Chapter 2
An Evolutionary History of Browsing and Grazing Ungulates

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2.1 Introduction

Browsing (i.e., eating woody and non-woody dicotyledonous plants) and grazing (i.e., eating grass) are distinctively different types of feeding behaviour among ungulates today. Ungulates with different diets have different morphologies (both craniodental ones and in aspects of the digestive system) and physiologies, although some of these differences are merely related to body size, as grazers are usually larger than browsers. There is also a difference in the foraging behaviour in terms of the relationship between resource abundance and intake rate, which is linear in browsers but asymptotic in grazers. The spatial distribution of the food resource is also different for the different types of herbage, browse being more patchily distributed than grass, and thus browsers and grazers are likely to have a very different perception of food resources in any given ecosystem (see Gordon 2003, for review).

Grass is a relatively recent type of food resource: extensive grasslands only emerged during the later Cenozoic, within the past 25 million years (Ma), while the first ungulates date back to the early Cenozoic, around 55 Ma. Browsing, probably with the incorporation of a fair amount of fruit, is thus the primitive diet of ungulates (Bodmer and Ward 2006). The general evolutionary perspective is that when the grazing species evolved later they eclipsed the browsers (Kowalevsky 1873; Matthew 1926; Pérez-Barbería et al. 2001). While this view of the later Cenozoic rise of grazing ungulates, and corresponding demise of browsing ones, is broadly correct, the actual evolutionary picture is of course much more complex. While the most familiar ungulates today (horses, cows, elephants, etc.) are mainly grazers, in fact specialised grazing is a fairly recent evolutionary adaptation: the first true grazers (i.e., animals subsisting primarily on grass year round) are no more than 10 million years old, and a predominance of tropical grazers as is familiar to us in Africa today has a history of only a couple of million years.

In order to understand the evolutionary history of diets and feeding adaptations in ungulates we need to first pose several questions. Firstly, what exactly are ungulates, and how are different ungulate groups related to each other? Secondly, how can we deduce the feeding behaviour of extinct species from their fossilised remains? And thirdly, how have differences in the earth's climate and environment

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in past times influenced the distribution and abundance of ungulates of different feeding behaviours?

2.1.1 Ungulate Phylogeny and Evolutionary History

While ungulates have long been considered as a clade, united by the possession of hooves (which is in fact not strictly true in any case), recent molecular phylogenies have refuted the monophyly of the 'Ungulata' (see Springer et al. 2005 for review). The paenungulates (elephants, hyraxes, and sea cows) are now united with other African endemic mammals in the basal placental clade Afrotheria. Although artiodactyls and perissodactyls are fairly closely related, they are not sister taxa: the perissodactyls are now considered to be more closely related to a clade consisting of carnivorans plus pangolins, and artiodactyls are now included with whales in the Cetartiodactyla. The name of the clade uniting this diverse assemblage is the Ferungulata.

It is difficult to state how extinct 'ungulate' groups, such as the condylarths and the endemic South American ungulates, fit within this new phylogenetic scheme. The South American orders Notoungulata and Litopterna paralleled northern ungulates in the later Cenozoic in their evolution of body morphologies (with types resembling rhinos, rodents, hyraxes, horses, and camels), and in similar evolutionary transitions to animals with skulls and teeth adapted for grazing, and limbs adapted for cursoriality (see Prothero and Schoch 2002). See the Glossary for terms of extinct ungulate groups (Box 2.1).

Box 2.1 Glossary Guide to extinct taxa. See chapters in Janis et al. (1998) and Rose (2006) for more details

ANCHITHERIINAE. A subfamily of horses (family Equidae), known from the late Eocene to late Miocene of North America and the Miocene of Eurasia, ranging from sheep-sized (earlier forms) to the size of a modern horse (later forms). More derived than the Hyracotheriinae in having more lophed teeth, indicative of a more folivorous diet (but all were brachydont, presumed browsers), and somewhat longer legs, with the loss of the fourth toe in the front foot, and no evidence of a foot pad.

BRONTOTHERIIDAE. A family of perissodactyls (also known as titanotheres), all members brachydont (indicative of browsing), known from the Eocene of North America and Eurasia. Early members were pig-sized and hornless, later forms became larger and grew forked bony nasal horns, and some of the latest forms were of a comparable size to a white rhino.

CHALICOTHEROIDEA. A superfamily of perissodactyls, all members brachydont (indicative of browsing). The earlier Eomoropidae, known from the Eocene of Asia and North America, were small (dog-sized), unspecialised forms. The later Chalicotheriidae, known from the Oligocene to Pleistocene of

Eurasia, the Miocene of North America, and the Miocene to Pleistocene of Africa, were large (camel-sized) forms that had substituted claws for hooves, and likely fed with a bipedal stance clawing down vegetation.

CONDYLARTHRA. A paraphyletic assemblage (order) of basal archaic ungulates, comprising at least eight families, known from the Palaeocene and Eocene of North America, South America and Eurasia, mostly ranging in size from the size of a squirrel to the size of a pig (some carnivorous forms reached bear size). Most forms had bunodont cheek teeth indicative of omnivory; some had more lophed teeth indicative of herbivory, while some were even carnivorous. None had cursorial (running-adapted) postcranial morphologies nor any degree of hypsodonty. The carnivorous mesonychid 'condylarths' are considered to be the sister taxon to the Cetartiodactyla, but the precise relationship of the other families to extant ungulates is not resolved.

DEINOTHERIIDAE. A family of proboscideans, known from the Miocene to Pleistocene of Africa and Eurasia. Characterised by very large size and the possession of recurved lower tusks only (no upper tusks). Cheek teeth were tapir-like, bilophodont and brachydont, indicative of a specialised browsing diet.

DINOCERATA. An order of ungulate-like (but probably not ungulate-related) mammals known from the Palaeocene and Eocene of North America and Asia, ranging from sheep-size to rhino-size, with later forms having a bizarre series of horns on their skulls and sabre-like upper canines. They had brachydont, bilophodont teeth indicative of a diet of soft browse, and later forms had postcranial adaptations indicative of a semi-aquatic mode of life.

GOMPHOTHERIIDAE. A family of Proboscidea, known from the Miocene to Pleistocene of North America, Eurasia, and Africa. Ranged from small rhino-sized to modern elephant-sized. Earlier forms had cheek teeth that were brachydont and bunodont to bunolophodont, indicative of omnivory and/or browsing. Included bizarre 'shovel-tusked' forms. Some later (Pliocene) forms developed highly lophed, hypsodont cheek teeth, indicative of mixed feeding and/or grazing.

HIPPARIONINI. Horses belonging to an extinct tribe of the subfamily Equinae (modern horses and their direct ancestors belong to the tribe Equini), known from the middle Miocene to Pliocene of North America, and late Miocene to Pliocene of Eurasia and Africa (survived into mid Pleistocene of Africa). Earlier hipparionines and equines were similar types of pony-sized animals, but hipparionines in general remained less hypsodont than later equines, and they retained a tridactyl foot. Dental microwear suggests mainly mixed-feeding diets rather than grazing (Hayek et al. 1992; Solounias and Sempebron 2002).

HYPERTRAGULIDAE. A primitive family of ruminants, known from the Eocene and Oligocene of North America and Asia. Diminutive forms, about the size of extant *Tragulus* (Tragulidae). Teeth range from brachydont to hypsodont (but not likely to have been grazing).

(continued)

Box 2.1 (continued)

HYRACOTHERIINAE. A subfamily of horses, known from the Eocene of North America. Small forms (cat to small dog-sized), with relatively bunodont cheek teeth indicative of a folivorous/frugivorous diet, and relatively short legs retaining three toes in the hind foot and four in the fore foot, with the likely presence of a tapir-like foot pad.

