

Testing the Role of Cursorial Specializations as Adaptive Key Innovations in Paleocene-Eocene Ungulates of North America

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Abstract Episodes of rapid faunal turnover in the fossil record are often used to examine processes driving macroevolutionary changes, such as competitive exclusion. The sudden appearance in the earliest Eocene of North America of artiodactyls and perissodactyls, and subsequent decline of endemic “condylarths” constitutes such an episode. It has been suggested that the specializations for high speed locomotion (cursoriality) that are present in artiodactyls and perissodactyls were key innovations of these orders accounting for their success in the Eocene and onwards. A quantitative geometric morphometric analysis of distal femoral articular morphology was used to examine changes in locomotor specializations in North American ungulates across the Paleocene-Eocene boundary. “Condylarths” were found to have displayed a broad range of locomotor adaptations, including cursoriality. The early Eocene had the broadest disparity in terms of taxonomic and locomotor contributions to morphological diversity. Changes in locomotor variety were associated with the disappearance of arboreal taxa, primarily “condylarths.” The initial impact of artiodactyls and perissodactyls in North America on existing locomotor diversity was limited and does not support a competitive exclusion hypothesis.

Keywords PETM · Mammal evolution · Geometric morphometrics · Macroevolution · Paleocology · Competitive exclusion

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Introduction

Adaptive radiation, a macroevolutionary process in which a clade diversifies as a result of evolving a key phenotypic feature, is often hypothesized to explain the success of modern eutherian orders (O’Leary et al. 2013). In the fossil record, evidence of active taxonomic displacement of endemic taxa by new arrivals is used to test hypotheses of adaptive radiation and competitive exclusion (Kitchell 1985). The Paleocene-Eocene boundary is marked worldwide by a major climatic event, the Paleocene-Eocene Thermal Maximum (PETM) (McInerney and Wing 2011). In North America, the PETM is associated with the first appearances of members of several orders of modern placental mammals (Rose et al. 2012; Secord et al. 2012). In contrast, the Paleocene fauna is primarily composed of a radiation of endemic mammals of uncertain affinities (Rose 1981; Secord 2008). Many of these groups are considered ecological analogues of the invasive modern orders, and so the Paleocene-Eocene boundary is used to study potential cases of competitive exclusion and ecological replacement (Maas et al. 1988; Jernvall et al. 2000; Wesley-Hunt 2005).

“Condylarths,” a diverse, para- or polyphyletic (Spaulding et al. 2009; Halliday et al. 2015) assemblage of small- to medium-sized herbivorous mammals (Rensberger 1986), rapidly decline in species diversity as the early Eocene progresses, while artiodactyls and perissodactyls diversify (Janis 1993). Recent fossil evidence supports an Asiatic origin for artiodactyls and perissodactyls (Cooper et al. 2014; Rose et al. 2014). The sudden appearance of these orders in North America at the beginning of the Eocene is thus consistent with a hypothesis of immigration of these orders from Eurasia into North America (Gingerich 2006). Thus, competitive exclusion of “condylarths” by invasive artiodactyls and perissodactyls has been proposed to explain the faunal turnover.

However, early Eocene (Wasatchian) artiodactyls and perissodactyls have teeth that are functionally similar to those of “condylarths” (Jernvall et al. 2000), suggesting that dietary based competitive exclusion may not have driven the radiation. In contrast, the cursorial specializations of artiodactyls and perissodactyls have been identified as distinguishing them from the more generalized “condylarths” (Van Valen 1978), and have been hypothesized to constitute a key innovation of the group (Van Valen 1971b; Rose 1987). The postcranial skeleton of early artiodactyls and perissodactyls includes distinctive diagnostic features of the ankle joint indicative of specialization for high-speed modes of locomotion (cursoriality) (Kitts 1956; Rose 1982; Wood et al. 2011). Modern artiodactyls and perissodactyls are either cursorial or secondarily graviportal (specialized for stability at large body mass).

To date, the role of locomotor specialization in the evolution of the Paleogene ungulates of North America has not been studied in a systematic and rigorously quantitative way. Articular surface morphology reflects behavior (Andersson and Werdelin 2003; Andersson 2004; Polly 2008; Fabre et al. 2013). In particular, distal femoral articular surface morphology and locomotion are strongly linked in modern placental mammals (Gould 2014). Undistorted distal femora are found relatively frequently in collections from the Paleogene of North America. This study uses geometric morphometrics to analyze quantitatively changes in distal femoral morphology shown by “condylarths,” artiodactyls, and perissodactyls through the Paleocene and early Eocene of North America.

The aim of this study is to test the hypothesis that cursorial morphology is a key adaptation of artiodactyls and perissodactyls that drives radiation and competitive exclusion of “condylarths” in the early Eocene of North America. It is hypothesized that the cursorially specialized distal femoral morphology of artiodactyls and perissodactyls will be functionally distinct from that of “condylarths”; thus, the appearance of the artiodactyls and perissodactyls post-PETM will be associated with an increased range of femoral morphology found in all early Eocene “ungulates.” It is further hypothesized that the extinction of the “condylarths” through the Eocene will result in a contraction of the range of distal femoral morphologies, associated with the limited locomotor diversity of artiodactyls and perissodactyls relative to “condylarths.” Finally, it is hypothesized that the distal femoral morphologies of Eocene artiodactyls and perissodactyls are similar to those of modern cursorial mammals. Together, these hypotheses will test whether the locomotor specialization of artiodactyls and perissodactyls were key macroevolutionary drivers of the diversification of these orders, and if this diversification is consistent with competitive exclusion playing a role in the disappearance of “condylarths.”

Methods

Taxon Sampling

A sample of fossil distal femora was assembled from five museum collections throughout North America. This sample covers the Paleocene through to the Middle Eocene Uintan North American Land Mammal Age (NALMA). Specimens were selected based on degree of distortion and confidence of taxonomic identification to family level, through dental association wherever possible. Only complete, undistorted distal femora with unambiguous identification to at least family level were retained. The final sample included eight genera (six families) of artiodactyls, ten genera (five families) of perissodactyls, and 19 genera (six families) of “condylarths.” The unit of analysis was the specimen. A full list of specimens and institutions is included in the supplementary data (supplementary information 1). A total of 118 fossil specimens were retained for the analysis.

In addition, a dataset of 165 extant placental mammal specimens (44 genera in five orders) was assembled to build a discriminant function analysis with which to assign locomotor modes to fossils. As most modern ungulate taxa are of similar locomotor mode, sampling was primarily from two orders of modern placentals with extensive locomotor variation, Carnivora and Rodentia. A number of artiodactyl and perissodactyl taxa that sampled a range of body sizes were also included. The hyrax *Procavia capensis* was also included, as it has morphological features associated with both scansoriality and arboreality. Specimens were from the permanent collections of the United States National Museum of Natural History. A complete list of extant specimens used is in the supplementary data (supplementary information 1).

