

POPULATION DYNAMICS OF *ARCHAEOHIPPIUS BLACKBERGI* (MAMMALIA; EQUIDAE) FROM THE MIOCENE THOMAS FARM FOSSIL SITE OF FLORIDA

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The Thomas Farm fossil site, Gilchrist County, Florida, is the most fossiliferous Hemingfordian terrestrial site east of the Mississippi River. Taphonomy indicates that the formation of the fossil deposit occurred over a period of at most thousands of years, a geologic instant. Thomas Farm contains one of the earliest and numerically largest populations of the small equid *Archaeohippus*. Although the sample of mandibles is small (MNI=30), I was able to recognize nine age grades for *Archaeohippus blackbergi*. As the age at which a female *Equus* gives birth to her first offspring (3-3.5 years) approximately correlates with eruption of the third molar (3.5-4 years), it is estimated from tooth eruption data that a female *A. blackbergi* yielded her first foal between 1.5-2 years of age. A mortality spike for individuals with m3 coming into occlusion is interpreted as representing mortality due to intraspecific combat between males. Potential longevity for *A. blackbergi* is estimated at about 5 years.

Key Words: *Archaeohippus*; Equidae; life table; Miocene; *Parahippus*; Thomas Farm

INTRODUCTION

The Miocene horse genus *Archaeohippus* (Gidley 1906) may be an example of phyletic dwarfism. Phyletic dwarfism, in its broadest sense, is size decrease in ancestral-descendant lineages, and is a form of pedomorphosis, the retention of ancestral juvenile character states in descendant species. It is either the result of neoteny, where somatic growth is retarded and sexual maturity is not, or progenesis, where somatic growth rate is unchanged but sexual maturation rate is accelerated, causing an early onset of sexual maturity. Attainment of sexual maturity is strongly correlated with a dramatic decrease in somatic growth rate in organisms with determinate growth such as vertebrates (Alberch et al. 1979).

Body size has a strong influence on mammalian physiology, life history, and ecology (McNab 1980; Eisenberg 1981). Thus, a single heterochronic dwarfing event can affect each of these (McKinney & Gittleman 1995). The ecological benefits of size reduction in *Archaeohippus* could include reduction of competition for resources with other ungulate species. In particular,

small herbivores are capable only of processing small amounts of food, and thus are dependent on high quality herbage (Janis 1976). However, they are well suited to survive in environments with a dry season during which resources are available only in small patches, and are thus good indicators of such environments (Ravosa et al. 1995).

Life history variables such as age of reproductive maturity and gestation length are correlated with body size (Eisenberg 1981). Compared with artiodactyls, perissodactyls have large neonates and long gestations (Millar 1981). Size reduction through dwarfing might have provided *Archaeohippus* with a way to reduce life history parameters such as gestation length and age of first reproduction relative to larger, plesiomorphic equids, thus increasing ecological distance and reducing interspecific competition.

The Thomas Farm fossil site of Gilchrist County, Florida, is an early Miocene (ca. 18 million years) terrestrial site (Simpson 1932; Pratt 1990). Taphonomic analysis indicates that the formation of the fossiliferous deposit occurred over a period of at most thousands of years (Pratt 1990). Thomas Farm contains one of the earliest and largest known samples of *Archaeohippus*. Although a wide array of vertebrate taxa has been iden-

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tified from Thomas Farm, fossils of three-toed equids account for 54% of the identifiable megafaunal specimens recovered (Pratt 1990). The most common taxon is *Parahippus leonensis*, the mesodont sister taxon of merychippine, hipparionine, and equine horses (Hulbert & MacFadden 1991). The largest and rarest of the Thomas Farm equids is the browser *Anchitherium clarencei* (MacFadden 2001), while the smallest is *Archaeohippus blackbergi*.

The brief period of fossil accumulation provides an almost instantaneous sampling of the fauna. The Thomas Farm fossil site formed as a sediment cone within a sinkhole; thus it is not as taphonomically biased as a stream deposit (Pratt 1990). Therefore, taxa can be treated as relatively intact populations in life table analyses of demographics. Hulbert (1984) performed such a study using mandibles of *Parahippus leonensis* from Thomas Farm. He determined that the mortality profile did not indicate a catastrophic accumulation of individuals, but rather an attritional assemblage that accumulated over many years.

The study presented here is an analysis of the population structure of *Archaeohippus blackbergi* from Thomas Farm with a comparison to *Parahippus leonensis* from the same locality (Hulbert 1984) and other equid populations. Although the present study does not attempt to resolve the question of which form of pedomorphosis produced this dwarf genus, exploring the population dynamics of this taxon is part of a larger study of heterochrony and the evolution of *Archaeohippus*. This study also provides insight into the workings of the dynamic life table as applied to fossil samples.

Abbreviations used in this study: m, molar; MCZ, Museum of Comparative Zoology, Harvard University; p, premolar; UF, Florida Museum of Natural History, University of Florida.

MATERIALS AND METHODS

A life table analysis of a fossil population uses the proportions of individuals in each age class to estimate population characteristics such as age-related mortality, average longevity, and fecundity. Such an analysis (Table 1) was performed on the population of *Archaeohippus blackbergi* from Thomas Farm (Table 2). *Miohippus obliquidens* (Table 3), a taxon from the Orellan Harvard Fossil Reserve in Goshen County, Wyoming, was included in the analysis to reflect the plesiomorphic condition of a larger equid modeled to be close to the ances-

try of *A. blackbergi*. At present, however, the identity of the nearest plesiomorphic sister taxon of *Archaeohippus* is unclear. In addition, comparisons will be made with Hulbert's (1984) study of the population of *Parahippus leonensis* (Table 3) from Thomas Farm.

Nine age classes are recognized for *Archaeohippus* jaws that correspond to those used by Hulbert (1984) on *Parahippus leonensis* from Thomas Farm. Figure 1 presents representative mandibles for age classes 2 through 9, and Table 4 lists these and additional referred specimens. Age classes one through five are based on patterns of tooth eruption, while classes six through nine are based on tooth wear criteria. Crown height measurements were taken at the metaconid. I will note how these classes differ for *A. blackbergi* versus other taxa to which they have been applied.

Unworn heights were rarely available because occlusion and wear coincide with full eruption. Not all of Hulbert's (1984) wear-based age class criteria for *Parahippus leonensis* are applicable to the *Archaeohippus blackbergi* sample. For example, the linguaflexid is not as strongly developed in *A. blackbergi* as in *P. leonensis*; thus the linguaflexid does not persist through as many classes in *A. blackbergi*. *Miohippus obliquidens* typically loses the p2 metaflexid after half the crown height is worn down.

In *Miohippus obliquidens*, permanent premolars display more wear than m2 throughout the life of the adult dentition, and this is very obvious by class 5. This wear pattern suggests that the permanent premolars erupt before m2 comes into occlusion. This was also observed in other *Miohippus* species (e.g. *Miohippus equinanus*) but is not characteristic of *Archaeohippus blackbergi* or *Parahippus leonensis*, which clearly erupt the m2 before the p2-p4.

