Fossil Evidence of Interactions between Plants and Plant-Eating Mammals [and Discussion]

Margaret E. Collinson, Jerry J. Hooker, P. W. Skelton, P. D. Moore, J. Ollerton and R. McN. Alexander

Phil. Trans. R. Soc. Lond. B 1991 **333**, 197-208
doi: 10.1098/rstb.1991.0068

Fossil evidence of interactions between plants and plant-eating mammals

MARGARET E. COLLINSON[1] AND JERRY J. HOOKER[2]

[1] *Division of Biosphere Sciences, King's College London, Campden Hill Road, London W8 7AH, U.K.*
[2] *Palaeontology Department, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*

SUMMARY

We document changes in mammalian dietary and foraging locomotor adaptation, and appearances and developments of angiosperm fruiting strategies and vegetation types since the late Cretaceous in the Euramerican region, and to some extent in low latitude Africa. These changes suggest: (i) an expansion in the exploitation of dry fruits and seeds by mammals on the ground as well as in the trees after the terminal Cretaceous dinosaur extinction; (ii) a relation between large nuts and rodents, which appear in the late Palaeocene and radiate in the late Eocene; (iii) a relation between primates and fleshy fruits established in the early–Middle Eocene when tropical forests reached their maximum latitudinal extent; (iv) a hiatus of several million years in the vertebrate exploitation of leaves after dinosaur extinction and before the first few mammalian herbivores in the Middle Palaeocene, followed by an expansion in the late Eocene when climates cooled and more open vegetation became established.

1. INTRODUCTION

A glance at a matrix plotting dietary against foraging locomotor adaptive types shows that nearly all possible combinations are fulfilled by modern mammals (figure 1). Understandable exceptions are scansorial, arboreal and aerial grazers and aquatic frugivores. In the late Cretaceous, however, the pattern was quite different with very few boxes being occupied. Adding the then dominant group of land-based vertebrates, the dinosaurs, fills more but still leaves many gaps. By examining the changes that have taken place in locomotor and dietary adaptations in mammals we can begin to understand the ways in which they interacted with angiosperm-dominated vegetation during the past 70 Ma.

2. SOURCES OF EVIDENCE

(*a*) *Plant fossils*

Plants are represented in the fossil record by a variety of parts ranging from minute dispersed pollen grains to large *in situ* tree stumps and from isolated fruits, seeds and leaves, to infructescences and foliage organically connected to one another. These provide direct evidence of the nature of plant material available to mammals.

In situ tree stumps with associated litter provide direct evidence of ancient forest vegetation. Even when only isolated organs are available, functional morphology combined with taphonomic and sedimentological evidence permit reconstruction of ancient vegetation. Ancient vegetation and climate can be reconstructed using evidence from leaf and wood physiognomy (Friis *et al.* 1987; Wolfe 1990; Wolfe & Upchurch 1987; Collinson 1990).

(*b*) *Mammal fossils*

Land-based mammals (marine ones are excluded here) most frequently occur as isolated teeth; jaws and postcranial remains are also common but complete skeletons are rare. Those which occur at the German Middle Eocene site of Messel are often enhanced by fur impressions and gut contents (Schaal & Ziegler 1988). Understanding of mammal–plant interaction requires knowledge of mammalian diet and locomotion. Dominant locomotor adaptation is almost always associated with foraging.

(i) *Locomotion*

Locomotion can be deduced from postcranial remains either from isolated limb bones or, if available, from complete skeletons. For instance, to show arboreality requires evidence of prehensility of hand, foot or tail (Jenkins & Krause 1983). Trunk-climbing ability (scansoriality) is more difficult to ascertain, but is typified by strong laterally compressed claws (Koenigswald in Schaal & Ziegler (1988)) and some mobility of the ankle (Szalay 1984). In contrast, a mammal restricted to the ground ('large' ground mammal (LGM) of Harrison (1962) and Andrews *et al.* (1979), but in effect not always large) is recognized especially by laterally restricted mobility of limb articulations, also often presence of hooves and reduction of digits. The class of 'small' ground mammal (SGM) (more

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

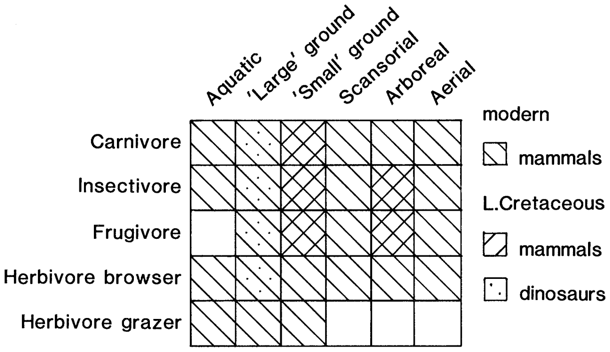


Figure 1. Matrix of dietary and locomotor categories for modern (world) and North American late Cretaceous (see figure 2) land-based mammalian and dinosaur faunas.

appropriately termed semiterrestrial) is probably the most difficult to recognize, as it is intermediate between LGM and scansorial, with the ability to move from the ground into bushes but may also be fossorial (burrowing). P. Andrews (personal communication, 1991) is currently revising Harrison's locomotor classes.

Postcranial information from the nearest relative (nearly always fossil) is used to infer locomotor class for any species with no known postcranials. Usually the relation is no more distant than intrafamilial. Late Cretaceous and Palaeocene taxa are relatively poorly known postcranially. Reliability for locomotor adaptations improves in younger strata.

(ii) *Diet*

Mammalian diet can be inferred from tooth morphology by using modern dental analogues with known diet (see Collinson & Hooker in Friis *et al.* (1987)). Relevant features of teeth are gross morphology, gross wear pattern and microwear, which are apparently interdependent. Mastication occurs in two principal modes: translatory and puncture–crush. Each produces a characteristic pattern of wear (comprehensively reviewed by Janis in Boucot (1990) pp. 241–259; Teaford 1988).

We are here concerned with fossil plant-eating mammals and thus with deducing frugivory (construed here as a diet of fruits and seeds) and herbivory (diet of the green parts of plants, including bark). Herbivory is divided into grazing (feeding on grassland grasses) and browsing (all other types of plant). Typically a herbivorous type of cheek tooth (see, for example, figure 4b) will have little emphasis on puncture–crush but strong cresting with emphasis on translatory movement. Buccal phase shearing facets form as the teeth move towards occlusion, and lingual phase grinding facets form as they move out of occlusion (resulting in distinct wear facets with mainly unidirectional microwear striations). A frugivorous cheek tooth (see, for example, figure 4c) will have low, rounded cusps with little cresting, and emphasis on puncture–crush over translatory movement. This enhances wear at the cusp tips which are dominated by multidirectional microwear striations (Rensberger 1986; Teaford 1988). Intermediate morphologies suggest intermediate (mixed) diets. Details of microwear may be influenced by variations in hardness of diet, occlusal pressure and size of animal (Janis & Fortelius 1988; Rensberger 1978).

3. MATERIAL

Fossil information is spatially patchy. Our data are largely restricted to the mid- to high latitudes of the Northern Hemisphere. Only those elements of ancient life which were living close enough to depositional settings to be preserved are ever available for study. Assemblages from southern England nevertheless have mammals and plants preserved in the same or adjacent levels (Collinson & Hooker in Friis *et al.* (1987)).

4. EARLY CRETACEOUS AND PALAEOCENE

(*a*) *Mammals*

The earliest mammals were late Triassic morganucodontids, kuehneotheriids and haramiyids (Lillegraven *et al.* 1979). These were small, mostly insectivorous types though the last probably included fruit in their diet. The multituberculates, the diet of which had a significant plant (fruit) component, first appeared in the late Jurassic and became abundant and diverse in the late Cretaceous.

Postcranial evidence is unknown for most Mesozoic mammals but nearly all late Cretaceous multituberculates with known postcranial remains were arboreal (Jenkins & Krause 1983). They possessed a prehensile tail, opposable hind toe and mobile ankle joint.

The teeth of ptilodontoid multituberculates include a large, ridged blade-shaped premolar in the lower jaw biting against a grooved, cuspate upper tooth. The nearest modern dental analogue is *Burramys* (mountain possum) which has a similar blade in both upper and lower premolars. *Burramys* holds hard-shelled seeds and insects with hard cuticles at the side of the mouth and cracks them with blade-like premolars extracting contents with forceps-like incisors. In addition, it takes dry seeds from opened capsules and tackles drupes by using lower incisors to dig through flesh and then crack the stone (Kerle 1984).

Ptilodontoids are thought to have chewed in a comparable way using slicing–crushing action (Krause 1982) to deal with a diet of mainly hard and dry seeds and fruits. The generally larger taeniolabidoid multituberculates lacked the blade-like premolar but had gnawing, although rooted, incisors and were probably dominantly frugivorous.

The only other group of plant-eating mammals in the late Cretaceous was the didelphoid marsupials (opossums). These also appear to have eaten insects and fruit but were much less specialized for their fruit eating, having teeth of insectivore type merely with less cresting. (One genus with blunter cusps may have fed principally on fruit (Lillegraven *et al.* 1979).) Very little postcranial evidence is available but a few astragali suggest that most early didelphoids were ground dwellers (Szalay 1984). A modern dental analogue is *Marmosa* (mouse opossum) which eats a mixture of small invertebrates and fruit (Walker 1975).

