

THE IMPACT OF REGIONAL CLIMATE ON THE EVOLUTION OF MAMMALS: A CASE STUDY USING FOSSIL HORSES

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One of the classic examples of faunal turnover in the fossil record is the Miocene transition from faunas dominated by anchitheriine horses with low-crowned molar teeth to faunas with hipparionine horses characterized by high-crowned teeth. The spread of hipparionine horses is associated with increased seasonality and the expansion of open habitats. It is generally accepted that anchitheriine horses did not display an evolutionary increase in tooth crown height prior to their extinction. Nevertheless, to test whether anchitheriines showed any changes interpretable as adaptation to local conditions, we analyzed molar teeth from multiple populations of *Anchitherium* in three dimensions. Our results show differences in tooth morphology that suggest incipient hypsodonty in Spain, the first region experiencing increasingly arid conditions in the early Miocene of Europe. Furthermore, analyses of tooth wear show that Spanish specimens cluster with present ungulates that eat foliage together with grasses and shrubs, whereas German specimens cluster with present-day ungulates that eat mostly foliage. Taken together, even a taxon such as *Anchitherium*, with a long and successful history of forest adaptation, did respond to regional environmental changes in an adaptive manner.

KEY WORDS: *Anchitherium*, dental durability, GIS, Miocene, palaeodiet, three-dimensional (3D) scanning, tooth crown height, tooth wear.

Anchitherium was a widespread genus that had a long history during the Miocene (Jernvall and Fortelius 2004). Its origins lie in North America where the first fossils are found in the latest Oligocene–earliest Miocene times (25–23 million years ago [mya], e.g., Marsh 1874; Forsten 1991). *Anchitherium* has been reconstructed to be a browser that was adapted to forest environments of Early Miocene times (Abusch-Siewert 1983; Forsten 1991). It has highly molarized teeth (premolars and molar are similar, see Fig. 1). *Anchitherium* migrated during the Early Miocene

(MN3, 20 mya) from North America to Eurasia (Forsten 1991) where it flourished in forest environments.

During the Late Miocene a great environmental change took place, with the spread of more arid conditions and C4 grasslands, and increased seasonality (Bernor 1983; Cerling et al. 1997; Utescher et al. 2000; Mosbrugger et al. 2005). This environmental change also caused modifications in the distribution and abundance of mammalian genera so that increasingly the most well-represented taxa had hypsodont teeth (Jernvall and Fortelius 2002). One of the taxa affected by this change was *Anchitherium*. The decline of *Anchitherium* is classically attributed to a failure to adapt to the changing conditions of the drying world.

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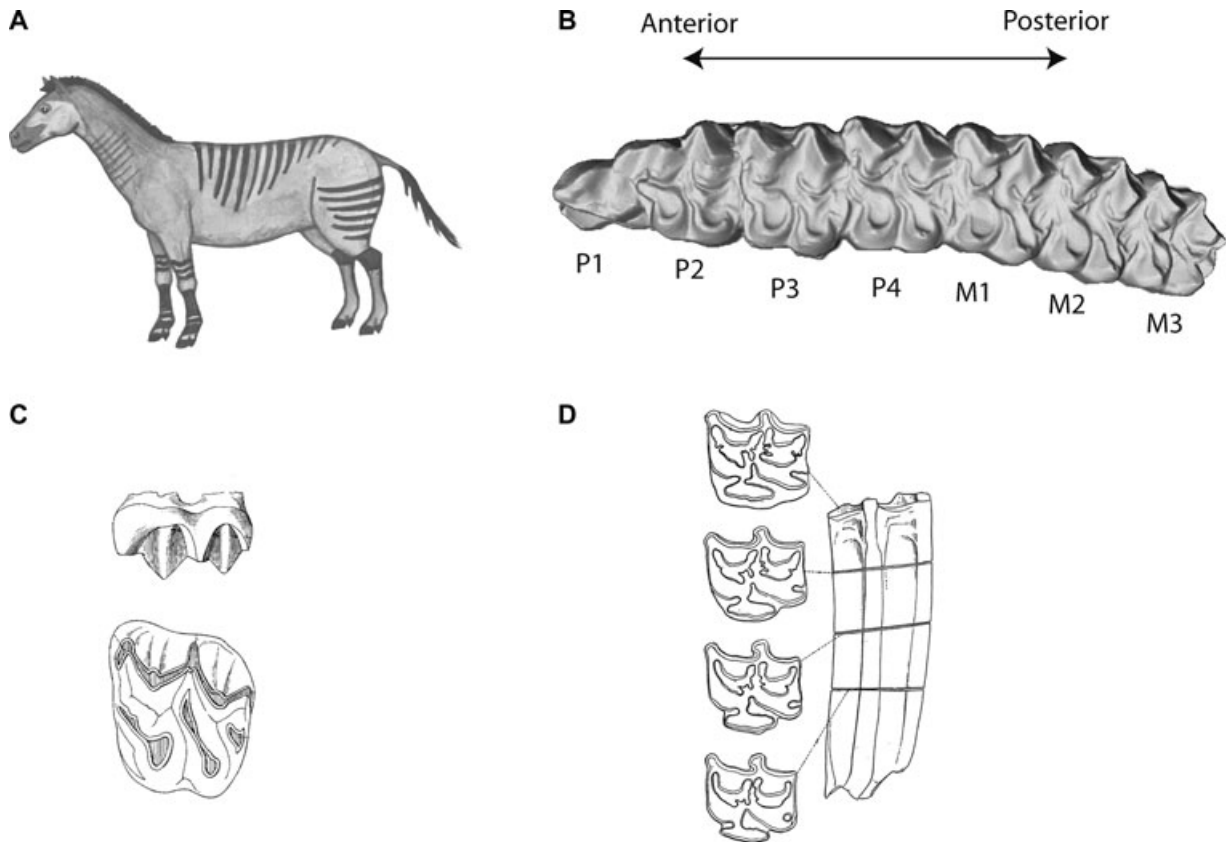