Analysis of Distal Femoral Surface Morphology

The analysis of distal femoral morphology followed a previously described protocol (Gould 2014). Distal femora were scanned using a Next Engine three dimensional (3D) surface laser scanner. The entire distal femoral articular surface from the resulting 3D surface model of each distal femur was manually segmented by tracing the edge of the articular surface in GeoMagic Studio 12 (Geomagic Inc.). A custom MatLab (Mathworks, Inc.) script was used to project a standardized grid of 321 points on the each distal femur, such that the entire articular surface was evenly sampled. These 321 landmarks were treated as sliding semi-landmarks (Bookstein 1997; Gunz et al. 2005). The process of using an even spacing approach to place landmarks on a continuous surface introduces systematic error in the analysis of shape variation. As the semi-landmark positions are defined in reference to other landmarks, the possibility exists that the same semi-landmark on two specimens may end up on what are

geometrically distinct portions of each specimens. This is particularly likely for landmarks that are along, or close to, edges or corners, and introduce spurious shape differences if not addressed. The sliding semi-landmark approach minimizes this error by allowing each landmark on each specimen to shift slightly on the surface in a way that minimizes distortion due to arbitrary equal spacing. This is done prior to the usual geometric morphometric analysis, such that the shape coordinates calculated for geometric morphometric analysis do not include this error. The resulting specimen specific landmark configurations are then treated as normal type I or type II landmarks in a landmark based geometric morphometric analysis. A full Procrustes superimposition was performed in MorphoJ (Klingenberg 2011) to scale, rotate, and translate the landmark configurations for extant and fossil taxa into the same shape space. Procrustes coordinates describing covariation in shape space resulting from this superimposition were exported for further analysis. These Procrustes coordinates, which identify only variation between landmark configurations that is invariant to scaling, rotation, and translation, can be analyzed using standard multivariate statistics.

Taxonomic Grouping

The fossil taxa were grouped into three assemblages for analysis: Artiodactyla, Perissodactyla and “condylarths.” Only Perissodactyla is likely strictly monophyletic (dos Reis et al. 2012). Artiodactyla in this case is paraphyletic, as none of the early archaeocetes are sampled (Gingerich et al. 2001). As they represent an ecologically and biogeographically (Thewissen et al. 2007) distinct lineage from the artiodactyls found in the Eocene of North America, this does not affect the scope of this study. The group “condylarths,” however, has long been recognized as a “wastebasket” taxon (Archibald 1998), and is polyphyletic (Spaulding et al. 2009; Hooker and Russell 2012; Halliday et al. 2015). There is, however, good evidence for dietary competition between some “condylarths” and artiodactyls and perissodactyls (Radinsky 1966; Jernvall et al. 2000). The monophyly of several

“condylarth” families is well supported, and these will be addressed in the discussion.

Functional Grouping

The extant taxa were classified into one of five locomotor categories (arboreal/scansorial, semi-aquatic, semi-fossorial, terrestrial, and cursorial) based on the literature (Table 1). A principal components analysis was run on the Procrustes coordinates of the extant taxa only. The first 24 principal components (PCs), accounting for 95 % percent of the variance, were retained for further analysis. As the assumptions of multivariate normality and between group equality of the variance-covariance matrix did not hold (as is often the case for cross taxonomic, observational datasets), a non-parametric MANOVA (Anderson 2001) was run with locomotor mode as a factor to test the effect of locomotor mode on variation in distal femoral morphology. Pairwise Kruskal-Wallis tests were then used to identify individual PCs associated with locomotor mode. These were then used to construct a discriminant function analysis (DFA). Percent correct classification was estimated using leave-one-out cross validation (Kovarovic et al. 2011) (supplementary data 2).

The Procrustes coordinates of the fossil specimens were then projected into the principal component space defined by the extant specimens. Principal components analysis is a linear transformation of the multivariate data used to quantitatively represent specimens. Thus, any shape representation with the same number of coordinates can be represented in the principal components coordinate space calculated using a subset of said shapes. One limitation of this approach is that the principal components scores of the added specimens no longer represent a hierarchical arrangement of the variation in all specimens (as this is only the case for the specimens used to calculate the original principal component space). However, the advantage of this approach in this

Table 1 Locomotor categories and definitions (following Gould 2014)

| locomotor mode | abbreviation | definition |
|---------------------|--------------|---|
| Arboreal/Scansorial | A | Resides almost exclusively in trees or makes extensive use of inclined/vertical substrates. May show substrate use specialization (e.g., ground foraging, tree nesting) |
| Terrestrial | T | Uses almost exclusively ground level substrate. Does not locomote fast for sustained periods of time. |
| Semi-aquatic | Taq | Makes use of ground and aquatic substrate. When in water is capable of underwater swimming. |
| Semi-fossorial | Tf | Digs burrows larger than itself. |
| Cursorial | C | Ground dwelling, frequently engages in sustained bouts of high speed locomotion. |

study is that the coordinate system into which the fossil specimens were projected was one based on a sample specifically selected for functional locomotor diversity. This approach allowed the fossil taxa to be used as unknowns to be classified by the discriminant function calculated on the extant taxa. The DFA was used to assign locomotor modes to the fossil taxa based on their calculated principal components coordinates. One hundred and sixty five extant placental mammal specimens were used to calculate the DFA.

Stratigraphic Binning

Stratigraphic data were obtained from specimen data and cross referenced with published accounts (Woodburne 2004) to place each specimen within a defined North American Land Mammal Ages (NALMA). The Eocene NALMAs covered by this study are the Wasatchian, Bridgerian, and Uintan ages. Owing to the small number of Paleocene specimens, the Paleocene was treated as a single time bin. The time span covered by the sample is roughly 65 Ma to 39 Ma, based on estimated ages of the beginning of the Paleocene and the end of the Uintan, respectively.

Changes through Time: Ordination and Testing

Ordination of the fossil specimens in the plane of principal components space defined by the first and second principal components was used to represent changes through time. These plots are only a shorthand for viewing major changes in variation in morphospace through time, as they are low dimensional representations of high dimensional datasets.