Most of these marsupials became extinct at the K/T boundary, at least in the Northern Hemisphere. The multituberculates continued undiminished through the Palaeocene where they were joined by the placental carpolestids (Plesiadapiformes), the teeth of which show strong convergent morphology with those of the ptilodontoid multituberculates and a similar diet is inferred (Biknevicius 1986). Related plesiadapids show evidence of scansorial locomotion; they probably also became frugivorous but there is much disagreement on details (Szalay & Delson 1979). The only distinct specializations for eating fleshy fruit in the Palaeocene are in two picrodontid genera (also Plesiadapiformes) with teeth like those of modern fruit bats. Three or four genera or paromomyids (recently recognized as dermopterans–colugos) are considered to be scansorial or aerial forms feeding extensively on tree exudates like modern sugar gliders (Beard 1990).

Most of the remaining Palaeocene mammals that included fruit in their diets were condylarths (primitive ungulates). Many are known only from jaws and teeth but the available postcranials suggest that they were ground dwellers. The earliest and probably most specialized for frugivory were the periptychids which had massive conical ridged premolars and dominant puncture-crush mastication. Hard seeds may have formed an important part of their diet (Rensberger 1986).

(*b*) *Plants*

Fossil palynofloras and leaf floras from mid- to high-northern palaeolatitudes show the diversification and rise to dominance of angiosperms during the mid Cretaceous (from near 0% at 120 Ma to 50–80% at 66 Ma at the end of the Cretaceous) (Lidgard & Crane 1990). A broader assessment of palynofloras from 80° N to 20° S (Crane & Lidgard 1990) also shows this pattern with diversifications of magnoliid dicotyledons and monocotyledons followed rapidly by non-magnoliid dicotyledons which account for most early angiosperm diversity. Evidence from flowers shows that the Cretaceous magnoliids included Chloranthaceae, Lauraceae, and forms close to extant Magnoliaceae; with pollen evidence alone also indicating Winteraceae and possibly Myristicaceae (Friis *et al.* 1987; Crepet *et al.*, this symposium; Crane & Lidgard 1990; Crane *et al.* 1989; Drinnan *et al.* 1990; Muller 1985; Doyle *et al.* 1990). Cretaceous non-magnoliids (hamamelids and rosids) included Platanaceae and Trochodendrales (Crane 1989).

Most Cretaceous leaf floras are much in need of systematic revision (Wolfe & Upchurch 1987) but include a range of Lauralean, Magnolialean and Nymphaealean forms along with forms referable to Trochodendrales and other Hamamelidae, platanoids and primitive Rosidae (sapindophylls) (Friis *et al.* 1987; Crane 1989, Crane *et al.* 1989, Crane & Blackmore 1990; Crabtree 1987). In the later Cretaceous flacourts and euphorbs, palms and *Fagopsis* (Fagaceae) are also important (Wolfe & Upchurch 1986; Crabtree 1987). In a recent revision using foliar architecture and cuticular anatomy, Upchurch & Dilcher (1990) recognize 70% of a Cenomanian leaf flora to be of magnoliid form (Magnoliales, Laurales and Illiciales). None of these leaves could be assigned to an extant family with certainty.

The late Cretaceous angiosperm-dominated vegetation included shrubs, small trees and large trees (Wolfe & Upchurch 1987). In North America, trunk woods from south-eastern sites (maximum diversity five species) show little evidence of seasonality and conductivity values suggest a range through large, medium-sized and small trees. Several are represented by trunk pieces at least 1 m in diameter. A late Cretaceous wood assemblage from California (Page 1981) is more diverse (47 angiosperm species). Most again show no growth rings, but although conductivity values show that some may have been large trees, most probably represent small trees or shrubs (Wolfe & Upchurch 1987). Seventy percent of the 100 sufficiently well-preserved specimens (of 200) represented small stems, branches or roots (Page 1981). Some of these words are sufficiently distinct to suggest close relation with modern groups. These include platanoids, lauracioids and forms similar to modern Sapindales and Symplocaceae.

Direct evidence from fossil fruits and seeds in late Cretaceous and early Palaeocene floras suggests predominance of small, dry seeds and nutlets (e.g. Platanaceae, Juglandaceae, Betulaceae, Trochodendrales, Magnoliales, Cercidiphyllceae, Hamamelidaceae, Ulmaceae and Theaceae) along with some small drupes (single-seeded stone fruits; e.g. Cornaceae, Icacinaceae, Aquifoliaceae, Sabiaceae, Sapindaceae and rarer Ulmaceae (Celtidoideae), Menispermaceae and Anacardiaceae) probably with little leathery flesh (Knobloch & Mai 1986; Mai 1987; Collinson 1990; Crane & Blackmore 1990; Friis *et al.* 1987). Angiosperms were of low diversity compared with those of the Eocene (Collinson 1990). The subordinate conifers and other seed plants included similar seed forms, for example, dry seeds of Taxodiaceae or the fleshy seeds of *Ginkgo* (Crane *et al.* 1990) (comparable in potential palatability to a drupe). Close-living relatives of leaf, pollen and wood floras discussed above do not imply the presence of other fruit types. Rare fleshy fruits are represented by an early Palaeocene lauracioid (M. E. Collinson, unpublished data) and late Palaeocene *Psidium* (Myrtaceae) and a 'fleshy fruit' (Crane *et al.* 1990). Vitaceae seeds also occur in the late Palaeocene (Mai 1987).

(*c*) *Interactions*

Wolfe & Upchurch (1987) interpret late Cretaceous vegetation as open canopy broad-leaved evergreen woodland which was replaced by rain forest in the early Palaeocene. Modern mammals with arboreal specializations similar to the multituberculates (e.g. most South American didelphids) are confined to dense forest. The North American Virginian opossum is, however, an exception and extremely adaptable regarding habitat. The expansion of multituberculates with angiosperms in the Cretaceous, their continuation through into the Palaeocene and the strong convergent

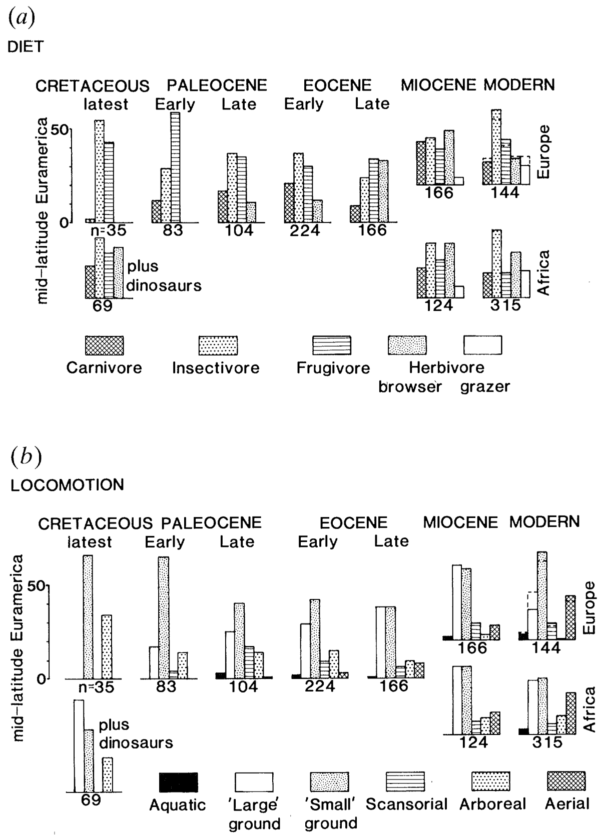


Figure 2. Ecological diversity histograms for dietary (*a*) and locomotor (*b*) adaptation, in mammal faunas from latest Cretaceous to modern, and in latest Cretaceous, the sum of mammal plus dinosaur faunas ('plus dinosaurs' histogram). Percentages of different dietary classes are shown, after the methodology of Andrews *et al.* (1979) and Collinson & Hooker (in Friis *et al.* 1987). Species of mixed classes are scored proportionally. Faunas are composite and originate from north hemisphere mid-latitudes as these are best known and easiest to interpret. The inclusion of European (temperate) and African (tropical) faunas for the Miocene and modern only shows that the pattern is independent of latitudinal control. Sources: latest Cretaceous: Lance Formation, Wyoming, U.S.A. and Scollard Formation, Alberta, Canada (Lillegraven *et al.* 1979; Weishampel *et al.* 1990); early Palaeocene: composite puercan, western U.S.A. (Savage & Russell 1983); late Palaeocene: Clarkforkian, Wyoming, U.S.A. (Rose 1981) and Cernay, France (mainly Russell *et al.* 1982); early Eocene: Wasatchian, Wyoming, U.S.A. (Schankler 1980) and European Sparnacian (mainly Russell *et al.* 1982); late Eocene: 15 English, French and Swiss sites (Hooker in Prothero (1991)); European Miocene: Pasalar, Turkey (Andrews 1990), la Grive (modified from Guérin & Mein (1971)) and Sansan (P. Andrews, unpublished data), France; African Miocene: Chamtwara, Fort Ternan, Koru and Songhor (P. Andrews, unpublished data); modern Europe (Corbet & Ovenden 1980); modern Africa: 23 low latitude sites covering a wide range of habitats (Andrews *et al.* 1979, pp. 184–185; P. Andrews, unpublished data). *n*, Number of species. Dashed lines on modern European histogram incorporates extinct mainland late pleistocene species (Kurtén 1968). This increases the similarity with tropical Africa but does not radically alter the histogram.

adaptation of carpolestids to a diet of mainly dry fruits suggests that the evolution of these mammals was linked to that of the angiosperms. Early Palaeocene GM periptychids had a similar diet. Mammalian and angiosperm fruit and seed dispersal interactions (Howe 1986; Estrada & Fleming 1986) involving small seeds carried or defecated away from the parent plant, may have commenced at this time, although much of the interaction probably resulted in seed predation rather than dispersal. Scatterhoarding usually involves larger dry fruits (Estrada & Fleming 1986; Vander Wall 1990) and thus is less likely to have been involved in the Cretaceous (see below).

