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Richard H. Madden
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1 Hypsodonty in South America

1.1 The tangled history of precocious hypsodonty

Increasing tooth crown height is an often repeated pattern in the evolutionary history of mammals. Probably the best-known example is the evolution of high-crowned teeth in horses (the family Equidae) and contemporary ungulates through a 12-million-year interval in the North American continental Miocene (MacFadden, 1992; Strömberg, 2006; Mihlbachler et al., 2011).

Other noteworthy examples of the evolution of high-crowned teeth are found among extinct herbivores (e.g., *Myotragus*, *Marremia*) from islands where they were subject to the magnifying effects of geographic isolation and the instability of island ecosystems. Conspicuous examples are also found among extant mammalian herbivores (e.g., *Antilocapra*, *Vicugna*) in high arid and volcanic mountain environments.

Presumably, when mineral particle ingestion is unavoidable, natural selection will enhance the physical structures in teeth that are useful for resisting abrasive tooth wear. However, neither the agencies nor mechanisms whereby continental, insular, or arid volcanic mountain environments present exceptionally abrasive environments to mammalian herbivores are understood very well.

Among South American mammals, the number of examples of the independent evolution of conspicuous structures for resisting abrasive tooth wear seems extraordinary. As many as 26 clades of South American mammals evolved high-crowned or hypsodont teeth, among xenarthrans, marsupials, rodents, archaic native ungulates, and more recent immigrants among mice and ungulates. Of special note, nearly half of these clades evolved ever-growing teeth; that is, teeth that grow throughout the animal's life, endlessly and continuously replacing tooth mineral substance lost through wear. Elodont or ever-growing teeth effectively neutralize the selective pressure imposed by environmental abrasives that would otherwise prematurely truncate the functional longevity of teeth and the reproductive life of the organism.

The inventory of South American mammals with high-crowned and elodont teeth was started by Karl von Linne in 1758 (*Vermilingua*, *Cuniculus*, *Silvilagus*) with the mammals of the territory of the Virrenato del Rio de La Plata. Cingulata was added to the roster between 1803 and 1804 by Desmarest and Geoffroy, and Rodentia added between 1782 and 1837 by Molina, Fischer, Olfers, Brandts, and Waterhouse. The first elodont fossil tooth from South America was described by Thomas Falkner (1774) and the first complete skeleton of an elodont fossil mammal was the *Megatherium*

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americanum brought from Buenos Aires to the Royal Cabinet in Madrid in 1789 and described by Cuvier in 1796 (Mones, 2002). Some forty years later, Sir Richard Owen (1837) described *Toxodon*, the first of several South American fossil mammals with ever-growing teeth collected by Darwin (Fernicola et al., 2009).

The evolutionary transformation from low to hypsodont tooth crowns in toxodonts and the increasing prevalence of hypsodonty among archaic South American ungulates were revealed along with their context of stratigraphic superposition by the discoveries of Carlos and Florentino Ameghino (1904, 1906).

1.1.1 Precocious hypsodonty

The apparent fact of an older or precocious evolution of hypsodonty among terrestrial herbivores in the late Eocene of Patagonia has been of interest to paleontology for a long time. Without a doubt, while there are examples of the evolution of high-crowned teeth in older rocks, there is nothing like the manifest and parallel evolutionary trends among so many different taxa at about the same time in the Eocene and Oligocene as in Patagonia.

Therefore, who actually “discovered” that the evolutionary trend to high tooth crowns in ungulates in Patagonia antedates similar evolutionary trends elsewhere? There are four contenders: (1) William Berryman Scott (1913, 1937a) at Princeton who, between 1913 and 1937, worked directly on fossil material from both North and South America while writing *A History of Land Mammals of the Western Hemisphere* in English; (2) Albert Gaudry in Paris who worked directly on fossils from both Europe and South America (the material collected by Tournoüer) and published on their morphology and evolution in French; (3) Karl von Zittel in Munich who was studying fossils from Patagonia purchased from the Ameghinos while compiling the *Grundzüge*, a comprehensive history, in German, of mammal evolution in the Cenozoic; or (4) Florentino Ameghino (1897, 1906) in Buenos Aires who, between 1897 and 1906 described, in Spanish and French, the original fossil material (collected by Carlos Ameghino), argued for phylogenetic affinities with mammals on other continents, and documented the evolutionary trend to higher tooth crowns in Patagonia.