Figure 1. (A) Life reconstruction of *Anchitherium aurelianense*. Illustration by Laura Säilä. (B) The left upper cheek-teeth row of *A. aurelianense*, showing teeth from first premolar to last molar (P1–M3). (C) Illustration of low-crowned *A. aurelianense* cheek tooth, from the side (upper) and top (lower). Modified from Osborn (1907). (D) Illustration of high-crowned horse (*Equus complicatus*) upper cheek tooth from the side, with sectioned slices to show crown shape at different levels of wear. Note that the crown retains its shape throughout the tooth, allowing functionality to be preserved with increased wear. Modified from Gidley (1901).

According to Forsten (1991), the only adaptation toward increased wear resistance in Middle to Early Late Miocene anchitheriine horses was a trend of increasing occlusal surface area caused by increased relative tooth size, observed in North America as well as in Eurasia from around the Middle-Late Miocene transition onwards. She also suggested that during Early and Early Middle Miocene (MN4–MN5, 18–15 mya) there was morphological stasis in *Anchitherium*.

The general question behind this study concerns niche conservatism and to what degree species and genera “track” their preferred environments and how their potential to adapt to changing local and regional conditions is determined. Here, we use tooth shape and wear analyses of *Anchitherium* from two different settings, Germany and Spain, to explore this question. The general question can be broken down into two specific and testable primary hypotheses: (1) There is a significant difference in degree of hypsodonty between the German and Spanish populations. (2) Differences in hypsodonty correlate with diet, and hence reflect more arid living environments in Spain compared to more mesic

conditions in Germany. For the latter hypothesis, the diet is inferred using tooth-wear analysis. We estimate whether differences in tooth height offset the life-span-reducing effects of increased tooth-wear rates due to eating more abrasive vegetation. For many present-day ungulates, tooth wear is a proximate cause of senescence (Skogland 1988; Loe et al. 2003; see also King et al. 2005) and tooth hypsodonty and wear rates differ among species with different dietary regimes (Solounias et al. 1994).

The questions outlined above are usually very hard to infer from the fossil record. Whereas the fossil record provides the benefit of hindsight, little material is usually available with limited temporal resolution. Here, we examine *Anchitherium* teeth collected from Spain and Germany from early Middle Miocene (17–14 mya) a time interval when *Anchitherium* was in its prime and the dispersal of hipparionine horses to the Old World was millions of years away. Our selected time interval postdates the arrival of anchitheriine horses in the Old World by millions of years, and is highly unlikely to reflect events related to the invasion process.

Hypsodonty

Hypsodonty refers to the tooth crown height. The higher the crown part of the tooth is, more hypsodont the animal. For example, the modern horses of the genus *Equus* are very hypsodont with high tooth crowns, whereas *Alces alces* (moose) and many deer species are brachydont, with low tooth crowns.

Hypsodonty is fundamentally an adaptive response to increasing demands for wear tolerance and functional durability brought about by the development of more fibrous or abrasive plants in a progressively more open and arid-adapted vegetation (Van Valen 1960; Fortelius 1985; Janis and Fortelius 1988; Solounias et al. 1994; Fortelius and Solounias 2000). Details reflecting regional ecology are recorded in the dental morphology (Fortelius and Hokkanen 2001; Fortelius et al. 2002; Jernvall and Fortelius 2002). The factors favoring hypsodonty are many, but virtually all increase in effect with increasing aridity and openness of the landscape (increased fibrousness, increased abrasiveness due to intracellular silica or extraneous dust, and decreased nutritive value resulting in requiring more food to be processed) (Fortelius 1985; Janis and Fortelius 1988).

We believe that hypsodonty implies a condition of the vegetation that might be termed “generalized water stress,” either in overall conditions, or perhaps more commonly as a regularly occurring extreme period, such as a dry season. Some previous analyses have concluded that habitat and climate do not play an important role in the evolution of hypsodonty (Williams and Kay 2001; Muhlbachler and Solounias 2006). Using present-day ungulate data Mendoza and Palmqvist (2008) argue that habitat and climate do play an important role in the development of hypsodonty. There is an ongoing discussion on the causes behind hypsodonty, especially on the exact roles that factors such as grasses and open habitats play in the evolution of hypsodonty (e.g., Williams and Kay 2001; Strömberg 2006; DeMiguel et al. 2008; Mendoza and Palmqvist 2008). Although we cannot completely exclude the possibility of nonadaptive causes behind hypsodonty, evolving hypsodonty requires extensive modification of skull structures to physically accommodate tall teeth. Hence, even if the underlying selective factors may not be detectable in each case of hypsodonty, we favor an adaptive explanation, as have many authors previously.

Here, we investigate minor changes in brachydont tooth morphology that are the first steps toward a higher tooth crown. As teeth become hypsodont, cusps slopes become vertical and through three-dimensional (3D) measurements, we can reveal early stages of these morphological differences relevant to tooth volume.

Environmental Setting

During the Cenozoic (last 65 mya), the climate successively changed from the warm-humid greenhouse climate of the Pa-

leogene into the Quaternary icehouse phase characterized by its glacial–interglacial cycles (e.g., Retallack 2001; Zachos et al. 2001 for reviews). The Miocene (23.8–5.3 mya) belongs to the late phase of the Cenozoic cooling. Corresponding to climate changes, vegetation also underwent large changes (e.g., Willis and McElwain 2002; Mosbrugger et al. 2005). Palaeobotanical data show considerable vegetation changes from the Early to the Late Miocene. For example the grasslands became dominant parts of the ecosystems and subtropical-temperate evergreen forests were replaced by deciduous forests in Europe (e.g., Strömberg 2002, 2004; Willis and McElwain 2002; Mosbrugger et al. 2005).

