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FROM THE EARLY MIOCENE (HEMINGFORDIAN)
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ABSTRACT

Anchitherium clarencei Simpson 1932 is described from the early Miocene (early Hemingfordian, ca. 18 million-year-old) Thomas Farm locality in north central Florida. This rare species of three-toed browsing horse demonstrates diagnostic characters including a reduced m3 hypoconulid heel and relatively robust metapodials, both of which also differentiate *Anchitherium* from its close relative *Kalobatippus*. The distinctness of these two genera has been questioned for 85 years. Some workers argue that *Anchitherium* Meyer 1844 is the senior synonym of *Kalobatippus* Osborn 1915, with the former genus being distributed throughout Holarctica during the Miocene. Other workers believe that *Kalobatippus* is restricted to the New World, whereas *Anchitherium* is restricted to the Old World during the Miocene. In the interpretation presented here, both *Kalobatippus* and *Anchitherium* occur as distinct genera in North America, with the former found principally in Arikareean faunas and the latter found principally in Hemingfordian faunas (although *A. clarencei* extends into the early Barstovian in Florida). New World *Anchitherium sensu stricto*, such as *A. clarencei*, has the derived characters shared with Old World species of *Anchitherium*. The postcranial morphology represented by *A. clarencei* from Thomas Farm indicates relatively flexible fore- and hind-limbs with functional tridactyly.

Key words: *Anchitherium*, Equidae, Florida, *Kalobatippus*, Miocene

RESUMEN

Se describe a *Anchitherium clarencei* Simpson 1932 de la localidad Thomas Farm, región centro-norte de Florida, Mioceno Temprano (Hemingfordiano Temprano, ca. 18 millones de años). Esta rara especie de équido tridáctilo ramoneador muestra rasgos diagnósticos que incluyen un talón con hipoconúlido reducido sobre el m3 y metapodiales relativamente robustos; ambos caracteres diferencían a *Anchitherium* de su pariente más cercano *Kalobatippus*. Por 85 años, la validez de estos dos géneros se ha cuestionado. Algunos investigadores argumentan que *Anchitherium* Meyer 1844 es el sinónimo senior de *Kalobatippus* Osborn 1915, y que el primero se encuentra distribuido al través del Dominio Holártico durante el Mioceno. Otros autores sugieren que para dicho intervalo de tiempo *Kalobatippus* se restringe al Nuevo Mundo y *Anchitherium* al Viejo Mundo. En la interpretación que se presenta aquí, tanto *Kalobatippus* como *Anchitherium* se encuentran como géneros diferentes en Norteamérica, el primero reconocido para las faunas arikareanas y el segundo fundamentalmente en las hemingfordianas (aunque *A. clarencei* se reconoce para el Barstoviano Temprano de Florida). El *Anchitherium sensu stricto* del Nuevo Mundo, tal es el caso de *A. clarencei*, presenta rasgos derivados que comparte con las especies del Viejo Mundo de *Anchitherium*. La morfología postcraneal de *A. clarencei* de Thomas Farm, indica extremidades anteriores y posteriores relativamente flexibles, con tridactilia funcional.

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[1]The author is Associate Director of Exhibits & Public Programs and Curator of Vertebrate Paleontology, Florida Museum of Natural History, University of Florida, Gainesville FL 32611-2710, email: bmacfadd@flmnh.ufl.edu.

INTRODUCTION

Thomas Farm is one of the best known Tertiary fossil mammal sites in eastern North America. Located in Gilchrist County, northern Florida, it preserves an exceedingly rich sink-hole accumulation of early Miocene (early Hemingfordian) land mammals (Pratt 1990). This locality is about 18 million years old based on correlations with similar sites in the western interior (Tedford et al. 1987). Since its discovery in 1931, Thomas Farm has produced literally tens of thousands of catalogable fossil vertebrate bones and teeth, of which about 80 percent of the macrofauna represent fossil horses. Although there have been different opinions about the number of equid species and their proper taxonmic names (e.g., compare Simpson 1932; White 1942; Bader 1956), as currently envisioned, Thomas Farm horses (Family Equidae) include three valid taxa, i.e., *Parahippus leonensis* Sellards 1916, *Archaeohippus blackbergi* (Hay 1924), and *Anchitherium clarencei* Simpson 1932. As a rough qualitative approximation based on specimens collected during the 1990s, the medium-sized three-toed *P. leonensis* is very common (representing ~90% of the equid fossils from this site), whereas the tiny three-toed *A. blackbergi* is uncommon (~9 percent) and the three-toed browser *A. clarencei* is very rare (<1 percent).

Parahippus leonensis has been the subject of numerous studies, including systematics (White 1942; Bader 1956; Forsten 1975; Hulbert and MacFadden 1991), taphonomy (Pratt 1990), and population dynamics/paleoecology (Hulbert 1984). Because of its rarity, *Archaeohippus blackbergi* from Thomas Farm is less well studied (e.g., Simpson 1932 as *A. "nanus"*; White 1942; Bader 1956; Forsten 1975) and this species is currently the subject of a Ph. D. dissertation by UF zoology student Jay O'Sullivan. The purpose of this paper is to describe the hypodigm of Thomas Farm *Anchitherium clarencei* and to discuss the question of the validity of the extinct equid genera *Anchitherium* Meyer 1844 and *Kalobatippus* Osborn 1915. Simpson (1932) and White (1942) represent the only detailed descriptions of Thomas Farm *Anchitherium* and these were published more than a half-century ago. Within the past two decades, renewed excavations have yielded more material, particularly of the lesser-known and/or previously undescribed postranial elements. Thus, a better understanding of this very rare horse is now possible.

HISTORY AND NONEMCLATURE OF *ANCHITHERIUM* MEYER 1844 and *KALOBATIPPUS* OSBORN 1915

An understanding of the nomenclature and taxonomy of *Anchitherium clarencei* from Thomas Farm spans two continents and two centuries of paleontological investigations. I will concentrate here primarily on North American material and only highlight selected studies of relevant Old World *Anchitherium*.

In the middle of the nineteenth century the German paleontologist Meyer (1844) erected the name *Anchitherium* (*anchi-*, Gr. near, probably in reference to near the ancestry of modern horses; *-therium*, Gr. beast) for early Miocene, low-crowned (brachyodont), three-toed fossil horse remains from western Europe. The type species of *Anchitherium*, *A. ezquerrae* Meyer 1844, was collected from Cerro de Isidro, Madrid, Spain (Abusch-Siewert 1983; Sánchez et al. 1998). Leidy (e.g., 1869; 1873) assigned remains of middle Tertiary fossil horses from numerous, widespread North American localities (e.g., Texas, Nebraska, and Oregon) to *Anchitherium*, and in so doing, implied a Holarctic distribution for this genus. In one of the classic monographs on *Anchitherium*, the Russian paleontologist Kowalevsky (1873) did a brilliant study of the anatomy and phylogeny of this genus based on specimens from Europe. Of relevance to this study, Kowalevsky also tacitly accepted a Holarctic distribution for *Anchitherium* by referencing the presence (as described by Leidy 1869) of this genus in North America.

Osborn (1915) erected the genus *Kalobatippus* (*kalobamon*- Gr., walking on stilts, in reference to gracile metapodials; -(h)*ippus*-Gr., horse) and used as the type species *Anchitherium praestans* (Cope 1879) from the early Miocene John Day basin of Oregon (Fig. 1). He described this new genus as follows (Osborn, 1915, plate CVIII): "Upper molars with metaloph united to ectoloph as in *Anchitherium*, but M3 and heel of m3 unreduced and like *Miohippus* in pattern. Limb bones and metapodials much elongated, lateral digits unreduced from *Miohippus* stage; phalanges short, inner cuneiform of pes abutting upon cannon-bone." Osborn (1918, p. 69) further elaborated upon the description of *Kalobatippus*, with the emended description to include the following:

1. Metaloph united to ectoloph (as in *Anchitherium*, *Hypohippus*, and *Archaeohippus*).
2. Anterior margin of orbit above posterior end of M3, as in *Archaeohippus*.
3. Size exceeding that of any of the known species of *Miohippus* and *Archaeohippus*.
4. Teeth more brachyodont than in *Anchitherium*.
5. No internal cingulum.
6. Protolophs of molars and metalophs of P3-4 incomplete.
7. Last upper molar, and heel of m3 unreduced.
8. No crochet.
9. Incisor row broadly rounded.
10. Lachrymal fossa shallow.
11. Malar fossa broad and not very deep.
12. Hind foot with elongate metatarsals and short phalanges; foot longer and more slender than in *Anchitherium* or *Hypohippus*.
13. Lateral digits not more reduced than in *Anchitherium*.
14. Metatarsal III-cuboid facet strong.
15. Metatarsal III with strong meso-entocuneiform facet, as in *Anchitherium* and *Hypohippus*.

In this same monograph Osborn (1918) proposed the species *Kalobatippus agatensis* from the late Arikareean of Nebraska. As also demonstrated in the type material of *K. praestans*, represented by an associated skeleton, both species clearly have the diagnostic characters of the genus, including, in particular, the relatively unreduced m3 heel and very elongated metapodials (Fig. 2). Comparison of the holotype of *K. praestans* (AMNH 7269) with that of *K. agatensis* (AMNH 14211) indicates character differences sufficent to justify these two distinct species. In particular,

relative to *K. praestans*, *K. agatensis* is larger and has relatively more elongated metapodials.

Hay (1924) described the new species *Miohippus navasotae* based on a small sample of isolated anchithere teeth from early Hemingfordian Garvin Gully Fauna, located about 8 km SE of Navasota in the Miocene Texas Gulf Coastal Plain. In addition to an overall complex of primitive equid dental characters, Hay (1924) mentioned that the upper molar contains some cement and a faint crochet. If this were the case, then this should probably be more properly referred to a parahippine. However, the illustrations provided in his paper (Hay, 1924, plate I) indicate that these characters are poorly represented. Because of its direct relevance to the present study, the importance of this species is further discussed in the context of Forsten's (1975) study of Texas Gulf Coastal Plain horses, as described below.

In his description of "*Anchitherium*" *agatense* from lateral equivalents of the type locality (Agate Springs National Monument) in the Harrison Formation of NW Nebraska and adjacent Wyoming, Romer (1926) provided a thorough and excellent review of the validity of the genus *Kalobatippus*. Of Osborn's (1918) fifteen points (listed above), Romer concluded that only one (# 12), i.e., metapodial length, served to differentiate these two genera. In view of the known metapodial variation of other recognized equid genera (e.g., he cites *Mesohippus* and *Miohippus*), Romer concluded that this character also was insufficent for recognition of both *Anchitherium* and *Kalobatippus* and hence they were synonymous. In the same year Matthew (1926) published a synthetic review of fossil Equidae. In his Fig. 25 (p. 167) he graphically indicated the distribution of *Kalobatippus* as North American, whereas *Anchitherium* was restricted to the Old World.

Simpson (1932) described *Anchitherium clarencei* from the Midway Local Fauna of the eastern Florida panhandle. In his discussion of the nomenclature and phylogenetic position of this species, he says that the available "characters place it at once as in the anchitheriine line and, in the American fauna, closest either to *Kalobatippus* or to the earlier and more primitive species of *Hypohippus*. It is very difficult to draw a good generic distinction between these two groups, or between either one and the European genus *Anchitherium*. . . . I would prefer to place all the species of *Kalobatippus* and the earlier species of *Hypohippus* in the genus *Anchitherium*, to which the present form would then obviously be referable" (p. 33).