Late Cretaceous and early Palaeocene floras evidently included angiosperm trees and shrubs on which were borne a variety of palatable leaves. These, in contrast to their fruit and seeds, were apparently not exploited by mammals at this time.

5. PALAEOGENE EVOLUTION OF NEW STRATEGIES

The evolution of new strategies may be considered by examining changes in both diet and locomotor adaptations. These are part of the broader study of ecological diversity (Fleming 1973; Andrews *et al.* 1979; Collinson & Hooker in Friis *et al.* (1987)). Adaptations are assessed for mammalian faunal assemblages and plotted as histograms (figure 2). Changing patterns in locomotor adaptation within frugivory and herbivore browsing are also illustrated (figure 3, see later). Faunas are presented as composite data, in an attempt to avoid bias from local communities (in particular habitats), but also to determine general trends (in contrast to our detailed studies of southern England (Collinson & Hooker in Friis *et al.* (1987); Hooker in Prothero (1991)).

(*a*) *Dietary adaptation* (*figure 2a*)

As noted above, late Cretaceous and early Palaeocene plant-eating mammals were frugivores. In fact, most plant-eating mammals developed first as frugivores, presumably because fruit is more easily processed than foliage. Mammals did not invade the herbivorous niche until the Middle Palaeocene. Evolution of large size was a prerequisite for the exploitation of leaves because longer residence time in the gut for bacterial fermentation is required to obtain sufficient nutrients from leaves. Small herbivorous rodents can exist today only because they have reduced the required gut residence time by more efficient mechanical preparation by the teeth (Janis & Fortelius 1988).

In the late Cretaceous, dinosaurs occupied the herbivorous niche and, with their addition, the late Cretaceous histogram resembles that of the Miocene or modern tropics except for the absence of grazers. These do not appear until much later, their explosive radiation being in the Miocene, coincident with a similar radiation of grassland-forming grasses (Thomasson & Voorhies 1990).

For mammals alone the late Cretaceous histogram is very different, being dominated by insectivores and frugivores with very few carnivores. After dinosaur extinction the early Palaeocene shows an increase in frugivores and a decrease in insectivores, indicating more specialization for plant-eating. Carnivores also diversify, as mammals increase in size after the extinction of the dinosaurs.

Herbivore browsers first appear in the Middle Palaeocene but they did not become significant until the late Eocene (see later). Frugivory declines first, with the appearance of herbivore browsing, and again with the appearance of grazers. The post-Miocene increase of grazers occurs at the expense of herbivore browsers.

(*b*) *Locomotor adaptation* (*figure 2b*)

In this case, even including the dinosaurs in the late Cretaceous plot does not make it similar to the modern because dinosaurs add only a strongly terrestrial (LGM) element. (We have not included aerial pterodactyls as they occur in marine settings distant from the mammal occurrences.) For mammals, only arboreal and 'small' ground classes existed in the late Cretaceous. 'Large' ground and scansorial mammals appeared in the early Palaeocene after dinosaur extinction; aquatic forms appeared in the Middle Palaeocene and aerial forms in the late Palaeocene. Aerial mammals became abundant by the late Eocene with the diversification of bats, which had appeared in the latest Palaeocene.

SGMs dominate over LGMs until the late Eocene, when LGMs increase to equivalent status. In modern temperate regions SGMs again dominate even when the extinct Pleistocene megafauna is included (dashed histograms). Arboreal forms are slightly reduced in the late Eocene and more markedly so from the Miocene onwards in temperate latitudes.

6. FRUGIVORY

(*a*) *Changes in locomotor adaptation within frugivory* (*figure 3a*)

At the Cretaceous–Tertiary boundary the first 'large' ground frugivores appear. Marsupials were essentially replaced by placentals that rapidly underwent a radiation from almost entirely insectivorous 'small' ground mammals. Many mixed frugivory with insectivory or carnivory, but others, like periptychids, were more specialized frugivores. Placentals also replaced most marsupials as SGM frugivores. LGM frugivores show a progressive reduction from early Eocene to modern, irrespective of latitude. The proportion of SGM frugivores is also reduced at low latitudes by the expansion of the arboreal primates and the aerial bats.

The late Palaeocene increase in scansorial frugivores is due to radiation of the (now extinct) primate-like Plesiadapiformes. The presence of this group reduced the proportions of LGM and SGM which resumed their previous importance with the near extinction of the Plesiadapiformes at the Palaeocene–Eocene boundary and the appearance of artiodactyls and perissodactyls.

The arboreal frugivore proportions have remained more or less stable to the present day, except where greatly reduced in modern temperate faunas.

The major category of aerial frugivores today, the fruit bats (Howe 1986; Marshall 1975; Estrada & Fleming 1986), do not appear until the Miocene when essentially modern forms are found in southern France and tropical Africa (Sigé & Aguilar 1987). Fossil fruits and seeds, the close living relatives of which are an important part of fruit bat diet (Marshall 1975), are known from the Kenyan Miocene (Chesters 1957; M. E. Collinson, personal observations). These include Annonaceae, Lauraceae, Tiliaceae, (*Grewia*), Sterculiaceae, Cucurbitaceae, Combretaceae, Euphorbiaceae, Rhamnaceae, Vitaceae, Sapindaceae, Burseraceae, Anacardiaceae, Meliaceae, Ehretiaceae, Rubiaceae and Arecaceae (*Phoenix*). Many of these are also known from much earlier fossils (see elsewhere herein) so do not reflect coevolution with bats.

(*b*) *'Large' ground frugivory*

The presence of quite high numbers of 'large' ground mammalian frugivores in the Palaeogene may

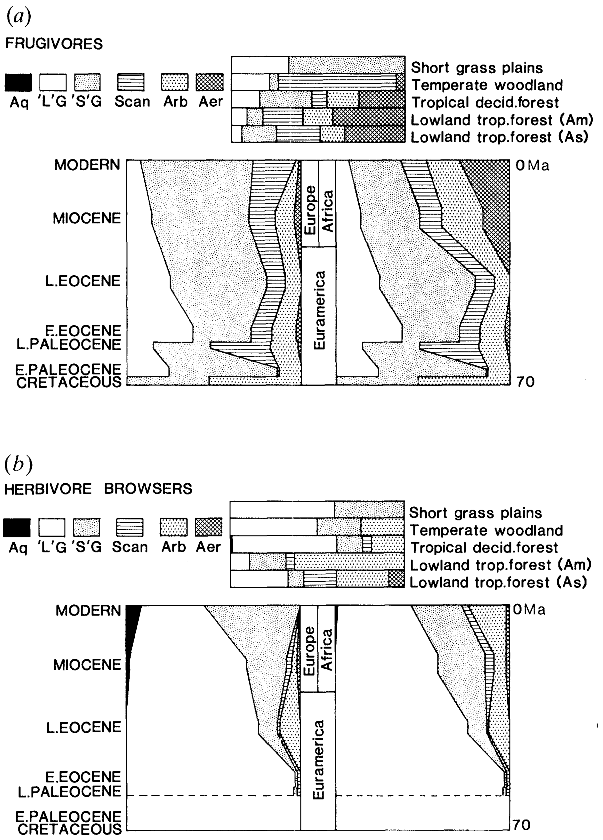


Figure 3. Proportions of locomotor classes among (*a*) frugivores and (*b*) herbivore browsers through time (faunas in figure 2). Plots for five modern habitat types (horizontal bar diagrams at top of each figure) show that changing vegetation is not the major control over past pattern, although tropical deciduous forest fits reasonably well with African Miocene. Faunas from short grass plains and tropical deciduous forest from Andrews (unpublished data); temperate woodland and American (Am) lowland tropical forest from Fleming (1973); S.E. Asian (As) lowland tropical forest from Davies (1962). Ma = millions of years before present. Note that the two diagrams at left and right are the same up to the late Eocene, whereas above that level separate versions are shown for Europe and Africa.

seem surprising in view of their rarity today. Modern examples are peccaries, agoutis and chevrotains. The proportion of 'large' ground frugivores falls from the late Palaeocene to the present day, regardless of latitude or of the increase in arboreal and aerial frugivores in the tropics.

Conclusive evidence for the terrestrial nature of Palaeogene frugivores is provided by the skeleton of the artiodactyl *Aumelasia* from Messel which has bunodont teeth like those of *Acotherulum* (figure 4c). The tooth gross morphology, gross wear and microwear of the latter all compare closely with fruit-eating monkeys. Cusps are rounded, there is little cresting and puncture-crush wear is much in evidence on the cusp tips. The gut contents of *Aumelasia* include fruits, seeds and sand grains which could only have been ingested when picking up fallen fruit (Franzen & Michaelis 1988).

Possible reasons for the subsequent demise of this strategy are as follows.

1. Reduction in fallen fruit abundance which may be due to a reduction in climatic equability resulting in alteration of patterns of fruit production (cf. Terborgh in Estrada & Fleming (1986)). Insufficient fallen fruit in the neotropics during the season of scarcity is a population-regulating factor for terrestrial frugivores today (Smythe 1986).
2. Competition with arboreal frugivores taking fruit at source. Multituberculates, in taking mainly dry fruits and seeds, may not have caused the same degree of competition as later primates.
3. Competition with rodents (especially outside the tropics) able to open all but the hardest of dry nuts and seeds, and which, because of their scatterhoarding (Estrada & Fleming 1986; Vander Wall 1990) might have been selected for as plant dispersers.