The later wear classes in *Archaeohippus blackbergi* are different than in *Parahippus leonensis*. This is due to the low crown height of *A. blackbergi* teeth. For example, the last wear stage of *P. leonensis* has all lingual reentrant angles worn away on all but m3 (Hulbert 1984:fig. 3). These features are present in the enamel of *A. blackbergi* down to the root of the tooth. Such complete loss of occlusal detail on all teeth would be much rarer in *A. blackbergi* than in the higher crowned dentition of *P. leonensis*, which does not possess detailed features near the roots.

Wear classes in *Archaeohippus blackbergi* are defined as follows:

Class 1 - dp2-dp4 erupted, no m1 eruption;

Table 1. Life table for *Archaeohippus blackbergi* from the early Miocene Thomas Farm fossil site in Gilchrist County, Florida. Quantity $n(x)$ is the number of mandibles and dp2s or p2s from the original sample that belong to a class. Quantity $d(x)$ is $N(x)$ adjusted to fit a hypothetical population of 1000, and it can be obtained with the following formula: $dx=[N(x)/N*1000]$. Quantity $l(x)$ of class 1 is set at 1000, but for subsequent classes $l(x+1)=l(x)-d(x)$. Quantity $m(x)$ is fecundity, and it has been estimated as described in the text. For class x , reproductive output $=l(x)*m(x)$. Age-specific mortality $q(x)=d(x)/l(x)$. Average longevity for a class is $e(x)=(0.5duration(x)*d(x) + 1.5duration(x)*d(x)+1 + 2.5duration(x)*d(x)+2 \dots \text{until the oldest cohort in the population})/l(x)$.

Class(x)	N(x)	dx [N(x)/N*1000]	Female N(x)	Female d(x)	Female l(x)	Male N(x)	Male d(x)	Male l(x)	l(x)
1	29	333	0.5N(1)	167	500	0.5N(1)	167	500	1000
2	4	46	0.5N(2)	23	333	0.5N(2)	23	333	667
3	6	69	0.5N(3)	34	310	0.5N(3)	34	310	621
4	11	126	0.3N(4)	38	276	0.7N(4)	76	276	552
5	22	253	0.3N(5)	76	238	0.7N(5)	177	200	425
6	5	57	0.8N(6)	46	162	0.2N(6)	11	23	172
7	3	34	0.7N(7)	24	116	0.3N(7)	10	11	115
8	4	46	0.8N(8)	37	92	0.2N(8)	9	1	80
9	3	34	0.7N(9)	24	55	0.3N(9)	10	-8	34
	totals	1000		469	31		518	-18	0

class (x)	m(x)	2m(x)	3m(x)	l(x)m(x)	2*l(x)m(x)	3*l(x)m(x)	q(x)	Duration(years)	e(x)
1	0.0	0.0	0.0	0	0	0	0.3	0.6	1.9
2	0.0	0.0	0.0	0	0	0	0.1	0.6	2.1
3	0.0	0.0	0.0	0	0	0	0.1	0.6	1.6
4	0.5	1.0	1.5	138	276	414	0.2	0.6	1.2
5	0.5	1.0	1.5	119	238	357	0.6	0.6	0.9
6	0.7	1.4	2.1	113	227	340	0.3	0.6	1.1
7	0.7	1.4	2.1	81	163	244	0.3	0.6	0.9
8	0.7	1.4	2.1	64	129	193	0.6	0.6	0.6
9	0.7	1.4	2.1	39	77	116	1.0	0.6	0.3
	totals	555	1109	1664					

Table 2. Number of jaws and second deciduous and permanent premolars of *Archaeohippus blackbergi* from Thomas Farm in each age class, and the proportion of the sample of either category these represent. Second premolars were placed in age classes based primarily on wear criteria. In both categories, a sudden increase occurs in class 5. This class is signaled by the occlusion of the m3, which is interpreted to correlate with the attainment of sexual maturity.

Class	Mandibles (N)	%	p2s (N)	%
1	0	0	0	0
2	2	6	2	8
3	4	12	2	8
4	4	12	7	28
5	11	33	11	44
6	4	12	1	4
7	2	6	1	4
8	3	9	1	4
9	3	9	0	0
Total	33		25	

Class 2 - m1 erupting or erupted, no m2;
 Class 3 - m2 erupting or erupted, no m3;
 Class 4 - p2-p4 erupting or erupted, m3 partially erupted (in *Equus*, the eruptions of p2 and p3 erupt during class 3 at 2.5 years, while p4 erupts during class 4 at 3.5 years, coincident with the start of m3 eruption);
 Class 5 - m3 fully erupted, some wear;
 Class 6 - m3 fully wearing except heel, which may have slight wear on enamel, but no exposed dentine in *Archaeohippus blackbergi*;
 Class 7 - m3 heel worn, m1 metaflexid is tiny (*Miohippus obliquidens* m2 metalophid fully attached to metastylid);
 Class 8 - m3 heel heavily worn (*M. obliquidens* m3 metalophid attached to metastylid);
 Class 9 - all teeth heavily worn.

In *Parahippus leonensis*, p3 and p4 (and probably p2) erupt at the same time and *A. blackbergi* erupts p2-p4 nearly simultaneously, not sequentially as in *Equus* (Hulbert 1984).

From a sample of mandibles (MNI=33) and 25 deciduous and permanent lower second premolars, a

dynamic life table (see Deevey 1947 for detailed description), was constructed for *Archaeohippus*. Convention requires an adjusted population of 1000. For a sample size of 58, this is achieved by multiplying N(x) by 17.24. Age at which adulthood is attained in fossil horse populations can be calculated by comparing estimated rates of tooth wear with eruption of the third molar, an ontogenetic event strongly correlated with attainment of sexual maturity in modern horses and other ungulates (Sisson 1927).

Wear rates are estimated at the constant 1 mm per year known for white-tailed deer (*Odocoileus virginianus*) (Hilson 1986), which share the browsing habit presumed for the low-crowned *Archaeohippus*. Uniformity of wear in fossil equids has been demonstrated in the past (Van Valen 1964). Unlike Van Valen's (1964) sample of *Merychippus primus* or Voorhies' (1969) sample of *Protohippus cf. perditus*, there is no evidence of seasonality of death assemblages at Tho-

Table 3. Number of jaws of *Miohippus obliquidens* from the Harvard Fossil Reserve and *Parahippus leonensis* from Thomas Farm (from Hulbert, 1984) in each age class, and the proportion of the sample these represent. The *M. obliquidens* distribution differs from that of *Archaeohippus blackbergi* in a) the greater representation of class 1 individuals; b) the lesser representation of juvenile classes 2-3; and c) the less distinct mortality spike in early adulthood, which extends through classes 4-6. The *P. leonensis* distribution differs from that of *A. blackbergi* in a) the greater representation of class 1 individuals; b) the very different mortality profile which lacks a spike at classes 4 and 5, but instead increases gradually through class 8.