INDRICOTHERIINAE. A subfamily of rhinos (of the extinct family Hyracodontidae), known from the late Oligocene and early Miocene of western Asia, all with brachydont cheek teeth (indicative of browsing). Known as 'giraffe rhinos' because of the evolution of long neck and long legs, including the largest ever known land mammal, weighing up to 15 tons.

LITOPTERNA. An extinct order of South American ungulates, known from the Palaeocene to the Pleistocene, comprising forms with brachydont cheek teeth (indicative of browsing), or somewhat hypsodont teeth (indicative of mixed feeding), generally resembling horses or camels.

MAMMUTIDAE. A family of Proboscidea (mastodons), known from the Miocene to Pleistocene of North America, Eurasia, and Africa. Ranged from small rhino-sized to modern elephant-sized, and had cheek teeth that were brachydont and bunolophodont, indicative of browsing.

NOTOUNGULATA. An order of South American ungulates, known from the Palaeocene to the Pleistocene, comprising forms with high-crowned or ever-growing cheek teeth (but were not necessarily all grazers), generally resembling rodents, hyraxes, or rhinos.

OREODONTOIDEA. Extinct superfamily of (possibly) tylopod artiodactyls, pig-like or hyrax-like in appearance, known from the late Eocene to late Miocene of North America. They combined relatively derived selenodont check teeth (albeit in a snub-nosed skull), earlier forms all brachydont, with a primitive postcranium that retained a digitigrade stance. The earlier and more primitive Agriochoeridae (cat-sized to dog-sized) had replaced their hooves with claws and were likely secondarily arboreal. The later Merycoidodontidae (hyrax-sized to tapir-sized) were the commonest mammals in the Oligocene and early Miocene of North America. Somve later Miocene forms showed a tendency to evolve somewhat longer legs and more hypsodont teeth.

PALAEOMERYCIDAE. A family of deer-like (and deer-related) artiodactyls, known from the Miocene and Pliocene of North America (subfamily Dromomerycinae) and Eurasia. Mostly brachydont (indicative of browsing), some forms slightly hypsodont and may have been mixed feeders; many forms characterised by a third, median occipital horn in addition to a pair of frontal horns.

PALAEOTHERIIDAE. A family of horse-like, and horse-related, perissodactyls, known from the Eocene of Eurasia, ranging from dog-size to modern horse-size. All brachydont (indicative of browsing).

PANTODONTA. An order of ungulate-like (but probably not ungulate-related) mammals, known from the Palaeocene and Eocene of North America, Eurasia, and South America, ranging from goat-sized to bison-sized, and later forms resembling ground sloths or hippos. All brachydont (indicative of browsing), and some forms were likely semi-aquatic.

Sivatheriinae. A subfamily of Giraffidae, known from the Miocene to Pleistocene of Africa and Eurasia. Differed from extant Giraffinae in being relatively short legged and heavily-built (often termed ‘moose-like’, but with shorter legs than a moose), with horns that were more lobate in form than giraffines. Cheek teeth were generally more hypsodont than giraffines, indicative of a more mixed-feeding type of diet.

Taeniodonta. An order of ungulate-like (but probably not ungulate-related) mammals, known from the Palaeocene and Eocene of primarily North America, ranging from cat-sized to pig-sized. Later forms had hypselodont (ever-growing) cheek teeth and showed adaptations for digging, rather resembling large pigs. Their hypselodont cheek teeth were probably related to grit found on excavated roots and tubers, as their diet otherwise appears to have been omnivorous.

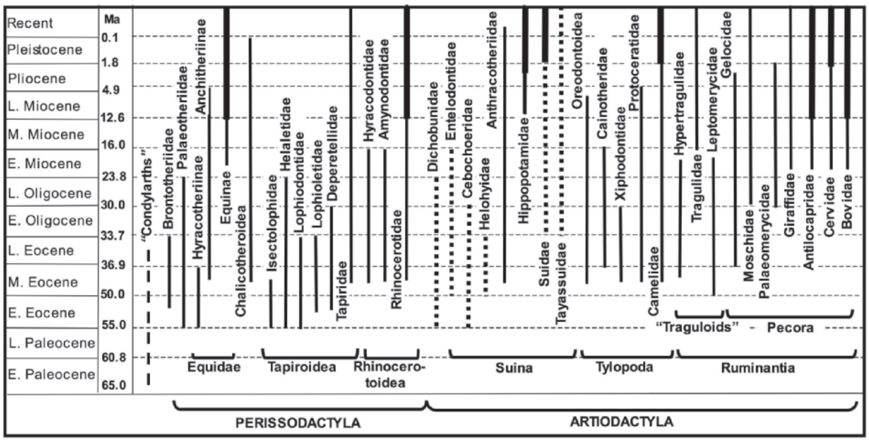

Fig. 2.1 Temporal ranges of ungulate families (adapted from range charts in Benton 1993 and Janis et al. 1998). Not all extinct families of artiodactyls shown; extinct subfamilies of Equidae included. *Dotted lines*: omnivorous groups. *Solid lines*: folivorous groups. *Thick solid lines* indicate time when there were at least some taxa in this lineage that likely took a fair amount of grass (>50%) in their diet

This chapter will mainly consider the evolution of feeding adaptations in the two major orders of extant ungulates: the Perissodactyla, or odd-toed ungulates, and the Artiodactyla, or even-toed ungulates (see Fig. 2.1). Both orders are of Northern Hemisphere origin, first appearing at the start of the Eocene (55 Ma) in North America and Eurasia. Both orders show considerable evolutionary parallelisms, including the evolution of hypsodont (high-crowned) cheek teeth, and elongated limbs with an unguligrade foot posture (i.e., standing on the tip of the phalanges, like a ballerina ‘en pointe’), but they differ profoundly in their morphophysiological adaptations to folivory (the eating of leafy material, whether browse or grass). Perissodactyls are specialised hindgut fermenters while camelid and ruminant artiodactyls (in the taxonomic sense) are foregut fermenting ruminants (in the physiological sense). Such differences in digestive physiology are reflected in differences in both craniodental morphology and feeding behaviour. For example: in terms of craniodental morphology, hindgut fermenters process more food per day than ruminants (all other things such as body size, diet, etc., being equal) so they have a greater volume of masticatory musculature, which is reflected in a deeper angle of the mandible. In terms of feeding behaviour, ruminants are more limited in their daily intake, due to their longer digestive passage time, and so they have to feed in a more selective fashion than a hindgut fermenter, and use their tongue for food selection to a much greater extent than other ungulates. Figure 2.1 shows the distribution of the major families of perissodactyls and artiodactyls through time. Note that forms that have craniodental adaptations for grazing are relatively few and appear relatively late in ungulate evolutionary history.

It is worth making a brief mention of the evolutionary history of the proboscideans and hyracoids (both hindgut fermenters), even though these orders are not closely related to other ungulates (see above). Present-day hyraxes are a relict specialised clade of small-bodied forms: the extinct family Pliohyracidae comprised the dominant small-to-medium sized herbivores in the Eocene and Oligocene of Africa, with a diversity of morphologies, including a long-legged antelope-like form, but none showing any craniodental adaptations for grazing (see Prothero and Schoch 2002; Turner and Antón 2004). This radiation was largely gone by the Miocene, perhaps related to the influx of modern ungulates into Africa, but some pliohyracids persisted into the Pleistocene (including a large, hippo-like form), and were also found across southern Eurasia in the later Cenozoic. The extant family Procaviidae first appeared in the late Miocene, and the modern genus *Procavia* (the rock hyrax) is the only one that takes a large amount of grass in its diet. Proboscideans also originated in Africa, and comprised around ten separate families. Only three families (including the Miocene to Recent Elephantidae) show craniodental morphologies indicative of grazing, such as hypsodont, complexly-lophed cheek teeth. Other proboscideans have bunodont cheek teeth indicative of omnivory, or bilophodont cheek teeth indicative of browsing (see Fig. 2.2 for tooth types; hyracoids and proboscideans are not shown in Fig. 2.1, for reasons of economy of space). However, as with the other ungulates, there is no evidence of any craniodental morphology indicative of grazing until the later Miocene.