Ameghino was the first to describe the actual fossils and fossil taxa from pre-Santacrucian levels in Patagonia, and through his phylogenetic reconstruction of horses, is among the originators of the idea of precocious hypsodonty. For Ameghino, age control (and global correlation) was provided by the marine invertebrates from interbedded strata in Patagonia, studied and described by Hermann von Ihering in São Paulo. Ameghino’s contemporaries in Europe, Gaudry and von Zittel, also studied original fossil mammal material from Patagonia; Gaudry through the collections made by his employee Tournoüer and von Zittel through material sold to the Bavarian State Collection in Munich by Ameghino. (Scott studied the type material from Patagonia in the Ameghino collection a little later, but after Ameghino’s death, and only type material of the younger Santacrucian.)

All four of these paleontologists (Ameghino, Gaudry, von Zittel, and Scott) were working with original fossils from Patagonia, but only three worked in positions that enabled them to make direct comparisons of material from different continents (Scott, Gaudry, and von Zittel), and of these three, only Gaudry and von Zittel benefitted by working directly with material from the older Cenozoic of Patagonia. Of these last two, only Gaudry (through the work of Tournoüer) had access to the stratigraphy and independent evidence from marine invertebrates (and global correlation) by which to make age assessments and intercontinental comparisons. But alas, nobody in the modern literature ever cites Gaudry as the originator of the idea of “precocious hypsodonty.” Why? Gaudry wrote in French, and language has a huge influence on citation history. For example, it explains why Patterson and Pascual (1968) are so often cited and Pascual and Odremán Rivas (1971) so often overlooked.

Ameghino (1906) placed South American Notohippidae near the base of horse evolution, and noticed the implication that notohippid hypsodonty in Patagonia antedated the evolution of hypsodonty in northern hemisphere horses. However, the endemism and monophyly of Notoungulata in characters of the basicranium, revealed by Roth (1903), removed the precociously hypsodont Notohippidae from any direct phylogenetic affinity with true horses.

More substantive evidence for an early occurrence of hypsodonty in South America was provided by Albert Gaudry (1903) and Andrés Tournouër (1903a, b) through a comparison of the European and Patagonian fossil mammal sequences. Using the new collections from Patagonia, Tournouër and Gaudry independently established the relatively older age of the deposits in Patagonia. Comparably high prevalences of hypsodonty among European mammals are attained only in much younger deposits. Tournouër (1903a, b) provided constraints on the age of the Patagonian sequence on the basis of the relationship of fossil-bearing continental units to marine beds along the Gulf of San Jorge. These marine beds contain rich and diverse fossils studied by French paleontologists at the Laboratoire, including molluscan taxa. On the basis of these studies, Tournouër and Gaudry concluded that the *Notostylops* and *Pyrotherium* beds could not be younger than *l’Oligocène supérieur*.

Gaudry (1902, 1903) commented about the age relationships of the *Pyrotherium* and Santa Cruz faunas with respect to the *le marche de l’évolution dans l’hémisphère boréal* (the course of evolution in the northern hemisphere). Gaudry went beyond the evidence from marine fossils to note “*jamais, à moins de recourir à l’étude des fossils marins places au-dessous, on n’aurait pu avoir l’idée de ranger dans le Miocène l’étage santacruzien où on ne trouve aucun Equidé ou aucun animal en voie de devenir Equidé*” (without resorting to the study of marine fossils below, we would not have had the idea about placing the Santacrucian stage in the Miocene, as there are no equids nor any animal becoming an equid). Then, after a long list of such comparisons with the Miocene mammals of Europe, Gaudry concludes that “*A en juger par les etudes faites dans nos pays, le Santacruzien devrait être du Tertiaire ancien, et pourtant e’est du Tertiaire relativement recent. La transformation des Mammifères en Patagonie s’est produite moins complètement que dans nos pays. Cela est d’un grand intérèt pour la paléontologie philosophique. L’évolution s’est avancée à travers des ages d’un pas*

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More information

inégal" (Judging by studies made in our country, the Santacrucian would be the older Tertiary, but it is relatively recent Tertiary. The evolutionary transformation of mammals in Patagonia was less complete than in our country. This is of great interest to philosophical paleontology. Evolution progresses through time at unequal rates.) (1903, p. 473).