Class	<i>Miohippus obliquidens</i>		<i>Parahippus leonensis</i>	
	Mandibles (n)	%	Mandibles (n)	%
1	3	13	3	4
2	1	4	5	7
3	1	4	9	12
4	4	16	8	11
5	6	24	6	8
6	4	16	12	16
7	3	12	14	19
8	2	8	14	19
9	2	8	3	4
Total	25		74	

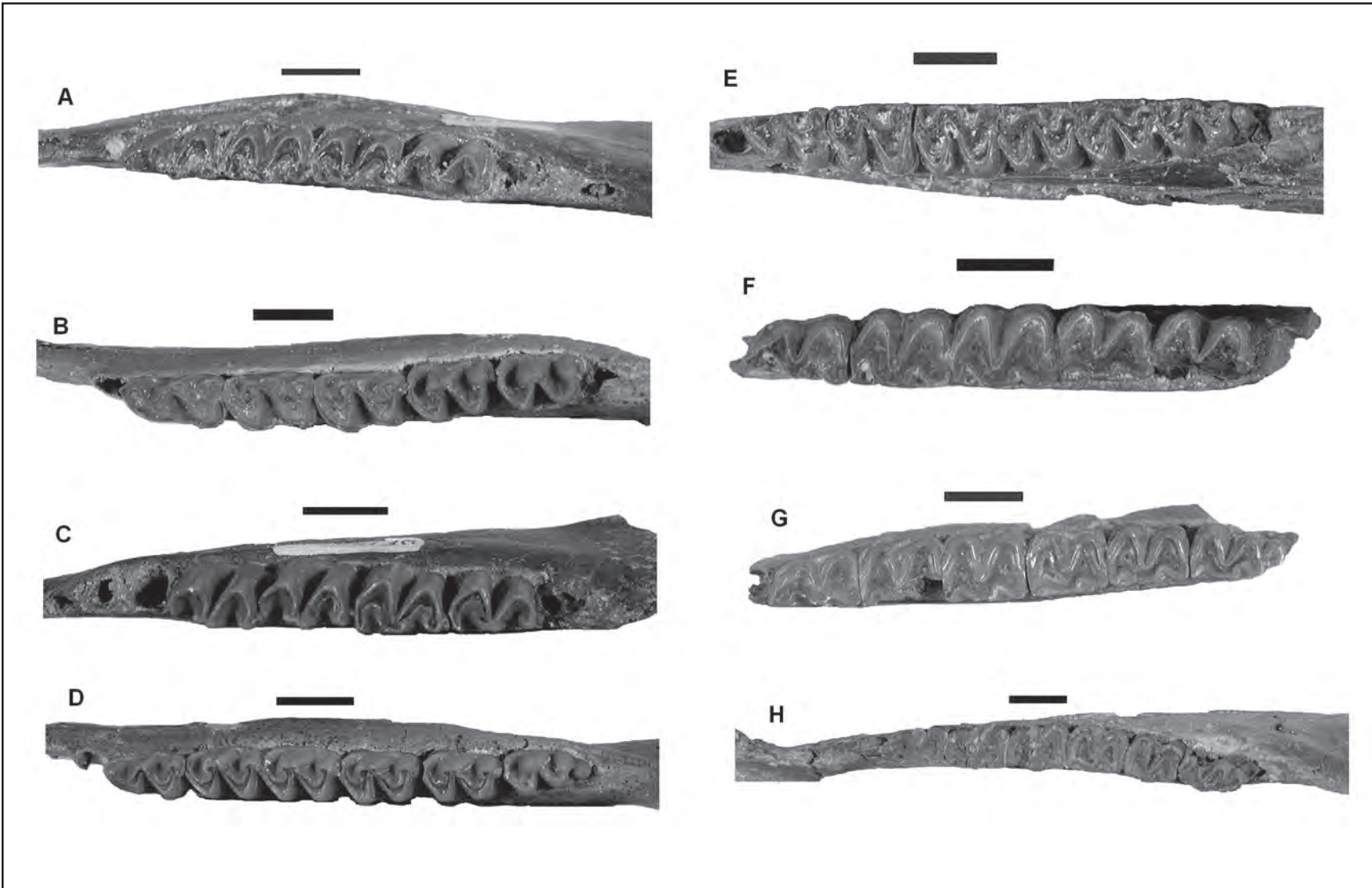


Figure 1. Occlusal views of representative specimens of *Archaeohippus blackbergi* from Thomas Farm, Gilchrist County, Florida, for age classes two through nine. A) UF 155953 Class Two; B) UF 19755 Class Three; C) UF 154015 Class Four; D) UF 165496 Class Five; E) UF 211314 Class Six; F) UF 19992 Class Seven; G) UF 164738 Class Eight; H) UF 3530 Class Nine.

mas Farm. Thus, one can not assume that each age class represents a cohort of births that occurred one year after the preceding age class. In the present study, the age of individuals must be estimated from tooth wear within each age class. This was complicated by the large degree of variation in initial crown height within the Thomas Farm sample. Variation in initial crown height exceeded estimated annual wear rate, a phenomenon observed by Van Valen (1964) for *M. primus* and *Pseudhipparion* (= *Griphippus*) *gratum*.

FIRST REPRODUCTION IN MODERN FEMALES

Some feral mares (*Equus caballus*) of the Granite Range of Nevada give birth at two years of age (Berger 1986). Relative to other *Equus*, this is unusually early, and may correlate with a period of rapid population growth, possibly in response to the removal of cattle from the region. Pregnancies were detected in 72% of yearlings in a Wyoming population (Wolfe et al. 1989). However, this study suggested that the method used to detect pregnancy in most study animals (measurement of progesterone levels) tended to greatly overestimate pregnancy rate. Observations of subsequent foaling by these yearlings were not included in their study. In other studies cited by Berger (1986; also Garrott & Taylor 1990), the earliest age of first reproduction for feral mares was three years. Density dependent increases of foaling rates were observed in the study of Garrott and Taylor (1990). Mares 3 to 5 years old experienced an increase in foaling in response to a 51% population decrease during the previous winter, however, 2-year-old mares were not observed to foal. According to Klingel (1969), mares of the Plains zebra (*E. burchelli boehmi*) attain puberty and exhibit mating behavior between 13-15 months, but do not deliver a foal until approximately 3.5 years. Considering the typical equid gestation length of 11-12 months, conception approximately correlates with the eruption of the second molar at 2 years (Sisson 1927), whereas first foaling correlates with the eruption of the third molar at 3.5-4 years (Sisson 1927).

LITTER SIZE IN MODERN FEMALES

Litter sizes in extant perissodactyls very rarely exceed one embryo per pregnancy (Millar 1981). Of the 10 pregnant palaeotheres recovered from the Messel fossil site, all were carrying single embryos (Briggs 2001). Multiple ovulations are common in *Equus*; multiple births are not (Stabenfield & Hughes 1977). Therefore, discrimination against additional ova after one is fertilized

must be a characteristic of equids (at least extant equids).

However, according to Bunnell (1987 p. 146), "(i)t is possible that the browsing habitat ...encourages multiple births," at least in artiodactyls, as a consequence of the furtive juvenile defense tactics available in that habitat. Litter size is negatively correlated with adult weight in eutherian mammals (Eisenberg 1981; Millar 1981); therefore, it is possible that the present limit on perissodactyl litter size is a consequence of large body size in all extant perissodactyls. Twinning is more common among small artiodactyls such as muntjacs and chevrotains than among large artiodactyls (Walker 1964); the Chinese water deer (*Hydropotes inermis*) bears litters of four to seven young. These points raise the possibility of multiple births in populations of small, forest-dwelling three-toed horses. It is likely that the modern perissodactyl reproductive pattern (annual cycle with one year gestation of a single embryo) is not an example of "phylogenetic constraint," but is instead an artifact of the recent evolutionary history of the group, a combination of allometric constraint and reduced diversity of perissodactyls in modern faunas. Also, it is likely that gestation length in *Archaeohippus* was less than the 11-12 months of *Equus*. In environments without pronounced seasonal availability of resources, births need not be seasonal. Thus, even if *Archaeohippus* produced only one offspring per birth, with short gestation and year-round reproduction it is probable that a repro-

Table 4. List of age classes of *Archaeohippus blackbergi* from Thomas Farm, Florida, and specimens assigned to each.