2.1.2 Determination of Feeding Adaptations

The large diversity of extant ungulates of known diet has made it possible to quantitatively determine features of cranial and dental morphology that correlate with feeding behaviour (Janis 1995; Mendoza et al. 2002). Ungulate cheek teeth (molars and premolars) are the most obvious dietary indicators. Omnivores have low-cusped molars with rounded, bumpy cusps (‘bunodont’), designed to process non-brittle food such as fruit and roots (Fig. 2.2A). Many different herbivorous forms have evolved from this type of dentition a more ‘lophed’ or ridged type of

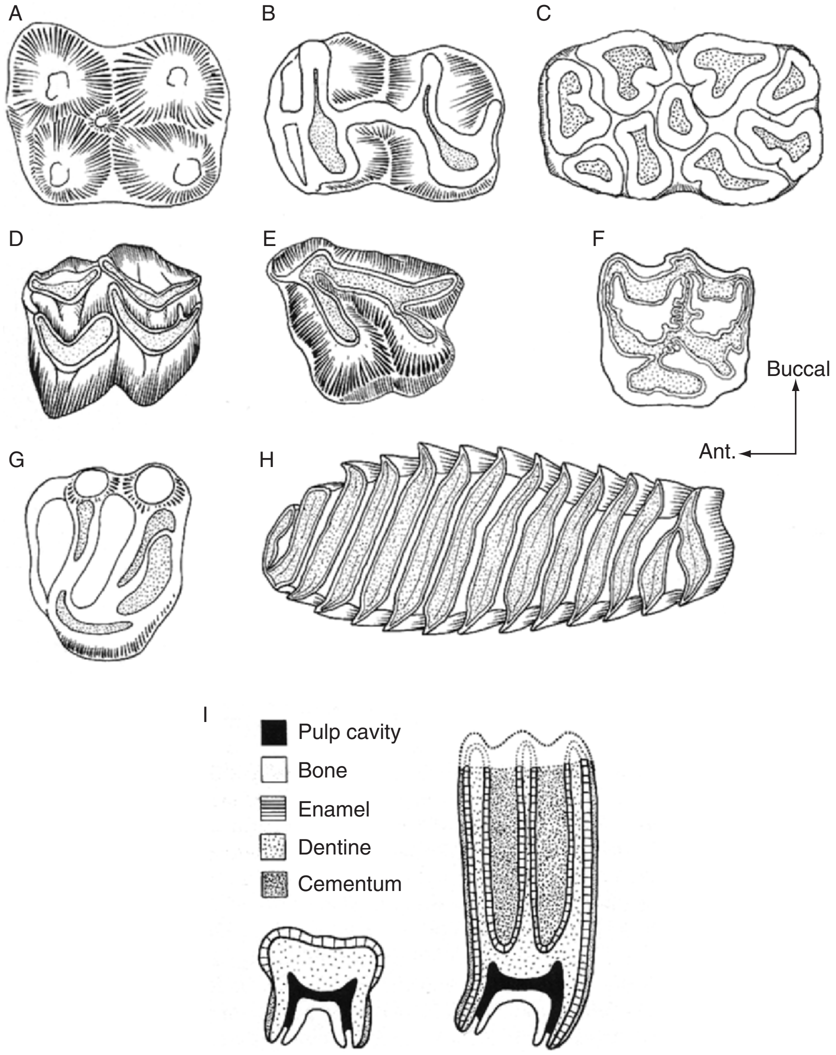

Fig. 2.2 Types of molar morphologies in herbivorous mammals. *A*. Bunodont (peccary). *B*. Bilophodont (kangaroo). *C*. Columnar (warthog). *D*. Selenodont (deer). *E*. Lophodont (rhinoceros). *F*. Plagiolophodont (horse). *G*. Bunolophodont (rodent – woodchuck). *H*. Multilophed (rodent – capybara). *I*. Longitudinal sections of molars, showing brachydont (human) form on the left and hypsodont (horse) form on the right. Modified from Janis and Fortelius 1988, with permission of Cambridge University Press

molar, where the individual cusps are thrown into higher occlusal relief, and are run together as longitudinal or horizontal ridges or lophs (Jernvall et al. 1996). These teeth have been evolved to have maximum efficiency after initial wear, so that the enamel is worn off the top of the lophs exposing a lake of dentine with enamel edges on either side, and these lophs act to shred more fibrous food, such a leaves. The different way in which the cusps have been linked into these lophs result in different patterns of occlusal anatomy: ruminant artiodactyls have ‘selenodont’ teeth (Fig. 2.2D), where the main pattern of the lophs is in an antero-posterior direction, while perissodactyls have ‘lophodont’ (Fig. 2.2E) or ‘bilophodont’ (Fig. 2.2B) teeth, where the main pattern of the lophs is in a labio-lingual direction. Other herbivorous mammals, such as warthogs (Fig. 2.2C) and rodents (Fig. 2.2G, H) have evolved lophed teeth independently in different fashion.

A more fibrous diet of grass rather than browse is reflected in both the level of hypsodonty (see below) and in the occlusal pattern. Highly specialised grazing ruminants and perissodactyls have more complex ‘plagiolophodont’ (Fig. 2.2F) occlusal enamel patterns, accomplished by cross-linking the enamel ridges. In other mammals, such as elephants, and also in many rodents and in wombats, the teeth become ‘multilophed’ with numerous parallel ridges of enamel that can no longer easily be homologised with the original mammalian tooth cusp pattern (Fig. 2.2H; Janis and Fortelius 1988). Any tooth in which the full crown is not visible above the gum line at eruption can be considered as ‘hypsodont’ to some extent, but there are varying degrees of hypsodonty, and in extreme cases the crown height may be six or seven times the width of the tooth. Hypsodont teeth usually have a layer of cementum that coats the tooth and fills in the spaces between the cusps (see Fig. 2.2I).

All dental dimensions scale isometrically: thus a simple ratio, or ‘hypsodonty index’ of the unworn crown height of the third molar (usually the highest-crowned tooth) to its width or length can be compared across taxa of different body sizes (Janis 1988). Fortelius et al. (2002) define a general rule of thumb for ‘hypsodonty classes’, based on the ratio of height to length of the second upper or lower molar. A brachydont tooth has a ratio of less than 0.8, a mesodont (partially hypsodont) tooth has a ratio of 0.8–1.2, and a hypsodont tooth has a ratio of greater than 1.2.

The traditional determinant of a browsing versus grazing diet in fossil ungulates has been the level of hypsodonty, or the degree of molar crown height, as the silica contained in grass tissue results in greater wear on the teeth. A year-round diet of grass in a (perforce) open habitat necessitates a hypsodont dentition, but other dietary or environmental factors may lead to hypsodonty. Fortelius et al. (2002) note that the factors that correlate with hypsodonty are: ‘increased fibrousness, increased abrasiveness due to intracellular or extraneous dust, and decreased nutritive value’. Hypsodonty has evolved numerous times within mammals, and probably represents a fairly simple developmental change, involving delaying the closure of the tooth roots (Janis and Fortelius 1988). For an animal with an abrasive diet, and hence a high rate of tooth wear, hypsodonty is an important adaptation as a dentition that is insufficiently durable will result in a shortened life span, and hence in a reduced reproductive output (Damuth and

Janis 2005). Thus there is a strong evolutionary imperative to make teeth hypsodont if the diet is abrasive.