During the early Middle Miocene (17–14 Ma), the German Molasse basin was a wetland area, a progressively drying part of the western end of the Paratethys (Rögl 1998; Steininger 1999). A low sea level allowed the development of wetlands with areas of marsh, fen, peatland, and forest. The climatic conditions of the late Early and Middle Miocene of Central Europe are well documented as warm and humid (Kovar-Eder et al. 1996; Esu 1999; Utescher et al. 2000; Ivanov et al. 2002; Böhme 2003; Jechorek and Kovar-Eder 2004; Reichenbacher et al. 2004; Jiménez-Moreno et al. 2005; Mosbrugger et al. 2005; Eronen and Rössner 2007).

During the early Middle Miocene, Spain seems to have been somewhat warmer than Central Europe (Bruch et al. 2004); Suc et al. (1992) describe the presence of mangrove-trees (*Avicennia*) and other warm-loving vegetation (megathermic) elements. There is also some evidence of the presence of open forests (Sanz de Siria 1981) in Spain during the early Middle Miocene. The Spanish locality La Retama contains the hypsodont rhinoceros *Hispanotherium*. The “*Hispanotherium*” faunas are known from localities in Asia, but in Europe they are known only from Spain (see Fortelius et al. 2002). Based on these studies and further evidence from fossil mammals (Fortelius et al. 2002; Eronen and Rook 2004; Van Dam 2006) it seems well established that during the Miocene the first indications of drier conditions in Europe come from Spain and the eastern Mediterranean region.

Here, we propose that *Anchitherium*, which disappeared from the fossil record of Europe in the earliest Late Miocene (11–10 mya), was undergoing adaptive evolution to local arid conditions as early as the late Early Miocene (17–14 mya). These adaptive changes were subtle and may be difficult to reveal using linear measurements.

Material

The *Anchitherium* teeth used in this study come from Bayerische Staatssammlungen für Paläontologie (Munich, Germany), Institut de Paleontologia M. Crusafont (Sabadell, Spain) and Museo de Ciencias Naturales (Madrid, Spain). All teeth from Germany (11 specimens) are from one locality, Sandelzhausen, which is dated as zone MN5 in the European mammal zonation (Mein 1975,

Table 1. Teeth examined in this study, with measured mean angle values.

Locality	Country	Species	Paracone angle	Protocone angle	Metacone angle	Hypocone angle	Mesial top angle	Distal top angle
Sandelzhausen	Germany	<i>A. aurelianense</i>	50.7	42.13	50.21	51.07	87.2	78.8
Sandelzhausen	Germany	<i>A. aurelianense</i>	50.87	40.92	54.48	46.93	88.3	78.6
Sandelzhausen	Germany	<i>A. aurelianense</i>	58.56	51.59	56.29	53.5	69.9	70.3
Sandelzhausen	Germany	<i>A. aurelianense</i>	50.55	43.84	54.52	48.95	85.7	76.6
Sandelzhausen	Germany	<i>A. aurelianense</i>	46.48	50.31	54.11	47.43	83.3	78.5
Sandelzhausen	Germany	<i>A. aurelianense</i>	40.75	46.93	33.18	47.12	92.4	99.7
Sandelzhausen	Germany	<i>A. aurelianense</i>	48.69	41.27	51.03	45.44	90.1	83.6
Sandelzhausen	Germany	<i>A. aurelianense</i>	52.27	56.23	48.6	51.05	71.5	80.4
Sandelzhausen	Germany	<i>A. aurelianense</i>	48.47	63.77	51.18	46.82	67.8	82
Sandelzhausen	Germany	<i>A. aurelianense</i>	57.89	51	42.4	56.23	71.2	81.4
Sandelzhausen	Germany	<i>A. aurelianense</i>	49.67	39.38	48.66	51.66	91	79.7
Puente de Vallecas	Spain	<i>A. aurelianense</i>	63.44	51.04	58.61	39.87	65.6	81.6
Puente de Vallecas	Spain	<i>A. aurelianense</i>	67.7	43.22	60.86	42.86	69.1	76.3
Puente de Vallecas	Spain	<i>A. aurelianense</i>	59.5	49.77	53.06	47.36	70.8	79.6
Puente de Vallecas	Spain	<i>A. aurelianense</i>	63.03	43.42	62.58	45.54	73.6	71.9
Puente de Vallecas	Spain	<i>A. aurelianense</i>	61.43	58.71	59.42	59.23	59.9	61.4
Montejo De La Vega	Spain	<i>A. aurelianense</i>	58.43	48.86	57.34	46.81	72.8	75.9
Alhambra	Spain	<i>Anchitherium</i> sp.	67.29	52.35	63.38	52.78	60.4	63.9
Puente de Vallecas	Spain	<i>Anchitherium</i> sp.	54.39	45.35	51.87	38.85	80.3	86.3
Puente de Vallecas	Spain	<i>Anchitherium</i> sp.	60.18	43.76	54.89	41.5	76.1	84.5
Puente de Vallecas	Spain	<i>Anchitherium</i> sp.	60.61	44.07	54.07	53.63	75.4	76.8
Puente de Vallecas	Spain	<i>Anchitherium</i> sp.	56.22	53.9	49.62	48.43	69.9	84.4
Puente de Vallecas	Spain	<i>Anchitherium</i> sp.	52.08	47.17	47.18	58.37	80.8	53.5
La Retama	Spain	<i>A. castellanum</i>	66.16	48.12	68.21	44.26	65.8	78.5
La Retama	Spain	<i>A. castellanum</i>	58.5	43.67	57.32	49.41	77.9	67.8
La Retama	Spain	<i>A. castellanum</i>	63.33	50.26	62.83	50.51	66.5	68.9
La Retama	Spain	<i>A. castellanum</i>	63.54	46.07	60.66	54.41	70.4	69.1
Alhambra	Spain	<i>Anchitherium</i> sp.	50.18	47.18	56.49		82.7	