Specific hypotheses of changes between and within time bins were tested using multivariate statistics. Differences between time bins and groups in the mean position show whether different groups occupy different regions of morphospace. Differences between time bins and groups in the variance reflect differences in the morphometric range occupied by different groups. Differences in mean were tested for using non parametric multivariate analysis of variance (Anderson 2001), using permutation tests with 5000 replicates. Differences in variances were tested using the complementary function (Anderson 2006), which uses the distribution of multivariate Euclidean distance from the mean as the basis for a Levene's test of equal variance. Pairwise comparisons were done using Tukey's Honestly Significant Difference test (HSD). Both tests were calculated on the 24 first PC scores calculated for the fossil specimens, a number which represents 95 % of the variation in the extant sample. All statistical calculations were done in R (R Core Team 2015) using the vegan package (Oksanen et al. 2013).

Partial Disparity

Partial disparity (Foote 1993) calculates the contribution of sub-groups to overall group disparity (morphological variation). Partial disparity works by using a measure of the distance between points in the morphological space to partition total morphological variation in a group among various subgroups. The method calculates the total morphological disparity as the sum of squared distances between each point and the overall centroid divided by the total group size, and the partial disparity (that is, the contribution of a given subgroup to that overall disparity) as the sum of squared distances to the overall group centroid of only the points in a given subgroup, divided by the total group size. Partial disparity was used to calculate the changing contribution of both taxonomic and functional groupings to ungulate disparity through time. The partial disparity was calculated using the first 24 principal component scores of the fossil specimens. All partial disparity calculations were done in the MDA package for MatLab (Navarro 2003).

Data Archiving

All data and code used in this study are archived on figshare.

Gould, Francois (2014): Data and code for distal femoral papers (Gould 2014, in review). **figshare**. <http://dx.doi.org/10.6084/m9.figshare.957635>

Results

Paleogene Artiodactyls, Perissodactyls, and “Condylarths” Occupy Different Areas of Morphospace

There is a significant difference in the centroid position of artiodactyls, perissodactyls, and “condylarths” across the entire time period (MANOVA, $F(1, 117) = 6.25, p = 0.0004$). There is no significant difference in variance between the three groups (Tukey's HSD: $p(\text{artiodactyls} = \text{perissodactyls}) = 0.0507, p(\text{perissodactyls} = \text{“condylarths”}) = 0.0967, p(\text{artiodactyls} = \text{“condylarths”}) = 0.9081$) (Fig. 1).

Overall Changes in Ungulate Morphospace Occur in the Eocene, not at the Paleocene-Eocene Boundary

Overall, there are significant differences between the mean of the distal femoral ungulate morphospace between the different time periods ($F(108,1) = 4.49, p = 0.0016$) (Fig. 2a). However, pairwise tests find no significant differences between the Paleocene and the Wasatchian ($F(57, 1) = 0.35, p = 0.9502$). Significant differences are recovered between the Wasatchian

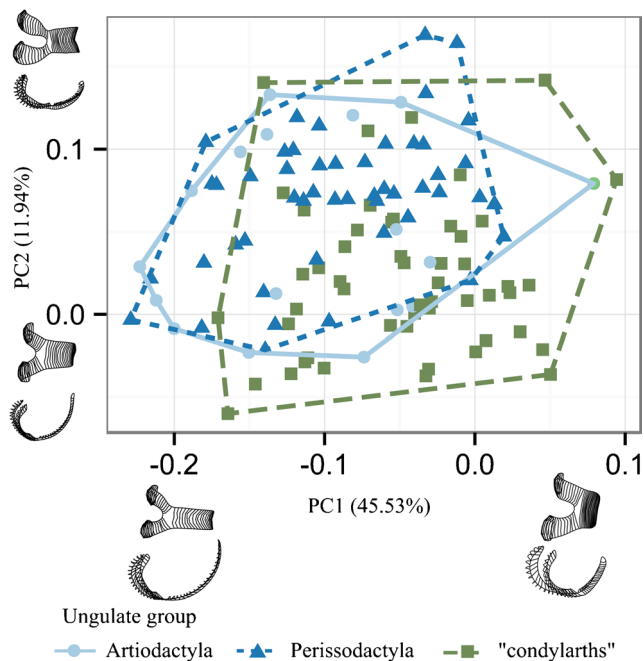


Fig. 1 Ordination plot of all fossils from all NALMAs along PC1 and PC2, by ungulate group. The shapes along the axes are lateral and distal views of theoretical distal femoral shape changes modelled along PC1 and PC2

and Bridgerian ($F(82, 1) = 4.16, p = 0.003$) and the Bridgerian and Uintan ($F(50, 1) = 759.85, p = 0.0002$). Significant differences in variance are found only between the Bridgerian and Uintan (Tukey's HSD, $p = 0.0241$).

Artiodactyls, Perissodactyls, and “Condylarth” Morphospaces Show Different Patterns of Change through the Time Period

There is a significant difference in the mean of the artiodactyl morphospace between the time bins ($F(15, 1) = 2.48, p = 0.0306$). Low sample size makes pairwise tests impossible, but the trend is for the mean to shift towards higher values of PC1, corresponding to a less cursorial morphology (Fig. 2b). Dispersion among artiodactyls is higher in the Uintan than in the Bridgerian (Tukey HSD, $p = 0.0072$).

There is a significant difference in the mean of the perissodactyl morphospace ($F(48, 1) = 3.83, p = 0.0042$). Pairwise comparison shows a change in the mean from the Wasatchian to the Bridgerian ($F(44, 1) = 3.66, p = 0.0060$) and from the Bridgerian to the Uintan ($F(32, 1) = 2.36, p = 0.0284$). The shift is associated with a change towards less cursorial morphologies in the distal femur. However, dispersion through time does not change significantly (Fig. 2b).

There is no significant difference in the mean of “condylarth” morphospace through time ($F(43, 1) = 0.80,$

$p = 0.5577$). There is also no significant change in “condylarth” dispersion through time (Fig. 2b).

Partial disparity shows that the contribution of each group to overall morphospace disparity in distal femoral morphology changes between time bins (Fig. 3a). In the Wasatchian, “condylarths” account for nearly two-thirds of total disparity, with perissodactyls accounting for most of the remainder. By the Bridgerian, “condylarths” account for less than a tenth of the total disparity, and most of the disparity comes from perissodactyls. In the Uintan, “condylarths” are extinct, and artiodactyls account for over three-quarters of the disparity, with the remainder attributed to perissodactyls.

Locomotor Diversity Varies between Ungulate Assemblages and Time Periods

Table 2 summarizes the locomotor classification of all the fossil specimens from each group in each time period by the discriminant function. Fig. 4 shows mean distal femoral shapes for each locomotor category as calculated from the extant taxa. Briefly, cursorial taxa have craniocaudally elongated, mediolaterally compressed distal femora with a deep patellar groove that is long, narrow, and extends proximally above the proximal height of femoral condyle. Conversely, arboreal taxa have mediolaterally broad and craniocaudally shallow distal femora with short, flat patellar grooves. Cursorial and terrestrial taxa are present in all ungulate assemblages and time bins. A significant number of “condylarth” specimens in the Wasatchian are recovered as arboreal/scansorial specialists. Phenacodontid “condylarth” specimens, like artiodactyls and perissodactyls, are either terrestrial or cursorial. Conversely, most arctocyonids are recovered as arboreal. Mesonychids and periptychids are recovered as primarily terrestrial. Hyposodontids show the greatest locomotor diversity among “condylarth” groups (supplemental information 3). The contribution of different locomotor categories to overall morphological disparity is shown in Fig. 3b.

