Thus, whilst some sexually dimorphic horned ungulates were present during the Miocene in North America, they largely represented immigrants from Eurasia, rather than endemic forms, and formed only a small percentage of the ungulate fauna (Fig. 1, Table 1). Tables 2 and 3 suggest an extension of Jarman's (1974) categories to include the combinations of feeding and social behaviour proposed for some of these extinct ungulates.

(2) Perissodactyls

After the early Miocene, equids were the dominant ungulates (Table 1). At the end of the Oligocene there was a split in the main line of equid evolution into browsing and grazing lineages. The first was represented by the brachyodont anchitherine and hypohippine equids, and the second by the progressively hypsodont parahippines and merychippines. Members of the genus *Merychippus* were the first equids to be found widespread in large numbers, and probably represented the first genus truly to frequent open habitats and form herds. The genus *Merychippus* was tridactyl, with different species exhibiting varying degrees of hypsodonty, but most species were around 100 kg in body weight. Later in the Miocene several lineages split off independently from the merychippines. Some (for example, the genera *Nanippus* and *Calippus*) became dwarf forms, ranging from approximately 30 to 50 kg in body weight. Most of the other equids were larger (ranging from 120 to 250 kg) and consisted of, amongst other lineages, the monodactyl Protohippini, leading ultimately to the present-day genus *Equus*, and the tridactyl Hipparionini. Members of the latter lineage migrated into Eurasia and Africa in the late Miocene, and underwent a highly successful radiation in savanna habitats of the Old World during the Plio-Pleistocene.

Other perissodactyls were also present in the Miocene. Tapirs, very similar in size and general morphology to those found today in Central America, were a persistent rare member of the Miocene faunas, probably confined to riverine forests. Rhinoceroses were also present. In the early Miocene the small rhinoceros *Diceratherium* was common. *Diceratherium* and related genera had a body weight of about 250 kg, and had paired nasal horns in the male only. Diceratheres were replaced in the middle Miocene by larger hornless rhinoceroses, with body weights of around 1500–2000 kg, which were apparently immigrants from Asia. These included the hypsodont short-legged genus *Teleoceras* and the brachyodont long-legged *Aphelops*. Also present in the early Miocene was the chalicothere *Moropus*, a hornless perissodactyl, but which possessed claws instead of hoofs. Chalicotheres appear to have been large tree browsers, rather horse-like in appearance but similar to giant ground sloths in their habitats (Borissiak, 1945), and *Moropus* would have weighed approximately 1200 kg.

Fig. 1 compares the relative abundance of perissodactyls and ruminant artiodactyls through the Tertiary in North America and the Old World. Fig. 6 compares the perissodactyls and ruminant artiodactyls of present-day East Africa with that of the early and late Miocene of North America.

(3) Suoids and proboscideans

In addition to the ruminant artiodactyls, a number of suoids were present in the Miocene. Peccaries, ranging in body weight from 30 to 100 kg, were a persistent small component of the North American ungulates, and have survived on this continent until the present day. In the early Miocene entelodonts, giant suines weighing up to 1000 kg, were present, as were the smaller (150–300 kg) hippo-related anthracotheres. Both forms were probably immigrants from Eurasia in the Oligocene, and they had become extinct in North America by the middle Miocene.

Proboscideans, in the form of brachyodont gomphotheres and mastodonts, made their first appearance in North America in the late Miocene being immigrants from Africa by way of Eurasia. Their appearance was coincident with the inception of the first animals inhabiting open savanna, with a predominance of grazing ungulates (Webb, 1977). They may in fact have contributed to the creation of a more open type of habitat on this continent, in a manner similar to the effect that living proboscideans have on woodland savanna (e.g. Laws, 1970). Proboscideans were reasonably abundant and diverse in North America until they became extinct in the late Pleistocene, along with most of the other ungulates present. Although they did exhibit a considerable size range, all were over 1000 kg.

The problem central to the pattern of ungulate evolution on different continents can be stated as follows: why should it be the case that the environmental conditions in Eurasia and Africa encouraged the evolution of sexually dimorphic combat weapons in the form of horns, when this was not so in North America (nor in South America or Australia)? Theories and speculation on the incidence of horns and sexual dimorphism in living ungulates have tended to regard the living equids and camelids as somewhat bizarre exceptions to the general ungulate rule (e.g. Geist, 1966; Leuthold, 1977). Yet it is highly unlikely that these groups failed to evolve horns because of some genetic incapacity. In the case of the equids, bony horns were seen in the closely related extinct brontotheres, although they were not dimorphic in their possession. The case is even more compelling for the camelids, where the closely related protoceratids appear to have been the one example of true parallelism with the Eupecora in the sexually dimorphic possession of elaborate bony horns amongst the ungulates endemic to North America. Amongst oreodonts, small nasal horns are actually found in one small genus, *Cyclopideus* (my own observation), so presumably other oreodonts would have been able to evolve horns should the evolutionary need have arisen.

VI. CORRELATION OF REPRODUCTIVE AND DIGESTIVE STRATEGIES IN UNGULATES

Whilst ungulates social behaviour can be shown to be related to the availability and dispersion of potential food items (Jarman, 1974), it is also the case that foraging strategies are closely related to digestive strategies (Janis, 1979, and unpublished data). It follows that social behaviour and reproductive strategies, together with such morphological correlates as dimorphic possession of horns,
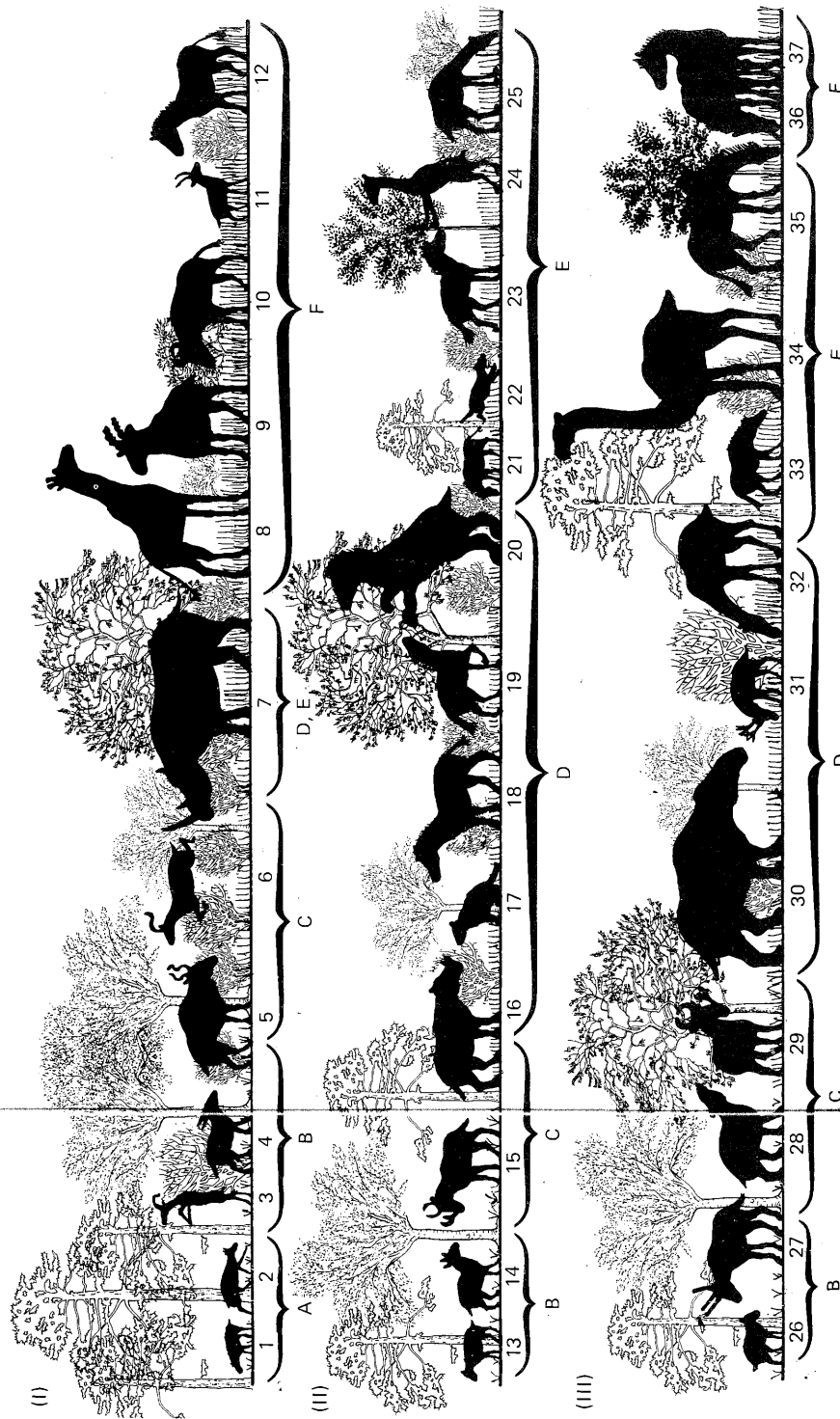
could be closely linked to both habitat structure and the structure of the digestive system.