1989). The teeth from Spain are from four different localities, Puente de Vallecas (MN5, 12 specimens), La Retama (MN4, 4 specimens), Alhambra (MN6, 2 specimens), and Montejo de la Vega (MN5, 1 specimen) (Table 1). The teeth have various degrees of wear. The molars of *Anchitherium* are hard to tell apart from each other, especially M1 and M2 (Abusch-Siewert 1983), so we pool them for the purpose of this study. All the procedures were also tested with tooth rows including both M1 and M2, and no differences were seen between M1 and M2.

Our sample includes different species (Table 1). We have only *Anchitherium aurelianense* from Germany. The material from Spain includes *A. aurelianense*, *Anchitherium castellanum*, and *Anchitherium* sp. We compare the *A. aurelianense* specimens from Germany to *A. aurelianense* from Spain, as well as *A. aurelianense* from Germany to all *Anchitherium* specimens from Spain. The sample sizes are small, as is typical for paleontological data. To compensate for the small sample size, we

will use a wide array of techniques to fully assess the available information.

Methods

To investigate the subtle changes in *Anchitherium* molar morphology, we used a new 3D analysis of features that show incipient shape changes related to changes in crown height. This analysis measures the mean slope of cusps on the buccal and on the lingual side. With steeper slopes the crown sides become more vertical, thus increasing the total tooth volume. An increasing steepness of cusp slopes is also a prerequisite for truly hypsodont molars to make the teeth taller. The use of 3D methods combined with a topographic analysis of tooth crown (using GIS techniques, see below) avoids the problem of identifying landmarks in a complex morphology that is gradually lost due to wear. This approach also circumvents the fact that tooth height can be measured directly

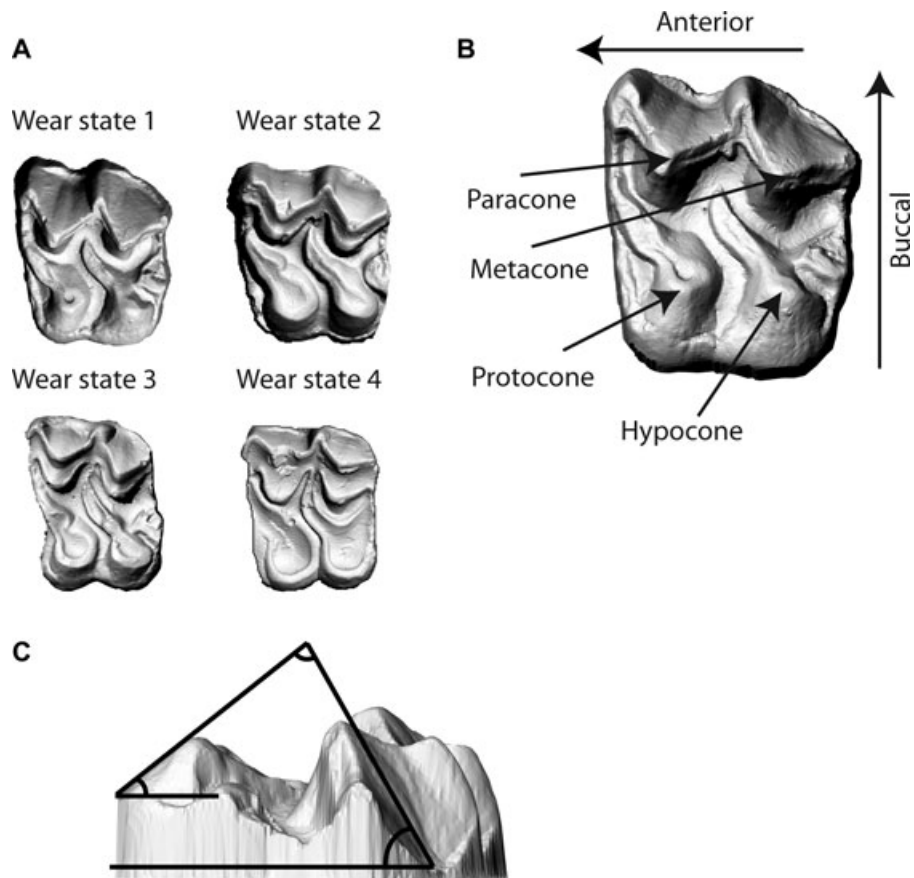


Figure 2. (A) Representative specimens from wear states 1–4. (B) Cusp nomenclature used in this study. (C) Measurement of the “top angle” from measurements of buccal slope (shown here for the metacone) and lingual slope (shown here for the hypocone), such that $\text{top-angle} = 180 - (\text{buccal slope} + \text{lingual slope})$.

from unworn teeth only, which would further limit the available specimens to study. We visually classified the specimens to four wear classes (1 = unworn or slight wear, 2 = moderate wear, 3 = heavy wear, 4 = almost completely worn) (Fig. 2A). However, we used all the teeth for the cusp slope measurements.

