A CLIMATIC EXPLANATION FOR
PATTERNS OF EVOLUTIONARY DIVERSITY IN
# UNGULATE MAMMALS

by CHRISTINE M. JANIS

ABSTRACT. The radiation of ruminant artiodactyls, bovids in particular, that characterized the latter part of the Neogene, appeared to be at the expense of the hindgut-fermenting ungulates (perissodactyls, proboscideans, and hyracoids), that showed a corresponding decrease in diversity and total numbers. However, climatic and vegetational changes may have been the cause for this decline, rather than direct competition with ruminants. The Tertiary change in relative diversity of hindgut fermenters, from initially more than 50% of the ungulate fauna to only 25–30%, occurred during the late Eocene and early Oligocene in higher latitudes, and in the mid-Miocene in lower latitudes. In both cases, this change was correlated with a climatic shift from low to high seasonality. Subsequently, the relative abundance of hindgut fermenters remained more or less constant in all latitudes until the end of the Pleistocene. The radiation of the ruminant artiodactyls appears to have taken place at the expense of less specialized selenodont artiodactyls such as anthracotheres, oreodonts, and traguloids, that were the first artiodactyls to show an increase in diversity after the late Eocene reduction in numbers of hindgut fermenters.

THE pattern of evolutionary diversity of ungulate mammals through the Tertiary period has long been seen as a success story for the Order Artiodactyla. The radiation and diversification of ruminant artiodactyls during the Neogene, reaching its apogee with the supreme Plio-Pleistocene success of the Family Bovidae, is often contrasted with that of the Order Perissodactyla. Perissodactyls reached their maximum species diversity in the late Eocene, and thereafter showed a decline in abundance and family diversity that was more or less synchronous with the onset of the diversification of the ruminating artiodactyls (members of the Suborders Tylopoda and Ruminantia). This contrasting pattern of radiation between the two orders is usually attributed to competitive interaction and ecological replacement of an inferior group by a better adapted one, the key cited feature being the forestomach site of fermentation in the ruminants, contrasted with the hindgut site of fermentation in the caecum and colon of the perissodactyls (e.g. Simpson 1953; Van Valen 1971; Stanley 1974).

This simple pattern of artiodactyl radiation versus perissodactyl decline is more complex than has previously been assumed. Perissodactyls reached their maximum diversity at the family level in the late Eocene with 13 families, 3 of which were extinct by the end of the Eocene, and a further 6 were extinct by the middle Miocene (text-fig. 1). However, the remaining perissodactyl families did not show a continuing Neogene evolutionary pattern of steady decline in diversity and abundance. The Rhinocerotoidea had a maximal diversity in the later Oligocene and early Miocene, and rhinocerotids were abundant throughout the Miocene. The Equidae had their maximal diversity in the late Miocene, the Chalicotheriidae had a moderate diversification during the Neogene (only suffering extinction during the Pleistocene) and, while the Tapiriidae never displayed a great diversification, they persisted little changed from the Oligocene to the present day (Janis 1984). All living perissodactyls, derived from a common early Eocene or late Palaeocene ancestry, are hindgut fermenters, and it thus seems parsimonious to assume that all extinct members of this order (which all possess lophed cheek teeth indicative of a folivorous diet) had a similar type of digestive physiology.

Only two out of a total of 37 Tertiary artiodactyl families (Bovidae and Cervidae) have a
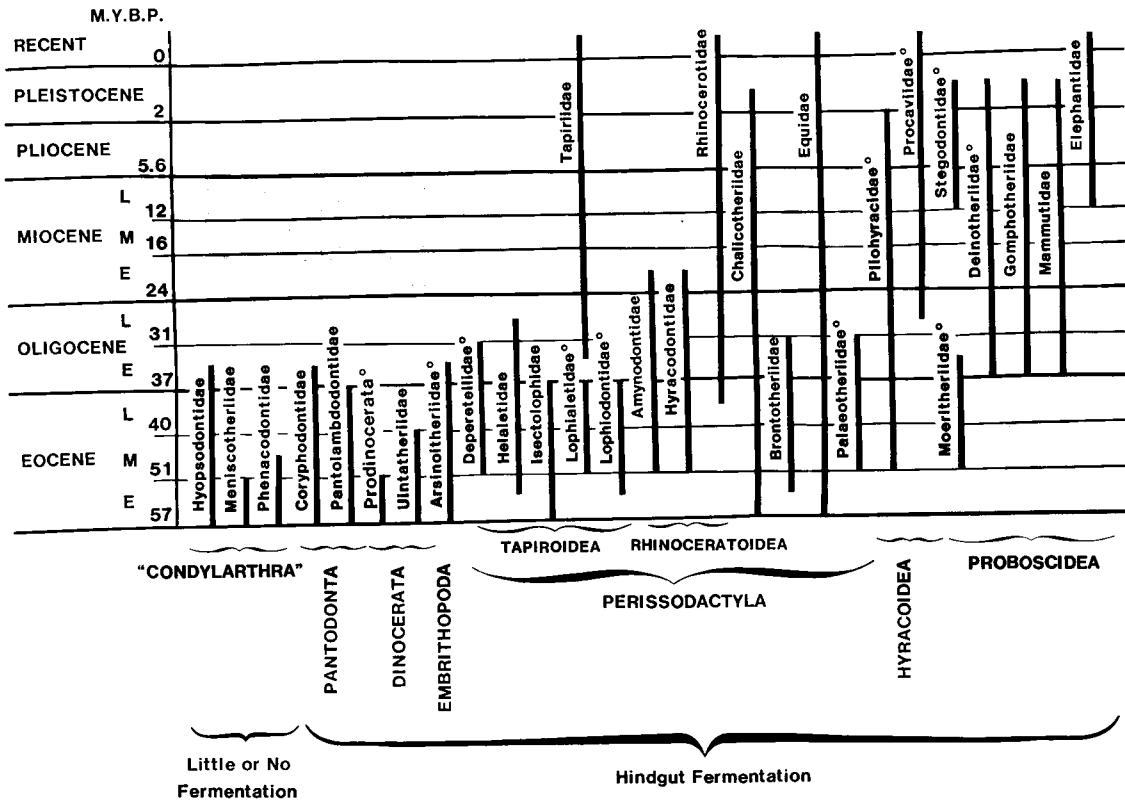
TEXT-FIG. 1. Distribution of ungulate families (with the exclusion of the Artiodactyla) through the Cenozoic (excluding the Palaeocene). Omnivorous 'condylarth' families (Arctocyonidae and Mesonychidea) and aquatic families (Desmostylia and Sirenia) excluded. ° = exclusively Old World families.

widespread distribution and diversity of species at present. The primitive artiodactyls in the Suborder Palaeodonta did not survive past the Oligocene, and the Suborders Suina and Tylopoda had considerable reduction in family diversity during the Neogene. Among the Ruminantia, only members of the Infraorder Pecora have continued to expand in range and diversity since the end of the Oligocene, though three families were extinct by the end of the Miocene, and several others showed a considerable decline in diversity in post-Miocene times (text-fig. 2). [It should be noted in this context that the terms 'Palaeodonta' or 'dichobunid artiodactyls' are widely used, but represent a paraphyletic or polyphyletic assemblage of primitive artiodactyls rather than a taxonomically cohesive group. The same is also true for the 'basal' pecoran family 'Gelocidae' (Janis 1987), the 'basal' ungulate order 'Condylarthra' (Prothero et al. 1988), and the artiodactyl suborders 'Suina' and 'Tylopoda' (Webb and Taylor 1980). However, it is not my intention to revise the phylogeny of the ungulates in this paper, and these terms remain useful, if cladistically invalid.]

The general evolutionary pattern of other ungulate orders has been for extinction or a decline in diversity during the early Tertiary, with later significant extinctions in those families that survived into the Plio-Pleistocene (text-fig. 1). Dental morphology and wear patterns suggest that the ungulate orders that experienced early Tertiary extinctions were either omnivorous (most condylarths), or selective folivores (all other orders) (Janis 1979). Those families that survived to the present day, the Elephantidae (Order Proboscidea) and the Procaviidae (Order Hyracoidea), have
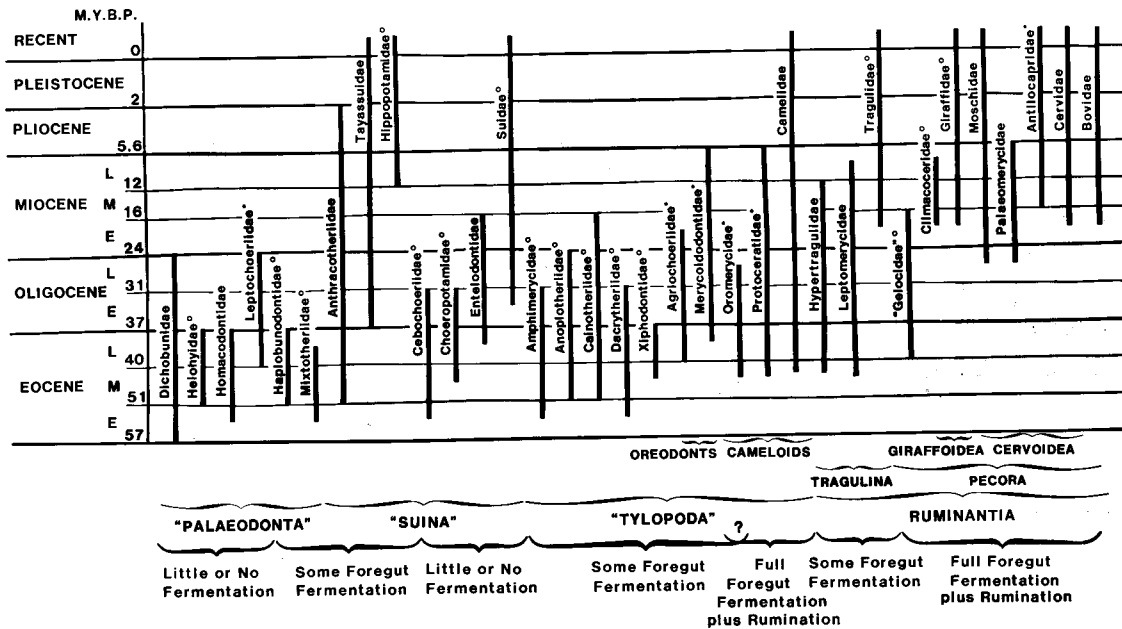
TEXT-FIG. 2. Distribution of ungulate families in the Order Artiodactyla through the Cenozoic (excluding the Palaeocene). * = exclusively North American families. ° = exclusively Old World families. Monotypic families [the Eocene to Oligocene Amphimerycidae ('Tylopoda'), the Oligocene Bachitheriidae and Lophiomerycidae (Tragulina), and the Miocene Hoplitomerycidae (Pecora)] not depicted. Ruminant taxonomy, including assignation of taxa from listings in Savage and Russell (1983) to families, from Janis (1987) and Janis and Scott (1987) (Palaeomerycidae includes the North American dromomerycids and the European taxon *Amphitragulus*). Note: the correct latinization of the giraffoid family Climacoceridae, derived from the genus *Climacoceras*, should be Climacoceratidae, but I am following the original nomenclature of Hamilton (1978).

