Revised age of the late Neogene terror bird (*Titanis*) in North America during the Great American Interchange

Bruce J. MacFadden
Joann Labs-Hochstein – Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, USA
Richard C. Hulbert, Jr.
Jon A. Baskin Department of Biology, Texas A & M University, MSC 158, Kingsville, Texas 78363, USA

ABSTRACT

The giant flightless terror bird *Titanis walleri* is known from Florida and Texas during the late Neogene. The age of *T. walleri* is problematic because this taxon co-occurs with temporally mixed (i.e., time-averaged) faunas at two key sites. Thus, prior to this study, *T. walleri* from the Santa Fe River, Florida (type locality), was either as old as late Pliocene (ca. 2.2 Ma) or as young as latest Pleistocene (ca. 15 ka). Likewise, *T. walleri* from the Nueces River, Texas, was either early Pliocene (ca. 5 Ma) or latest Pleistocene (ca. 15 ka). In order to better resolve this age range, the rare earth element (REE) patterns of *T. walleri* from the Santa Fe River, Florida, were compared to two biochronologically distinctive groups (late Pliocene versus late Pleistocene) of fossil mammals from the same locality. Similarly, the REE patterns of *T. walleri* from Texas were compared to two groups (early Pliocene versus latest Pleistocene) of fossil mammals from the same locality. The REE patterns of *T. walleri* from Florida are indistinguishable from those of the co-occurring late Pliocene mammals. Likewise, the REE pattern of *T. walleri* from Texas is indistinguishable from those of the co-occurring early Pliocene mammals. Given these REE constraints, the revised age of *T. walleri* is early Pliocene in Texas (ca. 5 Ma) and late Pliocene (ca. 2.2–1.8 Ma) in Florida. As such, *T. walleri* is interpreted as an early immigrant during the Great American Interchange prior to the formation of the Isthmian land bridge. No evidence currently exists for Pleistocene *T. walleri* in North America.

Keywords: bone, diagenesis, extinction, Florida, Pleistocene, Pliocene, rare earths, taphonomy, *Titanis walleri*, Texas, Great American Interchange.

Figure 1. Reconstruction of *Titanis walleri* based on 40 fragmentary bones known from Neogene of Florida. *T. walleri* is estimated to have been between 1.4 and 1.9 m high and ~150 kg (Gould and Quitmyer, 2005), similar in mass to large individuals of modern North African ostrich (*Struthio camelus camelus*; del Hoyo et al., 1992), although of more robust proportions.

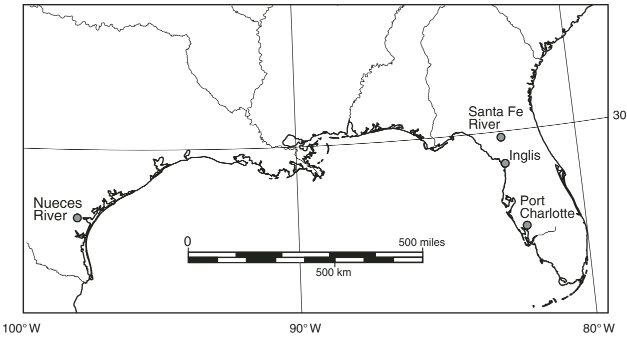

Figure 2. Map of four known localities that have yielded specimens of *Titanis walleri* from North America: Nueces River, Texas; time-averaged early Pliocene (late Hemphillian, ca. 5 Ma) and latest Pleistocene (late Rancholabrean, ca. 15 ka); Santa Fe River, northern Florida; time-averaged late Pliocene (late Blancan, ca. 2.2 Ma) and latest Pleistocene (late Rancholabrean, ca. 15 ka); Inglis 1A, latest Pliocene (latest Blancan, ca. 1.8 Ma); and Port Charlotte, late Pliocene (late Blancan, ca. 2.2 Ma). Modified from Gould and Quitmyer (2005) and reproduced with permission of Florida Museum of Natural History.