Eocene Artiodactyls and Perissodactyls Do not Have Distal Femoral Morphologies consistently Similar to Modern Cursors

Overall, there is no close match between the distal femoral morphologies of Eocene artiodactyls and perissodactyls and the distal femoral morphologies in the sample of extant cursorial mammals used in this study (Table 3). Only Bridgerian artiodactyls have a mean distal femoral morphology not significantly different from modern cursorial mammals.

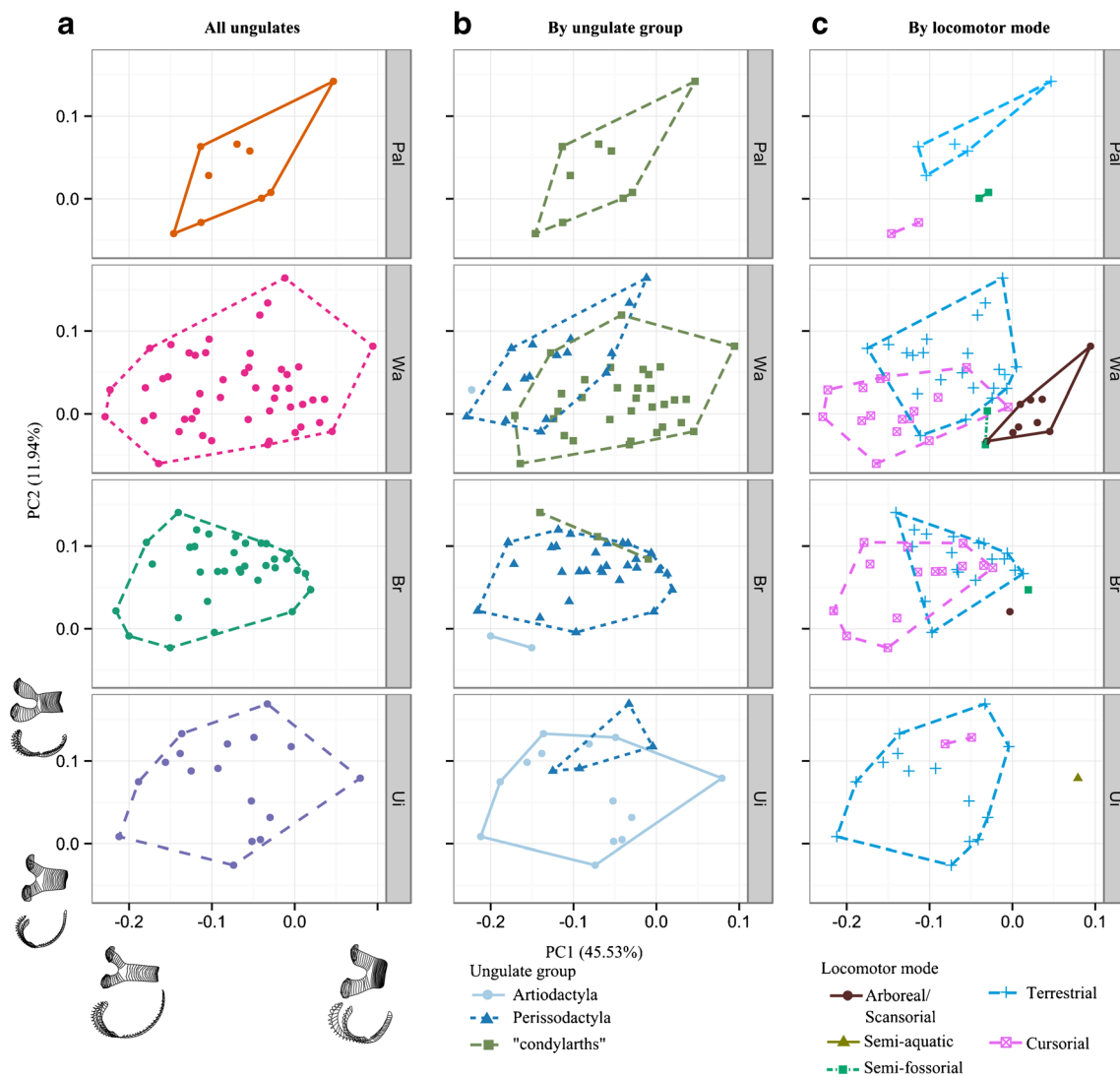


Fig. 2 Ordination plots of fossil specimens in all time bins along PC1 and PC2. Each row of panels represents data from a single time period: Pal: Paleocene, Wa: Wasatchian, Br: Bridgerian, Ui: Uintan. In column **a** all ungulates are shown; in column **b** specimens are grouped by ungulate

group; in column **c** specimens are grouped by locomotor mode (estimated from DFA classification). The shapes on the *bottom left graph* are lateral and distal views of theoretical distal femoral shape changes modelled along PC1 and PC2 and are applicable to interpret the data in each panel

Discussion

There Is Limited Evidence for Significant Overlap in Locomotor Mode between “Condylarths” and Artiodactyls and Perissodactyls