hindgut sites of fermentation (paralleling the condition in perissodactyls), and it is likely that this was also the case in the extinct families of these orders. The extinct African and northern hemisphere ungulate orders, Embrithopoda, Dinocerata, and Pantodonta, combined a folivorous type of dental morphology with large body size, and thus were most probably also hindgut fermenters (see Janis 1976, 1979; Van Soest 1982; Demment and Van Soest 1985 for discussion of body size in relation to digestive physiology).

I have previously argued that a hindgut site of fermentation is not inferior to a ruminant type of digestive system, and that the type of fermentation site developed is dependent on the body size of the members of that lineage at the time of the adoption of a folivorous diet (Janis 1976). Cifelli (1981) has shown that the patterns of evolutionary diversification of perissodactyls compared to artiodactyls, at both familial and generic levels, do not fit an evolutionary model of competition and ecological replacement. However the fact remains that ungulates with a hindgut site of fermentation became extinct or decreased in diversity during the later Tertiary. In contrast, the most widespread and speciose ungulate families today, the Cervidae and the Bovidae, are pecoran ruminants possessing an advanced type of foregut digestive physiology, combined with rumination (remastication) of the food. It should be emphasized that the type of digestive physiology is a critical aspect of the biology of a herbivorous mammal in terms of its ability to cope with any particular type of vegetation, irrespective of whether the animal is typed as a 'grazer' or 'browser' (see later discussion and e.g. Janis 1976; Bell 1982; Van Soest 1982; Guthrie 1984; Demment and Van Soest 1985; Owen-Smith 1985). Despite the fact that the late Tertiary saw the radiation of supposedly

grazing ungulates concurrent with the spread of low-biomass vegetation (Wolfe 1985), this time period also saw a decline in the diversity of hindgut fermenters regardless of dietary type.

Although Cifelli (1981) clearly demonstrated that the decline of perissodactyls (the most diverse of the hindgut-fermenting ungulates) could not be explained by competition with ruminant artiodactyls, he did not propose an alternative model to explain their later Tertiary demise. Cifelli obtained his faunal data from Romer (1966), while I have had the advantage of the later publication by Savage and Russell (1983). Although there are still problems with this data set (see discussion in following section), it provides the opportunity for the geographical division of mammalian faunas, to test the hypothesis that the decline of hindgut-fermenting ungulates was simultaneous in all geographical regions. This can be shown not to be the case: the more northern latitudes experienced an earlier decline than the more tropical regions, and this observation is the basis for the model proposed here.

This paper examines the evolutionary patterns of diversity of Old World and North American ungulate lineages, grouped by types of digestive physiology, and proposes that Tertiary climatic changes were responsible for both the reduction in diversity of hindgut fermenters and, independently, for the radiation of the specialized ruminant foregut fermenters. Hindgut fermenters and ruminants, by virtue of their different digestive strategies, are differentially adapted for using vegetation of climatic regimes of low and high seasonality respectively (see later discussion). Thus the vegetational changes accompanying Tertiary climatic changes may have been the key influence on the differential pattern in their relative abundance and diversities through time. Langer (1987) reviews changing diversities of artiodactyls and perissodactyls through the Tertiary in correlation with climatic and vegetational changes and, while he attributes these patterns to differences in digestive physiology, he does not propose a detailed type of causal mechanism as is advanced here.

MATERIAL AND METHODS

Faunal lists of different time periods and geographic regions were taken from Savage and Russell (1983). The faunal summaries have been deposited with the British Library, Boston Spa, Yorkshire, UK, as Supplementary Publication No. SUP 14037 (17 pages). The data are summarized in text-fig. 3. A problem exists with the 'Asian' faunas, as these are lumped in Savage and Russell from a wide geographical area spanning both temperate and tropical latitudes (i.e. above and below 23° N). Wherever possible I have chosen those faunas from more southern latitudes, but the problem remains that southern Asian (and African) faunas are simply not known from many critical time periods. Nevertheless, the data can still be used to provide a general test of my hypothesis and in any event it appears that the Asian faunas were more protected from climatic change than the European forms, regardless of absolute latitude, possibly because of their more continental setting. [Singh (1988) also notes that vegetational changes affected Central Asia relatively late in comparison with Europe.] Data for Palaeocene faunas were excluded as the orders Artiodactyla and Perissodactyla did not make an appearance until the Eocene or the latest Palaeocene (Cifelli 1981). There is a problem with the late Eocene faunas of North America. While the Unitan has commonly been termed the 'late Eocene', it is now considered to be equivalent to the European faunas of mid-Eocene age (Krishtalka et al. 1987). However, the Duchesnean faunas are poorly known, and I have included in my Duchesnean faunal composite listing (text-fig. 3) taxa that are known from earlier in the Eocene and, although as yet undiscovered in the Duchesnean, survive (or have surviving close relatives) in the Chadronian (early Oligocene).

Because no living members remain of the South American ungulate orders, any conclusions about the role of digestive physiology in their evolutionary diversifications remains highly speculative, and for this reason I have not considered faunal changes in South America in this paper. Likewise, I have not considered Australia, mainly because the Tertiary faunas are still poorly known, and herbivorous marsupials are not directly comparable with ungulates. The late Pleistocene fauna should perhaps be viewed as the 'final stage' in this pattern of ungulate diversification because of the bias in northern latitude faunas resulting from the end-Pleistocene extinctions of most of the endemic North American ungulates.

The relative diversities of ungulates were estimated from the number of described species of ungulates of higher taxa in the lumped faunas for each geographic region. Boucot (1978) has demonstrated that, for fossil invertebrates, the number of described species of a particular group is a good estimate of its abundance and distribution, and that assumption has been made here for ungulates. A similar approach was applied by Cifelli

(1981). Moreover, as almost all ungulates can be considered 'large' animals (i.e. over 5 kg in body weight), this data base is probably little biased due to differential preservation on the basis of body size (Behrensmeyer and Boaz 1980). The diversity of ungulate lineages was broken down into the following four main types of digestive physiologies for comparison of the patterns of evolutionary diversity.

1. Non-ruminant ungulates: this includes ungulates with low-crowned, bunodont cheek teeth, that are presumed to have a primarily omnivorous diet with little or no fermentation of cellulose (Janis 1979). That is, the 'condylarths', many of the primitive 'palaeodont' or 'dichobunid' artiodactyls, and most suines. Some living suines do have a certain degree of forestomach fermentation (but do not chew the cud), as seen in members of the families Tayassuidae (peccaries) and Hippopotamidae (Langer 1984a). In the Suidae, the warthog (*Phacochoerus aethiopicus*) subsists on a diet composed primarily of grass (Field 1970), although it does not practise extensive cellulose fermentation. However, all these taxa can be regarded as lacking a specialized system for cellulose fermentation in comparison with other ungulates.

2. Primitive selenodont artiodactyls: this category is further subdivided as follows.

a. Artiodactyls with the selenodont type of lophed cheek teeth, suggesting a folivorous (rather than omnivorous) diet, yet lacking the morphological specializations of an elongated diastema and long legs with the reduction of the lateral digits. (These features appear to be correlated respectively with the handling of a more fibrous diet and a greater foraging radius in camelids and ruminants.) This category includes the 'suine' family Anthracotheriidae, the 'tylopod' families Anoplotheriidae and Dacrytheriidae, the 'palaeodont' families Haplobunodontidae and Mixtotheriidae, and the oreodont families Agriochoeridae and Merycoidodontidae.