High-quality plaster casts (Fujirock EP, GC Europe, Leuven, Belgium) of teeth and tooth rows were made from silicone moulds (Coltene Lab-Putty, Coltène/Whalendent AG, Altstätten, Switzerland) of museum specimens. After casting they were scanned using a three-dimensional needle scanner (MDX-15, Roland) with 200 μm resolution. Teeth were oriented manually to maximize crown-base projection (resulting in a roughly horizontal occlusal plane), which remains relatively constant through wear. Three-dimensional point files were imported into GIS software (MFWorks 3.0, KeiganSystems, London, Ontario, Canada) and interpolated using inverse distance weighting (with the following criteria: search radius 0.5 mm, output precision 0.01 mm, first grid spacing 3 cells) to produce digital elevation models (DEMs).

The DEMs were converted to maps of the slope with the “Grade” procedure in MFWorks. We examined the sloping enamel surfaces on the occlusal surface on the buccal (for paracone and

metacone) and lingual (for protocone and hypocone) sides. The slope for each cusp was measured using a three-cell wide profile from the centre of each cusp tip to the base, and the average steepness of the cusp slope for that area was measured. To avoid the effect of wear and to maximize the sample size, we measured slopes from the base of the crown upwards toward the tip. For buccal and lingual cusps, we chose the base to be the point where a continuous crown slope began, typically just above the cingulum. If the baseline was different for anterior and posterior cusps, the higher was chosen for both cusps. Averages of local slope angles were calculated along the lines that were 10% of the crown length. This corrects for size differences among teeth and basically provides a measure of how vertical the crown sides are. In 14 of 111 cases, the cusps were so worn (wear class 4) that some of the lingual cusps were below the 10% cut of point (none of the *A. aureliense* from Germany). We still used the angles from the more worn cusps because only in five cases the line was shorter than 8% of the crown length (minimum was 5.4%). The average angles measured from individual pixels correspond closely with angles measured using only the final height at 10%. We prefer, however, the average angles because they do not depend on single points.

Because differences in buccolingual orientation of teeth may affect the slopes, we also calculated a “top-angle” for buccal-lingual cusp pairs (paracone-protocone, metacone-hypocone) by subtracting the individual cusp angles at the base of the cusp from 180 (e.g., $180 - (\text{metacone slope} + \text{hypocone slope})$) (Figs. 2B,C). In contrast to the individual cusp slopes, a small top-angle corresponds to more vertical, hypsodont, sides of the crown.

Because the data were nonrandomly distributed, we used nonparametric statistical tests (Kruskal–Wallis) to examine the differences in cusps slopes. Our sample size is typical for paleontological data and is enough to offer adequate statistical power. Nevertheless, to give further confidence to our results, we performed randomization test for all our samples. The randomizations were done by reshuffling the species assignments 1000 times and calculating the cusp slope values for each randomization.

To investigate the range of potential diets in our sample, we performed a mesowear analysis of teeth. Mesowear analysis was developed by Fortelius and Solounias (2000) to investigate ungulate diet based on the visible differences in tooth wear. The analysis is done by evaluating cusp shape and relief of upper second molars and using a dataset of modern mammals to see which species the fossils group with. The mesowear analysis was done as a blind test, with the person performing the scoring having no information about the locality of the tooth. We performed a hierarchical clustering based on the scores using the method and the modern dataset from Fortelius and Solounias (2000).

Results

To test whether there is a significant difference in the degree of hypsodonty between the German and Spanish populations, we

compared the specimens in two ways. In the first comparison we included all species (*A. aurelianense*, *A. castellanum* and *Anchitherium* sp. from Spain and *A. aurelianense* from Germany). In the second, we included only the species *A. aurelianense* from both Spain and Germany. Basal measurements between all Spanish and German specimens show that the anteroposterior length of molars is significantly greater in Spain than in Germany ($P = 0.0001$ Chi-square, Kruskal–Wallis). The difference remains highly significant within *A. aurelianense* from Spain and Germany ($P = 0.0001$). The other Spanish specimens from Puente del Vallecas (*Anchitherium* sp.) may be even slightly larger than *A. aurelianense* but this difference is not significant ($P = 0.4871$). Using buccal-lingual width as a basal measurement gives the same result. This shows that Spanish specimens used in this study are without exception larger than the German ones.

We investigated the degree of difference in tooth volume by measuring the steepness of the cusp slopes, a prerequisite for hypsodont teeth. A plot of individual cusp slopes is shown in Figure 3. The results show that all cusps of German *A. aurelianense* have roughly similar slopes, with the mean of specimens around 50 degrees (Fig. 3). Whereas the Spanish specimens have similarly sloped lingual cusps, the buccal slopes (cusps paracone and metacone) are more vertical than those of German *A. aurelianense*, around 60 degrees (Fig. 3). Both Spanish *A. aurelianense* and other taxa have comparable cusps slopes, although the non-*aurelianense* taxa are more variable, most likely because these specimens represent more than one taxon.

The top-angle (Fig. 4) comparison between German and Spanish specimens supports the results obtained from individual cusps: the Spanish specimens of *Anchitherium* have a smaller top-angle, reflecting the more vertical buccal walls of their