In the 1911 edition of the *Grundzüge der Paläeontologie (Paläeozoologie). II. Abteilung, Vertebrata*" (Text-book of Paleontology (Paleozoology), Part II, Vertebrata), Karl von Zittel, with F. Brioli, Ernest Koken, and Max Schlosser, summarized the middle Cenozoic sequence of Patagonia and provided a glimpse at broad patterns of crown height evolution among the notoungulates. Those of the Upper Eocene *Notostylops* beds were consistently brachydont, the notohippids of the Oligocene *Astraponotus* beds had moderate crown height, and the archaeohyracids had prismatic (apparently ever-growing) teeth, and by the Miocene *Pyrotherium* beds, the Typotheria and Toxodontia displayed complete elodonty.

In the first edition of *A History of Land Mammals of the Western Hemisphere*, William Berryman Scott (1913) argued that the explanation for high-crowned, persistently growing pattern of grinding teeth in horses, camels, ruminants, and rodents "is probably found in the spread of grassy plains at the expense of forests. . .[o]n account of the silica which they contain, the grasses are very abrasive and rapidly wear the teeth down. In adaptation to this new source of abundant and nutritious food, many kinds of mammals developed a form of tooth which was fitted to compensate by growth for the loss through abrasion" (p. 233).

Scott compared the Oligocene mammals of North and South America, and with respect to those of South America, wrote that a "large number of genera, especially among the toxodonts and typotheres. . .had high-crowned, cement-covered teeth. . .an indication that grazing habits had already begun to be prevalent" (p. 264) in the South American Oligocene. With respect to the older Eocene, Scott wrote that Casamayoran genera were "far more primitive and less specialized than their descendants in the Deseado and Santa Cruz stages. All of them had the low-crowned grinding teeth of the browsers, and no grazers were then in existence, so far as is known" (p. 282). He noted in passing that the mammals of the next successive level, the *Astraponotus* beds, or Mustersan, of either Eocene or Oligocene age, were scanty.

At the same time, Scott (1913) explicitly establishes the greater antiquity of hypsodonty in Patagonia relative to North America (and Europe); he describes hypsodont teeth in general, and notes they occur in "many plant-feeders, such as horses, cattle, elephants, beavers, etc." (p. 95). Note the diversity of mammals he includes in this statement. He goes on to note that "in very many instances the development of brachyodont into hypsodont teeth may be followed through every step of the change" and that "the advantage of the change is obvious in lengthening the animal's life, especially in those which feed upon abrasive substances, like grass" (p. 95).

In the second edition of *A History of Land Mammals of the Western Hemisphere*, Scott (1937a) acknowledges the fact of "prematurely specialized" Deseadan notoungulates "which had high-crowned (hypsodont), cement-covered teeth, and in which the

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More information

lower molars had a deceptively horse-like pattern (*Rhynchippidae* and *Notohippidae*). Next in frequency of occurrence were the *Typotheria*, of which many genera likewise had the hypsodont, cement-covered teeth" (p. 249). "This multiplication of grazing animals, with hypsodont, cement-covered teeth, is a very interesting parallel to the similar development which appeared in so many rodent, artiodactyls, perissodactyl and proboscidean families of the Miocene in the northern hemisphere, but the adaptation to grazing habits took place much earlier in South than in North America, from which fact it might be inferred that the extension of grasslands occurred much sooner in the southern continent." (p. 249). He also noted that Mustersan (lower Oligocene or Eocene) Typotheria "were small animals and most of them had the hypsodont, rootless and cement-covered teeth" (p. 251).