Of direct relevance to the present study, White (1942)
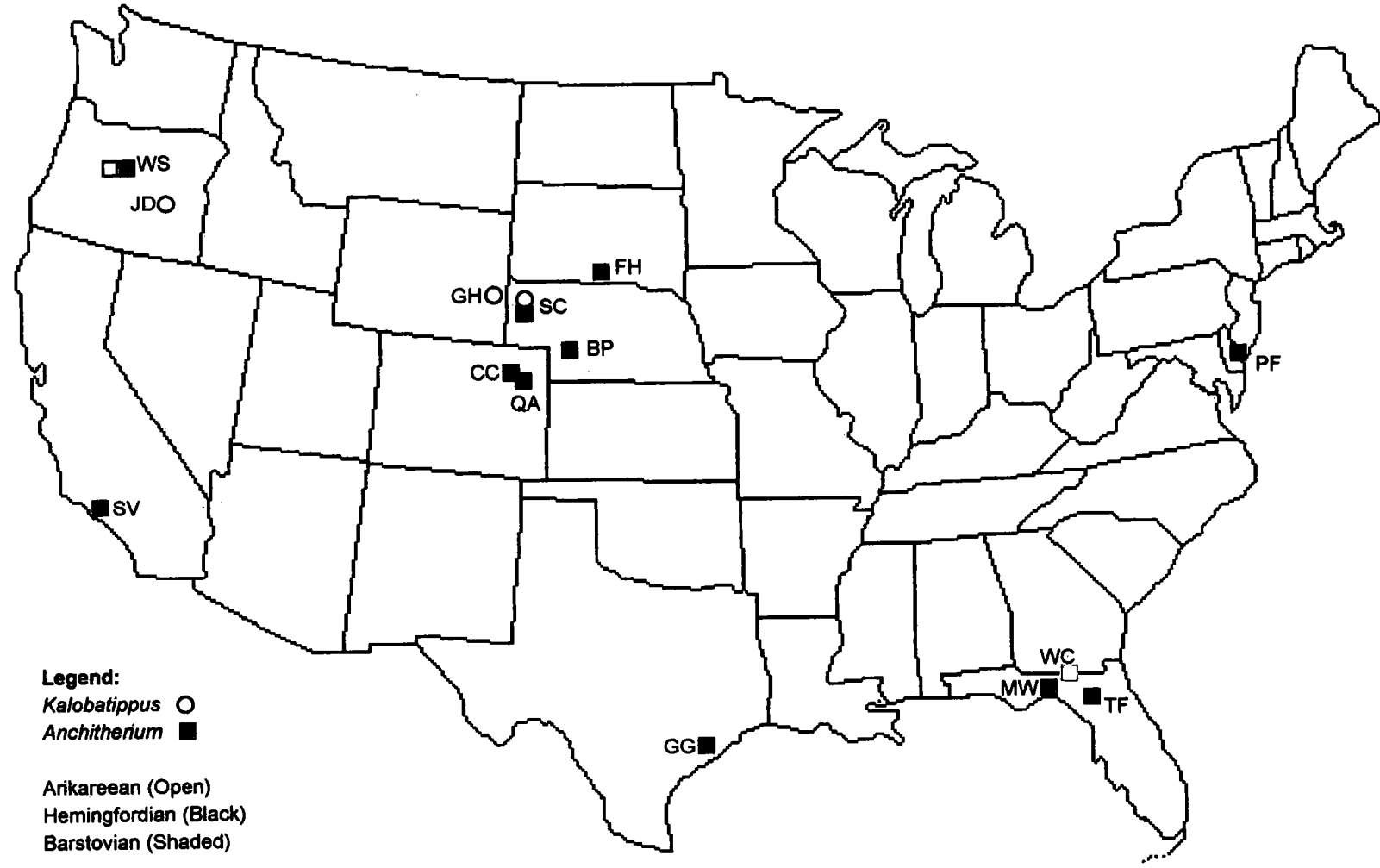
Figure 1. Map of localities discussed in text; BP, Bridgeport, NE; CQ, Clay Quarry, CO; FH, Flint Hills, SD; GG, Garvin Gully, TX; GH, Goshen Hole, WY; JD, John Day, OR; MW, Midway, FL; PF, Pollack Farm, DE; QA, Martin Canyon Quarry A, CO; SC, Sioux County, NE; SV, Sespe-Vaqueros formations, CA. TF, Thomas Farm, FL; WC, Willachoochee Creek, FL; WS, Warm Springs, OR.
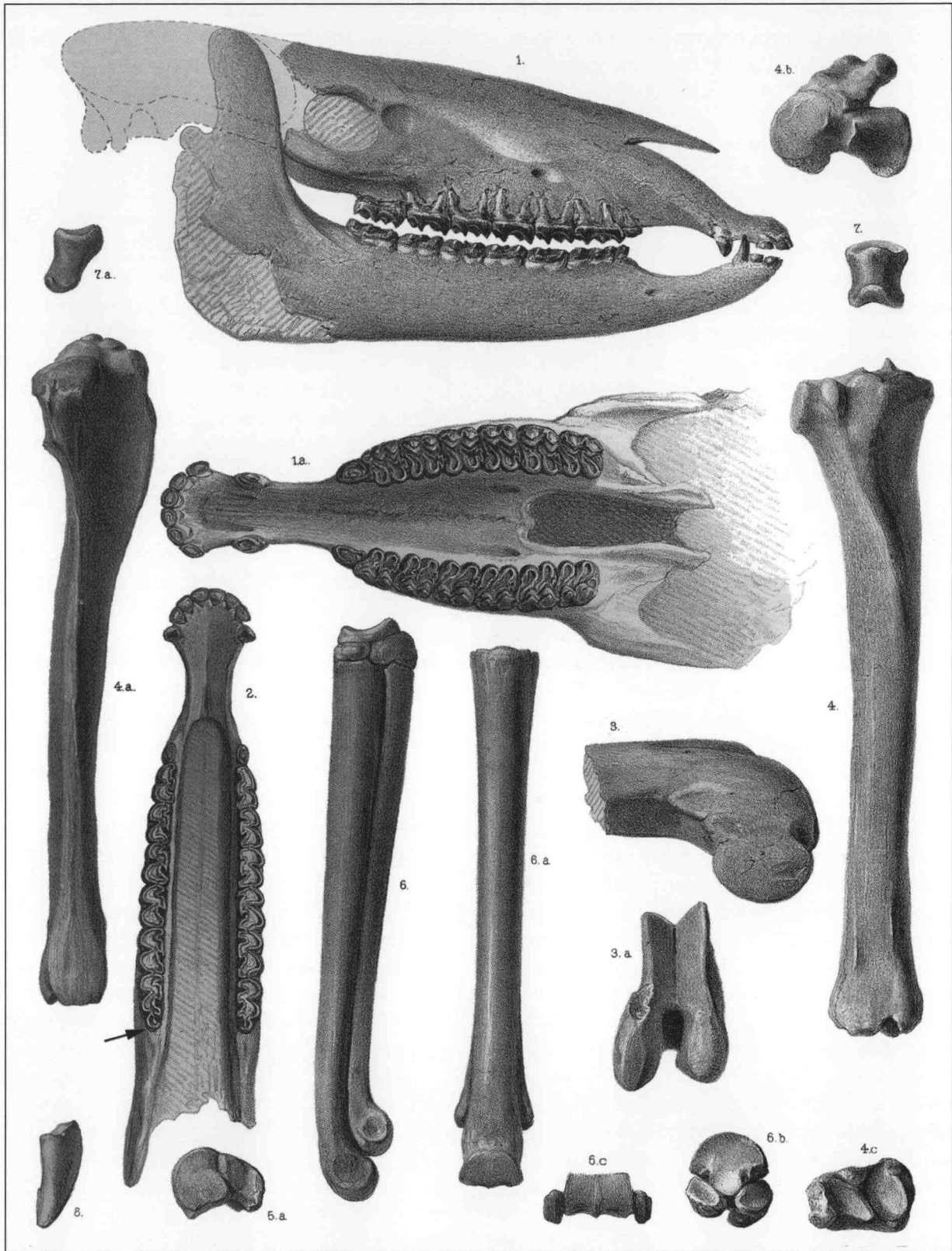
Figure 2. Original figure (modified) illustrating holotype of *Kalobatippus praestans*, AMNH 7269, from the John Day Fossil Beds, OR (from Osborn, in Cope 1915, plate CVIII). Note, in particular, the reduced m3 heel ("2," see arrow) and slender metapodials ("6" and "6a").

described a juvenile mandible of *Anchitherium clarencei* from the the middle Miocene Thomas Farm Local Fauna. He thus followed Simpson's (1932) generic and specific assignments and added another locality to the known distribution of this species.

Schlaijker (1935) described a new species of small equid, *Hypohippus avus*, from the early Miocene of Goshen County, Wyoming. The holotype (MCZ 2811) represents a beautifully preserved juvenile skull with M2 erupting. No other referred material is known from this locality. Some undescribed specimens in the AMNH (F:AM collection) from the Keeline locality of Niobrara County, Wyoming, which are believed to be referable to the Harrison Formation (Hunt, pers. comm. 2000), are probably referable to this species (MacFadden, pers. observ. 1999).

Wehrli (1938) presented a detailed description of *Anchitherium aurelianense* from 35 localities in southwestern Germany and Switzerland and also discussed the supposed distinction between *Kalobatippus* and *Anchitherium*. Like Romer (1926), Wehrli (1938) addressed each of Osborn's (1918) fifteen points and also concluded that the variation between these two genera was also seen within European *Anchitherium*. He therefore concluded that *Kalobatippus* was synonymous with *Anchitherium*. Stirton (1940), in his classic "Phylogeny of the North American Equidae," listed seven species of *Anchitherium* and did not mention the genus *Kalobatippus*.

In her review of Gulf Coastal Plain horses from the Miocene of Texas, Forsten (1975) makes *Anchitherium navasotae* (Hay 1924) and *A. clarencei* Simpson 1932 synonymous. This decision obviously has implications for the Thomas Farm sample because *A. clarencei* would therefore be rendered a junior synonym. More recent workers (e.g., Hulbert 1993), however, have not followed Forsten's (1975) synonymy. This distinctness of these two species is likewise followed here for the following reasons: (1) as Forsten (1975) noted, the mean length of the p3-m2 of the Garvin Gully *Anchitherium* is less than those from Florida; (2) the m3 in the type specimen of *A. navasotae* is not reduced as is the same tooth in the sample referred to *A. clarencei* from Florida. It is, however, noted that this decision is based on small samples that are not amenable to statistical analysis. If in the future more specimens referred to these species from both Texas and Florida became available, then it would be important to further test discrimination of these two species. But, with the presently available evidence, *A. navasotae* (Hay) 1942 and *A. clarencei* Simpson 1932 are considered to be dis-

tinct species. On a related subject, Forsten (1975) noted that in several characters, including the reduction of the M3/m3, *A. clarencei* from Thomas Farm is more advanced than *Kalobatippus* and resembles *Hypohippus* and Old World *Anchitherium*. This is corroborated by ideas presented here (also see Hulbert 1993), where *A. clarencei* from Florida possesses shared-derived characters that separate it from more primitive *Kalobatippus* and ally it with *Hypohippus* and Old World *Anchitherium*.

Bryant (1991) described two specimens, including a Lp2 (UF 114723) and partial left P3-M1 (UF 118529), of *Anchitherium clarencei* from the Willacoochee Creek Fauna from the Torreya Formation in the eastern Florida panhandle, ca. 20 km to the NW of the type locality for this species. This occurrence extends the biostratigraphic range of *A. clarenci* into the early Barstovian. As such, the temporal duration of this species in Florida is from about 18 to 15.5 (MacFadden et al. 1991).

Recent studies considerably extend the known geographic range, as well as further resolve the biochronology, of *Anchitherium* in North America. Emry and Eshelman (1998) report *A.* sp. from the Pollock Farm Local Fauna of Delaware, which contains a diagnostic early Hemingfordian assemblage (including the horses *Parahippus leonensis* and *Archaeohippus blackbergi*) and is calibrated by a Sr-isotope age of 17.9 ± 0.5 Ma on interbedded mollusk shells. Donohoo and Prothero (1999) described a new early Hemingfordian fauna from the Sespe and Vaqueros formations of northern Orange County, California. This local fauna is constrained paleomagnetically between 17-19 Myr and is reported to contain *A. clarencei* (Prothero, pers. comm. 1999). Dingus (1990) reports fragmentary teeth of *Anchitherium* from the late Arikareean to Hemingfordian John Day Formation near Warm Springs, Oregon.

In an overview of North American Equidae, Evander (1989) considered both *Anchitherium* and *Kalobatippus* to be distinct and valid, although he did not discuss the geographic distribution of these two genera. Interestingly, his cladistic analysis related *Anchitherium* to *Hypohippus* and *Megahippus*, whereas it placed *Kalobatipus* with the more derived Equinae. More recently, MacFadden (1992, 1998) used *Kalobatippus* as the North American genus and did not mention *Anchitherium* as being valid in North America. Given the diversity of opinions that have been presented over the years, the validity and distribution of *Anchitherium* and *Kalobatippus* have remained unresolved. The current study sheds additional light on this subject.

MATERIALS, METHODS, TERMINOLOGY, AND ABBREVIATIONS

Relevant fossil materials of anchithere horses were studied from the following museum collections (acronyms are used in the text):

AMNH; Department of Vertebrate Paleontology, The American Museum of Natural History, New York City.

F:AM; Frick:American Mammals, part of the AMNH collection.

MCZ; Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

UF/FGS; Florida Geological Survey Collection, now part of UF (see below).

UF; Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville. The following other abbreviations and terminology are used in the text:

Anchithere; an adjective or noun used to describe the polyphyletic, horizontal assemblage of low-crowned late Oligocene-Miocene horse species traditionally assigned to either advanced *Miohippus, Kalobatippus, Anchitherium, Sinohippus, Hypohippus*, or *Megahippus*. This is obviously not a strict phylogenetic category.

L; left side.

L.F., Local Fauna; a geographically and temporally restricted fossil assemblage

M, m; molar (upper, lower)

Ma; megannum, in reference to a point, in millions of years, on the geological time scale

Myr; million years ago on the geological time scale, usually in reference to a duration or span of time.

P, p; premolar (upper, lower).

R; right side.

Dental terminology follows the convention of upper case for upper teeth (i.e., I, C, P, M) and lower case for lower teeth (i.e., i, c, p, m). Anatomical terminology generally follows Getty (1975) and dental terminology follows Stirton (1941) and MacFadden (1984). Many of the measurements presented here follow the conventions of Eisenmann et al. (1988).

During this study a database was developed that for every specimen included the following possible suite of coded variables or measurements:

General—tooth row and ontogeny

U/l; Upper or lower tooth.

SIDE; right or left,

ONT; ontogenetic stage as assessed from teeth; J, juvenile (deciduous premolars and/or incompletely erupted

molars); E, early adult (molars erupted and in early wear); M, adult (all teeth in middle wear); L, late wear (all teeth heavily worn).

P1M3TRL (or p1m3trl); tooth row length from anterior-most part of DP1 (or dp1) to posteriormost part of M3 (or M3).

P2M3TRL (or p2m3trl); tooth row length from anterior-most part of P1 (or p1) to posteriormost part of M3 (or M3); = measurement 9 of Eisenmann et al. (1988, p. 7).

Upper dentitions (Fig. 3)

APL; greatest anteroposterior length of M1, M2, or M3; = measurement C2 of Eisenmann et al. (1988, p. 23).

TRN; greatest transverse width of M1, M2, or M3; = measurement C4 of Eisenmann et al. (1988, p. 23).

MSTHT; mesostyle height of enamel, excludes specimens for ONT = L (late wear).

CROCHET; crochet development; P=present, R= rudimentary, or A=Absent (not illustrated in Fig. 3).

RIBS; P=present; R=rudimentary; or A=absent (not illustrated in Fig. 3).

CINGULUM; internal (lingual) cingulum, P=present, R= rudimentary, or A=absent (not illustrated in Fig. 3).

Lower dentitions (Fig. 3)

apl; greatest anteroposterior length; = measurement C2 of Eisenmann et al. (1988, p. 29).

trn; greatest transverse width; = measurement C6 of Eisenmann et al. (1988, p. 29).

mtcmstht; metastylid/metaconid height of enamel, excludes specimens for ONT = L (late wear).

m3heel; greatest anteroposterior length of hypoconulid heel of m3 (see Fig. 4).

m3ratio; mapl/m3heel, an indication of the relative size of the hypoconulid heel on m3.

Metatarsal III (Fig. 3)

The metatarsal (MT) was chosen to charaterize the general morphology, size-related limb parameters, and relative limb robustness because: (1) the only complete metapodials for Thomas Farm *Anchitherium* are represented by MT III; and, fortunately, (2) the associated limb bones for relevant type specimens of closely related species also include MT III. Measured characters and ratios used here are as follows:

PRXW; greatest transverse (mediolateral) width across proximal articular surface; = measurement B3 of Eisenmann et al. (1988, p. 61).

GRTL; greatest proximodistal length; = measurement C1 of Eisenmann et al. (1988, p. 61).