b. Families in the infraorder Tragulina of the suborder Ruminantia which, by analogy with living tragulids, probably had a similar feeding strategy of selective browsing with little or no fermentation (Kingdon 1982). Members of other traguloid families were of a similar size to living tragulids, most under 5 kg in body weight, which would also militate against their evolving full rumination (Janis 1976).
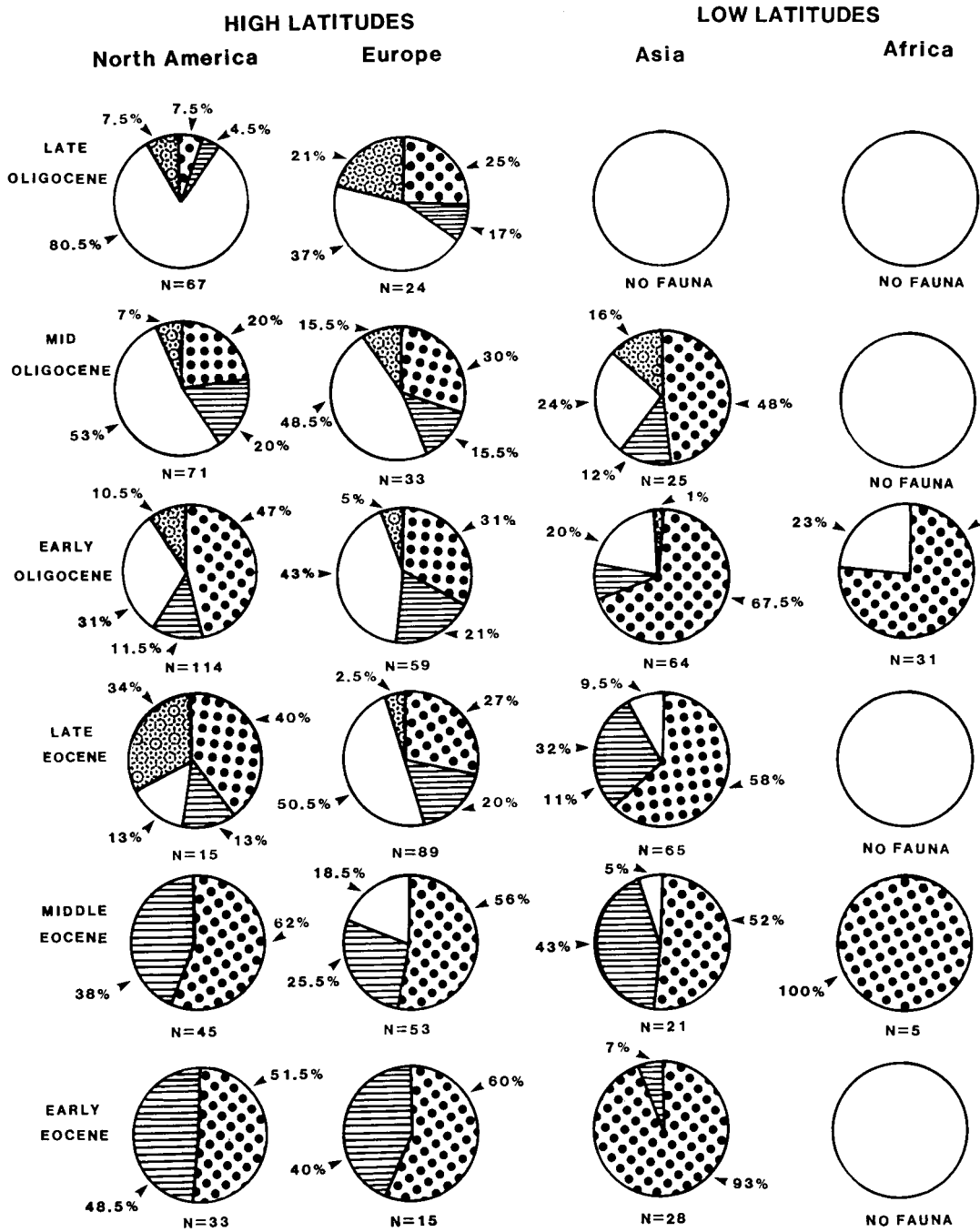
c. Other European early Tertiary 'tylopod' families, the Amphimerycidae, Cainotheriidae and Xiphodontidae, containing small, gracile animals that paralleled the traguloids in many aspects of their morphology.

Based on comparison with the cranial and dental morphology of living ungulates of known digestive physiology (e.g. Janis in press a), these 'primitive selenodont' taxa are assumed to have had a 'tragulid' type of digestive physiology. Tragulids have the capacity to handle a greater degree of fibre in the diet than non-ruminant herbivores, but lack the full foregut-fermentation capacity of camelids and ruminants (category 3). In terms of the absolute number of species, the most important ungulates in this category are the anthracotheres, oreodonts and traguloids.
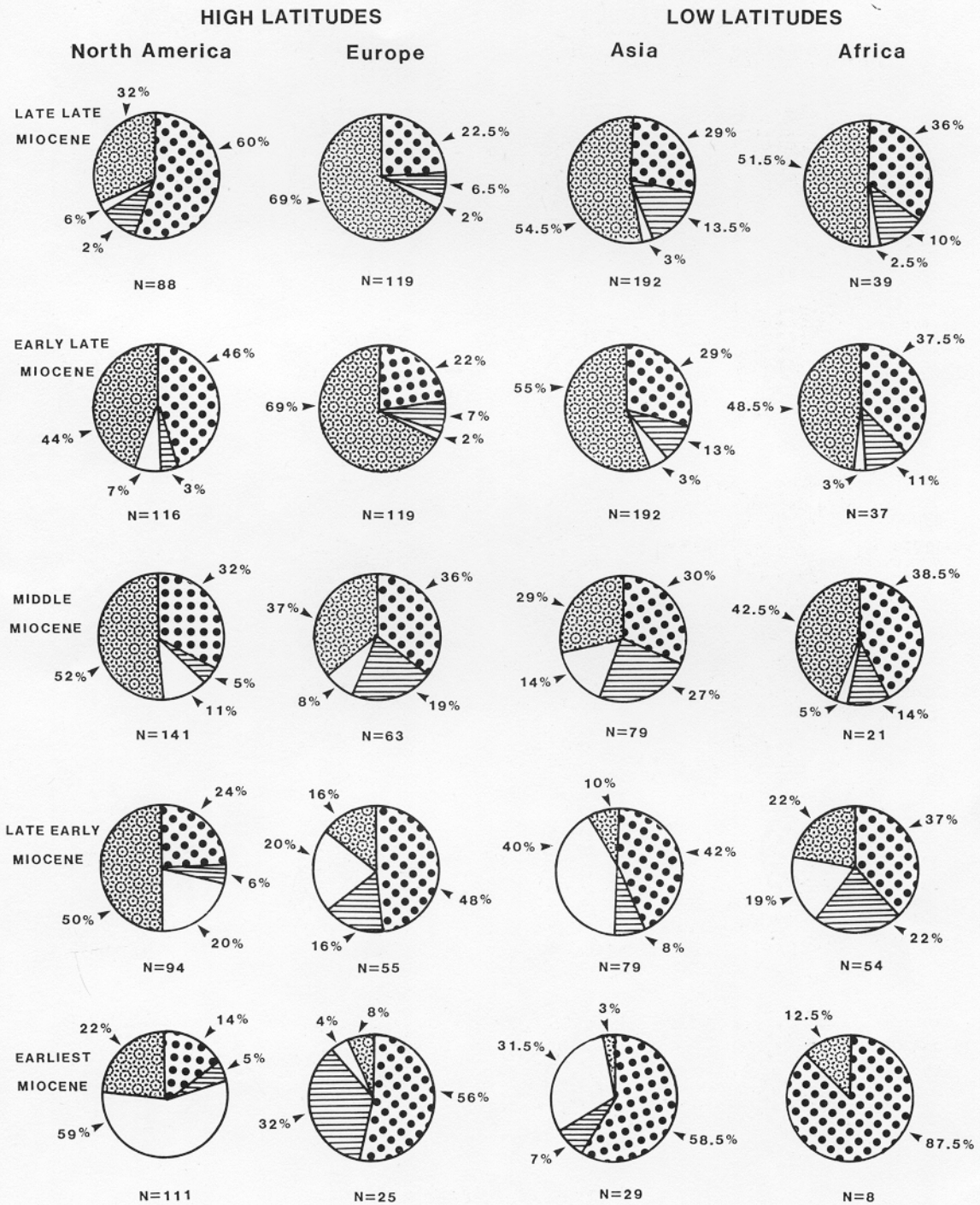
3. Ruminant artiodactyls. This includes living and fossil families in the infraorder Pecora, the living tylopod family Camelidae, and the extinct tylopod families Oromerycidae and Protoceratidae (which are closely related to the Camelidae). All living tylopod and ruminant artiodactyls, which had a common late Eocene ancestry (Gazin 1955), share a similar embryology of the enlarged forestomach (Langer 1974), as well as specialized selenodont cheek teeth typical of a folivorous type of diet (Webb and Taylor 1980). Additionally, camelids have evolved a type of forestomach fermentation, combined with cud-chewing, similar to that seen in the Pecora, but lacking in the Tragulina (Langer 1974). I have therefore assumed that the extinct close relatives of these living families also had a more fully developed type of forestomach fermentation than seen in the more bunodont traguloids. Additionally, protoceratids parallel camelids and ruminants in many aspects of their morphology (Janis 1982), and thus may be assumed to have had a similar type of physiology, although the oromerycids were smaller and more bunodont, and may be better classified as 'primitive selenodonts'.

4. Hindgut fermenters. This includes the living and fossil families of the extant orders Perissodactyla, Proboscidea, and Hyracoidea, and the extinct orders Embrithopoda (arsinoitheres), Dinocerata (uintatheres), and Pantodonta. (The reasons for assuming that these extinct taxa had a hindgut type of fermentation system were discussed previously.)

The diversities of ungulate faunas of different digestive feeding strategies were compared for both high latitudes (i.e. around 45° N) in the northern hemisphere (faunas from North America and Europe) and for low latitudes (faunas from Asia and Africa) (text-fig. 3). Climatic information for the time periods and geographical areas examined was obtained from current literature sources, using palaeobotanical data (e.g. Wolfe 1978, 1985), oxygen isotope ratios from marine benthic foraminifera (Burchardt 1978; Woodruff *et al.* 1981), and deep-sea sedimentary data (e.g. Keller and Barron 1983; Shackleton 1986). The time scale was taken from Woodburne (1987).

HIGH LATITUDES   LOW LATITUDES

North America   Europe   Asia   Africa

LATE
OLIGOCENE

7.5%   7.5%   4.5%
7.5%
80.5%
N=67

21%   25%
37%   17%
N=24

NO FAUNA

NO FAUNA

MID
OLIGOCENE

7%   20%
53%   48.5%   20%
N=71

15.5%   30%
48.5%   15.5%
N=33

16%
24%   48%
12%   N=25

NO FAUNA

EARLY
OLIGOCENE

10.5%   47%
31%   11.5%
N=114

5%   31%
43%   21%
N=59

20%   1%
67.5%
N=64

23%
N=31

LATE
EOCENE

34%   40%
13%   13%
N=15

2.5%   27%
50.5%   20%
N=89

9.5%
32%   58%
11%
N=65

NO FAUNA

MIDDLE
EOCENE

62%
38%
N=45

18.5%   56%
25.5%
N=53

5%   52%
43%
N=21

100%
N=5

EARLY
EOCENE

51.5%
48.5%
N=33

60%
40%
N=15

7%   93%
N=28

NO FAUNA

TEXT-FIG. 3A. For legend see p. 471.

TEXT-FIG. 3 B. For legend see p. 471.