Amongst living and fossil ungulates, horns are present in some perissodactyls, such as living and many fossil genera of rhinocerotids, and they were seen in the extinct brontotheres, but the evolution of sexually dimorphic bony horns has been restricted to the artiodactyl sub-orders Ruminantia and Tylopoda. Most species of perissodactyls and ruminant artiodactyls live on a diet of vegetation that has a high content of fibre and this requires for its utilization a fermentation chamber within the digestive tract containing cellulase-producing micro-organisms. Perissodactyls and artiodactyls differ in the siting of this fermentation chamber, and in consequence they also differ in foraging strategies (Janis, 1976). Ruminant artiodactyls have a forestomach or rumen for cellulose fermentation, and re-masticate their food after its initial ingestion by chewing the cud. This type of digestive strategy is well suited for dealing with herbage that has a low or moderate fibre:protein ratio, but makes it impossible for them to ingest the large quantities of vegetation of high fibre:protein ratio that they would need for daily maintenance. In contrast, perissodactyls have a hind-gut site, the large caecum and colon, for

Fig. 6.
    Savanna faunas. (I) Recent, East Africa. (II) Early Miocene, North America. (III) Late Miocene, North America.

Habitat types and associated fauna
    (A) Forest. Small selective browsers, non-dimorphic. Jarman's (1974) feeding category A.
    (B) Closed canopy woodland. Small to medium-sized browsers. Ruminants territorial, males with horns, Jarman's (1974) feeding category B.
    (C) Open canopy woodland. Medium-sized browsers/mixed feeders. Ruminants seasonally territorial, males with elaborate horns. Jarman's (1974) feeding category C.
    (D) Woodland–Savanna Grade 1. Medium- to large-sized browsers. Ruminants herd-forming, non-territorial, non-dimorphic.
    (E) Woodland–Savanna Grade 2. Medium- to large-sized browsers and mixed feeders. Ruminants herd- or harem-forming, non-territorial, non-dimorphic.
    (F) Open savanna. Medium- to large-sized grazers, mixed feeders and high-level browsers. Ruminants usually isomorphic, and herd-forming. Jarman's (1974) feeding categories D and E.

Animals
    (I) (1) *Hyemoschus aquaticus* (water chevrotain). (2) *Cephalophus nigrifrons* (duiker). (3) *Litocranius walleri* (gerunuk). (4) *Tragelaphus scriptus* (bushbuck). (5) *Tragelaphus strepsiceros* (greater kudu). (6) *Aepyceros melampus* (impala). (7) *Diceros bicornis* (black rhino). (8) *Giraffa camelopardalis* (giraffe). (9) *Taurotragus oryx* (eland). (10) *Connochaetes taurinus* (wildebeest). (11) *Gazella granti* (Grant's gazelle). (12) *Equus burchelli* (Burchell's zebra).
    (II) (13) *Parablastomeryx* (moschoid). (14) *Barbouromeryx* (dromomerycid). (15) *Lambdoceras* (protoceratid). (16) *Diceratherium* (diceratherine rhino). (17) *Merycoidodon* (oreodont). (18) *Hypohippus* (browsing equid). (19) *Anchitherium* (browsing equid). (20) *Moropus* (chalicothere). (21) *Archeohippus* (dwarf browsing equid). (22) *Merychyus* (oreodont). (23) *Parahippus* (browsing–grazing equid). (24) *Oxydactylus* (aepycameline camelid). (25) *Protolabis* (protolabine camelid).
    (III) (26) *Pseudoceras* (Moschoid). (27) *Yumaceras* (dromomerycid). (28) *Tapirus* (tapir). (29) *Synthetoceras* (protoceratid). (30) *Aphelops* (aceratherine rhino). (31) *Merycodus* (merycodontine antilocaprid). (32) *Hemiauchenia* (cameline camelid). (33) *Calippus* (dwarf tridactyl grazing equid). (34) *Aepycamelus* (aepycameline camelid). (35) *Neohipparion* (tridactyl grazing equid). (36) *Pliohippus* (monodactyl grazing equid). (37) *Astrohippus* (monodactyl grazing equid).

Fig. 6. For legend see facing page.

cellulose fermentation, and are not as limited in the nature of their diet. They can utilize herbage of a higher fibre content than a ruminant of similar body size, but they are unable to extract as much nourishment from a given quantity of vegetation, and they thus have to eat an absolutely greater amount a day. Ruminant artiodactyls are more limited by the nature of the herbage they can eat, but in a habitat where sufficiently high-quality food is available, they will be able to make more efficient use of it than a perissodactyl of similar body size (Bell, 1969; Janis, 1976, 1979).

Whilst perissodactyls can afford to be fairly indiscriminate feeders, it is simply not possible for a ruminant artiodactyl to forage unselectively. Nor can a small to medium-sized pecoran afford the time to search for appropriately high-quality food items in an unreduced stand of fibrous herbage, as the time taken to dis-cover them would militate against the animal's being able to eat enough per day (Jarman & Sinclair, 1979; Janis, 1979, and unpublished data). Such ruminants must confine their distribution to habitats where such items are more easily obtainable, such as sub-tropical woodland, or in more open habitats they must rely on other herbivores to alter the structure of the vegetation first so that the lower levels, containing herbage of higher protein content such as herbaceous plants, are more readily accessible (Bell, 1969).

The correlation of the sexually dimorphic possession of horns with the possession of a forestomach for cellulose fermentation suggests a correlation between these strategies of reproductive behaviour and food utilization. It can be seen that territory holding in ruminant artiodactyls is related to the structure of the habitat. Impala territories are larger in open woodland than in closed woodland. (Jarman & Jarman, 1979). This is presumably because the more dispersed the food resources (in this case represented by the trees), the larger must be the territory that provides an animal with sufficient food. However, territory maintenance is very costly (Jarman & Jarman, 1979), and for any animal there must be an upper limit to the size of territory that it can maintain as a reproductive strategy. This is why antelope in open habitats, in Categories D and E, rarely attempt to maintain exclusive feeding territories.

However, the resources available to an animal in a given area depend not only on the absolute amount and dispersion of suitable food, but also on the amount of energy that the animal can extract from the food. For medium-sized ruminants, of body weight 20–200 kg, living in a mixed sub-tropical woodland habitat, territory holding is apparently an economical proposition, as male antelope in this size range hold year-round territories in this type of habitat (Jarman, 1974). However, a perissodactyl of this body size would require greater amount of food per day. The smaller browsing perissodactyls that live in forests, such as the various species of tapir and the Javan and Sumatran rhino, are apparently solitary and non-territorial (Grzimek, 1972). It may be that perissodactyls never passed through an evolutionary stage where the combination of feeding and social behaviour seen in antelope in Jarman's Category B was possible, as at this body size the area required to provide a perissodactyl with sufficient food would be too

large to make territorial defence an economic reproductive strategy. Thus the digestive and foraging activities of perissodactyls precluded them from adopting the strategy in which a male holds exclusive territory, at the critical combination of body size and habitat type that was suitable for ruminant artiodactyls. Perissodactyls thus had no reason to evolve the type of sexually dimorphic bony horns that were developed by certain ruminant artiodactyls at this time.