MDSH; midshaft mediolateral width; = measurement B3 of Eisenmann et al. (1988, p. 61).
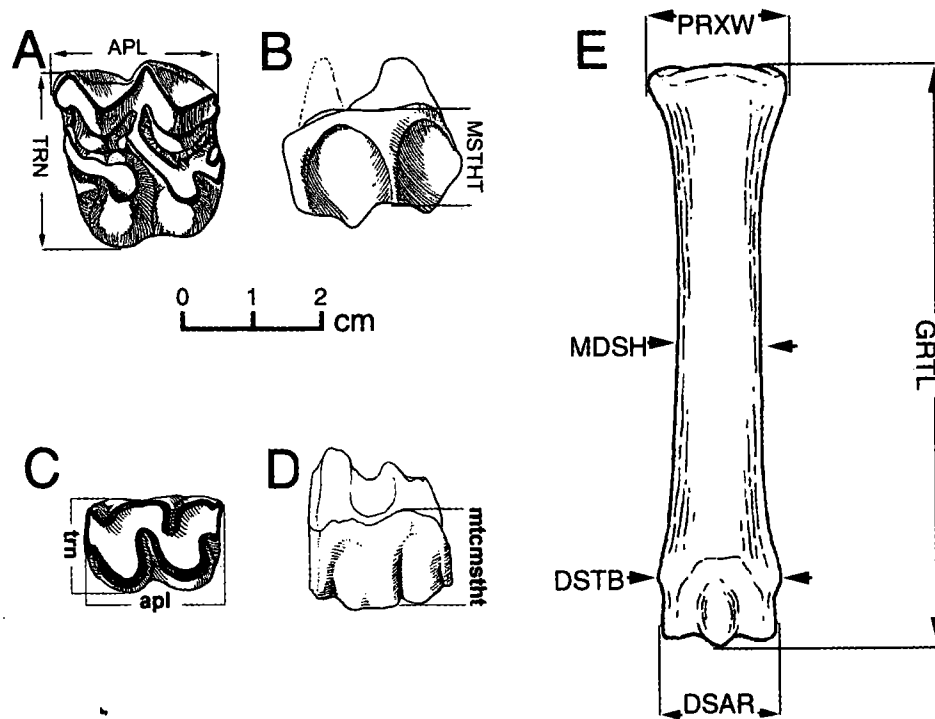
Figure 3. Dental and MT III measurements and abbreviations (also see text). Upper molar, occlusal (A) and external (B) views. Lower molar, occlusal (C) and internal (D) views. MTIII measured characters (E).

DSTB; transverse (mediolateral) width across distal tuberosities; = measurement B10 of Eisenmann et al. (1988, p. 61).

DSAR; greatest transverse (mediolateral) width across distal articular trochlea; = measurement D11 of Eisenmann et al. (1988, p. 61).

INDEX; metatarsal index of robustness (=GRTL/MDSH; not illustrated in Fig. 3).

All coded variables and measurements were analyzed using SAS (Statistical Analysis System; SAS Institute, 1985) provided on the University of Florida mainframe computer (NERDC, Northeastern Regional Data Center).

SYSTEMATIC PALEONTOLOGY
Class Mammalia Linnaeus, 1758
Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Genus *Anchitherium* Meyer, 1844

Generic diagnosis.—Moderately large, brachyodont, anchitheriine tridactyl horse. DP1/dp1-M3/m3 tooth row lengths ca. 120 mm to 135 mm; P2/p2-M3/m3 tooth row lengths ca. 113 mm to 127 mm. M1APL, M2APL, m1apl, or m2apl ca. 19 mm to 22 mm. Unworn or little-

worn maximum MSTHT or mtcmstht ca. 10 to 14 mm. Preorbital facial fossa large, oval, and moderately well developed excavated depression on maxillary, nasal, and lacrimal bones, but lacking a well defined rim or pocketing. Anteriormost part of orbit lying above M3. Upper and lower cheek teeth with cingula moderately developed, rudimentary, or absent. Upper cheek teeth lacking cement and crochet, ribs poorly developed, metaloph and protoloph connected to ectoloph except in unworn or little-worn teeth. M3 reduced relative to M2. Lower teeth with moderately separated metaconids and metastylids, m3 with characteristically reduced hypoconulid heel which does not come into wear until late maturity. Metapodials ca. 230 mm to 255 mm long and robust (mean metatarsal INDEX = 10.0; see Table 1). Well developed facets for cuboid and mesentocuneiform on MT III. Lateral metapodials relatively well developed in contrast to later equids, e.g., *Parahippus*. Proximal phalanges not elongated.

Anchitherium differs from *Kalobatippus* in having more reduced m3 hypoconulid heels and longer, broader (in mid-section), and more robust metapodials; *Anchitherium* differs from *Miohippus* and *Mesohippus*

Table 1. Dental and metatarsal III measurements for *Anchitherium* and *Kalobatippus* based on specimens examined during this study. These two genera were sorted into *a priori* groups based on qualitative differences (described in the text) that are frequently used to distinguish these two genera. For abbreviations, see text and Fig. 3.

Character	Taxon	N, x, s, range[1]	Taxon	N, x, s, range[1]	Probability	Different?[2]
P1M3TRL[3]	*Anchitherium*	9, 128.8, 7.0, 116.8-140.6	*Kalobatippus*	6, 117.6, 7.9, 109.3-128.9	0.012	Yes
P2M3TRL[3]	*Anchitherium*	17, 120.7, 7.6, 107.7-133.7	*Kalobatippus*	6, 109.3, 8.7, 100.4-121.2	0.006	Yes
U1MAPL[3]	*Anchitherium*	71, 20.8, 2.1, 16.2-25.3	*Kalobatippus*	19, 19.4, 2.7, 16.5-25.9	0.020	Yes
UMTRN[4]	*Anchitherium*	25, 23.6, 2.2, 19.2-27.4	*Kalobatippus*	6, 20.8, 1.2, 19.4-22.4	0.004	Yes
lmtrnw[4]	*Anchitherium*	47, 13.4, 1.6, 10.1-16.2	*Kalobatippus*	13, 13.2, 1.7, 10.9-16.2	0.723	No
HEIGHT[5]	*Anchitherium*	66, 10.0, 2.2, 5.2-16.7	*Kalobatippus*	15, 8.6, 1.0, 6.3-10.2	0.022	Yes
m3ratio	*Anchitherium*	12, 4.4, 0.9, 3.4-6.0	*Kalobatippus*	5, 3.4, 0.3, 3.1-3.9	0.013	Yes
GRTL	*Anchitherium*	22, 243.0, 12.8, 216.0-264.0	*Kalobatippus*	7, 212.6, 20.0, 194.0-254.0	0.001	Yes
PRXW	*Anchitherium*	20, 32.2, 2.4, 27.8-38.7	*Kalobatippus*	7, 24.9, 2.5, 21.6-28.0	0.000	Yes
MDSH	*Anchitherium*	24, 24.1, 2.2, 20.4-31.4	*Kalobatippus*	7, 17.5, 1.4, 15.8-20.0	0.000	Yes
DSTB	*Anchitherium*	22, 34.4, 2.1, 30.6-39.7	*Kalobatippus*	7, 27.4, 2.2, 24.6-31.4	0.000	Yes
DSAR	*Anchitherium*	20, 30.4, 1.2, 29.0-33.4	*Kalobatippus*	7, 23.1, 2.8, 18.9-26.9	0.000	Yes
INDEX	*Anchitherium*	22, 10.0, 0.7, 8.4-11.4	*Kalobatippus*	7, 12.1, 0.9, 11.1-13.1	0.001	Yes

[1]N, number of specimens measured; x, mean; s, standard deviation; range, i.e., observed minimum to maximum.

[2]Are *Anchitherium* versus *Kalobatippus* different (assuming an acceptable cutoff probability of $p < 0.05$) using either the *t*- or Wilcoxon tests for significance? All linear measurements were assumed to be normally distributed with equal variances (the latter of which usually resulted in lower probability levels than for unequal variances) and thus the *t*-test was used; RATIO and INDEX are both ratios and thus the non-parametric Wilcoxon test was used.

[3]Includes both upper and lower dentitions as combined data sets.

[4]Upper and lower transverse widths analyzed separately.

[5]HEIGHT = pooled sample of MSTHT (uppers) and mtcmstht (lowers); Well-worn teeth (ONT = "L") removed from analysis.

in larger size, stronger connection of the metaloph to the ectoloph, reduced internal cingula, weaker upper cheek-tooth ribs, better separated metaconids and metastylids, and more pronounced cuboid and ectocuneiform facets on MT III; *Anchitherium* differs from *Hypohippus* in being less hypsodont and having faint ribs in the upper cheek teeth (they are absent in the latter genus), relatively more pronounced m3 heel, and preorbital facial fossa lacking either pocketing or well defined rim, and in most species smaller size. *Anchitherium* differs from *Parahippus* (including *"Desmatippus"*) in lacking cement on the cheek teeth and a crochet on the upper pre-molars and molars, and having less elongated phalanges.

Included North American species.—*A. navasotae* (Hay 1924), *A. clarencei* Simpson 1932, and one or more undescribed species from the western U.S. (as represented in the AMNH collections).

Distribution.—Early Hemingfordian of Delaware, Florida, Texas, High Plains (Nebraska, Colorado, Wyoming, South Dakota, and California); late Hemingfordian of Florida; possibly late Hemingfordian of California (Fig. 1). Tedford et al. (1987) stated that the genus *Anchitherium* persists in North America through the Barstovian; this is corroborated in Florida (Bryant 1991). While it is indeed true that other anchitheres are found elsewhere in North America during the Barstovian (16.5 to 11.5 Myr; MacFadden, pers. observ. 1999), the exact biochronological range of *Anchitherium s. s.* in North America must await a comprehensive analysis of all Miocene anchithere horses on this continent.

Discussion.—Stirton (1940) listed seven species assignable to North American *Anchitherium sensu lato*. As currently envisioned, of these seven, three are referable to *Kalobatippus* as *K. praestans* (Cope 1879) (= *K. gracilis* Marsh 1892), *K. avus* (Schlaikjer 1935), and *K. agatensis* Osborn 1918, whereas *Anchitherium* includes *A. navasotae*, *A. clarencei*, and one or more new, undescribed species from western North America.

In many respects *Kalobatippus* and *Anchitherium* are very similar and hence the confusion about the validity of these two genera, particularly in North America. Most workers who have considered *Kalobatippus* to be distinct from *Anchitherium* have focused on the metapodial proportions, principally the relative robustness of MT III. This important, defining character has heretofore not been analyzed statistically, mostly due to the paucity of relevant specimens. During this study all available MT IIIs were measured for *Kalobatippus* and *Anchitherium* (Table 1). Upon examination and in a qualitative sense,

there were discernable differences between these two taxa, as had been previously described in the literature. It was, however, unclear which morphological characters would be most important in quantitative discrimination and to what extent these differences might be related to size (*Kalobatippus* is generally a smaller horse than *Anchitherium*).Results of *t*-tests of all five metapodial characters (GRTL, PRXW, MDSH, DSTB, and DSAR) indicate that there are statistically significant differences in all these size-related characters. In addition, a Wilcoxon non-parametric test of the metapodial character INDEX, which is an indicator of relative robustness, also yielded statistically significant results (Table 1). These characters all indicate that the MT III of *Anchitherium* is both larger and relatively more robust than that of *Kalobatippus*, thus confirming the observations of previous workers.

There also are dental characters that distinguish *Kalobatippus* from *Anchitherium*, most of which relate to relative size, including toothrow lengths, upper and lower molar lengths (UIMAPL), HEIGHT, and upper molar transverse width (UMTRN; Table 1). Many workers have indicated that the m3 heel of *Anchitherium* is reduced relative to *Kalobatippus* (Fig. 4). The character m3ratio, which takes into account the relative development of the m3 heel, is statistically significant ($p = 0.013$, assuming a cut-off of $p < 0.05$). In summary, there are quantitative characters of the MT III and dentition that serve to differentiate *Anchitherium* from *Kalobatippus*.

Anchitherium clarencei Simpson, 1932

Type specimen.—UF/FGS V-5074, R M1-M3, Midway L. F., Gadsden County, FL. (Also see other referred specimens from the Midway locality in Simpson [1932]). The holotype, which is an adult dentition in middle wear (Fig. 5), preserves diagnostic and important characters represented in this species, including weakly developed ribs on ectoloph, both protoloph and metaloph connected to ectoloph, rudimentary internal cingulum, triangular hypostyle connected to metaloph, M3 (APL = 16.7 mm, TRN = 21.4 mm) smaller than M2 (APL = 21.5 mm, TRN = 24.3 mm), and brachyodont teeth (M1 MSTHT = 7.7 mm, M2 MSTHT = 8.5 mm, M3 MSTHT = 7.8 mm; also see Table 2).

Referred material from Thomas Farm.—*Cranial and dental*: MCZ 19930, flattened but relatively complete skull of mature adult with R and L I1, I2, R and L P1-M3; UF/FGS V-5243, right mandible with p2-m3 (also see Simpson 1932); UF 17615, L mandibular fragment

with p2, p3, fragmentary p4; MCZ 3810, L mandible with ascending ramus, dp2-dp4, m1 erupting (also see White 1942); UF 19756, L mandible with ascending ramus, dp2-dp4, m1 erupting; MCZ 7595, L dP2; UF 156492, UF 164050, 164051, isolated incisors; UF 156492 L occipital condyle.

Axial skeleton: UF 171842, 181198, fragmentary cervical vertebra.

Forelimb: MCZ 7626, 2 L scapulae; MCZ 7598, L scapula; MCZ 7600, R humerus; UF 1473, 200364 distal R humerus; UF 172615, 174950, R radius; MCZ 7601, L radius; UF 44720, distal L radius; MCZ 7633, L ulna; MCZ 7603, L scaphoid; UF 19843, L lunar (intermediate); MCZ 7459, R pisiform; UF 190343, R proximal MC II; UF 45507, L proximal MC III.

Hindlimb: UF 174127, L innominate; UF 1325, fragment proximal L femur; UF 177675, fragment distal L femur; UF 1437, R patella; UF/FGS V-6595, MCZ 759, UF 43625, L astragalus; MCZ 7599, UF 157922, R calcaneum; MCZ 7458, L calcaneum; UF 43601, 44724, L navicular; UF 155689, 58605, R ectocuneiform; UF 60717, 182749, L ectocuneiform;UF 66944, 204045, R cuboid; MCZ 7608 (2 specimens), UF 155081, R MT III; UF/FGS V-6748, proximal R MT III; UF 47569, proximal L MT III.

