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EVOLUTION OF HORNS IN UNGULATES: ECOLOGY AND PALEOECOLOGY

BY CHRISTINE JANIS

Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K.

CONTENTS

I. INTRODUCTION

The predominant ungulates of the present-day savanna faunas of Africa are the horned bovids. However, the predominant ungulates of the savanna faunas in North America during the Miocene epoch were all hornless, with tylopod artiodactyls (camelids and oreodonts) and equids being the commonest faunal elements (Table 1). In this paper I review the climatic changes during the Tertiary and the evolution of the ungulates in the northern hemisphere, and propose a

Table 1. *Composition of past and present ungulate communities*

1. Recent: Africa (total no. in fauna = 8221)

Animal	No. of indiv.	Percentage of fauna	Body wt. (kg)
PROBOSCIDEANS			
Elephant	218	3	2575
Loxodonta africana			
EQUIDS			
Zebra	2200	27	200
Equus burchelli			
RHINOS			
Black rhino	40	0·1	816
Diceros bicornis			
GIRAFFIDS			
Giraffe	115	1	750
Giraffa camelopardalis			
BOVIDS			
Buffalo	457	6	450
Syncerus caffer			
Wildebeest	2473	30	165
Connochaetes taurinus			
Impala	700	9	40
Aepyceros melampus			
Grant's gazelle	1230	15	40
Gazella granti			
Thomson's gazelle	788	10	15
Gazella thomsoni			

Percentages	
Equids	27
Hind gut fermenters	30
Ruminants	70
Horned ruminants	70

2. Oligocene: North America (total no. in fauna = 868)

Animal	No. of indiv.	Percentage of fauna	Body wt. (kg)
EQUIDS			
Mesohippus	139	16	10
TAPIRS			
Colodon	3	0·3	30
RHINOS			
Hyracodon	19	2	60
Caenopus	10	1·1	250
DICHOBUNIDS			
Miscellaneous leptochoerids	2	0·2	2
SUOIDS			
Archaeotherium (entelodont)	10	1·1	600
Bothriodon (anthracothere)	4	0·5	200
Perchoerus (peccary)	3	0·3	35
OREODONTS			
Agriochoerus	11	1·3	50
Merycoidodon culbertsoni	143	16·5	50
M. gracilis	37	4·3	35
Bathygenus	1	0·1	13
CAMELIDS			
Pöebrotherium	17	2	8
TRAGULOIDS			
Hypertragulus	68	8	2·5
Leptotragulus	389	45	3
Hypisodus	12	1·3	0·5

Percentages	
Equids	16
Hind gut fermenters	19·4
Ruminants (including oreodonts and excluding traguloids)	23
Horned ruminants	0

Table 1. (cont.)

3. Early Miocene: North America (total no. in fauna = 42)

Animal	No. of indiv.	Percentage of fauna	Body wt. (kg)
EQUIDS			
Archaeohippus	4	9·5	25
Anchitherium	3	7	110
Hypohippus	2	4·5	200
Parahippus pawniensis	3	7	80
P. neocognatus	3	7	90
CHALICOTHERES			
? Moropus	1	2·5	1200
RHINOS			
Diceratherium	1	2·5	220
SUOIDS			
Daeodon (entelodont)	1	2·5	850
Arretotherium (anthracothere)	3	7	200
Dyschyus (peccaries)	2	4·5	50
Desmathyus (peccaries)	1	2·5	80
Hesperhyus (peccaries)	1	2·5	80
OREODONTS			
Merychyus	5	12	50
CAMELIDS			
Oxydactylus	1	2·5	80
PROTOCERATIDS			
Lambdoceras	4	9·5	80
DROMOMERYCIDS			
Barbouromeryx	1	2·5	20
MOSCHIDS			
Parablastomeryx galushai	4	9·5	15
P. advena	1	2·5	6
P. scotti	1	2·5	3

Percentages	
Equids	35
Hind gut fermenters	40
Ruminants (including oreodonts and moschids)	41
Horned ruminants	12

4. Late Miocene: North America (total no. in fauna = 506)

Animal	No. of indiv.	Percentage of fauna	Body wt. (kg)
PROBOSCIDEANS			
Amebelodon	13	1	2000
EQUIDS			
Pseudohipparion	1	0·5	100
Hipparion	8	3	120
Neohipparion	30	12	200
Calippus	1	0·5	40
Pliohippus	22	9	110
Astrohippus	17	6	200
Nannipus	1	0·5	90
TAPIRS			
Tapirus	20	8	150
RHINOS			
Teleoceras	40	16	1500
Aphelops	18	7	1500
SUOIDS			
Prosthenops (peccary)	11	4	40
CAMELIDS			
Aepycamelus	2	1	800
Hemiauchenia	24	9	300
Procamelus	31	12	40
DROMOMERYCIDS			
Yumaceras	12	5	250
MOSCHIDS			
? Pseudoceras	2	1	8
ANTILOCAPRIDS			
Antilocaprid	1	0·5	20

Percentages	
Equids	31·5
Hind gut fermenters	67·5
Ruminants (including moschids)	28·5
Horned ruminants	12·5

The African Recent fauna is from the Amboseli Game Park, Kenya, and is taken from Western (1980). The Oligocene fauna is from the lower nodular zone in the Brule Formation, South Dakota. The numbers of animals in the fauna are taken from Clark *et al.* (1967), and represent the summation of open plains and near plains facies from collections at the South Dakota School of Mines, and the University of Colorado Museum at Boulder. The fauna has been interpreted as being essentially an untransported death assemblage.

The early Miocene fauna is from the Batesland Formation, South Dakota, and is housed in the Museum of Paleontology at the University of California, Berkeley, California. The late Miocene fauna is from the Love bone bed, Florida, and is a stream bed assemblage, housed at Florida State Museum, Gainesville Florida. The data are taken from Webb, MacFadden & Baskin (1981).

The numbers of animals in the early Miocene fauna were estimated from the museum collection in the following manner: for each species, the single most common element was noted (this was usually either the mandible (ranked by age class according to eruption and wear sequence), or tarsal elements such as the astragalus or calcaneum). A count was then made of left- and right-hand elements, and the largest number was taken as an estimate of the minimum number of individuals of that species present.

reason why bony horns were evolved in the majority of the ruminant artiodactyls in the Old World, but only in a single family in North America. Reconstructions of both the feeding styles and the social behaviour of the endemic tylopod artiodactyls of North America in the middle Tertiary indicate, taken separately or together, a habitat in which the food resources were more widely dispersed than was the case for the contemporary Old World habitats, or in the present-day mosaic vegetation of the African savanna. A possible cause of this habitat difference may have been a more continental climate in North America than in Eurasia during the Tertiary, resulting in a more seasonal and arid habitat, in which the trees were more widely spaced. The distribution of feeding types in the Tertiary faunas supports this hypothesis of a greater tree density in the Old World.

The Eupecora* (*sensu* Webb & Taylor, 1980) are today the most abundant and

* The living members of the Eupecora are the bovid, cervid, giraffid and antilocaprid artiodactyls of the suborder Ruminantia. The group is considered by Webb & Taylor (1980) to be a division of the infra-order Pecora as originally defined by Flower (1883), which included the musk deer (*Moschus*) with the ruminants just named. Webb & Taylor separate the Pecora into the divisions Eupecora and Moschina, with the Moschina including the living musk deer plus some extinct hornless ruminants (gelocids and blastomerycids) which were previously assigned to the other infra-order of the Ruminantia, the Tragulina (see Fig. 2).

speciose of the ungulate orders (Figs. 1, 2). Eupecorans are conspicuous for their horns or horn-like organs, found in the males only in most species, and in their use of these frontal appendages for display, fighting and defence in intraspecific combat. This behaviour is related to the maintenance of territorial boundaries and dominance hierarchies, which in turn determine access to females and the possibility of reproduction (Geist, 1966).