Class	Referred Specimens
2	UF 155953
3	MCZ 7296, UF 19917, MCZ 6964, UF 19755
4	UF 158523, UF 165340, UF 19889, UF 154015, UF 165925, UF 165495
5	MCZ, 6996, MCZ 6934, UF 19760, UF 19977, MCZ 6998, UF 43012, UF 1246, UF 171652, UF 174141, UF 165496, MCZ 6933, MCZ 4455, MCZ 6247
6	MCZ 3685, MCZ 237, MCZ 7291, MCZ 3884
7	MCZ 6932, MCZ 4456
8	MCZ 6238, MCZ 7586, UF 164738, MCZ 6992
9	UF 3530

ductive output estimate of one offspring per year may be an underestimate.

Within the life table analysis, the impact of multiple birth litters on population maintenance will be explored. The duration of each age class is estimated at 7 months (see Results). This means that once a female had started to reproduce, her fecundity could be as high as 1.7 litters per year. The actual calculation of these rates is also presented in the Results section.

FIRST REPRODUCTION IN MODERN MALES EQUIDS

Male equids are fertile by about 3 years of age (between the eruptions of M2 and M3), but age of first reproduction for males is somewhat later than in females, approximately 5 years (Klingel 1969; Berger 1986), which corresponds with the eruption of the canine teeth (4 - 5 years according to Sisson, 1927). In species of *Equus*, access to females is limited to dominant males, and is often resolved between males by threat display and combat, which can involve the canines (Klingel 1969; Eisenberg 1981; Berger 1986). In the Granite Range study (Berger 1986), males aged 7 - 10 years were more successful at intraspecific conflict than older and younger males. Even though birth ratios indicate a bias toward male births (1.3:1.0), adult ratios indicate a reduction in the proportion of males to females (0.76:1.0) (Berger 1986). At least part of this male attrition must be due to the cost of intraspecific competition, including mortality and emigration of males in search of available females. Fecundity estimates for the population of *Archaeohippus* from Thomas Farm should include adjustments for a shift of sex ratios if evidence for such a shift exists in the data.

RESULTS

Average crown height loss on m1 from class 3 to class 5 is 1 mm. Although annual wear rates as low as 0.4 - 0.6 mm have been observed in the Norwegian red deer *Cervus elaphus* (Loe et al. 2003), ~1 mm is typically considered the annual cheek tooth wear rate for a browser (Hilson 1986). This suggests that a class 5 *Archaeohippus blackbergi* lived about one year longer than a class 3 specimen. A comparison of average crown heights at different classes reveals a consistent pattern. Class 4 p4 crown height is 5.5 mm and class 8 p4 crown height is 2.5 mm. Class 4 m3 crown height is 5 mm and class 8 m3 crown height is 2.5 mm. Class 9 did not differ substantially from class 8 in crown loss. Thus, on average, *A. blackbergi* lost ~ 3 mm crown height from p4 and ~ 2.5 mm crown height from m3 between classes

4 and 8. Based on wear, class 8 specimens lived approximately 2.5 - 3 years longer than class 4 specimens.

Potential longevity for individuals in the sample can be estimated by adding tooth wear from deciduous premolars to that of permanent teeth. I used the following two methods. 1) Average dp2 total crown height loss (representing tooth wear during classes 1 - 3) = 1.2 mm. This added to the average p2 total crown height loss (classes 4 - 9 = 3.96 mm) yields a total of 5.16 mm for classes 1 - 9. 2) Average dp2 total crown height loss (classes 1 - 3) = 1.2 mm plus average m1 total crown height loss (classes 2 - 9) = 4.34 mm yields a total of 5.54 mm. So, based on ~ 1mm loss/year, these two estimates give a maximum life expectancy (derived from observed dental wear) of ~ 5 - 5.5 years for the population of *A. blackbergi* from Thomas Farm.

Since the m1 erupts before the dp2 is lost, the lower of the two estimates may be the more accurate. An alternate estimate based on the tallest (relatively) unworn m1 at 6.34 mm (class 3 specimen UF 19755) plus the ~1 mm crown height loss from dp2 by class 3 divided by 1 mm annual wear yields a greatest potential longevity of 7.3 years, at which point the cheek teeth would be almost completely worn.

Estimation of age at which m3 erupts can be derived from dp2 loss from classes 1-3 of 1.2 mm + m1 loss from classes 3-5 of 1 mm as ~ 2.2 mm or 2.2 years.

There is a great amount of p2 wear associated with class 4. This is the ontogenetic period when *Archaeohippus blackbergi* sheds dp2-dp4, erupts p2 - p4, and begins to erupt m3, so this range of wear may indicate that this is a longer interval than the rest. Or, it may be an indication that p2 erupts slightly earlier than p3/p4, and thus bears a greater overall wear in class 4 than in later classes when it is accompanied by the p3/p4. In *Equus caballus*, these teeth erupt sequentially. The ages during which these teeth erupt are (from Sisson 1927): p2/P2 at 2.5 years, p3/P3 at 2.5/3 years, p4/P4 at 3.5/4 years (taken together these are equivalent to *A. blackbergi* class 4), and m3/M3 at 3.5 - 4 years. Therefore, the equivalent duration of this class in *E. caballus* is approximately 1.5 years, with these notable differences: the premolars do not erupt as simultaneously as in *A. blackbergi*, and there is greater overlap in the timing of eruption of P4 and M3 in *E. caballus*.

For *Archaeohippus blackbergi*, the average wear per class is ~ 0.6 mm, thus the average duration of a class is 7.2 months. The durations of the classes in *A. blackbergi*, *Parahippus leonensis* (from Hulbert 1984), and *Equus caballus* (from Sisson 1927) are given in

Table 5. Estimated durations of age classes in *Archaeohippus blackbergi*, *Parahippus leonensis* (from Hulbert, 1984), and *Equus caballus* (from Sisson, 1927) based on eruption sequence and tooth wear. No wear criteria have been devised to determine classes 6+ in *E. caballus*.

	<i>A. blackbergi</i> Age (years)	<i>P. leonensis</i> Age (years)	<i>E. caballus</i> Age (years)
Class 1	0 – 0.6	0 – 0.5	0 – 1
Class 2	0.7 – 1.2	0.6 – 1.2	1 – 2
Class 3	1.3 – 1.8	1.3 – 2.2	2 – 3
Class 4	1.9 – 2.4	2.2 – 2.8	3 – 4
Class 5	2.5 – 3.0	2.8 – 3.5	3.5 – 4
Class 6	3.1 – 3.6	3.6 – 4.6	n/a
Class 7	3.7 – 4.2	4.6 – 5.6	n/a
Class 8	4.3 – 4.8	5.6 – 7.0	n/a
Class 9	4.9 – 5.4	7.0 +	n/a

Table 5. Dental eruption in *E. caballus* is delayed relative to eruption in the Miocene taxa. The first two age classes in *A. blackbergi* and *P. leonensis* are of approximately equal duration, with subsequent classes in *P. leonensis* ranging in duration from 0.6 – 1.4 years.

