Sexual dimorphism and paleoecology in *Teleoceras*, a North American Miocene rhinoceros

Alfred J. Mead

Abstract.—Sexual dimorphism is documented in 35 articulated adult skeletons, 24 females, and 11 males, of the Miocene rhinoceros *Teleoceras major* from Ashfall Fossil Beds, Nebraska. Morphometric analysis of 51 cranial, mandibular, forelimb, and hindlimb characters reveals larger male mean values in 50 of the 51 measurements, of which 23 are significantly different ($p \leq 0.01$). The most clearly dimorphic feature is the i2 diameter. The dimorphism evident in additional mandibular and cranial characters is conservative when compared with the dimorphism present in the fore- and hindlimbs. Non-overlapping male and female ranges are recorded for humerus length, radius length, radius proximal width, and femur length, with corresponding dimorphism ratios (DR = male ÷ female) of 1.11, 1.12, 1.11, and 1.10. Maximum male longbone lengths exceed minimum female lengths by an average of 24% (20–29%). Developmental maturity is apparently asynchronous in *T. major*, with fusion of longbone epiphyses delayed a minimum of two relative adult age classes in males. Significant sexual dimorphism is evident in the radius (DR = 1.34) and femur (DR = 1.19) cross-sectional areas. Estimates of body mass suggest a DR value between 1.13 and 1.23. The cranial, mandibular, and body-size dimorphism in *T. major* approaches that seen in the extant rhinoceroses *Ceratotherium simum* and *Rhinoceros unicornis*. However, the apparent herd structure and breeding-age sex ratio for the Ashfall herd suggests a behavioral ecology for *T. major* different from that of extant rhinoceroses. *Teleoceras* was likely a herding polygynous species ecologically more similar to extant *Hippopotamus amphibius* of Africa.

Alfred J. Mead. University of Nebraska State Museum and Department of Geosciences, W436 Nebraska Hall, Lincoln, Nebraska 68588-0514

Introduction

Paleontologists are fully aware of the variability inherent in populations of extant mammals, but seldom are afforded the opportunity to examine the variability of a large group of spatially and temporally contemporaneous individuals of an extinct species. Not only is a thorough understanding of intraspecific variation necessary for proper systematic analyses, but it potentially provides information concerning life habits of the extinct taxon such as geographic range (possible clinal variations), developmental heterochrony (bimaturism), and probable social structure and mating system. Documentation of variability in fossil mammal species is not unusual (Kurten 1969), but the generally limited sample sizes in studies of large mammals restrict the significance of most analyses.

* Present address: Georgia College and State University, Department of Biological and Environmental Sciences, Milledgeville, Georgia 31061. E-mail: amead@mail.gcsu.edu

Ecological analyses of extant herbivores indicate a positive correlation between breeding system and adult dimorphism, with harem size increasing proportionately with degree of dimorphism (Alexander et al. 1979). In this context of mating systems and sexual dimorphism in herbivorous mammals, Jarman (1983: p. 488) predicted that (1) "dimorphism will characterize species in which some males monopolize matings," (2) "prolonged male growth in size of body and weapons will restrict this monopolization to certain age-classes of males," and (3) "dispersion of females relative to the males' range will limit the extent of dimorphism and affect the age at which males first breed." Jarman (1983: p. 487) also suggested that "timing of reproduction" (seasonal vs. aseasonal) is an important consideration for the development of polygyny and dimorphism. A strong correlation of Jarman's predictions with dimorphism in extant large mammalian herbivores suggests that these principles should be applicable to paleoecological interpretation of extinct large mammalian herbivores.

Berger (1983a) suggested caution when using fossil mammal assemblages to infer socioecological characteristics of extinct taxa. Studies in taphonomy indicate that the death assemblage may not accurately reflect the life assemblage. However, when catastrophic and attritional assemblages containing many individuals of a particular taxon are available for comparative analysis, robust socioecological inferences should be possible.

Questions concerning intraspecific variability are of paramount importance in rhinoceros systematics. Loose (1975: p. 26), referring to extant rhinoceroses and the Pleistocene Rhinocerotidae of western Europe, stated that he had "not been able to find any sex-character in the skull [$n = 56$] of these two [*Ceratotherium simum* and *Diceros bicornis*] species (the same holds for *Dicerorhinus sumatrensis*)" and that "sexing fossil rhino skulls is a waste of time." In contrast, Borsuk-Bialynicka (1973) found that bimodality in the occiput width, maximum skull length, orbit-nuchal crest length, and orbit-nares length supported the conclusion of sexual dimorphism in *Coelodonta antiquitatis*. In their discussion of the bimodality in body mass estimates for *Indricotherium transouralicum*, Fortelius and Kappelman (1993: p. 96) referred to "the perpetual problem of sexual dimorphism in fossil organisms." Of greater significance to the present study, the most recent systematic analyses of North American Miocene rhinoceroses are based to a large extent on the assertions that no "ceratomorphs (rhinos and tapirs), living or fossil, show significant dimorphism in size or, for that matter, in structures that are commonly dimorphic, such as horns . . . [The] only significant difference between sexes in the Rhinocerotidae occurs in the shape of the lower tusk" (Prothero and Sereno 1982: p. 16) and "extreme size dimorphism is unknown in the rhinocerotids" (Prothero and Manning 1987: p. 418). Furthermore, the general scheme of North American Miocene rhinoceros congeneric taxonomy is based largely on cranial and postcranial dimensions rather than actual differences in morphology (Tanner 1975; Prothero and Manning 1987).

The occurrence of a large number ($n = 100+$) of articulated skeletons of the North American Miocene rhinoceros *Teleoceras major* in a synchronous, nonselective, mass death assemblage allows a number of questions concerning intraspecific variation in this extinct taxon to be addressed: (1) To what extent are intra- and intersexual variability present in *T. major*? (2) How does the nature of variability in *T. major* compare with that in extant rhinoceros species? and (3) Do paleoecological inferences based on morphometric variability in *T. major* (using Jarman's predictions) agree with independently generated paleoecological interpretations?

Rhinoceroses are a common component of the Barstovian, Clarendonian, and Hemphillian (North American land mammal "ages," middle to late Miocene) mammalian faunas of the North American Great Plains. Of the three rhinoceros genera present (*Aphelops, Peraceras, Teleoceras*), *Teleoceras* is arguably the most common and has been found in large numbers in several localities such as the famous Long Island Quarry in Kansas and Mixon's Bone Bed in Florida. The vertebrate remains in these quarries are generally disarticulated, making reassociation of skeletal material difficult or impossible. The mass death occurrence of 100+ articulated skeletons of the Clarendonian *T. major* from the University of Nebraska State Museum (UNSM) Poison Ivy Quarry (now called Ashfall Fossil Beds) in Antelope County, Nebraska, has been briefly described by Voorhies (1985). The specific attributes of the locality are also discussed therein. The Ashfall rhinoceros skeletons are buried in volcanic ash and the vast majority are preserved in their three-dimensional death-pose, a few exhibit variable amounts of disarticulation. This group of skeletons, exhibiting a catastrophic age profile and apparently free from major taphonomic biases, is believed to represent a "snapshot" of a Miocene rhinoceros herd (Voorhies 1985) and provides an ideal sample in which to quantify the intrapopulational variability, both intrasexual and sexually dimorphic, in *T. major*.

Several previous studies have documented the existence of varying degrees of variability within samples of extinct North American perissodactyls. Coombs (1975) found that plots of radius and tibia lengths for the early Mio-

cene chalicothere *Moropus* suggest the presence of sexual dimorphism. Similarly, Gingerich (1981) attributed dental and cranial variations in the early Eocene horse *Hyracotherium* to sexual dimorphism. In an anecdotal manner, Radinsky (1963, 1967) suggested the presence of sexual dimorphism in the primitive tapiroids *Homogalax* and *Isectolophus* (based on canine morphology) and the primitive rhinocerotoid *Hyrachyus* (based on bimodality in molar row lengths).

Sexual dimorphism has been qualitatively recognized in additional extinct rhinoceros taxa. Osborn (1903) found that the gender of the Oligocene rhinocerotids *Subhyracodon occidentalis* and *S. tridactylum* (now *Diceratherium tridactylum fide* Prothero 1998) could be determined using lower-tusk morphology. Osborn (1903) also noted the dimorphic character of the nasals-horn bosses present in males—in the late Oligocene rhinoceros *Diceratherium*. Peterson (1920) pointed out the similarly dimorphic nature of the horn bosses in the early Miocene rhinoceros *Menoceras* (then recognized as *Diceratherium*).

Sexual dimorphism has been noted in *Teleoceras* as well. Osborn (1898) concluded that skulls of *Teleoceras* (Fig. 1) could be identified to gender on the basis of lower tusk (i2) diameter and possibly the size of the terminal horn boss, but he did not provide measurements. Voorhies and Stover (1978) confirmed the gender basis of the i2 dimorphism by describing the presence of fetal remains (Fig. 2) inside the articulated skeleton of an Ashfall *T. major* with the smaller-sized tusks. On the basis of a limited number of isolated postcranial elements, Voorhies (1990) suggested that sexual dimorphism is evident in ulna and radius dimensions of Barstovian *T. medicornutum* and Hemphillian *T. fossiger*, respectively. However, significant sexual dimorphism in postcranial characters has yet to be documented in extinct rhinoceroses, possibly because the gender of postcranial elements cannot be identified confidently or because adequate sample sizes are lacking. In fact, the lack of demonstrable dimorphism was used in part as evidence for the existence of sympatric species of *Teleoceras* in Miocene deposits of the Texas Gulf Coastal Plain (Prothero and Sereno 1982; Prothero and

Manning 1987: dwarf *T. meridianum* and larger *T. medicornutum*) and Miocene deposits of western Nebraska (Tanner 1975: an un-named smaller "tribe" and larger *T. schultzi* [cf. *fossiger*]).