Jarman (1974) analysed the types of morphology and social organization of African antelope in terms of the relationship of body size and group size to the
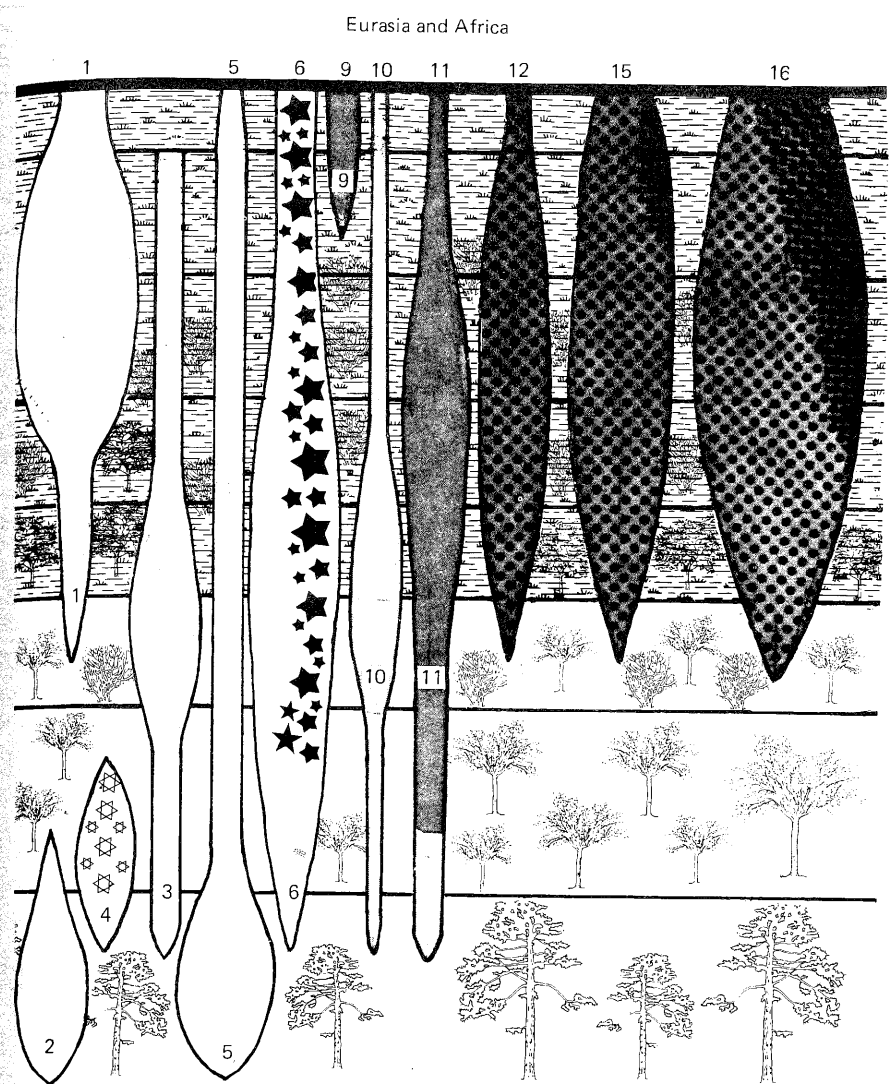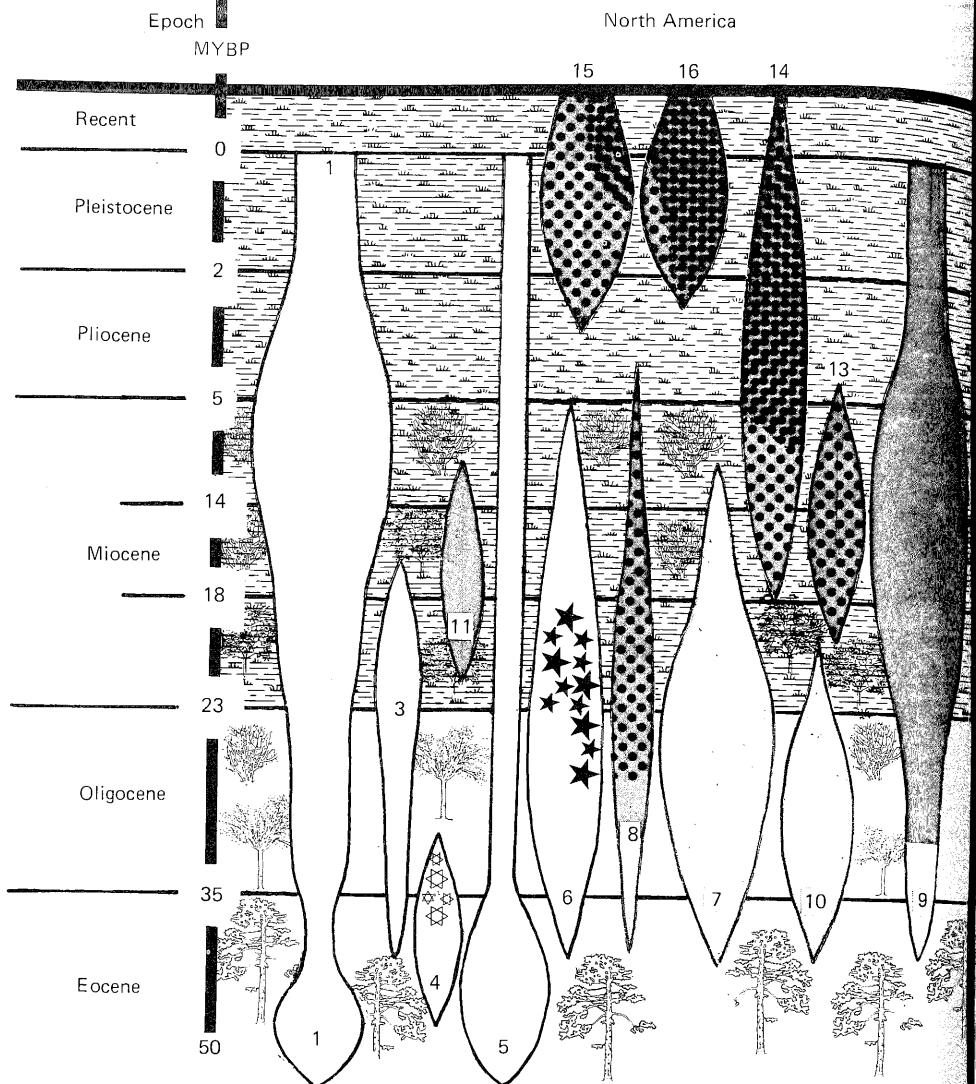
Fig. 1. Distribution of perissodactyls and ruminant artiodactyls in the New and Old World during the Cenozoic. The width of 'balloon' gives an approximate measure of the relative abundance of individuals in a family. Background vegetation types are indicated for approximately 40° N. MYPB, million years before present.

1. Digestive physiology

Hind-gut fermentation of cellulose

Partial forestomach fermentation (no regurgitation of food)

Full forestomach fermentation (rumination)

2. Possession of horns or horn-like organs

Bony horns in males only

Bony horns in both males and females, but horns in females smaller than in males

Keratin horns in males only

Keratin horns in males and females (may be larger in males)

Bony nasal horns in males and females

3. Habitat: vegetation types

Tropical forest

Closed woodland

Open woodland

Woodland savanna

Mixed woodland–open savanna

Open savanna

Steppe–temperate woodland

4. Ungulate families. 1, Equidae. 2, Paleotheriidae. 3, Chalicotheriidae. 4, Brontotheriidae. 5, Tapiriidae. 6, Rhinocerotidae. 7, Merycoidodontidae. 8, Protoceratidae. 9, Camelidae. 10, Tragulina. 11, Moschina. 12, Giraffidae. 13, Dromomerycidae. 14, Antilocapridae. 15, Cervidae. 16, Bovidae.
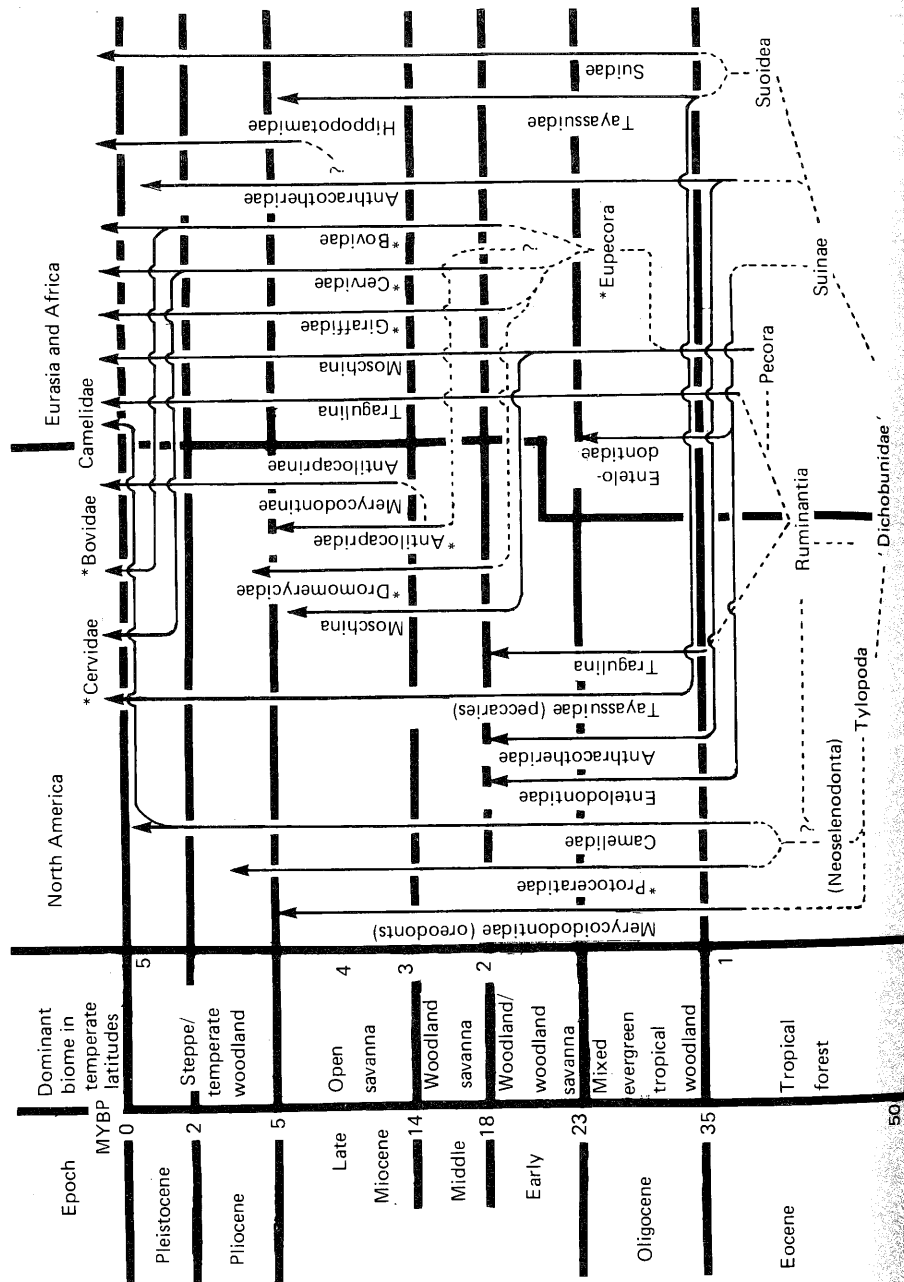
Fig. 2. For legend see facing page.

*(Figure 2 — rotated phylogenetic chart. Axis labels: "Eurasia and Africa", "North America"; "Dominant biome in temperate latitudes"; "MYBP"; "Epoch". Taxon labels include: Suidae, Hippopotamidae, Tayassuidae, Anthracotheriidae, *Bovidae, *Cervidae, *Giraffidae, Moschina, Tragulina, Antilocaprinae, Merycodontinae, *Antilocapridae, *Dromomerycidae, Tayassuidae (peccaries), Entelodontidae, Camelidae, *Protoceratidae, Merycoidodontidae (oreodonts), *Eupecora, Entelodontidae, Suoidea, Suinae, Pecora, Ruminantia, Dichobunidae, Tylopoda, (Neoselenodonta). Dominant biome categories: Steppe/temperate woodland, Open savanna, Woodland savanna, Woodland/woodland savanna, Mixed evergreen tropical woodland, Tropical forest. MYBP scale: 0, 2, 5, 14, 18, 23, 35, 50. Epochs: Pleistocene, Pliocene, Miocene (Late, Middle, Early), Oligocene, Eocene.)*

distribution of food resources in the habitat. He showed that both body and group size can be related to habitat choice and to aspects of behaviour such as reproductive strategy, as well as to the degree of sexual dimorphism (Table 2). Although Jarman presented this argument purely as an example of diversification in space, other authors (e.g. Geist, 1974a, b; Estes, 1974) have attempted to use this analysis as a model to explain ungulate diversity over time, in an analysis of their evolution from the original forest biome, through a woodland habitat to their present distribution in tropical and temperate grasslands. Implicit in all these evolutionary scenarios has been the idea that the Eupecora (bovids in particular) represent 'typical' ungulates, and that the development of horns or horn-like organs (such as cervid antlers or giraffid ossicones) are the norm amongst ungulates (e.g. Geist, 1966). A further assumption is that the faunal zonation and habitat types seen on the African continent in the present day represent some kind of static microcosm for the interpretation of mammalian evolution on a global scale during the Tertiary.

