

## LINKING SEXUAL DIMORPHISM AND SOCIALITY IN RHINOCEROSES: INSIGHTS FROM *TELEOCERAS PROTERUM* AND *APHELOPS MALACORHINUS* FROM THE LATE MIOCENE OF FLORIDA

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A strong relationship between sexual dimorphism and the degree of polygyny (i.e., the degree to which males compete for mates) is not apparent in living perissodactyls. For instance, in both monomorphic and dimorphic species of rhinos, about half of male mortality is attributable to tusk and horn mediated combat. Males of the North American Miocene rhinoceros *Teleoceras* had delayed tusk (i2) eruption, prolonged tusk root growth, and highly sharpened tusk facets maintained by honing on the upper incisor, thus predicting high levels of intermale aggression similar to living rhinos. The sex biases and elevated male mortality rates found in *Teleoceras* assemblages from Nebraska and Florida seem to confirm this prediction. However, the degree of body size dimorphism in these assemblages varies. Therefore, the intensity of intermale competition seems unrelated to the magnitude of body size dimorphism in *Teleoceras*.

Male individuals of *Aphelops*, a sympatric rhino, experienced more finite tusk growth and tusks were blunted with age due to the ancestral loss of the upper honing incisor, thus predicting lower levels of intermale competition. The *Aphelops* fossil assemblage from the Love Bone Bed of Florida is not sex-biased, shows more balanced sex-specific mortality rates, and seems to confirm the prediction of reduced intermale competition, thus suggesting a type of sociality that is different from both *Teleoceras* and modern rhinos. However, the same assemblage exhibits a degree of sexual dimorphism in tusk and body size that are not demonstrably different from *Teleoceras*. Thus, we are left with a perplexing relationship between dimorphism and sociality for rhinos, where levels of intermale competition seem uncorrelated to the degree of sexual dimorphism in both living and extinct species.

**Key Words:** *Teleoceras*; *Aphelops*; Miocene; rhinoceros; sexual dimorphism; sociality

### INTRODUCTION

#### SEXUAL DIMORPHISM AND SOCIALITY IN PERISSODACTYLS

Sexual dimorphism in mammals is best understood as a result of sexual selection in polygynous species where males invest large amounts of energy into competing with other males to monopolize access to females (Alexander et al. 1979; Jarman 1983, 2000; Clutton-Brock et al. 1988; Andersson 1994; Berger & Cunningham 1994a). Mature males commonly possess enlarged body size or enlarged weapon-like structures (e.g., horns, tusks, or antlers) that are used to compete for mates either directly through combat, or more indirectly through complex behaviors (e.g., ritualized displays). The identification and quantification of sexual dimorphism in fossils is potentially informative of the

degree of polygyny in extinct species (Plavcan 2000). The relationship of sexual dimorphism with sociality is most clear among ruminant artiodactyls where increasingly larger species tend to be extremely dimorphic and form large, herd-like social groups that enable males to monopolize large numbers of mates (Jarman 1983; Geist & Bayer 1988; Loison et al. 1999). Extant perissodactyls are unusual in the sense that, although all living species appear to be polygynous, sexual dimorphism is not prominent and there is no clear-cut relationship between sexual dimorphism and sociality. Tapirs and horses are both monomorphic in body size, yet tapirs tend to be solitary while most horse species form year-round harems (Berger 1986; Rubenstein 1986; Nowak 1999). Rhinos are the only living perissodactyls that possess conspicuous weapon-like structures in the forms of horns and tusks; therefore we might expect to find among rhinos a stronger relationship between dimorphism and sociality. The degree of sexual dimorphism in living rhinos varies from species to species and there are both mono-

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morphic (*Diceros bicornis*) and moderately dimorphic forms (*Ceratotherium simum*, *Rhinoceros unicornis*) (Groves 1982; Owen-Smith 1988; Dinerstein 1991, 1993; Berger 1994; Rachlow & Berger 1995). Despite some variability in the degree of dimorphism, all living rhinos are typically solitary. They rarely form small, temporary aggregations, and these appear to result from the chance clustering of critical food or water resources. Social bonding is minimal among adults, even among the most dimorphic species (Laurie 1982; Owen-Smith 1988; Dinerstein 2003). Despite the absence of coherent groups, intermale competition among rhinos is intense and they are among the most violent and aggressive of mammals. In the most well-studied populations of Africa and Asia, aggressive confrontations among males account for up to half of male mortality in both monomorphic (*D. bicornis*) and dimorphic species (*C. simum* and *R. unicornis*) (Hitchins & Anderson 1983; Owen-Smith 1988; Dinerstein & Price 1991; Berger 1994; Berger & Cunningham 1994b; Dinerstein 2003). Males are also aggressive towards females. For instance, *R. unicornis* males ram females to subdue them (Dinerstein 1991).

Sexual dimorphism is commonly reported for extinct perissodactyls, suggesting that sexual dimorphism was more prominent in the past. Dimorphism has been identified in an early "equoid" (Gingerich 1981), various ceratomorphs, including *Homogalax*, *Isectolophus* (Radinsky 1963), *Hyrachyus* (Radinsky 1967), *Indricotherium transouralicum* (Fortelius & Kappelman 1993), and the chalicothere *Moropus* (Coombs 1975). Horned species of the extinct family Brontotheriidae show high levels of intraspecific variation in horn size and zygomatic thickness, suggesting a degree of sexual dimorphism similar to modern ruminants (Osborn 1929; Muhlbachler et al. 2004a). Dimorphism has been recognized among many extinct members of the Rhinocerotidae. Osborn (1898a) reported dimorphism in the mandibular incisor and nasal horn bosses of Oligocene rhinos *Subhyracodon occidentalis* and *Diceratherium tridactylum*. The early Miocene *Menoceras arikareense* shows a degree of dimorphism in its horn bosses that is comparable to the level of dimorphism found in modern ruminants (Peterson 1920; Muhlbachler unpublished data). Osborn (1898b) recognized sexual dimorphism in the tusks of *Teleoceras fossiger* from the late Miocene Long Island Rhino Quarry, Kansas. Mead (2000) further quantified sexual dimorphism in tusk size and body size in *Teleoceras* from

the Ashfall site, Nebraska. Voorhies and Stover (1978) found fetal bones within the abdominal regions of skeletons of small-tusked individuals from the Ashfall site, confirming that the small-tusked individuals were females. Matthew (1932) and Lambert (1994) found that lower tusks of *Aphelops mutilus* from Coffee Ranch, Texas and Moss Acres, Florida could be easily divided into male and female groups based on size. Borsuk-Bialynicka (1973) discovered that several cranial dimensions of *Coelodonta antiquitatis*, the Pleistocene woolly rhino of Europe, were bimodal. Finally, Deng (2001, 2005) attributed intraspecific variation in the cranial osteologies of *Chilotherium wimani* and *Iranotherium morgani* to sexual dimorphism.

Frequent sexual dimorphism among fossil perissodactyls and less pronounced dimorphism among modern species resembles Wright's (1993) findings on peccaries; sexual dimorphism is not prominent among the few living species although pronounced dimorphism is found in extinct species. Perissodactyls were more diverse in the past, and extinction over the last several million years has resulted in drastic reductions in taxonomic diversity. Additionally, population sizes of most extant species have been greatly diminished in recent times. Population bottlenecks, geographic range restriction, artificial population management, and phenotypic alteration (e.g., dehorning of rhinos) can have dramatic effects on ecological relationships and social behaviors of large mammals (Berger 1994; Berger & Cunningham 1994a, 1994b). Consequently, recent perissodactyls might not serve as good models for the first ~99.9% of perissodactyl evolutionary history. For instance, sociality and sexual dimorphism might have been more strongly correlated in the past, during a time when anthropogenic effects were absent or minimal.

Among the three surviving families of perissodactyls (Tapiridae, Equidae, Rhinocerotidae), sexual dimorphism appears to have been most pronounced in rhinos. The family Rhinocerotidae is cladistically defined by a honing relationship between a chisel-like upper incisor (I1) and a dimorphic tusk-like mandibular incisor (i2) (Prothero 2005). The living Asian rhinos (*Rhinoceros unicornis*, *Rhinoceros sondaicus*, and *Dicerorhinus sumatrensis*) possess both tusks and horns. Surprisingly, the enlarged tusks, rather than the horns, are used to establish dominance hierarchies among Asian rhinos. In *R. unicornis*, incisor size is strongly related to male dominance and tusk mediated combat commonly results in mortal wounding (Laurie 1982; Dinerstein & Price

2001; Dinerstein 2003). African rhinos (*Diceros bicornis* and *Ceratotherium simum*) have secondarily lost their incisors and intermale aggression is mediated by the horn, which results in similarly high levels of mortal wounding (Owen-Smith 1988; Berger 1994). Age- and sex-specific mortality patterns in modern rhinoceros populations are strongly imprinted by tusk and horn mediated social behaviors. In populations of the three well-studied species of living rhinos, *C. simum*, *D. bicornis*, and *R. unicornis*, 50% or more of male deaths are directly related to tusk and horn mediated aggression (Hitchins & Anderson 1983; Owen-Smith 1988; Dinerstein & Price 1991; Berger 1994; Berger & Cunningham 1994b; Dinerstein 2003). Socially mediated mortality is more frequent in rhinos than other large mammals and is most heavily concentrated among young adult males during the life-history interval between the years of sexual maturity and the age of first reproduction.

#### OBJECTIVES

Rhinos are good cases for linking sexual dimorphism with paleosociality. Studies of rhino populations consistently indicate high rates of death among males due to horn and tusk mediated combat. Likewise, recent and fossil skeletal assemblages of rhinos contain clear evidence of elevated mortality rates for young adult males, whereas most other large mammal populations do not (Mihlbachler 2003). Because tusk and horn mediated behavior strongly influences the mortality patterns of modern rhinos in a predictable way, and similar patterns are discernable in fossil rhino assemblages, it is possible to approximate the levels of intermale competition by examining mortality patterns among fossil rhinos. Therefore, it is possible to compare sexual dimorphism in fossil rhinos with aspects of sociality relating to intermale competition. In this paper, sexual dimorphism is quantified in the tusks (i2) and limb bones of late Miocene assemblages of *Teleoceras proterum* and *Aphelops malacorhinus* from the Love Bone Bed (LBB), Florida, and *Teleoceras proterum* from Mixson's Bone Bed (MBB), Florida. Secondly, the ontogeny and sex-specific use wear patterns of the tusks are described. Thirdly, postcranial body size dimorphism in the Florida rhino assemblages is compared to body size dimorphism in an assemblage of *Teleoceras major* from Ashfall, Nebraska, previously described by Mead (2000). The ensuing discussion on the sexual dimorphism, mortality, and sociality of these rhinos draws from the results of

this paper as well as results reported in Mihlbachler (2003) on the age- and sex-specific demographics of these fossil assemblages.

#### MATERIALS AND METHODS

Mixson's Bone Bed (MBB) and Love Bone Bed (LBB) contain large assemblages of Miocene rhinos. Early MBB collections are at the Smithsonian Institution, Washington, D.C. (UNSM), while the bulk of the collection is housed at the American Museum of Natural History, New York (FAM). The LBB collection is housed in the Florida Museum of Natural History, Gainesville (UF). The taphonomic backgrounds of LBB and MBB are summarized elsewhere (Webb et al. 1981; Hulbert 1982; Mihlbachler 2003). LBB was dated biostratigraphically to the latest Clarendonian land mammal "age", or about 8.5 to 10 million years old (Webb et al. 1981). The MBB is biostratigraphically placed in the early Hemphillian land mammal "age", about seven million years old (MacFadden & Webb 1982). *Aphelops malacorhinus* and *Teleoceras proterum* are found at both localities, although the Mixson's *Aphelops* sample is too small for statistical analysis of sexual dimorphism. The taxonomy used in this paper follows Prothero (2005). Skulls from these localities are mostly fragmented and severely crushed (Fig. 1), limiting interpretation of sexual dimorphism to teeth and postcranial elements. I did not measure cheekteeth because these elements are usually not dimorphic, even among dimorphic species. Based on the relative frequencies of tusks, both the LBB and MBB *Teleoceras* assemblages contain superabundant numbers of adolescent or young adult males. The LBB assemblage is 77% male and the MBB assemblage is 72% male. The LBB *Aphelops* assemblage is not significantly age- or sex-biased (Mihlbachler, 2003). Although the dimensions of *Teleoceras* and *Aphelops* tusks overlap, they can be readily differentiated. *Teleoceras* tusks are more curved with a teardrop-shaped cross-section. The female tusk crown is short and somewhat triangular and in both sexes the enamel crown is notably wider than the root. Male tusks have longer crowns, but they are often worn extensively with well-developed honing facets. *Aphelops* tusks are less curved and have a more rounded cross-section. The diameter of the crown is not much greater than the root diameter. *Aphelops* male tusks lack the well-developed honing facet seen in *Teleoceras* males. *Aphelops* female tusks have a narrower and more elongate crown than those of *Teleoceras* females. Virtually every postcranial element of

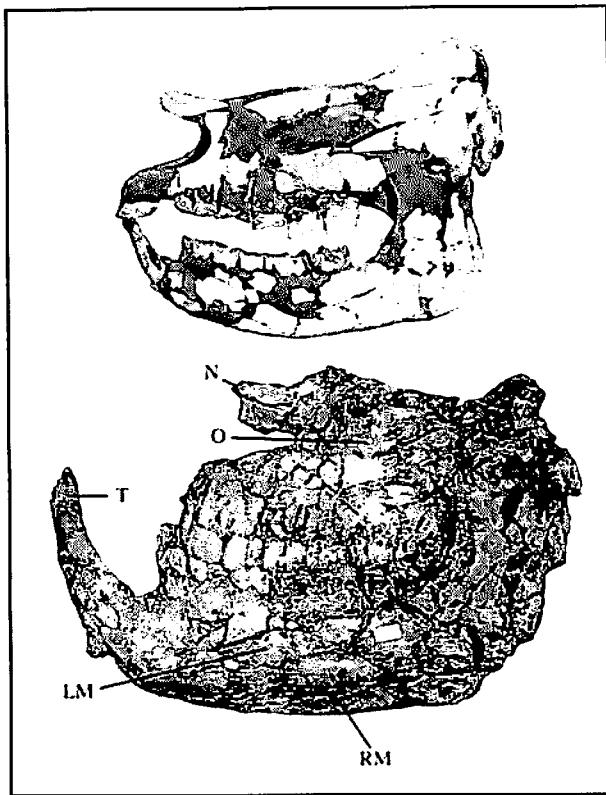


Figure 1. Male skulls and mandibles of late Miocene rhinos from Florida: (top) *Teleoceras proterum* (Love Bone Bed, UF 40253) and (bottom) *Aphelops mutilus* (Moss Acres, UF 69944). These skulls demonstrate the shape difference in the heads of these genera corresponding to the presence of a honing relationship among the incisors of *Teleoceras* and the lack of such a honing relationship in *Aphelops*. Although the *Aphelops* skull is laterally flattened, it is complete and the shape of the lateral profile is preserved. The following structures are labeled to aid orientation: (N) nasal, (O) orbit, (T) mandibular tusk, (LM) left mandible, and (RM) bottom of the right mandible.