Living camelids have a type of digestive system that is very similar to that possessed by pecorans (Langer, 1974). The presence of sexually dimorphic bony horns in the Protoceratidae demonstrates that tylopods have been able to parallel pecorans in this combination of feeding and reproductive behaviour, with the evolution of horns as its morphological correlate. The fact that this option was only adopted by one tylopod family, and that the two major tylopod families (Camelidae and Merycoidodontidae) did not evolve horns, suggests that a suitable habitat, with the appropriate distribution of food resources for the type of territorial behaviour seen in antelope in Category B, was in short supply in North America. In contrast, the fact that horns evolved independently as many as six times in Eurasia suggests that such a habitat represented the predominant type of vegetation on this continent. Floral and faunal evidence suggests a more open habitat in the mid Tertiary of North America than in Eurasia, and this must have been a habitat type less conducive to the evolution of horns. Corroborative evidence for this suggestion comes from the endemic ungulate fauna of South America. Here the available data suggest an even more open habitat during the mid Tertiary than in North America (Webb, 1978), and none of the ungulates evolved bony horns.

VII. EVOLUTION AND BIOLOGY OF NON-DIMORPHIC RUMINANT ARTIODACTYLS

A difference in habitat types between North America and the Old World during the middle Tertiary is suggested by the fact that the majority of the endemic ruminant artiodactyls of North America did not evolve horns. A difference in habitat type is also suggested by the morphology and patterns of molar wear in these animals, which in combination suggest types of foraging behaviour that are not displayed by ungulates in any present-day habitat. The combination of the surmised feeding and social behaviour of both camelids and oreodonts in turn leads to the conclusion that the dispersal of the food resources within the woodland vegetation of the middle Tertiary in North America was greater than that seen in comparable habitats, past and present, in the Old World.

This greater dispersal may have been the result of a greater average distance between the trees in the North American woodland. Although it could be argued that this situation would lead to a greater abundance of food resources, due to an increase in shrub undergrowth, studies on living ungulates indicate that tree products are of vital importance to maintenance of ruminant ungulates during the winter (Skinner & Telfer, 1974; Harlow, Whelan, Crawford & Skeen, 1975). It is also true that antelope hold larger territories in habitats where the tree density is reduced (Jarman & Jarman, 1979), implying an importance of trees in the

resource patterning of the habitat. In addition to the fact that the endemic ungulates of North America were appropriate to a highly open woodland habitat, the mid-Tertiary faunas of Eurasia and Africa contained a much larger number of large browsing ungulates (over 400 kg) than were seen in the contemporaneous North American faunas. These ungulates, such as the chalicotheres and giraffes, appear to have been specialized high-level browsers, supporting the idea that the tree density was greater in the Old World habitats than in North America.

The Eurasian land mass was broken up the incursion of the Tethys sea during the Tertiary (Adams, 1981), and the climate in the centre of the continent would not have been so severe as in North America. This difference in relative size of continental masses during the Tertiary could have resulted in a more seasonal climate in terms of temperature and rainfall in North America than in Eurasia. The effect of this on the vegetation could have resulted in greater spacing between the trees in North America than in Eurasia, and to a condition where the shrub undergrowth was less abundant, with growth being produced in pulses rather than in a steady fashion throughout the growing season. Seasonality is an important factor in determining territorial behaviour in living ungulates (Owen-Smith, 1977), and pronounced seasonality in North America would also have discouraged the evolution of territorial behaviour in the indigenous ungulates.

(1) *Diet and social behaviour of oreodonts*

Oreodonts are interesting and problematical animals in terms of reconstructing their behaviour and mode of life. Not only do they lack living descendants, but with their combination of a suid-like post-cranial skeleton and derived selenodont cervid-like cheek teeth, indicative of a folivorous diet, they do not resemble any living mammal. I submit that they are understandable in terms of an ungulate lineage adapted to a type of habitat that is no longer in existence, and that this is the reason that they do not resemble any living ungulate in present-day habitats.

Oreodonts, though tylopods, were not as closely related to the camelids as were the protoceratids. Webb & Taylor (1980) regard them as the sister group to all the other tylopods, with the Ruminantia, and they term this latter assemblage the Neoselenodonta (Fig. 2). Oreodonts retained a number of primitive features not seen in the Neoselenodonta, including a long tail; short limbs with unfused metapodials and little reduction of the side digits; a short face, with the lack of a post-canine diastema; and the retention of the upper incisors. Like other ruminant artiodactyls, they show some molarization of the fourth premolar, but little tendency to molarize the anterior ones (Fig. 3).

Oreodonts probably lacked the complex ruminal fermentation system common to the members of the Neoselenodonta, along with the lack of the other specializations of this assemblage. Embryological studies show that the mode of derivation of an enlarged forestomach is similar in living tylopods and pecorans, and probably inherited from a common ancestor (Langer, 1974), despite later independent development and modification of the forestomach in the two lineages. It is unlikely that oreodonts had a hind-gut site of fermentation, as ungulates possessing such

a site (perissodactyls and hyracoids) show a rapid tendency to molarization of the premolars in their evolutionary history, this being correlated with the large through-put required on the adoption of this digestive strategy (Janis, 1979, and my unpublished data). It seems probable that oreodonts had some sort of enlarged forestomach, but without the derived system of regurgitation and cud chewing seen in living tylopods and pecorans. This type of forestomach fermentation system has been evolved independently in a number of mammalian lineages, including peccaries (Langer, 1976), hippopotamuses (Langer, 1978) and macropod marsupials (Langer, 1979). The system in oreodonts might have been derived independently, or more likely they shared the feature of enlarged forestomach with the other tylopods.

Oreodont molar wear indicates a folivorous diet, without the evidence of the inclusion of components of an omnivorous nature, such as mushrooms, nuts and bark, that are taken during the winter by temperate-latitude cervids of the present day (Skinner & Telfer, 1974; Harlow et al., 1975). (Oreodonts differ in this regard from the predominantly European anthracotheres, Tertiary suoid artiodactyls that shared with oreodonts the combination of suid-like postcrania and selenodont molars, as in these animals the molar wear patterns suggest a largely omnivorous diet.) But unlike present-day sub-tropical folivorous ruminants, such as the browsing antelope, oreodonts did not have hypsodont cheek teeth, and their blunt snouts militate against the probability of their having selected a low-level leafy diet amongst a varied stand of herbage. From this combination of characters it seems likely that they were fairly wide-ranging animals, taking fresh young growth over a relatively large area, rather than making maximal use of the limited resources within a fixed home range.

Oreodonts showed no evidence of sexual dimorphism, and tend to be found preserved together in large accumulations, suggesting herding behaviour. Taphonomic studies of the North American Oligocene show that oreodonts were unusual compared with the other ungulate species present in that they were not predominantly restricted to a single habitat type, but were equally distributed between near-stream, swampy plain and open non-wooded habitats (Clark et al., 1967). This information, in combination with the dietary evidence, suggests that oreodonts were not territorial, but wandered in mixed-sex feeding bands, looking for fresh flushes of vegetation at young growth stages. Few present-day browsers are herd forming, as the clumping of the food resources militates against groupings of more than two or three animals, and there is also difficulty in maintaining group cohesion in present-day sub-tropical woodland habitats (Jarman, 1974). This suggests that the sub-tropical woodland habitat of the North American Oligocene was more open than that seen today, a condition that would discourage the maintenance of territories by small folivorous ungulates, but would make possible the cohesion by means of visual signalling and contact between members of a browsing herd. The seasonal nature of the habitat would probably make for pulses of new growth, constituting localized abundances of high-quality forage, which would sustain a herd of browsing ungulates for a limited amount of time. Such

a resource would not have been rapidly renewable, but it would be possible for oreodonts to utilize this type of food resource as long as they were prepared to move on in search of another suitable patch once the first source was depleted. [This would be similar to the manner in which present-day peccaries forage in bands on fallen fruit (D. H. Janzen, personal communication).]