Material and Methods

Fifty-one cranial and postcranial measurements were obtained from 35 adult (longbone epiphyses fused) skeletons, 24 females and 11 males, from Ashfall Fossil Beds (AFB). Eight of the skeletons remain in situ at AFB, the remaining 27 are housed in the UNSM collections. Not every measurement was obtainable on each skeleton, owing to factors such as breakage, distortion, concealment in blocks of ash, and, for those specimens in situ, extent of exposure. Only one element in a pair (left or right, depending on availability) was measured on each individual. The analysis included 12 cranial measurements and 13 measurements for each mandible, forelimb, and hindlimb. Measurements are defined in the corresponding table captions (Tables 1–4). I calculated radius and femur cross-sectional areas by initially making circumferal molds (using polyvinyl siloxane) at midshaft on the radius and immediately below the third trochanter on the femur. The molds were digitized on a flatbed scanner and the cross-sectional area analyses performed on a Macintosh computer using the public domain NIH Image program (developed at the U.S. National Institutes of Health and available on the Internet at http://rsb.info.nih.gov/nih-image/).

To facilitate the recognition of age-dependent variation, I placed each skeleton in a relative adult age class (AWG 1–9) based on the eruption and wear of the lower molars. I determined the sex of each skeleton using the i2 transverse diameter (Fig. 3A) as suggested by Osborn (1898) and Voorhies and Stover (1978). For each measurement and for each sex, I calculated the mean, observed range, standard deviation, and coefficient of variation, and used the Student's t-test to test the significance of the difference between male and female means. I then calculated dimorphism ratios (DR = male value ÷ female value) for the means of each measurement.

Intrasexual variability and dimorphism ra-
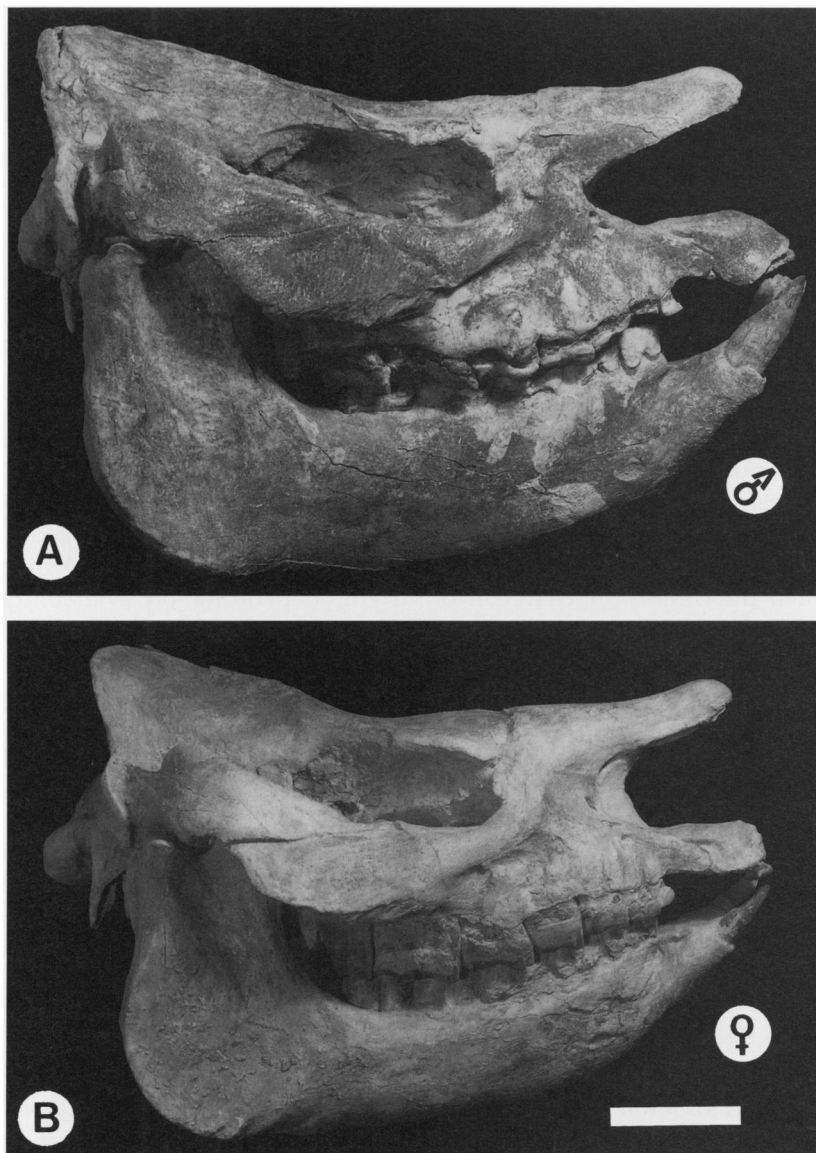
FIGURE 1.   Articulated skulls of *Teleoceras major* from Ashfall Fossil Beds. A, Male (UNSM 52288). B, Female (UNSM 52269). Ash is visible in the female nasal cavity. Skulls to same scale (=10 cm). Readily apparent dimorphic features in the male include enlarged I1, i2, greater jaw depth, and more massive mandibular-angle region.

tios were calculated both for the maximum and minimum male and female longbone lengths and for the maximum and minimum male and female body mass estimates. Body mass estimates were determined from published regression equations based on various cranial and postcranial dimensions. I determined relative limb-segment lengths for each sex in *Teleoceras* and for combined sexes in extant rhinoceroses (*Ceratotherium simum, Diceros bicornis, Dicerorhinus sumatrensis, Rhinoceros unicornis*), *Hippopotamus amphibius,* and the extinct (presumably semiaquatic [Scott 1941]) amynodont rhinoceros *Metamynodon planifrons.*

Isolated radii and tibiae attributed to *T. fossiger* from Long Island Quarry (medial Hemphillian), Kansas, and *T. proterum* from Mixon's Bone Bed (early Hemphillian), Florida, were also measured. The skeletal material in both quarries is disarticulated and the sex of the postcranial material is not independently

FIGURE 2. Fetal bones (f) found within the pelvic (p) region of a female *Teleoceras major* skeleton (UNSM 52373) exhibiting the smaller sized (20.1 mm × 22.5 mm) lower tusks. Material on display at Ashfall Fossil Beds.
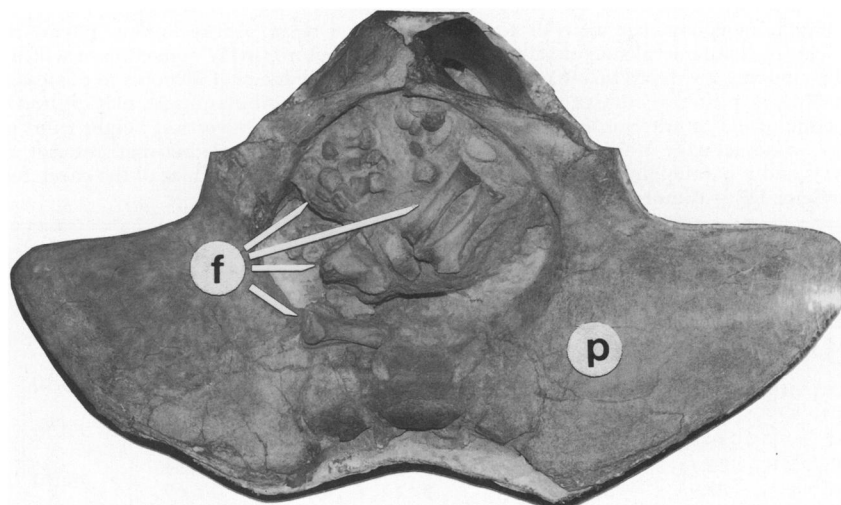
TABLE 1. Cranial morphometric analysis for adult (longbone epiphyses fused) *Teleoceras major* from Ashfall Fossil Beds, Nebraska. Abbreviations: DR = dimorphism ratio (male value ÷ female value); P2–M3, P2–P4, M1–M3 lengths measured at cervix along buccal side; M3C = posterior edge of M3 to the ventral edge of foramen magnum; P2C = distance from point on palatine suture perpendicular to P2 to the ventral edge of the foramen magnum; BPOP = maximum width at postorbital processes; LH = ventral edge of foramen magnum to the dorsal edge of lambdoid crest; TOW = greatest transoccipital width; SL = anterior tip of nasals to posteriodorsal edge of lambdoid crest; FNL = tip of nasals to posteriormost point of narial notch; PNL = anterior edge of premaxilla to posteriormost point of narial notch; MZW = maximum skull width at zygomatic arches. Linear dimensions in millimeters, areal dimensions in millimeters squared.