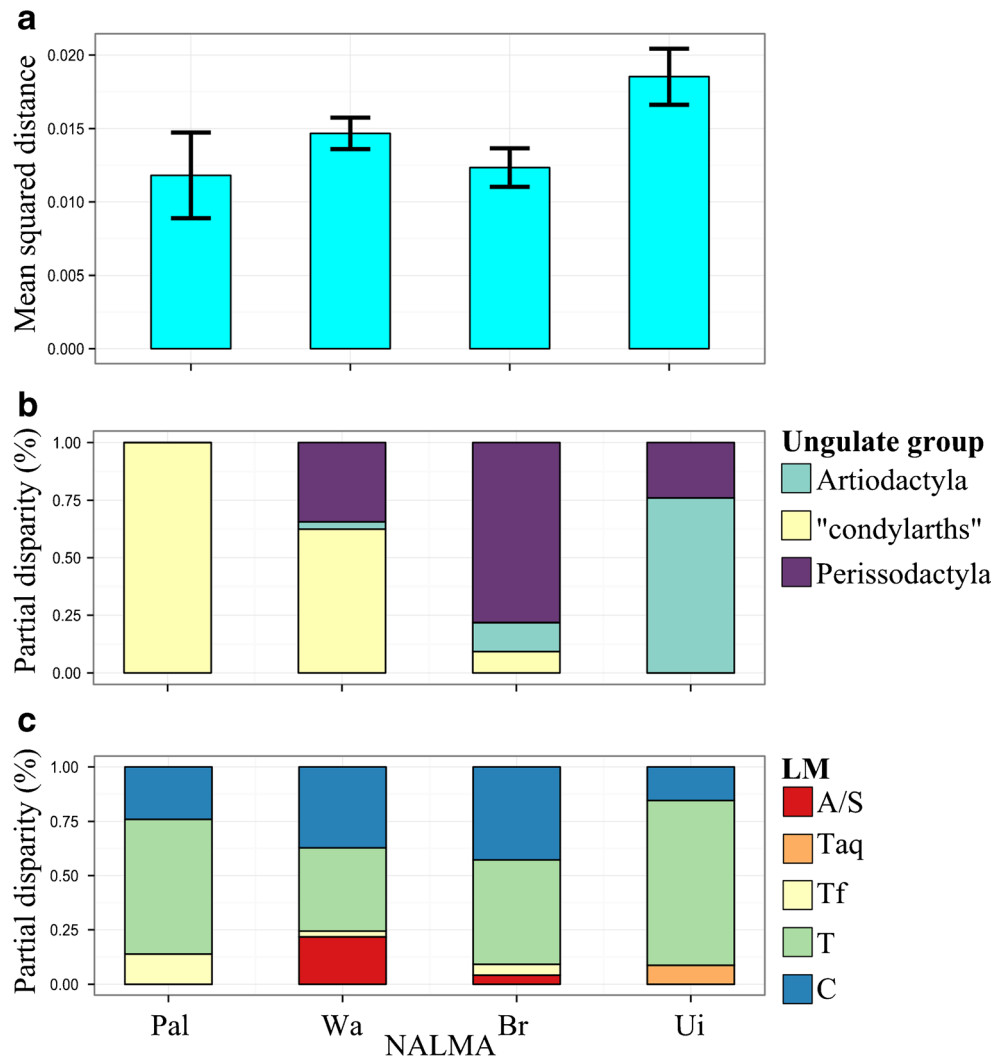
The distal femora of Paleogene “condylarths,” perissodactyls, and artiodactyls occupy different regions of morphospace. This differs from locomotor diversity, where “condylarths” are represented in all locomotor categories, but artiodactyls and perissodactyls are mostly restricted to the terrestrial and cursorial categories. Within each time bin, morphological overlap between artiodactyls, perissodactyls, and the assemblage of endemic “condylarths” is limited, challenging the simplistic model of ecological competition among Paleogene

ungulates, despite functionally similar dentitions (Jernvall et al. 1996). This undermines the idea that artiodactyl and perissodactyl cursorial locomotion per se represents a key innovation of these groups.

The distribution of “condylarths” among locomotor categories clusters taxonomically (supplementary data 3). Most of these results are in agreement with previously published accounts based on comparative anatomy (Rose 1982, 1987, 1990; Zack et al. 2005), although *Pachyaena* was previously described as cursorial (O’Leary and Rose 1995).

By the end of the time period examined, faunal turnover is complete (there are no more “condylarths” present). The effect on locomotor diversity is primarily reflected in the disappearance of taxa that are not terrestrial or cursorial. Thus, major changes in the ecological composition of Paleogene

Fig. 3 Disparity through time. **a** total ungulate disparity (+/- 1 st. dev.); **b** partial disparity (as proportion of total) by ungulate group; **c** partial disparity (as proportion of total) by locomotor mode (LM) (A/S: arboreal/scansorial; Taq; semi-aquatic; Tf: semi-fossorial; T: terrestrial; C: cursorial). Pal: Paleocene; Wa: Wasatchian; Br: Bridgerian; Ui: Uintan



ungulates are occurring outside the habitats of artiodactyls and perissodactyls. In terms of the first hypothesis put forward in

the introduction, artiodactyl and perissodactyl distal femoral shape differs on average from that of “condylarths,” but there

Table 2 Classification of fossil specimens to locomotor group by discriminant function analysis

| | Arboreal/Scansorial | Semi- Aquatic | Semi- fossorial | Terrestrial | Cursorial |
|----------------|---------------------|---------------|-----------------|-------------|-----------|
| Paleocene | | | 2 | 5 | 2 |
| “condylarths” | | | 2 | 5 | 2 |
| Wasatchian | 9 | | 2 | 22 | 16 |
| “condylarths” | 9 | | 2 | 13 | 8 |
| Artiodactyla | | | | | 1 |
| Perissodactyla | | | | 9 | 7 |
| Bridgerian | 1 | | 1 | 18 | 14 |
| “condylarths” | | | | 3 | |
| Artiodactyla | | | | | 2 |
| Perissodactyla | 1 | | 1 | 15 | 12 |
| Uintan | | 1 | | 14 | 2 |
| Artiodactyla | | 1 | | 10 | 2 |
| Perissodactyla | | | | 4 | |

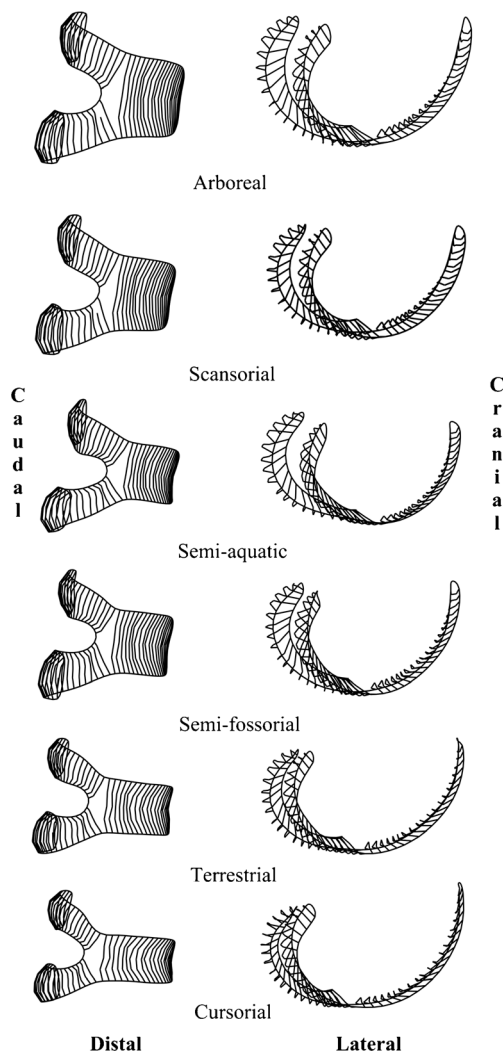


Fig. 4 Models of group means of distal femoral morphologies by locomotor category, calculated from the Procrustes scores of the extant taxon sample

is significant morphological and functional overlap in the cursorial/terrestrial region of morphospace. As such, the impact of the appearance of artiodactyls and perissodactyls on the range of morphology present in the Eocene is less than expected.