For each age class, the life table (Table 1) includes:

$N(x)$ = number of specimens in class x ;

$d(x) = N(x)/N * 1000$, the number if individuals of the adjusted population that dies during class x ; this was calculated separately for females and males as explained below;

$l(x)$ = population size at the beginning of class x ; this was calculated separately for females and males as explained below;

$m(x)$ = reproductive output of the population during class x ; this was calculated for litters including 1, 2, or 3 offspring;

$l(x)m(x)$ = number of offspring born to the population during class x ;

$q(x)$ = the proportion of mortality in class x ;

$e(x)$ = average life expectancy for individuals alive in class x . It is calculated $ase(x) = (0.5duration(x)*d(x) + 1.5duration(x+1)*d(x+1) + 2.5duration(x+2)*d(x+2) ...until the oldest class in the population)/l(x)$.

Mortality bias against males in adult classes reduces the proportion of males in each class. This affects estimates of fecundity per class. Female and male differential survival is here estimated (Table 6) by com-

parison of mortality [$q(x)$] for classes 1 – 5 in the populations of Thomas Farm *Archaeohippus blackbergi* and *Parahippus leonensis* (from Hulbert, 1984). For *P. leonensis*, $q(x)$ was combined for classes 4 and 5 (Hulbert 1984); for the present study, that figure was divided by 2. Compared with *P. leonensis*, *A. blackbergi* class 4 $q(x)$ is + 0.1 and class 5 $q(x)$ is + 0.46. It is assumed here that these increased rates are due to increased male mortality in these age classes. With two sets of $q(x)$, I was able to split the sample into two sets of $N(x)$ for *A. blackbergi*; one for females, and one for males. From these, I calculated separate $l(x)$ and $d(x)$, always with the goal of attempting to balance survivorship, mortality, and reproductive output. Totals for each of these deviate from their optima. For instance, final $l(x)$ for males is negative where it should be zero; this is probably due to small rounding errors magnified by the conversion of the original sample to a population of 1000.

Rate of reproduction in class 4 females is low (11–25%, mean = 18%) in various studies cited by Berger (1986), whereas births per female increase substantially in the later classes. In my analysis, class 4 $m(x)$ of 0.18 was always insufficient to replace the initial population of 1000, so I had to assume that reproductive output in class 4 matched that of class 5. If this mathematical manipulation represents a biological reality, it suggests that maturation of the reproductive system of *Archaeohippus blackbergi* occurred relatively earlier than in *Equus*.

Estimated average longevity $e(x)$ differs from potential longevity as calculated from tooth wear (see above). Estimated average longevity for a class is the average number of years an individual in that class (x) is expected to live, taking into account rates of mortality in that class and all subsequent classes. In Table 1, the highest longevity is for class 2 (2.1 years), which is greater than that of class 1 (1.9 years). Although no individuals of class 1 were found in the sample, probably due to taphonomic bias against such tiny neonates, I estimated 33% mortality, and inflated $N(x)$ by 29 to accommodate this increase. This estimate is comparable to that of Hulbert (1984), where class 1 mortality was estimated at 40%. Any class with such high mortality will have a reduced $e(x)$. Average longevity for the population is noticeably reduced during class 5 in response to a large increase in mortality in that class.

In addition to the standard survivorship curve, a particularly informative graphic display of life table data is the mortality curve (Dittus 1975). This is especially

Table 6. Sex-specific mortality for *Archaeohippus blackbergi* calculated from a comparison with $q(x)$ from Hulbert's (1984) study of *Parahippus leonensis*. The $q(x)$ of *P. leonensis* (Fig. 2) lacks the mortality spike seen in the $q(x)$ of *A. blackbergi*, and is assumed to represent $q(x)$ for *A. blackbergi* females. Additional mortality seen in *A. blackbergi* classes four and five is due to male combat. This is used to estimate adult sex ratios and fecundity in Table 1.

Class	<i>P. leonensis</i> All	<i>A. blackbergi</i> All	<i>A. blackbergi</i> Females	<i>A. blackbergi</i> Males
1	0.34	0.33	0.33	0.33
2	0.07	0.07	0.07	0.07
3	0.14	0.11	0.11	0.11
4	0.125	0.23	0.125	0.225
5	0.125	0.59	0.125	0.585
6	0.28	0.33	0.33	0.33
7	0.45	0.3	0.3	0.3
8	0.83	0.57	0.57	0.57
9	1.00	1.0	1.0	1.0

true with life tables derived from fossils, because fossil assemblages directly inform us of within-class mortality. Fecundity, total life expectancy, etc., must be estimated, but mortality is represented by actual specimens in all classes but those subject to taphonomic bias (e.g. the delicate-boned neonates of class 1). The curve for *Archaeohippus blackbergi* from Thomas Farm (Fig. 2) indicates that mortality is very high in classes 4 and 5, which correspond with the early phase of sexual maturity.

DISCUSSION

ESTIMATES OF FIRST REPRODUCTION IN FOSSILS

In modern horses, the eruption of the second permanent molar (class 3) occurs at about 2 years, the second premolar erupts at 2.5 years (class 4) and the eruption of the third permanent molar (class 4-5) occurs at about 3.5 to 4 years (Sisson 1927). As stated above, in a rapidly growing population of feral *Equus caballus*, early reproduction was observed to occur in two-year-old mares (which corresponds to dental class 3-4 of this study), with typical first foaling occurring among three-year-olds (class 4-5). Based on tooth wear, the approximate age range of *Archaeohippus blackbergi* during class 3 was 1.3-1.8 years, class 4 was 1.9-2.4 years, and class 5 was 2.5-3.0 years (Table 5). If the correlation between tooth eruption and reproduction as seen in *Equus* were present in *A. blackbergi*, then age at which precocious *A. blackbergi* females would deliver their

first foal would be ~1.5 years, and age of normal first foaling would be 2-2.5 years.

As stated above, in *Equus*, although physiological reproductive maturity is attained in classes 4-5, males are unable to win access to females until about classes 6-7 (coinciding with the completed eruption of the canine), with best success attained at ages 7-10 years (Berger 1986). This has bearing on the increased mortality in classes 4-5 (Fig. 2, see below for further discussion).

Estimated fecundity $m(x)$ for this sample produces 555 individuals over all reproductive age classes. This does not replace the original population of 1000. This may be due to: a) an age of first reproduction estimate that is too high; b) $m(x)$ estimates that are too low because females were more successful at foaling than the *Equus* populations studied by Berger (1986); c) $l(x)m(x)$ estimates that are too low because birth sex ratios were more female-skewed than the 1:1 ratio assumed here; or d) a combination of these factors.