Character	Sex	Mean	Range	n	SD	CV	p	DR
P2–M3	F	255.6	241–282	20	11.81	4.62	>0.10	1.03
	M	262.4	245–278	10	10.84	4.13		
P2–P4	F	97.6	85–107	20	5.74	5.88	>0.10	1.03
	M	100.7	88–112	10	7.23	7.18		
M1–M3	F	163.7	152–183	22	7.58	4.63	0.05	1.04
	M	169.9	162–178	10	6.98	4.11		
M3C	F	197.2	175–228	13	16.49	8.36	0.02	1.10
	M	216.0	201–233	7	12.65	5.86		
P2C	F	439.9	402–462	14	16.60	3.77	0.002	1.06
	M	466.4	443–481	7	12.67	2.72		
BPOP	F	160.2	148–181	11	9.89	6.17	>0.10	1.05
	M	169.0	162–184	4	10.10	5.98		
LH	F	176.3	150–188	13	11.84	6.72	0.10	1.06
	M	187.6	178–208	5	11.78	6.28		
TOW	F	214.1	187–232	13	11.56	5.40	0.01	1.08
	M	232.2	218–251	6	12.89	5.55		
SL	F	463.4	423–503	17	19.39	4.18	0.002	1.06
	M	490.6	464–508	8	14.87	3.03		
FNL	F	116.5	99–138	19	9.78	8.39	>0.10	1.01
	M	117.9	104–131	8	9.08	7.70		
PNL	F	126.3	111–138	17	7.33	5.80	0.001	1.12
	M	141.9	127–153	9	8.51	6.00		
MZW	F	308.3	280–344	13	19.56	6.34	>0.10	1.03
	M	318.0	297–339	6	15.31	4.81		

TABLE 2. Mandibular morphometric analysis for adult *Teleoceras major*. Abbreviations: p3–m3, p3–p4, m1–m3 lengths taken at cervix along buccal side; m1L = maximum length of m1; m1W = maximum width of m1; m1A = m1L × m1W; JD = buccal jaw depth below m1 cervix; JL = anterior edge of i1 alveolus to posterior edge of mandibular angle; m3MA = posterior edge of m3 to posterior edge of mandibular angle; m3C = horizontal distance from posterior edge of m3 to anterior edge of mandibular condyle; CH = vertical height from ventral edge of mandibular angle to dorsal edge of mandibular condyle; AMS = vertical angle between anterior margin of mandibular symphysis and a parallel line in the horizontal plane of the occlusal surface of the cheek teeth; i2D = mediolateral i2 diameter. DR = dimorphism ratio (see Table 1).

Character	Sex	Mean	Range	n	SD	CV	p	DR
p3–m3	F	228.1	207–251	23	10.88	4.77	0.10	1.04
	M	236.4	219–248	8	10.53	4.45		
p3–p4	F	68.3	62–75	23	4.07	5.96	0.05	1.05
	M	72.0	67–75	8	2.83	3.93		
m1–m3	F	158.7	145–175	23	6.57	4.14	>0.10	1.03
	M	163.1	149–171	9	7.91	4.85		
m1L	F	46.2	41.8–50.6	20	2.47	5.35	>0.10	1.01
	M	46.6	42.4–51.6	9	2.87	6.16		
m1W	F	32.1	26.4–37.0	15	2.74	8.54	>0.10	1.06
	M	33.9	31.0–35.9	8	1.93	5.69		
m1A	F	1489.3	1133–1872	15	187.68	12.60	>0.10	1.06
	M	1575.4	1395–1852	8	161.47	10.25		
JD	F	94.1	84–112	23	6.84	7.27	0.05	1.08
	M	101.4	92–125	9	10.13	9.99		
JL	F	465.2	451–506	20	13.62	2.93	0.001	1.07
	M	498.6	472–523	10	16.85	3.38		
m3MA	F	169.3	139–189	24	13.48	7.96	0.02	1.08
	M	182.7	161–210	9	13.88	7.60		
m3C	F	113.9	76–137	21	17.08	15.00	>0.10	1.07
	M	121.6	105–139	9	12.03	9.89		
CH	F	232.0	206–260	20	12.20	5.26	0.01	1.07
	M	247.1	231–269	8	13.34	5.40		
AMS	F	34.9	27–45	21	4.52	12.95	0.05	n/a
	M	30.6	25–38	9	4.98	16.27		
i2D	F	24.8	22–28	18	1.83	7.38	0.001	1.73
	M	43.0	38–49	8	3.34	7.77		

verifiable. The measured Long Island Quarry material is housed in the American Museum of Natural History (AMNH), University of Kansas Natural History Museum, and UNSM collections. The Mixon's Bone Bed material analyzed for this study is housed at AMNH.

Results

Significant sexual dimorphism is evident in *Teleoceras major* for cranial, mandibular, and postcranial characters (Tables 1–4). Analysis of male and female mean cranial values (Table 1) indicates a significant difference ($p \le 0.01$) in P2-condyle length, transoccipital width, skull length, and narial notch–anterior premaxilla length. Range overlap is evident in each of these characters. Male mean values for premolar and molar length, breadth of the postorbital process, length of the free nasals, and maximum width of the zygomatic arch are larger, but not statistically different. Male

and female intrasexual variability, as determined by coefficient of variation (CV) is approximately equal for all characters except the M3–condyle length, where females appear more variable. Male means are larger (DR values > 1.0) for all cranial characters. The large DR value (1.12) for the narial notch–anterior premaxilla length apparently reflects the enlarged I1 (Fig. 1A) rather than a more retracted narial notch in males. Considerable dimorphism is also evident in M3–condyle lengths (DR = 1.10).

For the mandibles (Table 2), jaw length, mandibular condyle height, and i2 diameter are significantly dimorphic ($p \le 0.01$). The difference in jaw length is attributable in part to the enlarged i2 in males (Fig. 1A). Range overlap is evident in all mandibular characters except the i2 diameter (Fig. 3A). Premolar and molar lengths (Fig. 3B), m1 occlusal surface area, jaw depth, m3–mandibular angle length,

TABLE 3. Forelimb morphometric analysis for adult *Teleoceras major*. Abbreviations in brackets correspond to standardized von den Driesch (1976) measurements. Abbreviations: HL = humerus length [GLC]; HPW = proximal width of humerus [Bp]; HDW = maximum distal width of humerus [Bd]; HDWC = distal articular surface width of humerus; RL = radius length [GL]; RPW = maximum proximal width of radius [Bp]; RDW = maximum distal width of radius [Bd]; RDD = maximum distal depth of radius; RXA = midshaft cross-sectional area of radius; MC3L = length of third metacarpal (MC3) [GL]; MC3PW = maximum proximal width of MC3 [Bp]; MC3DW = maximum distal width of MC3 [BT]; MC3D = anterior-posterior thickness of MC3 at 0.5 length. DR = dimorphism ratio (see Table 1).

Character	Sex	Mean	Range	n	SD	CV	p	DR
HL	F	296.1	283–314	17	8.72	2.94	0.001	1.11
	M	327.8	317–341	9	9.39	2.86		
HPW	F	80.1	75–87	14	3.15	3.93	0.001	1.09
	M	87.2	83–93	5	4.02	4.62		
HDW	F	122.2	115–130	15	3.97	3.25	0.01	1.05
	M	128.0	125–133	5	3.16	2.47		
HDWC	F	79.8	74–86	14	3.66	4.59	0.002	1.08
	M	86.0	82–90	6	3.03	3.52		
RL	F	239.6	230–253	20	6.93	2.89	0.001	1.12
	M	269.2	259–289	9	9.69	3.60		
RPW	F	75.3	71–79	16	2.75	3.65	0.001	1.11
	M	83.9	81–90	7	3.48	4.16		
RDW	F	86.2	78–96	17	4.75	5.51	0.02	1.07
	M	91.9	87–99	7	4.18	4.55		
RDD	F	47.6	45–52	16	2.00	4.20	0.001	1.15
	M	54.6	51–58	7	2.44	4.47		
RXA	F	977.6	826–1186	15	114.87	11.75	0.001	1.34
	M	1305.1	1024–1501	7	142.49	10.92		
MC3L	F	115.0	111–120	9	2.65	2.30	0.01	1.07
	M	123.2	111–131	6	6.74	5.47		
MC3PW	F	55.7	53–60	9	2.87	5.15	0.10	1.06
	M	59.2	56–63	5	3.11	5.25		
MC3DW	F	46.1	44–48	9	1.62	3.51	0.01	1.07
	M	49.2	48–51	5	1.30	2.64		
MC3D	F	18.7	15–20	9	1.50	8.02	0.02	1.22
	M	22.8	19–27	4	3.50	15.35		

m3–mandibular condyle length, and angle of the mandibular symphysis are not significantly different. Male and female intrasexual variability (CV) is similar for all mandibular characters except p3–p4 length, m1 occlusal surface area, m3–mandibular condyle length, jaw depth, and angle of the mandibular symphysis. Females are apparently more variable for the first three of these characters and males more variable for the last two. DR values are greater than 1.0 for all mandibular characters except the angle of the mandibular symphysis, the only nondimensional character recorded. In addition to the i2 diameter (DR = 1.73), m3–mandibular angle length (DR = 1.08) and jaw depth (DR = 1.08) appear to be the most dimorphic mandibular characters.

In comparison to the crania and mandibles, a greater degree of sexual dimorphism is evident in the postcranial skeleton. Distal width of the radius, proximal width of the third metacarpal (MC3), and midshaft thickness of MC3 are the only forelimb characters not significantly different (see Table 3). Male and female ranges do not overlap for humerus length, radius length, or radius proximal width. The bivariate plot of radius length and radius proximal width is clearly bimodal (Fig. 4A). A plot of radius length alone fails to show a clear bimodal distribution. Intrasexual variability (CV) is similar for all forelimb characters except the MC3 length and MC3 midshaft thickness, for which the males appear more variable. The DR values are greater than 1.0 for all forelimb characters. Sexual dimorphism is most evident in the radius cross-sectional area (DR = 1.34), MC3 midshaft thickness (DR = 1.22), and radius distal depth (DR = 1.15). DR values for humerus length, radius length, and radius proximal width also are greater than 1.10. A plot of radius distal depth versus relative age (not figured) suggests that

TABLE 4. Hindlimb morphometric analysis for adult *Teleoceras major*. Abbreviations in brackets correspond to standardized von den Driesch (1976) measurements. Abbreviations: FL = femur length [GLC]; FHD = anterior-posterior thickness of femoral head [DC]; FDW = maximum distal width of femur [Bd]; FXA = cross-sectional area of femur immediately below the third trochanter; TL = tibia length [GL]; TPW = maximum proximal width of tibia [Bp]; TDW = maximum distal width of tibia [Bd]; TDAW = width of distal articular surface of tibia; TDD = maximum distal depth of tibia [Dd]; MT3L = length of third metatarsal (MT3) [GL]; MT3PW = maximum proximal width of MT3 [Bp]; MT3DW = maximum distal width of MT3 [BT]; MT3D = anterior-posterior thickness of MT3 at 0.5 length. DR = dimorphism ratio (see Table 1).

