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# Mallee model for mammal communities of the early Cenozoic and Mesozoic

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## ABSTRACT

Mallee is an endemic Australian woodland and shrubland of semi-arid, summer–dry regions between dry woodland and desert shrubland. In other parts of the world, such as Africa and the Americas, such climatic regions support grassland ecosystems. Using Australian and African climofunctions and models gives very different reconstructions of paleoclimate (subhumid versus perhumid) and paleovegetation (woodland versus rainforest) for North American fossil mammal faunas before Cenozoic evolution of grassland ecosystems. Modern mammal faunas of Africa and Australia have different ecological spectra of taxonomic units, body size, feeding, and locomotion of species of mammals on precipitation gradients. Gradients in proportions of such categories yield transfer functions for mean annual precipitation from percent species of Artiodactyla or Macropodidae, percent species of moderately large animals (45–180 kg), percent species of arboreal mammals, and percent species of grazers. These transfer functions can be applied to fossil mammal faunas to estimate paleoprecipitation in Africa, Australia and North America. Modern transfer functions match well paleoprecipitation estimates based on depth to calcic horizons in paleosols at the same localities in Kenya and inland Australia back through the Miocene. For fossil mammal faunas of the Rocky Mountain region of North America, African transfer functions fail, but Australian transfer functions predict paleoprecipitation back to the Cretaceous–Tertiary boundary (66 Ma). Furthermore, modern mallee soils investigated in this study closely match Cretaceous to Eocene paleosols of the Rocky Mountains. Extinct mallee-like vegetation, such as pori woodlands of Kenya and cunhaka woodlands (newly defined) of the Rocky Mountains better explains the dominance of small, nocturnal, insectivorous, arboreal mammals of Paleogene and Mesozoic mammal faunas, than comparisons with African grassland or rainforest faunas.

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## 1. Introduction

Mammals of African grasslands are ecologically and taxonomically distinct from faunas elsewhere in the world (Gheerbrant and Rage, 2006; Shorrocks, 2007), yet are used to interpret the taphonomy and paleoecology of North American mammals (Bakker, 1983; Webb, 1983). Mammals of African grassland communities are geologically young, no more than 15 Ma, and as $C_4$-photosystem communities, no more than 7 Ma, based on evidence from the isotopic composition of pedogenic nodules and distinctive crumb ped structure of paleosols (Jacobs, 2004; Retallack, 2004a, 2004b, 2007a; Tipple and Pagani, 2007; Edwards et al., 2010). A modern analog widely applied to fossil mammalian faunas before evolution of grassland is the fauna of African rainforests (Andrews and Van Couvering, 1975; Archer et al., 1991), which have many small, nocturnal, arboreal mammals like Paleogene faunas (Andrews et al., 1979; Evans et al., 1981).

There are reasons to doubt that all Paleogene mammals lived in rainforest. Rainforests produce large leaves with drip tips, abundant vines, and dicot wood. Some Eocene fossil vertebrates are found at

localities with fossil plants of that description, such as the Clarno Nut Beds of Oregon (Manchester, 1994; Hanson, 1996). However, many vertebrate localities have associated fossil floras of medium to small leaves of legumes or eucalypts and few if any vines: such as the flora of the early Eocene (48 Ma) Green River Formation of Wyoming (MacGinitie, 1969), middle Eocene (46 Ma) Mahenge locality of Tanzania (Jacobs and Herendeen, 2004), and middle Miocene (16 Ma) Ngapakaldi locality of South Australia (Tedford, 1991). Evidence against rainforest is most convincing for fossil soils which entomb mammal fossils. Rainforest soils are thick, red and non-calcareous with hematite, boehmite, and kaolinite (Retallack, 2008a, 2010a), but many paleosols yielding mammals are smectitic with abundant carbonate nodules: such as the early Eocene Willwood Formation of Wyoming (Bown, 1979; Retallack, 1998; Kraus and Riggins, 2007), early Miocene sites of Songhor, Koru and Rusinga Island in Kenya (Retallack, 1991a; Retallack et al., 1995), and Miocene sites of Kangaroo Well and Lake Palankarinna in Australia (Metzger and Retallack, 2010). These are unlike soils of rainforest or grasslands, but indistinguishable from Australian mallee soils (Northcote, 1956; McKenzie et al., 2004). Quantitative estimates of mean annual precipitation fall well short of the minimum requirement (1750 mm) for rainforest (White, 1983), even in Australia, where rainforest is