INTRODUCTION

The geological development of Central America during the Neogene significantly affected the historical biogeography of terrestrial vertebrates. Native faunas from South America dispersed northward and those from North America dispersed southward during the Great American Interchange (GAI), starting about 2.5 Ma (e.g., Webb, 1985). An early phase of the GAI occurred during the late Miocene and early Pliocene before the Isthmian closure, with dispersal resulting from island hopping across southern Central America. Thereafter, the greatest degree of faunal mixing during the GAI occurred after the Panamanian land bridge formed during the early Pliocene, ca. 4.5–3.5 Ma (Coates and Obando, 1996; Haug et al., 2001; Gussone et al., 2004).

The giant (~1.4–1.9 m high, ~150 kg; Gould and Quitmyer, 2005) flightless terror bird *Titanis walleri* (Fig. 1) is traditionally considered a northward immigrant during the post-Isthmian phase of the GAI in the late Pliocene and Pleistocene (e.g., Webb, 1985). *T. walleri* is found at four late Neogene localities in Florida and Texas (Fig. 2). The exact ages of these occurrences are problematical because at two sites (Santa Fe River, Florida, and Nueces River, Texas), *T. walleri* co-occurs with temporally mixed mammals ranging in age from early Pliocene (ca. 5 Ma, Texas), to late Pliocene (ca. 2.2 Ma, Florida), to late Pleistocene (ca. 15 ka, both Texas and Florida).

In this paper we use differences in the relative uptake of rare earth elements (REEs) in fossil bones within these mixed faunas to resolve the age of *T. walleri*. This revised age for *T. walleri* has significant ramifications for the timing of northward dispersal during the GAI and subsequent extinction. The relevant North American Land Mammal Ages are used: Blancan, Pliocene, 4.9–1.7 Ma; Hemphillian, late Miocene–early Pliocene, 9–4.9 Ma; Rancholabrean, late Pleistocene, ca. 0.4 Ma to ca. 10 ka (Tedford et al., 2004; Bell et al., 2004).

Geology, February 2007; v. 35; no. 2; p. 123–126; doi: 10.1130/G23186A.1; 4 figures; Data Repository item 2007035.

FOSSIL BONE TAPHONOMY AND RARE EARTH ELEMENTS

Within the past decade, studies of diagenetic uptake of REE during bone fossilization have clarified time-averaged vertebrate faunas and faunal sequences in a wide range of examples in the fossil record (e.g., Plummer et al., 1994; Trueman and Benton, 1997; Metzger et al., 2004; Martin et al., 2005). REEs occur in very low abundances (ppb) in living vertebrate skeletal tissues, but are rapidly taken up and concentrated (as high as 10^3 ppm, or greater, depending upon the pore-water chemistry) during early diagenesis. This process begins within a few years after death (Trueman et al., 2004) and probably continues for as long as 10–30 k.y. (Patrick et al., 2001). Once altered during early diagenesis, fossil bones are not prone to additional trace element uptake or exchange (Trueman and Tuross, 2002). The relative concentrations of REEs in fossil bones reflect the geochemical conditions and redox potential within local pore waters at the time of diagenetic recrystallization (Henderson et al., 1983). As local pore-water chemistry subsequently changes, fossils deposited in younger sediments potentially have different REE patterns. Likewise, pore-water compositions potentially vary spatially as well as temporally. Bones initially deposited in different geochemical environments but subsequently reworked together can also be distinguished by their REE patterns.

PREVIOUS STUDIES AND GEOLOGICAL CONTEXT

Florida: Late Pliocene (ca. 2.2 Ma) or Latest Pleistocene (ca. 15 ka)?