During the calculation of $l(x)m(x)$ it was assumed that births occurred in each of the adult age classes. This requires a gestation length of 7 months or less (a realistic assumption given the relatively small body size of the animals involved, *Equus* having a gestation of 11-12 months), virtually no interval between broods, and no breeding seasonality. This last is questionable given the strong correlation between estrus and photoperiod in

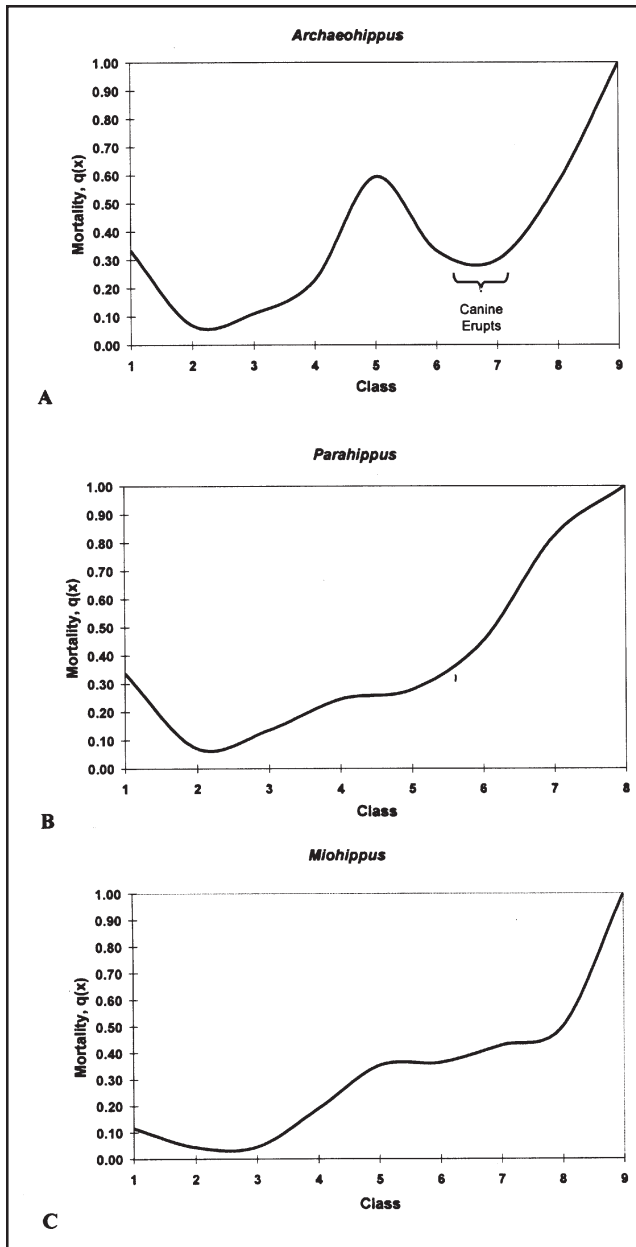


Figure 2. A) Age-specific mortality curve for *Archaeohippus blackbergi* from the Miocene Thomas Farm fossil site of Florida. Note the large increase in mortality at classes 4 and 5, which may be the consequence of male combat for access to females. This is followed by a reduction in $q(x)$ in the middle-adult classes, indicating that most individuals that survive the mortality spike will survive to old age. B) Age-specific mortality curve for *Parahippus leonensis* from the Miocene Thomas Farm fossil site of Florida. Mortality increases slightly in the mature classes, with highest $q(x)$ in the oldest classes. C) Age-specific mortality curve for *Miohippus obliquidens* from the Oligocene Harvard Fossil Reserve of Wyoming. Note the slight increase in mortality at classes 4 and 5, with a continually high mortality in all subsequent age classes.

Equus (Stabenfield & Hughes 1977), although this may be a consequence of the year-long gestation of *Equus* and a need therefore to time both mating and parturition in the summer. Only when $m(x)$ estimates were doubled was reproductive output sufficient to replace the original population, as can be seen in column $2 \cdot l(x)m(x)$ in Table 1. These calculations imply that multiple offspring litters, which are rare in *Equus*, were necessary to maintain the population of Thomas Farm *Archaeohippus blackbergi*.

AGE DEPENDENT MORTALITY

A comparison of the population dynamics of Thomas Farm *Archaeohippus blackbergi* with Hulbert's (1984) study of *Parahippus leonensis* demonstrates a fundamental difference between these sympatric equids. In the *A. blackbergi* sample, mortality in class 4 is high ($N = 11$ of the original sample of 58). Mortality in class 5 is higher ($N = 22$). The number of *A. blackbergi* mandibles in the Thomas Farm sample that preserve the symphysis and have canine teeth (and therefore permit assignment to sex) is low. However, this peak (seen clearly in Fig. 2A) in mortality mirrors a pattern of age dependent mortality observed in mammal taxa from feral horses (Berger, 1986) to monkeys (Dittus 1975), and many others (see Muhlbachler 2001 for a review). This mortality pattern indicates death due to wounds sustained by young males in battles over access to females with older, more experienced males.

While the *Archaeohippus blackbergi* data show a dramatic increase in mortality at attainment of age of first reproduction (classes 4 and 5), the *Parahippus leonensis* age-specific mortality curve (Fig. 2B) shows only a slight increase in mortality at this age, an increase that persists through class 8. An intermediate pattern can be seen in the age-specific mortality curve of *Miohippus obliquidens* (Fig. 2C), with a moderate increase in mortality at the start of the adult age classes.

In addition, using canine tooth size to identify the sex of specimens, Hulbert (1984) established that *Parahippus leonensis* at Thomas Farm exhibits some sexual dimorphism in body size. *Archaeohippus blackbergi*, while demonstrating dimorphism in canine tooth size, does not demonstrate body size dimorphism. For example, MCZ 3685 is a small individual (p4 anteroposterior length = 9.7 mm; depth of jaw at p2 = 14.4 mm) with small canines (female). MCZ 7291 is a small individual (p4 anteroposterior length = 10.0 mm; depth of jaw at p2 = 17.0 mm) with relatively large canines (male). MCZ 6997 is a large individual (p4 anteroposte-

Table 7. Comparison of mandibular and dental measurements (in mm) of Thomas Farm *Archaeohippus blackbergi* and *Parahippus leonensis*. Note the absolutely taller canines in *A. blackbergi*, the high standard deviations (due to greater canine wear) in indices calculated for *A. blackbergi*, and the *P. leonensis* index/*A. blackbergi* index, which demonstrates that the canine of *A. blackbergi* is relatively much larger than the canine of *P. leonensis*.

<i>P. leonensis</i>	Canine Height	m1 Antero- Posterior Length	Symphysis Medio- Lateral Width	Canine Height/ m1 Length	Canine Height/ Symphysis Width
UF 1289	4.3		21.6		0.20
UF 181919	4.6		16.5		0.28
UF 211464	3.9		20.2		0.19
UF/FGS 6426	4.5		18.3		0.24
UF 99392	5.2	13.7	16.5	0.38	0.32
UF 3514	5.6	14.2	18.0	0.40	0.31
UF 159629	5.1	14.5	20.4	0.35	0.25
average	4.8			0.38	0.26
standard deviation				0.02	0.05

<i>A. blackbergi</i>	Canine Height	m1 Antero- Posterior Length	Symphysis Medio- Lateral Width	Canine Height/ m1 Length	Canine Height/ Symphysis Width
UF 159954	7.8		11.6		0.67
UF/FGS 6561	3.3		9.5		0.35
UF 67023	4.4		12.8		0.35
UF 198915	7.2	9.5	12.2	0.76	0.59
UF 223350	7.6	10.2	12.4	0.74	0.61
UF 211616	3.9	8.6	12.0	0.45	0.32
UF 3530	5.4	9.7	12.6	0.56	0.43
average	5.7			0.63	0.48
standard deviation				0.15	0.15

rior length = 11.3 mm; depth of jaw at p2 = 19.4 mm) with small canines (female). The p4 anteroposterior length of MCZ 6997 is 16% larger than that of MCZ 3685 and 13% larger than that of MCZ 7291, and the mandibular depth beneath the p2 is 35% larger and 14% larger, respectively.