While almost all grazers have highly hypsodont cheek teeth, not all hypsodont ungulates are grazers, as the silica contained in grass is far from the sole abrasive element in a herbivorous diet. The exceptions to a high degree of hypsodonty in grazers include taxa such as the hippo, *Hippopotamus amphibius*, and the rock hyrax, *Procavia capensis*. These animals (both hypsodont, but at a relatively low level) both have relatively low metabolic rates for their size, resulting in less food consumed per lifetime and thus overall less dental abrasion. Grazing kangaroos are also less hypsodont than grazing ungulates, again probably due to the relatively lower metabolic rate of marsupials. Fresh grass grazers, such as the reduncine bovids, are also less hypsodont than grazers subsisting on grass in more dusty habitats. Open-habitat mixed feeders can also be highly hypsodont, approaching the level of hypsodonty of grazers in the same habitat, even if including little grass in the diet. Most gazelles fall into this category, and the pronghorn, *Antilocapra americana*, is among the most hypsodont of the ruminants despite having only about 12% of grass in its diet. The obvious interpretation of this correlation is that grit and dust accumulating on the food must also contribute to the abrasive nature of the diet (see Janis 1988; Janis et al. 2002). Hypsodont taxa in the fossil record clearly provide some form of palaeoecological signal: increasing levels hypsodonty in today's ungulate communities show a negative correlation with levels of rainfall (i.e., hypsodont ungulates are more prevalent in more arid habitats; Damuth et al. 2002; Fortelius et al. 2002).

A number of aspects of craniodental morphology can be shown to correlate with dietary behavior (see Solounias and Dawson-Saunders 1988; Janis 1995; Mendoza et al. 2002). The features distinguishing grazers from browsers relate to the different physical demands of feeding on grass versus browse. Grass is in general more fibrous and abrasive than browse, and a more fibrous and abrasive (i.e., lower quality) diet requires a greater intake and a greater degree of mastication. Grazers have bigger masseter muscles than browsers, reflected in a larger and deeper angle of the jaw, and a longer masseteric fossa on the skull. Browsers are selective feeders (as are most mixed feeders; Gordon and Illius 1988), and both these feeding types have a narrow muzzle in comparison with grazers, who have a broad muzzle for the intake of large bites. However, the majority of living ungulates are ruminant artiodactyls, and quantitative correlations of morphology and behavior derived from ruminants may not be directly applicable to other types of ungulates, although general qualitative observations may still hold true.

Dental wear (microwear, mesowear, or macrowear) is another way of determining past diets. Dental wear records the actual food preparation and mastication events that took place during the life of the animal, and thus holds the potential for recording the actual ecological history. But dental wear alone may be an insufficient guide to diet because of the continual abrasion of teeth during the life of the animal, and especially of the abrasion of the surface enamel that records microwear patterns. Solounias and Semprebon (2002), and Semprebon et al. (2004) summarise much of the current uses of dental wear in dietary determination in ungulates.

Another recently developed methodology is the use of carbon isotopes in dental enamel. Following the shift in photosynthesis in tropical grasses around 7 Ma, from a C3 carbon cycle to a C4 carbon cycle, the dental enamel of tropical grazers contains a different composition of enamel isotope from that of browsers, and mixed feeders have intermediate values between browsers and grazers. While dental isotopes are only applicable in the rather limited case of fairly recent ungulates (i.e., within the past 7 Ma or so) in tropical or subtropical settings, they can be extremely useful in such palaeoecological situations, especially in combination with morphological features (e.g., Sponheimer et al. 1999).

How does one, then, determine the diet of an extinct ungulate? To a good first approximation, molar occlusal morphology can distinguish omnivores from folivores, and hypsodonty (as well as occlusal morphology, to a certain extent) can distinguish browsers from grazers, but with a degree of caution. A low-crowned (brachydont) ungulate is extremely unlikely to be anything else but a browser, but hypsodont taxa may have a variety of diets. Within hypsodont taxa, craniodental features and/or microwear can be used to distinguish mixed feeders and grazers in most circumstances, and isotopes are useful for distinguishing diets among later Cenozoic taxa in dry, lowland tropical habitats.

2.1.3 Cenozoic Changes in Climate

Evolutionary transitions in ungulate diets can only be understood in the context of climatic changes on planet Earth over the past 60 million years or so. This environmental history is related to changes in the movement of the continents, which in turn have resulted in changes in ocean currents, mountain building, polar glaciation, etc. (see summaries in Janis 1993; Jacobs et al. 1999; Hooker 2000; Zachos et al. 2001). Understanding of the different environmental patterns on different continents comes from a variety of sources, including palaeotemperatures determined from deep sea foraminifera (Zachos et al. 2001) and palaeobotany (Jacobs et al. 1999). Figure 2.3 summarises the evolution of grassland habitats, and the changing global palaeotemperatures. [Note that grass phytoliths have now been isolated from the latest Cretaceous of India (Prasad et al. 2005), but there is no evidence for extensive grasslands in Asia until the later Cenozoic.]

At the start of the Cenozoic, 65 Ma, the entire globe was a fairly equable, warm place, with evidence of mainly forest cover, and tropical-like forests extending up into the high latitudes, although herbaceous (non-grassy) open habitats are recorded in places such as Central Asia. Rapid warming at the end of the Palaeocene was followed by the early Eocene climatic optimum (55–52 Ma; see Zachos et al. 2001). Following this optimum the climate cooled in the higher latitudes, with the arrival of winter frosts and more deciduous types of vegetation

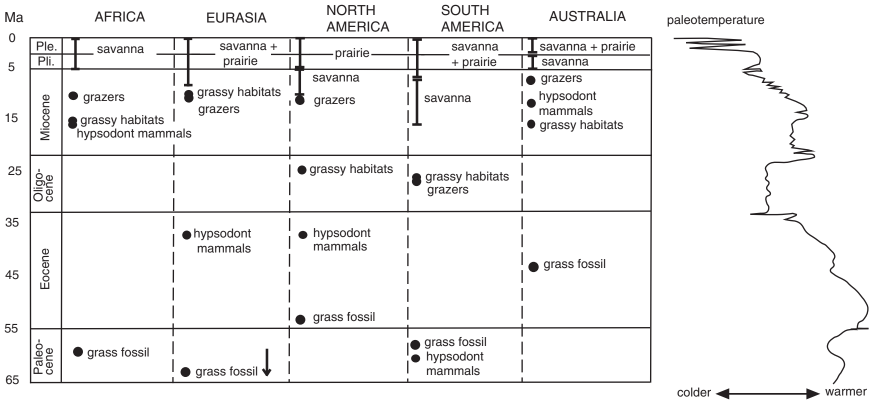

Fig. 2.3 Evolution of grasses and grazers on different continents. *Bars* indicate times of widespread grasslands: prairie (also equivalent to steppe or pampas) = treeless grassland; savanna = treed grassland. *Closed circles* record the first appearance of various events. Grassy habitats = habitats containing some grasses, probably woodland savanna or brushland. Grazers = mammals with craniodental adaptations (apart from hypsodonty) indicative of specialist grazing (i.e., >90% of grass in the diet on a year-round basis). Palaeobotanical information adapted from data in Jacobs et al. (1999) and Strömberg (2004). Palaeotemperature curve is from global deep sea oxygen isotopes (adapted from Zachos et al. 2001); as used here it represents relative temperatures only (for general comparison, mid latitude mean temperatures during the early Eocene climatic optimum were probably around 30° C). Modified from Janis et al. 2004

by the late middle Eocene (around 45 Ma). Although grass fossils are known from the Eocene, and there seem to have been areas of open habitat, such habitats have been termed ‘woody savannas’, not dominated by grasses, and have no analogues among modern habitat types (Leopold et al. 1992).