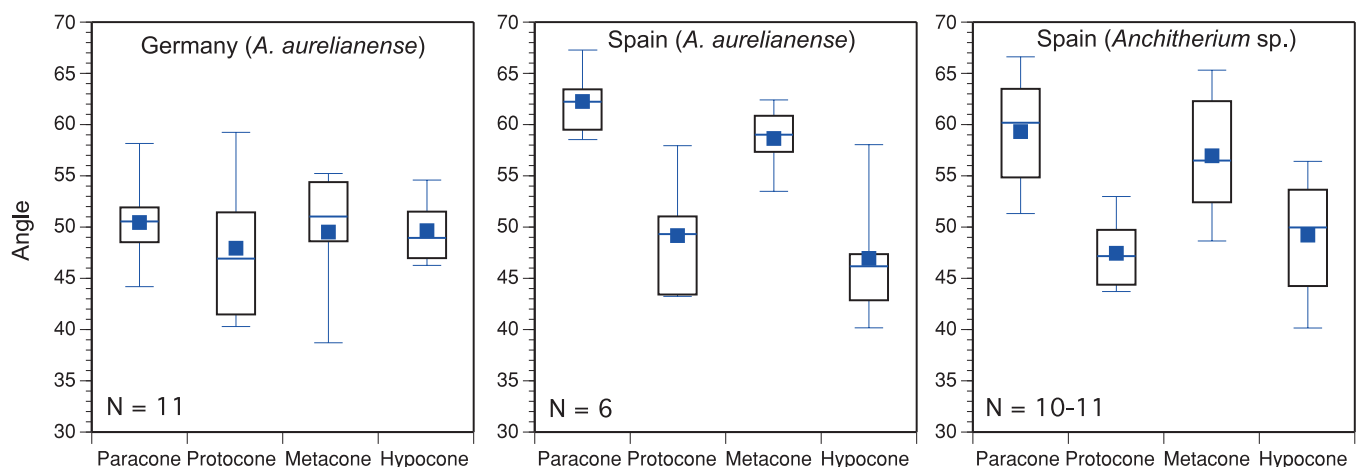


Figure 3. Cusp slope comparisons. Slope angles (90 degrees is vertical) for buccal (paracone and metacone) and lingual (protocone and hypocone) show steeper buccal cusps for the Spanish *Anchitherium*. Slopes were calculated along horizontal lines extending from the base of the crown 10% of the crown length toward cusp tips. Boxes enclose 50% of observations, the median and mean are indicated with horizontal bar and square, respectively, and whiskers enclose 95% of observations.

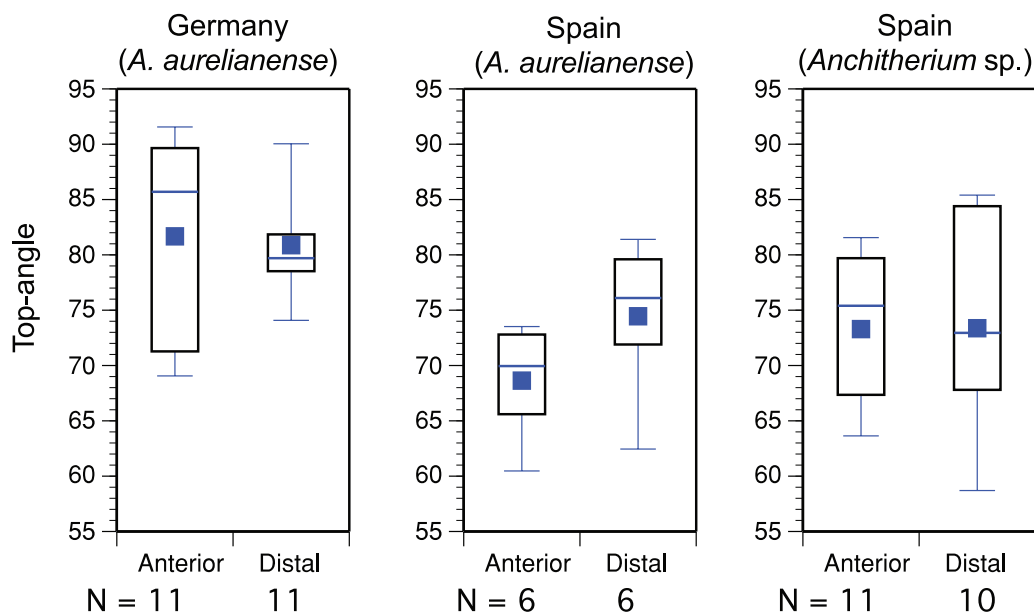


Figure 4. Top-angle, showing steeper cusps slopes for the Spanish *Anchitherium*. The difference between Spanish and German specimens appears to be the greatest for anterior cusps, which form first during development. See text for significance tests.

molars. The differences between German and Spanish specimens are greater using the pooled sample of all Spanish specimens (mesial $P = 0.0097$, distal $P = 0.0642$ Chi-square Kruskal–Wallis). If we use only *A. aurelianense* (Puente de Vallecas) specimens, the differences are less: the difference is significant at $P < 0.05$ level for the mesial top-angle ($P = 0.027$, *A. aurelianense* Chi-square Kruskal–Wallis), but not significant for the distal top-angle ($P = 0.0875$, *A. aurelianense*). Between Spanish *A. aurelianense* and *Anchitherium* sp. there are no significant differences. Additionally, because of the small sample sizes, we used a randomization test by randomly reshuffling the species assignments 1000 times and calculated the cusp slope values for each randomization. As Figures 3 and 4 indicate, the results show that compared to the Spanish specimens, the buccal cusp slopes of German *Anchitherium* appear to be shallower (both paracone and metacone are $P < 0.001$) than the lingual slopes (protocone $P = 0.476$ and hypocone $P = 0.731$). Furthermore, both the mesial and distal top-angles are larger, indicating less development toward hypsodont teeth in German specimens (mesial $P = 0.003$ and distal $P = 0.018$). All P values when comparing Spanish *A. aurelianense* to other Spanish specimens are ≥ 0.1 .