Table 3 Results of pairwise MANOVAs comparing means of fossil artiodactyls and perissodactyls in each time bin with the mean of a sample of extant cursorial mammals

| | Artiodactyla | | Perissodactyla | |
|------------|--------------|---------------|----------------|---------------|
| | F | p | F | p |
| Wasatchian | N/A | N/A | 4.35 | 0.0016 |
| Bridgerian | 1.48 | 0.146 | 12.47 | 0.0004 |
| Uintan | 5.26 | 0.0004 | 8.49 | 0.0004 |

Bold values indicate significant differences. (Test could not be performed on Wasatchian artiodactyls as sample size too small)

The Wasatchian Fauna Has More Locomotor Diversity than Both the Paleocene and the Later Eocene

The immediate post-PETM time period, the Wasatchian, was a period of elevated locomotor diversity. The Wasatchian is the only time period where a significant fraction of the disparity is due to locomotor modes other than terrestrial or cursorial. There is a trend towards increased overall disparity in distal femoral joint shape. Taxonomically, roughly one-third of the disparity is in the perissodactyls, with most of the remaining two-thirds in the various “condylarth” families. This distribution is more even than in either the Paleocene, or the Bridgerian.

The immigration of artiodactyls and perissodactyls (Rose et al. 2014) into North America after the PETM has a subtle impact on locomotor ecomorphospace diversification. Artiodactyls have little impact on disparity at the taxonomic level. Perissodactyls, in contrast, do expand the range of distal femoral morphology seen in ungulates. Just under half of artiodactyl and perissodactyl specimens in the Wasatchian are classified as cursorial, and the relative contribution of cursorial taxa to disparity increases in the Wasatchian relative to the Paleocene. However, as the number of cursorial “condylarths” is also larger in the Wasatchian than the Paleocene sample, it is unclear how much of this effect can be attributed solely to the invasive taxa. Furthermore, the Wasatchian differs significantly from the Paleocene sample in the presence of the arboreal arctocyonid “condylarths” *Thryptacodon* and *Chriacus*. Thus, the expansion and locomotor diversification of the distal femoral morphospace of Paleogene ungulates is only in part due to the appearance of artiodactyls and perissodactyls.

The extinction of the various “condylarth” families is associated with a trend towards a reduction in overall ungulate disparity. In terms of locomotor mode, the clearest change is the complete disappearance of the cluster of arboreal-type distal femora from the Bridgerian morphospace. Bridgerian “condylarths” (mesonychids) contribute little to overall disparity as they are similar in their locomotor adaptations to artiodactyls and perissodactyls. However, mesonychids are highly derived dentally (Szalay 1969), so there was likely no direct competition occurring. Thus, although we see a pattern that is superficially consistent with hypothesis 2 (a reduction in morphospace disparity associated with the decline of “condylarths”), the way in which the morphospace contracts is not consistent with a hypothesis of competitive exclusion.

Cursorial and Terrestrial Specialization Are Persistent through Time, though They Do Not Appear to Drive Patterns in the Fossil Record

Cursorial taxa are present in all time bins, including the Paleocene, where there are no artiodactyls or perissodactyls. Because cursorial and terrestrial “condylarths” overlap in

distal femoral morphology with early perissodactyls, cursorial specializations of the postcranial skeleton are not key innovation of perissodactyls. Artiodactyls, more rare than perissodactyls in the Wasatchian and Bridgerian sample, contribute little to overall ungulate disparity in those time periods. Thus, an adaptive radiation of artiodactyls did not result from their cursorial morphology in the immediate aftermath of the PETM, casting doubt on the idea that it may be the order's key innovation (Van Valen 1971b). Dental studies suggest that artiodactyl teeth also remain relatively conservative until later in the Cenozoic (Jernvall et al. 1996).

Paleogene artiodactyls and perissodactyls may not be specialized cursors. The DFA classifications favor a terrestrial over a cursorial classification for most of the specimens in our analysis. Artiodactyls and perissodactyls were distinct from extant cursors for most time periods. Part of this difference may be due to body size related differences (Biewener 1989). This contradicts hypothesis 3, and challenges the notion that cursorial locomotion is ecologically defining of artiodactyls and perissodactyls at all times.

The Uintan has the highest disparity of any of the intervals examined. Much of that disparity is accounted for by artiodactyls, unlike in the Bridgerian and the Wasatchian. A cluster of specimens of the agrochoerid *Diplobunops* is located close to the region of the morphospace occupied by semi-fossorial taxa. This unusual taxon has secondarily re-evolved claw-like unguals, and has been hypothesized to be semi-fossorial or even arboreal (Ludtke 2007). This may represent an artiodactyl taxon exploiting a niche previously occupied by “condylarths.”

This study indicates that more work is needed to understand the impact of the post-PETM migration of artiodactyls and perissodactyls on the endemic “condylarths” of North America. Dentally similar taxa (such as arctocyonid “condylarths” and dichobunid artiodactyls (Van Valen 1971a)) had different locomotor modes and substrate uses, suggesting they occupied different habitats (arboreal versus cursorial), whereas taxa that are similar in locomotor mode (mesonychids and perissodactyls) have very different dentitions. Certain groups (e.g., early equids and phenacodontids (Radinsky 1966; Thewissen and Domning 1992)) may have competed. Overall, climate and habitat changes through the Eocene may have driven indirect interactions affecting the three groups differently (Janis 1993; Chew 2009). This study finds little support for a key role of their derived cursorial morphology in the eventual success of artiodactyls and perissodactyls in the Paleogene. The pattern recovered in this study is consistent neither with a scenario of locomotor competitive exclusion between invasive modern ungulates and extant “condylarths,” nor with a scenario of adaptive radiation of perissodactyls and artiodactyls driven by a key locomotor innovation. In the early Paleogene at least, there is little evidence

of a sudden explosive success of the modern ungulate orders in terms of morphological disparity or taxonomic diversity.

Limitations of the Study

The specimens used represent the largest sample of distal femoral material yet on North American Paleogene ungulates. Sampling remains uneven between time periods. In particular, the Paleocene is undersampled, and the Wasatchian likely oversampled. Cross-referencing the specimens in this study with published taxon lists (Woodburne 2004; Secord 2008) shows that the data are relatively complete. However, differential sampling effort is known to affect disparity measures in particular. In most cases, samples were too small to allow rarefaction to be used. Thus, only variance based disparity estimators, which are less sensitive to outliers (Foote 1997), were included.