A million years or so after the end of the Eocene there was an episode of extreme cooling, setting the stage in the higher latitudes for the more temperate world of the Oligocene, when temperate deciduous woodlands spread in the mid latitudes along with patches of more arid habitat. Temperatures started to rise again in the late Oligocene, around 25 Ma, and after a brief fall reached a further peak at around 14 Ma, the ‘mid Miocene optimum’ (Zachos et al. 2001). Palaeobotanical evidence shows that grasslands spread during the Miocene in the higher latitudes, but tropical areas such as East Africa had only limited, if any, savanna regions at this time (Jacobs et al. 1999; see Fig. 2.3). The Antarctic ice cap, which had its inception in the late Eocene, was firmly in place by the Miocene.

After around 14 Ma temperatures fell in the higher latitudes, with additional evidence for increasing aridity. By the latest Miocene (around 6 Ma) the short-grass savannas of North America were replaced by tall-grass prairie (Retallack 2001), and there is evidence of woodland savannas in East Africa (Jacobs et al. 1999). Additional higher latitude cooling in the Plio-Pleistocene brought new types of cold-adapted and/or arid-adapted vegetational habitats: tundra and taiga to the high latitudes, and true deserts to tropical and subtropical regions. An extremely important event in establishing the modern grassland habitats was in the middle Pliocene, at 2.5 Ma. At this time the Isthmus of Panama appeared, linking North and South America (with subsequent animal migrations) and disrupting circum-equatorial circulation. This resulted in the aridification of East Africa, and the establishment of the extensive grasslands that support much of the diversity of grazing ungulates today. The Arctic ice cap first appeared in the Pliocene, and from the start of the Pleistocene around 2 Ma the periodic fluctuations in earth's climate, caused by the various aspects of the rotation of the earth on its own axis (Milankovitch cycles), were sufficient to regularly plunge the higher latitudes into periods of extended glaciation, which we term 'Ice Ages'.

2.2 Fossil Record Evidence of Dietary Evolution in Ungulates

2.2.1 Early Archaic Ungulates and Ungulate-like Mammals (65 to 40 Ma)

Palaeocene 'ungulates' were various taxa ascribed to the order 'Condylartha', that probably contains the ancestry of both artiodactyls and perissodactyls (see Glossary, Box 2.1). Other larger ungulate-like taxa (but probably not related to true ungulates) such as taeniodonts, pantodonts, and dinoceratans (see Glossary, Box 2.1) were also around in the Palaeocene in North America and Asia, persisting into the mid Eocene. These taxa were all apparently predominately omnivorous (taeniodonts and most condylarths) or were adapted to a diet of relatively nonfibrous browse (other condylarths, pantodonts, and dinoceratans). There was little evidence of any herbivores subsisting on fibrous vegetation (with the possible exception of a couple of smaller condylarth taxa in the latest Palaeocene).

2.2.2 The Eocene Emergence of Modern Ungulates (55 to 34 Ma)

The early Eocene saw a great diversification of artiodactyls and perissodactyls in the Northern Hemisphere, and the initial appearance of small to mid-sized mammals that appeared to be specialised folivores (primates as well as ungulates). This mammalian community shift suggests that something had happened to the structure of the vegetational habitat in the higher latitudes where these mammals were found, with leaves now available as a broad dietary resource. The early Eocene vegetation of mid to high latitudes was similar to that of modern tropical forests in terms of plant diversity (e.g., Collinson et al. 1981; Wolfe 1985). Eocene fossil localities supported a wide diversity of small-to-medium sized (5–100 kg) terrestrial herbivores, unlike the situation in present-day equatorial forest habitats, which have a paucity of small terrestrial herbivores (Hooker 2000; Janis 2000). The initial diversity of folivorous ungulates was among the perissodactyls (see Fig. 2.1). The main diversity at this time was among the 'tapiroids', mostly sheep-sized or smaller. Some of these were ancestral to modern tapirs, others to rhinos (first appearing in the middle Eocene), and others were evolutionary dead ends. Most tapiroids had bilophodont cheek teeth (see Fig. 2.2B), indicative of folivory. Hyracotheriine Equids, and the Eurasian equid-related palaeotheres were also common, especially in the early Eocene, most ranging in size from the proverbial wire-haired fox terrier to the size of a large sheep. In general, their teeth were more bunodont than those of the tapiroids and rhinos, indicative of a more omnivorous diet, although some European forms had more lophed teeth, suggestive of a greater degree of folivory. Other families of extinct browsing perissodactyls, included chalicotheres (dog-sized at this time) and brontotheres (see Glossary, Box 2.1).

Artiodactyls were also common in the early Eocene, at this time small (tragulid-sized) with bunodont cheek teeth (see Fig. 2.2A) indicative of a generalised omnivorous diet. Artiodactyls started to diversify into the modern lineages: suines (pig-related forms), tylopods (camel-related forms), and ruminants (see Fig. 2.1) in the late Eocene, coincident with the high-latitude climatic deterioration. Dental changes included more specialised bunodont cheek teeth in many of the suines, indicative of a more specialised omnivorous diet, and the evolution of more selenodont cheek teeth (see Fig 2.2D) in the tylopods and ruminants, indicative of more specialised herbivory. The common selenodont artiodactyls of the late Eocene and Oligocene were various types of now-extinct small to medium-sized traguloid ruminants and tylopods.

The declining temperatures in the higher latitudes during the late Eocene (see Fig. 2.3) basically resulted in the extinction of smaller, generalised omnivorous forms among all ungulate groups, and the rise of more specialised folivores among surviving artiodactyl and perissodactyl lineages, while the remaining condylarths and ungulate-like mammals became extinct (Janis 2000). Most higher latitude primates also disappeared during this time. The megaherbivore brontotheres also went extinct at the end of the Eocene, possibly unable to sustain their specialised browsing diet in higher latitudes at this time. Rhinos persisted through this time period, but tapiroids were badly hit, and equoids (horses and palaeotheres) became completely extinct in the Old World. The familiar story of horse evolution relates an unbroken phylogeny through the North American Eocene, but this masks the fact that the abundance of individual equid fossils decreased sharply following the early Eocene diversity of the subfamily Hyracotheriinae. Only in the late Eocene did equids return to the North American fossil record in abundance, with the first member of the subfamily Anchitheriinae, the sheep-sized *Mesohippus*. *Mesohippus* was a very different beast from the earlier hyracotheres, with more strongly-lophed teeth, indicative of committed folivory, and more cursorially-adapted limbs.

This pattern of late Eocene perissodactyl decline and artiodactyl diversification has often been held as indicative of competitive replacement, ascribed to the supposedly superior foregut system of digestion in ruminating artiodactyls (see discussion in Janis 1976), but this is not supported by the patterns in the fossil record (Janis 1989). The late Eocene fossil record shows a general shift from omnivory to folivory (in terms of adaptive dental morphologies) in rodents as well as ungulates (Collinson and Hooker 1991; Meng and McKenna 1998). Ruminating artiodactyls may have been fortuitously better-adapted than perissodactyls to cope with the changing vegetation of the later Eocene, due to their ability to subsist on smaller amounts of more selectively chosen vegetation. The climatic changes, including increased patterns of seasonality, of the later Eocene may have resulted in changes in vegetational abundance, but perhaps more importantly would probably have resulted in a greater differentiation of fibre content between plant leaf and stem, allowing for the selective feeding habits that characterise present-day ruminants (see Janis 1989). Foregut fermentation would also have been useful for the detoxification of plant secondary compounds (Bodmer and Ward 2006). Small-to-medium-sized ruminants fare better than hindgut fermenters where food is lower in quantity but higher in quality. The increased body size of many perissodactyls in the late Eocene (e.g., among the brontotheres) may also reflect an adaptation to changing patterns of food abundance and quality.