The idea of "prematurely specialized" hypsodont notoungulates in Patagonia was resuscitated in modern form for the English language audience by Patterson and Pascual in the late 1960s, and from that time forward, Pascual is the principal source of creative thinking about the environmental significance of hypsodonty in Patagonia. Pascual argued that the cause of early hypsodonty in Patagonia may be related to (1) Andean tectonism and mountain uplift leading to change in physiographic conditions immediately after deposition of middle Eocene sediments (Pascual and Odremán Rivas, 1973), (2) the establishment of extensive herbaceous steppes and the early diversification of grasses (Pascual and Odremán Rivas, 1971), and most recently, (3) the accumulation of pyroclastic sediments with abundant siliceous abrasives (Pascual and Ortiz-Jaureguizar, 1990). The two syntheses of Pascual and Odremán Rivas are seminal to the history of the growing complexity and sophistication of thinking about the environmental correlates of precocious hypsodonty in Patagonia.

1.1.2 Grasses

Fossil grasses were first discovered in Patagonia at the turn of the twentieth century (Dusen, 1899), but grasses are never a very prominent component of fossil macrofloras in Patagonia. Fossil grass leaves do not occur in any abundance in these classical floras, nor do they occur in circumstances that might have led paleobotanists to believe they indicated grasslands. For example, Berry (1925, 1928, 1934, 1937) described "Miocene" floras in Patagonia and his review cites all the available evidence for grasses; in sum, pitifully little. Hünicken (1955, 1966) studied the rich leaf floras of middle Eocene to Oligocene age along the Rio Turbio, and similarly found no grasses.

Romero (1986b) reviewed the composition and environmental significance of the Patagonian floras and did not mention evidence for grasses. Most recently, Barreda and Palazzesi (2010) describe the composition and sequence of Cenozoic macrofloras and pollen records from Patagonia, and mention the oldest record of Poaceae at Rio Turbio during the Eocene and the oldest evidence of a more arid-adapted vegetation with grasses in low abundance in the early Miocene. Their review of the establishment of arid-adapted vegetation in Patagonia (2007) convinces the reader that grasses do not make a significant appearance in Patagonia until after the early Miocene. Grasslands do

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More information

not appear in the pollen record of Patagonia until the Quaternary (Palazzesi and Barreda, 2012). Given there is little evidence from leaves or pollen for grasses in floras from Paleogene deposits in Patagonia, where did the evidence of early grassland evolution in Patagonia come from?

1.1.3 Phytoliths

The occurrence of phytoliths in Plio-Pleistocene sediments of the pampas of Argentina was established by Frenguelli (1930, 1955), Teruggi (1955, 1957), and Bertoldi de Pomar (1975). Their classification and affinities to modern plants were established by Bertoldi de Pomar (1970, 1971).

The first mention of plant phytoliths in the Mustersan of the Sarmiento Formation of Patagonia was made by Renato Andreis (1972), and these were interpreted as grasses in light of known phytolith systematics at that time. Bertoldi de Pomar's (1971) classification, while highly original, was based on descriptions of grass and monocot phytoliths then current in the botanical literature, and this literature had very limited phylogenetic scope. The insinuation of its implications into the literature about hypsodonty in the Patagonian fossil mammal record happened between 1970 and 1972.

Spalletti and Mazzoni (1977) remarked that Andreis found evidence of *escasas gramíneas* (sparse grasses) because of "*nidos de escarabéidos. . .requiere de superficies llanas libres de pastos*" (flat exposures of soil free of grasses). The combination of tuffaceous sediments on a broad flat land surface, paleosol microstructure, the presence of dung-beetle brood balls and biogenic silica, together with high-crowned fossil mammals suggested that wide plains with a low vegetation of grasses became established during the Mustersan (Pascual and Odremán Rivas, 1971; Andreis, 1972).