Giant fossil bird bones were discovered from alluvium in the Santa Fe River, Florida, in 1962 (Fig. 2; Ray, 2005). Brodkorb (1963) described these fossils as a new genus and species, *Titanis walleri*, within the family of extinct large flightless birds Phorusrhacidae, previously known from the Cenozoic of South America. Based on associated "Pleistocene indicators among the edentates, rodents, perissodactyls, and artiodactyls" from these Santa Fe River alluvial deposits, Brodkorb (1963, p. 115) interpreted *T. walleri* to be a late Pleistocene immigrant from South America at the end of the GAI. (We can confirm a late Pleistocene component to this fauna because the collections at the Florida Museum of Natural History [FLMNH] include diagnostic Rancholabrean *Bison*, armadillo-like *Holmesina septentrionalis*, ground sloth *Megalonyx jeffersonii*, peccary *Platygonus compressus*, mammoth *Mammuthus columbi*, dire wolf *Canis dirus*, and American lion *Panthera atrox*). This discovery extended the temporal range of phorusrhacids from the Pliocene (3.0 Ma), as known in South America, to the latest Pleistocene.

Additional fossils collected from the same Santa Fe River alluvium (in the FLMNH collections) indicate a temporally mixed vertebrate assemblage of both latest Pleistocene (ca. 15 ka) and late Pliocene (ca. 2.2 Ma) mammals (Hulbert, 2001), the latter consisting of diagnostic Blancan species, including the South American immigrant edentates (armadillo-like *Holmesina floridanus*, glyptodont *Glyptotherium arizonae*, and ground sloths *Glossotherium chapadmalense* and *Megalonyx leptostomus*), North American endemic hyena (*Chasmaporthetes ossifragus*), dog-like carnivores (*Borophagus diversidens* and *Canis lepophagus*), peccary (*Platygonus bicalcaratus*), llama (*Hemiauchenia blancoensis*), pronghorn antelope (*Capromeryx arizonensis*), and three-toed horse (*Nannippus peninsulatus*; Morgan and Hulbert, 1995; Hulbert, 2001; Bell et al., 2004; Morgan, 2005). These Blancan mammals, therefore, call into question the late Pleistocene age for *T. walleri* in this fauna. Furthermore, remains of *T. walleri* were subsequently reported from two other localities in Florida, Port Charlotte and Inglis 1A (Fig. 2; Gould and Quitmyer, 2005), associated with late Pliocene (late Blancan, ca. 2.2 Ma) and latest Pliocene (latest Blancan, ca. 1.8 Ma) mammals, respectively. Despite its ambiguous association with ca. 15 ka faunas (possibly indicating a late survival) in the Santa Fe River, several authors have indicated that *T. walleri* in Florida represents a Pliocene northward dispersal event during the GAI ca. 2.5 Ma and extinction during the Pleistocene (e.g., Webb, 1985; Morgan, 2005).

Texas: Early Pliocene (ca. 5 Ma) or Latest Pleistocene (ca. 15 ka)?

A toe bone of *T. walleri* was found in a late Pleistocene sand and gravel pit near Odem in the Angelina terrace fill deposits along the Nueces River (Fig. 2). These deposits have also yielded latest Pleistocene (Rancholabrean) mammals, including mammoth (*Mammuthus*) and *Bison*. A ^{14}C age of 13,230 ± 110 yr B.P. (SMU 2306; Baskin, 1995) was determined on wood from the next younger terrace unit at a gravel pit 20 km upstream from Odem (Cornish and Baskin, 1995). In addition, the terrace fill sequence has yielded early Pliocene (latest Hemphillian) horses, including *Astrohippus*, *Nannippus*, and *Neohipparion*, clearly indicating a time-averaged fauna. Despite the lack of obvious abrasion, these horses were probably transported 15–25 km from their most likely original source, the upper Goliad Formation (Baskin, 1991). Baskin (1995) inferred that *T. walleri* from the Nueces River was late Pleistocene primarily because it had previously been reported as a post-2.5 Ma immigrant during the GAI (e.g., Webb, 1985) and therefore could not be early Pliocene (ca. 5 Ma).

SAMPLES AND METHODS

Fossil bones from the two localities studied here are time-averaged, taphonomically mixed assemblages. Individual bones of unambiguous taxonomic affinity were allocated to one of the two biochronologically distinct groups from each locality, i.e., for Florida, either Blancan (n = 17) or Rancholabrean (n = 20), and for Texas, either Hemphillian (n = 9) or Rancholabrean (n = 10). For this analysis, the *T. walleri* specimens (Florida, n = 6; Texas, n = 1) are considered the unknowns. The REE patterns produced are used to compare *T. walleri* with the biochronologically distinct groups of fossil mammals.