The fossil record shows the true evolutionary picture to be considerably more complex than this. Horns and pronounced sexual dimorphism appear to be a specialized feature of Eupecoran artiodactyls, rather than the norm amongst large-bodied herbivorous mammals. Out of 91 living and fossil ungulate and sub-ungulate families (taken from Romer, 1966), only 10 have evolved bony horns. Of these only 6 (5 eupecoran and 1 tylopod family) showed sexual dimorphism in their possession. Two more families had bony horns in a single aberrant genus (a single median frontal horn in the extinct suid *Kubanochoerus*, and nasal bosses in the oreodont *Cyclopideus*). The Rhinocerotidae developed keratin horns, and a chalicothere genus evolved a domed head, possibly for combat purposes (Munthe & Coombs, 1979). Six more families evolved tusks such as those seen in present-day

Fig. 2. Summary of evolutionary phylogeny and zoogeography of the artiodactyla.

* Families with sexually dimorphic bony horns. MYPB, million years before Present.

(1) Terminal Eocene climatic event. Climate in northern latitudes changes from non-seasonal (temperature and rainfall) to seasonal.

(2) Change in ungulate faunal dominance in North America, from oreodont-dominated to equid-dominated plus first appearance of *Merychippus*.

(3) First appearance of proboscideans in North America.

(4) First appearance of hipparionid equids in Eurasia.

(5) North American Pleistocene extinctions.

This Figure shows the main artiodactyl families, excluding some short-lived lineages inhabiting Eurasia in the early Tertiary and uncertain affinities such as the Xiphodontidae, Anoplotheriidae and Cainotheriidae (usually grouped with the 'Tylopoda'). The small oreodont family Agriochoeridae has been omitted. The use of the superfamilies Moschina (including Gelocidae and Moschidae) and Tragulina (including Hypertragulidae, Tragulidae and Leptomerycidae) is *sensu* Webb & Taylor (1980), as is the term 'Neoselenodonta' to include the camelids and protoceratids with the Ruminantia. The commonly referred to 'basal ruminant' family, the Palaeomerycidae (e.g. Stirton, 1944) has been omitted. This family is not a monophylytic assemblage (Hamilton, 1978b), and most of the genera that were included in it have been transferred either to the Giraffidae (Hamilton, 1978a) or to the Moschidae (Webb & Taylor, 1980). The dromomerycids, often included in the Palaeomerycidae (e.g. Romer, 1966) have been represented here as a separate family.

Table 2. *Summary of Jarman's (1974) categories of feeding and social behaviour for African antelope, and proposed extensions to other living and fossil ruminant artiodactyls and perissodactyls*

Category	Habitat	Diet	Morphology	Body weight Range and (mean)	Group size and social behaviour	Reproductive behaviour	Sexual dimorphism	Some antelope included by Jarman	Some possible other living ungulates	Possible fossil ungulates
A	Forest-bushland-thicket. Remain in same habitat throughout year	Frugivorous-folivorous. Highly selective, take growth parts of plants containing little cellulose	Molars brachyodont. Limbs short	5–70 kg (10 kg). ♂ B.W. 95 % ♀	1–3. Found singly or in pairs, sometimes accompanied by recent offspring	Solitary, or ♂/♀ pairs defend territory. Olfactory marking of territories. Monogamous	Isomorphic– slight dimorphism: No horns in either sex or small horns in ♂♂ only or small horns in both sexes	Duikers (*Cephalophus*) Dik-dik (*Madoqua*) Royal antelope (*Neotragus*)	Chevrotains (*Tragulus* and *Hyemoschus*). Some cervids, e.g. *Pudu, Muntiacus*	Some chevrotains (e.g. small spp. of *Dorcatherium*) Eocene equoids and tapiroids
B	Forest-woodland-grassland. Small home range	Folivorous. Highly selective, feeding on browse or grass. Some seasonal variation in diet	Molars brachyodont– mesodont. Limbs medium length	15–110 kg (40 kg) ♂ B.W. 120 % ♀	1–12, commonly 3–6. Adult ♀♀ group together	♂♂ hold year-round exclusive feeding and breeding territories. Territorial defence by fighting. Polygamous	Dimorphic. Medium sized horns in ♂♂ only. ♂♂ may retain large canine	Reedbuck (*Redunca*) Bushbuck (*Tragelaphus scriptus*) Gerunuk (*Litocranius walleri*)	Some cervids, e.g. roe deer (*Capreolus capreolus*)	Protoceratids, most dromomerycids. ?Diceratherine rhinos. Probably most cervids
C	Woodland-grassland-savanna	Fairly selective, take range of browse and grass. Seasonal flexibility in diet	Molars mesodont– hypsodont. Limbs medium length	20–250 kg (85 kg). ♂ B.W. 140 % ♀	6–60 (up to 200). Adult ♂♂ occur singly, adult ♀♀ and young group together	Males hold seasonal territories or may lek. Polygamous	Highly dimorphic. Large and elaborate horns, usually in ♂♂ only	Greater kudu (*Tragelaphus strepsicerus*) Impala (*Aepyceros melampus*) Waterbucks (*Kobus*) Gazelles (*Gazella*)	Some cervids, e.g. possibly red deer (*Cervus elaphus*)	Meryeodontine antilocaprids
D	Grassland-savanna	Relatively unselective, predominantly grasses. May be migratory	Molars hypsodont. Limbs long	80–220 kg (150 kg). ♂ B.W. 110 % ♀	6–400. Mainly mixed-sex herds adult ♂♂ sometimes found singly	Males may hold temporary breeding territories when non-migratory. Polygamous	Isomorphic– slight dimorphism. Medium-sized horns in both sexes	Alcelaphines, e.g. wildebeest (*Connochaetes*) tsessebe and topi (*Damaliscus*)	Reindeer & caribou (*Rangifer*)	
E	Grassland-savanna-woodland	Wide-ranging diet of grass and browse. Mixed feeder	Molars hypsodont– mesodont. Limbs medium	180–700 kg (400 kg). ♂ B.W. 150 % ♀	100–2000. Large mixed-sex aggregations	Males develop dominance hierarchies within breeding	Highly dimorphic in body weight. Slight dimorphism in horns (larger in ♂♂ than ♀♀)	Eland (*Taurotragus*) Buffalo (*Syncerus*)	Bison (*Bison bison*)	

suids and proboscideans, although in none of these families was there such a pronounced tendency towards sexual dimorphism as in the horns of the protoceratids and the eupecoran artiodactyls. This leaves 72 families of ungulates that showed no evolution of specialized combat organs. The indigenous ungulates of South America and Africa (before the middle Tertiary invasion of the eupecoran artiodactyls) also showed no tendency for the evolution of sexually dimorphic combat weapons. Considering macropod marsupials as ungulate equivalents, this assertion also applies to Australian faunas.

I also examine the evolution of Tertiary ungulates in North America, and show that it cannot be interpreted in terms of an African model. As studies of living ungulates have shown that many aspects of their behaviour are correlated with their morphology, I have used the remains of extinct animals to interpret their foraging ecology and social behaviour. Although an approach of this type necessitates a good deal of speculation, it has at its base certain physical laws, expressed in such forms as Kleiber's Law (Kleiber, 1961) relating metabolic rate to the body size, that determine absolute limitations on the possible physiologies and morphologies of animals. This type of approach has been applied to animals that have no close living representatives, such as Paleozoic fish (Thompson, 1971) dinosaurs and mammal-like reptiles (Bakker, 1975) and Mesozoic mammals (Crompton, Taylor & Jagger, 1978), as well as to ungulates by Webb (1972) and myself (1976, 1979).

II. MATERIALS AND METHODS

Much of the fossil evidence in this paper comes from direct observation of collections at the British Museum of Natural History, London; the Museum of Geology at the Rijksuniversiteit, Utrecht; the American Museum of Natural History, New York; the Museum of Paleontology, University of California at Berkeley, California; Los Angeles County Museum, Los Angeles, California; and Florida State Museum, Gainesville, Florida.

The body weights quoted for the fossil ungulates were estimated from molar measurements, using regression lines calculated for living ungulates by relating upper second molar area to body weight. Other workers have used similar techniques for predicting body weights (e.g. Kay, 1975; Gingerich, 1977; Creighton, 1980). However, there are problems in using this method of weight estimation for extinct animals, as the relationship between molar area and body weight may not have been a constant feature during the evolution of Tertiary mammals (J. Damuth, personal communication). A better estimate can be made from the post-cranial elements (K. M. Scott, 1979, personal communication), but the appropriate calculations are not yet available for the range of ungulate species in this paper. The body weights quoted in this paper are intended to serve as a rough guide to the approximate size of the animal, and are not meant to be precise.

The basis for inferring diets of ungulates from the pattern of wear in their molar teeth, and a description of the correlation between diet and tooth wear in living herbivorous mammals, have been described elsewhere (Janis, 1979).

III. MAMMALIAN EVOLUTION AND CLIMATIC CHANGES DURING THE TERTIARY

The biomass of ungulates is greatest in the present-day habitats in the African savannas, and the species is high (Bourlière, 1964). However, the restriction of the tropical grassland biome to the equatorial zone is a relatively recent phenomenon in mammalian history. Although mammals first appeared at the end of the Triassic, some 200 million years ago, these mammals were all small and mainly insectivorous or omnivorous. The diversification of mammals, with the evolution of large-bodied herbivorous species, has been confined to the Tertiary period, commencing some 65 million years ago (Romer, 1966). At this time the breaking-up of the super-continent of Pangaea, which began in the late Triassic, was more or less complete, and by the early Tertiary the continents were close to their present-day positions (Lillegraven, Kraus & Bown, 1979; McKenna, 1980). Although a certain amount of faunal interchange took place throughout the Tertiary between North America, Eurasia and Africa, the Tertiary history of mammalian evolution has been primarily one of the evolution of different, albeit parallel, community types on the different continents. Australia has remained separate from the rest of the world since the early Tertiary (Clemens, 1979), and is well known for it highly distinctive marsupial and monotreme fauna. South America was largely isolated from the rest of the world until the late Pliocene, when the Panama land bridge connexion was formed. Unfortunately, at this time most of the endemic forms, including all the indigenous ungulates, became extinct (see Webb, 1976).