(*c*) ***Primate frugivory***

Our frugivorous category incorporates any fruit or seed eating. A combination of gross dental morphology and microwear can be used to provide some indications of types of frugivory i.e. soft fleshy versus hard dry. As noted earlier few mammals in the late Cretaceous and Palaeocene had distinct adaptations for eating fleshy fruit.

True primates appeared just before the Palaeocene–Eocene boundary in North America, Europe, Asia and North Africa. Today they are amongst the most important arboreal frugivores (Fleming *et al.* 1987; Howe 1986; MacKinnon 1978; Chivers 1980; Estrada & Fleming 1986). Initially primates were insectivorous, then combined insectivory and frugivory. In the late Early and Middle Eocene of Europe many primates (especially in the family Adapidae) were frugivorous. Their molars are typified by low blunt cusps showing much wear at the tips; their wear facets bear only very fine striations and very little pitting (observed by light microscopy). This suggests a fleshy fruit diet. It coincides with the widespread extent of tropical to paratropical forests reaching to 50°–60° North and South (Wolfe 1985; and see Collinson (1990) for review) represented in the fossil record by a diversity of fruits and seeds (Collinson 1983, 1990, in Franzen & Michaelis (1988), in Crane & Blackmore (1989); Mai & Walther 1985; Manchester in Knobloch & Kvaček (1990)) whose close living relatives include fleshy fruits important in the diets of primates today (Terborgh in Estrada & Fleming (1986); Chivers 1980; Gautier-Hion *et al.* 1985; Leighton & Leighton 1983). These include Annonaceae, Moraceae (especially *Ficus*), Vitaceae, Sapindaceae, Sapotaceae, Anacardiaceae, Euphorbiaceae, Burseraceae. The significance of several of these families in ancient vegetation of this time is supported by leaf and pollen fossils (Muller 1985; Wilde 1989; Manchester in Knobloch & Kvaček (1990)). Confirmation of the former existence of softer tissues in fruits is available, for example for Menispermaceae, Vitaceae, Lauraceae and Cornaceae at Messel (Collinson in Franzen & Michaelis (1988)), and in some permineralized fossils (e.g. Lauraceae in the London Clay flora (Collinson 1983)).

Many factors influence fruit and seed selection, and dispersal versus predation, in frugivory. These include fruit colour and composition of pulp, particularly with respect to lipids, proteins and sugars (Howe 1986; Estrada & Fleming 1986). These factors are unknown for fossils. Physical features can be observed. These include (rarely) pericarp texture and thickness and in almost every case the thickness and strength of the layer which would have been the major protection for the embryo (testa, endocarp, etc.). In most cases the ancient examples are very like their close living relatives and they offer no evidence for modification in response to frugivory.

The family Lauraceae is extremely abundant and diverse in these tropical or paratropical Eocene forests (Collinson 1983, in Franzen & Michaelis (1988); Wilde 1989; Mai & Walther 1985). Modern Lauraceae exemplify one extreme fruiting strategy, having large fruit, high in protein and lipid content (termed high quality, high investment fruit). In consequence fruits of many modern Lauraceae are dispersed by birds, although they can form a very subordinate element in some primate diets, e.g. howler and capuchin monkeys (Howe 1986; Fleming *et al.* 1987; Estrada & Fleming 1986, Herrera (in Estrada & Fleming 1986) quoted *Laurus* species from distinct modern habitats where fruits were identical (colour, form, composition) but were dispersed by quite unrelated birds, as evidence against any close coevolutionary relation between the fruit and bird dispersal agents. The fossil record of birds is fragmentary but there is no evidence to suggest that a wide range of frugivorous birds existed in the European early Eocene (Harrison 1979). The Eocene fruits are mostly only medium-sized and it is possible that they formed part of the arboreal mammalian frugivore diet.

Cornaceae are another group with mainly bird dispersers today although some mammals also take the fruit (Eyde 1988). The family (here taken to include Mastixiaceae) has an extensive fossil history with fruits recorded from the late Cretaceous onwards (Eyde 1988). Late Cretaceous and Palaeocene forms were restricted to mastixioids probably with scant leathery flesh. These were small in the late Cretaceous (Knobloch & Mai 1986) but one early Palaeocene example

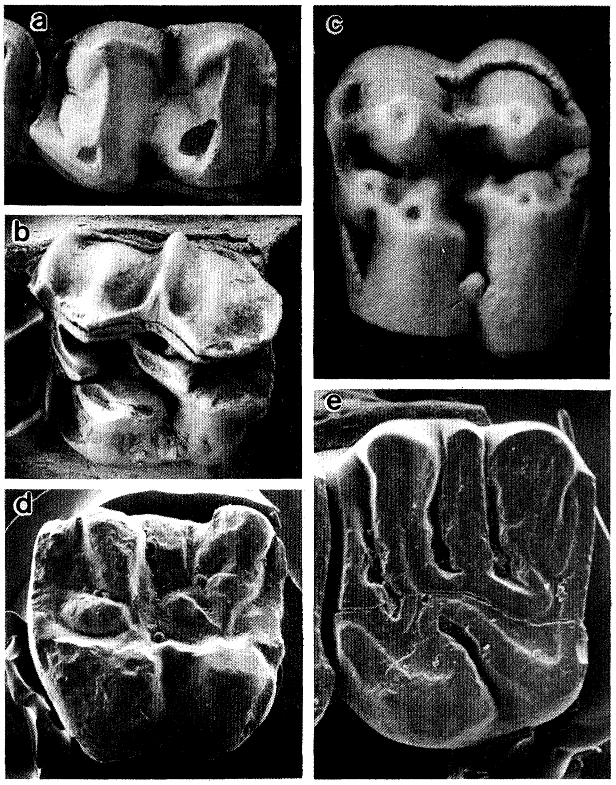


Figure 4. Upper (b–e) and lower (a) pre-ultimate molars of fossil mammals from the Eocene of southern England. (a–c) LM, coated with ammonium chloride; (d–e) SEM. Numbers refer to specimens in the Palaeontology Department, Natural History Museum (BM(NH)). (a) *Hyrachyus stehlini*, a bilophodont herbivore browser (perissodactyl), M50194, × 2.5. (b) *Plagiolophus annectens*, a selenodont semihypsodont herbivore browser (perissodactyl), 29715, × 2.3. (c) *Acotherulum quercyi*, a frugivore (artiodactyl), M29470, × 4.8. (d) *Sciuroides rissonei*, a frugivore (soft) (rodent), M37368, × 12. (e) *Thalerimys headonensis*, a semihypsodont herbivore browser (rodent), 30159a, × 18.

(Puercan, Colorado) is large (endocarp more than 20 mm long) (M. E. Collinson, unpublished results). Eocene forms included those with thicker soft tissues (Eyde 1988). Eocene fruits are typified by higher locule number than modern examples whereas Miocene forms often have thicker, strongly ornamented endocarps (Eyde 1988; Knobloch & Mai 1986). Rodent-gnawed examples occur in the Miocene (Boucot 1990, p. 263). A thorough survey of fruit trends in this family, so well represented in the fossil record, would be worthwhile. They too might have been food for early mammalian frugivores.

(*d*) *Rodent frugivory*

Rodents are another important group of frugivorous mammals today, tending to be specialized for feeding on hard dry fruit types (Estrada & Fleming 1986; Vander Wall 1990).

Rodents first appeared in the late Palaeocene: about 1 Ma earlier in North America than in Europe but in both cases coincident with drastic reduction in multituberculates (Krause 1986). However, the locomotor adaptations of the rodents appear to have been considerably less specialized for life in the trees than were the multituberculates (Szalay 1985). Generally they lack specific arboreal modifications and we have scored them as SGM/scansorial.

Rodents underwent a relatively modest radiation during the early and Middle Eocene, although they were abundant as individuals in nearly all faunas. They underwent a major radiation in the late Eocene to become a major component of faunas, as they are today. Many remained SGM/scansorial although some later became LGM, others arboreal and some partly aerial.

The early rodents would have been able to exploit the variety of dry seeds and fruits (see above) which had been exploited by multituberculates. Krause (1986) argued strongly for competitive exclusion of multituberculates by rodents. One major adaptive advantage possessed by rodents was evergrowing incisors, not possessed by the gnawing taeniolabidoid multituberculates. Angiosperm families that produce large, rodent-dispersed nuts today (Betulaceae, Fagaceae, Juglandaceae) were producing mainly smaller (often winged) nutlets during the late Palaeocene and earliest Eocene. The first production of the larger nuts in these families occurs during the latest Palaeocene or the early and Middle Eocene and they were not abundant until the late Eocene (Crane & Blackmore 1989). An earlier rodent expansion may have been contained by the abundance of soft fruit more suited to exploitation by primates in tropical forests during the early and Middle Eocene but as these forests became more restricted the deciduous nut-bearing families diversified (Crane & Blackmore 1989; Wolfe in Prothero (1991); Collinson in Prothero (1991)).

It is possible that these early rodents hoarded nuts, as do modern rodents. The earliest evidence of nut hoarding by rodents appears to be late Miocene heteromyid burrows containing *Celtis* endocarps (Boucot 1990, p. 57). *Celtis* endocarps are known in the Palaeocene and are abundant from the Eocene onwards (Manchester in Crane & Blackmore (1989)).