Character	Sex	Mean	Range	n	SD	CV	p	DR
FL	F	385.6	369–400	21	9.17	2.38	0.001	1.10
	M	422.9	401–446	10	13.35	3.16		
FHD	F	74.1	68–81	18	3.45	4.66	0.10	1.04
	M	76.9	74–80	7	2.34	3.04		
FDW	F	113.4	106–120	17	3.86	3.40	0.05	1.03
	M	117.3	112–124	9	3.81	3.25		
FXA	F	2004.1	1710–2327	17	156.76	7.82	0.001	1.19
	M	2383.3	2085–2974	7	306.79	12.87		
TL	F	235.1	223–247	18	8.37	3.56	0.001	1.11
	M	260.4	239–287	9	13.86	5.32		
TPW	F	94.0	88–102	14	3.78	4.02	0.001	1.07
	M	101.0	95–106	8	4.00	3.96		
TDW	F	74.2	69–81	14	3.62	4.88	0.01	1.08
	M	80.4	69–87	8	5.48	6.82		
TDAW	F	60.7	54–67	14	4.20	6.92	0.05	1.06
	M	64.3	62–67	7	1.80	2.80		
TDD	F	56.5	50–62	14	3.23	5.72	0.001	1.10
	M	62.3	60–66	7	1.98	3.18		
MT3L	F	95.3	89–100	8	4.10	4.30	>0.10	1.07
	M	102.3	92–112	3	10.02	9.79		
MT3PW	F	40.0	37–42	8	1.60	4.00	0.05	1.09
	M	43.7	41–48	3	3.79	8.67		
MT3DW	F	43.6	42–45	8	1.19	2.73	0.05	1.06
	M	46.3	44–49	3	2.52	5.44		
MT3D	F	18.8	18–20	8	0.89	4.73	>0.10	1.06
	M	20.0	19–22	3	1.73	8.65		

male radii continued to increase in mass with age, whereas once fused, the female radial mass remained relatively constant.

Dimorphism in the hindlimbs (Table 4) is not as pronounced as that observed in the forelimbs. However, femur length, femur cross-sectional area, tibia length, tibia proximal width, tibia distal width, and tibia distal depth are significantly different ($p \leq 0.01$). Range overlap is evident for all hindlimb characters except femur length. The bivariate plot of tibia length and distal depth (Fig. 4B) visually suggests sexual dimorphism but does not produce a clear bimodal distribution as seen in the radius plot (Fig. 4A). Males appear more variable (CV) for femur cross-sectional area, tibia distal width, third metatarsal (MT3) length, and MT3 proximal width, while width of the distal articular surface of the tibia is more variable in females. All hindlimb DR values are greater than 1.0. Dimorphism is

most pronounced in femur cross-sectional area (DR = 1.19). DR values for femur length, tibia length, and tibia distal depth are greater than 1.09. A plot of tibia distal depth and relative age (not figured) suggests, as in the radii, that the male tibia, but not the female, increased in mass with age.

Bimaturism in *T. major* is demonstrable in the postcranial skeleton. A young adult male (UNSM 121511, in situ at AFB) with humerus and femur epiphyses unfused exhibits a stage of lower-molar eruption and wear equivalent to that seen in an AWG 1 female (UNSM 52238) with longbone epiphyses fused. An additional male (UNSM 121510, in situ at AFB) with unfused longbone epiphyses (radius, ulna, femur and tibia) exhibits lower dentition eruption and wear equivalent to that in AWG 2 specimens (UNSM 52283 for comparison).

All DR values for maximum male versus minimum female longbone lengths (Table 5)
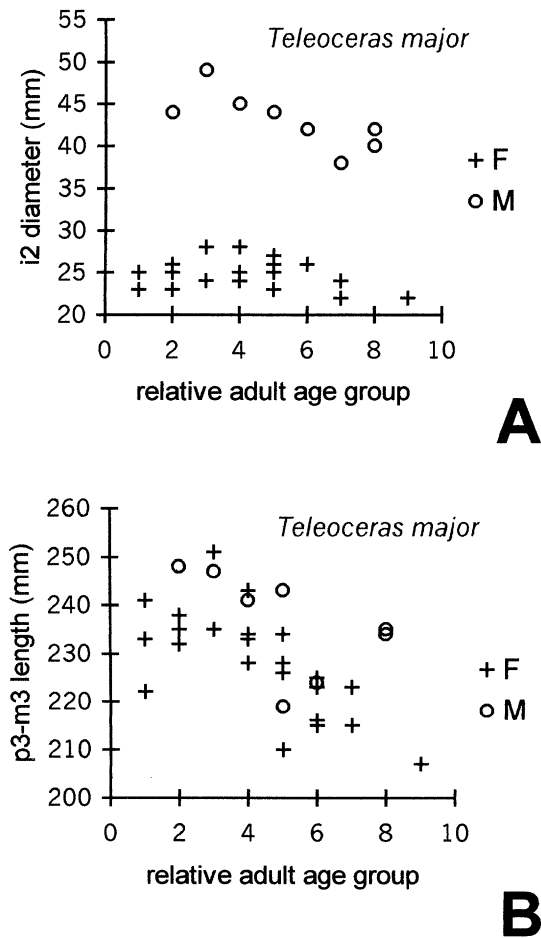
FIGURE 3. A, Tusk size in adult *Teleoceras major* from Ashfall Fossil Beds. Transverse (mediolateral) diameter of one lower tusk (i2) was measured in all ($n = 26$) skeletons in which this tooth is preserved. Relative ages were assigned on the basis of wear on lower permanent cheek teeth. Unambiguous sex determination for all Ashfall *Teleoceras* postcrania measured for this study are based on associated tusks or, in a few cases, their alveoli. B, p3–m3 lengths plotted against age, illustrating the progressive shortening of the tooth row with age.
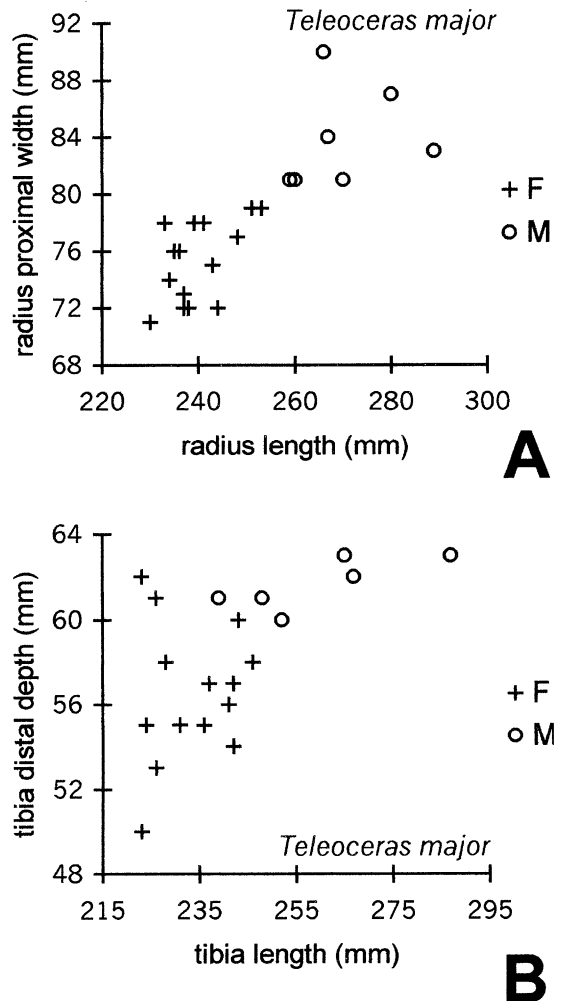
FIGURE 4. Radius length versus radius proximal width (A) and tibia length versus tibia distal depth (B) for adult (longbone epiphyses fused) male and female *Teleoceras major* from Ashfall Fossil Beds.

TABLE 5. Comparison of intrasexual variability and sexual dimorphism ratios for *Teleoceras major* male and female maximum and minimum longbone lengths and cross-sectional areas. Abbreviations: mM = minimum male; xM = maximum male; mF = minimum female; xF = maximum female; (L) = length; (A) = cross-sectional area.

Character	xM/mM	xM/xF	xM/mF	mM/xF	mM/mF	xF/mF
Humerus (L)	1.08	1.09	1.20	1.01	1.12	1.11
Radius (L)	1.12	1.14	1.26	1.02	1.13	1.10
Radius (A)	1.47	1.27	1.82	0.86	1.24	1.44
Femur (L)	1.11	1.11	1.21	1.00	1.09	1.08
Femur (A)	1.43	1.28	1.74	0.90	1.22	1.36
Tibia (L)	1.20	1.16	1.29	0.97	1.07	1.11

TABLE 6. Body mass estimates (kg) for the *Teleoceras major* skeletons judged (on the frequency of having the largest [smallest] value for each character) to be the maximum and minimum males and females in the Ashfall Fossil Beds herd. Estimates based on the following: m1 occlusal area (m1AL) from Legendre's (1986) Artiodactyl + Perissodactyl equation; m1 occlusal area (m1AD) and m1–3 length from Damuth's (1990) nonselenodont-ungulates equations; posterior length of skull (PSL = M3 to posterior edge of occipital condyles) from Janis's (1990) perissodactyls + hyracoids equation; radius distal width (RDW), humerus distal width (HDW), femur distal width (FDW), and femur length (FL) from Scott's (1990) all-ungulates equations; humerus (HC) and femur (FC) minimum midshaft circumference from Anderson et al.'s (1985) mammals > 300 kg equations; average of the HC and FC (AHFC); humerus (HL) and tibia (TL) length from Alexander et al.'s (1979) all-mammals equations; average of non-length longbone dimensions (ANLDLB). Other abbreviations the same as Table 5.