(1) *Post-Eocene climatic changes*

The course of mammalian evolution has been influenced not only by the separate evolution of communities (with varying amounts of interchange) on the different continents, but also by a more or less unidirectional change in global climate since the end of the early Tertiary. Most people are aware of the succession of ice ages that took place relatively recently during the Pleistocene, which greatly altered the nature of the local fauna and flora. Fewer are generally aware of the fact that, during the Paleocene and Eocene epochs in the early Tertiary, 'tropical' forest, similar to the type now confined to the equatorial regions, extended to within the confines of the Artic circle (the situation in the Southern hemisphere at this time is unknown) (see Wolfe, 1978; McKenna, 1980). Thus the initial habitat available for all mammals at the start of their radiation was a more or less global extension of this type of tropical or sub-tropical rain forest. The reasons for this difference in world climate are not known, although much speculation exists. Current theories include the notion of a shift in the earth's axis to a more vertical position (Wolfe, 1978), although this idea has been disputed (Daly, 1972). Other suggestions are that there has been a change in the amount of solar radiation or in overall world precipitation patterns; these, together with the known absence of the Arctic ice cap, would allow for an extension in the range of present-day tropical and sub-tropical plants (Daly, 1972).

At the end of the Eocene, some 35 million years ago, there was some kind of catastrophic climatic event. This has been postulated as having acted over a period as short as a million years in North America (Wolfe, 1978), although the changes in Europe appear to have been less dramatic and to have taken place more gradually over a longer period of time (Daly, 1972; Collinson, Fowler & Boulter, 1981). The resultant changes included a large fall in annual mean temperature (accompanied by an increase in the annual temperature range) in the present-day temperate latitudes, essentially switching the climate in these regions from non-seasonal (at least in terms of temperature and rainfall) to seasonal. The faunal, floral and geological evidence all points to a steady decrease in annual mean temperature, and a corresponding increase in temperature seasonality, in these latitudes from the end of the Eocene throughout the remainder of the Tertiary, although a temporary reversal of this trend was seen during the late Miocene (Leopold, 1969; Wolfe, 1978).

The global picture for climate and vegetation during the Tertiary would thus have been that of a steady post-Eocene retreat of the tropical forest belt to the lower latitudes, pulling with it first mixed evergreen woodland, then broad-leaved deciduous forests, and finally in the summer deciduous forests and the boreal coniferous forests of the middle and upper latitudes, as seen today (Leopold, 1969) (Fig. 1). Mixed evergreen woodland is a type of vegetation once widely distributed over the middle latitudes in both hemispheres, but now restricted to a few places such as northern New Zealand, south central Chile and the tip of the South African Cape region (Eyre, 1968). Grasslands can be formed in all vegetational habitats as the result of edaphic factors, or other influences such as rainfall, fire, and the influence of man and grazing animals (Andrews & Van Couvering, 1975; Harris, 1980). Tropical grasslands are termed savannas, and contain an admixture of trees with the grasses. (Drier conditions, which result in the absence of trees, lead to desert shrub or desert vegetation in tropical regions (Harris, 1980).) In the temperate latitudes grasslands are more or less devoid of trees, the grasses are shorter, and they are termed prairie or steppe (Eyre, 1968).

(2) *The evolution of the savanna environment*

The term 'savanna' has been used in a variety of ways in the recent literature. The usage by Webb (1977) implies any vegetational type that is not closed canopy forest or treeless prairie, with a division into 'woodland savanna' and 'open savanna' environments. Andrews & Van Couvering (1975) restrict the use of the term savanna to grasslands where shade covers less than 50 per cent of the ground, and term habitats of more dense tree cover than this 'woodland'. (They distinguish woodland from forest on the basis of single rather than multiple tree canopy.) However, my use of the term savanna in this paper approximates more closely to that used by Webb, and is taken from Harris's (1980) definition of savanna, as a tropical plant community with a continuous herbaceous layer, dominated by high grasses of the C_4 photosynthetic type (i.e. those with a photosynthetic pathway additional to the regular Calvin cycle, which accelerates

photosynthesis by concentrating carbon dioxide) with the woody component, varying from complete absence of trees to an almost closed canopy. Obviously a completely closed woodland would not allow sufficient light to reach the forest floor to permit the growth of grasses and herbs. Thus 'savannas' are here defined by the presence of grass as a dominant component of the vegetation, rather than by the absence of trees. I think that this is a more appropriate way of assessing the vegetation from the view of the ungulate community. Andrews & Van Couvering's use of the term 'savanna' approximates more closely to my use of 'open savanna'. Van Couvering (1980) uses the term 'savanna-mosaic' to describe the integrated mixture of habitats of woodland, wooded grassland, grassland and bushland as a single community type, as seen on the African continent in the present day, and I have adopted her term in this paper.

The development of the savanna mosaic environment was a prominent feature of the changing global vegetation during the middle Tertiary. As the tropical forest zone retreated towards the equatorial regions, the higher latitudes became covered with a woodland type of vegetation that was readily converted to grassland by climatic factors. Despite the assertion by various authors that widespread areas of grassland are features of the habitat that have come about only in the recent history of the earth, due to the activities of man (e.g. Eyre, 1968), mammalian evolution has shown a progressive tendency, since the end of the Eocene, for the development of animals with a morphology appropriate to locomotor activity suited to an open habitat (see Andrews, Lord & Evans, 1979). It seems likely that grasslands have always been an important biome since the middle Tertiary (Harris, 1980), although it may well be true that many of the current tracts of grassland in Africa have been augmented by human activity (Andrews & Van Couvering, 1975).

Unfortunately the paleobotanical record is of limited help in determining details of changing global habitats during the Tertiary. Although it can provide information on the types of plant species present, insufficient knowledge exists as to the biases inherent in the mode of preservation of fossil plants to be able to reconstruct the vegetational structure of the habitat, or even to give reliable information about the relative abundances of different species (R. Singer, personal communication). Thus palynological evidence can tell us that grasses first appeared commonly in the fossil record in the late Eocene and early Oligocene, probably in swampy and forest glade environments (Penny, 1969), and that wide-ranging grass species and their associated herbs evolved in the late Oligocene to early Miocene (Leopold, 1969). But it cannot tell us how widespread such grasslands were, nor how open the nature of the habitat. Added to this is the problem that fossil floras are rarely found preserved in the same deposits as the animals with which they were presumably associated. A more reliable method of determining fossil habitats comes from observations of the composition of the faunal community itself. Andrews et al. (1979) have shown that an analysis of the ecological diversity of the patterns of mammalian communities in Africa during the Recent period can differentiate statistically between five habitat types, even if the species composition of the faunas is unique to that community, by examining the spectra of feeding

and locomoter types, and the distribution of body sizes. This method has subsequently been applied to faunal communities of Africa in the Tertiary (e.g. Van Couvering, 1980; Nesbit Evans, Van Couvering & Andrews, 1981). It is apparent that in East Africa tropical rain forest was the dominant habitat type during the early Miocene, although a woodland component may have been mixed in with the forest (Van Couvering, 1980). There was a considerable amount of faunal change at the start of the middle Miocene, with a greater proportion of ground-dwelling browsers, indicating a change to a basically woodland environment. Wooded grasslands first appeared as a dominant habitat in the late Miocene (Van Couvering, 1980), with grasslands subsequently becoming an important component of the vegetation until the present day.

(3) Habitat changes in northern latitudes during the middle and late Tertiary

Unfortunately the faunas of North America and Eurasia have not as yet been subjected to a rigorous analysis of ecological diversity. But as these continents are at more northern latitudes than Africa, and so would have been subjected to a greater degree of climatic seasonality during the middle Tertiary, one would expect this shift from forest to woodland, and subsequently to a savanna mosaic habitat, to have taken place at a somewhat earlier date. The nature of the faunas of North America suggest the presence of limited areas of savanna habitats since the late Eocene (Webb, 1977). The radiation of the cricetid rodents in the middle Oligocene certainly indicates the trend towards an open type of savanna habitat as a major component of the vegetation (Wilson, 1972), although the palynological record suggests a predominance of a sub-tropical woodland habitat (Leopold, 1969). Clark, Beerbower & Kietzke (1967) describe the climate of South Dakota in the middle Oligocene as fairly dry, with annual precipitation of less than 30 inches, but with virtually frost-free winters. The habitat was composed primarily of well-drained gallery forests, interspersed with swamps, and in addition areas of more arid upland plains, each habitat having its characteristic mammalian community. By the early Miocene, the ungulate community in North America showed a diversity of morphological adaptations to grassland habitats that was more or less comparable to that seen in the late Miocene in Africa (Van Couvering, 1980), and pollen records from the middle Miocene of the Rocky Mountains region show a preponderance of temperate trees such as pine and spruce (Leopold, 1969). Much of the vegetation of North America in the late Miocene consisted of fairly open grassland (Webb, 1977) with some areas in the western part of the continent containing semi-arid steppe vegetation (Leopold, 1969).

The faunal record of Eurasia show that the Hsanda Gol fauna in the Oligocene in Mongolia had a composition indicating an open habitat (Mellett, 1968), but this was apparently not ancestral to the mosaic communities of the later Old World savanna. All well-known early Miocene faunas from Eurasia were dominated by aquatic-margin and temperate-forest mammals (Van Couvering, 1980). The pollen record indicates a mainly sub-tropical vegetation for Western Europe in the Oligocene, but in the early Miocene the more southern species of the present day,

such as oak and chestnut, were being replaced by species more typical of northern temperate forests, such as pine, beech and elm (Leopold, 1969). It appears that the vegetational and habitat changes in Eurasia took place in advance of those in East Africa, but later than those in North America. This is borne out, not only by the faunal communities, but also by the pollen record. Sub-tropical floral elements were found as far north as 50–55 degrees in Eurasia in the early Miocene, but only as far as 40 degrees north in North America. By the late Miocene, sub-tropical floral elements were restricted to latitudes below 40 degrees almost everywhere (although some warmer areas persisted in Western Europe) (Leopold, 1969), and steppe floras replaced woodland in the Soviet Union (Hambrey & Harland, 1981). In the early Miocene, the habitat of North America consisted of a fair amount of savanna mosaic, if not as yet any open grasslands, whereas Eurasia was dominated by woodland, and Africa by tropical rainforest. But by the late Miocene the savanna mosaic biome had spread south to encompass East Africa (Van Couvering, 1980), and areas of steppe and sub-arid scrub vegetation were apparent in the now desert areas of south central Russia (Leopold, 1969). In the Pliocene, the temperate plant ranges were decreased even further, evidence existing for glaciation at high latitudes (Hambrey & Harland, 1981), and boreal types of forest dominated by pine trees became increasingly abundant in the northern latitudes (Leopold, 1969). (See Fig. 1 for a summary of climate changes in the northern latitudes during the Tertiary.)