2.2.3 The Lull Before the Storm: Oligocene and Early Miocene Times (34 to 20 Ma)

The 10 million years of the Oligocene and the first few million years of the Miocene were a time of relative calm, following the high latitude temperatures of the later Eocene, the rapid plunge in temperatures just after the Eocene/Oligocene boundary (see Fig. 2.3), and the extinctions in Europe (the 'Grande Coupure') that resulted not only from climatic change but from an influx of taxa from Asia (Hooker 2000). The mid to high latitude climate would have been equable, but also temperate and seasonal, with winter frosts (see Wolfe 1985). The prominent vegetation was deciduous forest or woodland, with some areas of relative aridity in North America (Retallack 2001), but no true modern-type grasslands or deserts.

Among North American and Eurasian ungulates, tapiroids were few, and the modern family Tapiriidae was now well-established. (Note that at this time there was not yet faunal exchange between Eurasia and Africa, and India was still an isolated island.) Rhinos were represented by a variety of forms of medium to large body size, including the huge (up to 15,000 kg) indricotheres (see Glossary, Box 2.1). Anchitheriine equids underwent a moderate diversification in North America, and *Anchitherium* itself migrated to Eurasia in the early Miocene. All of these perissodactyls had skulls and dentitions suggestive of generalised browsing. The general artiodactyl diversity was primarily a continuation of the late Eocene radiation of small or medium-sized browsers and omnivores.

However, it was among the Oligocene artiodactyls that the first incidences of hypsodonty appeared among ungulates, at least in the Northern Hemisphere. (While some native South American ungulates had hypsodont teeth from Eocene times, this feature alone—as noted below—is not necessarily indicative of grazing behavior, and many hypsodont notoungulates in fact had dental microwear indicative of browsing or mixed feeding; Townsend and Croft 2005). Oligocene hypsodont ungulates include several North American taxa: the diminutive hypertragulid *Hypisodus*, rock-hyrax-like oreodonts such as *Sespia,* and gazelle-like camelids such as *Stenomylus* (see Glossary, Box 2.1). The appearance of these hypsodont ungulates has been used in support of the notion of an early spread of grasslands and grazers in North America at this time (Retallack 1983), but the cranial morphology of these animals does not support a grazing diet. These ungulates all had very narrow muzzles, typical of specialised mixed-feeders in open habitats, where grit or abrasive types of browse were the main cause of high rates of tooth wear. It is likely that they represented some sort of specialised selective feeders living in open, arid areas. Some grass may have formed some part of their diet, but they were far from being specialised grazers. All of these lineages went extinct without issue during the Miocene: they were not ancestral to any of the later groups of hypsodont mammals.

2.2.4 The Rise of the Grasslands (20 to 10 Ma)

During the late early Miocene, around 20–17 Ma, both floral and faunal change became prominent, with mid-latitude grasslands diversifying in North America and eastern Asia. Grasslands may have been established several million years earlier in southern South America, and a fauna characterised by ungulates with hypsodont teeth occurred as early as the early Oligocene (Jacobs et al. 1999; see Fig. 2.3). Sea levels fell, and a land bridge opened up between Africa and Eurasia, allowing the migration of proboscideans out of Africa and the immigration into Africa of northern types of ungulates (rhinos and various ruminants such as bovids and giraffoids; see Turner and Antón 2004). There is little evidence for grasslands in Africa at this time, although the middle Miocene (14 Ma) site of Fort Ternan in Kenya contains evidence of fossil grasses and some ungulates that were probably mixed feeders (Jacobs et al. 1999).

In North America palaeobotanical evidence exists for grasslands during the late Oligocene and earliest Miocene from both plant phytoliths (Strömberg 2004, 2006) and fossil soils (Retallack 2001). However, the soil evidence, as well as evidence from other organisms such as legumes and insects, points to initial arid bunchgrass shrubland with more savanna-like short sod grasslands developing in the late early Miocene (Retallack 2001). The advent of grasslands in North America before the evolution of hypsodont ungulates such as equids has been argued as evidence for ‘adaptive lag’ (Retallack 1983; Strömberg 2006)—that is, that morphological evolution had not yet caught up to behavioural evolution. This evolutionary scenario is highly unlikely: as mentioned previously, hypsodonty is essential for an animal eating an abrasive diet, and hypsodonty also seems to be an easy feature to evolve, as it has evolved so many times convergently among mammals (Janis and Fortelius 1988; Damuth and Janis 2005).

The first pecorans (horned ruminants), including early members of the modern families Bovidae, Cervidae, and Giraffidae, made their first appearance in Eurasia at around 18 Ma. The earliest definite bovid, *Eotragus*, is known from around 18 Ma in Europe and Pakistan, some cervids of a similar age are known from Europe, and some large giraffoids are known from the early Miocene of Spain (see Gentry 2000). New types of ruminant artiodactyls appeared in North America, including antilocaprids (pronghorns) and palaeomerycids (see Glossary, Box 2.1). Also in North America larger and more derived types of camelids appeared, along with a great radiation of the first member of the modern equid subfamily, Equinae, the genus *Merychippus*. However, at this point none of these ungulates had craniodental morphologies indicative of grazing, even though hypsodonty was apparent among the equids, antilocaprids, and camelids.

This initial rise in the numbers of hypsodont ungulates has long been interpreted as the radiation of a 'savanna-like' fauna (e.g., Webb 1977), but it is not at all clear that these hypsodont taxa were actually specialised grazers: the majority of the hypsodont Miocene equids have dental microwear indicating mixed feeding (Solounias and Semprebon 2002). Many lineages of camelids also became more hypsodont at this time, but again their craniodental morphology does not support the notion of a grazing habit (Dompierre and Churcher 1996), and all of these taxa display rather moderate levels of hypsodonty in comparison with modern grazers.

Until recently, the fate of the browsing ungulates during the Miocene was thought to have been one of gradual extinction, replaced by the 'better-adapted' grazers (see discussion in Janis et al. 2004). In the familiar story of horse evolution there is rarely a mention of the parallel diversification to the hypsodont forms of specialised browsing anchitheriine equids that survived into the late Miocene in both North America and Eurasia, ranging from the goat-sized *Archaeohippus* up to the horse-sized *Hypohippus* and *Megahippus* (Janis et al. 1994; Agustí and Antón 2002). This radiation of browsing horses is merely a portion of the diversity of late early and middle Miocene browsers. Others browsers included the palaeomerycids, the bizarrely-clawed chalicotheres, various types of rhinos, and a diversity of mid-sized proboscideans such as mastodons (Mammutidae) and gomphotheres (see Glossary, Box 2.1). The evolutionary pattern of these browsers has been best documented in North America (Janis et al. 2000, 2002, 2004), but similar patterns are apparent in western Europe (Fortelius et al. 1996). In North America, not only were browsing ungulates highly diverse taxonomically on a continental scale (see Fig. 2.4), but they were also exceedingly species rich at individual fossil localities. The numbers of browsing ungulates at mid-Miocene fossil sites in North America greatly exceeds those in any habitat today, and similar patterns appear to hold true for ungulates at localities in Eurasia and Africa (Janis et al. 2004), and for terrestrial herbivores in South America (Kay and Madden 1997) and Australia (Myers 2002). This abundance of browsers disappears from North America by the start of the late Miocene, around 11 Ma, and an overall decline of ungulates also occurs at this time in North America, Western Eurasia, and in Pakistan (Barry et al. 1995). These palaeocommunities clearly represent some sort of woodland savanna habitat, but with no precise modern analog.