HIGH LATITUDES　　　　　　　LOW LATITUDES

North America　　　Europe　　　　　Asia　　　　　Africa
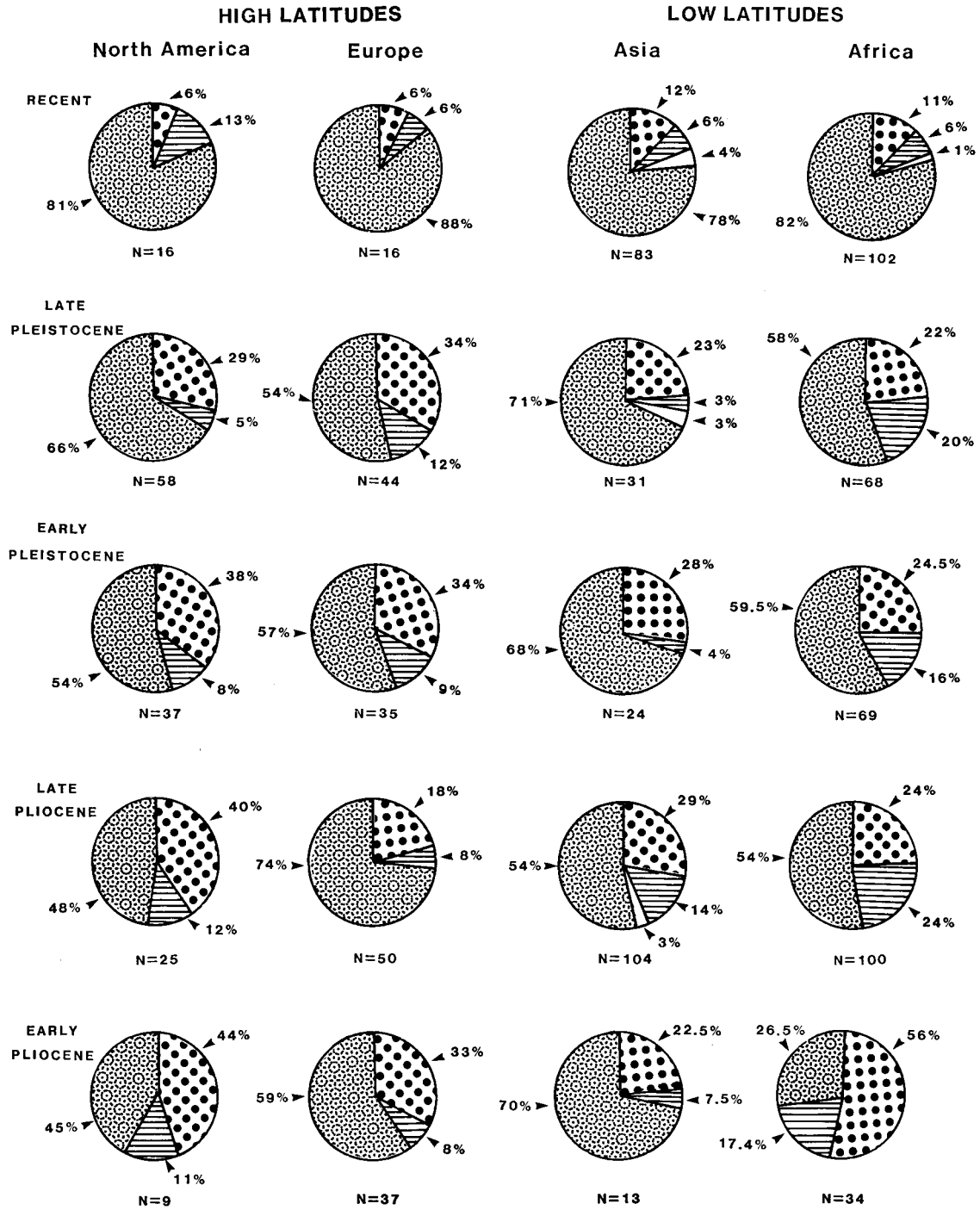
TEXT-FIG. 3C. For legend see opposite.

RESULTS

Text-fig. 3 summarizes the results presented in this section.

Eocene

The world of the earliest Eocene had a similar climatic and vegetational regime to that seen in the late Palaeocene (Wolfe 1985; Wing and Tiffney 1987), although the climate at this time was apparently both warmer and seasonally drier than that of the late Palaeocene (Rose 1981; Wing and Bown 1985). Hindgut fermenters comprised at least 50% of the ungulate fauna at all latitudes. Despite the fact that this epoch heralded the initial radiation of the orders Artiodactyla and

---

TEXT-FIG. 3. Summary of percentages of ungulate species of different dietary types (expressed in percentages of the total number of ungulate species in the fauna) in different geographic areas during the Cenozoic (taken from Savage and Russell, 1983). KEY: ▤, Little or no fermentation; ▨, hindgut fermentation; ☐, primitive selenodont artiodactyls (? some forestomach fermentation); ▨, ruminating artiodactyls (forestomach fermentation plus cud-chewing) (see text for further explanation of dietary categories, and assignation of ungulate taxa).

Faunal horizons are as follows: **Early Eocene (52 M.Y.B.P.):** North America: Composite Wasatchian (Greybullian) fauna. Europe: Composite Sparnacian fauna. Asia: Composite faunas from China. Africa: No fauna. **Middle Eocene (49 M.Y.B.P.):** North America: Composite Bridgerian fauna. Europe: Composite Lutetian fauna. Asia: Composite faunas from North India and Pakistan. Africa: Gouiret-el-Azib fauna (Algeria). **Late Eocene (40 M.Y.B.P.):** North America: Composite Duchesnean fauna. Europe: Composite Headonian fauna. Asia: Composite faunas from India and South China. Africa: No fauna. **Early Oligocene (34 M.Y.B.P.):** North America: Composite Chadronian fauna. Europe: Composite Suevian fauna. Asia: Composite faunas from North China and Mongolia. Africa: Fayum fauna (Egypt). **Mid Oligocene (Early Late Oligocene) (31 M.Y.B.P.):** North America: Composite Orellan fauna. Europe: Composite mid-Oligocene faunas (Antoignt, La Ferte-Alais and Montalban). Asia: Composite faunas from China, Kazakhstan and Mongolia. Africa: No fauna. **Late late Oligocene (28 M.Y.B.P.):** North America: Composite early Arikareean fauna. Europe: Composite Chattian fauna. Asia: No fauna. Africa: No fauna.

Early Early Miocene (22 M.Y.B.P.): North America: Composite late Arikareean fauna. Europe: Composite Agenian fauna. Asia: Composite Oligo-Miocene fauna (= 'Aquitanian') from China, Kazakhstan, and Mongolia. Africa: Early Rusinga fauna (East, North and Southwest Africa). **Late Early Miocene (18 M.Y.B.P.):** North America: Composite Hemingfordian fauna. Europe: Composite Orleanian fauna. Asia: Composite fauna of Agnean/Orleanian equivalent from Burma, China, Kazakhstan, Mongolia, Pakistan and Burma. Africa: Rusinga fauna (Egypt, Kenya and North Africa). **Middle Miocene (14 M.Y.B.P.):** North America: Composite Barstovian fauna. Europe: Composite Astaracian fauna. Asia: Composite fauna of Astaracian equivalent from Burma, China, India, Kazakhstan, Mongolia and Pakistan. Africa: Composite Ternian fauna (East and North Africa). **Early Late Miocene (10 M.Y.B.P.):** North America: Composite Clarendonian fauna. Europe: Composite Vallesian fauna. Asia: Composite fauna of Vallesian equivalent from China and Pakistan. Africa: Composite Ngororan fauna (East and North Africa). **Late Late Miocene (7 M.Y.B.P.):** North America: Composite Hemphillian fauna. Europe: Composite Turolian fauna. Asia: Composite fauna of Turolian equivalent from Afghanistan, Burma, China, Kazakhstan, Mongolia and Pakistan. Africa: Composite Lothaganian fauna (East and North Africa).

Early Pliocene (4 M.Y.B.P.): North America: Composite Blancan I fauna. Europe: Composite Ruscinian fauna. Asia: Composite fauna of Ruscinian equivalent from China and Turkey. Africa: Composite Langebaanian fauna (East, North and South Africa). **Late Pliocene (2·5 M.Y.B.P.):** North America: Composite Blancan III and IV faunas. Europe: Composite Villafranchian fauna. Asia: Composite fauna of Villafranchian equivalent from China, India, Israel and Pakistan. Africa: Composite Makapanian fauna (East, North and South Africa). **Early Pleistocene (1·5 M.Y.B.P.):** North America: Composite Irvingtonian fauna. Europe: Composite Biharian fauna. Asia: Composite fauna of Biharian equivalent from China. Africa: Composite faunas from East and South Africa: Koobi Fora (upper member), Kromdraai, Olduvai II–IV, Shungura and Upper Sterkfontein. **Late Pleistocene (0·5 M.Y.B.P.):** North America: Composite Rancholabrean fauna. Europe: Composite Steinheimian fauna. Asia: Composite late Pleistocene fauna (East Asia). Africa: Composite late Pleistocene fauna (East, North and South Africa). **Recent:** Faunal data obtained from Walker (1983).

Perissodactyla, the faunas were still dominated by pantodonts and uintatheres, and additionally by condylarths in northern latitudes. A global warming had occurred by the start of the middle Eocene, resulting in a climate that was fairly uniform globally, with high average temperatures and little range in the temperature means (Burchardt 1978; Wolfe 1978, 1985). However, in the early middle Eocene there was a drop in global temperature from the Tertiary maximum at the start of this time period (Shackleton 1986).