Character	xM UNSM 27803	mM UNSM 52239	xF UNSM 52228	mF UNSM 52282
m1AL	2405.7	2305.4	3441.3	2464.1
m1AD	1702.4	1633.9	2405.4	1742.3
m1–3	1834.7	2334.9	2549.2	1764.8
PSL	861.7	623.9	573.7	653.9
RDW	780.8	630.7	624.0	537.8
HDW	1400.5	1291.4	1187.7	1187.7
FDW	1067.3	805.5	858.7	793.5
FL	687.9	474.9	470.7	355.4
HC	941.6	917.4	758.6	686.2
FC	1358.3	771.5	771.5	720.5
AHFC	1150.0	844.5	765.1	703.4
HL	196.0	165.7	155.8	121.4
TL	69.1	39.0	42.7	31.4
ANLDLB	1109.7	883.3	840.1	785.1

exceed 1.20. DR values for longbone cross-sectional areas exceed 1.70. Male and female indices for maximum intrasexual variation are comparable except for the longbone cross-sectional areas, where the males appear more variable.

Estimated maximum and minimum body masses (Table 6) vary widely for both sexes, largely as a function of the original data used to formulate the regression equations. The uncertainties associated with body mass estimates in fossil taxa preclude meaningful statistical analysis of these data. Estimates based on dental measurements appear to be significant overestimates, while those based on longbone lengths are definitely underestimates. The estimates based on non-length longbone measurements appear to provide the most reasonable values and are comparable to estimates made by MacFadden and Hulbert (1990) for Clarendonian *Teleoceras* and

Aphelops from Florida. The apparent intrasexual variability is greater in males than in females (Table 7), and the body mass DR value based on the average of the estimates using mean values for radius, humerus, and femur distal widths is 1.13. The body mass DR value based on the average of the maximum and minimum non-length longbone dimensions (ANLDLB) is 1.23.

T. major males and females exhibit nearly identical relative limb-segment lengths (Table 8) that are similar to those of selected extant and extinct ungulates. *Teleoceras* MC3 / radius length is most similar to that of the extant *Diceros bicornis* and *Ceratotherium simum* and the extinct *Metamynodon planifrons*. Radius / humerus length is subequal with *C. simum, Rhinoceros unicornis,* and *M. planifrons*. Lengths of humerus / basal skull, humerus / femur, and tibia / femur most closely match those in *H. amphibius* and *M. planifrons. T. major* appears

TABLE 7. Intrasexual variability and sexual dimorphism indices for *Teleoceras major* minimum and maximum male and female body mass estimates. Abbreviations the same as in Tables 5 and 6.

Character	xM / mM	xM / xF	xM / mF	mM / xF	mM / mF	xF / mF
AHFC	1.36	1.50	1.63	1.10	1.20	1.09
ANLDLB	1.26	1.32	1.41	1.05	1.13	1.07

TABLE 8. Relative limb-segment lengths for *Teleoceras major* and selected extant and extinct ungulates. Data for *Diceros bicornis* (n = ?) from Hillman-Smith and Groves 1994; *Ceratotherium simum* (n = ?5) from Groves 1972; *Dicerorhinus sumatrensis* (n = ?) from Groves and Kurt 1972; *Rhinoceros unicornis* (n = 4) from Laurie et al. 1983; *Hippopotamus amphibius* No. 1 from Howell 1965, No. 2 from Prothero and Sereno 1982, and No. 3 from Gregory (Osborn 1929: p. 738); *Metamynodon planifrons* also from Gregory, except H/BSL from Scott 1941. Abbreviations: MC3 = third metacarpal; R = radius; H = humerus; BSL = basal skull length (basilar skull length used for *Teleoceras*); F = femur; T = tibia; f = female; m = male.

Species	MC3/R	R/H	H/BSL	H/F	T/F	T/R
T. major, f	0.482	0.812	0.592	0.769	0.609	0.978
T. major, m	0.462	0.822	0.623	0.778	0.615	0.954
D. bicornis	0.465	0.849	0.828	0.967	0.75	0.917
C. simum	0.492	0.82	0.737	0.932	0.73	0.952
D. sumatrensis	0.536	0.85	0.73	0.889	0.745	1
R. unicornis	0.518	0.805	0.768	0.873	0.735	1.04
H. amphibius-1	—	0.68	—	—	0.63	—
H. amphibius-2	—	—	0.562	0.794	0.741	—
H. amphibius-3	0.562	0.683	—	0.793	0.667	1.23
M. planifrons	0.478	0.814	0.804	0.819	0.583	0.875

most morphologically similar to the extant semiaquatic *H. amphibius* and the extinct, presumably semiaquatic (Scott 1941) *M. planifrons*.

Bivariate plots of radius length and proximal width for *T. fossiger* from the Long Island Quarry (Fig. 5A) and *T. proterum* from Mixon's Bone Bed (Fig. 5B) suggest the existence of sexual dimorphism in these species as well. The bivariate plot (Fig. 5A) for *T. fossiger* is clearly bimodal, as would be a plot of radius length alone. If the two natural groups in the *T. fossiger* plot are taken to represent males and females, the DR value is 1.13 for radius length and 1.12 for radius proximal width. The radius bivariate plot (Fig. 5B) for *T. proterum* is similar in form to that for *T. major* (Fig. 4A). On the basis of i2 diameters (Harrison and Manning 1983), the sex ratio of the AMNH *T. proterum* material from Mixon's Bone Bed is approximately 1:1. The *T. proterum* plot (Fig. 5B) is not as clearly bimodal as that for *T. fossiger* (Fig. 5A), yet a natural break appears to exist. DR values for the groups shown in Figure 5B are 1.11 for radius length and 1.09 for radius proximal width.

Discussion

Cladistic analyses suggest that *Teleoceras* does not lie within the lineage of the extant rhinoceroses (Prothero et al. 1986; Cerdeno 1995). However, because of similarities in gross morphology, dentition, and body size, it is legitimate to compare results of this study with what is known about dimorphism in modern rhinoceroses. Except for the crania, little quantitative information is available on the extent of skeletal dimorphism in extant rhinoceros species. Perhaps the questionable conclusions found in paleontological literature (Loose 1975; Prothero and Sereno 1982; Prothero and Manning 1987) indicating that modern rhinoceroses are not sexually dimorphic are a reflection of this scarcity of data.

Although measured live weights of free-ranging animals are not available for most extant rhinoceros species, body mass estimates for *Ceratotherium simum* males range from 25% to 43% greater than females (Owen-Smith 1988). Shoulder height (DR = 1.02) is apparently subequal (Owen-Smith 1988). Hillman-Smith et al. (1986) found that head circumference (around orbit region) (DR = 1.11), basal circumference of the nasal horn (DR = 1.14), and weight (DR = 1.6) are greater in *C. simum* males (4 ≤ n ≤ 9) than females (5 ≤ n ≤ 6). More recently, Rachlow and Berger (1997) also documented significantly larger horn bases in adult males. Although not as robust, female nasal horns are longer and thinner (Groves 1972). Male skull length is greater (average DR = 1.06) than that in same-aged females (Hillman-Smith et al. 1986). Territorial *C. simum* males also exhibit significantly larger neck and chest girths (Rachlow et al. 1998). The mixing of data attributable to different subspecies of *C. simum* may obscure or enhance the actual intersexual variation. Hellers data
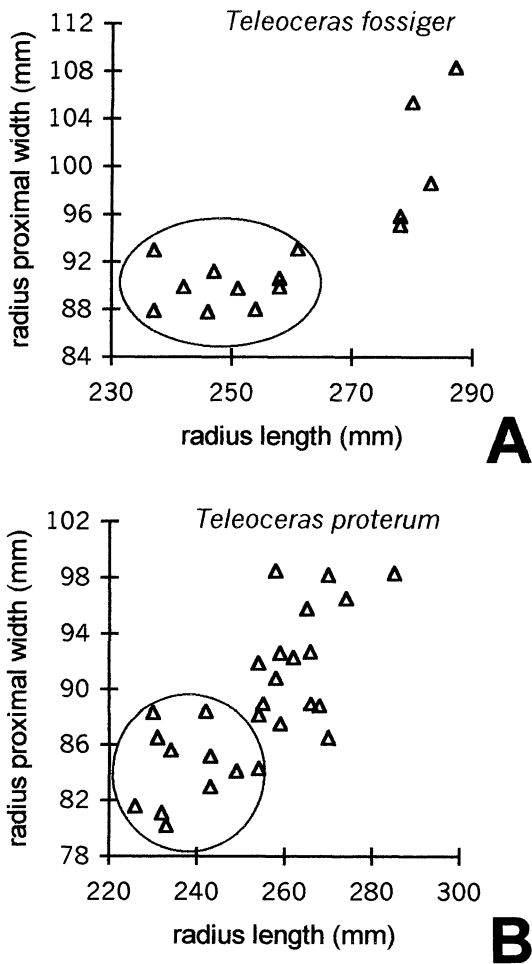
FIGURE 5. Radius length versus radius proximal width for adult *Teleoceras fossiger* from Long Island Quarry, Kansas (A) and *Teleoceras proterum* from Mixon's Bone Bed, Florida (B). Probable females within enclosure in each figure. *Teleoceras fossiger* appears to be more dimorphic and *T. proterum* less dimorphic than *T. major*.