Luis Spalletti and Mario Mazzoni first mentioned the presence of phytoliths (*ópalo biogénico*) in the Sarmiento Formation at Gran Barranca in 1977 (1977) and noted "*la notable abundancia de silicofitolitos (que contrasta con las deducciones de Feruglio, 1949 y Andreis*, 1972), *nos inducen a pensar–en coincidencia con las ideas de Pascual y Odreman* (1971)*–en amplias y temporalmente constantes estepas arbustivas*" (p. 278). This is the first in a series of detailed studies of phytoliths in the dominantly windborne tuffaceous sediments of the Sarmiento Formation and the oldest clear interpretation of the phytolith evidence for widespread low shrubland steppe in the Patagonian Eocene. Later, from phytolith separations, Mazzoni (1979) established the presence of *células de gramíneas* (grass phytoliths), and described the diversity and relative abundance of a wide variety of distinct morphological classes of phytoliths.

Alejandro Zucol and colleagues (1999, 2010) revised and updated the interpretation of the middle Eocene phytolith record from the Sarmiento Formation using Mazzoni's original separations, and found that graminoid phytoliths rarely comprise more than 50% of assemblages, a remarkably low relative abundance for such productive plants. Nevertheless, Zucol et al. (2010) argued for the presence of grassland ecosystems in Patagonia during the middle Eocene. The evidence for this is a relatively higher proportion of diagnostic panicoid phytoliths in a single stratigraphic level, Simpson's Y Tuff. This episodic occurrence of a relatively higher proportion of panicoid phytoliths

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More information

is the best available evidence for the establishment of grassland ecosystems in Patagonia in the late middle Eocene. Interestingly, this episode in Simpson's Y Tuff occurred during the Barrancan South American Land Mammal Age, a time when no active evolutionary change in mammalian hypsodonty occurred, and seems to have been ephemeral at best, perhaps reflecting only the local influence of an important volcanic eruption event.

Most recently, Strömberg et al. (2013) analyzed the phytolith content of the Sarmiento Formation at Gran Barranca, and while open-habitat grasses are indeed present, they are always at such low frequencies that there is no credible evidence for open grasslands or grassland ecosystems in the Sarmiento Formation anytime during the middle Cenozoic.

1.1.4 Grasses as sediment traps

Throughout the long history of ideas relating hypsodonty with grass diets, the grazing habit, grassy plains, or grassland ecosystems, there has been little mention of the role of grasses in the accumulation of erosion products or sediment deposition. Among the oldest published statements suggesting that intrinsic opaline silica abrasives in grasses may not be the sole cause of hypsodonty are those of Reuben Arthur Stirton who studied horse (1940, 1947) and beaver evolution (1935). Stirton believed hypsodonty was related more to soil ingestion than grass consumption (1947).

Most recently, earth surface processes have been invoked in relation to hypsodonty by Reguero et al. (2010). "As is interpreted for all ungulates, the hypsodonty solve the problem [sic] of increased tooth wear resulting from various dietary and environmental factors: (1) high phytolith abundance in especially coarse grasses, (2) prevalence of grass life-forms with areas of exposed soil around them, (3) high levels of soil disturbance or soil mineral mobility, (4) large areas of continuously available accumulations of volcanic ash (and other potential sources of mineral dust) subject to erosion–entrainment–transport–deposition cycles extending over evolutionary timescales" (p. 366). This invocation of earth surface processes extending over evolutionary timescales by Reguero et al. (2010), without attribution or empirical substantiation, must rank as one of the most prescient claims ever made about the evolution of high-crowned teeth in South American mammals.

However, the role of wind transport and trapping by grasses in the deposition of loessoid deposits in Argentina has long been recognized. "The wind-transported particles and grains which make up the loessoid deposits must have settled down slowly on the surface of the pampas, where they were trapped by a thick grass cover; the existence of this vegetation is shown in the sediments by the numerous siliceous cells found in all the levels of the Pampean Formation" (Teruggi, 1957; p. 330).