very broadly defined (Webb, 1968). The spike in mean annual precipitation during the transient warm-wet spike of the basal Eocene is $605 \pm 147$ to $804 \pm 147$ using paleosol depth to Bk in Utah (Retallack, 2009a), $683 \pm 182$ to $1316 \pm 182$ mm using paleosol geochemistry in Wyoming (Kraus and Riggins, 2007), and $769^{+332}_{-232}$ to $1470^{+636}_{-444}$ mm using leaves in Wyoming (Wilf, 2000; Wing et al., 2005). Cenograms of ordered mammalian body masses of mammal faunas show a continuous linear distribution in rainforest communities that is distinct from a disjointed size distribution of grassland communities, but Australian mallee cenograms are also continuous, not broken (Stirling Range of Travouillon and Legendre, 2009). Finally, climate modeling cannot find the amount of water needed for rainforest as widespread as has been inferred from Australian Miocene mammals (Herold et al., 2011). This paper explores whether mallee faunas of southeastern Australia or rainforest and grassland faunas of Africa (Tables 1–3) are better modern analogs for fossil mammal faunas of the early Cenozoic and Mesozoic (Background dataset for online publication Tables 4–7).

This study builds on a tradition of ecological diversity characterization established by Andrews et al. (1979) for reconstructing climate and vegetation from fossil mammal faunas. Fundamental to the method is number of species within particular categories of taxa, size, locomotion and diet, which can be used to calculate proportional representation in the fossil record (Evans et al., 1981; Maas and Krause, 1994; Alroy, 1998; Janis, 2000; Nieto et al., 2005). These data also can be used to generate transfer functions to predict from mammal assemblages such local environmental variables as precipitation and vegetation (Kay and Madden, 1997; Reed, 1998). In the studies cited above, this approach was used with local assemblages (alpha diversity of Whittaker, 1972), but comparable results come from studies of regional diversity (gamma diversity within grid squares 240 km in size by Badgley and Fox, 2000; 158 km by Andrews and O'Brien, 2000; and 0.5° or 55 km at the equator by Eronen et al., 2010a,b). The alpha diversity approach is extended here to modern faunas of Australia, in order to derive predictive equations for precipitation from mammalian community composition for application to fossil assemblages in Australia, Kenya, and North America.

## 2. Mallee ecosystems

Mallee is an Australian aboriginal word for a woody plant community of stature intermediate (2–10 m) between woodlands and shrublands, and a distinctive tree architecture with multiple thin trunks (Whittaker et al., 1979). Mallee covers a large area of western Victoria, southwestern New South Wales, southeastern South Australia and southwestern Western Australia (Fig. 1), mainly in the climatic region of Australia with a Mediterranean (summer dry) climate (Hill, 1989). Fossil plants, pollen and soils provide evidence that mallee is an endemic Australian vegetation type dating from at least the middle Miocene (Martin, 1989; Metzger and Retallack, 2010). Mallee soils, plants and animals are similar in some ways to those of other woodlands such as those of ancient Greece (Retallack, 2008b), but mallee has been less profoundly altered by humans (Whittaker et al., 1979; Nicolle, 2006).