Much of the pattern of mammalian evolution has been explained in terms of this pattern of changing habitat, although the emphasis is often on the idea of the animals 'moving out' from the forests to the savanna, rather than on the disappearance of wooded habitats in many parts of the world. An oft-quoted example is that of the evolution of the horse, where a progressive tendency to increasing body size, increasing degree of cursorial adaptation of the limbs, and an increase in the height and surface complexity of the cheek teeth, have been interpreted as being consistent with a change in habitats from those of a woodland browser to a plains-dwelling grazer (e.g. Simpson, 1950). Popular books and articles on horses tend to depict a scenario of the early horse boldly venturing forth from the swampy forests onto the open plains in search of a new diet of grass (e.g. Smythe, 1965). (This event was recently interpreted by one American horse journal as being contemporaneous with the disappearance of the carnivorous dinosaurs from this dangerous open habitat!) But a more likely explanation is that the changing global climate forced animals to change their feeding strategies (and hence both their social behaviour and morphology) if they were to survive at the same latitudes. This would have been especially critical in the case of North America, which was not joined to South America for the majority of the Tertiary, as there would have been no equatorial zone for the animals to retreat to along with the receding forest. Scientific studies of this phenomenon, such as Geist's (1974a) dispersal theory of ungulate evolution, also often fail to distinguish fully between the dispersion of animals into different habitats and evolution *in situ* due to long-term climatic changes.

IV. EVOLUTION OF HORNS IN RUMINANT ARTIODACTYLS

Geist (1966) noted that horns in present-day ungulates are found only in animals above a certain body size (about 5 kg). His explanation for this is that fighting by a combination of lunging, striking with the limbs and biting, as seen in small mammals, is too dangerous for ungulates of larger body size (because of size-scaling effects). So larger ungulates have evolved a more ritualized form of combat by the elaboration of these initially simple weapons, in which the risks of injury to the individual are minimized. However, this explanation seems untenable in the light of the fact that large-bodied equids and camelids lack horns, and still fight by means of this supposedly hazardous primitive method (Grzimek, 1972; Klingel, 1972). This reopens the question of the reason for the evolution of horns amongst the ruminant artiodactyls.

Studies of African antelope have shown that, in bovids at least, the degree of sexual dimorphism in the possession or the relative size of the horns is correlated with social behaviour and reproductive strategy, which in turn appear to be closely related to the structure of the habitat and the availability of potential food items (Jarman, 1974). Jarman's five categories of feeding and social behaviour are summarized in Table 2. [Studies on other animals (e.g. Crook, 1970, for primates; Laurie, 1982, for rhinos) have shown that Jarman's categories are broadly applicable to a wide range of herbivorous mammals.] Category A includes small (about 10 kg) non-dimorphic monogamous territorial browsers (although it has been noted that not all small ruminants of this feeding are territorial, and some may be solitary (see Barrette, 1977a)). Larger woodland browsers (20–200 kg) show a considerable degree of sexual dimorphism, with horns usually present in males only. Category B includes browsers that hold territories for the entire year, and Category C includes mixed browsers and grazers, living in more open habitats, that hold territories for part of the year only. Larger, open-country grazers, ranging from 150 to 250 kg, belong in Category D, and in these animals the females possess horns as well as the males, but differences in body size between males and females are not great. Finally, Category E comprises very large bovids (up to 700 kg) that live in herds and are predominantly grazers. In these animals, both sexes possess horns, but the males are much bigger than the females, and establish a dominance hierarchy amongst themselves which determines access to females. In contrast, males in Category D set up temporary breeding territories at times in the year when the herd is non-migratory. The mating system is polygamous in all categories except Category A.

(1) *Evidence for living small ruminants being secondarily small*

Although horns are seen in the present-day small forest-living bovids in Jarman's Category A, and may be present in the female as well as the male (for example in duikers of the genus *Cephalophus*), it seems likely that these animals are not in fact representative of the primitive eupecoran morphology and behaviour, despite common assumption to the contrary (e.g. Estes, 1974), but are secondarily

small. Thus the size of the smallest living horned ruminant (about 5 kg) may not represent the body size at which horns were initially evolved. Geist (1966) suggested that the dwarf antelope genera were secondarily small on the basis of their gestation period, which is much longer than would be predicted for an animal of this body size. I have argued the case for these animals being secondarily small on the basis of their digestive physiology (Janis, 1976). Cephalophines are also derived in their behaviour in that the males fight by means of head-to-head combat (Ralls, 1975), rather than adopting the primitive type of anti-parallel stance in fighting (Geist, 1966), as seen in the other small ungulates such as the mouse deer *Tragulus napu* (Ralls, Barasch & Minkowski, 1975) and the rock hyrax *Procavia habessinica* (Janis, 1979).

There is also evidence to suggest that other small living horned eupecorans are secondarily small, or at least that they have secondarily readopted a traguloid type of habitat, feeding style and social behaviour, typical of animals in Category A. The living species of muntjac (genus *Muntiacus*) are the most primitive of the antlered cervids. The male possesses small antlers but also retains the large sabre-like canines characteristic of the traguloid and moschoid members of the Ruminantia, while the female has smaller canines and does not possess antlers. However, despite this considerable degree of sexual dimorphism, more typical of antelope in Category B, their social behaviour is more like that of antelope in Category A in certain respects, as they are solitary and non-territorial (Barrette, 1977a). Their method of male/male fighting however, is more derived than that seen in the chevrotain or mouse deer *Tragulus*, involving head-to-head combat, although it is not as advanced as that seen in other cervids. The male apparently uses his small antlers to ward off canine slashes from his opponent, and also to wrestle with him until he produces a situation where his own canine slash can be effectively administered (Barrette, 1977b). The South American cervid of this same small body size and feeding category, the pudu (genus *Pudu*), is almost certainly an example of a secondary reversal in both behaviour and morphology to a small forest dweller, as all the other members of the Odocoiline radiation are considerably larger (Whitehead, 1972).

It is interesting to note, in this context, that despite the abundance of remains of small-sized traguloid and moschoid artiodactyls in the fossil record of the early Miocene in the Old World, these present-day small-sized bovid lineages are not found amongst the early eupecoran remains in the early and middle Miocene. The first dwarfed antelope was not seen until the end of the middle Miocene (Gentry, 1978), and the tribes Cephalophini and Neotragini were not a significant component of the African fauna until the late Miocene (Pickford, 1981). Similarly, the first fossil record of the genus *Muntiacus* is in the Pleistocene (Barrette, 1977a), although the subfamily Cervulineae, to which the living muntjac belongs, made its first appearance in the middle Miocene with the genus *Stephanocemus* (Colbert, 1936). (Although negative evidence of this nature does not constitute proof of the absence of these animals before these dates, it is interesting inasmuch as it correlates with other lines of evidence presented here.)

(2) Critical body size for horn evolution

In conjunction with the behavioural evidence that the small living eupecorans may be secondarily small, there is a considerable amount of evidence from the fossil record that the evolution of horns, initially in males only, occurred independently in a number of lineages of ruminant artiodactyls at a critical body weight of 15-20 kg, that is, at a size somewhat greater than that of living antelope placed in Jarman's (1974) Category A.

Horned ruminants first appeared in the fossil record in the late Oligocene of North America, about 27 million years ago, in the tylopod family Protoceratidae. Protoceratids are known from the late Eocene, but *Protoceras* was the first genus to possess horns, and also the first genus in this lineage to attain a body size of this critical value (Patton & Taylor, 1973) (Fig. 1). The males had a complex array of paired orbital and nasal horns, and retained a large canine (in the manner of *Muntiacus*), whilst the females were hornless with small canines. Horned pecorans did not appear in the fossil record of the Old World until the late early Miocene, some 7 million years later (Fig. 1). The members of the Ruminantia present during the Oligocene and early Miocene in the Old World were traguloids such as *Dorcatherium*, or moschoids such as *Gelocus*, *Amphitragulus* and *Dremotherium*. The first true bovid, as identified by the presence of a horn core, was *Eotragus*, found in Europe (Ginsberg & Heintz, 1968) and in Africa (Hamilton, 1973) at the end of the early Miocene, about 20 million years ago. *Eotragus* had a skull of about the same size as a Thomson's gazelle *Gazella thomsoni*, although it probably had shorter legs than this species, and must have weighed about 18 kg. Hornless skulls of this genus have been found (Thomas, 1977), which suggests that the primitive condition for the Bovidae is for horns to be present in the male only. The first positively identified cervids and giraffids occurred at about the same time. The first cervids (e.g. *Stephanocemus*) were of comparable body size, whereas the first giraffids were a little larger [e.g. *Climacoceras*, the most primitive member of the Giraffidae (Hamilton, 1978a) would have had a body weight of about 40 kg].

Eotragus did not retain large upper canines in the males, and retention of the upper canines was not seen in primitive giraffids. However, as the sexually dimorphic possession of large upper canines is a primitive feature of the Eupecora (Webb & Taylor, 1980), they were probably present in the immediate ancestors of these families. Large canines were retained in the smallest and earliest genera of the Dromomerycidae, *Barbouromeryx* and *Aletomeryx* (Frick, 1937), horned ruminants which also weighed approximately 20 kg (K. M. Scott's and my unpublished data). (Smaller canines were retained in some later genera of dromomerycids, as they are in many genera of living cervids.) Although the other immigrant lineage of eupecoran artiodactyls in North America in the Miocene, the merycodontine antilocaprids, were of smaller body size than this (about 8-12 kg), they were certainly not occupants of a present-day type of traguloid niche. Their hypsodont cheek teeth and elongated limbs indicate that they were open-country dwellers (Webb, 1977; K. M. Scott's and my unpublished data). As antilocaprids are

probably derived from Eurasian cervoid stock (Leinders & Heintz, 1980), it seems likely that their as yet undiscovered Old World ancestors would have been larger than this, close in size to *Eotragus* or *Stephanocemus*.

The primitive eupecoran condition appears to be the absence of any frontal appendages (Hamilton, 1978*b*), and horn-like organs seem to have evolved independently in the various eupecoran families. Cervid antlers are clearly formed by an ontogenetic process different from that responsible for appendages of giraffids and bovids. Bovid horns and giraffid ossicones develop from independent dermal ossifications, which later fuse to the frontal or parietal bones, whereas cervid antlers are outgrowths of the frontal bone (Bubenik, 1966). The existence of a true cervid lacking antlers in the living genus *Hydropotes* (Chinese water deer) also suggests that the Cervoidea split off from the eupecoran stock before the acquisition of antlers. Hamilton (1978*b*) suggests that the Giraffoidea and Bovoidea (including the Antilocapridae) are sister groups, with their common ancestor possessing a simple giraffoid type of skin-covered ossicone, from which the bovid horn, with its heavily keratinized dermal sheath, was later derived. However, evidence presented by Todd (1975) on chromosome morphology in the Ruminantia indicates that giraffids are considerably more primitive than either cervids or bovids, suggesting the independent evolution of this form of frontal appendage in the two superfamilies.