*Teleoceras* and *Aphelops* can be differentiated. *Teleoceras* is smaller and has extremely shortened limb elements. *Aphelops* is larger and proportioned more like living rhinos (e.g., *Diceros bicornis*).

To quantify size dimorphism, a series of measurements were taken on the tusk (i2) and on major weight-bearing limb elements including humerus, radius, third metacarpal (MC3), femur, tibia, and third metatarsal (MT3). All tusks with a fully formed crown and at least partial root formation were measured. Only adult bones with fully fused epiphyses were measured. Linear mea-

surements up to 15 cm were taken with digital calipers, while longer measurements and diameter measurements were taken with a cloth tape measure accurate to the mm. For cross sectional area measurements, the cross sections of limb bones were replicated with polyvinyl siloxane and scanned on a flatbed scanner. Area was calculated with ImageJ v1.33. Humeri and femora were not measured for the LBB assemblages because those elements were mostly crushed or incomplete.

Mead's (2000) study of *Teleoceras major* from Ashfall, Nebraska is the most rigorous analysis of sexual dimorphism for fossil rhinos to date; however my initial data on the Florida assemblages, described in Muhlbachler (2001a), was taken before Mead's (2000) analysis was published. The measurements of the LBB assemblages are similar to those of Mead (2000), but not all of them are homologous. The landmarks are slightly different in some cases, and limb bone circumferences were measured rather than cross-sectional areas. However, I have since been able to make a more extensive set of measurements on the MBB *Teleoceras* assemblage, including measurements that are homologous to those of Mead (2000), so that dimorphism in the MBB and Ashfall assemblages can be more directly compared.

Because of the articulated nature of the Ashfall material, Mead (2000) was able to determine the sex of the skeletons apriori due to their association with the extremely dimorphic mandibular tusk. This enabled him to simply compare the mean values of male and female data with Student's *t*-tests. Because of the disarticulated nature of the Florida assemblages, sex could not be determined in any element other than the dimorphic tusks. Therefore, it was necessary to adopt different methods. Rather than comparing means of males and females, it was necessary to test for patterns of bimodality in the sex-combined assemblage of bones against the null expectation of a unimodal normal distribution. To facilitate a more direct comparison of the Ashfall assemblage with the Florida assemblages, the raw data on the *Teleoceras* Ashfall assemblage (Mead 1999a) were used to calculate sex-combined statistics like those calculated for the Florida assemblages.

A highly dimorphic species will be distinguished from a monomorphic one by a bimodal distribution. A Shapiro-Wilk test of normality (*W*) was used to test for deviation from a unimodal normal distribution. Significant results indicate deviation from normality. The recommended alpha level for this test is  $p < 0.1$  (Sall &

Lehman 1996). Because a large number of variables were tested simultaneously, statistical error is a concern. The chance of statistical error increases with the number of tests, turning the analysis into a 'fishing expedition.' A significant result is bound to eventually come about due to the sheer number of tests. There is no simple solution to the inevitability of statistical error. A Bonferroni correction (Rohlf & Sokal 1994) is one means of diminishing the chance of type one errors (falsely rejecting the null hypothesis, monomorphism). A Bonferroni correction can be calculated by dividing the alpha level of the test by the number of tests. This correction raises the standard for what is accepted as significant, thus eliminating the 'fishing expedition' aspect of the analysis. However, the Bonferroni correction has the adverse effect of greatly magnifying the chance of type 2 error (falsely accepting the null hypothesis, monomorphism), particularly for the relatively small sizes analyzed in this paper. Indeed, the Bonferroni corrections on the Ashfall *Teleoceras* data (see below) seemed to result in what appear to be numerous type 2 errors. Therefore, the Bonferroni corrected results are reported for their heuristic value in evaluating the strength of the Shapiro-Wilk tests, but the uncorrected results were found to be more precise in terms of identifying sexual dimorphism, despite the likelihood of some type 1 errors.

A second means of evaluating dimorphism is the coefficient of bimodality ( $b$ ):

$$b = \frac{m_3^2 + 1}{m_4 + 3}$$

where  $m_3$  is skewness and  $m_4$  is kurtosis. A value of  $b$  greater than 0.555 usually indicates a bimodal or polymodal distribution (SAS Institute Inc. 1985; Bryant 1991).

## RESULTS

### TELEOCERAS TUSK LIFE-HISTORY

The life history patterns of the tusks are reported in terms of three basic ontogenetic processes, (1) formation of the crown and initial eruption, (2) growth of the root, and (3) use-wear. Among *Teleoceras* tusks, clear sex-specific differences are evident in all three of these processes. The age of tusk eruption was apparently delayed in males. A male mandible from LBB (UF 24221) with cheekteeth wear equivalent to a five- or six-year-old rhino (Hitchins 1978) contains an unerupted enamel tusk crown. Two female mandibles from MBB (FAM 141392 and FAM 141393) with a similar degree of cheekteeth wear have fully erupted tusks.

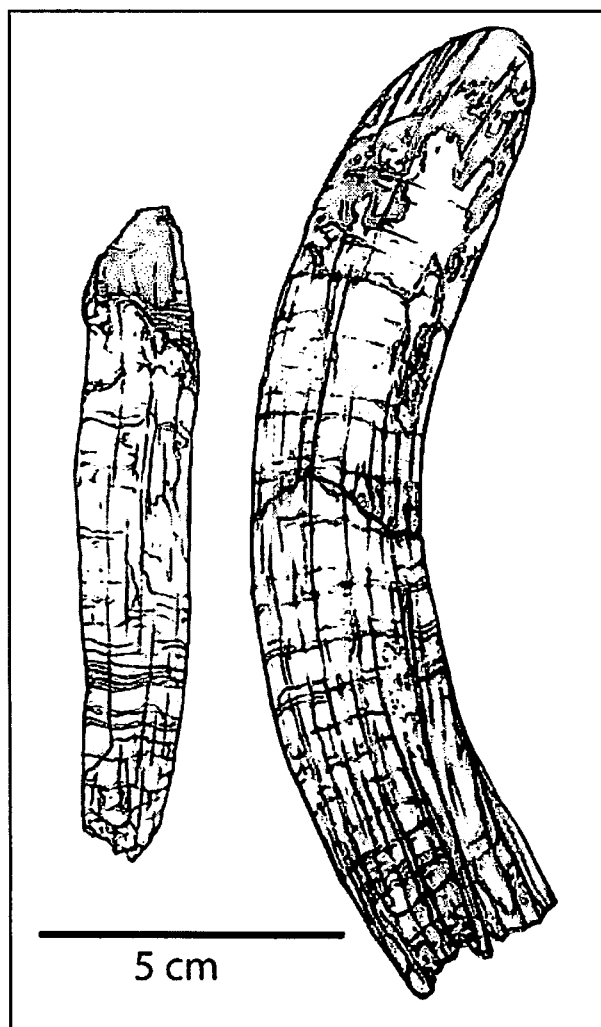


Figure 2. A pair of male and female *Teleoceras proterum* i2s (male: UF 41256; female: UF 41339) from the Love Bone Bed, Florida.

The root of male tusks continued to lengthen and erupt until very old age, while female tusks were fully formed in just a few years. Growth increments similar to the annual and subannual growth increments observed in the dentin of mammoth tusks (Fisher 1996) are clearly visible on the root surfaces of many of the male *Teleoceras* tusks (Fig. 2). The most conspicuous increments are traceable to light and dark bands that are visible in polished longitudinal sections and most likely represent annual increments like those found in the incisors of other mammals (Fig. 4; Klevazal & Kleinberg 1969). A detailed study of these growth increments is beyond

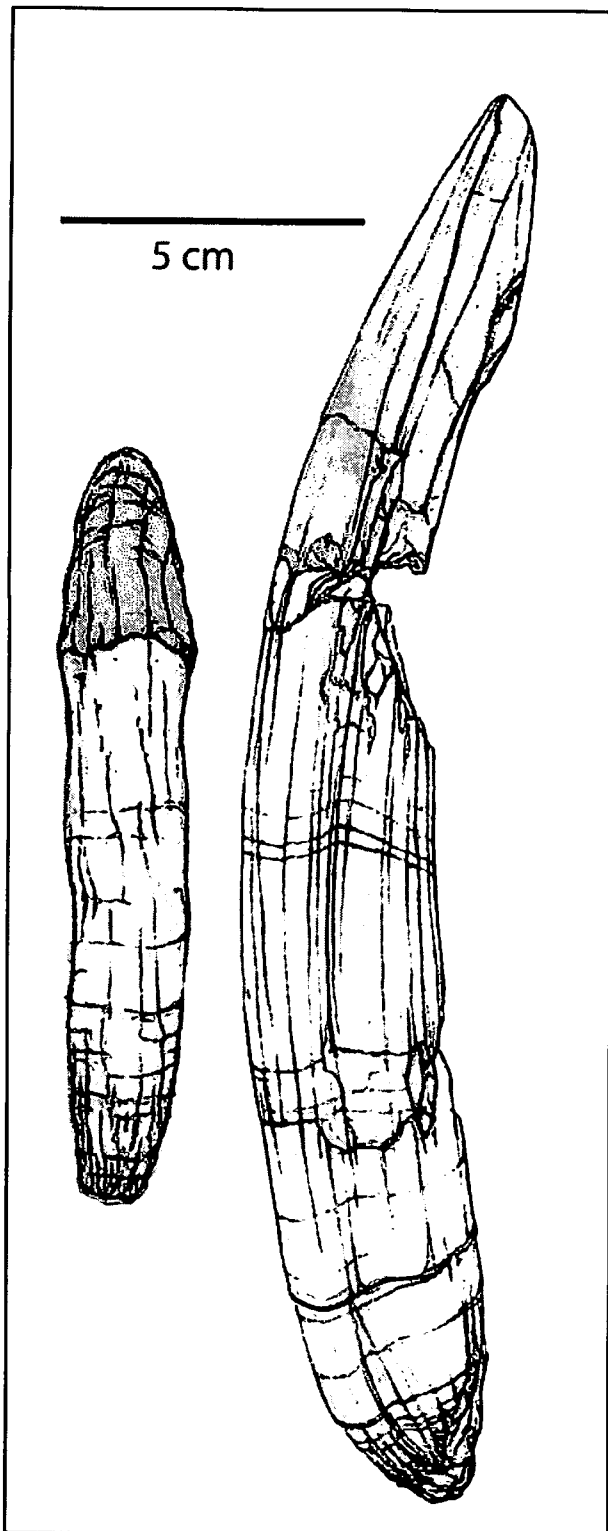


Figure 3. A pair of male and female *Aphelops malacorhinus* tusks (male: UF 41311; female: UF 41326) from the Love Bone Bed, Florida.

the aim this paper. However, the increments on the root surface make it possible to preliminarily quantify the rate of tusk eruption by measuring the distance of the increments that I have interpreted as most likely annual from the base of the enamel crown. Figure 5A shows the rate of eruption of male (UF 41256) and female (UF 41339) *Teleoceras* tusks. The tusks of both sexes appear to have increased in length at an initially rapid rate. Lengthwise growth in the female tusk slowed after three years, followed by two more years of minor lengthwise growth, after which the pulp cavity was closed off at the proximal end, terminating lengthwise growth. In the male tusk, lengthwise growth was initially fast and gradually slowed to a nearly continuous rate after a few years and continued for 16 more years until the death of the animal. In this particular specimen, the pulp cavity flares open at the proximal end of the tusk, indicating that eruption was still occurring at the time of death.