Complex interactions between fruit and scatter-hoarders are discussed by several authors in Estrada & Fleming (1986). For example Stapanian describes the relative value of *Juglans*, *Carya* and *Quercus*; the two former being more digestible and having a higher lipid content but being thick walled, whereas the latter yields more energy per unit time (even though twice the mass is needed to compensate for lower nutrient content) because the wall is thin. Relative sizes of nuts influence distance carried; this and timing of germination influence recovery and predation. Platt & Hermann show that the scatterhoarding of these species is essential for their persistence as codominants in a subtropical forest in northern Florida. Papers by Janzen and Hallwachs discuss the role of rodents in removing seeds from dung of megaherbivores. Here the size of seed and its visibility in dung are important. Miocene rodent-gnawed mastixioid Cornaceae (Boucot 1990, p. 263) would have possessed pulp so may have been secondarily predated by rodents.

Some aspects of significance to these rodent dispersal factors such as size of nuts and wall thickness can be assessed from the fossil record; especially that of

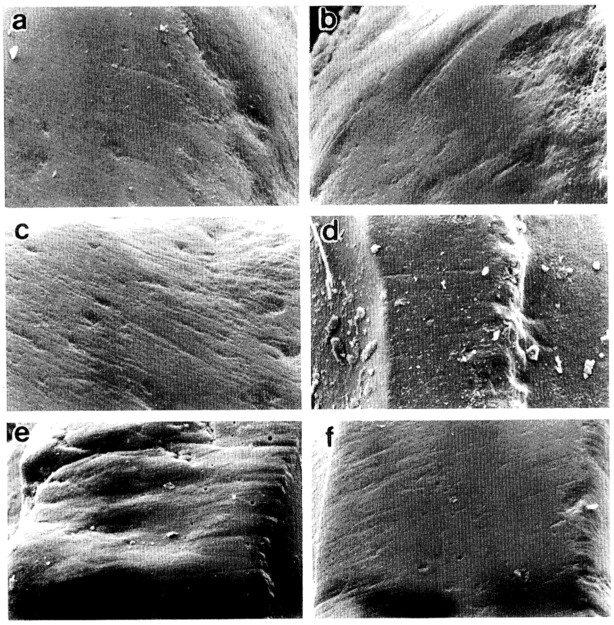


Figure 5. SEMS of microwear of fossil and modern mammal upper pre-ultimate molars (casts); buccal phase. Numbers refer to specimens in the Natural History Museum (BM(NH)); ZD indicates modern in Zoology Department, M or no prefix indicates fossil in Palaeontology Department. (a) *Ratufa affinis*, ZD9.4.1.218; (b) *Sciuroides rissonei*, (figure 4d); (c) *Treposciurus mutabilis*, M51685; 9d) *Capreolus capreolus* (modern); (e) *Alcelaphus buselaphus* (modern); (f) *Plagiolophus annectens*, M52683 (cf. figure 4b). (a–c) ×200; (d–f) ×60.

Juglandaceae. Detailed studies would be worthwhile to help elucidate the role of early rodents as seed dispersers.

(*e*) *Evidence of diet in southern England*

Some of the early and Middle Eocene rodents seem to have exploited the soft fruit availability at this time. Indeed, in southern English faunas (Collinson & Hooker in Friis *et al.* (1987)) and also in Europe we see a trend from softer to harder diet in rodents during the Eocene. A modern dental analogue for pseudosciurids (figure 4d) and manitshine paramyids in the middle Eocene is the giant squirrel (*Ratufa*). These eat both soft and hard fruit and a few flowers (MacKinnon 1978). The teeth have square outlines (which gives an increased crushing area) with low blunt cusps.

We have examined the microwear of one Middle and one late Eocene Pseudosciurid genus, shown here (figure 5) with *Ratufa* for comparison. This seems to indicate that *Sciuroides* (figure 5b) with few scratches on overall very smooth facets was eating a softer food than *Treposciurus* (figure 5c) with many, stronger, parallel striations and more pits. The modern *Ratufa* (figure 5a) is similar to *Sciuroides*.

This dietary modification coincides with reduction in individual abundance and species diversity of pseudosciurids at the Middle–late Eocene boundary; followed by a modest radiation of new types in the late Eocene with coarser diet including some fruit and some leaves. The frugivorous pseudosciurids were replaced by theridomyids (see herbivore browsing) and glirids (Collinson & Hooker in Friis *et al.* (1987)).

The small glirids (dormice) have low-crowned molars characterized by low ridges with enhanced grinding capacity suggesting a frugivorous diet different from that of the pseudosciurids. The plant items in the diet of modern glirids comprise a range of hard and soft fruits (Walker 1975). We have evidence for at least part of the diet for one species, as seeds of *Stratiotes* (with appropriate-sized gnaw marks) occur at two distinct late Eocene horizons (Collinson 1990); at one of these, in association with a glirid tooth.

7. HERBIVORE BROWSING

(*a*) *Changes in locomotor adaptation within herbivore browsing* (*figure 3b*)

The earliest herbivore browsers appeared in the Middle Palaeocene; almost all were LGMS. Pantodonts dominated with dinocerates and tillodonts in the later Palaeocene. They appear to have developed herbivory directly from insectory by increase in size and little initial tooth modification other than increased cresting.

Early Eocene herbivore browsers were also mainly LGMS but Palaeocene forms were replaced by new groups which evolved from LGM frugivores; especially perissodactyls and, as the Eocene proceeded, also artiodactyls. This contrasts with the picture just presented for frugivores where major changes in locomotor category occurred at this time.

LGM herbivore browsers show a decline from early Eocene to present in Europe and Africa; but not as marked as the LGM frugivore decline. This is balanced by an expansion of SGM and arboreal herbivore browsers in the Eocene. Most arboreal forms in the late Eocene were primates whose diet had shifted from frugivory (Szalay & Delson 1979). After this the arboreals declined and the SGMS continued to expand in Europe but both continued expanding in Africa.

(*b*) *Large ground herbivore browsing*

(i) *Bilophodonty*

The simplest dental modifications for leaf eating were developed in Eocene herbivores such as the rhinocerotoid *Hyrachyus* and occur today in tapirs and tree kangaroos. These teeth (figure 4a) had straight transverse crests (usually two per tooth) and are termed bilophodont. These performed mainly a shearing action slicing up leaves into quite large pieces. Bulk food was processed rapidly and inefficiently, a method typically used by perissodactyls to exploit mainly cell contents (Janis 1989). The modern tapir diet is restricted almost entirely to leaves of forest trees (Terwilliger 1978).

(ii) *Selenodonty*

A major radiation of LGM herbivore browsers occurred in the late Eocene (Collinson & Hooker in Friis *et al.* (1987)). Probable fossil grasses go back to the Eocene (Thomasson & Voorhies 1990). However, the earliest fossils securely attributed to the grasses are late Oligocene, and rapid diversification and spread of grasslands was not until the Middle Miocene. Fossil soils similar to those of modern grasslands have also been found in the Oligocene (Retallack 1986). In the light of these reports, and the fact that horse evolution is intimately connected with grazing adaptation, it is relevant to look at *Plagiolophus* (a palaeothere, figure 4b), which is both an equoid and the highest crowned (semi-hypsodont) herbivore in the European late Eocene, to see if its microwear suggests it was a browser or a grazer. Hypsodonty is generally associated with a more abrasive diet.

We have compared the microwear of *Plagiolophus* with *Capreolus* (roe deer), a moderately high-crowned browser and *Alcelaphus* (hartebeest) a grazer. *Alcelaphus* (figure 5d) shows a typical coarse-scale irregular pattern with fine-scale strong striations. *Capreolus* (figure 5e) shows a flat surface with no coarse pattern and a fine-scale pattern of fine striations. *Plagiolophus* (figure 5f) is very similar to *Capreolus* and thus a browser.

(*c*) **'*Small*' *ground herbivore browsing***

SGM herbivore browsers expanded from the late Eocene to the present day. Many of these are rodents such as theridomyids (e.g. *Thalerimys*, figure 4e). These are semi-hypsodont which implies the need to process a greater quantity of food than low-crowned pseudosciurids.

We can conclude that most theridomyids were eating a high proportion of leaves. A modern dental analogue, *Thryonomys* (the cane rat) (Collinson & Hooker in Friis *et al.* (1987), eats the roots and shoots of coarse grasses and shrubs as well as nuts, fallen fruit and bark (Walker 1975).

8. DISCUSSION AND CONCLUSIONS

In the case of frugivory two processes have operated during the Cainozoic. There has been a shift in locomotor adaptation (from the ground into the trees and the air) and a shift in diet (from insectivory or carnivory to frugivory in nearly all the locomotor classes). This implies pressure to change locomotor adaptation to obtain fruit at source and to change dietary adaptation to exploit a new food resource.

The situation is different for browsing herbivores. The earliest herbivores were ground dwelling and achieved their dietary specializations mainly through evolution from already large, ground-dwelling frugivores (or, in the Palaeocene, by size increase from small insectivorous ancestors). Large size limited them to the ground. Most browsing herbivores in other locomotor niches changed their diet from frugivory without changing their locomotor adaptation. Notable exceptions today are the tree kangaroo and the tree hyrax. The dietary shifts probably resulted from reduction in fruit availability, especially in the late Eocene.

A period of nearly 30 Ma existed between the dominance of angiosperms and their exploitation by mammalian herbivores. Even after dinosaur extinction several million years intervened without any evidence for dietary interaction between angiosperms and vertebrate herbivores. Expansion of this interaction did not occur until the late Eocene.