The closet parallel to oreodonts amongst living ungulates are probably Asian cervids such as the chital *Axis axis* and the hog deer *Axis porcinus*. These animals are about 45 kg in body weight, and have a life style similar to that which I have postulated for oreodonts. They rove in mixed-sex herds of up to 70 animals, and take a variety of food types, ranging from young green grass in the spring to fruit in the winter, and the males determine access to the females by establishing dominance hierarchies (Schaller, 1967). Of course, these deer are sexually dimorphic, with the males possessing antlers, but it may well be the case that the present-day Asian climate is a relatively recent phenomenon, and that the indigenous cervids have been trapped there as the result of Pleistocene climatic changes, and forced to adapt their social behaviour. The climate in India where these deer are found is highly seasonal, although the total rainfall for the whole year is high and there are a few frosty nights (Schaller, 1967). This type of seasonality may be more similar to that seen in the continental sub-tropical climate of the North American mid Tertiary, rather than to the Tertiary climate of Eurasia, which was insulated by the Tethyan sea for most of the period.

(2) *Diet and social behaviour in North American camelids*

The camelids pose a different problem to the oreodonts for the understanding of their feeding style and social behaviour. The earliest camelids, such as *Pöebrotherium*, had a body weight of approximately 20 kg, but showed no tendency to evolve horns of any type. *Pöebrotherium* had molar wear resembling that of a mixed-feeding bovid, such as the impala, but it did not possess hypsodont cheek teeth, implying that it was able to locate browse of relatively high quality all the year round. However, unlike contemporaneous oreodonts and protoceratids, the early camelids had relatively elongated legs and necks, suggesting an open-country habitat. They also had long tubular snouts, suggesting a highly selective mode of feeding, for in living bovids the length of the snout is correlated with the degree of selection in the diet (Jarman, 1974). In the Oligocene and early Miocene they probably lived on the woodland edges in the open habitat available at the time. Grasses indicative of more open habitats appeared for the first time in the Oligocene, and the floral evidence suggests a certain amount of woodland savanna habitat (McGinitie, 1953; Webb, 1977). This combination of relatively low-crowned teeth and long tubular snouts suggests that they were highly selective and browsed predominantly at ground level, using the long snout to reach down between tall stands of more fibrous vegetation and select the low-level herbaceous plants and succulent leaves.

The African bovids that feed at the lower levels of open-habitat vegetation, such as the gazelles, do not have snouts that are as long and tapering as those seen in

many Tertiary camelids. They can only obtain low-level herbs and grass leaves after the vegetational stand has been altered in composition by other, larger ungulates. Equids play an important role in altering the structure of the vegetation in present-day Africa, because of their ability to make use of the upper levels of fibrous grasses, and the classic example of this type of feeding succession was Bell's (1969) study of the succession of zebra, wildebeest and Thomson's gazelle on a catena in the Serengeti. The shorter snouts of the Old World ruminants suggest that they were primitively predominantly tree browsers.

Long tubular snouts were a constant feature in camelid evolution during the Tertiary, but were absent in the Pleistocene Camelinae which must have been inhabited short grass prairies. Present-day camelines, such as the llama *Llama glama* are predominantly low-level selective browsers (Koford, 1957). Later camelids never became truly hypsodont in the manner of Old World bovids, despite their adherence to open-country habitats. The only lineage that evolved highly hypsodont molars were the small gazelle-like stenomylines, which became extinct in the middle Miocene. The place taken in present-day Africa by alcelaphine and bovine bovids, such as the wildebeest *Connochaetes taurinus* and the buffalo *Syncerus caffer*, was probably taken by equids in the savanna habitats of the late Miocene of North America. During this time there were six sympatric genera of grazing equids, ranging in body weight from 30 to 250 kg (Table 1 and Fig. 6). Antilocaprids may have filled some of the smaller open-country grazing niches in the late Tertiary, such as are occupied in Africa today by the gazelles and the impala.

The two major lineages of Tertiary camelids, the protolabines and the aepycamelines, appear to have had divergent foraging strategies, with protolabines being predominantly ground-level feeders, and aepycamelines predominantly tree browsers. Both lineages had elongated limbs, but the aepycamelines were more giraffe-like in their proportions, with a greater degree of elongation of the metapodials and cervical vertebrae (Honey & Taylor, 1978). Protolabines had more hypsodont cheek teeth than the aepycamelines, and ground-level feeders are more likely to have hypsodont molars than tree browsers, because of the inclusion of grit and dust in the diet. For example, the North American pronghorn has extremely hypsodont molars, and is predominantly a ground-level browser (Smith & Malachek, 1974; Olsen & Hansen, 1977). This suggested difference in feeding levels is also supported by the fact that the snout of the aepycamelines was shorter and broader than that of other camelids, although still longer than that of most living bovids (Fig. 5). This indicates that aepycamelines had to practise less extreme selection in locating suitable dietary items. The proportions of the snout in many of the smaller aepycamelines, such as the early Miocene genus *Oxydactylus*, were very similar to those of the living gerunuk *Litocranius walleri*. This antelope possesses, in addition to a relatively long snout, a long sinuous neck more reminiscent of camelids than other bovids. The post-cranial proportions of the gerunuk differ from those of most other bovids in the greater relative length of the tibia, a feature that may be correlated with its habit of standing on its hind

legs to browse, and thrusting its long snout into the middle of thorny bushes (Scott, 1979). Relatively long tibia were also a feature of Tertiary camelids (M. K. Scott's and my unpublished data). The smaller aepycamelines may well have been gerunuk-like in their feeding behaviour, balancing on their hind legs in feeding, whilst the later larger aepycamelines were more like present-day giraffes in both behaviour and post-cranial proportions.

The proposed greater dispersal of the trees in the woodland savanna of the North American Oligocene would have meant that the majority of ruminants could not afford to rely on tree foliage as a major source of food, and would have been forced to select amongst the vegetational stands at ground level, if they did not adopt the oreodont strategy of roving in mixed feeding bands. Exclusive tree browsing appears to have been a viable option in certain limited habitats only, exploited by the relatively rare protoceratids, which paralleled the Ruminantia in the complete loss of the upper incisors, suggesting similar use of a long mobile tongue to strip leaves from branches (Kingdon, 1979). Taphonomic studies of the North American Oligocene show that camelids were found predominantly in the open plains environment. However, the contemporaneous equids, such as the genus *Mesohippus*, were found near streams in swampy environments (Clark *et al.*, 1967). The molar wear of *Mesohippus* is suggestive of an unselective browser living in mixed woodland, and the molar wear in equids indicative of a significant proportion of grass in the diet was not seen until the middle Miocene genus *Merychippus* (Janis, 1979, and unpublished data). In conformity with this interpretation, the long tubular snouts of the early camelids would have enabled them to select low-level browse in a tall stand of fibrous herbage without the benefit of equids first to reduce the level of the vegetational stand. This type of open habitat, exploited by the early North American camelids, does not seem to have existed during the Oligocene in the Old World.