The horn cores of antilocaprids have been interpreted as being very similar to those of bovids (O'Gara & Matson, 1975), which has led to the suggestion that the Antilocapridae and Bovidae are sister groups, with the common ancestor possessing a grooved horn core with a keratin sheath (Hamilton, 1978*b*). However, if Leinders (1979; and Leinders & Heintz, 1980) is correct in his assertion that antilocaprids are cervoids, this type of horn must have been developed independently in both giraffids and bovids. Dromomerycids may also be cervoids on Leinders's criteria, and at any rate probably also represent an independent acquisition of frontal appendages. In addition, a further cervoid family existed in the late Miocene, the Hoplitomerycidae, in which true horns, rather than antlers, were developed (J. J. M. Leinders, personal communication). Appropriately enough, the first representatives of this family had a body weight of approximately 18 kg!

Thus horn-like organs were evolved in ruminant artiodactyls at least three times on reaching this threshold body weight of approximately 18 kg: in the tylopod protoceratids in North America, and in cervoid and bovoid eupecorans in the Old World. Considering the likelihood of the independent acquisition of frontal appendages by the eupecoran families Giraffidae, Cervidae, Hoplitomerycidae, Dromomerycidae, Antilocapridae and Bovidae, it seems that horns may have been independently evolved as many as seven times as the various lineages attained this body size.

(3) *Importance of horns in territorial defence*

The appearance of horned ruminant artiodactyls in both North America and the Old World appears to have been correlated with the development of a more

seasonal climate and a more open type of woodland habitat (Fig. 1). The coincidence of the evolution of horns with the change in dominant vegetational type suggests a correlation of change in morphology with change in ecology and behaviour.

The ruminants in Jarman's (1974) Category A are mostly under 10 kg in weight, depend on olfactory marking for definition of territorial boundaries and hide to avoid predation. The diet of these animals is limited by their small body size, and hence their relatively large metabolic requirements. They must select a non-fibrous diet of high protein content, such as buds, fruit, berries and young leaves. Food items of this nature are usually small in size, and widely dispersed, which means that the home range of such an animal would be large, apparently too large for a male to maintain as an exclusive feeding and breeding territory. The time taken in locating food items of this nature, and the relatively large size of the territorial perimeter that would contain sufficient high-quality items for maintenance, both militate against maintenance by boundary patrol as an energetically feasible reproductive strategy. The relationship between resource dispersal and territorial behaviour in small selective browsing ruminants is illustrated by the behaviour of the lesser Malay chevrotain *Tragulus javanicus*. The male chevrotains engage in territorial disputes with neighbouring males only at those times of the year when fruit fall is abundant, guaranteeing the clumping of appropriate food items (Davison, 1980).

In contrast, the larger size of antelope in Category B means that they can tolerate a diet of higher fibre content, consisting primarily of leaves (Jarman, 1974). Thus the potential food resources within a given area are greatly increased. As a result the effective home range can be smaller, and because of the greater abundance of food the animals need not be so dispersed in their foraging, but can feed together in small groups. So the increased body size of these animals, which allows for the adoption of a different type of diet, in turn allows for the adoption of the reproductive strategy by the males of exclusive territorial behaviour. The effective costs of boundary patrol are less, because the perimeter of the home range is relatively less, and the dispersion of a folivorous food resource makes it possible for females to feed together in small groups, thus allowing the possibility of polygamous behaviour for a male with a fixed territorial base.

The body size at which horns appear in artiodactyl evolution marks the transition between living antelope in Categories A and B, and correlates with a change in climate in temperate latitudes that would result in an alteration in the spectrum of available herbivorous diets. Observations on the molar morphology and dental wear of early eupecorans also bear out this suggestion of change to a more folivorous diet at this time. The evolution of horns, therefore, is apparently correlated with the evolution of boundary patrol by territorial males. However, it is necessary to stress that not all ruminants evolved horns at this time, and there were probably a variety of possible combinations of feeding and reproductive strategies within the mid-Tertiary sub-tropical woodland. Although they were never as numerous as the eupecorans, the hornless tragulids and moschoids

persisted in the Eurasian faunas until the Pleistocene. Some of these animals were quite large (up to 100 kg), with molar wear indicating a more folivorous diet than that seen in present-day tragulids and dwarfed antelope, and they may have survived in the higher latitudes in the late Tertiary by taking more fibrous food in the cold season only. They were probably broadly classifiable in Jarman's (1974) Category A, and the living musk deer *Moschus* and the hornless Chinese water deer *Hydropotes* may represent survivors of animals of this type (Table 3).

If Barrette (1977b) is correct in interpreting the fighting behaviour of muntjac as truly primitive, horns may have originally arisen as organs of defence. The increase in male–male encounters that would result from territorial maintenance in early ruminants would act as a strong selective force for the development of such defensive organs. Horns subsequently became elaborated into weapons that were a reflexion of the growth stage and physical condition of the animal, and would thus act as display organs to advertise age and status. This would reduce the number of actual physical encounters, as ruminants usually only engage in fights with animals of their own relative age and condition (Geist, 1971). In addition, elaboration of the horns would mean that they could now be used to interlock the heads of fighting animals, resulting in encounters that were essentially ritualized tests of strength, rather than ones in which the horns were used to inflict injury (Geist, 1966).

(4) Evolution of horns in Old Word ruminants

The original radiation of the Ruminantia was of small hornless traguloids and moschoids, but they declined in diversity and abundance coincident with the diversification of horned pecorans, this being especially noticeable in Africa (Pickford, 1981). It seems likely that, when the bovids first appeared in Africa (the exact site of their origin, Africa or Eurasia, being as yet undetermined), the members of several lineages became secondarily small, after an initial diversification of medium-sized animals, and took over many of the niches occupied by their ancestors. The eupecorans would probably have been competitively superior to the contemporary traguloids, as their derived digestive system, with full rumen fermentation, although not necessary for fermentation of a low-fibre diet, now probably acted to assist in the detoxification of secondary plant constituents abundant in tropical vegetation (Freeland & Janzen, 1974; Janis, 1976). It appears that, once horns had been evolved, there may have been no good reason to lose them, nor reason to abandon the fighting style associated with their possession. Horns may have been evolved in the females of some of these small bovids, for example in the Cephalophini (duikers), to enable the female to defend herself against aggression from a horned male partner in a monogamous pair, where the two sexes feed together.

Amongst the larger members of the eupecoran radiation, occupying a more open habitat, most cervids and giraffids retained relatively low-crowned cheek teeth and a diet of browse, or mixed browse and grass. Hence they remained in Jarman's (1974) Categories B or C, where horns are the prerogative of the male of the

species. Giraffids have always been a tropical or sub-tropical group. Their predominant radiation was in Africa, but during the late Tertiary and early Pleistocene they were also found in the lower latitudes of Eurasia (Churcher, 1978). Cervids, on the other hand, had their radiation predominantly in the more northern parts of Eurasia, and have never been found on the African continent south of the Sahara (Hamilton, 1978b). Amongst the bovids, whilst some tribes retained relatively brachyodont cheek teeth and remained in what was left of the old temperate and sub-tropical woodland habitats (e.g. the Tragelaphini), others evolved more hypsodont teeth and longer limbs, and exploited the newly created more open areas (e.g. the Alcelaphini).

In the bovids of more open habitats, in Jarman's (1974) Categories D and E (plus a few in Category C), horns are found in the females as well as in the males. The reasons for this are not known for certain, although speculation is frequent. It seems that, once horns are present in the male of the species, if selection pressure comes into effect for isomorphy of the sexes, then the pressure will be on the female to mimic the male by evolving horns, rather than on the male to mimic the female by losing his. Once horns and a certain style of fighting have been adopted by the male, there could be strong selection pressure against losing those features. A possible reason for isomorphy in bovids inhabiting open country and forming herds is to minimize the selection of one sex over the other by predators of the open country, so that pregnant females would not be put at a greater risk (R. Estes, personal communication). Another is that horns allow females equal access to food in the intraspecific disputes over resources seen in mixed-sex feeding groups (P. Jewell, personal communication). Various other lines of evidence support the hypothesis that evolution of horns amongst female bovids is correlated with environmental features. Gazelles of the Recent epoch live in open habitats, and the females have small horns. But species of gazelles found in the middle and late Miocene in Europe, where the availability of non-wooded habitats would have been restricted (Leopold, 1969), had horns in the males only (Heintz, 1969). In addition, the only genus of cervid that occupies permanently open habitats, and forms migratory herds, is *Rangifer* (reindeer and caribou), which has horns in the female as well as in the male: this is also the sole instance of horns in female cervids.

Few cervids today are known to be territorial, the only good instance being in the roe deer (Bramley, 1970). This behaviour may, however, be a consequence of the present-day latitudinal zonation of habitats. The type of seasonal sub-tropical woodland that covered the temperate latitudes in the Northern hemisphere in the Miocene is no longer in existence, and the distribution of food resources within present-day temperate woodland is probably too great to make male territorial behaviour a viable strategy. Most living cervids rove in mixed herds of fluctuating composition, and a dominance hierarchy is maintained amongst the males, with reproductive behaviour limited to the end of the growing season when the males have built up food reserves. This is represented by 'rutting', when the males engage in a period of intense activity in establishing this dominance hierarchy, which in turn determines access to females. The relation of this type of behaviour

Table 3. *Proposed addition to Jarman's (1974) categories to cover other living and fossil ungulates (ruminant artiodactyls and perissodactyls)*

Category	Habitat	Diet	Morphology	Body weight Range and (mean)	Social and reproductive behaviour	Dimorphism	Possible living ungulates included	Possible fossil ungulates included
A1	Forest—seasonal woodland. Small home range	Folivorous, but take non-fibrous food when available. Diet seasonally variable	Molars brachyodont. Limbs short–medium	15–200 kg (25 kg) (artiodactyls) 150–1000 kg (perissodactyls)	Solitary or ♂/♀ pairs defending territory. Monogamous–solitary	Isomorphic (Slightly dimorphic). No horns in either sex (or small horns in ♂♂)	Chinese water deer (*Hydropotes*) ?Okapi (*Okapia johnstoni*) Tapirs (*Tapirus*) Small rhinos (*Rhinoceros sondaicus* and *Dicerorhinus sumatrensis*)	Some traguloids (e.g. large species of *Dorcatherium*) and moschoids (e.g. *Dremotherium*)
A2	Savanna—seasonal grassland. Medium home range	Highly selective for non-fibrous parts of open habitat plants (e.g. grass seeds)	Molars mesodont–hypsodont. Limbs long	2–40 kg (6 kg)	Solitary, or ♂/♀ pair bonding. Monogamous	Isomorphic–slight dimorphism. (No horns in either sex, or small horns in ♂♂ only)	Open country antelope in Category A. e.g. Steinbok (*Raphiceros campestris*) Orebi (*Ourebia ourebi*) Musk deer (*Moschus*)	North American traguloids and moschoids e.g. *Hypertragulus*, *Leptomeryx*, *Blastomeryx*. ?Stenomyline camels
B1	Open woodland. Large home range	Browse, fruit. Some seasonal variation in diet	Molars brachyodont–mesodont. Limbs short	10–200 kg (50 kg)	Mixed sex feeding herds. Males maintain dominance hierarchy. Polygamous	Primitively Isomorphic. (No horns in either sex)	Peccaries (although more folivorous than oreodonts.) Many cervids in post-Pleistocene habitats, e.g. North American odocoilenes, and Asian cervids, e.g. chital (*Axis axis*)	Oreodonts (families Agriochoeridae and Merycoidodontidae.) Browsing equids