We removed ~5–10 mg of cortical bone from each fossil specimen using a slow-speed rotary drill. In order to remove organic matter and other potential contaminants and insoluble residues, these specimen powders were weighed, placed in clean Savillex vials, dissolved with 1 mL of 3 M HNO_3, and heated overnight on a hotplate. Samples were then cooled and dried on a hot plate. The resulting dried sample was then weighed and dissolved with 2 mL of 5% HNO_3, and heated again overnight on a hot plate. The necessary weight for the samples was then calculated in order to dilute each sample by a factor of 2000 for the addition of 3 mL of 5% HNO_3. The weighed samples were placed in cleaned, clear, 4 mL plastic cups and the 3 mL of 5% HNO_3 was added. These samples were then analyzed for bulk REE concentrations on a Thermo Finnigan ELEMENT2 inductively coupled plasma–mass spectrometer (ICPMS) in the University of Florida Department of Geological Sciences. The analytical error on elemental analyses ranges from 0.002 to 5 ppm. Samples were run with internal standards and bone ash (NBS SRM 1400) and then corrected for instrument drift to obtain bulk REE concentrations. Of the 15 REE (excluding Pm [promethium], Z = 61), 14 were analyzed during this procedure. The REE concentrations reported here are normalized to Post-Archean Australian Shale (PAAS; McLennan, 1989), and indicated by REE_N. Statistical analyses were done using XLSTAT Pro 7.5. A complete list of fossil specimens, localities, age, analytical results, and individual specimen REE_N plots are presented in the GSA Data Repository (Table DR1 and Figs. DR1–DR6[1]).

RESULTS AND STATISTICAL ANALYSES

Florida

The graphical discrimination of the REE_N patterns of the Blancan versus Rancholabrean samples (Fig. 3A; see also Figs. DR–DR3) is compelling, as is the almost identical overlay of the *T. walleri* specimens with the Blancan mammals from Florida. The pattern of the mean sample populations of 14 REE_N values is relatively flat for the Rancholabrean speci-

---

[1] GSA Data Repository item 2007035, Table DR1 (post-Archean Australian Shale normalized rare earth elemental data) and Figures DR1–DR6 (individual specimen REEN plots), is available online at www.geosociety.org/pubs/ft2007.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