I have observed hundreds of *Teleoceras* tusks, but have found only a few male tusks from very old-aged individuals in which the proximal opening of the pulp cavity was completely closed off, indicating that lengthwise growth does eventually cease, but not until very old age. One tusk in the LBB sample, belonging to the individual with the most advanced cheekteeth wear in the sample (UF 24258), has a solid root and has 22 prominent rings visible on the root surface. From MBB, the oldest male tusk (USNM 3277a) has 19 or 20 growth increments visible on the outer surface of the tusk. The

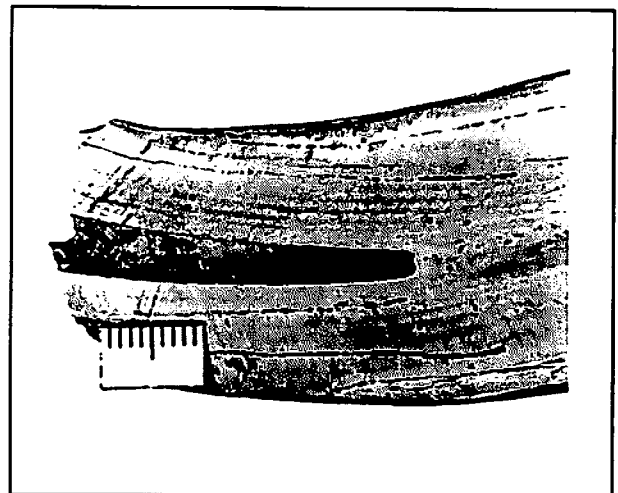


Figure 4. Polished longitudinal section of a broken male *Teleoceras proterum* tusk (UF 41319) showing annual growth bands. Increments on the scale are millimeters.

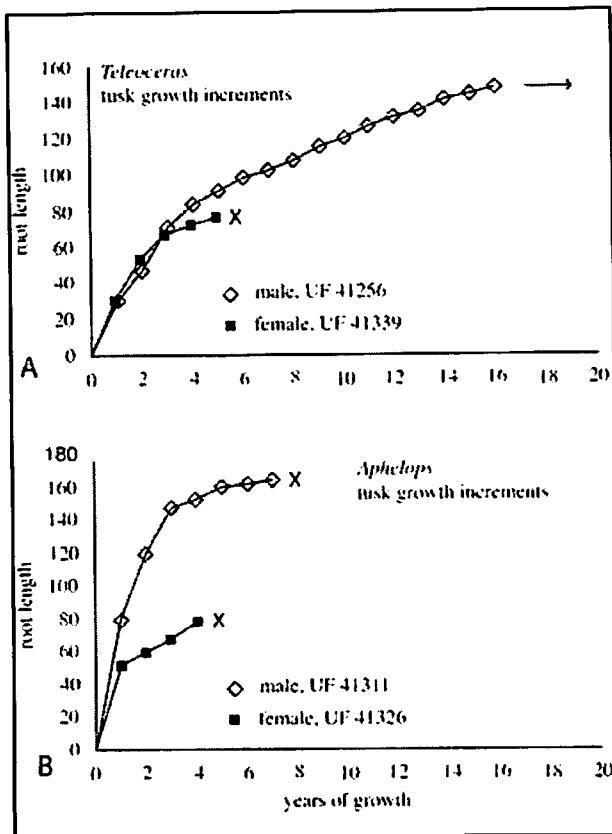


Figure 5. Years of lengthwise tusk growth in (A) *Teleoceras proterum* and (B) *Aphelops malacorhinus* based on measurements of the distance of presumably annual growth lines on the outer surface of the root from the base of the enamel crown. The resulting curves document the sex-specific lengthwise growth history of tusks. An arrow signifies the presence of a pulp cavity and continued lengthwise root growth while an X signifies a solid root and discontinued growth.

proximal tip is broken off but the root is completely solid indicating lengthwise growth had ceased sometime after 19 or 20 years. Because tusk growth ceased prior to death, it is impossible to determine the maximum age of these individuals, however they lived a minimum of 20-22 years. If the subadult years prior to the formation of the tusk root are added, these individuals must have lived more than 25 years. In the wild, modern rhinos live a maximum of 30 to 40 years (Owen-Smith 1988) and it seems that the potential lifespan in *Teleoceras* was similar or possibly somewhat shorter.

For males, the extensive incisor honing results in a progressive volumetric loss of material at the distal end

of the tusk. The crown is initially about 10 cm tall, but in old individuals the tusk is worn beyond the crown. Both UF 41256 (Fig. 2) and UF 41256 (Fig. 6A), are nearly worn to this stage. Male tusks maintain a sharp edge at the distolingual margin (Fig. 6A). The wear facet typically exhibits coarse parallel striations that match striations on the I1 (Fig. 7A). Continuous growth and eruption of the root coupled with the continuous honing of the crown seems to have allowed males to maintain sharpened tusks but without a progressive loss of total

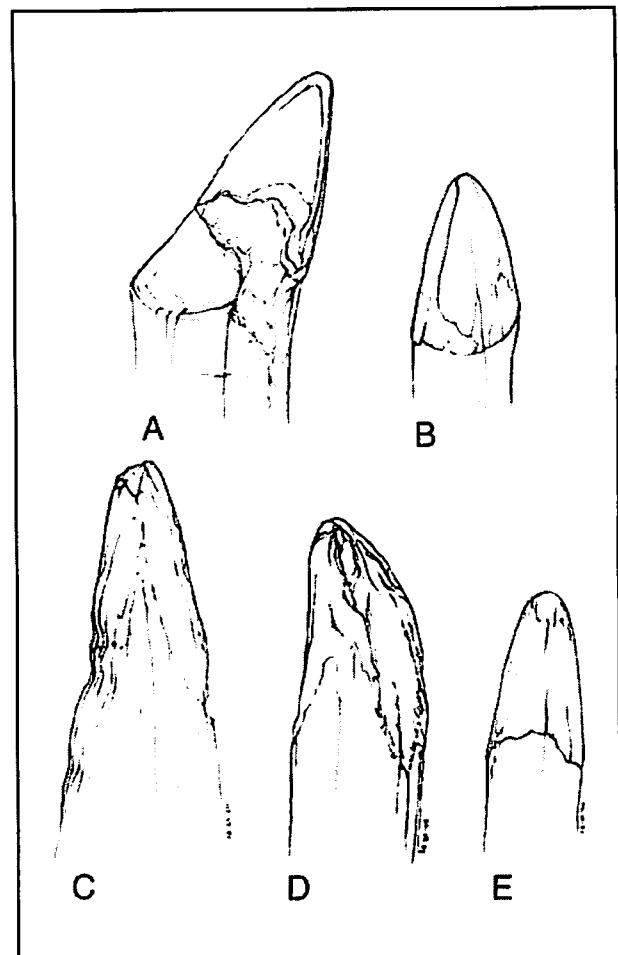


Figure 6. Distal ends of tusks exhibiting different types of wear: (A) right *Teleoceras proterum* male, UF 41256, with honing facet; (B) left *Teleoceras proterum* female, UF 41337, with light polished wear; (C) right *Aphelops malacorhinus* young male UF 14229, with light wear and shallow lingual grooves; (D) left *Aphelops malacorhinus* old male (UF 41328) with obliterated tusk crown; (E) right *Aphelops* female, UF 41357, with light polished wear.

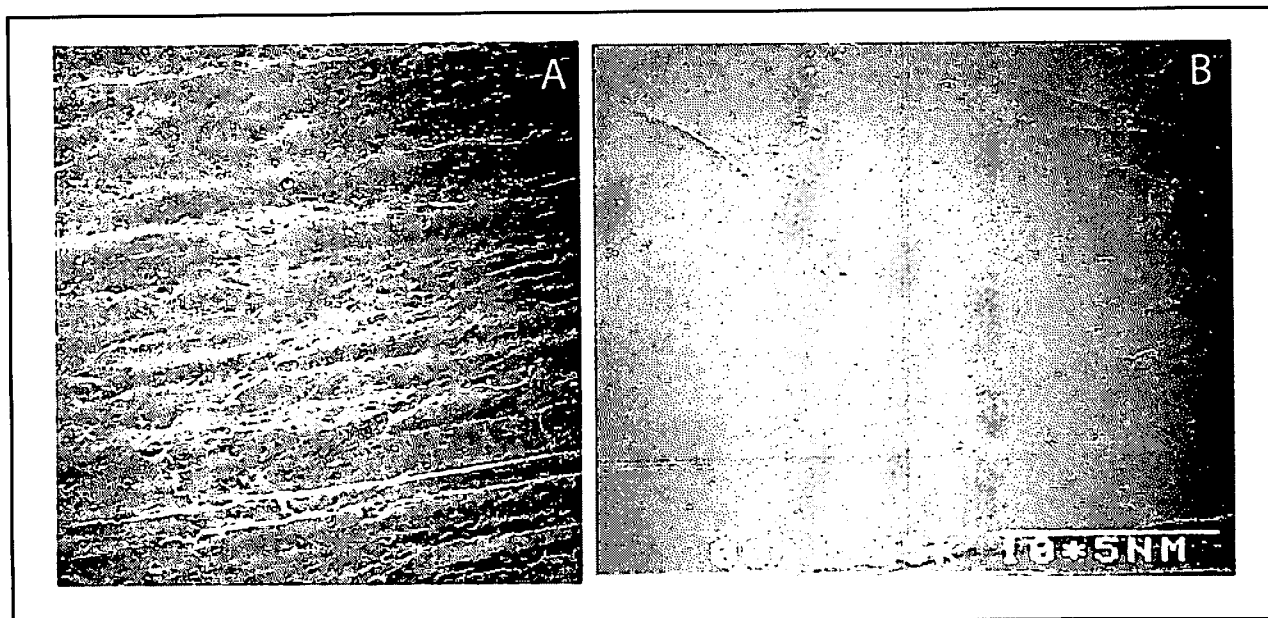


Figure 7. Scanning electron microscope close-ups of the wear surfaces of male rhinoceros mandibular tusks. *Teleoceras* wear facets (A) frequently show coarse parallel striations that correspond to similar striations in the upper incisor. *Aphelops* wear facets (B) are smoother and show fewer numbers of wear striations of variable widths and orientations. Both photos were taken at the same magnification.

tusk length. In older adults, the tusks are often worn beyond the original enamel crown, although because of the additional years of root growth, the tusk is similar in length to the tusk of a younger adult. Many female tusks show some evidence of honing, but it is not extensive and does not result in the loss of significant amounts of dental material.

#### APHELOPS TUSK LIFE-HISTORY

I was not able to determine the relative timing of male and female tusk eruption in *Aphelops* because I have never encountered a female mandible of the right age. However, many of the ontogenetic and functional morphology aspects of *Aphelops* tusks differ from *Teleoceras* in ways that are wedded to the loss of the upper honing incisor. The tusks are straighter (Fig. 3) and they tend to extend more horizontally from the mandible, rather than curve upward to meet the upper incisors, as in *Teleoceras* (Fig. 2). The crown does not experience gradual lengthwise reduction due to honing wear. The crowns of male *Aphelops* tusks initially form a sharp distal point and sharp lingual blade. As life progresses, these initially sharpened edges become blunted and rounded (Fig. 6C-6D). Male tusks lack regular wear facets. Gross wear patterns range from light

polishing to severe rounding and splintering, to breakage of the distal end. In female tusks, wear is mainly restricted to a slight lingual or distal polishing (Fig. 6E). Microwear features are sporadically distributed across wear surfaces and consist primarily of scratches of various widths, lengths, and orientations (Fig. 7B).

While many growth increments (> 100) appear on the outer surface of most male *Aphelops* tusks, a clear annual growth pattern is not discernable in most specimens. A small set of more prominent lines appear at intervals of some specimens that I preliminarily interpret as annual growth increments. This interpretation suggests that male and female *Aphelops* tusks formed over a finite period of time (Fig. 5B). A female tusk (UF 41326) grew rapidly for one year. Lengthwise growth ceased after four years. The first three years of growth in a male tusk (UF 41311) were rapid, followed by about five years of minor increase in tusk length, after which the pulp cavity was sealed off at the proximal end, terminating lengthwise root growth. Tusk growth in *Aphelops* appears to have been initially rapid and without the prolonged period of root growth seen among *Teleoceras* males. This seemingly rapid and finite interval of root growth in *Aphelops* is functionally consistent with the lack of honing wear; continuous root growth



is not needed to replenish dental material lost to extensive honing.

TUSK DIMORPHISM

Statistical results on tusk dimorphism are summarized in Tables 1-3. Most of the male tusks are broken at one or both ends or they are extensively worn, thus limiting the number of available length measurements (CL and RL). Diameter measurements of the crown (WBC) and root (RD) are more commonly available and show no overlap between males and females. Length (CL) and width (WBC) data for complete crowns clearly contain size clusters (Figs. 8A, 9A, 10A). The ratios (M/F) calculated from the average proportions of male and female *Teleoceras* tusks range from 1.6-2.7. In all groups, the length of the enamel crown (CL) was the most dimorphic character (M/F = 2.7 at LBB and 2.5 at MBB). The ratios of enamel crown width (WBC), and root diameter (RD) ranged from 1.6-1.8. This level of dimorphism is similar to the "tusk diameter" ratio of 1.53 reported for the Ashfall *Teleoceras* assemblage (Mead 2000). *Aphelops* tusk dimorphism is generally the same with M/F ratios ranging from 1.6-2.4. Large samples of modern rhinos are not available to calculate a ratio of mean male and female values, but I calculated similar ratios for WBC (M/F = 1.7) and RD (M/F = 1.6) from a male (AMNH 81892) and a female (AMNH 54763) of *Dicerorhinus sumatrensis*. A male (AMNH 35759) and female (AMNH 54456) of *Rhi-*

*noceros unicornis* yielded lower ratios of WBC (M/F = 1.4) and RD (1.1).