At the latitude of approximately 45°, the dominant vegetation of the middle Eocene was a tropical type of broad-leaved evergreen multi-storied forest, and the flora of the early middle Eocene of England contained the largest proportion of tropical elements seen in the Tertiary (Collinson 1983). The middle Eocene faunas contained mammals similar to those restricted today to the tropical forests of equatorial regions (e.g. primates and dermopterans), and a large proportion of small and arboreal mammals in general (Collinson and Hooker 1987). However, it should be noted that present-day equatorial forests do not support the Eocene diversity of small to medium-sized terrestrial folivores, suggesting that these Eocene 'tropical' forests were not directly comparable to those of the present day. Both plant and animal diversity of these forests was high, suggesting high vegetational biomass and high levels (but seasonal distribution) of rainfall (Wolfe 1985). Higher- and lower-latitude ungulate faunas in the middle Eocene were similar, with hindgut fermenters again comprising at least 50 % of the total ungulate fauna. Ruminant artiodactyls were not present until the late middle Eocene, and primitive selenodonts were the only folivorous artiodactyls for most of this time period. The non-fermenting ungulates were primarily represented by the palaeodont artiodactyls, and the diversity of condylarths showed considerable decline over the faunas of the early Eocene. The later middle Eocene vegetation was less tropical in aspect than that of the early and early middle Eocene, suggesting a more open habitat (MacGinitie 1969; Collinson and Hooker 1987), which might explain the reduction in diversity of the more omnivorous condylarths, and the radiation of the more folivorous perissodactyls in the higher latitudes.

The late Eocene climate was cooler than that of the middle Eocene (Shackleton 1986). Sclerophyll taxa first appeared in vegetational assemblages in southwestern North America and southwestern Asia at this time, suggesting some seasonal aridity and the possible emergence of a scrub type of vegetation in certain areas (Singh 1988). In England, there was a large reduction in the numbers of smaller and frugivorous mammals, with an increase in the numbers of ungulates possessing lophed cheek teeth, which suggests a habitat consisting of a more fibrous type of vegetation (Collinson and Hooker 1987). The proportion of hindgut fermenters in the higher-latitude faunas dropped from around 60 % to around 40 % between the middle and late Eocene, with an especially profound drop in Europe. Cameloids made their first appearance in North America at the end of the middle Eocene, 'gelocids' first appeared in Europe at the start of the late Eocene, and primitive selenodont artiodactyls (primarily oreodonts in North America and anthrocotheres in the Old World) showed a considerable increase in diversity over the situation in the middle Eocene faunas. However, vegetation in the lower latitudes showed little change at this time (Wolfe 1985), and the Asian faunas of South China and Burma still maintained a high (almost 60 %) variety of hindgut fermenters, represented by a diversity of rhinocerotoids and tapiroids, despite a radiation of traguloids and anthracotheres.

At the end of the Eocene, both oxygen isotope data (Burchardt 1978) and palaeobotanical data (Wolfe 1978, 1985; Collinson et al. 1981) suggest a sudden and profound climatic change in the northern hemisphere. Most significantly, a rise in the annual temperature range would have resulted in less equable winters (Collinson et al. 1981; Wolfe 1978). There may have been winter frosts, and there were certainly profound seasonal differences in the availability and abundance of vegetation [see Prothero (1985) and Singh (1988) for a review of the possible causal mechanisms for this climatic change]. Prothero (1985) provides faunal evidence for a more gradual pattern of extinction in the northern latitudes throughout the late Eocene, suggesting a less abrupt climatic change, and Shackleton (1986) points out that the profound 'climatic event' of the Eocene/Oligocene boundary actually postdates the late Eocene faunal changes.

Oligocene

During the Oligocene, the vegetation in latitudes 35–50° N consisted of microthermal broad-leaved deciduous forests, a vegetational type previously unknown (Wolfe 1985). The global ungulate faunas of the early Oligocene were similar to those of the late Eocene, even with a slight increase in the relative numbers of hindgut fermenters. In England, there was a further decrease in the number of small and arboreal mammals, both this and the palaeobotanical data suggesting a slightly more open habitat than present in the late Eocene (Collinson and Hooker 1987). However, between the early and mid (early late) Oligocene the number of hindgut fermenters in the high-latitude faunas fell drastically to around 25% of the fauna, accompanied by an increase in the relative numbers of primitive selenodont artiodactyls. Although the Asian faunas at this time also showed a slight decrease in the numbers of hindgut fermenters, this does not represent a substantial drop below the middle Eocene values. Prothero (1985) provides evidence for a second wave of general mammalian extinctions and higher-latitude climatic deterioration at this mid-Oligocene time. Late late Oligocene faunas are known only from North America and Europe. The European faunas showed a similar number of ungulates of various types to mid-Oligocene faunas, although ruminants were more abundant. The very low percentage of hindgut fermenters, and the very high percentage of primitive selenodonts, in North America during this time is probably an artifact of the method of data collection by species counting, as the number of oreodont species (here representing 76% of the fauna) is probably overestimated by a factor of 2 or 3 (Lander 1977), although there is no doubt that oreodonts were exceedingly abundant. Thus the real percentage diversity difference between North American and European faunas at this time (and also in the earliest Miocene) was probably considerably less than presented in text-fig. 3.

The drop in the numbers of hindgut fermenters in the higher-latitude faunas during the Oligocene represents the extinction of several perissodactyl families (text-fig. 1). However, the Asian faunas retained an abundance of rhinocerotoids. Throughout the Oligocene in the northern hemisphere, there was a reduction in the diversity of non-fermenting ungulates, and suines were substituted in this category for 'condylarths' and primitive artiodactyls. Although ruminating artiodactyls were present in both North America and Eurasia during the Oligocene, they did not radiate to comprise a large proportion of the ungulate faunas during this epoch. The main Oligocene artiodactyl radiation was of the primitive selenodonts, oreodonts in North America and anthracotheres in the Old World, although traguloids also diversified across the Northern Hemisphere. These primitive selenodont artiodactyls expanded at the apparent expense of the non-fermenting ungulates in the lower latitudes, and at the expense of both non-fermenting and hindgut-fermenting ungulates in the higher latitudes.

Miocene

Temperatures increased world-wide during the early Miocene, with the latest early Miocene representing the thermal maximum of the Neogene (Burchardt 1978; Wolfe 1978, 1985; Woodruff *et al.* 1981; Keller and Barron 1983; Singh 1988). However, at the start of the middle Miocene there was a profound drop in global temperatures (Singh 1988). Additionally, there was an increase in the latitudinal temperature gradient, which would have produced an intensified subtropical high-pressure system, with a change in precipitation patterns resulting in summer drought along the western sides of continents, and low-biomass vegetation types (savanna and steppe) appeared for the first time in both higher and lower latitudes (Wolfe 1985; Singh 1988). Elevation of mountain ranges at this time (e.g. the Himalayas, the Rockies, and the East African ridge system) would also have resulted in a continental rain-shadow effect (Wolfe 1985). A further temperature drop occurred at the start of the late Miocene, and there was an expansion of vegetation typical of open and arid habitats, a floral change that was especially marked in Africa owing to the elimination of the Tethys sea at this time (Singh 1988). Late Miocene faunal changes in Pakistan (Barry *et al.* 1985), southern Europe (Gabunaia and Chochieva 1982) and North America (Janis 1982; Webb 1983) also indicate a change from a woodland savanna to an increasingly open and drier prairie type of habitat. Floral

evidence suggests that intense Arctic cold fronts affected the North American vegetation by the latter part of the Miocene (Wolfe 1985), and widespread grasslands were seen both in North America (Chaney and Elias 1936; Stebbins 1981) and in northwest China (Li, in Wolfe 1985).

The earliest Miocene faunas had a greater diversity of hindgut fermenters in all latitudes than in the mid to late Oligocene, possibly correlating with the global warming. However, a profound decrease in their abundance occurred in the lower latitudes in the late early Miocene; by the middle Miocene, hindgut fermenters comprised only around 30% of the total ungulate fauna in more equatorial regions, resembling the condition seen in the higher latitudes at the start of the Miocene. However, the proportion of hindgut fermenters then remained more or less constant in all latitudes throughout the rest of the epoch, although a certain amount of fluctuation (both up and down) was seen in different regions. Ruminant artiodactyls initially radiated and diversified in the Miocene, with the Bovidae first appearing in the late early Miocene (Ginsburg and Heintz 1968).

Looking only at the change in ungulate faunal diversity in the lower latitudes, one might interpret the diversity changes as a radiation of the ruminants, resulting in a decrease in the diversity of hindgut fermenters. However, in the North American late Miocene faunas, an even greater radiation of ruminant artiodactyls is actually accompanied by a considerable increase in the proportion of hindgut fermenters, reflecting for the most part an increase in the diversity of equids with high-crowned (hypsodont) cheek teeth, presumably grazers, and the influx of proboscideans from the Old World. The ungulates that suffered the most profound reduction in numbers and diversity worldwide in the middle Miocene were the primitive selenodont artiodactyls. They fell to around 3% of the ungulate fauna worldwide by the early late Miocene, were completely absent from higher latitudes by the start of the Pliocene, and today are represented only by four tragulid species in the Old World tropics. The radiation of the ruminant artiodactyls in the Neogene appeared to occcur more at the expense of the less specialized anthracotheres, oreodonts, and traguloids than of the hindgut fermenters.

Although the spread of a savanna type of vegetation in the middle Miocene between 0 and 50° N would have affected both high and low latitudes, this vegetational change indicates the first significant occurrence of high levels of seasonality on the lower-latitude floras and faunas, with seasonality in precipitation affecting the availability of vegetation to the ungulates on a year-round basis. At this time, the proportion of hindgut fermenters in the lower latitudes dropped below 50% of the total ungulate fauna for the first time during the Tertiary. Moreover, the change in the abundance of hindgut fermenters in the lower latitudes, following the early middle Miocene drop in global temperature, and the onset of seasonality in precipitation in the lower latitudes, almost exactly paralleled the events in the higher latitudes that followed the onset of temperature seasonality in the late Eocene and mid-Oligocene. The fact that higher-latitude faunas did not suffer a further decrease in numbers of hindgut fermenters in the mid-Miocene suggests that those remaining taxa in the early Neogene were already adapted to a seasonal climatic regime. Thus, it would seem that it is the inital onset of seasonality, whether of temperature or of rainfall, that has an effect on the diversity of hindgut fermenters in the ungulate faunas, reducing their relative abundance from around 60% of the fauna to around 35%. Further types of seasonality do not appear to affect these already 'adapted' faunas, at least in terms of the relative numbers of species of ungulates with this type of digestive physiology, although a general decline of hindgut fermenters to around 25% of the fauna in all latitudes was seen with the further climatic deterioration of the later Cenozoic (see below).