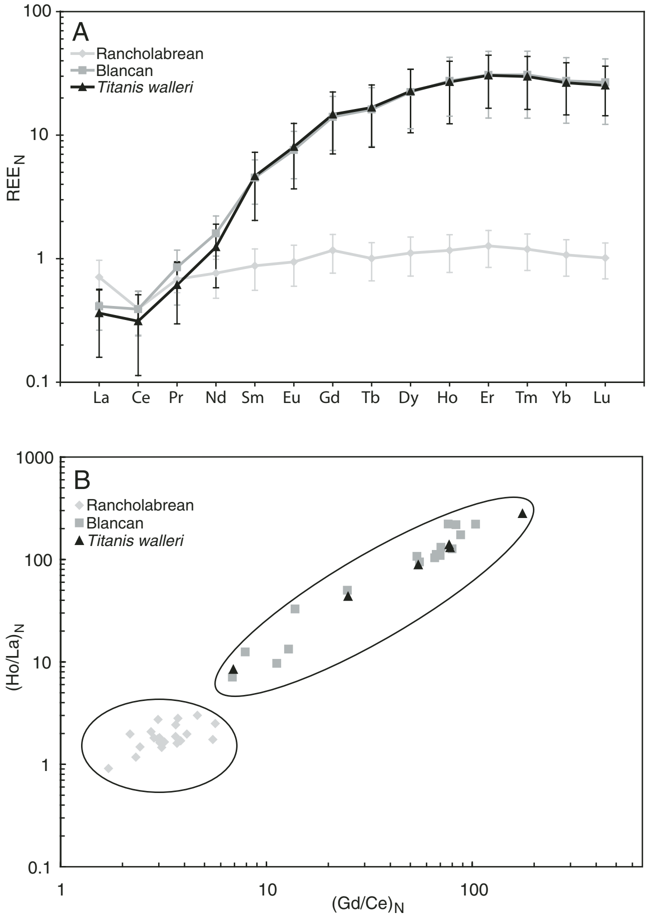

Figure 3. Rare earth element (REE_N—normalized to post-Archean Australian Shale; McLennan, 1989) data for *Titanis walleri* and associated time-averaged mammalian associations from Florida. A: Plot of mean (±2 standard errors) REE_N patterns for Blancan, Rancholabrean, and *T. walleri* samples. B: Plot of selected REE_N ratios.

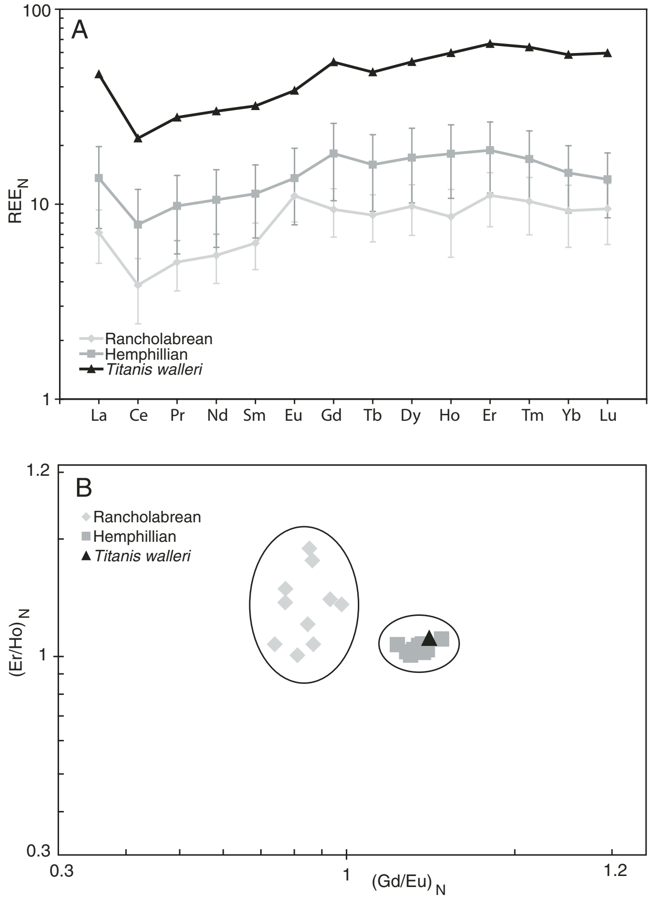

Figure 4. Rare earth element (REE_N—normalized to post-Archean Australian Shale; McLennan, 1989) data for *Titanis walleri* and associated time-averaged mammalian associations from Texas. A: Plot of mean (±2 standard errors) REE_N patterns for Hemphillian and Rancholabrean mammals, and one available specimen of *T. walleri*. B: Plot of selected REE_N ratios.

mens, but increases sharply in the middle (M) REE_N and heavy (H) REE_N for both the Blancan specimens and *T. walleri*. In addition to the compelling graphical evidence, regardless of whether one looks at parametric (Student's t) or nonparametric (Mann-Whitney U) tests for Σ REE_N (sum of all 14 elemental values), log Σ REE_N, or ratios expressing the relative change in values (a proxy of slope and overall pattern) for light (L)REE_N (La, Ce), $MREE_N$ (Gd), and $HREE_N$ (Ho; as exemplified by Fig. 3B), in all cases: (1) *T. walleri* is indistinguishable (probability level, p, > 0.05) from the Blancan mammals; and (2) both *T. walleri* and the Blancan mammals are significantly different from the Rancholabrean mammals ($p < 0.001$).