Miscellaneous podial elements: UF/FGS V-5301, V-6592, fragments of distal articular surface of metapodial III; UF 58782, 175395, proximal phalanx of medial digit III; UF 47450, 98400, 175396, 2nd (medial) phalanx of medial digit III; UF 203700, 204948, distal (ungual) phalanx of medial digit III; UF/FGS V-5273, fragment of lateral metapodial with distal articular surface; UF/FGS V-6593, UF 19985, 43624, 164118, 172006, MCZ 7605 and uncataloged; proximal phalanx of lateral digits (II or IV); UF/FGS V-10077, UF 59091, 161068, 165150, 165914, 196874, MCZ uncataloged (6); medial phalanx of lateral digits (II or IV); UF 19833, 19839, 47571, 204949, ungual (distal) phalanx of lateral metapodial; UF 1418, 165811, 180631, 183658, 183294, 183603, 185254, 195643, sesamoids.

Geographic location.—early Hemingfordian (18 Ma) to early Barstovian (~15.5 Ma) of Florida, early Hemingfordian Flint Hill L.F., South Dakota, and possibly early Hemingfordian Sespe and Vaqueros formations, California; possibly also from Frick (AMNH) Clay Quarry and Martin Canyon Quarry A, Colorado.

Revised Diagnosis.—Same as for the genus, with the following specific complex of characters: elongated cranium, preorbital facial fossa shallow and developed

Figure 4. Left m3s of selected anchithere horses showing the development of the posterior heel (right). In the primitive condition, as seen for example in *Miohippus equiceps* (bottom, which includes m2and m3), the heel is relatively well developed. In the advanced condition, as seen for example in *Hypohippus osborni* (top), the heel is relatively reduced and usually does not form part of the occlusal surface of the tooth until late wear. Taken from Osborn (1918, plate 5). Natural size.

on the nasal, lacrimal, and maxillary bones, malar fossa absent, rounded incisor arcade; teeth brachyodont; moderately large horse, similar in size to modern donkey (*Equus asinus*), mean P1M3TRL = 125.3 mm; P2M3TRL = 117.5 mm. Upper cheek teeth with well developed styles in the molars; relatively large dP1, cement absent, no crochet, metaloph connects to the ectoloph; internal cingula well developed on the upper premolars,
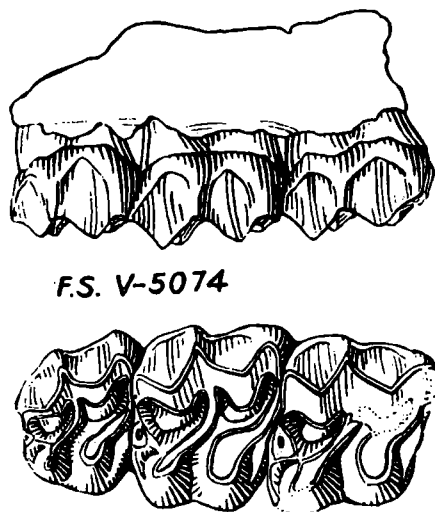
F.S. V-5074

Figure 5. Holotype of *Anchitherium clarencei*, UF/FGS
V-5074, R M1-M3, from the Midway L. F., Gadsden
County, Florida, external (top) and occlusal (bottom)
views. From Simpson (1932, p. 32, Fig. 18). Natural
size.

moderately developed or rudimentary on the molars;
mean M1/M2 APL = 20.8 mm; mean M1/M2 TRNW =
23.3 mm; MSTHT/mtcmstht = 9.6 mm (Table 2).

Mandible shallow (mean depth beneath posterior part
of m3 ≅ 53 mm); internal cingula poorly developed
relative to upper premolars; well developed and distinct
metaconids and metastylids, m1/m2trnw = 13.8 mm;
m3 hypoconulid heel reduced and is not part of the occlusal
surface until late wear. MT III short relative to other
Anchitherium (mean GRTL = 218.7 mm) but relatively
more robust than *Kalobatippus* (mean INDEX = 9.8, N =
3, s = 0.3 mm, observed range = 216 to 222 mm).
Proximal phalanges of MT III relatively unreduced.

Anchitherium clarencei differs from the closely
related species *A. navasotae* because the former is slightly
larger in size and has a more advanced reduction of the
m3 hypoconulid heel.

Description.—Although there have been previous
descriptions of the morphology of *Anchitherium clarencei*
from Thomas Farm, recent collecting and integration of
the hypodigm from the UF, FGS, and MCZ collections
warrants further description here.

Cranium and dentition. A single crushed skull, MCZ
19930, of *A. clarencei* is known from Thomas Farm (Fig.
6). In contrast to other middle Miocene horses (e.g.,
Parahippus leonensis and *Archaeohippus blackbergi*),

the skull indicates a relatively large horse, with a greatest
skull length of ~373 mm and a condylar-basal skull length
of ~342 mm (both measurements are approximate
because of postmortem distortion). This size is similar
to a modern donkey, *Equus asinus* (UF 156889), con-
tained in the UF VP collection. The upper incisor arcade
is rounded and the incisors (R and L I1 and I2 preserved)
have cups (infundibula). The precanine diastema (R =
15.0 mm, L = 14.4 mm; from posteriormost part of I3
alvoeli to anteriormost part of C alvoeli) is shorter than
the postcanine diastema (R = 32.7 mm; L = 29.0 mm;
from posteriormost part of C alvoeli to anteriormost part
of P1). The nasal notch, which lies anterodorsal to dP1,
is unretracted relative to the condition seen in advanced,
later Cenozoic equids. Although located in a badly
crushed region, the infraorbital foramen (IOF) appears
to lie dorsal to the posterior half of P3. The anterior
margin of the orbit lies dorsal to the junction of M1 and
M2. The cheek region (not illustrated) is dorsoventrally
crushed, but indicates a shallow, large, dorsally positioned
preorbital facial fossa lacking either a distinctive rim or
posterior pocket. There does not appear to be a ventrally
positioned malar fossa. The maximum transverse width
across the occipital condyles is 54.2 mm.

In the upper cheek teeth the dP1, which is retained
in adult dentition, is anteroposteriorly longer than its
transverse width; lingually there is a well delevoped
cingulum; the labial half of the tooth is in occlusal wear.
The anterostyle of P2 is well developed. The internal
cingulum is relatively well developed on the premolars
and poorly developed or absent on the molars. The dental
pattern of P2 through M3 is similar, with a well developed
W-shaped ectoloph with high crests indicating transverse
shear; the protoloph and metaloph are well developed,
lack proto- or metaconules or crochets, and are connected
to the ectoloph (Fig. 7). Ribs on the ectoloph between
the styles vary from rudimentary to moderately developed.
A prominent hypostyle is located in the posterior portion
of the cheek teeth. As Simpson (1932, p. 32) described,
the hypostyles for *A. clarencei* are "triangular, circular,
pitted, united by crest to hypocone." The M3 is smaller
than either the M1 or M2 (Table 2). There are very strong
and well developed external cingula that extend upward
on the teeth to form the parastyles and mesostyles. The
mesostyle crown heights are brachyodont (with
hypsodonty index [MSTHT/APL] of << 1) and higher
crowned relative to primitive horses such as *Miohippus*,
but shorter than *Hypohippus* and more advanced forms
like *Parahippus* (also compare with MacFadden 1992,
p. 240, Fig. 11.6).

Table 2. Cheek tooth (P2 or p2 through M3 or m3) measurements of *Anchitherium clarencei* from Florida. For each entry, the sequence represents APL or apl, TRN or trn, and MSTHT or mtcmstht. See text for abbreviations.

Specimen no.	Locality	Position	P2/p2	P3/p3	P4/p4	M1/m1	M2/m2	M3/m3	m3heel
UF/FGS V5074 type	Midway	RU				22.0, 23.0, 7.7	21.5, 24.3, 8.5	16.7, 21.4, 7.8	
MCZ 19930[a]	Thomas Farm	RU	24.7, 20.3, 7.4	21.4, 26.3, 8.6	20.9, 24.8, 8.7	21.3, 23.3, 8.8	20.0, 22.5, 8.2	18.1, 20.8, 7.2	7.2
UF/FGS V5243[b]	Thomas Farm	Rl	20.9, 11.4, 9.1	20.4, 12.7, 10.2	20.7, 14.6, 10.4	21.1, 14.2, 11.3	20.0, 13.2, 11.8	24.0, 11.4, 10.8	6.2
MCZ 3810	Thomas Farm	Ll	22.0, 12.1, 6.1	19.7, 14.4, 7.2	21.6, 13.4, 7.5	20.0, 13.9, 11.0	20.0, 12.7, —	—	—
UF 17615[c]	Thomas Farm	LL	20.5, 12.8, 9.0	20.0, 15.6, 10.4	20.0, 15.6, 10.4	—	—	—	—
AMNH 22684	Midway	Ll	—	—	—	—	—	23.4, 11.0, 8.9	5.5
UF 118529	Willacoochee	LU	—	21.2, 22.2, 7.1	19.6, 22.3, 7.3	19.7, 21.6, 5.5	—	—	—
UF 114723	Willacoochee	Ll	21.0, 11.9, 9.3	—	—	—	—	—	—

[a] P1M3TRL = 124.2; P2M3TRL = 115.2.
[b] p1m3trl = 126.3; p2m3trl = 119.8.
[c] Deciduous premolar series (not used in statistics presented in Table 1).
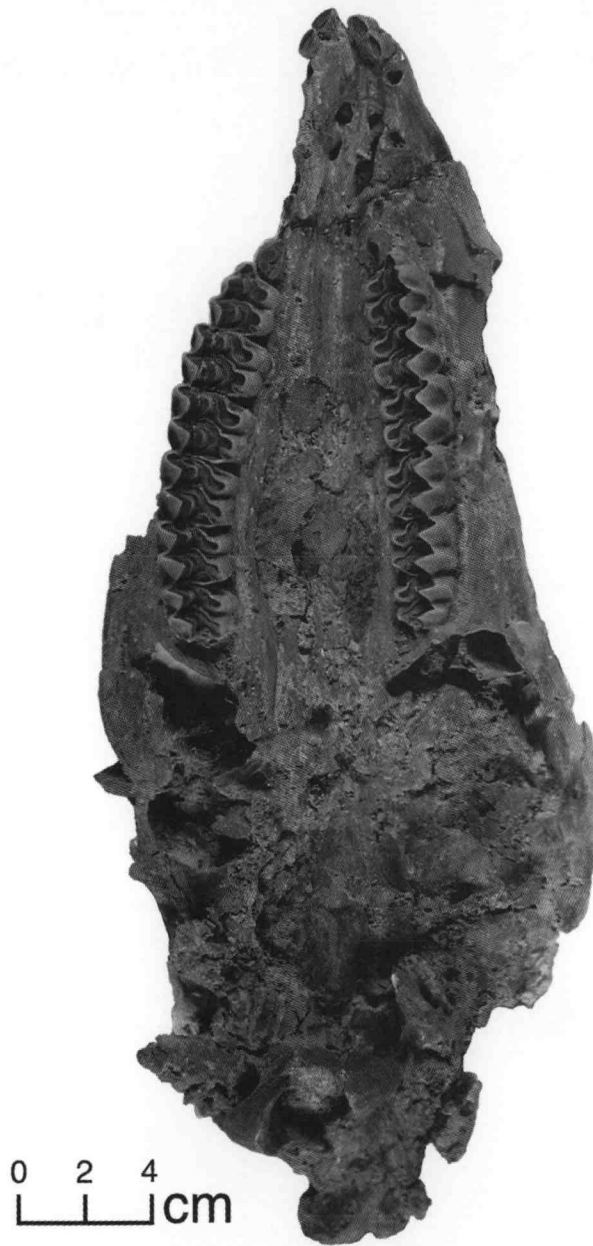
Figure 6. Ventral view of crushed cranium of *Anchitherium clarencei*, MCZ 19930, from Thomas Farm, early Hemingfordian of Florida.

As represented in MCZ 3810, the alveoli for the lower symphysial dentition indicate a rounded incisor series. There is no precanine diastema, as the canine is appressed to the i3. On the L side of MCZ 3180 a single mental foramen lies about midway between, and ventral to, the canine and p1 (Figs. 8, 9); on UF 17615 four foramina lie between, and ventral to, c and p1. The postcanine diastema (posteriormost part of c to anteriormost part of p1) is 31.6 mm in MCZ 3810 and >40.8 mm in UF 17615. With regard to p2-m3, the labial cingulum is poorly developed, whereas the lingual cingulum is strong and well developed. The p2 has a relatively elongated
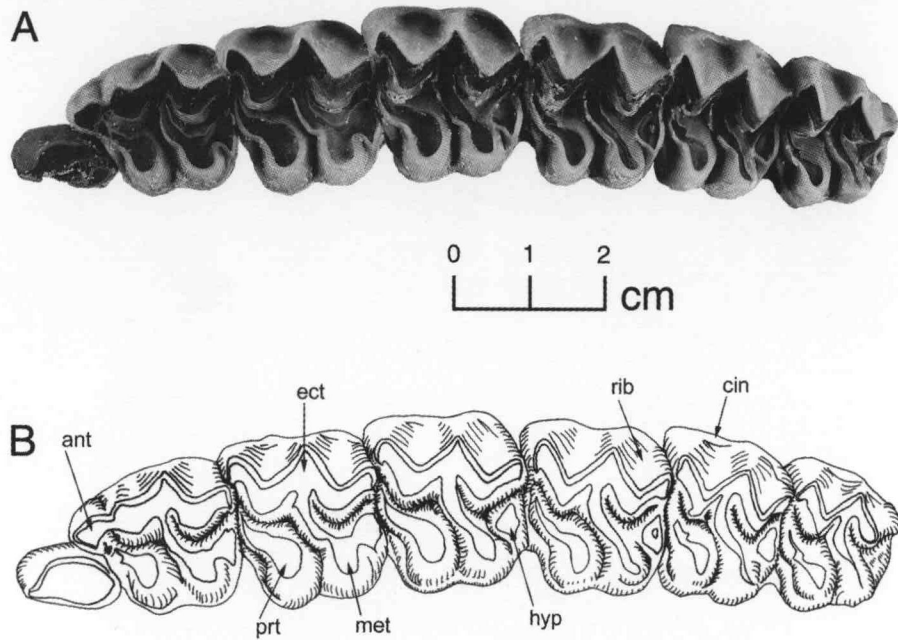
Figure 7. Photograph (A) and line drawing (B) of LP1-M3 of *Anchitherium clarencei*, MCZ 19930, from Thomas Farm, early Hemingfordian of Florida. ant, anterostyle; cin, cingulum; ect, ectoloph; hyp, hypostyle; met, metaloph; prt, protoloph; rib, rib.

and expanded region anterior to a well developed paraconid, a single metaconid/metastylid, and a well developed metalophid with a well developed entoconid posterolingually (Fig. 8). In p3-m3 the protolophids and metalophids are equal/subequal in size and there are distinct and relatively well separated metaconids and metastylids. The m3 is characterized by a moderately developed hypoconulid heel. In most respects the dental pattern of *Anchitherium clarencei* demonstrates a stage of evolution similar to primitive anchitheriines such as *Miohippus*, with the principal difference being that the former genus is larger in overall size-related characters.