Due to the limited availability of unworn specimens ($N = 2$ and 7 for German and Spanish specimens, respectively), estimates of the hypsodonty index (crown height/crown length) are highly provisional. In our sample, the mean hypsodonty index for the German and Spanish specimens are 0.38 and 0.58 , respectively, suggesting that the steeper slopes in Spanish specimens do contribute to crowns that are initially taller, although still very

brachyodont. Generally, teeth with hypsodonty index less than 0.8 are considered brachyodont (Fortelius et al. 2002). At a given crown height, tooth volume is greater in the Spanish *Anchitherium* compared to the German specimens, and this difference is greatest at the tips of the crown, corresponding to early wear stages. These results suggest that, compared to German population, Spanish populations of *Anchitherium* have subtle morphological features related to higher dental durability.

For dietary reconstructions, the grouping for the mesowear analysis (Fig. 5) shows that the *Anchitherium* from Germany (Anchi-G) are in the same cluster with *Antilocapra americana* (pronghorn), *Antidorcas marsupialis* (springbuck), *Capreolus capreolus* (roe deer) and *Giraffa camelopardis* (giraffe). Pronghorn, roe deer and giraffe are browsers and springbuck is a mixed feeder (Fortelius and Solounias 2000). These are all within the browser cluster (Fortelius and Solounias 2000) of the browser–mixed feeder–grazer continuum. The Spanish *Anchitherium* (Anchi-S) are in the same cluster with *Cervus canadensis* (wapiti), *Odocoileus hemionus* (mule deer), *Tragelaphus scriptus* (bushbuck) and *Taurotragus oryx* (eland). Wapiti, bushbuck and eland are mixed feeders whereas the mule deer is a browser. In Fortelius and Solounias (2000), these group at the mixed feeder end of the browser continuum. Taken together, and in concordance with our results on tooth morphology, it seems that the Spanish specimens are more firmly in the mixed feeding category whereas the German specimens are more at the browsing end. The higher dental durability in Spanish *Anchitherium* may thus have compensated for its more abrasive diet.

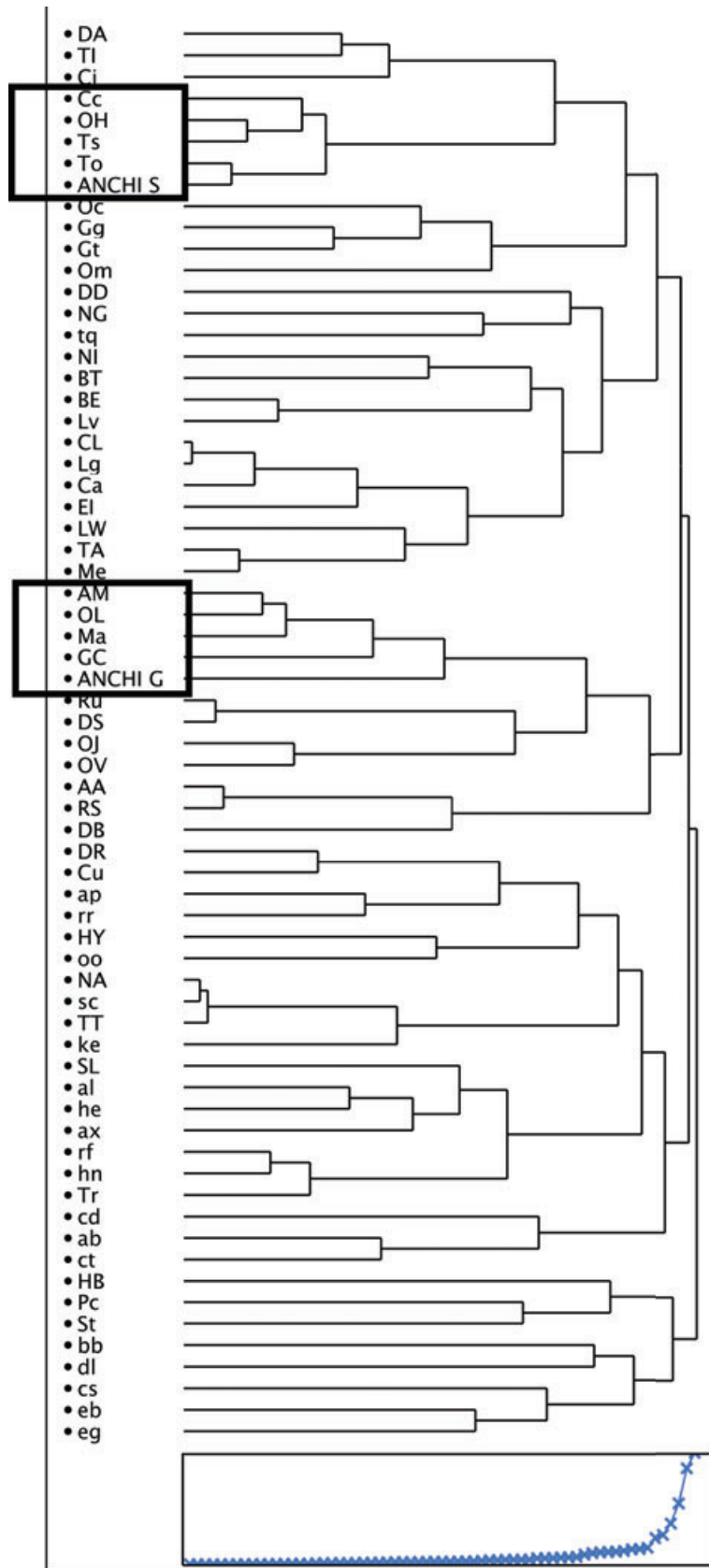


Figure 5. Mesowear grouping showing the place of Spanish (ANCHI S) and German (ANCHI G) populations. AM, *Antilocapra americana*; Ma, *Antidorcas marsupialis*; OL, *Capreolus capreolus*; GC, *Giraffa camelopardis*; Cc, *Cervus canadensis*; OH, *Odocoileus hemionus*; Ts, *Tragelaphus scriptus*; To, *Taurotragus oryx*. See Fortelius and Solounias (2000) for remainder of species abbreviations.