In studies of modern ungulates, it has been suggested that annual competition for females selects for larger body size in males (Eisenberg 1981; Janis 1982). However, this probably holds true for animals that use their entire body weight in attacks with horns or antlers. Hornless ungulates such as equids and chevrotains use their teeth and hooves, and are characteristically dimor-

phic in canine size and monomorphic in body size (Eisenberg 1981). Morphology and age-specific mortality indicate that *Archaeohippus blackbergi* fits this latter pattern. However, age/sex dependent mortality and sexual dimorphism in fossil and extant ungulates have been examined in detail by Muhlbachler (2001), who emphasized that any attempt to interpret social behavior in fossil perissodactyl populations is handicapped by the relictual status of modern perissodactyl taxa. Many extinct perissodactyl taxa can have no living analogues within the surviving equids, rhinos, and tapirs.

A comparison of the lower canines of *Archaeohippus blackbergi* and *Parahippus leonensis*

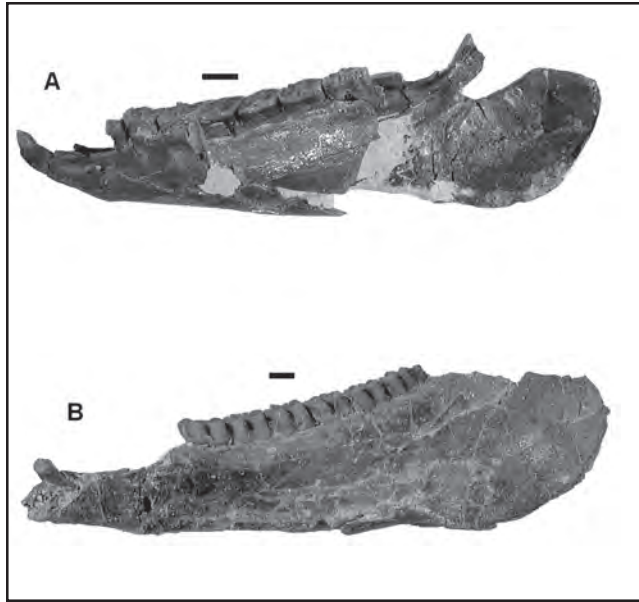


Figure 3. Lateral views of mandibles of Thomas Farm equids comparing A) the more tusk-like canine of *Archaeohippus blackbergi* (UF 211616) and B) the incisiform canine of *Parahippus leonensis* (UF 3514). Cheek teeth on UF 211616 are heavily worn, and the canine has a wear facet that made this tooth even more sharply pointed than canines of younger individuals.

reveals distinct differences in structure and function. The lower canines of *A. blackbergi* are long and tusk-like (Figs. 3A, 4A-B). The lower canines of *P. leonensis* are relatively small and incisiform (Figs. 3B, 4C-D). While wear on the occlusal surface of the canines of *P. leonensis* indicates they functioned like incisors, wear on the anteromesial surface of the canines of *A. blackbergi* made them shorter but sharper, as can be seen upon inspection of class 9 specimen UF 211616 (Fig. 3A). Measurements (Table 7) demonstrate that the canines of *A. blackbergi* were not only relatively larger than those of the larger equid *P. leonensis*, but they were absolutely larger, as well. All of this evidence supports the idea that, unlike *P. leonensis*, *A. blackbergi* males used their canines as weapons.

ESTIMATES OF AVERAGE AND POTENTIAL LONGEVITY

Average longevity $e(x)$ is an estimate made using lifetable data to determine the amount of time the average individual in a particular class will live. Average longevity is a function of the amount of time contained in the class of interest and in all subsequent classes versus the number of individuals alive at the start of that

class. As stated above, this differs from estimated potential longevity as derived from observed dental wear data. In equids, a third measure, greatest potential longevity, is estimated by dividing the height of unworn cheekteeth by the rate of wear that will eventually render those teeth useless, a development that should result in the death the animal by starvation. It should be noted that, given the rarity of dentitions in this condition at from Thomas Farm, greatest potential longevity is rarely achieved.

The greatest average longevity in the Thomas Farm sample of *Archaeohippus blackbergi* is found in class 2 at 2.1 years. In Thomas Farm *Parahippus leonensis*, greatest $e(x)$ is 4.06 in class 2, or 1.9 times that of *A. blackbergi*. This difference is a consequence of the very different mortality patterns of *A. blackbergi* and *P. leonensis* discussed above, which may indicate different modes of social organization in these two taxa.

Van Valen (1964) estimated potential longevity for the early Miocene equid *Merychippus primus* (~10 years) and middle Miocene equid *Pseudhipparion gratum* (~11 years). These are surprisingly similar, considering the cheek teeth of *P. gratum* are approximately 1.5 times the height of the cheek teeth of *M. primus*. The close correspondence in longevity appears to be the result of an increase in the rate of tooth wear in the younger taxon, probably the result of an increase in the amount of grass in the diet of *P. gratum* relative to the diet of *M. primus*. Thus, with its more abrasive diet, *P. gratum* needed taller teeth than *M. primus* in order to live ~1.1 times as long as *M. primus*.

A very similar relationship is seen in potential longevity in the sympatric horses from Thomas Farm. Hulbert (1984) estimated annual cheektooth-wear rates between 1.75 and 2.1 mm and greatest potential longevity between 8.2 and 9.6 years for *Parahippus leonensis*. The present study estimates annual cheektooth-wear rates of ~1 mm and observed potential longevity of 5 years and greatest potential longevity of 7.5 years for *Archaeohippus blackbergi*. Although the rate of tooth wear for *P. leonensis* is estimated at nearly twice that of the rate for *A. blackbergi*, the greatest potential longevity of the former is only about 1.09 to 1.28 times that of *A. blackbergi*.