Certain Wasatchian taxa are known from dental remains to be present in the Paleocene, most notably arctocyonid “condylarths,” which affects the conclusions of this work regarding the Paleocene-Eocene transition. The ranges of these taxa were not extended into the Paleocene, to do so would have made questionable assumptions about stasis in postcranial morphology given published accounts of these taxa (Rose 1987, 1996). A few “condylarths” do survive into the Uintan that are not represented in this sample (Gunnell et al. 2009). Again, the ranges were not extended from other ages, owing to the generally poorly known postcranial variation.

The absence of a phylogenetic framework for this study limits the evolutionary conclusions that can be drawn from the ecological patterns. The relationship of artiodactyls and perissodactyls to each other is unclear (Spaulding et al. 2009; dos Reis et al., 2012). As for the phylogenetic position of the various “condylarth” families, there is no consensus (Spaulding et al. 2009; Zack 2009; Halliday et al. 2015). Of particular interest would be to clarify the relationship between phenacodontids and perissodactyls, as well as the affinities of artiodactyls to other “condylarths.”

Conclusion

The migration of artiodactyls and perissodactyls into North America around the PETM is accompanied by an increase in morphological disparity of the distal femoral articular surface. The increase is driven by both taxonomic and ecological factors, but there is no indication that cursoriality is a key innovation of artiodactyls and perissodactyls when compared to endemic “condylarths.” Cursorial and terrestrial distal femora occur in all time periods. Extinction primarily affects arboreal and semi-fossorial taxa, but there is little evidence of concomitant radiation of artiodactyls and perissodactyls. Further work will clarify the effects of PETM migration events on the

ecology of the mammalian faunas of North America in the Paleogene, but it appears that, among ungulates, Paleogene ecological success is driven primarily by abiotic factors such as a climate change. The invasive modern orders may have been opportunists (although the dominance of early equids in certain faunas suggests they were highly successful at this). Postcrania are integral to understanding changing biota in the Eocene.

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Compliance with Ethical Standards

Conflict of Interest The author reports no conflict of interest.

References

- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26: 32–46
- Anderson MJ (2006) Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62: 245–253
- Andersson K (2004) Elbow-joint morphology as a guide to forearm function and foraging behaviour in mammalian carnivores. *Zool J Linn Soc* 142: 91–104
- Andersson K, Werdelin L (2003) The evolution of cursorial carnivores in the tertiary: implications of elbow-joint morphology. *Proc Roy Soc B: Biol Sci* 270: S163–S165
- Archibald JD (1998) Archaic ungulates (“Condylarthra”). In: Janis CM, Scott KM, Jacobs LL (eds) *Evolution of Tertiary Mammals of North America Volume 1: Terrestrial Carnivores, Ungulates and Ungulate-like Mammals*. Cambridge University Press, Cambridge, pp 292–329
- Biewener AA (1989) Scaling body support in mammals: limb posture and muscle mechanics. *Science* 245: 45–48
- Bookstein FL (1997) Landmark methods for forms without landmarks: morphometrics of group differences in outline shape. *Med Image Anal* 1: 225–243
- Chew AE (2009) Paleocology of the early Eocene Willwood mammal fauna from the central Bighorn Basin, Wyoming. *Paleobiology* 35: 13–31
- Cooper LN, Seiffert ER, Clementz M, Madar SI, Bajpai S, Hussain ST, Theewissen JGM (2014) Anthracobunids from the middle Eocene of India and Pakistan are stem perissodactyls. *PLoS One* 9 (10): e109232
- dos Reis M, Inoue J, Hasegawa M, Asher RJ, Donoghue PCJ, Yang Z (2012) Phylogenomic datasets provide both precision and accuracy in estimating the timescale of placental mammal phylogeny. *Proc Roy Soc B: Biol Sci* 279: 3491–3500
- Fabre A-C, Cornette R, Slater G, Argot C, Peigné S, Goswami A, Pouydebat E (2013) Getting a grip on the evolution of grasping in musteloid carnivores: a three-dimensional analysis of forelimb shape. *J Evol Biol* 26: 1521–1535
- Foote M (1993) Contributions of individual taxa to overall morphological disparity. *Paleobiology* 19: 403–419
- Foote M (1997) The evolution of morphological diversity. *Annu Rev Ecol Syst* 28: 129–152
- Gingerich PD (2006) Environment and evolution through the Paleocene–Eocene thermal maximum. *Trends Ecol Evol* 21 (5): 246–53
- Gingerich PD, ul Haq M, Zalmout IS, Khan IH, Malkani MS (2001) Origin of whales from early artiodactyls: hands and feet of Eocene Protocetidae from Pakistan. *Science* 293: 2239–2242
- Gould FDH (2014) To 3D or not to 3D, that is the question: do 3D surface analyses improve the ecomorphological power of the distal femur in placental mammals? *PLoS one* 9: e91719
- Gunnell GF, Murphy PC, Stucky RK, Townsend KEB, Robinson P, Zonneveld J-P, Bartels WS (2009) Biostratigraphy and biochronology of the latest Wasatchian, Bridgerian, and Uintan North American Land Mammal “Ages.” In: Albright LB III (ed) *Papers on Geology, Vertebrate Paleontology, and Biostratigraphy in Honor of Michael O. Woodburne*. Museum of Northern Arizona Bulletin 65, Flagstaff pp. 279–330
- Gunz P, Mitteroecker P, Bookstein FL (2005) Semilandmarks in three dimensions. In: Slice DE (ed) *Modern Morphometrics in Physical Anthropology*. Plenum Press, New York
- Halliday TJD, Upchurch P, Goswami A (2015) Resolving the relationships of Paleocene placental mammals. *Biol Rev*. doi:10.1111/brv.12242
- Hooker JJ, Russell DE (2012) Early Palaeogene Louisinidae (Macroscelidea, Mammalia), their relationships and north European diversity. *Zool J Linn Soc* 164: 856–936
- Janis CM (1993) Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annu Rev Ecol Syst* 24: 467–500
- Jernvall J, Hunter JP, Fortelius M (1996) Molar tooth diversity, disparity, and ecology in Cenozoic ungulate radiations. *Science* 274: 1489–1492
- Jernvall J, Hunter JP, Fortelius M (2000) Trends in the evolution of molar crowntypes in ungulate mammals. In: Teaford MF, Smith, MM, Ferguson MWJ (eds) *Development, Function and Evolution of Teeth*. Cambridge University Press, Cambridge, pp 269–281
- Kitchell JA (1985) Evolutionary paleocology: recent contributions to evolutionary theory. *Paleobiology* 11: 91–104
- Kitts DB (1956) American *Hyracotherium* (Perissodactyla, Equidae). *Bull Am Mus Nat Hist* 110: 1–60
- Klingenberg CP (2011) Morpho J: an integrated software package for geometric morphometrics. *Mol Ecol Res* 11: 353–357
- Kovarovic K, Aiello LC, Cardini A, Lockwood CA (2011) Discriminant function analyses in archaeology: are classification rates too good to be true? *J Archaeol Sci* 38: 3006–3018
- Ludtke JA (2007) Family Agriocheridae. In: Prothero DR, Foss SE (eds) *The Evolution of Artiodactyls*. Johns Hopkins University Press, Baltimore, pp 151–156
- Maas MC, Krause DW, Strait SG (1988) The decline and extinction of Plesiadapiformes (Mammalia: ?Primates) in North America: displacement or replacement. *Paleobiology* 14: 410–431
- McInerney FA, Wing SL (2011) The Paleocene-Eocene thermal maximum: a perturbation of carbon cycle, climate, and biosphere with implications for the future. *Annu Rev Earth Planet Sci* 39: 489–516
- Navarro N (2003) MDA: a MATLAB-based program for morphospace-disparity analysis. *Computers & Geosciences* 29: 655–664
- O’Leary MA, Rose KD (1995) Postcranial skeleton of the early Eocene mesonychia *Pachyaena* (Mammalia: Mesonychia). *J Vertebr Paleontol* 15: 401–430