The delay in developing herbivory may have resulted from the early Palaeocene equable climate which turned late Cretaceous open canopy woodland into rainforest (Wolfe & Upchurch 1987; Wolfe 1990) with an ample supply of fruit and dense vegetation which might have discouraged evolution of large size in mammals. We are unsure how much influence the removal of dinosaur herbivory had on plant communities following the K/T boundary (Friis *et al.* 1987) but the strong temporal link between the various later radiations of herbivore specializations and climate-induced vegetational changes seem inescapable (herein; Collinson & Hooker in Friis *et al.* (1987); Janis 1989). Definite examples of coevolution seem elusive but we can suggest the timing of certain events that may represent the beginnings or major development of interactions which some authors consider examples of coevolution. Opinions vary greatly on coevolution in fruit and seed dispersal (Estrada & Fleming 1986). One extreme is represented by Janzen's and Hallwach's claims (p. 252 and p. 285 respectively in Estrada & Fleming (1986)) for coevolution between large legume seeds like *Hymenaea* (Guanipol) and *Enterolobium* (Guanacaste) with extinct megaherbivores in South America. The other is favoured by many workers on avian frugivory and is specifically supported by documentary evidence by Herrera (p. 14 in Estrada & Fleming (1986)) who argues: 'insofar as plant adaptations are concerned, there exists little or no basis for assuming generally gradualistic change and environmental tracking in evolutionary formulations of plant-vertebrate seed disperser interactions'.

Possible examples of diffuse coevolution are: the late Cretaceous and Palaeocene expansion of arboreal dry fruit- and seed-eating multituberculates and angiosperm-dominated vegetation; the late Palaeocene appearance and late Eocene radiation of large nuts and rodents; the early to Middle Eocene expansion of fleshy fruits and the evolution of frugivorous arboreal primates.

Three features characterize the late Eocene. There is a change in frugivore diet from soft to hard fruit (to some extent a reversal of early Eocene trends); dietary shifts in nearly every locomotor class from frugivory to herbivore browsing and the existing herbivore browsers show evidence of increasing coarseness of diet. In addition, 'large' ground mammals reach equivalent abundance to small ground mammals and there is a slight reduction in arboreal forms. These changes are all consistent with patterns of vegetational and climatic change during the late Eocene in which previously widespread megathermal, tropical to paratropical, broad-leaved evergreen forests became increasingly restricted to low latitudes; being replaced in mid-high latitudes by mesothermal to microthermal, mixed evergreen and deciduous forests (Wolfe 1985, 1987; Collinson 1990; Wolfe in Prothero (1991); Collinson in Prothero (1991)).

We thank Peter Andrews, Mikael Fortelius and Jack Wolfe for helpful discussion. Peter Andrews also made available unpublished information and critically read the text. This work was undertaken by M.E.C. while in receipt of a Royal Society 1983 University Research Fellowship, which is gratefully acknowledged.

REFERENCES

Andrews, P. 1990 Palaeoecology of the Miocene fauna from Paşlar, Turkey. *J. hum. Evol.* **19**, 569–582.

Andrews, P., Lord, J. M. & Nesbit Evans, E. M. 1979 Patterns of ecological diversity in fossil and modern mammalian faunas. *Biol. J. Linn. Soc.* **11**, 177–205.

Beard, K. C. 1990 Gliding behaviour and palaeoecology of the alleged primate family Paromomyidae (Mammalia, Dermoptera). *Nature, Lond.* **345**, 340–341.

Biknevicius, A. R. 1986 Dental function and diet in the Carpolestidae (Primates, Plesiadapiformes). *Am. J. Phys. Anthrop.* **71**, 157–171.

Boucot, A. J. 1990 *Evolutionary paleobiology of behaviour and coevolution.* Amsterdam: Elsevier.

Chesters, K. I. M. 1957 The Miocene flora of Rusinga Island, Lake Victoria, Kenya. *Palaeontographica* B **101**, 30–71.

Chivers, D. J. (ed.) 1980 *Malayan forest primates.* New York: Plenum.

Collinson, M. E. 1983 *Fossil plants of the London Clay.* Palaeontological Association Field Guides to Fossils No. 1. London: The Palaeontological Association.

Collinson, M. E. 1990 Plant evolution and ecology during the early Cainozoic diversification. *Adv. Bot. Res.* **17**, 1–98.

Corbet, G. & Ovenden, D. 1980 *The mammals of Britain and Europe.* London: Collins.

Crabtree, D. R. 1987 Angiosperms of the northern Rocky Mountains: Albian to Campanian (Cretaceous) megafossil floras. *Ann. Missouri Bot. Gard.* **74**, 707–747.

Crane, P. R. 1989 Palaeobotanical evidence on the radiation of the non-magnoliid dicotyledons. *Pl. Syst. Evol.* **162**, 165–191.

Crane, P. R. & Blackmore, S. 1989 *Evolution, systematics and fossil history of the Hamamelidae*, vol. 1 (*Introduction and 'lower' Hamamelidae*); vol. 2 (*'Higher' Hamamelidae*). Systematics Association Special Volumes 40A & 40B. Oxford: Clarendon Press.

Crane, P. R., Friis, E. M. & Pedersen, K. R. 1989 Reproductive structure and function in Cretaceous Chloranthaceae. *Pl. Syst. Evol.* **165**, 211–226.

Crane, P. R. & Lidgard, S. 1990 Angiosperm radiation and patterns of Cretaceous palynological diversity. In *Major evolutionary radiations.* (ed. P. D. Taylor & G. P. Larwood), pp. 377–407 (Systematics Association Special Volume no. 42). Oxford: Clarendon Press.

Crane, P. R., Manchester, S. M. & Dilcher, D. L. 1990 A preliminary survey of fossil leaves and well-preserved reproductive structures from the Sentinel Butte Formation (Paleocene) near Almont, North Dakota. *Fieldiana Geology* n.s. **20**, 1–63.

Davies, D. D. 1962 Mammals of the lowland rain-forest of North Borneo. *Bull. natn. Mus. St. Sing.* **31**, 1–129.

Doyle, J. A., Hotton, C. L. & Ward, J. V. 1990 Early Cretaceous tetrads, zonasulcate pollen and Winteraceae. II. Cladistic analysis and implications. *Am. J. Bot.* **77**, 1558–1568.

Drinnan, A. N., Crane, P. R., Friis, E. M. & Pedersen, K. R. 1990 Lauraceous flowers from the Potomac Group (Mid-Cretaceous) of Eastern North America. *Bot. Gaz.* **151**, 370–384.

Estrada, E. & Fleming, T. H. 1986 *Frugivores and seed dispersal.* Dordrecht: W. Junk.

Eyde, R. H. 1988 Comprehending Cornus: puzzles and progress in the systematics of the dogwoods. *Bot. Rev.* **54**, 233–351.

Fleming, T. H. 1973 Numbers of mammal species in north and central American forest communities. *Ecology* **54**, 555–563.

Fleming, T. H., Breitwisch, R. & Whitesides, G. H. 1987 Patterns of tropical frugivore diversity. *A. Rev. Ecol. Syst.* **18**, 91–109.

Franzen, J. L. & Michaelis, W. (eds) 1988 Eocene Lake Messel. *Cour. Forsch.-Inst. Senckenberg* **107**, 1–452.

Friis, E. M., Chaloner, W. G. & Crane, P. R. 1987 *The origins of angiosperms and their biological consequences.* Cambridge University Press.

Gautier-Hion, A. *et al.* 1985 Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia, Berl.* **65**, 324–337.

Gingerich, P. D. (ed.) 1980 Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming. *Pap. Paleont. Mus. Paleont. Univ. Mich.* **24**, 1–146.

Guérin, C. & Mein, P. 1971 Les principaux gisements de mammifères miocènes et pliocènes du domaine Rhodanien. *Docum. Lab. Géol. Lyon. H.S.* 131–170.

Harrison, C. J. O. 1979 Small non-passerine birds of the Lower Tertiary as exploiters of ecological niches now occupied by passerines. *Nature, Lond.* **281**, 562–563.

Harrison, J. L. 1962 The distribution of feeding habits among animals in a tropical rain forest. *J. Anim. Ecol.* **31**, 53–63.

Janis, C. M. 1989 A climatic explanation for patterns of evolutionary diversity in ungulate mammals. *Palaeontology* **32**, 463–481.

Janis, C. M. & Fortelius, M. 1988 On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. *Biol. Rev.* **63**, 197–230.

Jenkins, F. A. & Krause, D. W. 1983 Adaptations for climbing in North American multituberculates (Mammalia). *Science, Wash.* **220**, 712–715.

Kerle, J. A. 1984 The behaviour of Burramys parvus Broom (Marsupialia) in captivity. *Mammalia* **48**, 317–325.

Knobloch, E. & Kvaček, Z. 1990 *Proceedings of the Symposium Paleofloristic and paleoclimatic changes in the Cretaceous and Tertiary.* Prague: Geological Survey Publisher.

Knobloch, E. & Mai, D. H. 1986 *Monographie der früchte und Samen in der Kreide von Mitteleuropa.* Edice Rozpravy Ustredniho ustavu geologickeho 47, Geological Survey Prague.

Krause, D. W. 1982 Jaw movement, dental function and diet in the Paleocene multituberculate Ptilodous. *Paleobiology* **8**, 265–281.

Krause, D. W. 1986 Competitive exclusion and taxonomic displacement in the fossil record: the case of rodents and multituberculates in North America. *Univ. Wyoming. Contrib. Geol. Spec. Pap.* **3**, 95–117.

Kurtén, B. 1968 *Pleistocene mammals of Europe.* London: The World Naturalist, Weidafeld & Nicholson.

Leighton, M. & Leighton, D. R. 1983 Vertebrate responses to fruiting seasonality within a Bornean rain forest. In *Tropical rain forest: ecology and management* (ed. S. L. Sutton, T. C. Whitmore & A. C. Chadwick), pp. 181–196. Oxford: Blackwell Scientific Publications.