Based on the Shapiro-Wilk test for normality (*W*), none of the sex-specific tusk data deviated significantly from normality in the MBB *Teleoceras* assemblage (Table 1). When the sexes were combined, the diameter measurements, WBC and RD, were highly bimodal ( $p < 0.1$ ). The length variables, CL and RL, did not deviate significantly from normality. The tusk length measurements are more difficult to evaluate because of smaller sample sizes (most of the tusks are broken and are not measurable for length). Moreover, most of the male tusks are from young individuals with poorly formed tusk roots. However, it is clear that older males achieve much longer tusk roots than females. Likewise, most of the older males have tusks that are worn almost to the base of the crown, or in some cases, past the crown. These factors introduce overlap in the ranges of male and female tusk length variables in the MBB sample. Nonetheless, unworn male tusk crowns are far longer than unworn female tusk crowns. The coefficients of bimodality (*b*) confirm that most of the data are more strongly bimodal when the sexes are combined. The sex-combined data for WBC, CL, and RD are strongly bimodal ( $b > 0.55$ ). Only RL yielded a coefficient suggesting unimodality ( $b = 0.31$ ), but, as noted above, this result is related to the number of young males with poorly developed roots.

Table 1. Statistics for the mandibular tusks (i2) of *Teleoceras proterum* from Mixson's Bone Bed, Florida.

Variable	Sex	Mean	SD	Min	Max	N	CV	Skew	Kurt	<i>b</i>	Pr.< <i>W</i>	M/F
WBC	M	51.4	4.20	44	59	17	8.2	0.12	-1.11	0.54	0.57	-
WBC	F	30.2	3.49	24	35	14	11.6	-0.27	-0.65	0.46	0.80	-
WBC	F+M	41.8	11.39	24	59	31	27.2	-0.11	-1.62	0.73	0.00	1.7
CL	M	96.9	23.06	56	132	17	23.8	-0.52	-0.78	0.57	0.33	-
CL	F	38.5	12.23	20	60	8	31.8	0.46	0.23	0.37	0.93	-
CL	F+M	78.2	34.22	20	132	25	43.7	-0.14	-1.40	0.64	0.11	2.5
RD	M	43.9	3.91	39	52	16	8.9	0.82	-0.25	0.61	0.14	-
RD	F	27.5	2.76	23	33	15	10.0	0.29	-0.57	0.45	0.79	-
RD	F+M	36	9.01	23	52	31	25.1	0.12	-1.45	0.65	0.01	1.6
RL	M	142.7	27.47	111	193	6	19.3	1.33	2.87	0.47	0.22	-
RL	F	76.5	28.75	27	106	7	37.6	-0.85	-0.27	0.63	0.29	-
RL	F+M	107.1	43.69	27	193	13	40.8	0.03	0.28	0.31	0.93	1.9

Abbreviations: SD = standard deviation; Min = minimum; Max = maximum; N = number of observations; CV = coefficient of variation, Skew = skewness; Kurt = kurtosis, *b* = coefficient of bimodality; Pr.<*W* = *P* value for Shapiro-Wilk test of normality; M/F = male/female ratio, WBC = width at base of crown, CL = crown length, RD = root diameter, RL = root length.

Table 2. Statistics for the mandibular tusks (i2) of *Teleoceras proterum* from the Love Bone Bed, Florida. See Table 1 for abbreviations.

Variable	Sex	Mean	SD	Min	Max	N	CV	Skew	Kurt	<i>b</i>	Pr.< <i>W</i>	M/F
WBC	M	39.9	4.42	33	46	13	11.1	-0.46	-0.74	0.53	0.27	-
WBC	F	21.9	2.29	18	26	18	10.4	0.00	-0.04	0.40	0.77	-
WBC	F+M	29.5	9.58	18	46	31	32.5	0.48	-1.45	0.80	0.00	1.8
CL	M	75.2	32.10	24	119	11	42.7	-0.38	-1.26	0.64	0.39	-
CL	F	28.0	9.06	13	43	16	32.3	-0.04	-0.90	0.48	0.88	-
CL	F+M	47.2	31.66	13	119	27	67.0	1.08	-0.15	0.77	0.00	2.7
RD	M	36.0	2.35	32	40	19	6.4	0.16	-0.18	0.36	0.77	-
RD	F	19.6	1.90	16	21	17	9.8	0.15	0.28	0.31	0.81	-
RD	F+M	28.3	8.56	16	40	36	30.3	-0.07	-1.85	0.88	0.00	1.8
RL	M	136.5	19.09	123	150	2	13.9	-	-	-	-	-
RL	F	67.3	7.25	60	80	12	10.8	0.74	-1.16	0.84	0.03	-
RL	F+M	77.2	26.54	60	150	14	34.4	2.19	4.29	0.80	0.00	2.0

Table 3. Statistics for the mandibular tusks (i2) of *Aphelops malacorhinus* from the Love Bone Bed, Florida. See Table 1 for abbreviations.

Variable	Sex	Mean	S.D.	Min	Max	N	CV	Skew	Kurt	<i>b</i>	Pr.< <i>W</i>	M/F
WBC	M	35.1	2.27	30	38	17	6.5	-0.88	0.22	0.55	0.17	-
WBC	F	21.3	3.23	17	27	19	15.2	0.28	-0.91	0.52	0.18	-
WBC	F+M	27.8	7.52	17	38	36	27.0	-0.04	-1.65	0.74	0.00	1.6
CL	M	91.9	23.3	49	120	7	25.3	-1.05	1.33	0.49	0.58	-
CL	F	38.9	12.23	16	57	16	31.4	-0.21	-0.06	0.36	0.34	-
CL	F+M	55.0	29.5	16	120	23	53.6	0.91	-0.23	0.66	0.01	2.4
RD	M	33.5	2.82	28	39	22	8.4	0.15	-0.12	0.36	0.84	-
RD	F	20.5	2.88	17	27	19	14.0	0.86	0.19	0.55	0.15	-
RD	F+M	27.5	7.12	17	39	41	25.9	-0.10	-1.53	0.69	0.00	1.6
RL	M	149.9	17.89	117	168	9	11.9	-0.78	-0.50	0.64	0.23	-
RL	F	73.6	7.13	63	83	11	9.7	-0.32	-0.96	0.54	0.33	-
RL	F+M	108.0	40.98	63	168	20	38	0.39	-1.72	0.90	0.00	2.0

In the LBB *Teleoceras* sample, the sex-specific distributions of the tusk data generally did not differ significantly from a normal distribution, except RL for females (Table 2). However all of the sex-combined tusk data deviated significantly from normality ( $p < 0.1$ ). Although the tusk wear patterns and unbalanced age distribution of the LBB *Teleoceras* assemblage are similar to those of Mixson's, the bimodality of the data is more obvious. The sex-combined coefficients of bimodality (*b*) were all above 0.55, indicating strong bimodality.

The LBB *Aphelops* tusk data are the most straightforward because young males with poorly developed roots are less frequent (Table 3). None of the sex-specific data deviated significantly from normality and all of the sex-combined data were not normal ( $p < 0.1$ ). The coefficients of the sex-combined data were very high ( $b = 0.66-0.90$ ) indicating strong bimodality.

#### BODY SIZE DIMORPHISM

The disarticulated condition of the Florida rhino assemblages prevented an analysis comparable to that of

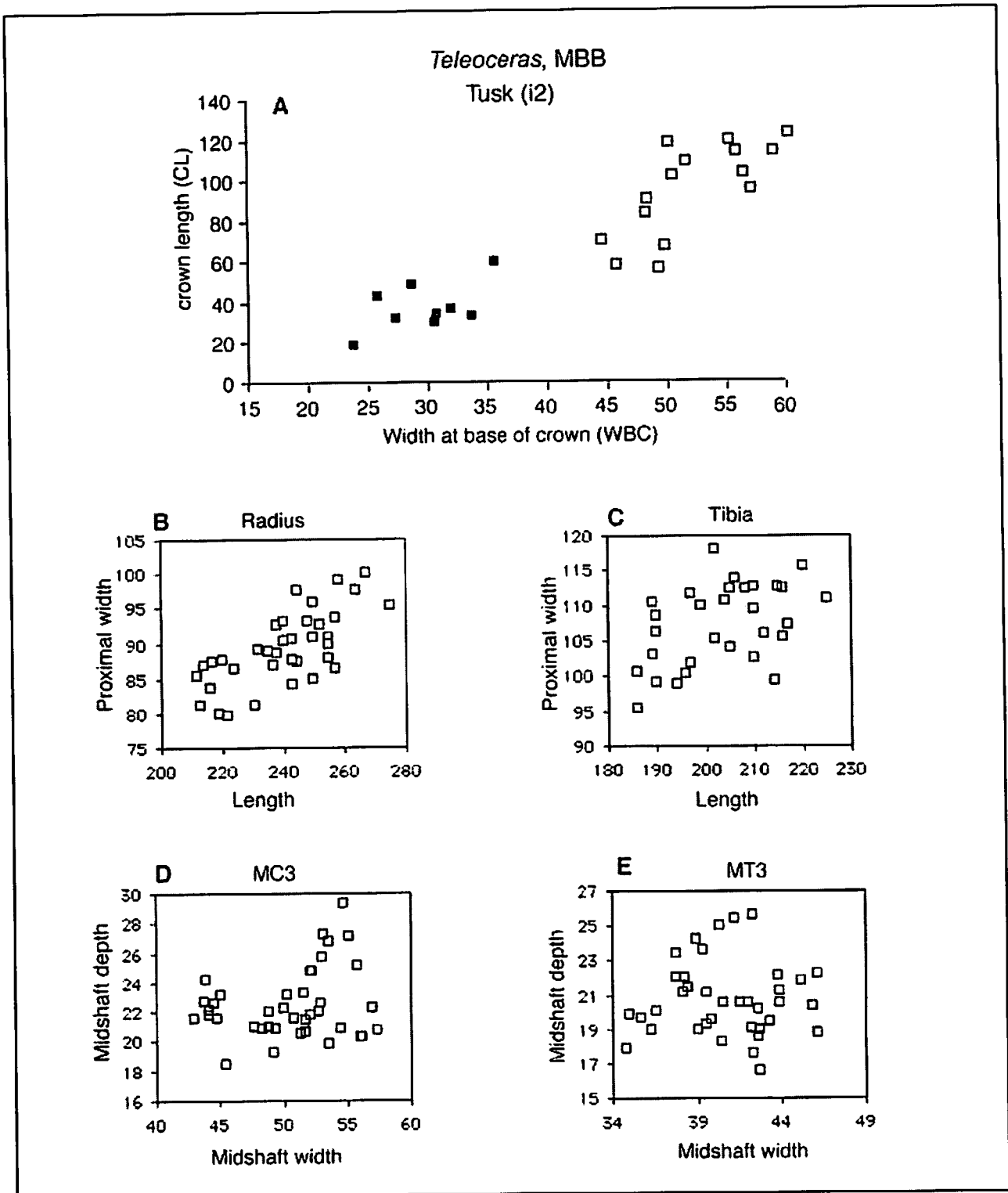


Figure 8. Bivariate plots of various linear dimensions of the mandibular tusks (i2) and the central weight-bearing limb elements of *Teleoceras proterum* from Mixson's Bone Bed.