Table 3. (*cont.*)

Category	Habitat	Diet	Morphology	Body weight Range and (mean)	Social and reproductive behaviour	Dimorphism	Possible living ungulates included	Possible fossil ungulates included
C1	Woodland savanna—grassland	Selective for plant parts, grass and browse	Molars mesodont–hypsodont. Limbs long	15–1000 kg (80 kg) or (300 kg)	Some mixed sex feeding. Males hold small breeding territories and/or harems. Polygamous	Isomorphic. (No horns in either sex.) Or slight dimorphism (small horns in ♀♀, larger horns in ♂♂)	Gazelles (*Gazella*) Pronghorn antelope (*Antilocapra americana*) South American camelids (*Lama* and *Vicuna*)	Most fossil camelids. Some dromomerycids (*Aletomeryx* and *Pediomeryx*) Antilocaprine antilocaprids
C2	Woodland–savanna	Predominantly high level tree browsing, or take both browse and shrubs	Molars mesodont. Limbs medium length, or highly elongate	40–2000 kg (1000 kg)	Loose aggregation mixed sex feeding herds. Some male territorial–hierarchical dispute, no fixed territories. Polygamous–serially monogamous	Isomorphic. No horns in either sex, or small horns in both sexes	Giraffe (*Giraffa cameleopardis*) Indian rhino (*Rhinoceros unicornis*) Black rhino (*Diceros bicornis*)	Most fossil giraffes. Aepycameline camels. Chalicotheres. Aceratherine rhinos
D1	Open woodland–savanna-grassland	Predominantly grass, or grass plus low level browse	Molars mesodont–hypsodont, or highly hypsodont. Limbs long	80–400 kg (200 kg)	Males hold harems with fixed female membership. Polygamous	Isomorphic. (No horns in either sex, or similar sized horns in both sexes)	Most equids (e.g. Burchell's zebra *Equus burchelli*)	Most fossil grazing equids. ?Some protolabine and cameline camels. ?Brachypotherine rhinos
D2	Arid savanna—grassland	Predominantly grass	Molars hypsodont. Limbs long	250–2500 kg	Males hold exclusive feeding and breeding territories. Polygamous	Isomorphic. (No horns in either sex, or similar size horns in both sexes)	Some equids (e.g. Greyvi's zebra *Equus greyvi*) White rhino (*Ceratotherium simum*)	?Some grazing equids. Some rhinos (e.g. *Elasmotherium*)

to present-day latitudinal zonation is illustrated by the fact that the more northern cervid species tend to be the ones that have the most distinct rutting seasons, are the most polygamous, and have the largest and most elaborate antlers (Geist 1974a; Clutton-Brock, Albon & Harvey, 1980). This type of behaviour is also seen in the northern latitude bovids, members of the tribes Bovini, Caprini and Rupicaprini (Geist, 1974a; Owen-Smith, 1977). However, the most primitive member of the Bovini, the nilgai *Boselaphus tragocamelus*, does display territoriality in sub-tropical Asia (Schaller, 1967), suggesting that the absence of this behaviour in more advanced members of the tribe is the result of their adopting a behavioural strategy suitable to their recent habitat, rather than evidence of phylogenetic conservatism.

The present-day ungulates of temperate latitudes are probably a poor model for studying the reasons for the evolution of horns and sexual dimorphism, as their behaviour may well be a relatively recent adaptation to the post-Pleistocene range of habitats. Study of sub-tropical South American cervids would be interesting in this regard, as they may be living in habitats more typical of the ones occupied by most cervids for the greater part of their evolutionary history.

This section presents the argument that the evolution of horns in ruminant artiodactyls was related to a combination of climatic and vegetational change, and an associated change in body size and foraging strategy of the animals. At a critical combination of body size and resource dispersal in the habitat it became possible for male ruminants to adopt the reproductive strategy of defending an exclusive territory for feeding and breeding, together with a change from a monogamous mating system to a polygamous one. The evolution of horns was related to self-defence in the increased number of male–male interactions dictated by the defence of territorial boundaries. The fact that a number of different lineages evolved horns and adopted this type of reproductive strategy independently, at this threshold body weight of approximately 18 kg, suggests that such a mating system is highly advantageous for male ruminants, if their foraging behaviour and the structure of the habitat allow for its evolution. However, this does not explain why horns of this type were never evolved in perissodactyls, nor in most of the endemic North Amerian tylopods. These problems will be dealt with in subsequent sections.

V. UNGULATES OF THE NORTH AMERICAN SAVANNA

The Miocene epoch, ranging from approximately 23 million to 5 million years ago, was the time when savanna mosaic was the prevalent vegetation type in North America. Mixed woodland savanna was the dominant biome at the beginning of the epoch, and more open savanna dominant at its end, although broad stretches of riparian forest were probably present throughout the epoch (Webb, 1977) (Fig. 1).

The North American Miocene faunas have often been compared with those of the present-day African savanna, and appear to have been broadly similar to them in diversity of ungulate species and feeding categories (Webb, 1977). Popular reconstructions of the North American faunas in somewhat overcrowded panor-

amas (e.g. Halstead, 1978) appear to display a diversity of forms similar to that of present-day African game parks. In the foreground there are usually a number of bizarrely horned antelope-like animals, such as protoceratids and dromo-merycids, with a variety of equids, camelids, rhinos, proboscideans and pig-like forms (entelodonts and oreodonts) relegated to the background. (Fig. 2 summarizes the evolution of the Artiodactyla.) To the casual observer, the correspondence between the savanna faunas of present-day Africa and the North American Miocene is great, and an obvious example of parallel evolution, with similarity in habitat resulting in a similarity of morphological types. However, closer exami-nations of the fossil record shows this apparent similarity to be fallacious. Whilst in the present-day African fauna the sexually dimorphic horned bovids form a large percentage of the total ungulate fauna in terms of numbers of individuals, in North America the predominant species in the fossil assemblages all lack horns in both sexes, and there is no evidence that they possessed a significant degree of sexual dimorphism in body size (although a certain amount of dimorphism may have existed in canine size, comparable to that seen in living equids and camelids) (Fig. 1, Table 1).

(1) *Ruminant artiodactyls*

The term 'ruminant' artiodactyl is used in this paper to describe those artiodactyls whose living representatives are known to ruminate (ferment food in the forestomach and regurgitate it and rechew it as 'cud'), i.e. the members of the sub-orders Tylopoda and Ruminantia. Almost all of the ruminant artiodactyls in the Old World during the Cenozoic were of the sub-order Ruminantia, the exceptions being some early Tertiary lineages of uncertain affinities, such as the xiphodonts, and of course the Pleistocene immigrant genus *Camelus*. However, the indigenous ruminant artiodactyls of North America were represented mainly by the sub-order Tylopoda, although some small 'traguloids' such as *Hypertragulus* and *Leptomeryx* also appear to have originated on this continent (Webb & Taylor, 1980) (Figs. 1 and 2).

The family Camelidae represented a significant component of the fauna throughout the middle and late Tertiary. No camelid species ever showed evidence of possessing horns of any type. They ranged in body weight from approximately 20 kg to 1200 kg, with most Miocene genera being between 100 kg and 300 kg in weight. Amongst the Miocene camelids there were four main lineages: the short-legged, brachyodont (low-crowned cheek teeth) miolabines; the long-legged protolabines, with cheek teeth that were moderately hypsodont (high crowned); the giraffe-like aepycamelines, with extremely elongated legs and mesodont cheek teeth (teeth higher crowned than brachyodont teeth, but not as high crowned as hypsodont teeth); and the small, gazelle-like, highly hypsodont stenomylines.

In the Oligocene and woodland savanna conditions of the early Miocene the oreodonts (families Agriochoeridae and Merycoidodontidae) formed a prominent component of the fauna. These were small- to medium-sized ungulates, weighing on average 20–50 kg, though they ranged in weight from 2 to 200 kg. They were
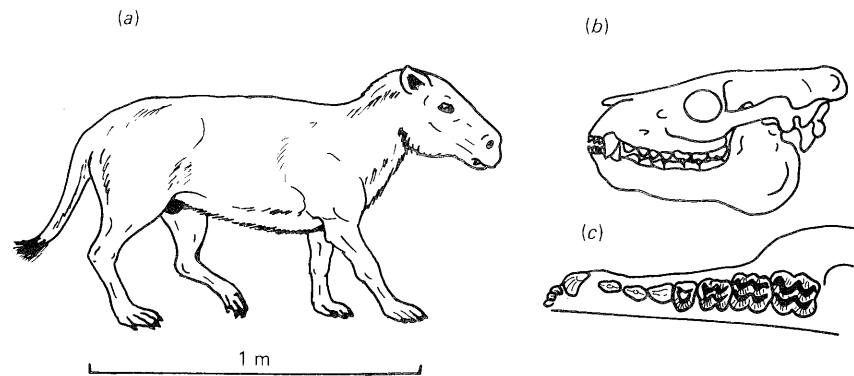
Fig. 3. (a) Reconstruction of *Merycoidodon*, an Oligocene oreodont (adapted from Beneš, 1979).
(b) Skull, and (c) palate of *Merycoidodon* (adapted from Schultz & Falkenbach, 1968).

entirely restricted to North America, and left no descendants. Their post-cranial morphology was similar to suids in its degree of modification from the primitive ungulate condition. They lacked any form of frontal appendages (although as previously mentioned nasal bosses were seen in one small genus), and in overall shape their heads, with short snout and deep cheek region, would have been very similar to that of a large hyrax (Fig. 3).