The relative amount of scatter (Fig. 3B) for the Rancholabrean versus Blancan/*T. walleri* ratios has interesting implications for either the amount of time represented by each sample population, or the rate of change of surrounding pore waters. Thus, the tight Rancholabrean cluster could indicate that these fossils underwent diagenesis during a relatively short interval of time, accumulated with relatively little transport, and/or the local pore-water chemistry remained relatively constant. In contrast, the more scattered Blancan/*T. walleri* cluster could indicate that these fossils represent longer time averaging, greater spatial accumulations, and/or that the local pore-water chemistry changed relatively rapidly during this interval.

Texas

The graphical representation of the REE_N patterns [Fig. 4A; Figs. DR4–DR6 (see footnote 1)] indicates that the one *T. walleri* specimen has higher total REE concentrations than either those of the Rancholabrean or Hemphillian. The Rancholabrean mammals have an increased Eu enrichment in contrast to either the Hemphillian mammals or *T. walleri*. In terms of the same parametric and nonparametric statistics (as for Florida), the ΣREE_N and log ΣREE_N are marginally nonsignificant ($0.056 < p < 0.142$), indicating an overlap of the Hemphillian and Rancholabrean data sets. This marginally insignificant difference probably results from the smaller sample sizes available. Nevertheless, analyses of $MREE_N$ versus $HREE_N$ ratios (Fig. 4B) indicate statistically significant ($p < 0.001$) differences between the Hemphillian and Rancholabrean samples. Thus, the *T. walleri* specimen is graphically indistinguishable from the Hemphillian mammals (Fig. 4B).

DISCUSSION

The REE_N data presented here have important implications for the timing of dispersal and extinction of *T. walleri* in North America. Previous studies have shown that the Panamanian land bridge formed during the early Pliocene between ca. 4.5 and 3.5 Ma (Coates and Obando, 1996; Haug et al., 2001; Gussone et al., 2004). It has traditionally been thought that the first overland dispersal of land mammals during the GAI occurred during the late Pliocene, ca. 2.5 Ma (Webb, 1985). *T. walleri* from the Blancan of Florida was previously interpreted as having been part of this initial wave of overland immigrants (Webb, 1985; Hulbert, 2001; Morgan, 2005); it was thought to have persisted into the latest Pleistocene (latest Rancholabrean), ca. 15 ka, based on the initial age interpretation (Brodkorb, 1963) and from the more recently reported evidence from Texas

(Baskin, 1995). These biochronological and paleobiogeographical interpretations now have to be revised significantly.

Unless REE signatures remained static throughout the Pliocene, the evidence from Texas indicates that *T. walleri* first occurred in North America during the early Pliocene (latest Hemphillian). This immigration at ca. 5 Ma is earlier than either the completion of the Panamanian land bridge or the initial phase of land-based northward dispersal. Therefore, *T. walleri* is interpreted to have been part of a pre–land bridge northward dispersal in the early Pliocene that resulted in a recently recognized earlier phase of dispersal during the GAI that is well documented in central Mexico (Flynn et al., 2005). The mode of dispersal probably occurred by island hopping through Central America or the Caribbean.

In Florida *T. walleri* first occurs during the late Pliocene, ~2.2 Ma. Its last occurrence in Florida, rather than indicating a range extension into the latest Pleistocene, is now revised to be from the latest Pliocene (latest Blancan Inglis 1A locality), ~1.8 Ma. The extinction of this top carnivore *T. walleri* and other phorusrhacids throughout the Americas during the late Pliocene may have resulted from competition with large placental (canid, felid, and possibly ursid) carnivores that radiated in the same ancient terrestrial ecosystems during the GAI (Webb, 1985).

CONCLUDING COMMENTS AND PERSPECTIVE ON FUTURE RESEARCH

REE patterns preserved in fossil bones during early diagenesis can be used to refine age estimates in taphonomically time-averaged faunas. When such faunas have end-member (older, younger) taxa that are biochronologically diagnostic, then other taxa of uncertain age (e.g., *T. walleri*) within this assemblage can be resolved by comparing REE patterns. The relatively small amount of sample required (5–10 mg), relative ease of preparation, and short amount of analytical time on the ICPMS together yield a cost-effective relative dating method when the circumstances described here are met. Analyses of REE preserved in vertebrate fossils have the potential to elucidate a broad range of age-related questions in the fossil record.