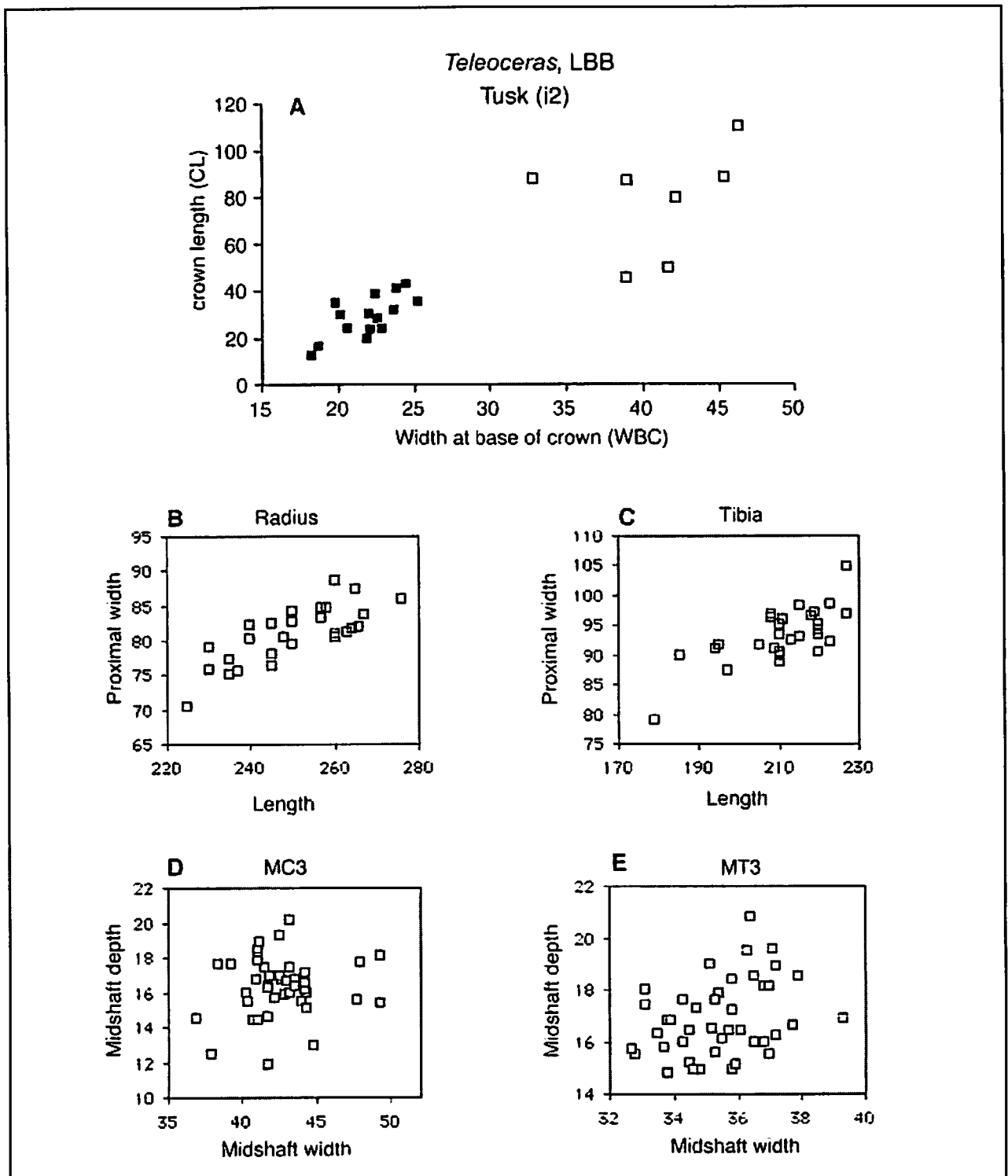


Figure 9. Bivariate plots of various linear dimensions of the mandibular tusks (i2) and the central weight-bearing limb elements of *Teleoceras proterum* from the Love Bone Bed.

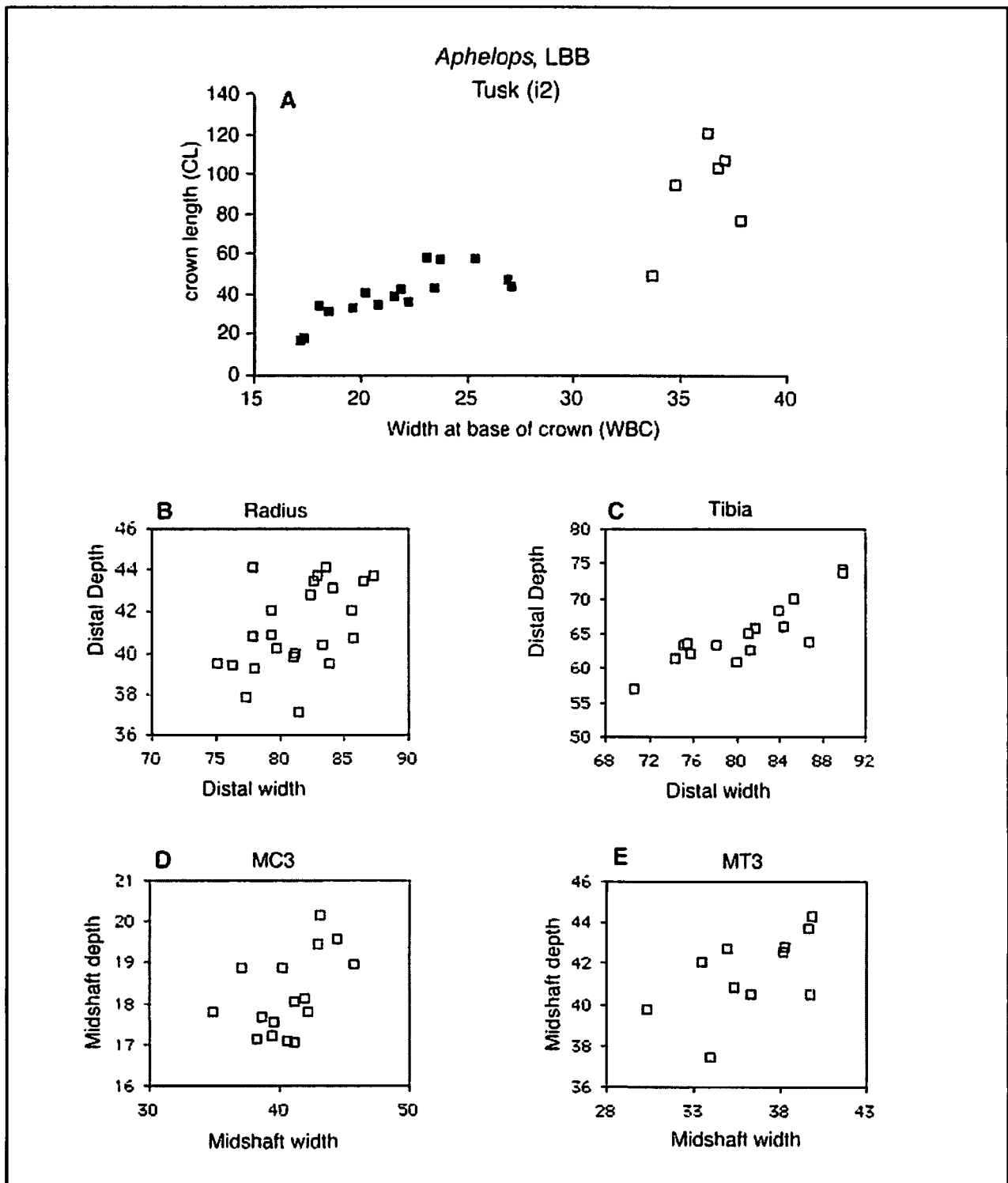


Figure 10. Bivariate plots of various linear dimensions of the mandibular tusks (i2) and the central weight-bearing limb elements of *Aphelops malacorhinus* from the Love Bone Bed.

Table 4. Statistics for the *Teleoceras major* assemblage from Ashfall, Nebraska, calculated from raw data in Mead (1999a). Column *t* includes the *p*-values of Mead's (2000) Student's *t*-tests used to compare male and female averages. See Table 5 for abbreviations.

Variable	<i>t</i>	Mean	SD	Min	Max	N	CV	Skew	Kurt	<i>b</i>	Pr. < <i>W</i>
HL	0.001	306.5	17.6	283	341	27	5.74	0.59	-0.87	0.63	0.03
HPW	0.001	82.3	4.3	75.3	92.7	19	5.24	0.71	0.71	0.43	0.67
HDW	0.01	123.7	4.5	115	133	20	3.65	0.18	-0.30	0.38	0.99
HDWC	0.002	81.4	4.62	73.6	89.9	21	5.68	0.14	-1.21	0.57	0.18
RL	0.001	248.5	15.7	229	289	30	6.34	0.93	0.05	0.61	0.01
RXA	0.001	1078	193.7	826	1126	23	17.96	0.605	-0.745	0.61	0.67
RPW	0.001	77.8	4.9	70.7	89.9	24	6.26	19.20	0.32	0.46	0.32
RDW	0.02	87.6	5.244.5	77.6	98.9	25	5.93	0.24	-0.40	0.41	0.86
RDD	0.001	49.6	3.74	44.5	57.5	24	7.54	0.73	-0.50	0.61	0.07
MC3L	0.01	118.0	6.1	110.5	131.2	15	5.20	0.78	-0.25	0.59	0.23
MC3PW	0.10	56.9	3.5	51.6	63.4	14	6.07	0.37	-0.32	0.42	0.83
MC3DW	0.01	47.1	2.1	43.7	50.8	14	4.44	-0.12	-0.42	0.39	0.76
MC3D	0.02	20.0	2.8	15.4	26.8	13	14.06	1.18	2.37	0.45	0.05
FL	0.001	397.6	20.6	369	446	31	5.17	0.79	-0.34	0.61	0.02
FXA	0.001	2115	269.5	1710	2974	24	12.75	1.43	3.58	0.46	0.01
FHD	0.10	74.8	3.4	67.6	81.0	25	4.55	-0.06	-0.21	0.36	0.72
FDW	0.05	114.7	4.15	106	123.7	26	3.62	-0.02	0.01	0.33	0.93
TL	0.001	243.6	15.9	223	287	27	6.53	0.88	0.67	0.48	0.06
TPW	0.001	96.5	5.2	88.3	106.3	22	5.37	0.29	-0.70	0.47	0.45
TDW	0.01	76.5	5.2	68.9	87.4	22	6.75	0.36	-0.57	0.47	0.66
TDAW	0.05	61.8	3.9	54.1	66.9	21	6.31	-0.47	-1.12	0.65	0.05
TDD	0.001	58.5	3.9	50.4	66	21	6.63	-0.13	-0.45	0.40	0.88
MT3L	>0.10	97.0	6.2	88.6	111.7	12	6.41	1.07	1.89	0.44	0.38
MT3PW	0.05	40.7	2.7	37.3	47.5	12	6.60	1.39	3.37	0.46	0.07
MT3DW	0.05	44.1	2.0	41.6	48.6	12	4.45	0.87	1.35	0.41	0.37
MT3D	>0.10	19.1	1.2	17.6	22.1	12	6.51	1.42	2.16	0.58	0.07

Mead (2000) where male and female averages were compared using Student's *t*-tests. Using *t*-tests, Mead (2000) found significant differences between male and female averages in 69% (18 out of 26) of the postcranial variables of the Ashfall *Teleoceras* assemblage (Table 4). The Bonferroni corrected alpha value for Mead's original *t*-tests is 0.002 (alpha level of 0.05 divided by 26). Even with this correction, 46% of the original *t*-tests (12 out of 26) are still significant, thus maintaining a very strong signal for dimorphism in the Ashfall sample. The Shapiro-Wilk test for normality (*W*) identified ten (38%) variables that differed significantly from normality ( $p < 0.1$ ). The Bonferroni corrected alpha value of the Shapiro-Wilk tests is 0.004 (alpha value of 0.1 divided by 26). This correction completely neuter the Shapiro-Wilk tests of all significance. Therefore, because we know this sample to be dimorphic, based on the *t*-tests, type 2 errors (wrongly accepting the null

hypothesis, monomorphism, when the sample is actually dimorphic) are clearly made when the correction is applied to the Shapiro-Wilk tests. Although there is no easy solution to discriminating real significant results from statistical error, out of the ten uncorrected significant results of the Shapiro-Wilk tests, six of these were also identified as dimorphic by the original *t*-tests. The uncorrected Shapiro-Wilk tests seem to have captured the signal for dimorphism, though not as strongly as the original *t*-tests. The coefficients of bimodality also seem to capture a signal of dimorphism. Nine of the 26 variables (35%) yielded coefficients of bimodality higher than 0.55 (Fig. 11). Out of these nine, seven were characters identified as dimorphic by Mead (2000). The Shapiro-Wilk test of normality and the coefficient of bimodality flagged six common variables; four of these are in common with the results of Mead's (2000) original *t*-tests. To summarize, the analysis of the sex-combined data

identified a little more than half as many variables as Mead's (2000) analysis of sex-segregated data. It can be concluded that the Shapiro-Wilk test and coefficient of bimodality were less effective than the original *t*-tests at identifying dimorphism in the Ashfall sample. However, these analyses flagged several of the variables identified as dimorphic by the original *t*-tests, and it indicated some other variables as potentially dimorphic. This suggests that the analysis of sex-combined data was effective at identifying size dimorphism, albeit not as effectively or thoroughly as the original *t*-tests.