Given this suggestion that the camelids adopted a fairly open habitat very early in their evolutionary history, they would have passed straight from a forest habitat and a selective-browsing foraging habit, to this type of open environment, where territory maintenance would be uneconomical. Thus they would never have passed through a stage at which they could have adopted the combination of feeding style and social behaviour seen in antelope in Category B, and at no point in their evolution would the appropriate circumstances have arisen for the development of sexually dimorphic combat weapons. Early camelids probably formed loosely associated mixed-sex feeding herds, and may at an early stage have adopted the strategy of harem possession by the males, as seen in present-day camelids (Koford, 1957; Franklin, 1974). Thus males might have fought with other males for the exclusive possession of females, as do living equids (Klingel, 1974; Rubenstein, 1981), but they would not have experienced the type of repeated confrontation with other males that is attendant on the maintenance of territorial boundaries, which probably resulted in the evolution of horns in the closely related protoceratids. On both morphological and taphonomical evidence, protoceratids appear to have been restricted to near-stream environments during this time period (Wilson, 1975).

Two objection could be made to this scenario of camelid evolution. The first is relatively minor, namely that living camelids, such as the South American llamas, do show male territoriality (Koford, 1957). However, their type of territorial behaviour is quite unlike that seen in living eupecorans in that they combine this territoriality with a harem system, where the male defends a band of females of fixed membership. This type of reproductive behaviour is unique to camelids and equids amongst living ungulates. In addition, territorial behaviour in ungulates is highly dependent on local habitat type (Owen-Smith, 1977; Rubenstein, 1981), and as the present-day habitat of the llama is very different from that experienced by Tertiary camelids, there is no reason to suppose that llamas represent 'typical' camelid behaviour. The problem here is the lack of diversity of living camelid species for a behavioural comparison.

The second problem, that also applies to the absence of horns in equids, is that amongst the living eupecoran species the frequency of male–male antagonistic encounters is at least as great, if not more so, amongst males living in herds, which determine access to females via a rank-dominance hierarchy (Owen-Smith, 1977). If the evolution of horns really is related to the frequency of male encounters, then why are they not found in animals that supposedly passed straight from a solitary existence to a mixed-sex group in the course of their evolution, such as camelids, equids and oreodonts? Could it just be that the original fighting style amongst pecorans were different from those in other ungulates, encouraging the evolution of a particular type of weapon in this lineage only? But this interpretation begs the question of why the protoceratids, alone amongst the tylopods, paralleled the eupecorans so closely. The presence of horns in male protoceratids suggests that the processes involved in the evolution of horns were due to some interaction with a particular type of habitat, rather than the result of phylogenetic behaviour patterns.

The type of male–male interaction seen in eupecorans living in mixed-sex associations may be a legacy of the type of male–male interactions associated with territorial boundary patrol. This type of association contrasts with that seen in camels and equids, which have female groups of fixed membership associated with a single adult male (harems), with juvenile and secondary males forming bachelor herds. A similar social system also exists in the rock hyrax *Procavia*, which is also hornless (Kingdon, 1971). I do not know of any reliable evidence that male–male encounters are less in harem-holding ungulates than in those forming mixed-sex associations, but one would imagine this to be the case, as the harems tend to be spatially separated and the males are not in constant confrontation with each other. Even in bachelor herds, where dominance ranking amongst the males exist, they are not subjected to continual challenges over females as in mixed-sex herds. Evidence presented by Owen Smith (1977) shows that wildebeest encounter at least three times as many aggressive interactions with other males per day as do llamas. But a problem with studies of this type is that encounters between herd-forming antelope are concentrated in the breeding season, and it is difficult to assess the relative costs of fighting, and hence the evolutionary selection pressure of evolving

specialized defensive and offensive weapons, in this situation relative to the costs of maintaining a year-round territory.

The fact that male eupecorans do tolerate such a system of continual encounters in mixed-sex herds may be because they had already evolved horns when they adopted the social system of herd formation in open habitats, and thus continual fighting was not so costly in terms of injury. In contrast, those animals that did not possess horns when they first moved into open habitats, such as equids, camelids and hyraces, may have had more selective pressure to develop a behavioural alternative to continual male interaction, such as a harem system. The fact that a very similar social system is found in ungulates as different as equids and camels suggests a similar history of interaction between behaviour and habitat in both lineages.

Certainly camelids and equids cannot be directly compared with living eupecorans. Owen-Smith (1977) estimates the 'potential mating enhancement factor' of reproductive strategies for territorial and non-territorial ungulates, and concludes that it is greater for the males in those species that maintain a system involving rank-dominance hierarchy than for those that are territorial. However, the values he obtains for the llama and the zebra, which maintain rank–dominance hierarchies, are similar to those for the territorial eupecorans. This emphasizes the need for a historical evolutionary approach when trying to understand the diversity of behavioural strategies amongst living animals.

VIII. EVOLUTION AND BIOLOGY OF PERISSODACTYLS

(1) *Evolution of horns in the Rhinocerotidae*

Greater difficulties arise in trying to understand the evolution of social and foraging behaviour of perissodactyls than with ruminant artiodactyls, as so few species of perissodactyls are extant, and most of these, especially the forest-dwelling ones, are inadequately studied. I do not propose to undertake a full-scale study into the reasons for the evolution of horns in the Rhinocerotidae, but it would seem inappropriate to fail to mention rhinos in a paper about horn evolution in ungulates!

An important point to make concerning the Rhinoceratoidea is that, despite the fact that all living rhino species possess keratin horns, horns have not been the predominant feature of rhino evolution (Fig. 1). The Rhinoceratoidea comprises three families, only one of which, the Rhinocerotidae, survived past the early Miocene. But the initial rhino radiation was comprised of two other families, the large hippo-like Amynodontidae and the small equid-like Hyracondontidae, both of which were hornless. Amongst the Rhinocerotidae, two important sub-families in the middle and late Tertiary, the Aceratherini and the Brachypotherini, were also hornless. In all Old World rhinos that developed horns, horns were present in the female as well as in the male, although they may well have been larger in the males, and thus it seems unlikely that they were initially used for sexual display and combat between males. Although the living African rhinos use their horns in

display and fighting, the Asian rhinos, which are more primitive in their morphology than the African genera, predominantly use their tusks for this purpose (Laurie, 1982). Horns in rhinos may have originally been evolved for some non-sexual purpose, such as rooting in mud to obtain food, and only later became elaborated for intraspecific combat (A. Laurie, personal communication). A similar argument might be extended to the early Tertiary perissodactyl family Brontotheriidae. Brontotheres were large rhino-like animals, but with a greater proportion of fruit in their diet than rhinos (Janis, 1979, and my unpublished data), in which the larger and later members developed bony nasal horns in both sexes.

The only exception to this lack of dimorphism in horn possession amongst perissodactyls was the sub-family Diceratherini. These were small rhinos, with a body weight of about 250 kg, and the males alone possessed a pair of forked horns on the nose. They were found in both North America and Eurasia in the late Oligocene, but were most abundant in the early Miocene of North America, at the time of the peak in oreodont diversity, along with the large tree-browsing chalicotheres. It may be that some feature of the structure of the woodland habitat at this time allowed the males to hold exclusive territories, and to adopt a combination of feeding and reproductive strategies similar to antelope in Jarman's (1974) Category B. It should be noted, however, that they were considerably larger than these antelope and the contemporaneous protoceratids, and the situation is unlikely to have been one of simple equivalence. The Diceratherini were replaced later in the Miocene by larger, hornless rhinos of the families Aceratherini and Brachypotherini.

(2) *Evolution of equoids in the Old World*

Equoids were numerous in the early Eocene of both North America and Europe, but were rare in Asia (Savage, Russell & Louis, 1965). North American equoids (family Equidae) were greatly reduced in numbers by the late Eocene in North America, but in the early Oligocene they were once again a dominant component of the ungulate biomass on this continent. However, the European equoids (family Palaeotheriidae) became extinct at the end of the early Oligocene, whereas other perissodactyls such as tapirs and chalicotheres remained a constant feature of the Eurasian faunas (Savage, Russell & Louis, 1966).