Forelimb. The scapula (not illustrated) contains a well developed and rugose olecranon process for attachment of the biceps brachii tendon. The mean greatest width (N = 3) of the glenoid fossa is 44.1 mm. On the blade the coracoid process is poorly developed. There is a well developed coracoid crest that is recurved ventrally as it extends the length of the scapula.

The complete humerus (MCZ 7600) is 225 mm in greatest length, with a mediolateral (transverse) proximal width of 59.9 mm and width across the distal trochlea of 55.6 mm. In general proportions and morphology the humerus of *A. clarencei* is distinctly equine, although with some notable exceptions (Fig. 10). The deltoid tuberosity is relatively poorly developed and the teres major tuberosity is absent. The morphology of the proximal articular surface is different from advanced, i.e., equine, horses (e.g., *Equus*). In *Equus* this region between the greater and lesser trochanters has a trochlear region with a well developed intermediate tubercule for accommodation of the biceps brachii tendon, which acts as a passive stay apparatus during standing (Hermanson and MacFadden 1992). In *A. clarencei* the trochlear region is curved to form a fossa defined by the greater and lesser tubercules and the INT is rudimentary (Fig. 10). In this morphology, *A. clarencei* is similar to *Mesohippus*, *Merychippus*, and extant *Tapirus terrestris*, as illustrated in Hermanson and MacFadden (1992, p. 379-380, Figs. 1, 2).

The radius has a mean greatest length of 255 mm (N = 2), a mean greatest transverse width (proximal to, and excluding the radial tuberosities) of the proximal
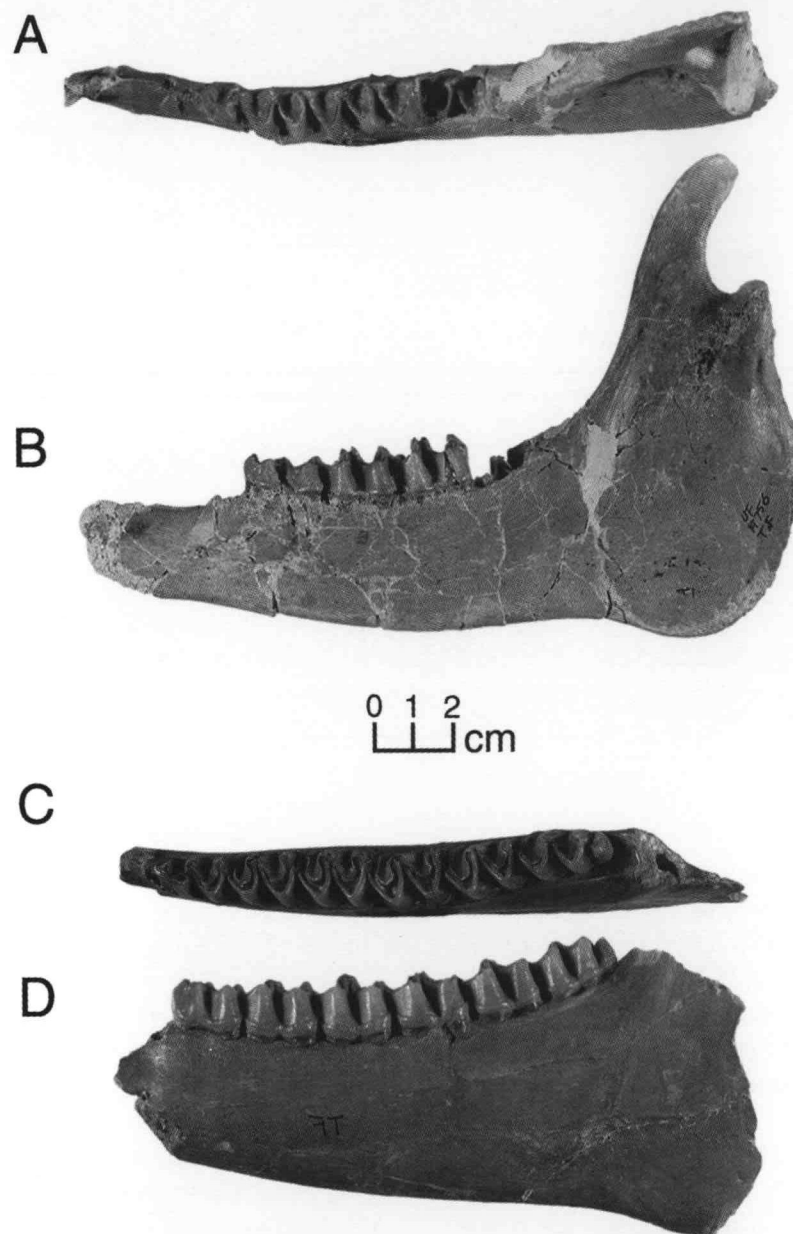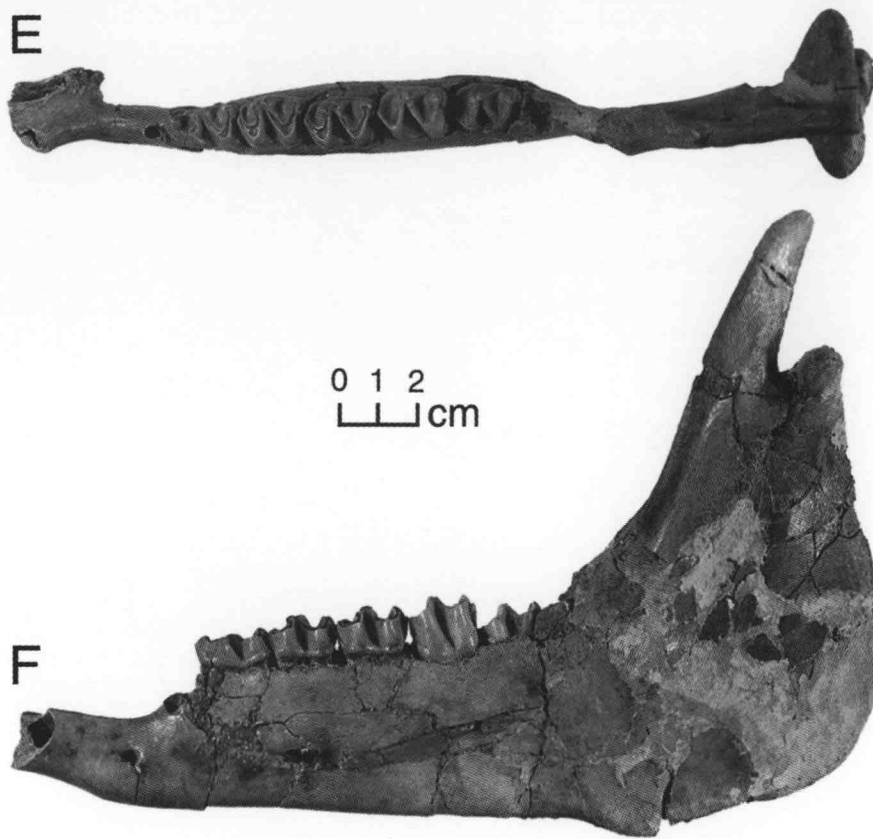
Figure 8. Mandibles of *Anchitherium clarencei* from Thomas Farm, occlusal (A, C, E) and external (B, D, F) views, UF 19756, L mandible with dp2-dp4, m1 erupting (top); UF/FGS V-5243, R mandible with p2-m3 (bottom); MCZ 3810, L with dp2-dp4, m1 erupting (next page). Note: C and D are reversed.

articular surface of 46.0 (N = 4), and a mean greatest transverse width (distal to, and excluding) of the distal articular surface of 39.8 mm (N = 2). The shaft of the radius is crushed, but the anterior surface is convex and the posterior surface is concave. In life, the radial shaft would have been slightly bowed. In general proportions and morphology the radius of *A. clarencei* is distinctly equine, although with some notable exceptions (Fig. 11). In particular, on the distal articular surface the medial facet for the lunar (intermediate) carpal bone is relatively small in contrast to its development in advanced equines such as *Equus*. This condition in *A. clarencei* reflects the lesser development of the central (III) carpal, metacarpal, and phalanges relative to their lateral (II or IV) equivalents.

The ulna (MCZ 7633), although broken distally, indicates a shaft that extends more than halfway down the shaft of the radius (Fig. 11). In contrast to the strong fusion of the ulna and radius in advanced equines (e.g., *Equus*), the ulna of *A. clarencei* appears to have been loosely affixed to the radius.

The carpus is represented by three bones (not illustrated). On the antero-internal face of the scaphoid (MCZ 7603) there are two well developed facets for the lunar and posteriorly there is a well developed volar tuberosity. The lunar (intermediate) of *A. clarencei* is represented by a single specimen (UF 19843). Other than being relatively less broad transversely relative to the radial and ulnar bones, in most characters this element resembles advanced equines. The pisiform (MCZ 7459) is concave internally, convex externally, and, relative to *Equus*, has a very large cuneiform facet and smaller ulnar facet.

Hindlimb. A partial left pelvis is represented by UF 174127 (not illustrated; also other specimens in the MCZ). It has a relatively elongated ilial shaft in contrast to primitive horses like *Mesohippus* (Hussain, 1975). The region of the obturator foramen is not preserved.

A single specimen (UF 177675, not illustrated) preserves the distal articular region of the R femur. The greatest transverse width across the medial and laterial condyles (distal to the epicondyles) is 57.4 mm. The lateral ridge of the trochlea has a well defined
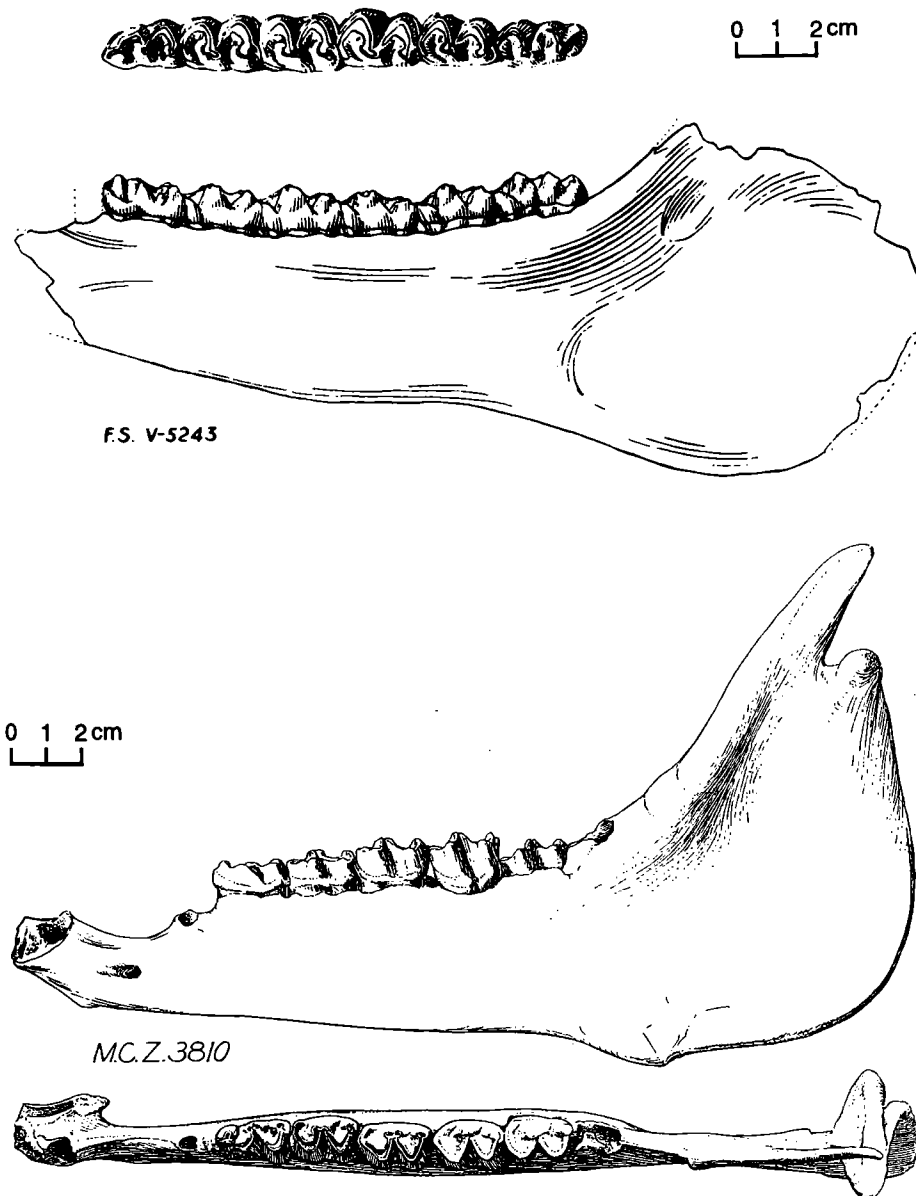
Figure 9. Mandibles of *Anchitherium clarencei* from Thomas Farm. UF/FGS V-5243 (top), occlusal and internal views (modified from Simpson 1932, p. 32, Fig. 19). MCZ 3810 (bottom), external and occlusal views (modified from White 1942, plate 9).

and distinct ridge; the corresponding medial ridge is not preserved.