(1913: p. 28) for *C. simum simum* and *C. simum cottoni* indicate that size differences existed between the two races. Nonetheless, *C. simum simum* males exhibit longer occipital-nasal lengths (DR = 1.09; male n = 5, female n = 3), greater zygomatic breadths (DR = 1.16; n = 5, 3), greater nasal-boss widths (DR = 1.18; n = 4, 3), and approximately equal lower tooth-row lengths (DR = 1.01; n = 5, 2) when compared with *C. simum simum* females. *C. simum cottoni* males also show longer occipital–nasal lengths (DR = 1.07; male n = 6, female n = 7), greater zygomatic widths (DR = 1.04; n = 6, 7), greater nasal-boss widths (DR = 1.19; n =

6, 7), and subequal lower tooth-row lengths when compared with *C. simum cottoni* females. "The general massiveness of the skull is considerably greater in the male [*C. simum*] where it is especially marked by greater length" (Heller 1913: p. 24).

Diceros bicornis does not show the same degree of body mass dimorphism as in *C. simum*. Owen-Smith (1988) reported similar male and female ranges and maximum values for body mass estimates and shoulder heights. Females exhibit generally longer horns (Hillman-Smith and Groves 1994), with the relative length of the frontal horn (both sexes $n \leq 59$), in comparison to the nasal horn, also longer (Hamilton and King 1969; Freeman and King 1969). Berger and Cunningham (1998: Table 1) provided data from three study populations in Etosha National Park, Namibia, indicating that males (n = 5, 14, 8) and females (n = 5, 12, 8) exhibit nearly identical nasal-horn lengths, horn basal widths, and head size.

In the Asian rhinoceroses, Pocock (1946) found that males tend to exhibit longer horns with greater basal circumferences. Estimates of male and female body masses in *Rhinoceros unicornis* differ by approximately 30%, males being larger (Owen-Smith 1988). Males are approximately 16% taller at the shoulder and exhibit more pronounced skin folds around the neck (Laurie 1982). Dinerstein (1991) indicated that among fully adult wild animals (males, $4 \leq n \leq 15$; females, $3 \leq n \leq 9$), males show significantly larger values for neck circumference (DR = 1.16), skull circumference (DR = 1.09), width behind the head (DR = 1.15), length of lower lateral incisor (tusk) (DR = 1.28), and basal circumference of the horn (DR = 1.28). Comparison of mean values for additional wild males ($5 \leq n \leq 6$) and females ($8 \leq n \leq 11$) indicates greater occipitonasal length (DR = 1.03), basal skull length (DR = 1.02), zygomatic breadth (DR = 1.08), nasal breadth (DR = 1.27), mastoid breadth (DR = 1.06), and occipital height (DR = 1.05) in males (Groves 1982: Table 1).

Data are limited for *Rhinoceros sondaicus* and *Dicerorhinus sumatrensis*. In wild *R. sondaicus*, mean values (males, $8 \leq n \leq 9$; females, $6 \leq n$ ≤ 9) for occipital length (DR = 0.96), basal skull length (DR = 0.97), zygomatic breadth

(DR = 0.99), and occipital height (DR = 0.95) are greater in females, and nasal breadth (DR = 1.17) and mastoid breadth (DR = 1.03) are greater in males (Groves 1982: Table 2). The difference in nasal breadth reflects the condition of generally more well developed horns in males (Pocock 1946). Dinerstein (1991) reported no apparent size differences in wild-caught *D. sumatrensis*. However, mean values for wild males ($n = 5$) and females ($8 \leq n \leq 9$) indicate greater occipitonasal length (DR = 1.06), basal skull length (DR = 1.04), zygomatic breadth (DR = 1.05), nasal breadth (DR = 1.20), occiput width (DR = 1.05), and occiput height (DR = 1.02) in males (Groves 1982: Table 4).

Osborn's (1898) inference that *Teleoceras* males had larger tusks than females is fully borne out by the present study. In the Ashfall sample of *Teleoceras major*, i2 diameter (Fig. 3A) is the most striking sexually dimorphic feature (DR = 1.73). Other craniodental measurements (Tables 1, 2) that clearly separate the sexes are M3–condyle length (DR = 1.10), premaxilla length (DR = 1.12), transoccipital width (DR = 1.08), m3–mandibular angle length (DR = 1.08), jaw depth (DR = 1.08), and mandibular condyle height (DR = 1.07). Taken together these dimensions show that *T. major* males had more massive heads, and probably necks as well. As in extant *C. simum* (Heller 1913), the massiveness of the male head and neck appear to have increased for a number of years after the longbone epiphyses fused, another example of bimaturism (discussed below) in this taxon. In contrast, linear dimensions of cheek teeth, as in extant rhinoceroses, are minimally different (average DR = 1.03), apparently owing in part to the pattern of interstitial wear evident in *Teleoceras*. Wood (1938) noted that *Teleoceras* cheektooth series shorten with age, shown clearly in Figure 3B. The two primary causes of toothrow shortening in *T. major* appear to be the beveling effect of erupting teeth pressing against already erupted teeth (p4 and m2 appear to trim the anterior and posterior edge of m1) and interstitial wear between neighboring teeth as they move in their sockets. Heller (1913) pointed out the same progressive anterioposterior shortening of m1 in *C. simum*.

Sexual dimorphism in *T. major* is most pro-nounced in the postcranial skeleton. The significantly larger humerus (DR = 1.11), radius (DR = 1.12), and MC3 (DR = 1.07) indicate more massive forequarters in males (Table 3). Bivariate plots of radius length and proximal width for *T. fossiger* (Fig. 5A) and *T. proterum* (Fig. 5B) suggest a similar pattern of sexual dimorphism in these Hemphillian species. The significantly larger femur (DR = 1.10) and tibia (DR = 1.11) indicate larger hindquarters (Table 4) in males. Significant body-size dimorphism (DR = 1.13–1.23) in *T. major* is supported by substantial differences both in the cross-sectional areas of the radius (DR = 1.34) and femur (DR = 1.19) and in body mass estimates (Tables 6, 7). Apart from AFB, *Teleoceras* longbones are seldom found in known association with cranial material. Comparison of the maximum and minimum lengths of male and female longbones (Table 5) indicates that *Teleoceras* longbones found in other Miocene localities could vary as much as 29% (tibia) in length.

The developmental heterochrony (bimaturism) evident for longbone epiphyseal fusion suggests that male *T. major* may have continued to develop several years after same-aged females matured, possibly reflecting the nature of the breeding system. If the timing of dental development in extant *D. bicornis* (Goddard 1970) is used as a proxy for age in *Teleoceras* (Mead 1999), then the fusion of longbone epiphyses may have been delayed at least two years in male *T. major*. Extant, sexually dimorphic, herbivorous mammals exhibit similar bimaturism (Jarman 1983). Growth curves (not figured) for *T. major* longbones suggest determinate bimaturism as seen in several dimorphic African bovids, including *Kobus ellipsiprymnus* (waterbuck) and *Syncerus caffer* (African buffalo) (Jarman 1983: Figs. 7, 8). Growth data for extant polygynous mammalian species indicate that males tend to take longer to mature than females (Alexander et al. 1979).

The degree of dimorphism evident in linear dimensions of upper and lower cheek teeth in *T. major* is conservative in comparison to postcranial differences, a condition not wholly unexpected. In the analysis of *R. unicornis*, Groves (1982) found that although certain cra-

nial characters were dimorphic (mentioned above), cheek-tooth measurements were not significantly different. Heller (1913) reported no apparent sexual differences in tooth-row lengths in *C. simum*. Several studies (see Fortelius 1985 for review) have demonstrated that the relative difference in body size is generally greater than the relative difference in cheek-tooth size in sexually dimorphic mammals.

Theoretically, the degree of sexual dimorphism in ungulates should reflect the nature of the breeding system. Alexander et al. (1979) demonstrated significant correlation between the degree of sexual dimorphism and harem size in extant ungulates, indicating that most polygynous ungulates live in large groups in open grassland environments. Sexual dimorphism in ungulates should be favored in breeding systems where females congregate in small areas (Owen-Smith 1988). Jarman (1983) included synchronous estrous as an additional factor favoring the development of sexual dimorphism. The large grazing *C. simum* and mixed-feeding *R. unicornis* show a greater degree of sexual dimorphism and higher female-to-male ratios than the browsing rhinoceros species (Laurie 1982). However, both *C. simum* and *R. unicornis* breed throughout the year. *C. simum* bulls defend exclusive territories where a number of females are likely to congregate, and large size in males (significantly larger neck and chest girths [Rachlow et al. 1998]) is beneficial for territory defense (Owen-Smith 1988). *R. unicornis* does not exhibit true territories, but the dominant bulls live in the area of highest adult female concentration (Laurie 1982). The enlarged tusks and shoulder musculature in bulls are advantageous in intrasexual dominance displays (Dinerstein 1991). In the browsing *D. bicornis*, where the sexes are monomorphic, females are widely dispersed and bulls exhibit overlapping home ranges (Owen-Smith 1988). In this species, horn size correlates with dominance in mature bulls (Berger and Cunningham 1998) and male death (excluding poaching) due to intrasexual combat may be as high as 50% (Berger 1994). As in *C. simum* and *R. unicornis*, *D. bicornis* is polygynous and breeding occurs throughout the year (Goddard 1966).

The nature of the cranial and mandibular dimorphism in *T. major* is similar to that seen in *C. simum* and *R. unicornis*. The dimorphism evident in the forelimbs of *T. major* is comparable to the shoulder-height dimorphism in *R. unicornis*. However, in general, *Teleoceras* appears to have been more sexually dimorphic than any of the extant rhinoceros species. Wright (1993) has documented a similar occurrence of sexual dimorphism in extinct tayassuids and a lack thereof in closely related extant taxa. It appears that ecological analogues rather than closest living relatives may provide the best models for exploring the expected degree of sexual dimorphism in extinct taxa.