Why did equoids disappear from Europe at the same time that they were achieving success in North America? The answer may be as follows: it appears that during the Eocene, equoids (at least in North America) were already specialized in terms of dietary habits amongst the perissodactyls, taking herbage of the highest fibre content amongst the dietary ranges of the contemporaneous ungulates (Janis, 1979, and unpublished data). In the seasonal climate of the North American Oligocene they would have been at an advantage over other ungulates during the winter, when fibrous vegetation would have been the only readily available source of food. North America was a large stable continent during the entire Tertiary, and thus would have been particularly vulnerable to the effects of seasonality following the global climatic changes at the end of the Eocene,

particularly in the interior regions. However, during the Oligocene the European continent was marked by a series of marine incursions and regressions, and of a periodic splitting up of the continental mass into islands of varying sizes (Heissig, 1979). This insularity would have tended to shield the European fauna and flora from the more extreme effects of the climatic changes of the late Eocene. Indeed, the fossil record shows that the post-Eocene floral changes were abrupt in North America (Wolfe, 1978), but more gradual in Europe (Daly, 1972; Collinson et al., 1981). Such conditions would have resulted in an overall higher quality of vegetation available year-round, and may have rendered the European equoids more vulnerable to competition from ruminant artiodactyls. It was not until the more stable continental conditions of the post-Oligocene period that the European continent again proved to be a suitable habitat for equoids. Three radiations of immigrant equids from North America were seen in the Old World. The browsing genus *Anchitherium* arrived in the early Miocene, the tridactyl grazing genus *Hipparion* first appeared in the late Miocene, and the monodactyl grazing genus *Equus* first appeared in the Pleistocene.

An interesting corollary to the differences proposed here between early camelid and pecoran feeding types, with primitive pecorans being exclusive tree browsers whereas camelids were always more open-habitat animals, is that bovids did not diversify into a variety of open-habitat types until grazing equids appeared in the Old World. The first appearance of the open-country grazing bovid tribes Hippotragini and Alcelaphini, about 10 million years ago, was coincident with the appearance of *Hipparion* in the Old World (Pickford, 1981). In Eurasia, a great change in faunal composition was seen at the first appearance, or slightly after the first appearance, of this equid. A shift from forest habitat to open habitat was indicated at this time by a relative and absolute decrease in the number of suoids, tragulids and giraffids in the faunas (Moonen et al., 1978). In the faunas outside India, *Hipparion* was very abundant at its first appearance, and its presence was correlated with a decrease in the relative proportion of bovids. In the Siwalik faunas of India, the first appearance of *Hipparion* was not marked by a great faunal change, and only a few equid individuals were present. However, shortly after this there was a great increase in the numbers of equid individuals, and a consequent change in faunal composition similar to that seen elsewhere in Eurasia (Moonen, Sondaar & Hussain, 1978). The bovids in the Siwalik faunas showed little change in morphology at the first appearance of *Hipparion*, but once the equids became numerous the bovids present showed an increase in body size, developed more hypsodont cheek teeth and showed a greater degree of molarization of the premolars (personal observation). This suggests a shift amongst the bovids to a more fibrous diet and the utilization of the vegetation available in a more open type of habitat in the wake of the radiation of the invading equids.

Hipparion was persistently tridactyl, but in its molar wear patterns and degree of hypsodonty it closely resembled the living genus *Equus*, although there was considerable variation within the various species of this genus. However, it seems likely that *Hipparion* resembled living equids in having a high-fibre diet and in

being relatively unselective in its foraging behaviour. Bovids all have relatively short snouts, and have difficulty in selecting low-level vegetation of high quality from amongst tall stands of vegetation (Jarman & Sinclair, 1979). It may well be the case that the Eupecora were originally predominantly tree-browsing animals, and that bovids have always been dependent on grazing equids to take the topmost fibrous layer of the grass stand, thus giving them easier access to the more nutritive items at lower levels (Bell, 1969). Thus, instead of the oft-quoted idea that the rise of the open-habitat bovids during the Miocene caused the demise of the less efficient equids (e.g. Kingdon, 1979), it seems more likely that the invasion of the North American grazing equids into the Old World actually permitted the radiation of the grazing bovids, and paved the way for the evolution of the present-day African savanna fauna.

(3) *Territorial behaviour in perissodactyls*

Despite the claim in this paper that, with the possible exception of the Diceratheriinae, perissodactyls never passed through a stage in their evolution when it was possible for them to combine territorial behaviour with the type of feeding behaviour seen in antelope in Jarman's (1974) Category B, it should be mentioned that some living perissodactyls are in fact territorial. The males of some species of equids and rhinos do hold exclusive year-round or seasonal feeding and breeding territories. However, their combination of territorial behaviour with diet and habitat type is in diametric opposition to that seen in ruminant artiodactyls. In ruminants, territory holding is most commonly seen in small- to medium-sized browsing animals, living in wooded habitats with high productivity and with a clumped dispersion of high-quality food (Jarman, 1974). But in perissodactyls, territory holding is most common in large grazing animals, living in open habitats of low productivity, with a continuous dispersion of low-quality food.

Territorial behaviour is not seen in tapirs (Grzimek, 1972), nor in small forest-dwelling rhinos such as the Javan rhino *Rhinoceros sondaicus* and the Sumatran rhino *Dicerorhinus sumatrensis* (Laurie, 1982). The larger Indian rhino *Rhinoceros unicornis*, which lives in a mixture of grassland and forest, and eats a mixture of grass and browse, and the African black rhinoceros *Diceros bicornis*, which browses in a wide range of habitats, both show a certain amount of territorial behaviour. They establish dominance hierarchies amongst neighbouring males, and occupy defined, although overlapping, home ranges, but they do not defend specific fixed areas of territory (Mukinya, 1973; Laurie, 1982), although other workers report a greater degree of territorial behaviour in the black rhino (e.g. Hitchins, 1971). This is in contrast to the African white rhino *Ceratotherium simum*, which is the largest living rhino species and the sole grazer. It lives in the most open habitats amongst living rhinos, and the males defend feeding and breeding territories from which other males are excluded (Owen-Smith, 1974). Similarly, amongst equids, most species are harem-forming and non-territorial, but male territorial behaviour is seen in those species living in the most arid environments, in Grevy's zebra *Equus grevyi* and in the African wild ass *Equus asinus* (Klingel,

1974, 1977). Amongst feral horses *Equus caballus*, social behaviour is flexible, these animals being harem-forming under conditions of plentiful food, and territorial in more sparse conditions (Rubenstein, 1981).

This difference between perissodactyls and artiodactyls must be related to the difference in digestive and foraging strategies. Whereas perissodactyls are at an advantage in conditions where the quality of the food is the limiting factor, the ruminant foraging strategy is best suited to those habitats where the quantity of the food is in limited supply. In the woodland habitat, with a clumped distribution of food items, the quality of the food will be relatively high, but the quantity within a given area will be limited. In such a habitat the greater digestive efficiency of the ruminant allows it to forage within an area small enough to patrol as a territory, whereas the high intake necessitated by the perissodactyl prohibits this animal from being territorial. But in an open habitat with a continuous dispersal of food of high fibre content, such as grass, the reverse is true, as in this case the quality rather than the quantity of the food will be the limiting factor. A large-bodied grazing perissodactyl could make maximal use of the poor-quality but readily available food in such a habitat, but a ruminant would have to search further afield each day to find the requisite amount of food of sufficiently high quality for maintenance. Under such conditions a perissodactyl would require a smaller home range than a ruminant artiodactyl, and at this combination of habitat structure and body size it is apparently advantageous for male perissodactyls to maintain an exclusive feeding and reproductive territory.