Lidgard, S. & Crane, P. R. 1990 Angiosperm diversification and Cretaceous floristic trends: a comparison of palynofloras and leaf macrofloras. *Paleobiology* **16**, 77–93.

Lillegraven, J. A., Kielan-Jaworowska, Z. & Clemens, W. A. 1979 *Mesozoic mammals, the first two-thirds of mammalian history.* Berkeley, California: University of California Press.

MacKinnon, K. S. 1978 Stratification and feeding differences among Malayan squirrels. *Malay. Nat. J.* **30**, 593–608.

Mai, D. H. 1987 Neue Früchte und Samen aus paläozanen Ablagerungen Mitteleuropas. *Feddes Repert.* **98**, 197–229.

Mai, D. H. & Walther, H. 1985 Die obereozänen Floren des Weisselster-Beckens und seiner Randgebiete. *Abh. St. Mus. Miner. Geol. Dresd.* **33**, 5–176.

Marshall, A. G. 1985 Old world phytophagous bats (Megachiroptera) and their food plants: a survey. *Zool. J. Linn. Soc.* **83**, 351–369.

Muller, J. 1985 Significance of fossil pollen for angiosperm history. *Ann. Missouri Bot. Gard.* **71**, 419–443.

Murray, D. R. 1986 Seed dispersal. Sydney: Academic Press.

Page, V. M. 1981 Dicotyledonous wood from the Upper Cretaceous of central California. III. Conclusions. *J. Arn. Arb.* **62**, 437–455.

Prothero, D. R. 1991 *Eocene-Oligocene climatic and biotic evolution*. Princeton University Press. (In the press.)

Rensberger J. M. 1978 Scanning electron microscopy of wear and occlusal events in some small herbivores. In *Development, function and evolution of teeth* (ed. P. M. Butler & K. A. Joysey), pp. 415–438. London: Academic Press.

Rensberger, J. M. 1986 Early chewing mechanisms in mammalian herbivores. *Paleobiology* **12**, 474–494.

Retallack, G. J. 1986 The fossil record of soils. In *Paleosols: their recognition and interpretation.* (ed. V. P. Wright), pp. 1–57. Oxford: Blackwell Scientific Publications.

Rose, K. D. 1981 The Clarkforkian land-mammal age and mammalian faunal composition across the Palaeocene–Eocene boundary. *Pap. Paleont. Mus. Paleont. Univ. Mich.* **26**, 1–197.

Savage, D. E. & Russell, D. E. 1983 *Mammalian paleofaunas of the world.* Reading, Massachusetts: Addison–Wesley.

Schaal, S. & Ziegler, W. (eds) 1988 *Messel – ein Schaufenster in die Geschichte der Erde und des Lebens*. Frankfurt am Main: Kramer.

Sigé, B. & Aguilar, J.-P. 1987 L'extension stratigraphique des megachiroptères dans le Miocène d'Europe méridionale. *C.r. Acad. Sci., Paris* **304**, 11, 9, 469–474.

Smythe, N. 1986 Competition and resource partitioning in the guild of neotropical terrestrial frugivorous mammals. *A. Rev. Ecol. Syst.* **17**, 169–188.

Szalay, F. S. 1984 Arboreality: Is it homologous in metatherian and eutherian mammals? *Evol. Biol.* **18**, 215–258.

Szalay, F. S. 1985 Rodent and lagomorph morphotype adaptations, origins, and relationships: some postcranial attributes analyzed. In *Evolutionary relationships among rodents – a multidisciplinary analysis.* (ed. W. P. Lucket & J.-L. Hertenberger), pp. 83–132. New York: Plenum Press.

Szalay, F. S. & Delson, E. 1979 *Evolutionary history of the primates.* New York: Academic Press.

Teaford, M. F. 1988 A review of dental microwear and diet in modern mammals. *Scanning Microsc.* **2**, 1149–1166.

Terwilliger, V. J. 1978 Natural history of Baird's Tapir on Barro Colorado Island, Panama Canal zone. *Biotropica* **10**, 211–220.

Thomasson, J. R. & Voorhies, M. R. 1990 Grasslands and Grazers. In *Palaeobiology a synthesis* (ed. D. E. G. Briggs & P. R. Crowther), pp. 84–87. Oxford: Blackwell Scientific Publications.

Upchurch, G. R. & Dilcher, D. L. 1990 Cenomanian angiosperm leaf megafossils, Dakota Formation, Rose Creek locality, Jefferson County, Southeastern Nebraska. *U.S. Geol. Surv. Bull.* **1915**, 1–52.

Vander Wall, S. B. 1990 *Food hoarding in animals*. University of Chicago Press.

Walker, E. P. 1975 *Mammals of the world*, 3rd edn. Baltimore: The Johns Hopkins University Press.

Weishampel, D. B., Dodson, P. & Osmolska, H. (eds) 1990 *The Dinosauria.* Berkeley: University of California Press.

Wilde, V. 1989 Untersuchungen zur Systematik der Blattreste aus dem Mitteleozän der Grube Messel bei Darmstadt (Hessen, Bundesrepublik Deutschland). *Cour. Forsch.-Inst. Senckenberg* **115**, 1–214.

Wolfe, J. A. 1985 Distribution of major vegetational types during the Tertiary. *Am. Geophys. Union Geophys. Mon.* **32**, 357–375.

Wolfe, J. A. 1987 Late Cretaceous-Cenozoic history of deciduousness and the terminal Cretaceous event. *Paleobiology* **13**, 215–226.

Wolfe, J. A. 1990 Palaeobotanical evidence for a marked temperature increase following the Cretaceous/Tertiary boundary. *Nature, Lond.* **343**, 153–156.

Wolfe, J. A. & Upchurch, G. R. 1986 Vegetation, climatic and floral changes at the Cretaceous–Tertiary boundary. *Nature, Lond.* **324**, 148–151.

Wolfe, J. A. & Upchurch, G. R. 1987 North American nonmarine climates and vegetation during the late Cretaceous. *Palaeogeogr. Paleoclimatol. Palaeoecol.* **61**, 33–77.

Discussion

P. W. SKELTON (*Department of Earth Sciences, The Open University, Milton Keynes, U.K.*). Because of the apparent absence of mammalian browsers in the early Palaeocene, what does Dr Collinson suppose were the bulk feeders upon vegetation at this time? Or was the world covered in mulch?

M. E. COLLINSON. Today, the most important bulk feeders on vegetation are insects. This is especially the case in tropical rainforests (Wint 1983). On the evidence from physiognomy of North American leaf floras, Palaeocene mid-latitude vegetation is inferred to have been closed-canopy forest (Wolfe & Upchurch 1987). Evidence from fossil leaf damage suggests that insects were active herbivores well before the Palaeocene (Chaloner *et al.* this symposium). Assuming that leaf litter was as actively processed then as today, it is unlikely that the absence of mammalian herbivores in the early Palaeocene (and their negligible numbers during the rest of the Palaeocene) would have meant a Palaeocene world covered in mulch. Much of the continental Palaeocene sequence of the western U.S.A. does contain extensive coals. These coals are not interpreted as reworked forest floor litter, but as former mire deposits resulting from a post-Cretaceous increase in precipitation (Wolfe & Upchurch 1987).

Reference

Wint, G. R. W. 1983 Leaf damage in tropical rain forest canopies. In *Tropical rain forest: ecology and management* (ed. S. L. Sutton, T. C. Whitmore & A. C. Chadwick), pp. 229–239. Oxford: Blackwell Scientific Publications.