Plio-Pleistocene

Following the Miocene, global climate was characterized by increased cooling and drying in the higher latitudes. By this time there was an extensive ice cap in the Antarctic, with ocean temperatures approaching those seen today (Woodruff *et al.* 1981), and corresponding changes in the type of grasses comprising the dominant floral elements in the higher latitudes (Stebbins 1981). The numbers of hindgut fermenters in both higher- and lower-latitude faunas were somewhat lower in the early Pliocene in comparison with the latest Miocene, and showed a further decline

throughout the Plio-Pleistocene from around 40% to around 25% of the total ungulate fauna, while the numbers of ruminants showed a corresponding rise (from around 50% to around 62%). However, this decline may not be directly attributable to ruminant competition. For example, in Africa there is little proportional increase in the number of ruminant species from the late Miocene to late Pliocene, and the decrease in the numbers of hindgut fermenters is accompanied by an increase in the numbers of suids of modern aspect.

As previously mentioned, the late Pleistocene may be viewed as the 'end point' in this evolutionary pattern of ungulate diversification. The late Pleistocene extinctions eliminated almost all the endemic ungulates in North America, including the hindgut-fermenting equids and proboscideans, and the present-day ungulate fauna is certainly not representative of the evolutionary history of that continent. The Pleistocene extinctions in the Old World eliminated most of the large species, including the majority of the rhinos and proboscideans, resulting in the extremely low numbers of species of hindgut fermenters (in comparison with the rest of the Cenozoic) seen in lower latitudes today. Demment and Van Soest (1985) provide a physiological explanation for the fact that the largest ungulates are generally hindgut fermenters, and Guthrie (1984) provides an explanation for the vulnerability of hindgut fermenters to the climatic and vegetational changes at the end of the Pleistocene. However, it shold be remembered that, while present-day hindgut fermenters may be of low species diversity, they still represent a large percentage of the total number of individuals and the total biomass of tropical ungulate faunas (Bell 1982). Additionally, because their digestive physiology allows them to feed more selectivity, ruminants are more speciose in any given environment than hindgut fermenters of similar dietary type (Owen-Smith 1985). Thus the relatively low species diversity of hindgut fermenters at present should perhaps not be considered as so much of an evolutionary disaster as a simple comparison of species numbers might suggest.

DISCUSSION

Evolutionary patterns of ungulate diversity

The data presented here do not support the hypothesis that hindgut fermenters were replaced over evolutionary time in an ecologically competitive sense by ruminant artiodactyls for the following reasons. Firstly, the initial decrease in the proportion of hindgut fermenters in higher latitudes was not accompanied by an immediate increase in the numbers of ruminants; rather, there was a diversification of primitive selenodont artiodactyls that probably lacked a complex system of fermentation. Secondly, hindgut fermenters experienced a worldwide rise in diversity at the time of global warming at the start of the Miocene, despite the radiation of ruminant artiodactyls throughout the Oligocene. Thirdly, the increase in the percentage of ruminants in higher-latitude faunas during the Miocene was not inevitably accompanied by a decrease in the proportion of hindgut fermenters; in contrast, the percentage of hindgut fermenters actually increased in North America, and the most significant decrease was in the numbers and proportional representation of primitive selenodont artiodactyls (the latter event was also paralleled in the lower-latitude faunas).

However, the data do suggest that the diversity of hindgut fermenters depends on climatic and vegetational factors, and that climates of low seasonality are able to support a greater diversity of hindgut fermenters than are highly seasonal climates, whether this seasonality is manifested in terms of temperature or precipitation, or of both factors. This low versus high seasonality difference in the diversity of hindgut versus foregut fermenters is seen to hold true today for all mammalian herbivores (Langer 1984b), although equids alone out of the range of hindgut fermenters appear to be well adapted to a seasonal regime, provided that the absolute quantity of food is not limiting. Why should the type of vegetation found in low-seasonality climates support a greater diversity of hindgut fermenters, while vegetation typical of climates with a greater degree of seasonality apparently promoted the diversification of ruminant artiodactyls? The answer may lie in the different mode of food selection between foregut and hindgut fermenters.

Ecological consequences of different digestive strategies

Hindgut fermenters rely on bulk-processing large quantities of food to make maximal use of a fibrous diet (Janis 1976). Van Soest (1982) terms them 'cell content specialists', in that they rely on mechanical measures (mastication) to release cell contents orally, which are then digested before the site of fermentation in the stomach and small intestine. The remaining cellulose is then fermented in the caecum and colon but, as this strategy depends on a large throughput of material, the food in not retained for a great length of time, and the digestion of forage is not complete (Janis 1976). Grazing ruminant artiodactyls, at least, are 'cell wall specialists' (Van Soest 1982), retaining fibrous vegetation for a longer period of time in the foregut site of fermentation, and making maximal use of the energy contained in the cellulose of the plant cell wall.

In a comparison of grazing ruminant artiodactyls (domestic bovids) and hindgut fermenters (equids) it is apparent that, although a ruminant can ingest less food per day than a hindgut fermenter of similar body size, it must retain the food for longer, and so the amount of food that can be ingested per day is more limited. This is probably due, at least in part, to the reticulo-omasal orifice in the ruminant stomach, which limits the rate at which the food can pass from the rumen to the rest of the digestive system (Janis 1976), although the exact mechanism for food retention in the ruman is not fully understood (Demment and Van Soest 1985). Smaller, more selectively feeding ruminants may have a more rapid rate of food passage (Hoppe *et al.* 1977; Hofmann 1985), but there is no comparable living perissodactyl for study. Tapirs and equids, which are of similar body size, have similar rates of passage, and both reduce this rate when switched from a diet of coarse hay to one of lesser fibre content (Foose 1982). Hay is hardly a natural diet for the browsing tapirs, but this experiment suggests that perissodactyls may also reduce the retention time of the digesta if feeding more selectively. Thus it remains a likely hypothesis that a ruminant cannot process as much food in a given time period as a hindgut fermenter of similar body size and dietary type.

In present-day habitats of low seasonality, the foliage is generally of poorer quality (i.e. containing a higher proportion of cellulose), and the distribution of cellulose between the different parts of the plant is fairly uniform (i.e. the leaf has a similar cellulose content to the stem). In more seasonal habitats, where plants 'expect' to lose their leaves during the course of the year, plants invest less in heavy structural or chemical protection of the leaves, and the leaves are generally more palatable and contain less fibre (Minson and McLeod 1970; Deinum and Dirven 1975). In addition, grasses (more typical vegetation in areas with a seasonal distribution of precipitation) protect their leaves less completely than do dicotyledonous plants, as the growing point is at the base (rather than at the apex). Thus grass leaves are less protected from herbivore consumption than are trees and shrubs. (It is common knowledge that pruning trees and clipping shrubs tends to keep them at bay for the season, whereas the more one mows the lawn, the faster it grows!)

Although tropical vegetation of high cellulose content may initially appear more suitable for a ruminant 'cell wall specialist' type of digestive strategy, large amounts of plant material would have to be processed per day in order to obtain enough protein and other cell-content nutrients. (The more fibrous the plant, the greater the proportion of cell wall to cell contents.) While more selectively feeding ruminants may be able to increase their food intake and rate of digestion to a certain extent (Hofmann 1984, 1988), hindgut fermenters seem to be better able to maintain high levels of intake on a fibrous diet (Hume 1984), and it remains true that living ruminants apparently fare poorly on tropical dicotyledonous material (Demment and Van Soest 1985). Today, ruminants are conspicuously rare as folivores in tropical forests.

Present-day ruminants are best able to function in seasonal habitats, especially in extremely seasonal environments where the abundance of vegetation is severely reduced, because of their superior ability to make maximal use of a limited quantity of vegetation. Present-day hindgut fermenters specialize on tropical browse (tapirs and the smaller rhinos), or on the fibrous parts of grasses (equids), whereas the more intermediate hindgut feeders are of very large body size, over 1500 kg (elephants and larger rhinos). [Van Soest (1982) has demonstrated that the ruminant

digestive physiology confers no nutritional advantage over hindgut fermentation at body sizes above 1000 kg.] No small ruminants (under 15 kg) subsists on a diet of fibrous vegetation, but certain hindgut-fermenting hyraxes and lagomorphs fare well on a fairly exclusive grass diet.

Climatic explanation of ungulate evolutionary patterns

The following evolutionary scenario may be proposed, considering the physiological explanations behind the diversity of body sizes, feeding types and habitat distribution of present-day hindgut and foregut fermenters.

The worldwide forests of a low-seasonality regime of the middle Eocene supported a large diversity of hindgut fermenters of small to medium body size; tapiroids in North America and Eurasia, equids in North America and Europe, and palaeotheres in Europe. The change to greater levels of seasonality in higher latitudes, because of climatic changes during the late Eocene and early Oligocene, restricted their diversity. Families that survived must have been able to cope with seasons when herbage was sparse or unavailable. Rhinos, first appearing in the middle Eocene, were initially small animals, but by the Oligocene were of larger body size, better able to withstand a seasonal decrease in vegetation availability. Chalicotheres and equids also increased in body size. Tapiroids, with the exception of the specialized larger browsing forest tapirids, became extinct in higher latitudes. Many ungulates showed changes in dental morphology suggestive of an increase in the dietary fibre content (Collinson and Hooker 1987). Although brontotheres and palaeotheres also showed an increase in body size in the early Oligocene, their dental wear suggests that they were heavily dependent on fruit in the diet (Janis 1979). The fact that these forms survived the end of the Eocene, while the large-bodied uintatheres and pantodonts did not, suggests that perissodactyls may have had some superiority of digestive physiology over the original Palaeogene ungulate radiation. In any event, these perissodactyl groups did not survive the Oligocene epoch, possibly as the result of the decrease in availability of fruit on a year-round basis. The differential survival of equids in North America and Europe at this time is problematical, and may be related to geographical differences in habitat (Janis 1982). In contrast, the lower-latitude Asian faunas retained a diversity of medium-sized perissodactyls (mainly rhinocerotoids) throughout the Oligocene epoch and the early Miocene.