In support of this idea that it is easier for a perissodactyl to be territorial in poor-quality habitats, it can be seen amongst living rhinos that the browsing species have larger home ranges than the grazing ones (Laurie, 1982). It is not possible to compare rhinos directly with ruminant artiodactyls in this respect, as grazing ruminants tend to be herd-forming and migratory, and do not establish discrete permanent home ranges (Leuthold, 1977), but data presented by Owen-Smith (1977) suggest that forest-dwelling antelope may have smaller home ranges than more open-country ones, which is the reverse of the situation in the rhinoceroses.

The question might then be posed why have such perissodactyls not evolved sexually dimorphic combat weapons, as it was this type of combination of habitat structure and body size that was postulated as being a feature of the evolution of ruminant artiodactyls. It may be that such a major change in behaviour is only possible in a group at a relatively early stage of its evolution (Boucot, personal communication), and that these animals have too much 'phylogenetic inertia' tied up in their existing methods of display and fighting behaviour to make such a radical change at this point in their evolution. Or it may be sure that such habitats have only been in existence since the Pleistocene, and that the change in territorial behaviour and reproductive strategy has not been in existence for long enough to result in a change in the correlated morphology.

IX. CONCLUSIONS

The fossil record shows that bony horns evolved in certain lineages of ruminant artiodactyls, initially in the male of the species only, at a critical body size of approximately 18 kg, at a point in time when the dominant local habitat was changing from a closed, non-seasonal type of sub-tropical woodland to a more open, seasonal one. The fact that horns evolved independently amongst both eupecoran and tylopodan artiodactyls under these conditions suggests that the evolutionary reasons for developing horns were a consequence of the interaction of body size, diet and habitat type, rather than a peculiarity of ruminant artiodactyl behaviour, as horns were evolved in all six lineages of eupecorans but in only a single tylopod lineage.

The body size at which horns evolved corresponds to the point at which present-day sub-tropical ruminant artiodactyls shift from a selective browsing diet and a pair-bonded monogamous mating system, to a folivorous diet, with a polygamous mating system where the male defends an exclusive feeding and breeding territory. It is therefore proposed that the evolution of horns in ruminant artiodactyls was correlated with the adoption of the reproductive strategy of male territorial defence, and is associated with the increased number of male–male antagonistic interactions, consequent on the adoption of such a strategy. Territorial behaviour is only possible for a ruminant ungulate in a habitat where the distribution of the food resources is sufficiently clumped to allow for an effective home range to be patrolled as an exclusive territory. The fact that the evolution of horns occurred in multiple Old World eupecoran lineages, but only in a single North American tylopod lineage, suggests that the resources were more dispersed in North America during the Tertiary than in Eurasia. This suggestion is supported by floral and faunal evidence, and by an analysis of the effects that the different geographies of the continents would have on their respective climates. It is further supported by the surmised combination of feeding and social behaviours seen in the endemic hornless North American tylopods, the camelids and the oreodonts.

Horses and other non-ruminant ungulates (with the possible exception of a single rhino family) never evolved horns of this type, that were essentially sexually dimorphic in nature. This was because their foraging and digestive strategies necessitated a greater daily intake than seen in ruminant artiodactyls. Hence their feeding home range in the available woodland habitats in the middle Tertiary, when they reached a similar critical point in their evolution, would have been too large for territorial defence to have been a worthwhile behavioural strategy in energetic terms.

I have presented a model that offers an explanation for the difference in habitats between the two northern hemisphere continental masses in terms of differences in the spacing of the trees in the woodland and savanna-mosaic habitats, with a greater average distance between the trees in North America (Fig. 6). It is proposed that the more stable mass of the North American continent during the

Tertiary resulted in a more continental type of climate, with the effects of the increasing post-Eocene seasonality in these latitudes being felt more strongly than in Eurasia, resulting in this difference in the vegetation. However, the proposed differences in resource distribution need not have entailed an actual physical difference in the spacing of the trees. Other factors, such as a difference in the number of low-level branches, in the annual productivity of the vegetation, or in the admixture of conifers and angiosperm trees might also have resulted in a difference in the distribution of the food resources as perceived by the ungulates. The argument might even be presented in reverse, with the same conclusions. That is, that a greater amount of spacing between the trees would result in a greater availability of food resources in the form of undergrowth, implying that there was a greater density of trees in North America than in the Old World. However, the diversity of feeding behaviours in the faunas of both continents supports my original hypothesis of a greater tree density in the Old World during the middle Tertiary, although it is clear that, at our present state of knowledge of the fossil record, information about the structure of the habitat cannot be obtained from paleobotanical evidence, and must be deduced from the spectrum of feeding types and morphologies of the herbivore community (see also Andrews, et al., 1979; Van Couvering, 1980; Nesbit Evans et al., 1981).

In reconstructing evolutionary scenarios it is a grave mistake to extrapolate directly from present-day spatial distributions of animals, and to assume that the present-day diversity of habitat types, and the mammalian communities that they support, represent the spectrum of available possibilities throughout time. Present-day communities may serve as useful guides, to understanding evolutionary radiations, but it is a mistake to assume that a fossil community can be made to fit a model of an existing one. The North American faunas of the middle Tertiary have frequently been compared with those of the present-day African savannas, but this paper shows that the North American savannas supported ungulates with a combination of feeding and social behaviours not seen in the present-day African savannas, nor anywhere else in the world, to my knowledge. The evolution of these ungulates cannot be made to fit an evolutionary model based rigorously on African bovids, and on the types of vegetation seen in Africa today.

Other paleontologists, working on the evolution of both plant and animal communities, have also pointed out the dangers inherent in trying to make a fossil community conform to a model of one existing today (e.g. Daly, 1972; Van Couvering, 1980). Equally, when considering the evolutionary history of animals abundant today (such as the Bovidae), fossil animals or relics of extinct communities (such as equids and camels in Africa today) must be given due consideration in any explanation of how animals are adapted to their current habitat types. They cannot be dismissed as bizarre exotic types, nor as some sort of 'exception that proves the rule'. Primary reference to the fossil record is essential for the understanding of the evolution of animal communities. It is not enough, as suggested by Geist (1974b), to make use only of reference text-books in the reconstruction of evolutionary scenarios and in speculations on paleobiology.

Such books of necessity present information only on phylogenies and morphology, and do not provide sufficiently detailed information on distribution, species richness and relative abundance of the animals within the communities. Equally, it is not enough for evolutionary biologists to regard the fossil record as 'yet one more approach' to evolutionary studies of this nature (e.g. Ruse, 1973). The fossil record provides the historical facts on which such studies should be based.

I have not discussed the endemic 'ungulate' faunas of South America or Australia in this paper, but it is clear that they can also be understood only in terms of the type of approach presented here, and not by direct analogy to present-day faunas. Neither have I discussed the evolution of carnivores, but inasmuch as carnivore diversity is dependent on herbivore diversity, the radiation of carnivorous mammals on different continents must also be considered in relation to the structure of the habitat.

X. SUMMARY

(1) The savanna ungulate faunas of the North American Miocene were broadly similar to those of present-day East Africa in terms of overall morphological and taxonomic diversity. However, the predominant ungulates of the African faunas are bovids, which possess bony horns that are primitively sexually dimorphic in their occurrence. The predominant ungulates of the North American Tertiary were equids, camelids and oreodonts, which all lacked horns. A limited number of horned ruminants were present, but these were largely Miocene immigrants from Eurasia. Horns were also absent from the large-bodied herbivores in the endemic faunas of South America and Australia.

(2) The absence of horns in equids and tylopod artiodactyls is unlikely to be due to genetic insufficiency. Bony horns were present in brontotheres, which were closely related to equids, and in protoceratids, which were closely related to camelids. Nasal horns were present in one oreodont genus.

(3) Studies on living ungulates show that a strong correlation exists between habitat type, feeding behaviour, social behaviour and morphology. It is possible to use the morphological remains of extinct ungulates to reconstruct the types of feeding and social behaviour, and to use the distribution of morphologies and body sizes in a community of mammals, in conjunction with geological and paleobotanical evidence, to reconstruct the type of habitat.