ACKNOWLEDGMENTS

We thank D. Fastovsky, Clive Trueman, T. Vennemann, and M. Woodburne for comments that improved the manuscript, and Carl Buell for permission to reproduce his reconstruction of *Titanis walleri* (presented in Fig. 1). Ian Breheny prepared Figure 2. The analytical results presented here were done on the inductively coupled plasma–mass spectrometer in the Department of Geological Sciences, University of Florida, with permission granted by Paul Mueller and the help of George Kamenov. University of Florida Contribution to Paleobiology 591.

REFERENCES CITED

Baskin, J.A., 1991, Early Pliocene horses from late Pleistocene fluvial deposits, Gulf Coastal Plain, south Texas: Journal of Paleontology, v. 65, p. 995–1006.

Baskin, J.A., 1995, The giant flightless bird *Titanis walleri* (Aves: Phorusrhacidae) from the Pleistocene coastal plain of south Texas: Journal of Vertebrate Paleontology, v. 15, p. 842–844.

Bell, C.J., Lundelius, E.L., Jr., Barnosky, A.D., Graham, R.W., Lindsay, E.H., Jr., Ruez, D.R., Jr., Semken, H.A., Jr., Webb, S.D., and Zakrzewski, R.K., 2004, The Blancan, Irvingtonian, and Rancholabrean mammal ages, *in* Woodburne, M.O., ed., Late Cretaceous and Cenozoic mammals of North America: New York, Columbia University Press, p. 232–314.

Brodkorb, P., 1963, A giant flightless bird from the Pleistocene of Florida: The Auk, v. 80, p. 111–115.

Coates, A.G., and Obando, J.A., 1996, The geological evolution of the Central American isthmus, *in* Jackson, J.B.C., et al., eds., Evolution and environment in tropical America: Chicago, Illinois, University of Chicago Press, p. 21–56.

Cornish, F.G., and Baskin, J.A., 1995, Late Quaternary sedimentation, lower Nueces River, south Texas: Texas Journal of Science, v. 47, p. 191–202.

del Hoyo, J., Elliot, A., and Sargatal, J., eds., 1992, Handbook of the birds of the world. Volume 1. Ostriches and ducks: Barcelona, Lynx Edicions, 696 p.

Flynn, J.J., Kowallis, B.J., Nuñez, C., Carranza-Casteñeda, O., Miller, W.E., Swisher, C.C., III, and Lindsay, E.H., 2005, Geochronology of Hemphillian-Blancan aged strata, Guanajuato, Mexico, and implications for timing of the Great American Biotic Interchange: Journal of Geology, v. 113, p. 287–307, doi: 10.1086/428806.

Gould, G.C., and Quitmyer, I.R., 2005, *Titanis walleri*: Bones of contention: Florida Museum of Natural History Bulletin, v. 45, p. 201–229.

Gussone, N., Eisenhauer, A., Tiedemann, R., Haug, G.H., Heuser, S., Bock, B., Nägler, T.F., and Müeller, A., 2004, Reconstruction of Caribbean Sea surface temperature and salinity fluctuations in response to the Pliocene closure of the Central American Gateway and radiative forcing, using $\delta^{44/40}$Ca, δ^{18}O and Mg/Ca ratios: Earth and Planetary Science Letters, v. 227, p. 201–214, doi: 10.1016/j.epsl.2004.09.004.

Haug, G.H., Tiedemann, R., Zahn, R., and Ravelo, A.C., 2001, Role of Panama uplift on oceanic freshwater balance: Geology, v. 29, p. 207–210, doi: 10.1130/0091–7613(2001)029<0207:ROPUOO>2.0.CO;2.