Long before Reguero and Teruggi, the basic principles were recognized by William Diller Matthew in his description of the fossil mammals of the Tertiary of northeastern Colorado (1901): "In view of the important bearing that the origin of the sediments must of necessity have on the discussion of the character and relationships of the fauna found in them" (p. 360). Matthew argued for the eolian origin of the White River beds and invoked the interaction of eolian and fluvial surface processes. “I think too that the importance of river flood-plains as a source of [sediment] supply is likely to be underestimated. The areas [of exposure] are limited it is true, but the supply of sediment is unlimited and the conditions for sorting and removal by the wind are exceptionally favorable, if we take as example the modern rivers of the Plains. It should be remembered that while rivers bring large amounts they also take away large amounts, whereas whatever windborne sediment is caught in prairie grasses is not likely to escape again” (p. 363).

Somewhat later, in the same paper he wrote “The sediments brought down by the various rivers from the mountains are deposited largely in the vast semidesert tract of eastern Wyoming, Colorado, and New Mexico. Here the prevalent westerly winds sift and sort them, rolling the sands but a short distance and leaving them as residual deposits, while all the finer material is carried much farther and caught by the grassy surface of the prairies to the east, finally merging perhaps into true flood-plain or lacustrine mud in the valley of the Mississippi. The denser the grass the more dust it sifts out and holds, hence the tendency to fill all lagoons and hollows, and bring the prairie surface to one uniform level. . .The fossils found in the loess are the fauna of the Plains. . .” (p. 367).

Then he notes “the analogy of the clay fauna is with that of the modern plains. . .The species from the clays are comparatively small, slender-limbed, with much more advanced reduction in the lateral toes, and the ungulates have cropping incisors and comparatively hypsodont molars” (p. 371).

1.1.5 Mountain uplift and volcanism

The relationship between tectonism and volcanism is complex in Patagonia and all along the Andes and their influence on South American environments has been considerable throughout the Cenozoic. Thomas Falkner observed “the volcanoes, or fiery mountains, of the Andean cordillera in western Mendoza, and was witness to a vast ash cloud carried by the wind that spread over a great part of the jurisdiction of Buenos Aires, beyond the Rio de La Plata, and scattered on both sides of the river in so much that the grass was covered with ashes” (1774).

Pascual and colleagues explored the possible causes and correlates of the evolutionary transformation of tooth crown shape and their discovery of a latitudinal gradient in hypsodonty (1985) and identified: (1) change in physical conditions related to the regional uplift that accompanied deposition of Mustersan age sediments, (2) the establishment of extensive herbaceous steppes, and (3) the deposition of pyroclastic sediments with abundant silicious abrasives (Pascual and Ortiz-Jaureguizar, 1990).

Given there is not much discussion of volcanism and hypsodonty in the paleontology literature, how did Pascual come to his suspicion? In the words of Ortiz–Jaureguizar. . .“*[A] Rosendo (y, por contagio, también a mi) lo le inquietaba era la diferente composición de las faunas mamalíferas de Patagonia y los sedimentos equivalentes del noroeste y el oeste argentino (Casamayorense, Mustersense y Divisaderense de aquellos tiempos). Una de las principales diferencias (ya notada por*

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More information

Pascual en su trabajo de 1970 y en el escribieron luego con Odreman Rivas en 1973) es que los sedimentos mamalíferos al norte del río Colorado eran epiclásticos y los patagónicos piroclásticos. Y mientras en el norte los mamíferos eran predominantemente braquiodontes, en Patagonia eran cada vez más hipsodontes. Consecuentemente, era probable que los mamíferos patagónicos incrementasen la altura de sus molares como una respuesta a la presencia de sedimentos abrasivos que se incorporaban junto con el alimento" (Ortiz-Jaureguizar, personal communication, November 29, 2011).

The idea that pyroclastic sediments played a role in the evolution of precocious hypsodonty is a uniquely South American contribution to the discussion about the possible and potential causes of tooth shape evolution.

1.2 Explaining the prevalence of hypsodonty in South American mammals

Formulating a plausible explanation for the precocious appearance and prevalence of high tooth crowns among South American mammals requires several things.

First is an understanding of the prevalence of tooth structures for resisting abrasive wear among living mammals in South America. Geographic patterns of variation in the prevalence of hypsodonty can be amply demonstrated among living mammals. Among these mammals, special significance is given to sigmodontine rodents, recent immigrants into South America, which encountered the continent's unique and varied environmental conditions and geography. The significance of their evolutionary accommodation to this physical reality will be explored using multivariate approaches.