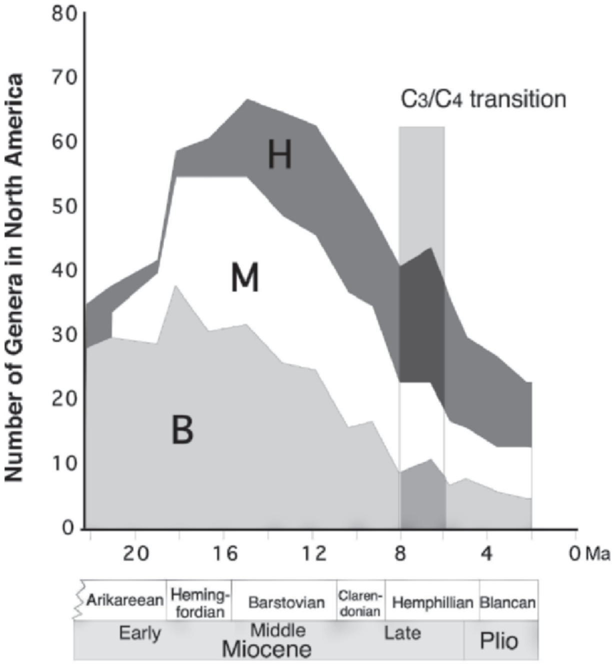

Fig. 2.4 Continent-wide generic diversity of ungulates in North America. *H* = hypsodont (i.e., probable grazers or mixed feeders in open habitats); *M* = mesodont (somewhat hypsodont; i.e., probable mixed feeders in open or closed habitats); *B* = brachydont (i.e., probable browsers). Modified from Janis et al. 2004

It is not clear how these mid Miocene habitats achieved a greater density of species, especially in terms of the numbers of browsers, than in their modern-day equivalents. Our (Janis et al. 2004) preferred explanation is for greater levels of atmospheric carbon dioxide than the preindustrial levels, leading to greater levels of primary productivity, but we acknowledge that this hypothesis is at odds with the current geochemical evidence. Additionally, species richness does not correlate in a simple fashion with productivity in modern ungulate faunas: Prins and Olff (1996) note that species richness of African grazers is actually highest at intermediate levels of grass productivity. Whatever the explanation, this great diversity of mid-Miocene browsers, occurring concurrently with the early diversification of more hypsodont, open-habitat forms, is an unappreciated evolutionary event.

2.2.5 *The Rise of Grazing Ungulates (10 to 2 Ma)*

It was not until the start of the late Miocene, around 10 Ma, that ungulates appeared with morphologies consistent with more specialised grazing adaptations. Note that, in general, the browsing lineages of the earlier Miocene went extinct without issue: although all grazers were obviously derived from browsers at some point in evolutionary history, the lineages that remained as browsers in the mid Miocene did not later transform into grazers. The remaining browsers in the late Miocene of North America were considerably bigger in body size than previously, indicating a declining quality and abundance of suitable forage (Janis et al. 1994).

A classic evolutionary pattern of distinct grazing versus browsing lineages can be seen among the North American horses. In the early Miocene the equid lineage split into the one leading to the modern Equinae (with the emergence of the genus *Parahippus*) and the lineage leading to the specialised large browsing horses of the later Miocene (derived members of the Anchitheriinae). These browsing horses (e.g., *Anchitherium, Hypohippus, Megahippus*) were a successful radiation for a good ten million years, but went extinct without issue during the climatic changes of the later Miocene. They did not change their diet at this time: instead the radiation into the grazing niche came from the Equinae line that had opted for a more mixed feeding diet back in the early Miocene. Another example is the North American dromomerycids (palaeomerycid ruminants). The final members of this predominantly browsing lineage showed some craniodental changes indicative of a more mixed-feeding strategy in the latest Miocene, but still declined in numbers and went extinct fairly rapidly, while at the same time there was an expansion of the antilocaprids that were previously more adapted for mixed feeding (Semprebon et al. 2004). The general evolutionary pattern in the late Miocene is for browsing lineages to be replaced by ones adapted for more fibrous diets (e.g., the replacement of tragulids and cervids by bovids in the Siwalik faunas of Pakistan; see, e.g., Barry 1995 and Barry et al 1995), rather than the browsers themselves undergoing evolutionary change. Likewise ungulate lineages do not transform back into browsing forms once they have evolved the more derived craniodental apparatus of grazers or mixed feeders. (A possible exception to this is the evolution of the specialised high-level browsing gerunuk, *Litocranius walleri*, that has a brachydont dentition presumably evolved from the more hypsodont dentition of other gazelles.)

In North America hypsodont horses, members of the extant tribe Equini and the extinct tribe Hipparionini (see Glossary, Box 2.1), diversified immensely in the late Miocene, and one lineage of hipparionines (or perhaps a couple) migrated into Eurasia by 10 Ma and from there into Africa. This time marks the appearance of the classic mid-latitude savanna faunas, the ‘Clarendonian chronofauna’ in North America and the ‘*Hipparion* fauna’ in Eurasia. These later equines were generally larger than early members of the Equinae (such as *Merychippus*), approaching the size of modern equids (although some secondarily dwarfed lineages also existed), and had more hypsodont cheek teeth and craniodental features indicative of a more fibrous diet, such as deeper mandibles and broader muzzles. However, patterns of dental microwear suggest that these equids were still predominantly mixed feeders (Hayek et al. 1992; Solounias and Sempebron 2002).

The taxonomic diversity of early late Miocene (around 11–8 Ma) North American equids was very high: continent-wide there were ten sympatric genera, each with a large diversity of species, and individual fossil localities commonly contained half a dozen different equid species (Janis et al., 2004), making equids as taxonomically diverse as grazing bovids are today in Africa. With the exception of the short-legged rhinoceros *Teleoceras*, no other ungulates in North America appeared to challenge equids as grass specialists until the very end of the Miocene, when hypsodont proboscideans (gomphotheres) first appeared (Lambert and Shoshoni 1998). During the late Miocene there was a significant radiation of hypsodont camelids, and also of more derived antilocaprids (the antilocaprines, which include the modern pronghorn, and which were more hypsodont than the earlier merycodontine antilocaprids); but the craniodental features of these taxa (e.g., relatively narrow muzzles) are indicative of mixed feeding rather than grazing.

In the early late Miocene of Eurasia there was a reduction in numbers of browsers such as suids, tapirs, tragulids, and brachydont rhinos, suggesting a loss of forest habitat, and a radiation of bovids, equids, and more hypsodont rhinos and giraffoids, suggesting the spread of more grass-dominated habitats (Barry 1995; Fortelius et al. 1996; Agustí and Antón 2002; Costeur et al. 2004.). However, these faunas contained few undoubted grazing species, the hypsodont forms most likely being mixed feeders, and the habitat of these localities appears to have been woodland and shrubland rather than open savanna (Solounias and Dawson-Saunders 1988; Prins 1998). Few highly hypsodont bovids were present in Africa: the late Miocene fauna contained a large diversity of suids, rhinos, proboscideans, and giraffids, as well as bovids and hipparionine equids, probably representing an assemblage of browsers and mixed feeders (Turner and Antón, 2004).

2.2.6 The Late Cenozoic Dawn of the Modern Ungulate Fauna

Global temperatures fell dramatically in the latest Miocene (see Fig. 2.3), as did mammalian taxonomic diversity, and the mid-latitude vegetational habitats apparently became more arid (see e.g., Fortelius et al. 2002). Around 8 Ma, there was a shift in grass photosynthetic biochemistry from the C3 cycle to the C4 cycle in lower latitudes in North America and Asia (Cerling et al. 1993, 1997). It has been claimed that this event had a significant impact on the grazing mammals: a greater diversity of hypsodont artiodactyls, including bovids, appeared in Pakistan at this time while brachydont taxa such as suids and giraffids declined (Barry et al. 1995), but there was little overall impact on the hypsodonty levels of ungulates in North America (Janis et al. 2000).