The calcaneum has a mean greatest length of 92.1 mm (N = 3) and greatest mean transverse width across the sustentaculum of 39.9 mm (N = 3). In general morphology the calcaneum is as Hussain (1975)

described for tridactyl horses. Relative to a similar-sized *Equus*, e.g., a donkey (*E. asinus*, UF 156889, that was also used for other postcranial comparisons below), the tuber calcis in *A. clarencei* has a more pointed surface (Fig. 12) for articulation with the Achilles tendon. The development of the proximal lanceolate facet, which

Figure 10. Humerus of *Anchitherium clarencei* (MCZ 7600) from Thomas Farm, anterior view (A), proximal articular surface (B), and posterior view (C). bbt, fossa for biceps brachii tendon; dt, deltoid tuberosity; gt, greater tubercle; lt, lesser tubercle.

articulates with the astragalus, deserves some discussion here. As reviewed in Hussain (1975), this facet is absent in primitive equids and Old World *Palaeotherium*, rudimentary in Old World *Anchitherium*, and well developed in New World *Anchitherium* and advanced equines, e.g., *Equus*. If this were the case, then differences in this character could be used to separate Old and New World *Anchitherium*. In all three specimens of *A. clarencei* from Thomas Farm, the proximal lanceolate facet is either absent, poorly developed, or confluent with the facet of the processus cochlearis for articulation with the astragalus. This observation is thus different from
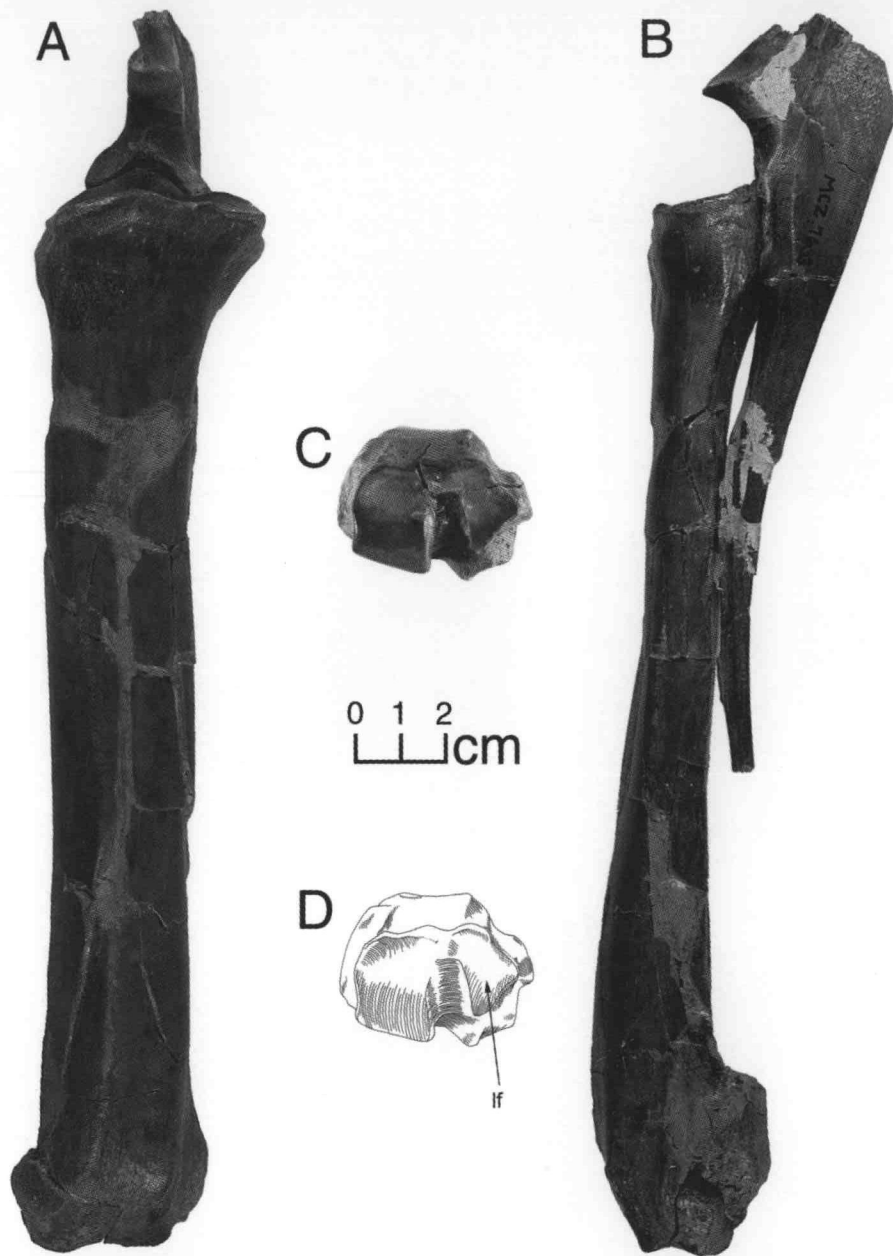
Figure 11. Lower forelimb of *Anchitherium clarencei* from Thomas Farm. Anterior view (A) of left radius (MCZ 7601) and ulna (MCZ 7633); externolateral view (B) of left radius (MCZ 7601) and ulna (MCZ 7633) showing development of ulnar notch and length of reduced ulnar shaft (distalmost part of which is missing); photo (C) and line drawing (D) of distal articular surface of radius (MCZ 7601). lf, lunar facet.

that of Hussain (1975). Further analysis of the distribution of the character and its various states in fossil horses is necessary before it warrants the definitive phylogenetic significance suggested by Hussain (1975).

In the astragalus, the mean greatest length (measured from the dorsalmost part of the medial trochlear ridge to the navicular facet) is 48.5 mm (N = 2) and mean greatest transverse width across the navicular facet is 33.3 mm (N = 3). All three astragali of Thomas Farm *A. clarencei* demonstrate similar morphology and relatively little
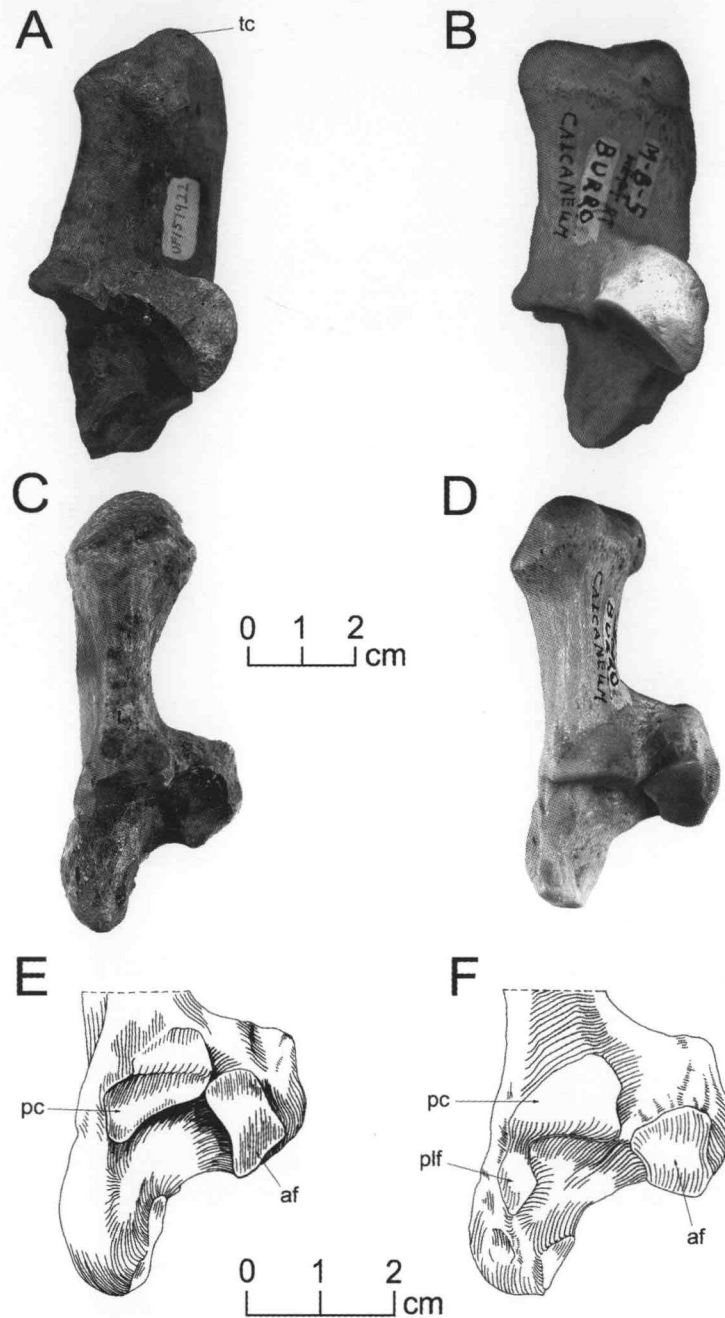
Figure 12. Right calcaneum (UF 157922) of *Anchitherium clarencei* from Thomas Farm, internolateral (A) and dorsal (C, E) views as compared to donkey, *Equus asinus* (UF 156889; B, D, and F). af, astragalar facet; pc, processus cochlearis facet; plf, proximal lanceolate facet; tc, tuber calcis.

variation in the development of the articular facets. The medial trochlear ridge contacts, or nearly contacts, the navicular facet. As noted by Hussain (1975), the medial and lateral trochlear ridges in *A. clarencei* are slightly more inclined relative to the sagittal plane than they are in *Equus* (Fig. 13). Kowalevsky (1873) reported that the posterolateral calcaneal facet was absent in *Anchitherium*. As Hussain (1975) also observed for all North American equids, this facet is distinct and well developed in *A. clarencei* from Thomas Farm (Fig. 13).
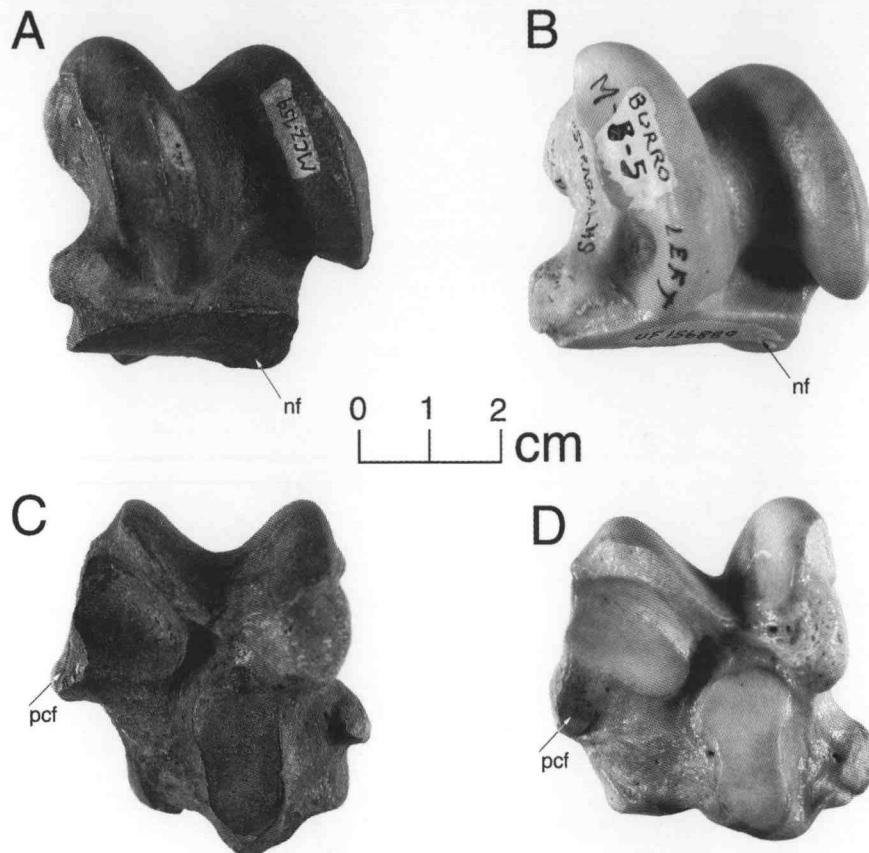
Fig. 13. Left astragalus (MCZ 759) of *Anchitherium clarencei* from Thomas Farm dorsal (A) and plantar (C) views as compared to donkey, *Equus asinus* (UF 156889; B, D); nf, navicular facet; pcf, posterolateral calcaneal facet.

The distal articular surface contains a large navicular facet and a small, but distinct, cuboid facet (not illustrated).

With regard to the other more distal ankle bones, the mean anteroposterior length (26.5 mm, N = 2) of the navicular is essentially the same as the mean transverse width (26.9 mm, N = 2). These proportions are similar to more advanced equines, and contrasts with *Mesohippus*, where in the latter genus the anteroposterior length is greater than the transverse width (Hussain 1975). This increased transverse width in *Anchitherium clarencei* reflects the emphasis on MT III relative to either MT II or IV. The proximal (astragalar) facet of the navicular in *A. clarencei* is concave and lacks the non-articular area seen in more advanced horses. The distal articular surface of the navicular is convex and has a well developed continuous ectocuneiform facet (Fig. 14)

in contrast to the larger development of non-articular areas seen in advanced equines such as *Equus*. On the ectocuneiform the proximal and distal articular surfaces contain, respectively, continuous navicular and MT III facets and lack the separation (or subdivisions) of these facets seen in advanced equines such as *Equus* (Hussain 1975). The proximal surface of the cuboid contains a large calcaneal facet and small astragalar facet (Fig. 15). There are well developed posterior navicular and ectocuneiform facets on the internal surface of the cuboid. The distal part of the cuboid (UF 66944) contains facets for articulation of the MT III and MT IV; both of these are relatively smaller in their development in contrast to the condition in advanced equines such as *Equus*. The presence of well developed facets for MT III and MT IV in *Anchitherium* is advanced relative to *Mesohippus*, the latter of which lacks the cuboid-MT III articulation. As
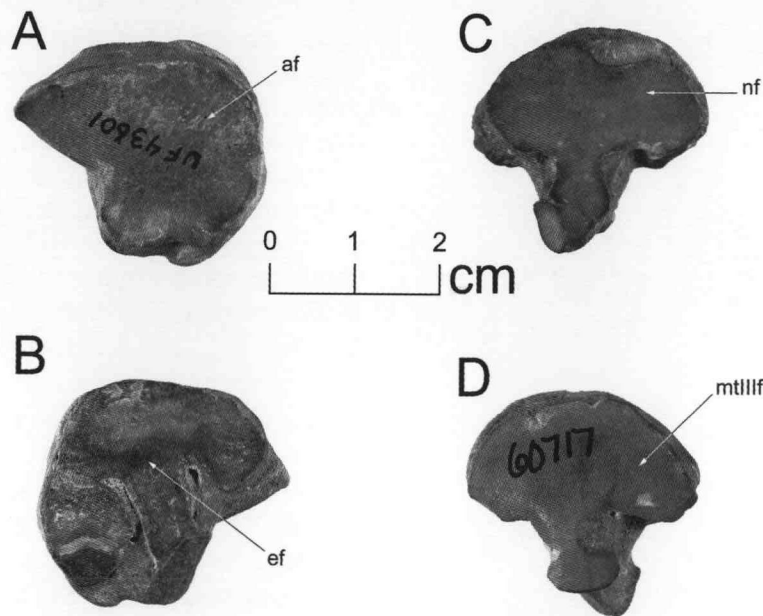
Figure 14. Navicular (UF 43601, A, B) and ectocuneiform (UF 60717, C, D) of *Anchitherium clarencei* from Thomas Farm, proximal (A, C) and ventral (B, D) views, respectively. af, astragalar facet; ef, ectocuneiform facet; nf, navicular facet; mtIIIf, metatarsal III facet.

noted by Hussain (1975), on the cuboid of *Anchitherium* there is a well developed tubercle for attachment of the plantar ligament.