A total of 38 variables were measured for the MBB *Teleoceras* sample (Table 5), including the 26 variables used by Mead (2000). Of these 26 variables, only six (23%) deviated significantly from a normal distribution, based on the Shapiro-Wilk test for normality. Only three (12%) of the 26 variables used by Mead (2000) have bimodality coefficients above the 0.55 threshold. Out of

all 38 variables, only 8% yielded coefficients of bimodality above 0.55 (Fig. 11) and only 18% yielded significant Shapiro-Wilk tests. The Bonferroni correction strips the Shapiro-Wilk tests of all significance; however, because of the probability of type 2 error in the corrected results, complete monomorphism is unlikely. At any rate, a fewer number of variables were flagged as being potentially dimorphic, suggesting a lesser degree of dimorphism in comparison to the Ashfall sample. Bivariate plots of selected variables of the MBB *Teleoceras* assemblage seem to confirm some size dimorphism by suggesting two size clusters, particularly for the radius and MC3 (Fig. 8B, D). In both plots there are more specimens in the larger cluster. This pattern is consistent with the numerical domination of members of the larger sex in the sample based on counts of tusks (72% male) (Mihlbachler 2003). Similar size clusters are evident in the plots of tibia and MT3 data (Fig. 8C, E), but

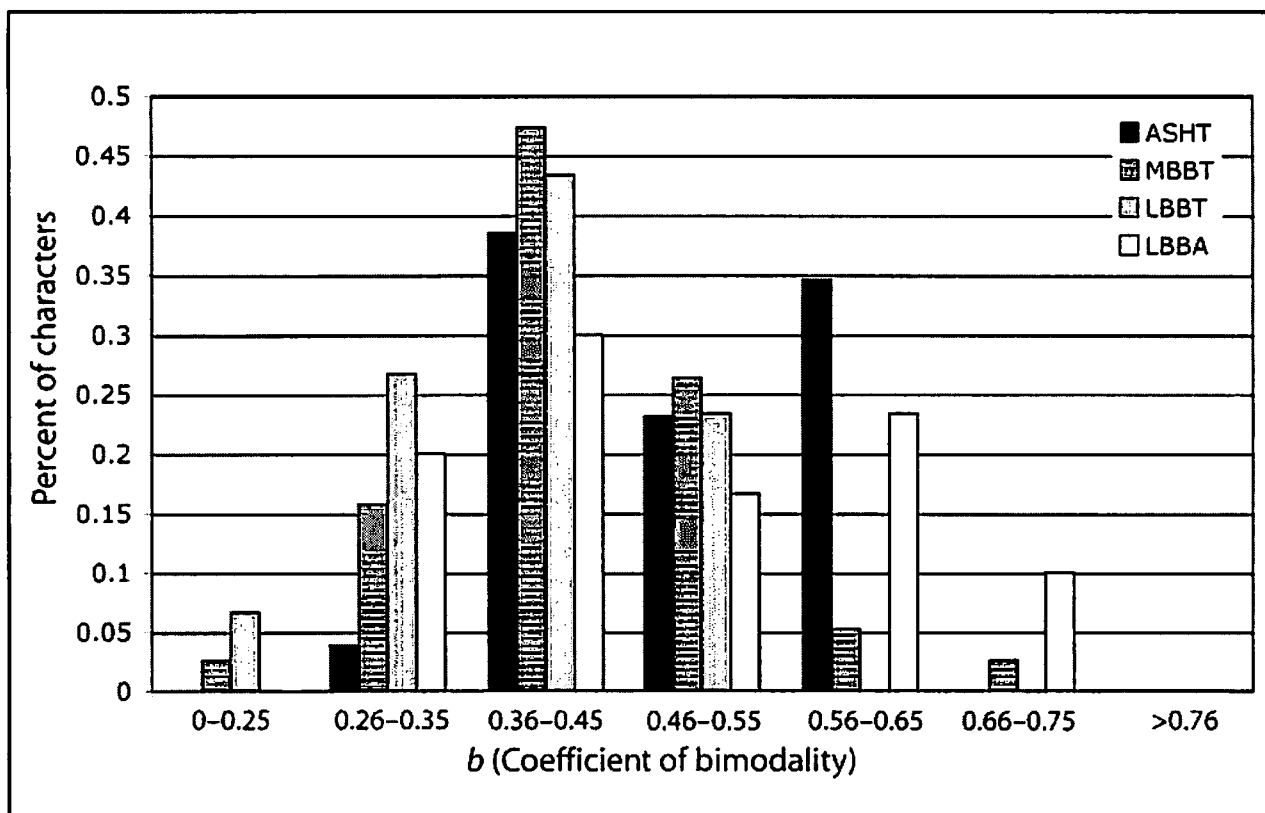


Figure 11. The distributions of coefficients of bimodality (*b*) for limb bone measurements of *Teleoceras* and *Aphelops* fossil assemblages. Abbreviations are as follows: ASHT = Ashfall *Teleoceras major*; MBBT = Mixson's Bone Bed *Teleoceras proterum*; LBBT = Love Bone Bed *Teleoceras proterum*; LBBA = Love Bone Bed *Aphelops malacorhinus*.

Table 5. Statistics for limb bone variables of *Teleoceras proterum* from Mixson's Bone Bed, Florida. See Table 1 for statistical abbreviations.

Variable	Mean	SD	Min	Max	N	CV	Skew	Kurt	<i>b</i>	Pr. < <i>W</i>
HL	310.2	13.75	286	342	28	4.4	0.36	-0.24	0.41	0.72
HPW	91.1	5.69	82	107	29	6.3	0.88	1.99	0.42	0.06
HDW	138.5	7.19	127	152	22	5.2	0.46	-0.91	0.58	0.15
HDWC	93.9	4.87	82	101	24	5.2	-0.21	-0.28	0.39	0.06
HMC	189.8	11.77	172	212	26	6.2	0.30	-0.89	0.52	0.19
RL	240.0	16.35	212	275	42	6.8	-0.01	-0.79	0.45	0.17
RPW	89.3	5.17	80	100	37	5.8	0.15	-0.33	0.38	0.58
RDW	85.8	5.02	76	98	40	5.9	0.30	0.58	0.30	0.25
RPD	47.3	2.98	41	53	38	6.3	0.01	-0.56	0.41	0.63
RDD	44.4	3.25	38	50	41	7.3	0.10	-0.62	0.42	0.22
RMC	137.0	11.70	114	158	41	8.5	0.05	-0.87	0.47	0.34
RXA	505.3	76.40	374	700	60	15.1	0.48	-0.15	0.43	0.20
MC3L	108.46	6.20	94	123	39	5.7	-0.21	0.68	0.28	0.53
MC3PW	64.82	3.25	60	73	36	5.0	0.71	-0.35	0.57	0.14
MC3MW	50.56	4.18	43	57	39	8.2	-0.33	-0.96	0.54	0.03
MC3DW	52.21	3.32	46	58	36	6.4	-0.10	-1.18	0.55	0.08
MC3PD	41.06	4.30	32	48	37	10.5	-0.25	-0.78	0.48	0.25
MC3MD	22.50	2.37	18	29	39	10.5	1.01	0.83	0.53	0.01
MC3DD	38.50	2.08	34	43	38	5.4	-0.58	0.34	0.40	0.05
FL	414.9	15.82	380	440	19	3.8	-0.71	0.59	0.42	0.25
FHD	78.2	3.51	74	86	21	4.5	0.83	0.49	0.48	0.06
FDW	124.9	4.88	118	134	15	3.9	0.53	-1.18	0.71	0.11
FMC	182.9	11.35	164	205	19	6.2	0.38	-0.63	0.48	0.65
FXA	889.8	106.20	698	1219	53	11.9	0.43	0.75	0.32	0.62
TL	201.8	11.20	177	225	37	5.6	-0.06	-0.71	0.44	0.59
TPW	107.2	5.76	95	118	30	5.4	-0.23	-0.84	0.49	0.44
TDW	79.5	4.15	70	90	40	5.2	0.26	0.43	0.31	0.76
TPD	90.9	5.19	82	104	33	5.7	0.40	0.07	0.38	0.84
TDD	67.3	4.01	60	75	40	6.0	0.15	-1.09	0.54	0.06
TDAW	69.8	3.18	63	75	38	4.6	-0.31	-0.40	0.42	0.54
TMC	150.7	8.63	133	167	34	5.7	-0.19	-0.63	0.44	0.45
MT3L	88.8	4.82	79	98	37	5.4	0.10	-0.78	0.45	0.48
MT3PW	46.8	2.26	43	53	36	4.8	0.35	-0.24	0.41	0.62
MT3MW	40.7	3.08	35	46	37	7.6	-0.09	-0.68	0.43	0.96
MT3DW	45.6	1.31	41	51	36	2.9	0.12	-0.87	0.34	0.43
MT3PD	37.2	3.01	31	45	33	8.1	0.09	0.10	0.33	0.21
MT3MD	20.7	2.19	17	26	37	10.6	0.59	-0.01	0.45	0.36
MT3DD	37.3	1.31	33	41	36	3.5	-0.41	1.62	0.25	0.97

Morphological abbreviations: HL = humerus length; HPW = humerus proximal width; HDW = humerus distal width; HDWC = humerus distal width of condyle; HMC = humerus midshaft circumference; RL = radius length; RPW = radius proximal width; RDW = radius distal width; RPD = radius proximal depth; RDD = radius distal depth; RMC = radius midshaft circumference; RXA = radius cross sectional area of midshaft; MC3L = third metacarpal length; MC3PW = third metacarpal proximal width; MC3MW = third metacarpal midshaft width; MC3DW = third metacarpal distal width; MC3PD = third metacarpal proximal depth; MC3MD = third metacarpal midshaft depth; MC3DD = third metacarpal distal depth; FL = femur length; FHD = femur head diameter; FDW = femur distal width; FMC = femur midshaft circumference; FXA = femur cross sectional area of midshaft; TL = tibia length; TPW = tibia proximal width; TDW = tibia distal width; TPD = tibia proximal depth; TDD = tibia distal depth; TDAW = tibia width of distal articular surface; TMC = tibia midshaft circumference; MT3L = third metatarsal length; MT3PW = third metatarsal proximal width; MT3MW = third metatarsal midshaft width; MT3DW = third metatarsal distal width; MT3PD = third metatarsal proximal depth; MT3MD = third metatarsal midshaft depth; MT3DD = third metatarsal distal depth.



Table 6. Statistics for limb bone variables of *Teleoceras proterum* from the Love Bone Bed, Florida. See Table 5 for abbreviations.

Variable	Mean	SD	Min	Max	N	CV	Skew	Kurt	<i>b</i>	Pr. < <i>W</i>
RL	250.3	12.65	225.0	276.0	30	5.1	-0.20	-0.62	0.44	0.71
RPW	81.0	3.83	70.3	91.6	69	4.7	-0.02	0.47	0.29	1.00
RMW	43.5	2.46	38.5	51.5	61	5.7	0.56	0.57	0.37	0.37
RDW	76.9	3.42	69.5	84.9	40	4.4	-0.40	0.14	0.37	0.31
RPD	45	3.47	39.4	53.5	62	7.7	0.61	-0.43	0.53	0.01
RMD	32.4	3.15	25.6	43.7	59	9.7	0.72	1.64	0.33	0.22
RDD	38.6	2.30	33.1	41.6	38	6.0	-0.83	0.13	0.54	0.01
RMC	123.7	6.96	108.0	139.0	58	5.6	-0.03	-0.32	0.37	0.63
MC3L	112.2	4.39	101.3	119.4	41	3.9	-0.37	-0.48	0.45	0.28
MC3PW	53.7	3.84	44.1	61.7	41	7.1	-0.22	-0.07	0.36	0.60
MC3MW	42.6	2.67	36.9	49.3	41	6.3	0.63	1.16	0.34	0.04
MC3DW	43.0	1.73	39.9	46.0	38	4.0	0.05	-1.16	0.54	0.10
MC3PD	35.6	2.98	29.8	41.0	41	8.4	-0.25	-1.05	0.54	0.07
MC3MD	16.3	1.71	11.9	20.1	41	10.5	-0.44	0.77	0.32	0.55
MC3DD	32.5	1.68	29.0	35.7	38	5.2	0	-0.39	0.38	0.35
TL	211	11.4	179	227	31	5.4	-1.09	1.23	0.52	0.01
TPW	93.5	4.68	79.0	104.8	29	5.0	-0.56	2.73	0.23	0.23
TMW	40.4	3.31	32.2	49.4	37	8.2	0.18	1.15	0.25	0.75
TDW	74.3	4.13	60.8	81.0	34	5.6	-1.16	2.49	0.43	0.05
TPD	91.8	7.20	74.9	107.4	26	7.8	0.04	0.46	0.29	0.90
TMD	42.1	3.49	31.8	48.6	37	8.3	-0.61	1.10	0.33	0.42
TDD	54.0	3.99	44.4	62.8	34	7.4	0.23	0.59	0.29	0.26
TMC	132.4	8.41	113.0	152.0	37	6.4	-0.09	-0.18	0.36	0.94
MT3L	89.4	3.38	82.1	96.2	41	3.8	-0.32	-0.17	0.39	0.23
MT3PW	38.5	1.68	35.0	41.0	42	4.4	-0.24	-0.91	0.51	0.13
MT3MW	35.4	1.52	32.7	39.3	42	4.3	0.14	-0.34	0.38	0.75
MT3DW	40.2	2.12	34.3	43.8	39	5.3	-0.52	0.09	0.41	0.43
MT3PD	31.0	1.39	28.7	34.3	41	4.5	0.17	-0.43	0.40	0.25
MT3MD	16.9	1.46	14.8	20.8	42	8.6	0.61	-0.15	0.48	0.11
MT3DD	33.8	1.8	31.0	39.7	42	5.3	0.76	1.55	0.35	0.07

they are subtler.

For LBB *Teleoceras*, eight out of 30 variables (27%) deviated significantly from normality based on the Shapiro-Wilk test. The Bonferroni correction again neutered the Shapiro-Wilk results. The coefficients of bimodality do not offer a strong signal for dimorphism; none of the variables yielded values above 0.55 (Fig. 11). However six variables had coefficients of variation approaching 0.55 ( $b > 0.5$ ). Five of these variables were also identified by the uncorrected Shapiro-Wilk test, so these two sets of results may indicate moderate dimorphism. However, in comparison to the Ashfall sample, body size dimorphism seems diminished in the LBB *Teleoceras* assemblage. Bivariate plots do not reveal any obvious size clustering (Fig. 9B-E).