Various examples of gigantism existed among ungulates at this time. There were four sympatric genera of oversized browsing or mixed-feeding camelids (i.e., ~1,500 kg) in the latest Miocene and the Pliocene of North America. The North American rhinos (one browsing and one grazing lineage) also increased in size throughout the Miocene to reach a similar size to present-day African rhinos by the end of the epoch. In the Old World, elephantids (all grazers) diversified at this time, as did large browsers such as chalicotheres, deinotheres (see Glossary, Box 2.1), and modern types of giraffids. There was also a radiation of the sivatheriine giraffids (see Glossary, Box 2.1) of similar size to the giant camelids.

In North America the rhinos were gone by the end of the Miocene, and the giant camelids did not survive past the Pliocene, but the diversity of large browsers survived in the Old World through the Pleistocene. Again, the situation of North America as an island continent probably accounts for its greater (and earlier) pattern of extinctions of large mammals. The only megaherbivores to survive into the Pleistocene in North America were the mammutid and gompthotheriid proboscideans, which were joined by the elephantid *Mammuthus* (mammoths, including the woolly mammoth and the Imperial mammoth) at this time, along with a small number of equids, antilocaprids, and camelids, and the newly immigrant bovids and cervids. The extinction of all the North American endemic ungulates and proboscideans at the end of the Pleistocene, with the exception of the pronghorn, *Antilocapra americana*, remains enigmatic, with numerous arguments for climatic change, human hunting, or some combination of the two.

African savanna habitats were first prominent in the Pliocene (Jacobs et al. 1999), with the initial radiation of specialised grazing bovids such as the hippotragines (e.g., sable) and alcelaphines (e.g., wildebeest). But the establishment of extensive open savannas of dry, secondary grasslands, versus woodland savanna or seasonally-flooded edaphic grasslands, was not apparent until the start of the Pleistocene, around 2 Ma, which is also when C4 grasses first appeared in Africa (Cerling 1992). At this time the first bovids with definitive specialised craniodental grazing adaptations appeared (Spencer 1997), evolving from earlier mixed feeding forms, and the total numbers of grazing taxa approached those of today (Reed 1997). The modern equid genus *Equus*, first evolving in North America, appeared in the Old World the late Pliocene, around 2.5 Ma; some remaining hipparionine equids (persistently three-toed forms) survived alongside *Equus* for a while, but eventually became extinct by the mid Pleistocene (Turner and Antón 2004). The grazing white rhino (genus *Ceratotherium*) also made its first appearance in the African Pliocene.

During the Pleistocene grazing megaherbivores such as the woolly mammoth (*Mammuthus*), and several types of hypsodont rhinos, including the woolly rhino (*Coelodonta*), were prevalent at mid to high latitudes, as were horses and large grazing bovids such as bison (*Bison*) and musk oxen (*Ovibos*). This array of large grazing ungulates, along with some smaller mixed-feeders [e.g., saiga antelope (*Saiga*) and reindeer (*Rangifer*)] comprised the fauna of the late Pleistocene 'steppe tundra' biome of northern Eurasia and Alaska, a habitat type with no modern analogue (Prins 1998; Agustí and Antón, 2002). In both North America and the Old World today bovids remain the prime grazers, although their diversity is much less in the Northern Hemisphere than it is in Africa. A few low latitude Asian cervids are today at least fresh-grass grazers, such as the barasinga (*Cervus duvaucelli*) and Père David's deer (*Elaphurus davidianus*; there is no equivalent radiation among cervids to bovids such as alcelaphines and hippotragines). However, it is not clear why cervids never really expanded into the grazing niche, and never colonised Africa south of the Sahara.

Ungulates such as deer, tapirs, and camelids (llamas), as well as now-extinct or extirpated forms such as gomphothere proboscideans and equids, dispersed into South America in the Pliocene, around 2.5 Ma (Webb 1991). The equids and gomphotheres diversified into the grazing niche, but no ungulate is a true grazer there today. Tapirs have remained as specialised browsers; llamas never diversified much beyond their present day high-altitude, mixed-feeding ecological role; and while cervids underwent the most profound diversification, they never evolved true grazing forms, although the marsh deer (*Blastocerus dichotomous*) is a fresh grass grazer. Bovids never reached South America until introduced by humans, and it is unclear why no cervid evolved there to be a specialised grazer.

2.3 Discussion and Conclusions

Grazing is a fairly recent evolutionary specialization among ungulates. Although extensive grasslands first appeared around 25 Ma—and along with them ungulates with hypsodont teeth designed to withstand a greater amount of abrasion—specialised grazers did not appear until around 10 Ma, and most true grazers are of Plio-Pleistocene age (Fig. 2.3). Many different lineages have evolved intermediate feeding types, but few have progressed to specialised grazing.

Although the majority of grazers today are bovids—and specialised grazing evolved a minimum of four times within this clade (within the Bovini, Caprini, Hippotragini, and Alcelaphini)—no other ruminant, past or present, has evolved a specialised grazing form (although a few modern cervids, such as *Blastocerus, Elaphurus* and species of *Cervus* and *Axis*, have a grass-dominated diet). Within other artiodactyls, grazers have appeared recently (Plio-Pleistocene) among suids (the warthog) and hippos, but were not in evidence before this time. In contrast, grazing appears to have been easier to evolve among hindgut fermenters.

Clauss et al. (2003) present an elegant argument for why ruminants, past and present, do not attain the size of rhinos and elephants. Ruminants have longer passage times of the digesta than hindgut fermenters of a comparable body size (around 40 hours for a horse versus around 60 hours for a cow), and the time for passage of the digesta increases with body size. However, if the passage time approaches 4 days, an acute problem develops with the growth of methanogenic bacteria, which convert acetic acid (the main volatile fatty acid product of cellulose fermentation) to methane and carbon dioxide, with resultant high energy losses. Elephants solve this problem by adopting relatively shorter and broader guts, thus speeding up the passage rate of the digesta; but this would not be a possible solution for a ruminant, where the rumenoreticulum portion of the stomach is specifically adapted to delay food passage. Thus ruminants are limited to body sizes where their digesta passage time is less than four days (likely under 1,500 kg).

Within the equids, several different clades in the subfamily Equinae progressed from mixed feeding to grazing (although only *Equus* survives). Grazing appeared independently within several different clades of rhinos, including the white rhino, and among extinct forms the North American *Teleoceras*, and the Old World woolly rhino (*Coelodonta*) and steppe rhino (*Elasmotherium*). Grazing also evolved three times within the Proboscidea (within the Elephantidae, Stegodontidae, and Gomphotheriidae), and once in the Hyracoidea (*Procavia*).

It is commonly thought that bovids somehow out-competed equids, but this is erroneous. Equids were predominantly a New World radiation, and their decline in taxonomic diversity in the late Cenozoic was due to being stranded in an island continent, with no tropical refuge zone when the more productive savanna grasslands turned to less productive prairie. North American equids never encountered bovids until the immigration of sheep and bison in the Pleistocene, by which time only one genus, *Equus,* remained. However, this taxon was still a very prominent part of the Pleistocene faunas, and the fossils are extremely numerous, suggesting individual abundance in life. North American equids only went extinct in the end-Pleistocene extinctions that decimated the megafauna. Equids that migrated into the Old World encountered an existing bovid-dominated faunal community, which may explain their lack of taxonomic diversification there in comparison with North America. While modern equids have diversified into a variety of different species (e.g., asses in Asia, zebras in Africa), and are individually numerous when encountered, there is still usually only one species of equid in any faunal community (this was also broadly true of Old World fossil communities), and all extant equid species belong to a single genus with essentially the same ecology (i.e., herd-living, specialised grazing).

The bias of today's world suggests a normality of the predominance of ruminant grazers, and also a diversity of grazers among other ungulates. However, the fossil record shows us that we need to think more about why grazing is so difficult to attain in non-bovid ruminants, and why in general it appears to be easy to evolve an animal that takes some grass in its diet, but not to evolve a specialised grazer.

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