The MT III of *A. clarencei* is at the lower end of the observed range (mean GRTL = 218.7 mm) for the sample of New World *Anchitherium* measured during this study (Table 1). On the proximal articular surface (Fig. 16) there is a large and continuous ectocuneiform facet that lacks the non-articular area seen in advanced equines such as *Equus* (Fig. 16). On the posteromedial part of the proximal articular surface there is a mesentocuneiform facet; posterolaterally there is a well developed cuboid facet. Just distal to the proximal articular surface on the caudal part of the MT III shaft there are well developed facets for articulation with MT II and MT IV. These prominent facets indicate a high level of functionality of the lateral metapodials relative to more advanced equids (Hussain 1975). In primitive horses, the mean width of the distal tuberosities (DSTB) is greater than the width across the condyles of the distal articular surface (DSAR, Table 1). In advanced, monodactyl horses the reverse is normally observed (Hussain 1975). For *A. clarencei*, the

mean (N = 3, MCZ 7608 [2], UF 155081) observed ratio of DSTB/DSAR is 31.5/29.2, indicating the more primitive morphology. In anterior view and at the distal-most part of the MT III shaft there is a distal articular concavity which allows for more rotation of the proximal phalanx. The distal sagittal (trochlear) ridge of the distal articular surface is well developed posteriorly, is faint along the distalmost curve, and is absent on the corresponding anterior trochlear surface (Fig. 16). This development of the sagittal ridge is characteristic of tridactyl horses. In more advanced monodactyl horses such as *Equus*, this ridge extends for a greater part of its circumference onto the anterior articular surface; its function is to restrict lateral motion of the foot (Hussain 1975).

Miscellaneous podials. Given the lack of association of skeletal elements (i.e., virtually all bones collected at Thomas Farm are disassociated), it is unclear whether the remainding footbones listed above in "Referred Specimens" belong to the fore- or hindlimbs. Nevertheless, there are some important characters preserved in these podials.

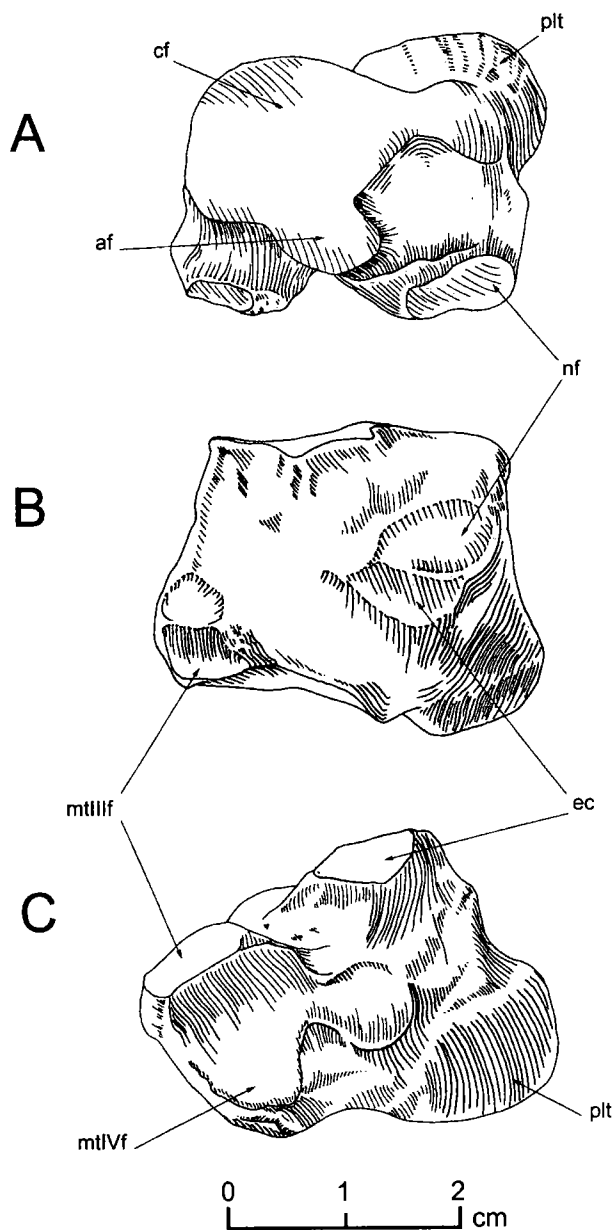A partial lateral metapodial (either II or IV,

Figure 15. Right cuboid (UF 66944) of *Anchitherium clarencei* from Thomas Farm. (A) proximal articular surface, (B) internal (medial) view), (C) distal articular surface. af, astragalar facet; cf, calcaneal facet; ec, ectocuneiform facet; mtIIIf, MT III facet; mtIVf, MT IV facet; nf, navicular facet; plt, plantar ligament tubercle.

undifferentiated, UF/FGS V-5273), which preserves the distal one-quarter of this bone (Fig. 17), indicates a relatively robust shaft with no evidence of distal reduction seen in more advanced, particularly monodactyl, horses. The distal articular surface has a weak sagittal ridge (not illustrated) for articulation of the proximal phalanx. This ridge extends only about halfway along this surface.

The proximal medial (III) phalanx of *A. clarencei* is short in contrast to more advanced horses in which this element is elongated relative to the medial (2nd) phalanx III (Fig. 17). The proximal articular surface of the proximal central phalanx has a groove that is developed on the plantar half of this area, but does not extend dorsally to the extent seen in advanced equines. This groove articulates with the distal sagittal ridge of the MT III. On the plantar side of the proximal medial phalanx there is a prominent proximal V-scar that extends about one-third the length of the shaft (Fig. 18). This V-scar for the attachment of digital ligaments is shorter than is seen on more advanced equines (Camp and Smith 1942; Sondaar 1968; Hussain 1975). The mean length (27.8 mm, N = 2) of the medial central (III) phalanx is 72 percent the mean length (38.4 mm, N = 3) of the proximal central (III) phalanx. The mean transverse width of the medial central phalanx is approximately equal to the mean length (29.4 mm, N = 2).

The proximal (Fig. 17) and medial phalanges of the metapodials II and IV of *A. clarencei* from Thomas Farm are characteristically equid as described in Sondaar (1968) and Hussain (1975). The distal articular surface of the proximal lateral metapodial lacks a sagittal ridge, indicating increased lateral flexibility of the side toes relative to more advanced equids. As represented by UF204948, the distal (ungual) phalanx of the medial digit III of *A. clarencei* is primitive in several aspects. Relative to *Equus*, in life the proximal articular surface (for articulation with the medial phalanx) would have indicated a less digitigrade stance, where more of the sole of the hoof would contact the ground during normal resting stance. The "V-shaped slit" (Fig. 17F) is well developed in *A. clarencei* relative to *Equus* and other advanced, monodactyl equids (Hussain 1975). Several specimens are preserved of the lateral distal (ungual) phalanx (Fig. 17G). This forms an assymetrical, well developed hoof core for the side toe. It has a prominent extensor process developed on the proximal articular surface. Hussain (1975) noted that the extensor process is present in fossil equids such as anchitheres and *Merychippus* and indicates muscular activity and functioning lateral digits.
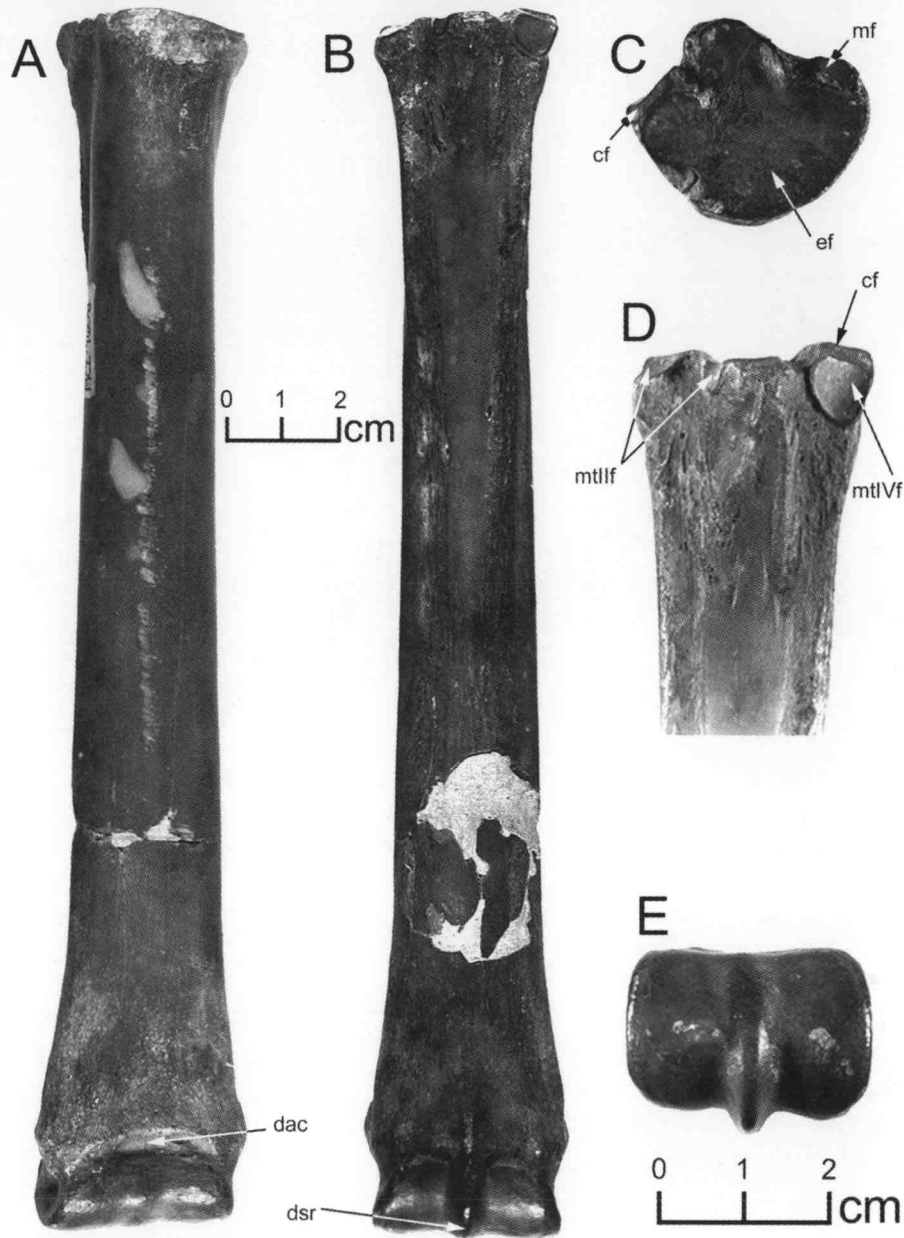
Figure 16. Right metatarsal III (MCZ 7608) of *Anchitherium clarencei* from Thomas Farm, (A) anterior view, (B) posterior view, (C) proximal articular surface, (D) posterior view of proximal one-quarter, showing facets, (E) distal articular surface, with anterior aspect above and posterior aspect below showing development of distal saggital ridge. cf, cuboid facet; dac, distal articular concavity; dsr, distal saggital ridge; ef, ectocuneiform facet; mf, mesentocuneiform facet; mtIIf, MT II facet; mtIVf, MT IV facet.
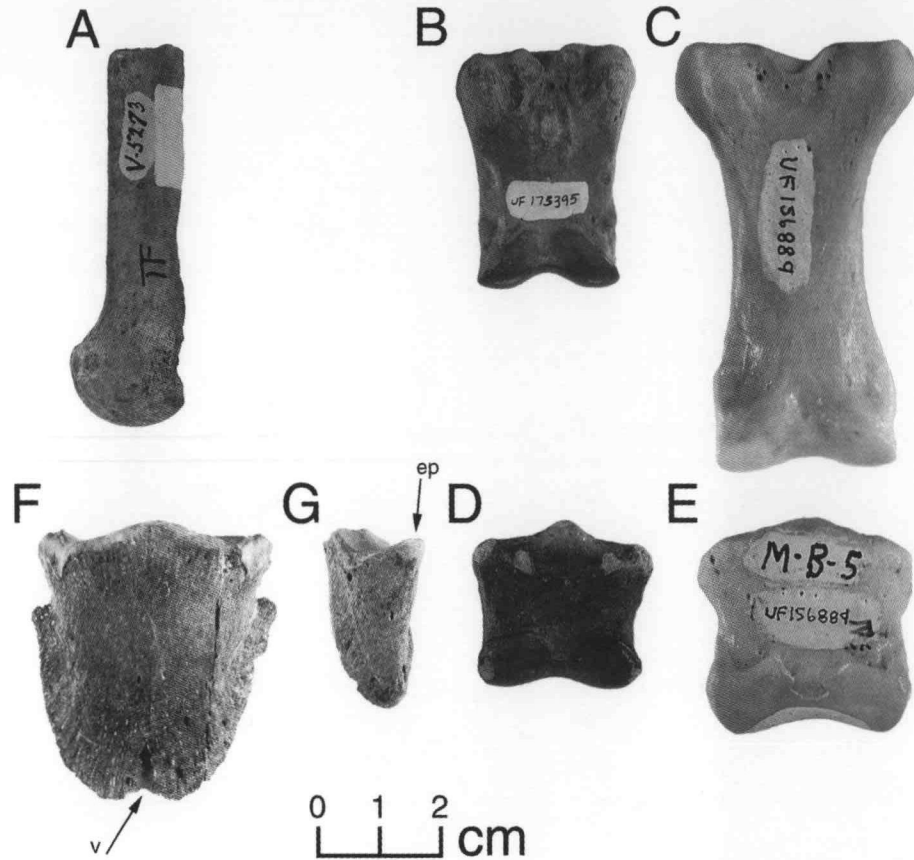
Figure 17. (A) External view of lateral metapodial (UF/FGS V-5273) of *Anchitherium clarencei* from Thomas Farm.
Ventral views of proximal (B, UF 98400) and medial (D, UF 175395) phalanges III of *Anchitherium clarencei* from
Thomas Farm compared to proximal (C) and medial phalanges (E) of extant donkey *Equus asinus*, UF 156889. (F)
Dorsal view of distal (ungual) phalanx III of *A. clarencei*, UF 204948. v, V-shaped slit. (G) Dorsal view of lateral
distal phalanx. ep, extensor process.