The late Eocene to early Miocene saw the emergence of a diversity of primitive selenodont artiodactyls. The traguloids, and the traguloid-mimicking European tylopods, were all of small body size and presumably were able to sustain themsevles on a selective browsing diet with little fermentation. It is interesting to consider the question of why perissodactyls did not retain a smaller body size at this point in time, and adapt to this type of feeding niche (a possible traguloid parallel did in fact exist in the form of the late Eocene long-legged deperetellid tapiroids of Asia). Possibly a lineage committed to extensive hindgut fermentation might be less able to adopt a selective-browsing foraging strategy than small, initially omnivorous, artiodactyls. Alternatively, the uniquely specialized double-pulley astragalus of artiodactyls (Schaeffer 1947) might have conferred a locomotory advantage in animals of small body size. The Oligocene success of the larger-sized oreodonts and anthracotheres may have been the result of an ability to utilize a wider spatial variety of food resources, by virtue of the retention of more scansorial types of postcranial adaptations.

The higher ruminant lineages that emerged in the late Eocene and early Oligocene were characterized by the progressive development of cursorial limbs, reflected in the lengthening and fusion of the metapodials and the development of a compact, parallel-sided astragalus (Webb 1977; Webb and Taylor 1980). Such morphological changes could reflect the adoption of a more open type of habitat, and/or of a greater foraging radius for suitable food items (Janis 1982, in press *b*). Similar morphological changes took place in the limbs of Oligocene equids (Sondaar 1969). Equids appear to have paralleled the patterns of evolutionary diversification of ruminant artiodactyls in a number of ways, but probably avoided direct competition with ruminants by their ability, as hindgut fermenters, to subsist on a diet of higher fibre content than a ruminant of similar body size (Janis 1976; Demment and Van Soest 1985). The Oligocene also showed a diversification of

medium-sized, somewhat cursorially adapted browsing rhinos (the hyracodontids and the diceratherine rhinocerotids). Their increase in size over the Eocene browsing tapiroids probably allowed them to cope better with seasonal fluctuations in vegetation abundance.

The worldwide drying event in the mid-Miocene resulted in a decrease in the diversity of hindgut fermenters in the lower-latitude faunas, and in the spread of grassland savanna vegetation over much of the continental land mass between latitudes 0° and 45°. This time period saw the first extensive diversification of the pecoran ruminants. While the proportions of hindgut fermenters held steady, or even increased slightly in higher latitudes, the composition of this fauna changed from a mixture of browsers and grazers of various sizes to one dominated by animals of large body size (proboscideans and large rhinos) or specialized grazers (hypsodont equids). Similar changes did not occur in lower latitudes until the Plio-Pleistocene. However, these climatic changes also provided an ideal environment for selectively foraging ruminants. Choosing plant parts with low cellulose content was now a viable feeding strategy, and the digestive physiology of these animals would have allowed them to survive on smaller amounts of plant material than is possible for a hindgut fermenter of similar body size. Guthrie (1984) points out that the mid-Miocene climatic changes would have resulted in a decrease in the favourable season for plant growth, resulting in a more mosaic type of vegetational habitat (a mixture of shrubs, trees, grasses, and forbs rather than a single woodland type of cover). This increased diversity in the vegetation would have favoured a greater diversity of folivorous ungulates, especially assisting the radiation of the ruminants because of the lesser investment in antiherbivory systems of defence by the shorter-growth-season plants, both mechanical (cellulose) and chemical (plant secondary compounds). Both pecorans and tylopods increased in size and developed a greater degree of cursorial specializations, and some groups became hypsodont (Webb 1977).

Among the hindgut fermenters, the equids showed two divergent tendencies from the ancestral medium-sized browsing equids of the Oligocene and early Miocene. Several clades, radiating from the middle Miocene genus *Merychippus*, diversified into larger, more cursorially adapted hypsodont species. These equids were probably more specialized for open habitats, and depended on a higher proportion of grass in the diet. In contrast, members of the Anchitheriini and the Hypohippini, originating from an Oligocene ancestor, apparently retained a preference for a more closed habitat and a browsing diet, as evidenced by relatively shorter limbs and low-crowned cheek teeth, but they also showed a significant increase in body size. The smaller hyracodontid and diceratherine rhinos became extinct, to be replaced by larger forms, including specialized grazers (teleoceratine rhinocerotids). The middle Miocene of Africa saw the demise of the larger hyracoids (family Pliohyracidae), the tapir-like listriodont suids and the anthracotheres, their place in more seasonal habitats being taken by giraffids, bovids, proboscideans, large rhinos and, in the latest Miocene, immigrant hipparionine equids.

However, the mid-Miocene saw the decline of all groups of primitive selenodont artiodactyls, presumably because seasonality in precipitation further restricted the availability of non-fibrous types of vegetation for the greater part of the year, making it essential for a large folivorous ungulate to have a full capacity for the fermentation of cellulose. By the late Miocene the traguloid families had disappeared from North America, and the tragulids were restricted to the Old World tropics. Suoids maintained their numbers, perhaps because their primitive bunodont type of dentition allowed for a greater flexibility in maintaining an omnivorous diet. The middle and late Miocene also saw the radiation and diversification of proboscideans over the northern hemisphere, their large body size presumably compensating for the seasonal fluctuations in availability of vegetation, since large-bodied mammals have a greater capacity for fat storage to weather out periods of food shortage.

A further steady increase in seasonality occurred in northern latitudes from the late Miocene to the late Pleistocene. By the end of the Miocene, chalicotheres and browsing equids had disappeared from all higher-latitude faunas, rhinos and oreodonts had disappeared from North America, and there was a severe reduction in the numbers of browsing ruminants. North America was particularly affected by the climatic changes at the end of the Miocene, as it was an island continent with few

opportunities for tropical refuges for the more specialized browsing ungulates. In the Old World, by the end of the Pleistocene, there was a reduction in diversity of giraffids, rhinos, and proboscideans, and the restriction of many of these ungulates to equatorial regions, with the extinction of chalicotheres and anthracotheres. Most of these extinctions affected the large browsing species adapted to subtropical vegetation. Smaller browsers that were adapted to a more temperate type of vegetation, such as members of the Cervidae, diversified at this time, as temperate-adapted vegetation encroached on previously subtropical zones.

CONCLUSION

The data presented in this paper support the hypothesis proposed that the reduction in the numbers and diversity of hindgut-fermenting ungulates is better correlated with climatic and vegetational changes than with the diversification of ruminant artiodactyls. However, ruminating artiodactyls may have replaced less specialized types of folivorous artiodactyls (here termed 'primitive selenodonts'). Despite the fact that the later Tertiary showed a rise in the diversity of ruminants, and a decline in the diversity of hindgut fermenters, this cannot truly be regarded as an 'ecological replacement', since the vegetational habitat changed during the course of the Tertiary, resulting in a change in ecological conditions. The ruminant artiodactyls came to dominate the ungulate faunas of the Neogene as a result of fortuitous circumstances that provided a more suitable vegetational regime for their particular type of digestive strategy, rather than because of overall superiority of design.

REFERENCES

BARRY, J. C., JOHNSTON, N. M., RAZA, S. M. and JACOBS, L. L. 1985. Mammalian faunal change in the Neogene of Southern Asia and its relation to global climatic and tectonic events. *Geology*, **13**, 637–640.

BEHRENSMEYER, A. K. and BOAZ, D. E. D. 1980. The recent bones of Amboseli National Park, Kenya, pp. 72–93. *In* BEHRENSMEYER, A. K. and HILL, A. P. (eds.). *Fossils in the making.* University of Chicago Press, Chicago.

BELL, R. H. V. 1982. The effect of soil nutrient availability on community structure in African ecosystems, pp. 193–216. *In* HUNTLEY, B. J. and WALKER, B. H. (eds.). *The ecology of tropical savannas.* Springer-Verlag, Berlin.

BOUCOT, A. J. 1978. Community evolution and rates of cladogenesis. *Evol. Biol.* **11**, 545–655.

BURCHARDT, B. 1978. Oxygen isotope palaeotemperatures from the Tertiary period in the North Sea area. *Nature, Lond.* **275**, 120–123.

CIFELLI, R. L. 1982. Patterns of evolution among Artiodactyla and Perissodactyla (Mammalia). *Evolution*, **35**, 433–440.

CHANEY, R. W. and ELIAS, M. K. 1936. Late Tertiary floras from the High Plains. *Publ. Carnegie Inst. Washington*, **476**, 1–72.

COLLINSON, M. E. 1983. *The fossil plants of the London clay.* The Palaeontological Association, London.

—— and HOOKER, J. J. 1987. Vegetational and mammalian faunal changes in the Early Tertiary of southern England, pp. 259–304. *In* FRIIS, E. M., CHALONER, W. G. and CRANE, P. R. (eds.). *The origin of angiosperms and their biological consequences.* Cambridge University Press, Cambridge.

—— FOWLER, K. and BOULTER, M. C. 1981. Floristic changes indicate a cooling climate in the Eocene of Southern England. *Nature, Lond.* **291**, 315–317.

DEINUM, B. and DIRVEN, J. G. P. 1975. Climate, nitrogen and grass. 6. Comparison of yield and chemical composition of some temperate and tropical grass species grown at different temperatures. *Neth. J. agric. Sci.* **23**, 69–82.

DEMMENT, M. W. and VAN SOEST, P. J. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* **125**, 641–672.

FOOSE, T. J. 1982. Trophic strategies of ruminant versus nonruminant ungulates. Ph.D. thesis (unpubl.), University of Chicago, U.S.A.

FIELD, C. R. 1970. Observations on the food habits of tame warthog and antelope in Uganda. *East Afr. Wildl. J.* **8**, 1–17.

GABUNAIA, L. K. and CHOCHIEVA, K. I. 1982. Co-evolution of the *Hipparion* fauna and vegetation in the Paratethys region. *Evol. Theory* **6**, 1–13.

GAZIN, C. L. 1955. A review of the upper Eocene Artiodactyla of North America. *Smithson. Misc. Coll.* **128** (8), 1–96.

GINSBURG, L. and HEINTZ, E. 1968. La plus ancienne antilope d'Europe, *Eotragus artenensis* du Burdigalian d'Artenay. *Bull. Mus. natl. Hist. nat., Paris (2° ser.)*, **40**, 837–842.