Only one tylopod family ever evolved frontal horns, the Protoceratidae. Proto-ceratids are often quoted as being members of the sub-order Ruminantia (e.g. Romer, 1966), but are now confirmed as being closely related to camelids (Patton & Taylor, 1973; Webb & Taylor, 1980). They ranged in size between 20 kg and 350 kg, with the majority of the middle Miocene genera weighing about 150 kg. Their horns were non-deciduous, present in the males only in all species, and it is not known whether or not they possessed any form of covering (although they did not have a bovid type of horny sheath). They possessed a median forked horn in addition to the paired frontal horns, and had relatively short legs, with unfused metapodials, and large heads, with brachyodont or mesodont cheek teeth (Fig. 4a). They were of low population density and species diversity in the Miocene faunas, and after the middle Miocene were restricted to the more sub-tropical environments of the Gulf coastal plains of Texas (Patton & Taylor, 1971). Their purely folivorous type of molar wear (my unpublished data) and broad moose-like snout suggest a semi-aquatic mode of feeding, in which vegetation containing little cellulose would be taken. It is interesting to note in this context that the sole genus to survive in the Great Plains region of North America after the early Miocene, *Prosynthetoceras* (*Lambdoceras*), had molar wear resembling that of present-day cervids, with evidence of a more omnivorous diet for at least part of the year. *Lambdoceras* also had a narrower snout than the other Miocene protoceratids, suggesting a tree-browsing habit. It may have been maintaining a Category B type of combination of feeding and social behaviour in the northern part of the continent in the later Miocene.
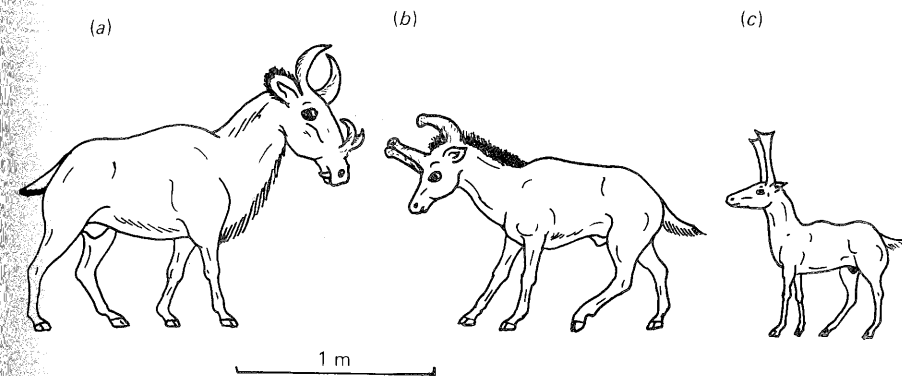
Fig. 4. Reconstructions of sexually dimorphic North American horned ungulates (approximately to scale)
(a) *Syndyoceras* (Early Miocene protoceratid)
(b) *Procranioceras* (Middle Miocene dromomerycid)
(c) *Paracosoryx* (Middle Miocene merycodontine antilocaprid)

The indigenous members of the sub-order Ruminantia, traguloids such as *Leptomeryx* and *Hypertragulus*, appear to have been associated with more open types of habitat than their Eurasian counterparts (Clark *et al.*, 1967). They had selenodont teeth and relatively elongated limbs, but as they were all hornless and small in body size they were probably all broadly classifiable in Category A in terms of social and reproductive behaviour. In their diet and foraging behaviour they may well have been like present-day small open-country antelope such as the steinbok *Raphicerus campestris* and Thomson's gazelle *Gazella thomsoni*, which are highly selective feeders on the growing parts of grass and other ground-level plants (Leuthold, 1977) (Table 3).

Three families of the sub-order Ruminantia, from the infra-order Pecora, appeared in North America in the Miocene, presumably as immigrants from Eurasia. These included the small hornless Blastomerycinae, members of the family Moschidae and closely related to the living musk deer *Moschus* (Webb & Taylor, 1980), and two families of horned eupecorans, the Dromomerycidae and the Antilocapridae. Blastomerycids all remained under 20 kg in body weight, and probably were similar in general biology and life style to the traguloids, probably largely replacing the endemic traguloids in this niche during the Miocene.

Dromomerycids made their first appearance late in the early Miocene. Their affinities amongst the Eupecora are uncertain, and they are variously claimed to be giraffoids (e.g. Stirton, 1944) or cervoids (e.g. Frick, 1937; J. J. M. Leinders, personal communication). They ranged in body weight from 20 to 300 kg, with most Miocene genera weighing around 100 kg. They possessed horns in the males only in most genera, and these were non-deciduous and unbranching. Although they were not covered by a bovid-type horny sheath, the skin covering the horns was probably keratinized to some extent, especially at the bulbous tips, in the manner of present-day giraffes. One sub-family, the Craniocerotinae, had a single
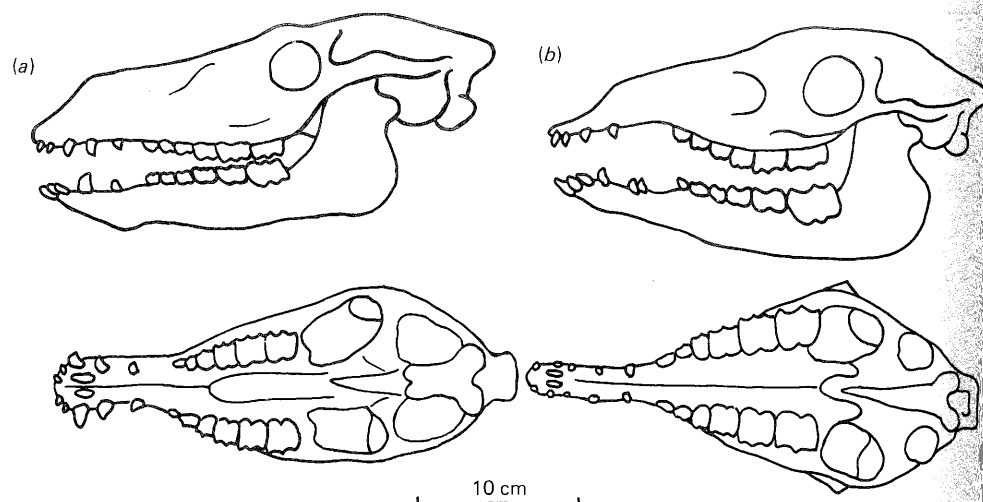
Fig. 5. Skull and palate of Early Miocene camelids of North America (lower jaw cut away to show height of M₃). (Drawn from specimens in the Frick Collection, American Museum of Natural History, and adapted in part from Frick & Taylor (1971).)

    (a) *Oxydactylus* (Aepycameline camelid)
    (b) *Michenia* (Protolabine camelid)

median occipital horn in addition to the paired frontal horns. They had moderately long legs, with fused metapodials, although remnants of the side metapodials were retained in the front limbs in some genera. Their post-cranial proportions would have been reminiscent of present-day forest-dwelling cervids or bovids (Fig. 4b), and their cheek teeth were brachyodont or mesodont.

    The dromomerycids were the principal occupants of the main cervoid–giraffoid type of niche in the middle and late Miocene but, although they were not as restricted in their distribution as the protoceratids, they were limited in species diversity and in relative abundance, when compared to both the contemporary camelids and equids, and also to living antelope. They appear to have been dependent on a woodland habitat, were absent from the southwestern part of the continent after the middle Miocene, and became extinct in the Pliocene when the main biome in North America turned to steppe (Webb, 1977). The increasing seasonality and aridity of the climate throughout the Miocene, with increasing fibre content of the available browse, is reflected by the trend in both dromomerycids and protoceratids to increasing body size and increasing height of the cheek teeth throughout the epoch, although neither family attained true hypsodonty.

    In the early Miocene the small but moderately hypsodont genus *Aletomeryx* was seen to have small horns in the female as well as slightly larger horns in the male. On the basis of its post-cranial proportions, *Aletomeryx* lived in a more open habitat than other Miocene dromomerycids (K. M. Scott's and my unpublished data), and may have lived in herds in mixed-sex feeding groups, rather than the males holding territories (Table 3). On a more speculative note, it is interesting

in this context that the last surviving genus of dromomerycid, the latest Miocene–early Pliocene *Pediomeryx*, was the most addicted to open-habitat living of the entire family (K. M. Scott's and my unpublished data), and yet no horn material has ever been found in association with the skeletal remains. Admittedly, such remains are rare, and no complete skulls have ever been found. But remains of the slightly earlier genus, *Yumaceras*, are equally if not more rare, and yet they are definitely known to have possessed large horns of the *Cranioceras* type. Speculation remains premature, but it may well be the case that sexual isomorphy was achieved in this genus by the loss of the horns in the male.

    The family Antilocapridae comprised two sub-families – the small-sized (7–30 kg) Merycodontinae, which made their first appearance in the middle Miocene, and the medium-sized (30–80 kg) Antilocaprinae, which first appeared in the late Miocene. Antilocaprids were an entirely North American radiation, and survive today as a single species, the pronghorn antelope *Antilocapra americana*. Their eupecoran affinities are uncertain. On the basis of their horn morphology they have generally been held to be closely related to bovids (e.g. Romer, 1966; O'Gara & Matson, 1975), although more recent work has shown that, on a number of morphological criteria, they are best considered as cervoids (Leinders, 1979; Leinders & Heintz, 1980). Living antilocaprids have an unbranched non-deciduous horn core, which supports a branched keratin sheath that is shed annually. Fossil antilocaprines also had horn cores that were unbranched, or simply forked, and that presumably supported a similar type of keratin sheath. Small horns were present in the females in all antilocaprines. The living pronghorn, the sole surviving representative of a moderately large Plio–Pleistocene radiation of antilocaprine antilocaprids, is an open-country herd-forming animal, but the males exhibit seasonal territorial behaviour (Kitchen, 1974), and their general life-style is similar to gazelles in Jarman's (1974) Category C (Table 3). However, unlike the African antelope, and despite the fact that their cheek teeth are highly hypsodont, they do not take much grass in the diet but rather select lower-level herbaceous plants (Olsen & Hansen, 1977).

    In contrast to the antilocaprines, the merycodontine antilocaprids had horns in the males only, and these horns had complex and variable branching. Despite the fact that the horns frequently had long pedicles and possessed cervid-like burrs, they were non-deciduous (Voorhies, 1969). In contrast to the other Miocene horned ruminants, they had hypsodont cheek teeth, were relatively more abundant and were found in more open habitats (K. M. Scott's and my unpublished data) (Fig. 4c). However, they were restricted to a small body size, and so would not have been in direct competition with most of the larger open-country equids and camelids, although they may have been in competition with stenomyline camels of similar size. (In fact, this camelid lineage showed a distinct decline in numbers, leading to extinction later in the middle Miocene, coincident with the appearance of the merycodonts.) Merycodonts were abundant in the middle and late Miocene, but became extinct at the end of the epoch, when they were superseded by the larger antilocaprine antilocaprids.