Second, a better understanding of the patterns and scale of geographic variation in the environment–crown height relationship in South America and in mammals around the world serves to identify the environmental conditions that are associated with it. Geographic coincidences are found among the prevalence of high tooth crowns, sources of environmental mineral abrasives, and the mechanisms that mobilize and transport these mineral particles. These coincidences lead to the proposition that earth surface processes, or more specifically, the intensity of soil erosion is the cause of much dental evolution, or mammalian herbivores, having evolved high-crowned teeth elsewhere for other reasons, once having acquired these adaptations, disperse into and exploit more marginal highly erosive environments.

Third, to distinguish coincidence from cause, a more detailed review of what is known about tooth wear in mammalian herbivores and of the causal agents that underlay variation in excess tooth wear and tooth wear rates is undertaken. The record of tooth wear in sheep on the North Island of New Zealand and southeastern Australia reveals that tooth wear varies as a function of geographic distribution in the intensity of soil erosion. In addition to this geographic coincidence, tooth wear rates in sheep vary seasonally, annually, and at longer timescales consistent with the intensity of soil erosion. Seasonal variation in soil ingestion may be explained by reproductive demand and grazing density, but interannual variation is more difficult to explain except by invoking earth surface processes. The geographic and temporal patterns in tooth wear convincingly point to the primary role of soil ingestion in the otherwise complex etiology of excess tooth wear.

Fourth, the findings at ecological timescales naturally lead to a set of expectations or predictions about what might be observed at evolutionary timescales in the fossil record. For these tests of the proposition, three examples are explored: (1) The fossil and rock record of mammalian herbivores on Mediterranean islands is examined where the independent evolution of high tooth crowns are a conspicuous feature of island history. These islands provide potential examples of the relationship between the rock record of volcanism and the earth surface processes known to drive tooth wear. (2) The potential universality of this finding is examined through a comparison of tooth wear rates among feral ungulate populations on oceanic islands where environments contrast in mineral soil substrate, the style and intensity of surface erosion, and the climate variables that mobilize and transport mineral particles. (3) Comparisons of tooth wear rates can be made between forested and non-forested islands, between islands with mineral soils and with organic soils, and contrasts between feral herbivore species traditionally classified as browsers and grazers. These contrasts point to earth surface processes, specifically the amount and type of exposed mineral soil at the surface, the susceptibility of the land surface to erosion, and the intensity of erosion, as contributors to the observed variation in tooth wear rates.

Fifth, better examples are found in the East African Plio-Pleistocene, where a marine record of soil erosion intensity can be coupled directly to the terrestrial record of evolutionary change in tooth structures. Here again, the coincidence of mountain uplift and volcanism in the Rift System and a record of surface denudation preserved in the sediments on the floor of the Indian Ocean, provide a detailed temporal record of the intensity of erosion. When this record of soil erosion intensity is compared directly with evolutionary rates of change in tooth shape among diverse mammalian lineages, temporal coincidences indicate that threshold levels of atmospheric particle flux trigger evolutionary response. These diverse examples appear to confirm the proposed model for the environmental causation of some important structural features of mammalian tooth shape evolution.

These findings are then related back to the fossil and rock record of South America, and specifically the Eocene–Oligocene transition in Patagonia and the southern oceans. In the fossil record at Gran Barranca in Patagonia is found evidence for multiple species undergoing independent and simultaneous evolutionary increase in tooth crown height. There were three episodes in this history. The first or oldest occurred through a one-million-year interval in the late middle Eocene in at least three monophyletic families of native herbivores at a time of significant local environmental change. The explanations for these are found to relate to the intimacy of terrestrial environments in Patagonia to oceanographic and atmospheric conditions associated with the circum-Antarctic current and West Wind Drift through the later Eocene and into the Oligocene, and their influence on widespread surface accumulations of volcanic ash.

Finally, I explore the significance of ever-growing teeth. I review the evidence for their evolution in South American mammals, their evolutionary and developmental morphology, possible explanations for their evolution and prevalence, and then their