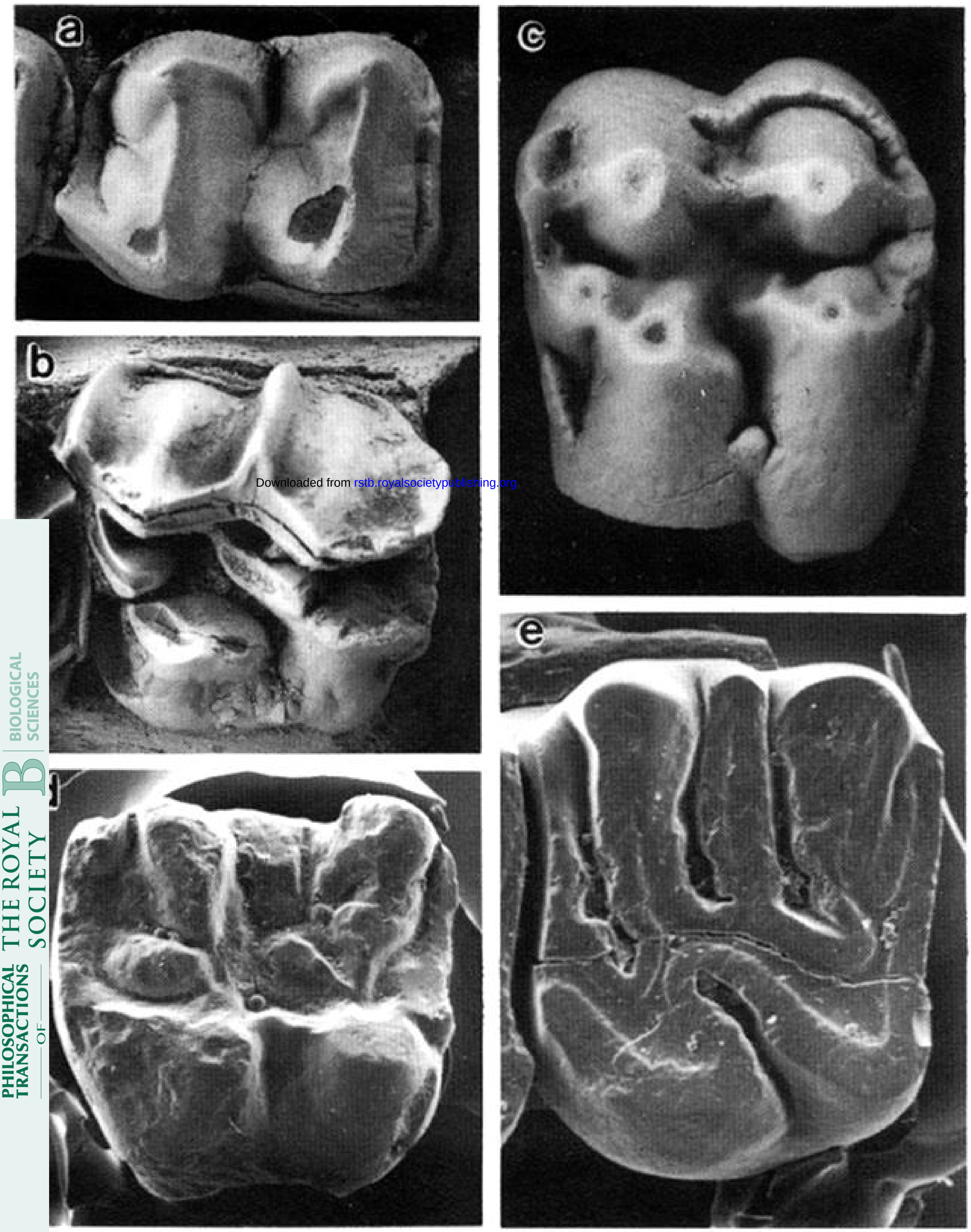
P. D. MOORE (*Division of Biosphere Sciences, King's College London, U.K.*). Dr Collinson has emphasized the importance of mammals in determining the course of fruit evolution in the angiosperms. Is it not possible that bird vectors may have played just as important a part in the evolution of dispersal mechanisms and hence in fruit structure?

M. E. COLLINSON. It is indeed possible that bird vectors played an important role in the evolution of fruit dispersal. Unfortunately, birds generally have a poorer fossil record than mammals and, except at certain sites, articulated skeletons are very rare. Nevertheless, there is direct evidence of frugivory in birds as early as the Middle Eocene from gut contents at Messel in Germany (see, for example, Schaal & Ziegler (1988), figures 82 and 217). This is clearly an area ripe for future study.

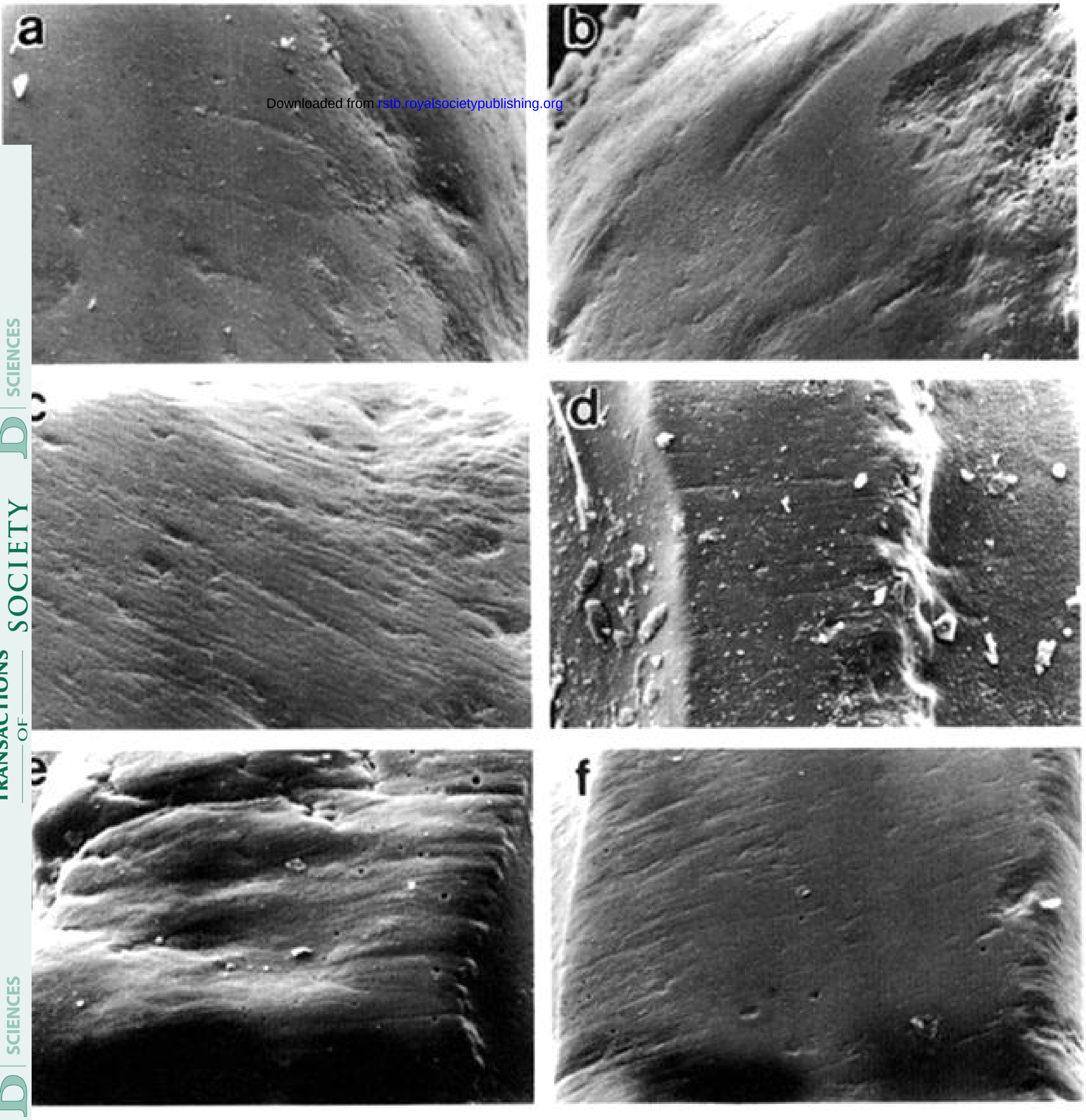
J. Ollerton (*Oxford Polytechnic, U.K.*). Apologies for being an ignorant plant ecologist, but what exactly does Dr Collinson mean by the term 'scansorial'?

R. McN. Alexander (*Department of Pure and Applied Biology, University of Leeds, U.K.*). I have an uncomfortable feeling that if I were given a selection of mammalian postcranial skeletons I might have difficulty in judging which belonged to small ground-living mammals, which to scansorial mammals and which to arboreal ones. Has Dr Collinson clear criteria for such distinctions? A multivariate analysis of skeletal form might make it easier to formulate reliable criteria.

M. E. Collinson. The criteria for recognizing tree-dwelling mammals relate to the necessity to rotate the feet to appropriate positions on the uneven substrate and to grip surfaces that depart significantly from the horizontal. Degree of rotation of the hind foot for instance can be judged from the distribution of articular facets on the astragalus and calcaneum (ankle joint). Gripping broad tree surfaces (e.g. trunks) is effected by strong laterally compressed claws (covering similarly shaped terminal phalanges) and describes the scansorial habit. Gripping narrow branches describes the arboreal habit and is effected by foot or tail prehensility, which can be assessed from the distribution of articular facets on the foot bones or from length of the tail plus degree of development of transverse processes and haemal arches on the tail vertebrae. A 'small' ground (semiterrestrial) mammal is one which lacks both these specializations and those typifying the 'large' ground (fully terrestrial) mammal, such as hooves, reduction of digits, or wrist and ankle joints that restrict lateral movement. It is thus the most difficult to recognize, but is a widespread locomotor mode today. We agree that a more rigorous classification of morphotypes relating to these locomotor modes is desirable.



gure 4. Upper (b–e) and lower (a) pre-ultimate molars of
sil mammals from the Eocene of southern England. (a–c)
, coated with ammonium chloride; (d–e) SEM. Numbers
er to specimens in the Palaeontology Department, Natural
story Museum (BM(NH)). (a) *Hyrachyus stehlini*, a
ophodont herbivore browser (perissodactyl), M50194,
2.5. (b) *Plagiolophus annectens*, a selenodont semihypsodont
rbivore browser (perissodactyl), 29715, ×2.3. (c) *Aco-
rulum quercyi*, a frugivore (artiodactyl), M29470, ×4.8.
) *Sciuroides rissonei*, a frugivore (soft) (rodent), M37368,
12. (e) *Thalerimys headonensis*, a semihypsodont herbivore
owser (rodent), 30159a, ×18.



igure 5. SEMs of microwear of fossil and modern mammal pper pre-ultimate molars (casts); buccal phase. Numbers efer to specimens in the Natural History Museum 3M(NH)); ZD indicates modern in Zoology Department, 1 or no prefix indicates fossil in Palaeontology Department. a) *Ratufa affinis*, ZD9.4.1.218; (b) *Sciuroides rissonei*, (figure d); (c) *Treposciurus mutabilis*, M51685; 9d) *Capreolus capreolus* nodern); (e) *Alcelaphus buselaphus* (modern); (f) *Plagiolophus nnectens*, M52683 (cf. figure 4b). (a–c) ×200; (d–f) ×60.