- O'Leary MA, Bloch JI, Flynn JJ, Gaudin TJ, Giallombardo A, Giannini NP, Goldberg SL, Kraatz BP, Luo ZX, Meng J, Ni X, Novacek MJ, Perini FA, Randall ZS, Rougier GW, Sargis EJ, Silcox MT, Simmons NB, Spaulding M, Velazco PM, Weksler M, Wible JR, Cirranello AL (2013) The placental mammal ancestor and the post-K-Pg radiation of placentals. *Science* 339: 662–667
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2013) *Vegan*: community ecology package. R package
- Polly PD (2008) Adaptive zones and the pinniped ankle: a three-dimensional quantitative analysis of carnivoran tarsal evolution. In: Sargis EJ, Dagosto M (eds) *Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay*. Springer, Dordrecht, pp 167–196
- R Core Team (2015) *R*: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Radinsky LB (1966) The adaptive radiation of the phenacodontid condylarths and the origin of the Perissodactyla. *Evolution* 20: 408–417
- Rensberger JM (1986) Early chewing mechanisms in mammalian herbivores. *Paleobiology* 12: 474–494
- Rose KD (1981) The Clarkforkian land-mammal age and mammalian faunal composition across the Paleocene-Eocene boundary. *Univ Michigan Pap Paleontol* 26: 1–182
- Rose KD (1982) Skeleton of *Diacodexis*, oldest known artiodactyl. *Science* 216: 621–623
- Rose KD (1987) Climbing adaptations in the early Eocene mammal *Chriacus* and the origin of Artiodactyla. *Science* 236: 314–316
- Rose KD (1990) Postcranial skeletal remains and adaptations in early Eocene mammals from the Willwood Formation, Bighorn Basin, Wyoming. In: Bown TM, Rose KD (eds) *Dawn of the Age of Mammals in the Northern Part of the Rocky Mountain Interior, North America*. *Geol Soc Am Spec Pap* 243: 107–134
- Rose KD (1996) On the origin of the order Artiodactyla. *Proc Natl Acad Sci USA* 93: 1705–1709
- Rose KD, Chew AE, Dunn RH, Kraus MJ, Fricke HC, Zack SP (2012) Earliest Eocene mammalian fauna from the Paleocene-Eocene thermal maximum at Sand Creek divide, southern Bighorn Basin, Wyoming. *Univ Michigan Pap on Paleontol* 36: 1–122
- Rose KD, Holbrook LT, Rana RS, Kumar K, Jones KE, Ahrens HE, Missiaen P, Sahni A, Smith T (2014) Early Eocene fossils suggest that the mammalian order Perissodactyla originated in India. *Nature Commun* 5, doi:10.1038/ncomms6570
- Secord R (2008) The Tiffanian land-mammal age (middle and late Paleocene) in the northern Bighorn Basin, Wyoming. *Univ Michigan Pap Paleontol* 35: 1–192
- Secord R, Bloch JI, Chester SGB, Boyer DM, Wood AR, Wing SL, Kraus MJ, McInerney FA, Krigbaum J (2012) Evolution of the earliest horses driven by climate change in the Paleocene-Eocene thermal maximum. *Science* 335: 959–962
- Spaulding M, O'Leary MA, Gatesy J (2009) Relationships of Cetacea (Artiodactyla) among mammals: increased taxon sampling alters interpretations of key fossils and character evolution. *PLoS One* 4: e7062
- Szalay FS (1969) Origin and evolution of function of the mesonychid condylarth feeding mechanism. *Evolution* 23: 703–720
- Thewissen JGM, Domning DP (1992) The role of phenacodontids in the origin of the modern orders of ungulate mammals. *J Vertebr Paleontol* 12: 494–504
- Thewissen JGM, Cooper LN, Clementz MT, Bajpai S, Tiwari BN (2007) Whales originated from aquatic artiodactyls in the Eocene epoch of India. *Nature* 450: 1190–1194
- Van Valen L (1971a) Toward the origin of artiodactyls. *Evolution* 25: 523–529
- Van Valen L (1971b) Adaptive zones and the orders of mammals. *Evolution* 25: 420–428
- Van Valen L (1978) The beginning of the age of mammals. *Evol Theory* 4: 45–80
- Wesley-Hunt GD (2005) The morphological diversification of carnivores in North America. *Paleobiology* 31: 35–55
- Wood A, Bebej R, Manz C, Begun D, Gingerich P (2011) Postcranial functional morphology of *Hyracotherium* (Equidae, Perissodactyla) and locomotion in the earliest horses. *J Mammal Evol* 18: 1–32
- Woodburne MO (ed) (2004) *Late Cretaceous and Cenozoic Mammals of North America*. Columbia University Press, New York
- Zack SP (2009) The phylogeny of eutherian mammals: a new analysis emphasizing dental and postcranial morphology of Paleocene taxa. Dissertation, Johns Hopkins School of Medicine, Baltimore
- Zack SP, Penkrot TA, Bloch JI, Rose KD (2005) Affinities of 'hyposodontids' to elephant shrews and a Holarctic origin of Afrotheria. *Nature* 434: 497–501