The results of the LBB *Aphelops* assemblage are more perplexing. Eleven out of 30 variables (37%) pro-

duced coefficients of bimodality exceeding 0.55 (Fig. 11). This suggests a level of dimorphism approaching that of the Ashfall *Teleoceras* assemblage. But only two (7%) of these variables yielded a significant result for the Shapiro-Wilk test for normality. Of course, the Bonferroni correction strips these results of their significance. Bivariate plots do not reveal any obvious size clustering in the *Aphelops* assemblage (Fig. 10B-E). The coefficient of bimodality strongly suggests sexual dimorphism for *Aphelops*, but other analyses give inconclusive results.

## DISCUSSION

### TELEOCERAS, HERDS, AND HIPPO MYTHS

Because of its conspicuous abundance at many Miocene localities and its distinctive short-legged, broad-torsoed appearance, *Teleoceras* is one of the most in-

Table 7. Statistics for limb bone variables of *Aphelops malacorhinus* from the Love Bone Bed, Florida. See Table 5 for abbreviations.

Variable	Mean	SD	Min	Max	N	CV	Skew	Kurt	<i>b</i>	Pr. < <i>W</i>
RL	344.7	13.28	328	369	12	3.9	0.52	-0.75	0.56	0.51
RPW	86.6	3.35	81.2	93.4	26	3.9	0.12	-0.58	0.42	0.66
RMW	47.3	3.96	38.1	53.4	29	8.4	-0.55	-0.45	0.51	0.28
RDW	81.5	3.40	75.1	87.4	23	4.2	-0.08	-0.87	0.47	0.80
RPD	51.6	3.89	42.4	59	23	7.5	-0.38	-0.30	0.42	0.96
RMD	36.3	3.69	30.1	43	29	10.2	0.66	-0.99	0.71	0.43
RDD	41.1	2.05	37.1	44.1	25	5	-0.09	-0.99	0.50	0.25
RMC	136.5	10.21	116	153	29	7.5	-0.16	-0.70	0.45	0.45
MC3L	178.0	9.46	167.0	196.0	8	5.3	1.15	0.75	0.62	0.23
MC3PW	52.8	2.53	47.6	57.1	21	4.8	-0.42	0.30	0.36	0.34
MC3MW	40.6	2.67	35	45.8	19	6.6	-0.07	-0.09	0.35	0.99
MC3DW	53.4	1.67	51.4	56.4	9	3.1	0.78	-0.38	0.61	0.39
MC3PD	45.0	2.96	39.0	51.9	20	6.6	0.09	0.70	0.27	0.77
MC3MD	18.1	0.98	17.0	20.1	17	5.4	0.66	-0.75	0.64	0.08
MC3DD	40.2	2.44	37.0	44.3	9	6.1	0.53	-0.53	0.52	0.71
TL	342.6	14.06	325.0	366.0	8	4.1	0.52	-0.77	0.57	0.57
TPW	107.2	7.26	95.0	121.2	12	6.8	0.18	0.08	0.34	0.96
TMW	47.4	2.03	44.4	51.1	12	4.3	0.13	-0.60	0.42	0.70
TDW	81.0	5.50	70.6	90.0	17	6.8	-0.02	-0.58	0.41	0.82
TPD	101.9	6.78	92.0	112.0	12	6.7	0.39	-1.39	0.72	0.07
TMD	43.5	1.91	39.3	46.3	14	4.4	0.66	0.41	0.42	0.62
TDD	65.0	4.60	56.9	74.2	16	7.1	0.68	0.40	0.43	0.26
TMC	155.3	8.18	140.0	171.0	18	5.3	0.23	0.28	0.32	0.56
MT3L	143.0	4.26	135.6	148.4	11	3.0	-0.43	-0.89	0.56	0.58
MT3PW	45.0	3.79	57.5	51.3	11	8.4	-0.48	0.58	0.34	0.92
MT3MW	36.4	3.08	30.4	39.9	11	8.5	-0.54	-0.41	0.50	0.38
MT3DW	35.9	2.14	31.4	39.7	11	6	-0.40	1.40	0.26	0.78
MT3PD	18.1	0.57	17.3	19.0	11	3.16	0.31	-1.30	0.64	0.41
MT3MD	41.5	1.99	37.4	44.3	11	4.8	-0.68	0.42	0.43	0.67
MT3DD	36.5	2.56	32.2	39.3	11	7.0	-0.60	-1.19	0.75	0.14

teresting North American rhinos. Speculation about its paleobiology in the scientific and popular literature is abundant and almost always refers dogmatically to modern hippos as an analogy (see Prothero, 2005 for review). Because of this popular association, no discussion of *Teleoceras* paleobiology will make sense without clarifying the degree to which this analogy is supported by empirical evidence. The association of *Teleoceras* with hippos began with Cope (1879) who first observed that *Teleoceras* superficially resembles *Hippopotamus amphibius* due to its unusually short limbs and broad torso. Osborn (1898b, 1898c) first suggested that *Teleoceras* lived in large herds in rivers and lakes. This interpretation has remained popular for more than a century (Scott 1913; Webb 1983; Voorhies 1985; Prothero et al. 1989; Webb & Opdyke 1995; Prothero 1998; Wall & Heinbaugh 1999). In my judgment, the traditional hippo analogy for *Teleoceras* is not strongly

supported from any angle of investigation (Mihlbachler 2001b). The question of whether or not *Teleoceras* was aquatic or terrestrial is still unresolved. The adaptive nature of the shortened limbs of hippos and *Teleoceras* are not well understood. Previously, the shortened limbs of these taxa were presumed to indicate a semiaquatic lifestyle (e.g., Wall & Heinbaugh 1999). However, Mihlbachler (2001a) and Mihlbachler et al. (2004b) argued, from a biomechanical perspective, that the shortened limbs of extinct hippo-like ungulates, including *Teleoceras*, are not clearly indicative of an aquatic lifestyle. An alternative hypothesis put forth by W. D. Matthew (1932), that the shortened limbs may have had more to do with open terrain and grazing habits, is equally plausible and has not been adequately tested. Functional morphology (Hermanson & MacFadden 1996) and stable isotopes also give inconclusive or conflicting results on the question (MacFadden

1998; Clementz & Koch 2000; Muhlbachler 2001). Although analogies are commonly used to generate inferences of the paleobiologies of extinct taxa, such analogies are only reliable when superficial similarities represent common adaptations and that these adaptations are understood. I suggest that this is not the case for the popular hippo analogy for *Teleoceras*.

Because of the popular hippo analogy, patterns of mortality and sexual dimorphism in *Teleoceras* fossil assemblages are commonly seen as indicative of herds (Webb 1983; Voorhies 1985; Prothero et al. 1989; Berger et al. 2001). Herd behavior for *Teleoceras* was most elaborately argued by Mead (2000), who found the levels of sexual dimorphism and sex-biased nature of the assemblage of *Teleoceras major* from Ashfall, Nebraska to be more consistent with herding ruminant artiodactyls, such as *Bison bison* or *Synceras caffer*, with mixed sex herds and separate male bachelor groups. Like others, Mead (2000) concluded from this finding that *Teleoceras* was different from modern rhinos and more analogous to *Hippopotamus amphibius*.

However, the high degree of body size dimorphism in the Ashfall *Teleoceras* assemblage contradicts the hippo analogy because hippos are not particularly dimorphic. In a large sample of hippos culled in Uganda, average male weight was only 8% greater than average female weight (Owen-Smith 1988). Some modern rhinos are more dimorphic in body mass than *Hippopotamus*. *Ceratotherium simum* males are 21-48% heavier than females (Owen-Smith 1988) and *Rhinoceros unicornis* males can be 31% heavier than females (Laurie et al. 1983; Owen-Smith 1988). At any rate, body size dimorphism is not strongly correlated to group size, group structure, or the degree of social bonding among modern perissodactyls; therefore the degree of dimorphism may not be a sound basis for inferring such behaviors in *Teleoceras* or other extinct perissodactyls.

An additional problematic aspect of the inference of herding behavior based on the hippo analogy is that it relies on oversimplified characterizations of group sociality. For instance, hippo societies are considerably different from typical herding ruminants. Hippos form partially sex-segregated clusters of individuals during the day in shallow rivers, lakes, and wallows, but unlike herding ruminants, there are no coherent social bonds between adults. Hippos emerge from their aquatic habitats at night and graze solitarily (Klingel 1991; Eltringham 1999). Therefore, if *Teleoceras* was a hippo "analog" this does not specifically indicate behaviors analogous to herding ruminants. Muhlbachler (2003) argued that

the age- and sex-specific demographics of the Ashfall and Florida *Teleoceras* assemblages are consistent with a number of interpretations including social behaviors similar not only to hippos and herding ruminants, but also with modern rhinos. Rhinos do not form herds, although some dominant males are territorial (*Ceratotherium simum*) (Owen-Smith 1972, 1988), while others are extremely aggressive towards subdominant males (*Rhinoceros unicornis*), driving them away from areas where females are most densely concentrated, particularly near water (Laurie 1982; Dinerstein & Price 1991; Dinerstein 2003). Incidentally, shallow water (ponds, rivers, wallows) is where fossil accumulation tends to occur, suggesting that fossil assemblages of extinct species whose behaviors resemble those of living rhinos will be strongly sex-biased. Despite the absence of coherent groups in rhinos, such behaviors result in elevated mortality rates among young adult males and promote partially sex-segregated societies that are not fundamentally different from the sex biases typical of *Teleoceras* assemblages (Muhlbachler 2003).

Phylogeny, rather than analogy, is a more appropriate framework for establishing a null hypothesis for an unpreserved character, including behavior (Witmer 1995). Patterns of sexual dimorphism and mortality found in the fossil record can be used to test a null hypothesis of *Teleoceras* sociality that is based on its extant phylogenetic bracket. *Teleoceras* is phylogenetically positioned outside the clade of living rhinos (Prothero et al. 1986; Cerdeño 1995; Antoine 2002), therefore the bracketing clades are extant members of the Rhinocerotidae and Tapiridae. Neither rhinos nor tapirs form herds and although rhinos may form ephemeral clusters of individuals there is no a priori reason to presume *Teleoceras* to have formed herds. To infer herd behavior in *Teleoceras*, patterns of sexual dimorphism and/or the population demographics of fossil assemblages must first falsify the null hypothesis that *Teleoceras* social behaviors resembled those of rhinos and tapirs.

Comparing the degree of size dimorphism of fossil and living rhinos is problematic because sexual dimorphism in extinct animals is most easily quantified with measurements of bones, while sexual dimorphism data on extant large mammals are mostly body mass data and whole-body measurements (Dinerstein 1991; Owen-Smith 1998). As noted above, sexual dimorphism is a poor indicator of sociality in modern perissodactyls and it does not offer strong evidence for or against group forming behaviors. The phenotypic expression of size dimorphism is also plastic and effected by varying levels

of ecological stress (see below). This introduces additional uncertainty in drawing inferences of sociality from sexual dimorphism.

Mortality patterns, on the other hand, contain strong signals of sociality in *Teleoceras* assemblages. The following is a summary of arguments elaborated by Muhlbachler (2003). The Ashfall assemblage is catastrophic in nature and represents a cluster of individuals that was quickly buried by rapid deposition of volcanic ash (Voorhies 1985). A catastrophic assemblage must be treated as an instantaneous sample from a living population (Voorhies 1969; Lyman 1994). This assemblage contains superabundant numbers of females (72% female), while young adult males are conspicuously underrepresented (Mead 2000). This pattern suggests a sex-segregated society of some sort. The missing males could have been rare in the localized deposits because they formed bachelor herds (ruminant analogy), semi-segregated clusters of individuals in water (hippo analogy), or because they were threatened by older dominant males in areas where females were concentrated (modern rhino analogy). Alternatively, they may have been already removed from the population by elevated male mortality rates. In contrast to the catastrophic nature of the Ashfall assemblage, the Florida *Teleoceras* assemblages are attritional in nature; such assemblages must be treated as localized mortality events that accumulated over a period of time and will reflect mortality patterns rather than the structure of a standing aggregation of individuals (Voorhies 1969; Lyman 1994). These assemblages show nearly the exact inverse sex ratio of the Ashfall assemblage (72%-77% male) with a superabundance of young adult males (Muhlbachler 2003). The mortality patterns in these assemblages indicate that males suffered locally from elevated mortality rates over an extended period of time. Age estimates based on cheekteeth wear (Hitchins 1978) suggest that males experience elevated mortality risk at an age equivalent to the years between the onset of sexual maturity and the age of first reproduction in modern rhinos, years where young males are particularly at risk from aggressive confrontations of older, dominant males (Laurie 1982; Dinerstein & Price 2001; Dinerstein 2003). The biased sex-ratios of both catastrophic and attritional assemblages of *Teleoceras* suggest similarly polygynous societies with partially sex-segregated populations and consistently high levels of intermale competition, even though the specific type of sociality (herd-like, hippo-like, rhino-like) is indiscernible. Recent bone assemblages of modern rhinos (*Diceros bicornis*) show mor-

ality patterns essentially identical to *Teleoceras*, with discrete mortality spikes for young adults. Recent bone assemblages of hippos and large ruminants lack these age-specific mortality spikes (Muhlbachler 2003).