Grazing habits have been suggested for *Teleoceras* on the basis of, among other evidence, the occurrence of fossil grass anthoecia within the oral cavities of *T. major* skeletons from AFB (Voorhies and Thomasson 1979). Unlike the generally solitary, aseasonally breeding, extant grazing rhinoceros species, *T. major* is thought to have bred seasonally (based on discrete tooth-wear categories) and formed herds (Voorhies 1985). This proposed ecology is more similar to that of some extant large bovids, such as *Bison bison* (American bison) and *Syncerus caffer*, both large-bodied, herding, mammalian herbivores exhibiting sexual dimorphism and a restricted breeding season. Mature *B. bison* males do not maintain year-round harems and associate with the mixed herd only during rut. Male mating success is determined by fighting skill, which is dependent in part on body mass (Berger and Cunningham 1994). In *S. caffer*, mature bulls interact more often with the herd (yet do not maintain harems) and male fights are infrequent; dominance is related to size, condition, and age (Sinclair 1977; Prins 1996). An additional extant herding herbivore that may provide an ecological analogue for *Teleoceras* is *Hippopotamus amphibius*. Although data are limited for extant *H. amphibius*, a body mass DR value of 1.08 was reported for a "large sample" ($n = ?$) culled in Uganda (Owen-Smith 1988: p. 14). Pooling of data from a number of sources suggests a body mass DR of 1.11 (Owen-Smith 1988: Table I1). Daytime congregations of *H. amphibius* in small pools (the exclusive terri-

tory of the dominant bull) consist of 10–30 animals including the large dominant bull, several females, young, and usually two to six subordinate males (Owen-Smith 1988). Territorial males monopolize breeding of females in his territory. Mature males not holding territories often form bachelor groups (Eltringham 1999). Dominant males with bordering territories generally avoid physical contact. However, when challenged by a mature bachelor, fights (using the enlarged canines as primary offensive weapons) become violent, sometimes resulting in death (Eltringham 1999).

In *T. major*, the greater male body mass, enlarged lower incisors, and more massive head and forequarters suggest size differences related to sexual dimorphism in a breeding system where dominant males fight for mating rights. Webb (1969: p. 141) interpreted "two healed-over wounds" on the nasals of a male *Teleoceras* cranium from Burge Quarry as evidence of intrasexual aggression. "The direction of attack and the evidence of great impact suggest that these wounds were acquired in a butting contest with another male *Teleoceras*" (Webb 1969: p. 141). Two of the adult *T. major* skulls from AFB exhibit features that may also represent healed wounds. UNSM 52272 has a patch of pathologic rugose bone right of center on the anterior edge of the frontals, and UNSM 27805 displays a near-circular (15.5 mm × 17.0 mm) patch of remodeled bone near the posterior edge of the right nasal. As indicated by Webb (1969), it is likely that the terminal nasal horn in *Teleoceras* was more significant than the "little callused knob" suggested by Matthew (1932: p. 436). It apparently was not uncommon for *T. major* to sustain breakage of anterior ribs, as evidenced by a number of AFB individuals with "healed" ribs (M. R. Voorhies personal communication 1999). Unfortunately, the relative frequency of rib breakage in each sex cannot be determined at this time.

If the AFB sample is truly a "snapshot" of a Miocene herd, the herd structure should reflect the nature of the breeding system. After the initial excavation of AFB, Voorhies (1985) reported an adult female-to-male sex ratio of 6.4 to 1 and suggested that *T. major* exhibited

a breeding system in which dominant bulls monopolize breeding. As noted by Voorhies (1985), young adult males are conspicuously underrepresented. Although the breeding age of *T. major* females is unknown, for this study it is judged to coincide with the full eruption of p4 and m2. *D. bicornis* jaws exhibit this stage of eruption at approximately six years of age (Goddard 1970), the average age of female sexual maturity in *C. simum* and *D. bicornis* (Owen-Smith 1988). Excavations continue at AFB and the present breeding-age sex ratio is 2.6 to 1. However, if unlikely breeders (the two males mentioned above with unfused epiphyses, two additional males [AWG 2 and 3] with lower tusks not fully erupted, and one old AWG 9 male) are removed, the ratio becomes 4.25 to 1, again suggesting a breeding system in which dominant bulls monopolize the cows and young adult males are mostly excluded from the herd. This conclusion agrees with that predicted by Jarman's (1983) model using only the degree of sexual dimorphism in the taxon.

As pointed out by Voorhies (1985), it is unlikely that young adult males are absent from this sample merely by chance. Bachelor herds would account for their absence. Mihlbachler (1999) inferred social behaviors for *Teleoceras* from attritional fossil assemblages from the Love Bone Bed and Mixon's Bone Bed localities in Florida. The high proportion (>50%) of young adult males in these deposits was interpreted as an indication of elevated death frequencies resulting from intrasexual competition beginning at the onset of sexual maturity. This interpretation agrees with Berger's (1983b) conclusions that skewed adult sex ratios in large mammals most often indicates intramale reproductive competition.

The breeding system inferred for *T. major*—dominant bulls monopolizing cows—is similar to that of extant *H. amphibius*, with which *Teleoceras* also shares postcranial morphological similarities, first noted by Cope (1879) and further emphasized by Osborn (1898). The AFB *T. major* herd, consisting mostly of adult females and young, contains approximately 54% subadults plus calves, 30% young adults, and 16% older adults (Voorhies 1985: Table 2), a herd structure remarkably similar to extant

H. amphibius. *H. amphibius* has been described as the African "ecological vicar of *Teleoceras*" (Webb 1983: p. 288). Prior to the present study, quantitative analyses supporting the morphological aspect of this analogy were lacking. Comparisons of relative limb-segment lengths (Table 8) document the postcranial similarities between *T. major*, *H. amphibius*, and the other extinct, assumed semiaquatic rhinoceros, *M. planifrons*. The low tibia/femur ratio in *T. major* suggests an adaptation for graviportal locomotion (Howell 1965), more similar to *H. amphibius* than any extant rhinoceros. Using carbon and oxygen isotope values from tooth enamel, MacFadden (1998: p. 274) concluded that *Teleoceras* from Florida likely exhibited grazing habits, yet was not "principally aquatic" like modern *H. amphibius*. *Teleoceras* lacks aquatic adaptations such as elevated orbits and nares found in *H. amphibius*.

Conclusion

Quantifiable sexual dimorphism is present in the herd of early Clarendonian *Teleoceras major* from Ashfall Fossil Beds, Nebraska. The most clearly dimorphic feature is the enlarged lower tusk (i2) in males. The degree of dimorphism in other mandibular and cranial characters is rather conservative when compared with that evident in the appendicular skeleton and in body mass estimates, a pattern noted in extant sexually dimorphic mammals.

The recognition of sexual dimorphism and bimaturism in *T. major* furthers our understanding of the paleoecology of this extinct taxon. The DR values for body mass approach those of *R. unicornis* and *C. simum*, the two extant, sexually dimorphic, polygynous rhinoceros species. However, sexually dimorphic, large-bodied, herding artiodactyls may provide better ecological analogues. Adult *T. major* males appear to have exhibited significantly larger heads, necks, and forequarters, similar to extant *R. unicornis* males, which use their massive forebodies to engage in fierce contests for breeding privileges. The significantly larger i2's in *T. major* males were likely the primary offensive weapons for intraspecific confrontations, although evidence suggests that the horns may have been used as well. The large concentration of mature and immature rhinoceroses at the AFB locality, along with a "breeding" sex ratio (female to male) of approximately 4 to 1, suggests herding habits and a breeding system in which dominant males monopolized matings. The herd structure, evidence of seasonal estrous, unbalanced adult sex ratio, body mass dimorphism, evidence of bachelor herds, and relative limb-segment proportions in *T. major* suggest ecological affinities to extant *H. amphibius* rather than to extant rhinoceros species.

Literature Cited

Alexander, R. D., J. L. Hoogland, R. D. Howard, K. M. Noonan, and P. W. Sherman. 1979. Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates, and humans. Pp. 402–435 *in* N. A. Chagnon and W. Irons, eds. Evolutionary biology and human social behavior: an anthropological perspective. Duxbury, North Scituate, Mass.

Alexander, R. McN., A. S. Jayes, G. M. O. Maloiy, and E. M. Wathuta. 1979. Allometry of the limb bones of mammals from shrews (*Sorex*) to elephant (*Loxodonta*). Journal of Zoology 189: 305–314.

Anderson, J. F., A. Hall-Martin, and D. A. Russell. 1985. Long-bone circumference and weight in mammals, birds and dinosaurs. Journal of Zoology 207:53–61.

Berger, J. 1983a. Ecology and catastrophic mortality in wild horses: implications for interpreting fossil assemblages. Science 220:1403–1404.

———. 1983b. Predation, sex ratios, and male competition in equids (Mammalia: Perissodactyla). Journal of Zoology 201: 205–216.

———. 1994. Science, conservation, and black rhinos. Journal of Mammalogy 75:298–308.

Berger, J., and C. Cunningham. 1994. Bison: mating and conservation in small populations. Columbia University Press, New York.

———. 1998. Natural variation in horn size and social dominance and their importance to the conservation of black rhinoceros. Conservation Biology 12:708–711.

Borsuk-Bialynicka, M. 1973. Studies on the Pleistocene rhinoceros *Coelodonta antiquitatis* (Blumenbach). Palaeontologia Polonica 29:1–95.

Cerdeno, E. 1995. Cladistic analysis of the family Rhinocerotidae (Perissodactyla). American Museum Novitates 3143:1–25.