PALEOENVIRONMENTAL RECONSTRUCTION OF THE THOMAS FARM FOSSIL SITE BASED ON INTERPRETATIONS OF SOCIAL STRUCTURE

Hulbert (1984) suggested that the Thomas Farm environment was woodland, which implies a forest with

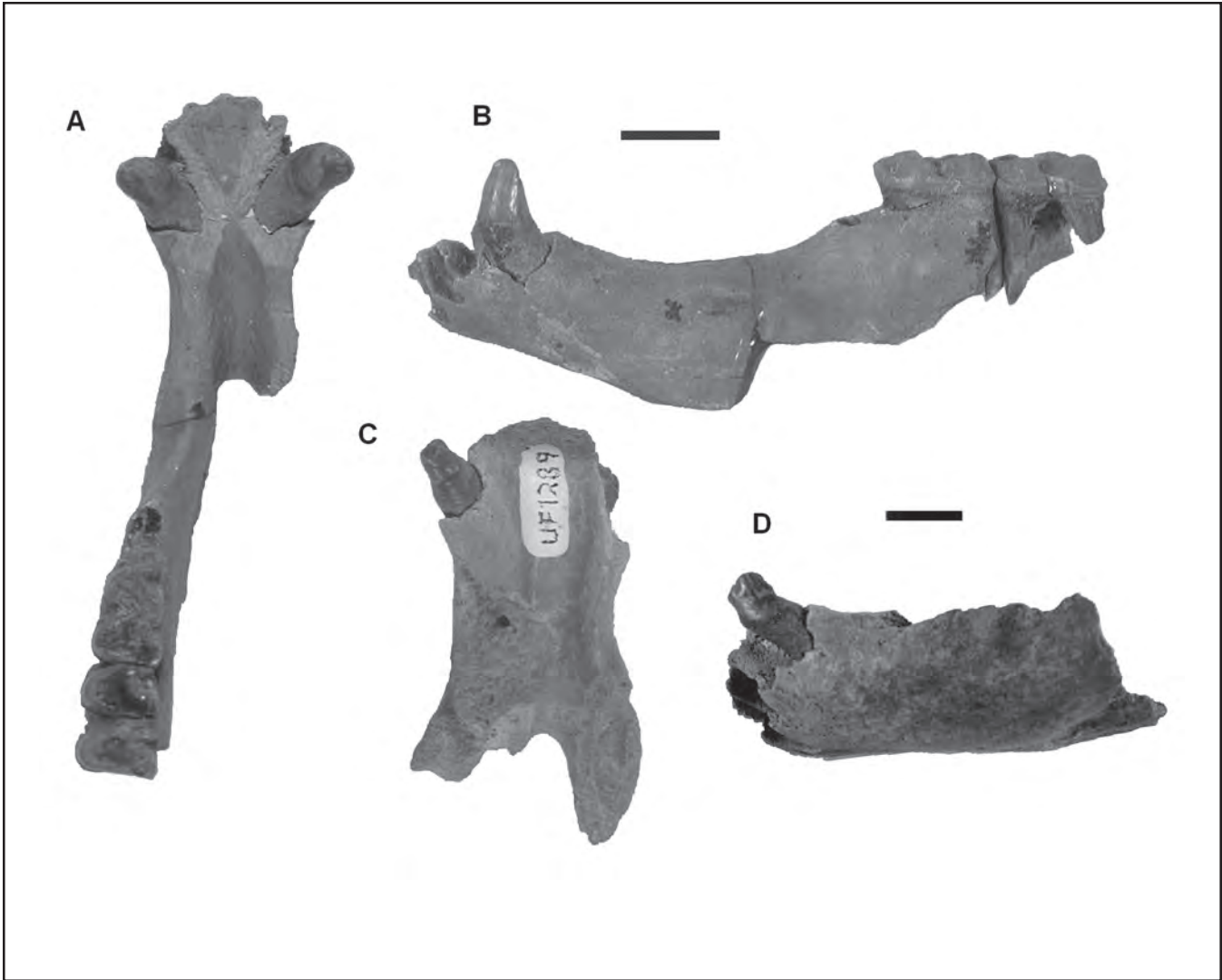


Figure 4. Additional views of mandibular symphyses with canines. A) Occlusal and B) lateral views of *Archaeohippus blackbergi*, UF 223350. C) Occlusal and D) lateral views of *Parahippus leonensis*, UF 1289.

open patches in it. His evidence for this comes from his interpretation of the diet of *Parahippus leonensis* as being a mix of browse and graze and his reconstruction of the social structure of *P. leonensis* as being similar to that of forest-dwelling deer. However, this social structure may have persisted in *P. leonensis* long after its subsistence base had shifted toward more open country, where both browse and graze are available. Herding and harem defending as seen in some species of modern *Equus* may be relatively recent innovations, since they are by no means universal among extant equids. These are not at all typical reproductive strategies in burros (*Equus asinus*) (Eisenberg 1981). In addition, objections raised above as to the validity of reconstruct-

ing the social dynamics of extinct equid species as being necessarily homologous to the social dynamics of the few extant equid species available to study apply to the question of then using those interpretations for environmental reconstruction. The evidence of male combat is not in itself informative of group structure or resource availability, as such behavior is exhibited by harem-maintaining modern *Equus* in open country (Berger 1986) as well as by more solitary deer in forests (Eisenberg 1981).

CONCLUSIONS

This study of *Archaeohippus blackbergi* from Thomas Farm adds to the body of knowledge concerning the most productive early Miocene terrestrial fossil site

in the eastern United States. It provides an interesting contrast with Hulbert's (1984) study of the sympatric equid *Parahippus leonensis*. These populations differ in mortality profile as demonstrated by plotting age-specific mortality [$q(x)$]. As interpreted here, this is suggestive of greater mortality due to intermale combat in the population of *A. blackbergi*.

These sympatric equids are also distinct in the estimated rate of tooth wear (indicative of a less abrasive diet in *Archaeohippus blackbergi*) and in the duration of age classes (shorter in *A. blackbergi*). Potential longevity for these two taxa are quite close (as a consequence of the lower rate of tooth wear in *A. blackbergi*), although average longevity of *A. blackbergi* is much less than that of *Parahippus leonensis* (as a consequence of the large amount of mortality in classes 4 and 5 in *A. blackbergi*).

The mortality pattern of *Miohippus obliquidens* from the Oligocene of Wyoming more closely resembles that of *Parahippus leonensis*. Assuming that spatial bias in mortality assemblages is not an overwhelming factor in this pattern, the possibility arises that the difference in age-specific mortality indicates a biologically significant difference. One possibility is that male intraspecific competition was more ritualized in *M. obliquidens* and *P. leonensis*. Another possibility is that *Archaeohippus blackbergi*, with its relatively large head and canines, was capable of inflicting more serious wounds on conspecifics than were the larger taxa.

An alternative explanation exists. Instead of reflecting actual behavioral differences between *Parahippus leonensis* and *Archaeohippus blackbergi*, these different mortality profiles may instead indicate taphonomic bias due to age-specific or sex-specific differences in spatial patterns of mortality (Mihlbachler 2001). For instance, Thomas Farm may have been a locale where bachelor males congregated. This would explain their strong presence in the fossil deposit. In this case, the sample of *A. blackbergi* at Thomas Farm may represent a biased fraction of the original population, whereas the sample of *P. leonensis* may accurately sample the original population of that taxon. Barring further evidence of such assortative spatial mortality, the hypothesis forwarded by the present study is that a relatively accurate sample of *A. blackbergi* is present at Thomas Farm, and that the age-specific mortality seen in the sample indicates intensive intrasexual competition among males.

This study demonstrates differences in population dynamics between closely related sympatric ungulates,

including the probable presence of intense male intraspecific competition in the population of *Archaeohippus blackbergi*. It adds to the growing body of published analyses of population dynamics of fossil mammals that increase our knowledge of the evolution of mammalian ecology, life history, and social behavior.

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