DISCUSSION

Until recently a comparison of North American
Anchitherium and *Kalobatippus* has been hampered by
the lack of relevant material and sufficently large
statistical samples with which to evaluate intraspecific
versus higher-level variation. Therefore, the sample of
A. clarencei accumulated over more than a half-century
of sporadic digging at Thomas Farm is important to an
understanding of the phylogeny and distribution of
anchithere horses, which are characteristically rare in
the fossil record.

***Anchitherium* Meyer 1844 and *Kalobatippus*
Osborn 1915.**—The question of the potential validity
of these two genera relates to the variation of their
fundamental differentia, some of which cannot be
assessed given the available material, whereas others can
be addressed at this time. Two salient characters of
generic significance include the reduction in the m3
hypoconid heel and the relative slenderness/robustness
of the metapodials. From the specimens examined during
this study it seems that there is a morphocline in the
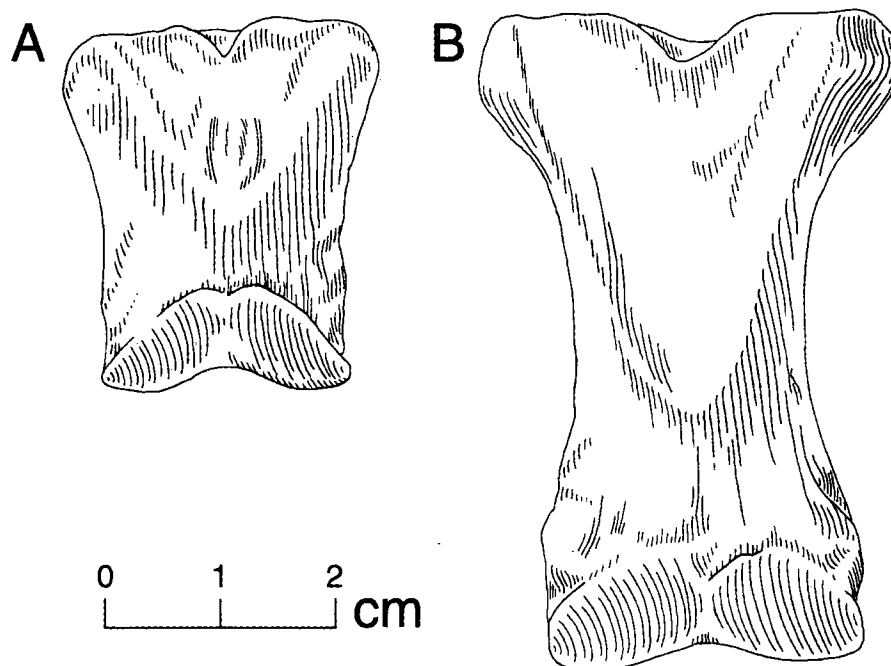reduction of the m3 heel from *Miohippus* to *Kalobatippus*

Figure 18. Ventral views of proximal phalanx III showing the development of the V-scar of *Anchitherium clarencei* (UF 175395) from Thomas Farm (A) compared to that of extant *Equus asinus* (UF 156889, B).

to *Anchitherium* to *Hypohippus* (Fig. 4). As described above the relative development (length) of the m3 heel in *Anchitherium* is shorter than in *Kalobatippus* (Table 1; m3ratio). This, therefore, seems to be a valid character to discriminate these two genera.

The population variation of metapodials can be assessed from a sample of *Anchitherium* sp. from the early Hemingfordian Bridgeport L. F. of Nebraska. Statistical analyses (N = 15) indicate that specimens from this quarry form a tight group, all of which are more robust than in the type and referred specimens of *Kalobatippus* (Fig. 19). Furthermore, the Coefficents of Variation (CVs) for all measured MT III characters are less than 5% (Table 3), which fall within acceptable limits for a uniform sample population of a fossil morphospecies (Simpson et al. 1960; MacFadden 1989). Thus, it seems that there is not continuous variation in the relative robustness of metapodials of *Kalobatippus* and

Anchitherium and this hallmark character serves, along with the relative reduction of the m3 heel, to differentiate these two taxa.

Thomas Farm *Anchitherium clarencei* and Old World dispersal.—The reduction of the m3 heel in UF/ FGS V-5243 and the relatively robust MT III proportions (Fig. 19) justify assignment of the Thomas Farm anchithere to *Anchitherium*. Simpson's species *A. clarencei* seems valid, although a detailed comparison with the closely related, slightly smaller *A. navasotae* (Hay 1924; Forsten 1975) and other currently undescribed species (e.g., as preserved in the Frick Collection) is warranted. *A. clarencei* possesses many characters that make this species similar to Old World *Anchitherium*, including size, reduction of the m3 heel, robust metapodials, triangular shape of the hypostyle, and presence of an internal cingulum on the upper premolars.
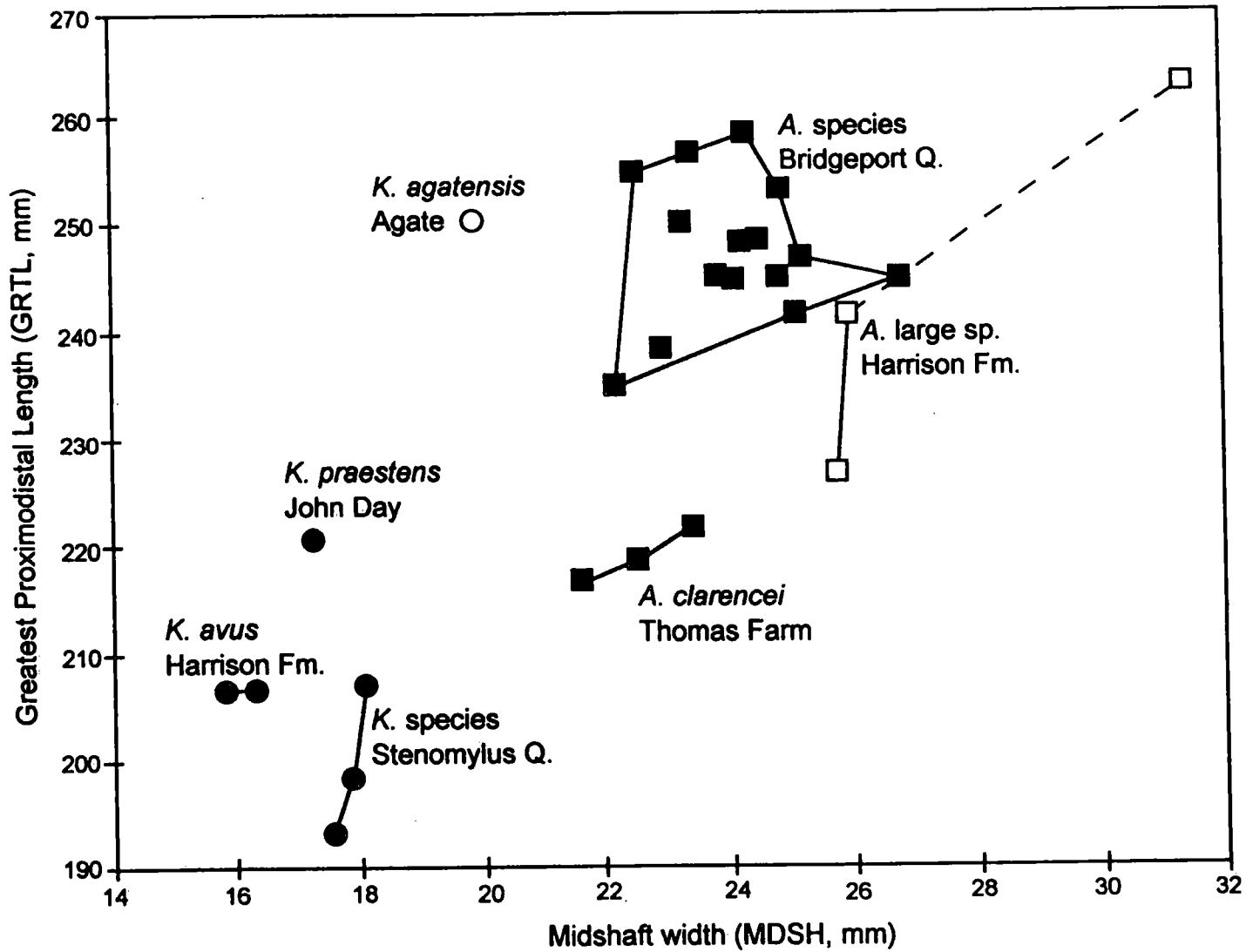
Figure 19. Bivariate plot of midshaft width of MTIII versus greatest proximodistal length for North American species of *Kalobatippus* and *Anchitherium* measured during this study.

Table 3. Univariate statistics, including variation parameters, from a population of *Anchitherium* sp. from the Bridgeport Quarry, Hemingfordian of western Nebraska (University of Nebraska State Museum locality MO 113 and 114). For character abbreviations see text and Figure 3.

Character	N	Mean	s	CV (%)	Range (minimum to maximum)
GRTL	15	247.6	6.5	2.62	235.5—259.0
PRXW	12	32.8	1.0	3.05	31.2—34.1
MDSH	15	24.1	1.2	4.98	22.1—26.8
DSTB	15	34.2	1.4	4.09	31.1—36.9
DSAR	14	30.5	1.1	3.61	29.2—33.4

The postcranial elements represented in Thomas Farm *A. clarencei* mostly confirm previous ideas about the functional morphology and stage of evolution of *Anchitherium* in general (e.g., Camp and Smith 1942; Sondaar 1968; Hussain 1975). In particular, the shape and relative development of articular facets on the metapodial, wrist, ankle, and phalangeal bones indicate a functionally tridactyl horse in which the fore- and hind-feet retained some of the flexibility seen in more primitive horses. *A. clarencei* lacked the passive stay apparatus developed in the forelimb of advanced horses such as *Dinohippus* and *Equus* (Hermanson and MacFadden 1992).

So far as the available evidence indicates, *Anchitherium* dispersed into the Old World, but *Kalobatippus* did not. Species like *A. clarencei* demonstrate the morphological complex of characters seen in Old World *Anchitherium*, particularly size, reduced m3 heel, triangular hypostyle, and internal cingulum development. In addition to morphological similarities, the occurrence of *A. clarencei* during the early Hemingfordian makes it a reasonable temporal candidate for dispersal during a major time of Holarctic faunal interchange at about 18 Ma. (Tedford et al. 1987; Woodburne and Swisher 1995; Sánchez et al. 1998) and thereafter when they become part of the middle Miocene "*Anchitherium* faunas" of the Old World.

SUMMARY AND CONCLUSIONS

For over a half-century fossil horses have been collected from the rich Hemingfordian Thomas Farm locality in north-central Florida. The accumulation of these fossils during this time now allows a better understanding of the morphology and systematics of *Anchitherium clarencei* Simpson, 1932, and such other primitive brachyodont horses as *Kalobatippus*. A reappraisal of the validity and distribution of *Kalobatippus* and *Anchitherium* indicates that both genera existed in North America. *A. clarencei* was widespread in North America during a very narrow time interval between about 18 and 17 Myr ago; it also persisted locally in the early Barstovian of Florida. *A. clarencei* is morphologically very similar to Old World *Anchitherium* and its occurrence at 17-18 Myr ago, which corresponds to Planktonic Foraminiferal zones N5 to N7, is consistent with this horse being a part of the middle Miocene intercontinental Holarctic dispersal across the Bering land bridge. So far as is known, *Kalobatippus* did not disperse into the Old World. The morphology of the foot of *A. clarencei* indicates a relatively high degree of flexibility and functional tridactyly.

Although many studies over the past several decades have concentrated on unravelling the complex interrelationships of fossil horses, fertile ground remains for a detailed phylogenetic study of the anchitheres, currently a horizontal assemblage of species traditionally referred to the North American genera *Miohippus*, *Anchitherium*, *Kalobatippus*, *Hypohippus*, and *Megahippus*. Once this is accomplished, then comparative evolutionary and ecological studies can be undertaken to better understand the paleobiology of this interesting, yet relatively poorly known, group of fossil horses.

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    Eisenberg, J. F. and J. R. Polisar. 1999. The mammal species of north-central Venezuela. Bulletin of the Florida Museum
        of Natural History, 42 (3):115-160.
Books:
    Lundell, C. L. 1937. The Vegetation of Petén. Carnegie Institute of Washington, Publication 478. Washington, D.C.
Composite Works:
    Gardner, A. L. 1993. Didelphimorpha. Pp. 15-24 *in* D. Wilson and D. M. Reeder, eds. Mammal Species of the World.
        Washington, D.C.: Smithsonian Institution Press, 1206 pp.
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