Henderson, P., Marlow, C.A., Molleson, T.I., and Williams, C.T., 1983, Patterns of chemical change during bone fossilization: Nature, v. 306, p. 358–360, doi: 10.1038/306358a0.

Hulbert, R.C., Jr., 2001. The fossil vertebrates of Florida: Gainesville, University of Florida Press, 350 p.

Martin, J.E., Patrick, D., Kihm, A.J., Foit, F.F., Jr., and Garndstaff, D.E., 2005, Lithostratigraphy, tephrochronology, and rare earth element geochemistry at the classical Pleistocene Fossil Lake area, south central Oregon: Journal of Geology, v. 113, p. 139–155, doi: 10.1086/427665.

McLennan, S.M., 1989, Rare earth elements in sedimentary rocks: Influence of provenance and sedimentary processes, *in* Lipin, B.R., and McKay, G.A., eds., Geochemistry and mineralogy of rare earth elements: Mineralogical Society of America Reviews in Mineralogy, v. 21, p. 169–200.

Metzger, C.A., Terry, D.O., Jr., and Grandstaff, D.E., 2004, Effect of paleosol format on rare earth element signatures in fossil bone: Geology, v. 32, p. 497–500, doi: 10.1130/G20376.1.

Morgan, G.S., 2005, The Great American Interchange in Florida: Florida Museum of Natural History Bulletin, v. 45, p. 271–311.

Morgan, G.S., and Hulbert, R.C., Jr., 1995, Overview of the geology and vertebrate biochronology of the Leisey Shell Pit Local Fauna, Hillsborough County, Florida: Florida Museum of Natural History Bulletin, v. 37, p. 1–92.

Patrick, D., Terry, D.O., Jr., and Grandstaff, D.E., 2001, Rare earth element (REE) variation in fossil and modern bones: The influence of osteological materials and time: Geological Society of America Abstracts with Programs, v. 33, no. 1, p. 27.

Plummer, T.W., Kinuyua, A.M., and Potts, R., 1994, Provenancing of hominid and mammalian fossils from Kanjera, Kenya using EDXRF: Journal of Archaeological Science, v. 21, p. 553–563, doi: 10.1006/jasc.1994.1054.

Ray, C.E., 2005, An idiosyncratic history of Floridian vertebrate paleontology: Florida Museum of Natural History Bulletin, v. 45, p. 143–170.

Tedford, R.H., Albright, L.B., III, Barnosky, A.D., Ferrusquia-Villafranca, I., Hunt, R.M., Jr., Storer, J.E., Swisher, C.C., III, Voorhies, M.R., Webb, S.D., and Whistler, D.P., 2004, Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs), *in* Woodburne, M.O., ed., Late Cretaceous and Cenozoic mammals of North America: New York, Columbia University Press, p. 169–231.

Trueman, C.N., and Benton, M.J., 1997, A geochemical method to trace the taphonomic history of reworked bones in sedimentary settings: Geology, v. 25, p. 263–266, doi: 10.1130/0091–7613(1997)025<0263:AGMTTT>2.3.CO;2.

Trueman, C.N., and Tuross, N., 2002, Trace elements in recent and fossil bone apatite, *in* Kohn, M.J., et al., eds., Phosphates—Geochemical, geobiological and materials importance: Mineralogical Society of America Reviews of Mineralogy and Geochemistry, v. 48, p. 489–522.

Trueman, C.N.G., Behrensmeyer, A.K., Tuross, N., and Weiner, S., 2004, Mineralogical and compositional changes in bones exposed on soil surfaces in Amboseli National Park, Kenya: Diagenetic mechanisms and the role of sediment pore fluids: Journal of Archaeological Science, v. 31, p. 721–739, doi: 10.1016/j.jas.2003.11.003.

Webb, S.D., 1985, Late Cenozoic mammal dispersal between the Americas, *in* Stehli, F.G., and Webb, S.D., eds., The Great American Biotic Interchange: New York, Plenum Press, p. 201–217.

Manuscript received 11 July 2006
Revised manuscript received 12 September 2006
Manuscript accepted 16 September 2006

Printed in USA