Discussion

A basic assumption underlying our study is that differences in dental morphology and diet link the fitness of individuals to environment. Dental wear is widely regarded as a proximate cause of senescence in mammals generally, and the wear rate of teeth is known to be an important life-history variable in several investigated cases (Skogland 1988; Loe et al. 2003; King et al. 2005). If an individual has more durable teeth, it can survive longer with abrasive food and its potential reproductive life span is higher. Obviously, we could not measure these life-history parameters directly from extinct taxa, and even in the case of teeth, we had to devise ways to measure dental durability indirectly. Nevertheless, by being widespread, *Anchitherium* offers a good example of taxon that should have experienced different environmental conditions in different parts of its range.

According to our results, there were functionally significant differences in dental morphology between Spanish and German populations of *Anchitherium*. We interpret this to imply that the Spanish populations of *Anchitherium* were undergoing adaptive evolution to local or regional arid conditions. These adaptations were steeper slopes (larger realized tooth volume) and larger teeth. The development of steeper slopes and larger teeth are adaptations toward more durable teeth (see Janis and Fortelius 1988 for review). Interestingly, the study of Forstén (1991, fig. 6) identified Puente de Vallecas as the locality in which tooth size was the greatest relative to astragalus size. This, in combination with our results, suggests that Spanish *Anchitherium* show incipiently features that more fully characterize the European and North American faunas during the latter parts of the Miocene. We note that these conclusions do not exclude the possibility that the German populations of *Anchitherium* were evolving more brachyodont teeth in response to less-abrasive foods, perhaps simply due to relaxed selective pressure on dental durability. We also cannot completely exclude the possibility of nonadaptive causes behind hypsodonty. Still, according to our results, the differences in diet inferred through mesowear are at least suggestive that the morphologies are adaptive between the populations, regardless of polarity of these changes. We also note that during the Neogene of Europe, ungulate genera show predominantly an increase in hypsodonty (Jernvall and Fortelius 2002), suggesting that the Spanish *Anchitherium* is the derived form.

The difference in crown volume between Spanish and German specimens, after correcting for size, is progressively greater toward the tip of the crown. This is noteworthy because the difference in slopes was also greatest in the anterior cusps (Fig. 4), which are initiated first during ontogeny. This indicates that the incipient hypsodonty in Spanish *Anchitherium* has early developmental origins rather than simple longer continuation of the crown formation, a hallmark of advanced hypsodonty (which should af-

fect anterior and posterior cusp slopes equally). Taken together, selective and developmental processes appear to have affected tooth shape at early stages of the wear in Spanish *Anchitherium*. Although one effect of these changes is the prolonged functional “life span” of a tooth, these changes also increase functional efficiency of teeth earlier in the life. This prolongation of tooth functionality is reflected in a longer life span because individuals can tolerate more abrasive food for longer (see King et al. 2005). This directs the selection toward more durable teeth, especially in habitats where much (or most) of the food is abrasive.

To put the above-mentioned selective and developmental processes into ecological context, it is useful to relate the effect of more durable teeth to tooth wear rates and expected life span. For roe deer (*C. capreolus*), a strict browser, the published wear rate is 0.33 mm/year (Solounias et al. 1994) whereas mixed feeder wear rates range typically from 0.92 to 1.63 mm/year (*Rangifer tarandus groenlandicus* [0.93], Island of Rhum *Cervus elaphus* [0.92], *Gazella granti* [1.63], *A. marsupialis* [1.41]). Yet, for similar body size, browsers and mixed feeders have approximately comparable life spans (Solounias et al. 1994). In addition to interspecies differences, tooth wear rate differences can be detected even within species. The Island of Rhum red deer (*C. elaphus*) diet is composed mainly of different grasses, *Calluna* shrubs and heath herbs (Gordon 1989a,b). In comparison, red deer from southern Norway eats mostly grasses and shrubs, together with a large proportion of conifer browse and some browse from deciduous trees (Myserud 2000). Compared to the wear rate of Island of Rhum red deer (0.92 mm/year), the tooth wear rate is lower, ranging from 0.61 (young male) to 0.45 (old female) in the Norwegian red deer (Loe et al. 2003). According to our results, the Spanish *Anchitherium* were closer to being mixed feeders whereas the German specimens were more toward the browsing end of the continuum. These dietary differences between different populations of *Anchitherium* were similar to the range of diets in present-day *C. elaphus* from different areas. In general, our results are suggestive that opening and fragmentation of habitats may exert detectable selective responses in taxa typically associated with forest environments.

Anchitherium had high site occupancy throughout most of its temporal range (Jernvall and Fortelius 2004). Compared to the much rarer Miocene primates, which seem to have tracked their preferred habitat narrowly (Eronen and Rook 2004), *Anchitherium* appears to have been a habitat generalist, able to adapt to local conditions to some degree. The subtle changes in dental morphology reported in this study suggest that “niche tinkering” was rooted in adaptive evolution, responding to local conditions at a regional scale. Considering dental evolution and the eventual extinction of *Anchitherium*, although it is not part of the hypsodont horse lineage, our results show that *Anchitherium* was in fact able to evolve toward hypsodonty. Why it did not proceed further along this

trajectory remains unknown. It could hardly have been because it started too late. In the Early Miocene, overwhelming competition from the few and rare hypsodont ungulates is unlikely. Whatever the factors were, the lack of advanced hypsodonty indicates limited success in competing outside forest environments.

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