Coombs, M. C. 1975. Sexual dimorphism in chalicotheres (Mammalia, Perissodactyla). Systematic Zoology 24:55–62.

Cope, E. D. 1879. On the extinct American rhinoceroses and their allies. American Naturalist 13:771a–771j.

Damuth, J. 1990. Problems in estimating body masses of archaic ungulates using dental measurements. Pp. 229–253 *in* Damuth and MacFadden 1990.

Damuth, J., and B. J. MacFadden, eds. 1990. Body size in mammalian paleobiology: estimation and biological implications. Cambridge University Press, Cambridge.

Dinerstein, E. 1991. Sexual dimorphism in the Greater one-horned rhinoceros (*Rhinoceros unicornis*). Journal of Mammalogy 72:450–457.

Eltringham, S. K. 1999. The hippos, natural history and conservation. Academic Press, London.

Fortelius, M. 1985. Ungulate cheek teeth: development, functional, and evolutionary interrelations. Acta Zoologica Fennica 180:1–76.

Fortelius, M., and J. Kappelman. 1993. The largest land mammal ever imagined. Zoological Journal of the Linnean Society 107: 85–101.

Freeman, G. H., and J. M. King. 1969. Relations amongst various linear measurements and weight for black rhinoceroses in Kenya. East African Wildlife Journal 7:67–72.

Gingerich, P. D. 1981. Variation, sexual dimorphism, and social structure in the early Eocene horse *Hyracotherium* (Mammalia, Perissodactyla). Paleobiology 7:443–455.

Goddard, J. 1966. Mating and courtship of the black rhinoceros (*Diceros bicornis* L.). East African Wildlife Journal 4:69–75.

———. 1970. Age criteria and vital statistics of a black rhinoceros population. East African Wildlife Journal 8:105–121.

Groves, C. P. 1972. *Ceratotherium simum*. Mammalian Species 8: 1–6.

———. 1982. The skulls of Asian rhinoceroses: wild and captive. Zoo Biology 1:251–261.

Groves, C. P., and F. Kurt. 1972. *Dicerorhinus sumatrensis*. Mammalian Species 21:1–6.

Hamilton, P. H., and J. M. King. 1969. The fate of black rhinoceroses released in Nairobi National Park. East African Wildlife Journal 7:73–83.

Harrison, J. A., and E. M. Manning. 1983. Extreme carpal variability in *Teleoceras* (Rhinocerotidae, Mammalia). Journal of Vertebrate Paleontology 3:58–64.

Heller, E. 1913. The white rhinoceros. Smithsonian Miscellaneous Collections 61:1–77.

Hillman-Smith, A. K. K., and C. P. Groves. 1994. *Diceros bicornis*. Mammalian Species 455:1–8.

Hillman-Smith, A. K. K., N. Owen-Smith, J. L. Anderson, A. J. Hall-Martin, and J. P. Selaladi. 1986. Age estimation of the

White rhinoceros (*Ceratotherium simum*). Journal of Zoology 210:355–379.

Howell, A. B. 1965. Speed in animals: their specialization for running and leaping. Hafner, London.

Janis, C. M. 1990. Correlation of cranial and dental variables with body size in ungulates and macropodoids. Pp. 255–299 *in* Damuth and MacFadden 1990.

Jarman, P. 1983. Mating system and sexual dimorphism in large, terrestrial, mammalian herbivores. Biological Reviews of the Cambridge Philosophical Society 58:485–520.

Kurten, B. 1969. Sexual dimorphism in fossil mammals. *In* G. E. G. Westermann, ed. Sexual dimorphism in fossil Metazoa and taxonomic implications. International Union of Geological Sciences A 1:226–233.

Laurie, A. 1982. Behavioural ecology of the Greater one-horned rhinoceros (*Rhinoceros unicornis*). Journal of Zoology 196:307–341.

Laurie, W. A., E. M. Long, and C. P. Groves. 1983. *Rhinoceros unicornis*. Mammalian Species 211:1–6.

Legendre, S. 1986. Analysis of mammalian communities from the late Eocene and Oligocene of Southern France. Palaeovertebrata 16:191–212.

Loose, H. 1975. Pleistocene Rhinocerotidae of W. Europe with reference to the recent two-horned species of Africa and S.E. Asia. Scripta Geologica 33:1–59.

MacFadden, B. J. 1998. Tale of two rhinos: isotopic ecology, paleodiet, and niche differentiation of *Aphelops* and *Teleoceras* from the Florida Neogene. Paleobiology 24:274–286.

MacFadden, B. J., and R. C. Hulbert. 1990. Body size estimates and size distribution of ungulate mammals from the Late Miocene Love Bone Bed of Florida. Pp. 337–363 *in* Damuth and MacFadden 1990.

Matthew, W. D. 1932. A review of the rhinoceroses with a description of *Aphelops* material from the Pliocene of Texas. University of California Publications in Geological Sciences 22: 411–480.

Mead, A. J. 1999. Enamel hypoplasia in Miocene rhinoceroses (*Teleoceras*) from Nebraska: evidence of severe physiological stress. Journal of Vertebrate Paleontology 19:393–399.

Mihlbachler, M. C. 1999. Population structure and implications for social behavior in Miocene Florida rhinoceroses. Journal of Vertebrate Paleontology 19(3):64A.

Osborn, H. F. 1898. A complete skeleton of *Teleoceras fossiger*. Notes upon the growth and sexual characters of this species. Bulletin of the American Museum of Natural History 10:51–59.

———. 1903. The extinct rhinoceroses. Memoirs of the American Museum of Natural History 1(3):75–164.

———. 1929. The titanotheres of ancient Wyoming, Dakota, and Nebraska. U.S. Geological Survey Monograph 55:1–953.

Owen-Smith, R. N. 1988. Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge.

Peterson, O. A. 1920. The American Diceratheres. Memoirs of the Carnegie Museum 7:399–477.

Pocock, R. I. 1946. A sexual difference in the skulls of Asiatic rhinoceroses. Proceedings of the Zoological Society of London 115:319–322.

Prins, H. H. T. 1996. Ecology and behaviour of the African Buffalo: social inequalities and decision making. Chapman and Hall, London.

Prothero, D. R. 1998. Rhinocerotidae. Pp. 595–605 *in* C. M. Janis, K. M. Scott, and L. L. Jacobs, eds. Evolution of Tertiary mammals of North America. Cambridge University Press, Cambridge.

Prothero, D. R., and E. Manning. 1987. Miocene rhinoceroses from the Texas Gulf Coastal Plain. Journal of Paleontology 61: 388–423.

Prothero, D. R., and P. C. Sereno. 1982. Allometry and paleo-ecology of medial Miocene dwarf rhinoceroses from the Texas Gulf Coastal Plain. Paleobiology 8:16–30.

Prothero, D. R., E. Manning, and C. B. Hanson. 1986. The phylogeny of the Rhinocerotoidea (Mammalia, Perissodactyla). Zoological Journal of the Linnean Society 87:341–366.

Rachlow, J. L., and J. Berger. 1997. Conservation implications of patterns of horn regeneration in dehorned white rhinos. Conservation Biology 11:84–91.

Rachlow, J. L., E. V. Berkeley, and J. Berger. 1998. Correlates of male mating strategies in white rhinos (Ceratotherium simum). Journal of Mammalogy 79:1317–1324.

Radinsky, L. 1963. Origin and early evolution of North American Tapiroidea. Peabody Museum of Natural History Bulletin 17:1–106.

———. 1967. Hyrachyus, Chasmotherium, and the early evolution of helaletid tapiroids. American Museum Novitates 2313:1–23.

Scott, K. M. 1990. Postcranial dimensions of ungulates as predictors of body mass. Pp. 301–335 in Damuth and MacFadden 1990.

Scott, W. B. 1941. Perissodactyla. The mammalian fauna of the White River Oligocene. Transactions of the American Philosophical Society 28:747–980.

Sinclair, A. R. E. 1977. The African Buffalo: a study of resource limitation of populations. University of Chicago Press, Chicago.

Tanner, L. G. 1975. Stratigraphic occurrences of Teleoceras, with a new Kimballian species from Nebraska. Bulletin of the University of Nebraska State Museum 10:23–33.

von den Driesch, A. 1976. A guide to the measurements of animal bones from archaeological sites. Peabody Museum Bulletin 1:1–136.

Voorhies, M. R. 1985. A Miocene rhinoceros herd buried in volcanic ash. Research Reports, National Geographic Society 19:671–688.

———. 1990. Vertebrate paleontology of the proposed Norden Reservoir Area, Brown, Cherry, and Keya Paha Counties, Nebraska. Division of Archeological Research, Department of Anthropology, University of Nebraska, Lincoln, Technical Report 82-09:A1–A275.

Voorhies, M. R., and S. G. Stover. 1978. An articulated fossil skeleton of a pregnant rhinoceros, Teleoceras major Hatcher. Proceedings, Nebraska Academy of Sciences 88:47–48.

Voorhies, M. R., and J. R. Thomasson. 1979. Fossil grass anthoecia within Miocene rhinoceros skeletons: diet of an extinct species. Science 206:331–333.

Webb, S. D. 1969. The Burge and Minnechaduza Clarendonian mammalian faunas of north-central Nebraska. University of California Publications in Geological Sciences 78:1–191.

———. 1983. The rise and fall of the Late Miocene ungulate fauna in North America. Pp. 267–306 in M. H. Nitecki, ed. Coevolution. University of Chicago Press, Chicago.

Wood, H. E. 1938. Causal factors in shortening tooth series with age. Journal of Dental Research 17:1–13.

Wright, D. B. 1993. Evolution of sexually dimorphic characters in peccaries (Mammalia, Tayassuidae). Paleobiology 19:52–70.