#### SEXUAL DIMORPHISM AND SOCIALITY IN *TELEOCERAS*

Neither sexual dimorphism nor the population demography of *Teleoceras* falsifies the null hypothesis, based on its phylogenetic bracket, that *Teleoceras* had evolved a highly polygynous, non-herding type of sociality. Due to their closer phylogenetic association and similar mortality patterns, modern rhinos, rather than hippos, are better models for *Teleoceras* sociality. The cranial weaponry of *Teleoceras* consists of a small nasal horn and dimorphic tusks. *Teleoceras* shares tusk dimorphism with living Asian rhinos (Pocock 1945; Groves 1982; Dinerstein 1991). In *Rhinoceros unicornis* males, tusks function in establishing dominance hierarchies and in coercing females into mating. Tusk mediated confrontation is the cause of 50% of male deaths. Tusk size determines dominance hierarchies among males. Young males with poorly developed tusks are most at risk (Dinerstein 1991, 2003). The best functional interpretation of *Teleoceras* tusks is that they had the same role as in *R. unicornis*. *Teleoceras* males maintained sharpened tusks into old age by extensive incisor honing coupled with continuous root growth. Delayed tusk eruption, tusk dimorphism, and sex-specific tusk growth and use-wear patterns all suggest high levels of intermale competition for *Teleoceras*. The consistently biased sex ratios and high rates of young adult male mortality rates that are apparent in *Teleoceras* assemblages are consistent with this prediction.

Given the lack of comparable data (bone measurements versus whole body measurements) one cannot readily determine whether or not *Teleoceras* was more dimorphic for body size than are modern rhinos, however the overall pattern of dimorphism is very similar. In *Diceros bicornis*, *Ceratotherium simum*, and *Rhinoceros unicornis* males reproduce at a later age than females (Laurie et al. 1983; Owen-Smith 1988; Dinerstein & Price 1991). There is evidence, from longbone epiphyseal fusion (Mead 2000) and the eruption schedule of tusks (this paper) that *Teleoceras* males reached maturity at a later age than females. Dinerstein (1991) found that *Rhinoceros unicornis* males were significantly larger than females in head, neck, and shoulder measurements. He concluded that between the sexes "the most conspicuous differences in morphometrics are directly related to the dental weapons and the enlarged

neck and shoulder musculature of males relied upon during the frequent intermale fights that determine dominance and access to females" (p. 455). In the Ashfall *Teleoceras* assemblage, the forelimbs appear to be more dimorphic than the hindlimbs (Mead 2000). Though less dimorphic overall, the MBB data indicate greater forelimb dimorphism as well.

Although the degree of dimorphism in *Teleoceras* cannot easily be compared to modern rhinos, there is strong evidence for variation in the degree of body size dimorphism from sample to sample. The Ashfall assemblage of *Teleoceras major* from Nebraska is more dimorphic than the Florida assemblages of *Teleoceras proterum*. An additional assemblage of *Teleoceras fossiger* from the Long Island Rhino Quarry, Kansas shows signs of being even more dimorphic than the Ashfall assemblage (Mead 2000), although this assemblage has not yet been thoroughly investigated. This variation may represent species-specific differences in body size dimorphism, perhaps corresponding to variations in social behaviors as they relate to the degree of intermale competition among different species of *Teleoceras*. However, the mortality patterns of these fossil assemblages suggest consistently high levels of intermale competition for both *Teleoceras major* and *Teleoceras proterum*, thus suggesting no relationship between dimorphism and the degree of intermale competition.

Body size is a phenotypically plastic character that is highly influenced by environmental factors (Falconer 1989; Geist 2000). Dinerstein (1991) noted that male zoo specimens of *Rhinoceros unicornis* can be up to 1,000 kg heavier than females, indicating a strong genetic potential for body size dimorphism. However, in a wild population at the Royal Chitwan National Park, Nepal, male and female sizes are similar. Dinerstein (1991) attributed the reduced state of phenotypic body size dimorphism to the fact that young adult males are subjected to greater levels of nutritional stress than females during important growth years due to forced emigration from optimal habitat. A similar phenomenon of phenotypic plasticity in body size may explain the variable levels of size dimorphism among *Teleoceras* assemblages. The intensity of intermale competition among polygynous species is strongly influenced by population density and other environmental factors such as resource distribution and abundance that determine the abundance and distribution of females. These factors have an effect on the degree to which males can compete by controlling female distribution. Shifts in these factors can

cause shifts in the strategies that males employ to monopolize mates (Byers & Kitchen 1988). In Florida populations of *Teleoceras*, young males may have experienced stunted growth because of higher population pressure, decreased habitat range, or clustered resource distribution, which enabled dominant males to behaviorally exclude younger males from optimal resource areas. Alternatively, in the Great Plains populations of Nebraska and Kansas, males may have achieved larger body sizes because of lower population pressure, larger ranges, and/or more homogenous habitats that reduced the ability of dominant males to exclude subdominant males from optimal habitat. Mead (1999b) noted frequent hypoplasias (interruptions in enamel growth that are caused by metabolic disruption or nutritional deficiency) in the dp4s and p4s of *Teleoceras* from Nebraska. Similar hypoplasias are found in the Florida assemblages (Mihlbachler personal observations). The dp4 and p4 hypoplasias are consistent with the life-history stages of birth and mother-calf separation (Mead 1999b), but are too early to indicate stress resulting from competition among viable adults. However, other forensic clues, such as Harris lines (osteological markers of recovery from an episode of growth arrest) may provide clues about ecological stress levels in different *Teleoceras* populations. For instance, Duckler and Van Valkenburgh (1998) demonstrated, with Harris line frequencies in long bones, that late Pleistocene large carnivore populations from the Rancho La Brea tar pits were less stressed than the highly endangered Florida panther population.

#### SEXUAL DIMORPHISM AND SOCIALITY IN *APHELOPS*

The extant phylogenetic bracket for *Aphelops* is the same as that of *Teleoceras*, with rhinos and tapirs forming the bracketing clades, and suggests a non-herding but highly polygynous type of sociality. However, tusk-ontogeny and use wear patterns in *Aphelops* offer a conflicting prediction of sociality. Unlike *Teleoceras* and modern Asian rhinos, *Aphelops* does not possess an upper honing incisor. The ability to hone the i2 tusk was lost with the loss of the I1. The more finite lengthwise growth of the tusk in males seems related to the loss of the honing feature, which no longer resulted in extensive loss of dental material due to honing wear. Wear patterns in male tusks indicate that the initially sharp tusk crown was progressively blunted with age, thus decreasing its effectiveness as a weapon among intermediate and old aged males. Perhaps tusk mediated behaviors consisted of non-lethal ritualized confrontations to establish dominance hierarchies. Hypotheses

of non-social tusk functions are suggested by the wear patterns. Dalquest (1983) described the wear patterns of male *Aphelops mutilus* tusks from Coffee Ranch, Texas. He noted that the wear in Coffee Ranch specimens was mainly confined to the lingual portion of the tusk and suggested that such wear was the result of attrition with the tongue or upper lip. Because there was no evidence of extensive wear on the tusk tip it indicated to him that the tusks were not used in feeding. Dalquest's conclusion, however, was based upon his belief that *Aphelops* fed on plants low to the ground. In addition, he suggested that the procumbent tusks might have physically limited the male's ability to crop low plants. Lambert (1994) made a similar conclusion regarding *Aphelops mutilus* material from Moss Acres. Many of the LBB *Aphelops malacorhinus* tusks have similar lingual wear patterns but also with wear and breakage on the tip of the tusk in some specimens, particularly individuals with extensive cheekteeth wear, indicating old age. The most heavily worn tusks resemble the polished, rounded and splintered distal tips of elephant tusks. Much of the wear on elephant tusks is a result of their use in digging, debarking trees and other feeding activities (Haynes 1991). These wear patterns suggest that at least some *Aphelops* males used their tusks in a manner similar to elephants, with possible uses in digging, debarking, or stripping woody branches. Some male *Aphelops* tusks have distinctive, highly polished lingual grooves that could be the result of cropping or stripping woody vegetation with the aid of the lip or tongue. These grooves are visible in an *A. mutilus* specimen from the Withlacoochee River, Florida (UF 14229, Fig. 6C). The smaller female tusks typically lack extensive use wear. The larger tusks of males may have allowed access to a wider array of food items, suggesting that tusk dimorphism resulted in some degree of ecological separation between males and females that could not have existed in a dentally monomorphic animal.

The loss of the I1 in the ancestry of *Aphelops* suggests that the social function of the tusk was altered or that its significance to male reproductive success was reduced, perhaps by a shift in reproductive strategy involving diminished male competition. Other lineages of rhinos, including the African rhinos, have lost their incisors entirely although they possess elongated nasal horns which function socially like the tusks of Asian rhinos because they are used in fights that frequently result in lethal wounds (Berger 1994; Owen-Smith 1988). *Aphelops*, like most extinct rhinos, never evolved a horn and was probably less capable of inflicting lethal wounds

then either *Teleoceras* or living rhinos. The LBB *Aphelops* assemblage seems to confirm the prediction of diminished intermale competition in *Aphelops*. It lacks a significant sex bias, suggesting less sex-segregated societies. Moreover, there is no evidence for the elevated mortality rates among young adult males that characterize *Teleoceras* and modern rhino populations (Mihlbachler 2003), suggesting that intermale aggression was either reduced, or dominance hierarchies were determined through non-lethal confrontations. Preliminary examination of the Coffee Ranch *Aphelops* assemblage shows that it has the same sex-balanced structure (Mihlbachler 2003). The diminished lethality of the tusk and the more balanced mortality rates of males and females seem to falsify the null hypothesis of a highly polygynous sociality. *Aphelops* sociality appears to have been significantly different from both *Teleoceras* and modern rhinos, and although its exact nature cannot be deciphered from the evidence at hand, it clearly seems to have resulted in less sex-segregated societies and lower levels of intermale competition.

Given the likelihood of reduced intermale competition, the degree of sexual dimorphism in *Aphelops* is perplexing. A lesser degree of sexual dimorphism is expected. However, the magnitude of tusk dimorphism in *Aphelops* is not different from *Teleoceras*, with male tusk dimensions that are 60-100% greater on average than the dimensions of female tusks. Although the analysis of body size dimorphism in *Aphelops* is somewhat inconclusive, the coefficients of bimodality suggest a degree of body size dimorphism in the LBB *Aphelops* assemblage that exceeds that of *Teleoceras* from the same locality, and was similar in magnitude to the more pronounced dimorphism in the Ashfall *Teleoceras* assemblage (Fig. 11).

## CONCLUSION

Extant rhinoceroses are both dimorphic and monomorphic. Unlike ruminant artiodactyls there is no apparent relationship between dimorphism and sociality in extant rhinos or other perissodactyls. Although no living rhinos form large groups, they are all highly polygynous and tusk and horn mediated behaviors lead to heightened mortality risks, particularly for young viable males. Because a very high frequency of tusk and horn mediated mortality leads to predictable death patterns in rhinos, sexual dimorphism can be indirectly related to intermale competition in fossil rhino populations. Patterns of tusk ontogeny and use-wear very strongly indicate that *Teleoceras* and *Aphelops* had adopted different social behaviors. *Teleoceras* tusks are potentially lethal weap-

ons. The sex- and age-biases typical of *Teleoceras* assemblages consistently indicate partially sex-segregated societies and elevated rates of male mortality. These patterns are not fundamentally different from modern rhinos and indicate high levels of intermale competition, thus predicting high levels of sexual dimorphism. The lethality of *Aphelops* tusks was diminished due to the loss of the upper honing incisor. Wear patterns on the tusks suggest that some males utilized the tusks for non-social purposes such as feeding. Likewise fossil assemblages of *Aphelops* lack sex-biases, suggesting less sex-segregated societies and more balanced mortality rates for males and females. These patterns are fundamentally different from modern rhinos and suggest reduced levels of intermale competition, thus predicting lower levels of sexual dimorphism. Patterns of sexual dimorphism found in assemblages of *Teleoceras* and *Aphelops* are not consistent with these predictions and suggest that, as in modern perissodactyls, there was not a consistent relationship between dimorphism and sociality in these rhinos.

Because large assemblages of *Teleoceras* are relatively common, perhaps more details about sexual dimorphism and population variation can be learned from this rhino than from highly endangered populations of living species. It was previously argued that *Teleoceras* was more dimorphic than modern perissodactyls (Mead 2000). However analysis of multiple fossil assemblages of *Teleoceras* indicates variation in the degree of body size dimorphism. Great Plains populations of the late Miocene appear to have been more dimorphic than Florida populations. This variation does not relate to differences in the level of intermale competition because the mortality patterns of all *Teleoceras* assemblages seem to indicate very high levels of intermale competition. However, variation in body size dimorphism among *Teleoceras* assemblages may relate to varying levels of ecological stress. Similar phenotypic plasticity in the degree of body size dimorphism in *Rhinoceros unicornis* is related to ecological stress exerted on young males due to forced emigration from optimal habitats. According to analysis of large fossil assemblages, patterns of mortality and sexual dimorphism in *Teleoceras* are similar to those of modern rhinos and provide no direct support for the popular idea that *Teleoceras* had evolved herd behavior or that it was behaviorally convergent upon *Hippopotamus*.

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