(4) The importance of the post-Eocene climatic changes to the history of mammalian evolution is stressed. Continents at higher latitudes have become increasingly seasonal in terms of temperature and rainfall since the equable global conditions of the early Tertiary. Savanna mosaic were the predominant biome in North America by the early Miocene, and in Eurasia by the middle Miocene. Living temperate-latitude species of ungulates may not be a reliable guide for the assessment of the interrelationship between behaviour and morphology in an evolutionary perspective, as their behaviour may have been recently adapted to a habitat type that has only been in existence since the Pleistocene.

(5) The primitive condition in eupecorans and protoceratids is the absence of horns, with the presence of large sabre-like canines in the males. The first horned

members of these divisions had horns in the males only. Small present-day antelope, where horns may also be present in the females of the species, are probably secondarily small.

(6) Horns were acquired independently in ruminant artiodactyls at least three times, and a maximum number of seven times is not unlikely. In each case, horns first appeared at a critical body weight of about 18 kg, and in correlation with a change in habitat from closed to open woodland.

(7) Horns in living ruminants are associated with territorial defence by males holding exclusive feeding and reproductive territories in woodland habitats. Such behaviour in present-day antelope is correlated with a body size of greater than 15 kg and a folivorous diet. It is argued that horns evolved in ruminant artiodactyls on the adoption of this type of territorial behaviour once the critical combination of body size, diet and habitat type had been attained in their evolution from small, essentially frugivorous, forest-dwelling animals.

(8) Perissodactyls never evolved sexually dimorphic bony horns of the type seen in ruminant artiodactyls. This is because their foraging and digestive strategies necessitate a larger daily intake of food. In a woodland habitat they were never able to adopt a feeding area small enough to make exclusive territory maintenance an economical proposition. Territory holding in male perissodactyls is seen, but under the opposite conditions of habitat to territorial behaviour in ruminant artiodactyls.

(9) Study of the morphology and paleoecology of oreodonts suggests that they were woodland herd-forming browsers with exclusively folivorous diets. They probably had some forestomach fermentation, but did not chew the cud. Similar studies of Tertiary camelids suggest that they were predominantly selective browsers eating herbage at a low level in open country and formed mixed-sex feeding groups. These combinations of feeding and social behaviour suggest a more open structure of the mid-Tertiary habitat in North America than in Eurasia.

(10) Studies of the behaviour and morphology of living members of the Ruminantia, and of the morphology and paleoecology of their fossil ancestors, suggest that they were primitively tree browsers living in closed woodland habitats. Such habitats were abundant in the Old World, but in limited supply in North America during the Oligocene, where the protoceratids were the only ungulates to parallel the eupecoran type of feeding and social behaviour. South America appears to have had an even more open habitat in the Oligocene than North America, and no parallel to the eupecorans was seen amongst the indigenous ungulates. The radiation of the Bovidae into open grassy habitats in the Pliocene may have been dependent on the immigration of grazing equids into the Old World.

(11) I conclude that there was a difference in habitat structure between North America and the Old World during the Tertiary. The food resources in North America were more widely dispersed, and this may have been the result of the trees being more widely spaced. A possible causal mechanism for this was the stable land mass of the North American continent during the Tertiary, resulting in a more continental climate, with a more severe effect of the post-Eocene seasonality on

the vegetation. The faunal record of the two continents also implied a greater density of trees in the Old World.

(12) Thus most endemic North American ruminants did not evolve horns because, at the critical combination of body size and diet seen in the evolution of horns in the Old World ruminants, the dispersal of the food resources within the vegetation was too great for an effective home range to be maintained as an exclusive territory.

(13) Attention is drawn to the dangers of constructing evolutionary stories about living animals without primary reference to the fossil record to see if the hypotheses are upheld, and of assuming that fossil animal communities can be made to fit models of existing communities.

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XIII. ADDENDUM

(1) Since writing this paper, my attention has been drawn to the fact that, contrary to my assertion that the North American brachypotherine rhinos were all hornless, small horns were probably present in late Miocene members of the genus *Teleoceras*. This genus also exhibited considerable sexual dimorphism in canine tooth size throughout the Miocene.

(2) A paper on the social behaviour in white-tailed deer (Hirth, 1977), supports my contention that social behaviour and group size in ungulates is highly dependent on habitat type. Data presented also suggests a greater amount of male–male aggressive interaction in woodland habitats than in more open areas.

Recent field work has shown that the present-day Himalayan musk deer is essentially solitary in its behaviour, and primarily a selective grazer in its dietary habits (M. Green, personal communication). Most fossil moschoids (including the North American blastomerycids) had relatively long limbs and mesodont teeth, like the living genus *Moschus*, and may have occupied a similar open habitat niche. Living moschids differ from tragulids in the possession of an advanced pecoran type of rumen fermentation, and in the fossil record moschoids are generally larger (15–40 kg) than most traguloids. It may be that horns never evolved in moschoids precisely because their initial diversification was as open-habitat grazers, and they were thus similar to the camelids in never passing through an evolutionary stage where the development of male territoriality was an advantageous reproductive strategy.

(3) Gingerich's (1981) recent assertion that early equids such as *Hyracotherium* were open-habitat dwelling, polygamous animals apparently contradicts my view of early equids as forest-dwelling browsers. His argument is based on the measure of sexual dimorphism in the early Eocene species *H. tapirinum*, in terms of both canine dimorphism and body size (although the latter estimate is based on only three complete specimens, and definitive predictions of body weight dimorphism from this data may be premature). He points out that this degree of dimorphism in primates and larger ungulates studied is correlated with polygamous behaviour in the males following female grouping in open habitats, and suggests that early equids were open-habitat forms with a polygamous mating system.

Whilst I would not dispute Gingerich's interpretation of North American Eocene habitats containing more in the way of open habitat and parkland than was available in the Paleocene, the tooth morphology and molar wear of Eocene equids clearly suggest a frugivorous/folivorous diet more compatible with a selective browsing niche in a forest undergrowth habitat. (The more open habitat of Eocene woodland would have contributed to the greater availability of low level browse in the woodland areas, whereas the predominantly closed canopy woodland of the Paleocene did not support a diversity of terrestrial folivores.) A better living model for *Hyracotherium* are the chevrotains (genera *Tragulus* and *Hyemoschus*) which have a very similar type of molar wear. These animals also show a considerable degree of canine dimorphism, yet they are solitary in their social behaviour, maintaining non-exclusive home ranges (Ralls, Barasch & Minkowski, 1975). A similar combination of morphology and social behaviour exists in other small ruminants, such as muntjac and musk deer, and Ralls and co-workers (1975) relate this type of social system to the type of habitat and the dispersion of food items. As the diet of *Hyracotherium* was apparently so similar to chevrotains (see Janis, 1979), it seems likely that the similar degree of canine dimorphism was also a reflection of a similar type of social organization and habitat use.

Gingerich interprets the increased brain size and cursorial adaptations in *Hyracotherium* as indicative of the use of a more open type of habitat than seen in the phenacodontid condylarth *Ectocion*, which was superficially similar to *Hyracotherium* but apparently replaced by this genus in the Eocene. However, brain size and cursorial adaptations continue to increase throughout the Tertiary in the equid lineages, and yet later equids (such as the Oligocene *Mesohippus*) were not notably dimorphic. Neither are living equid species, which have the same type of mating system and habitat preference as postulated by Gingerich for *Hyracotherium*. It seems unlikely to me that, if equids had indeed adopted this type of behavioural strategy at the start of their evolution, they would later have lost the very same morphological modifications that were supposedly correlated with it. It seems more probable that the pronounced sexual dimorphism of *Hyracotherium* was the reflection of a traguloid type of diet, habitat and social system, and that the later loss of dimorphism in the Oligocene, which was also correlated with a shift to an apparently more fibrous diet (Janis, 1979) was a reflection of the isomorphy characteristic of living ungulates that associate in permanent mixed-sex herds.

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