GUTHRIE, R. D. 1984. Mosaics, allochemicals and nutrients: an ecological theory of late Pleistocene megafaunal extinctions, pp. 259–298. *In* MARTIN, P. S. and KLEIN, R. G. (eds.). *Quaternary extinctions*. University of Arizona Press, Tucson, Arizona.

HAMILTON, W. R. 1978. Fossil giraffes from the Miocene of Africa, and a revision of the phylogeny of the Giraffoidea. *Phil. Trans. R. Soc.* B **282**, 165–229.

HOFMANN, R. R. 1984. Comparative anatomical studies imply adaptive variations of ruminant digestive physiology. *Can. Jl Anim. Sci.* **64** (Suppl.), 203–205.

—— 1985. Digestive physiology of the deer: their morphophysiological specialisation and adaptation. *Bull. R. Soc. N.Z.* **22**, 393–407.

—— 1988. Morphophysiological evolutionary adaptations of the ruminant digestive system, pp. 1–20. *In* DOBSON, A. and DOBSON, M. J. (eds.). *Aspects of digestive physiology in ruminants*. Comstock Publishing Associates, Ithaca.

HOPPE, P., QVORTRUP, S. A. and WOODFORD, M. H. 1977. Rumen fermentation and food selection in East African sheep, goats, Thomson's gazelle, Grant's gazelle and impala. *J. agric. Sci.* **89**, 129–135.

HUME, I. D. 1984. Evolution of herbivores – the ruminant in perspective, pp. 15–31. *In Ruminant physiology: concepts and consequences. A tribute to R. J. Moir.* Symposium Proceedings of the University of Western Australia, Perth.

JANIS, C. 1976. The evolutionary strategy of the Equidae, and the origins of rumen and cecal digestion. *Evolution*, **30**, 757–774.

—— 1979. Aspects of the evolution of herbivory in ungulate mammals. Ph.D. thesis (unpubl.), Harvard University, U.S.A.

—— 1982. Evolution of horns in ungulates: ecology and paleoecology. *Biol. Rev.* **57**, 261–318.

JANIS, C. 1984. Tapirs as living fossils, pp. 80–86. *In* ELDREDGE, N. and STANLEY, S. M. (eds.). *Living fossils*. Springer-Verlag, New York.

—— 1987. Grades and clades in hornless ruminant evolution: the reality of the Gelocidae and the systematic position of *Lophiomeryx* and *Bachitherium. J. vertbr. Paleont.* **7**, 200–216.

—— (in press *a*). Correlation of cranial and dental variables and dietary preferences: a comparison of macropodid and ungulate mammals. *In* TURNER, S., THULBORN, R. A. and MOLNAR, R. (eds.). *Problems in vertebrate biology and phylogeny – an Australian perspective. Mem. Qld Mus.*

—— (in press *b*). Do legs support the arms race in mammalian predator–prey relationships? *In* HORNER, J. R. and CARPENTER, K. (eds.), *Vertebrate behavior as derived from the fossil record*. Columbia University Press, New York.

—— and SCOTT, K. M. 1987. The interrelationships of higher ruminant families with special emphasis on the members of the Cervoidea. *Am. Mus. Novit.* **2893**, 1–85.

KELLER, G. and BARRON, J. A. 1983. Paleoceanographic implications of Miocene deep sea hiatuses. *Bull. Geol. Soc. Am.* **94**, 590–613.

KENNETT, J. P. 1977. Cenozoic evolution of Antarctic glaciation, the Circum-Atlantic Ocean, and their impact on global paleoceanography. *J. Geophys. Res.* **82**, 3843–3859.

KINGDON, J. 1982. *East African mammals, Vol. IIIC.* 393 pp. Academic Press, London.

KRISHTALKA, L., WEST, R. M., BLACK, C. C., DAWSON, M. R., FLYNN, J. J., TURNBULL, W. R., STUCKY, R. K., MCKENNA, M. C., BOWN, T. M., GOLZ, D. J. and LILLEGRAVEN, J. A. 1987. Eocene (Wasatchian through Duchesnean) biochronology of North America, pp. 77–117. *In* WOODBURNE, M. O. (ed.). *Cenozoic mammals of North America*. University of California Press, Berkeley.

LANDER, E. B. 1977. *A review of the Oreodonta (Mammalia, Artiodactyla), parts I, II and III.* Ph.D. thesis (unpubl.). University of California, Berkeley, U.S.A.

LANGER, P. 1974. Stomach evolution in the Artiodactyla. *Mammalia*, **38**, 295–314.

—— 1984a. Comparative anatomy of the stomach in mammalian herbivores. *Q. Jl Exp. Physiol.* **69**, 615–625.

—— 1984b. Anatomical and nutritional adaptations in wild herbivores, pp. 185–203. *In* GILCHRIST, F. M. C. and MACKIE, R. I. (eds.). *Herbivore nutrition in the tropics and subtropics*. Science Press, Craighall, South Africa.

—— 1987. Evolutionary patterns of Perissodactyla and Artiodactyla (Mammalia) with different types of digestion. *Z. zool. Syst. Evol.-forsch*. **25**, 212–236.

MACGINITIE, H. D. 1969. The Eocene Green River flora of northwestern Colorado and northeastern Utah. *Univ. Calif. Publ. Geol. Sci*. **83**, 1–140.

MINSON, D. J. and MCLEOD, M. N. 1970. The digestibility of temperate and tropical grasses, pp. 719–732. *In* NORMAN, M. J. T., (ed.). *Proc. 11th international grassland congress, Surfer's Paradise, Australia*. University of Queensland Press, St. Lucia.

OWEN-SMITH, N. 1985. Niche separation among African ungulates, pp. 167–171. *In* VRBA, E. S. (ed.). *Species and speciation*. Transvaal Museum Monograph No. 4. Transvaal Museum, Pretoria, South Africa.

PROTHERO, D. R. 1985. North America mammalian diversity and Eocene–Oligocene extinctions. *Paleobiology*, **11**, 389–405.

—— MANNING, E. and FISCHER, M. 1988. The phylogeny of the ungulate mammals, pp. 201–234. *In* BENTON, M. J. (ed.). *Phylogeny and classification of tetrapods, Vol. 2*. Systematics Assocation Special Vol. 35B. Clarendon Press, Oxford.

ROMER, A. S. 1966. *Vertebrate paleontology* (3rd edn), 468 pp. University of Chicago Press, Chicago.

ROSE, K. D. 1981. Composition and species diversity in Paleocene and Eocene mammal assemblages: an empirical study. *J. vertebr. Paleont*. **1**, 367–388.

SAVAGE, D. E. and RUSSELL, D. E. 1983. *Mammalian paleofaunas of the world*. 432 pp. Addison-Wesley, Reading, Mass.

SCHAEFFER, B. 1947. Notes on the origin and function of the artiodactyl tarsus. *Am. Mus. Novit*. **1356**, 1–24.

SHACKLETON, N. J. 1986. Palaeogene stable isotopes. *Palaeogeogr. Palaeoclimatol. Palaeoecol*. **57**, 91–102.

SIMPSON, G. G. 1953. *The major features of evolution*. 434 pp. Columbia University Press, New York.

SINGH, G. 1988. History of aridland vegetation and climate: a global perspective. *Biol. Rev*. **63**, 156–196.

SONDAAR, P. Y. 1969. Some remarks on horse evolution and classification. *Sonderb. Z. Saugetier*. **34**, 307–311.

STANLEY, S. M. 1974. Effects of competition on rates of evolution, with special reference to bivalve molluscs and mammals. *Syst. Zool*. **22**, 486–506.

STEBBINS, G. L. 1981. Coevolution of grasses and herbivores. *Ann. Mo. bot. Gard*. **68**, 75–86.

VAN SOEST, P. 1982. *The nutritional ecology of the ruminant*, 373 pp. O. & B. Books, Corvallis, Oregon.

VAN VALEN, L. 1971. Adaptive zones and the orders of mammals. *Evolution* **25**, 420–428.

WALKER, E. P. 1983. *Mammals of the world* (4th edn), 1362 pp. Johns Hopkins University Press, Baltimore.

WEBB, S. D. 1977. A history of savanna vertebrates in the New World. Part 1: North America. *Ann. Rev. Ecol. Syst*. **8**, 355–380.

—— 1983. The rise and fall of the late Miocene ungulate fauna in North America, pp. 267–306. *In* NITECKI, M. H. (ed.). *Coevolution*. University of Chicago Press, Chicago.

—— and TAYLOR, B. E. 1980. The phylogeny of hornless ruminants and a description of the cranium of *Archaeomeryx*. *Bull. Am. Mus. nat. Hist*. **167**, 121–157.

WING, S. L. and BOWN, T. M. 1985. Fine scale reconstruction of late Paleocene–early Eocene paleogeography in the Bighorn Basin of northern Wyoming, pp. 93–105. *In* FLORES, R. M. and KAPLAN, S. S. (eds.). *Cenozoic paleogeography of West-Central United States*. Rocky Mountain Section. S.E.P.M., Denver, Colorado.

—— and TIFFNEY, B. H. 1987. The reciprocal interaction of angiosperm evolution and tetrapod herbivory. *Rev. Palaeobot. Palynol*. **50**, 179–201.

WOLFE, J. A. 1978. A paleobotanical interpretation of Tertiary climates in the Northern hemisphere. *Am. Sci*. **66**, 694–703.

—— 1985. Distribution of major vegetational types during the Tertiary, pp. 357–375. *In The carbon cycle and atmospheric carbon dioxide*. Geophysical Monograph 32.

WOODBURNE, M. O. (ed.) 1987. *Cenozoic mammals of North America*, 336 pp. University of California Press, Berkeley.

WOODRUFF, F., SAVIN, S. M. and DOUGLAS, R. G. 1981. Miocene stable isotope record: a detailed deep Pacific Ocean study and its paleoclimatic interpretation. *Science*, **212**, 665–668.

CHRISTINE M. JANIS

Program in Ecology & Evolutionary Biology,
Division of Biology and Medicine
Box G, Brown University
Providence, R.I. 02912, U.S.A.