### 2.1. Plants

Mallee is dominated by many species of *Eucalyptus* with lignotubers and multiple, thin, spreading trunks (Fig. 2G, I). The mallee region however includes a variety of other small trees, including cypress pine (*Callitris columellaris*: Fig. 2C) and belah (*Casuarina cristata*; Fig. 2E). Mallee trees decline in stature from box woodlands (Fig. 2A) of regions receiving more than 500 mm mean annual precipitation to desert shrublands (Fig. 2K) receiving less than 200 mm mean annual precipitation (Fig. 3). In the data collected here (Table 3), the decline in average tree height (*H* in m) is related to mean annual precipitation (*P* in mm) and to depth to calcareous nodules (Bk) in soil (*D* in cm) by the following relationships (both $R^2 = 0.91$, standard error $= \pm 2.3$ m):

$$H = 16.13 \ln P - 84.71 \qquad (1)$$

$$H = 12.39 \ln D - 35.74. \qquad (2)$$

Mallee is easy to walk through, but has a continuous canopy, unlike the meadow-and-glade structure of African wooded grassland (Shorrocks, 2007). The ground under mallee is littered with branches and bark, rather than leaves, because mallee plants are evergreen. Mallee eucalypts (mallets) have a variety of adaptations to aridity: leaves which are small, rolled, reflective, hanging edgewise to the sun, and roots which are stout and deep. Mallee plants are also superbly adapted to fire: resprouting leafy branches from lignotubers in the ground and from epicormic shoots on charred trunks, and releasing seeds after scorching of gum nuts (Nicolle, 2006). Mallee is not vegetation early in ecological succession, but a mature community (Holland, 1986) of high plant diversity (Whittaker et al., 1979).

### 2.2. Soils

Mallee soils are silty to sandy, brown to red, and have common subsurface calcareous nodules (Figs. 2–3). In soil taxonomy (Soil Survey Staff, 2000) mallee soils are Aridisols, lacking the highly-organic surface horizons of grassland soils (Mollisols) and deeply weathered clayey subsurface horizons of rainforest soils (Ultisols, Oxisols). Australian mallee soils were regarded by Northcote (1956) as distinct enough for the name "Mallisol", but in modern Australian classifications (Isbell, 1998; McKenzie et al., 2004) these soils are Calcarosols, distinct from rainforest soils (Ferrosols) and bunch grassland soils (Vertosols). Mallee vegetation is found in rocky outcrops, such as Iron Knob (South Australia) and Stirling Range (Western Australia), but for most of its range grows on alluvium and loess of large sedimentary basins likely to be preserved in the sedimentary record (Wasson, 1989).

**Table 1**
Comparison of modern mallee, grassland and rainforest ecosystems.

| Mallee | Grassland | Rainforest |
|---|---|---|
| Low multiple bole trees (ca. 8 m) | Dense grasses (<1 m) | Large trees (10–100 m) |
| Sclerophyll leaves | Mesophytic leaves | Mesophytic leaves |
| Bunch grasses | Sod grasses | Bambusoid broad-leaved grasses |
| Bare ground showing | Complete ground cover | Bare ground showing |
| Low carbon soil (2 wt.% C) | High carbon soil (8–10 wt.% C) | Low soil carbon (<1 wt.% C) |
| Low soil moisture | High soil moisture | High soil moisture |
| Blocky angular soil peds | Granular-crumb soil peds | Spherical micropeds |
| Soil calcareous nodules | Soil calcareous nodules | Non-calcareous soils |
| Smectite soil clays | Smectite soil clays | Kaolinite soil clays |
| Endemic mammal clades | Cosmopolitan mammal clades | Endemic mammal clades |
| Few large (>180 kg) mammal species | Many large (>180 kg) mammal species | Few large (>180 kg) mammal species |
| Many non-bat mammal gliders | Few non-bat mammal gliders | Many non-bat mammal gliders |
| Many mammal fungivores and omnivores | Few mammal fungivores and omnivores | Many mammal fungivores and omnivores |
| Mammals different 500–1500 mm MAP | Mammals different 500–1500 mm MAP | Mammals similar 1800–4000 mm MAP |
| Mostly nocturnal mammals | Mostly diurnal mammals | Mostly nocturnal mammals |
| Paws | Hooves | Paws |
| Common cursorial bipeds | Rare bipeds | Rare bipeds |
| Noncursorial quadrupeds | Cursorial quadrupeds | Noncursorial quadrupeds |
| Brachydont molars | Hypsodont molars | Brachydont molars |
| Plagiaulacid premolars | Conical premolars | Conical premolars |

**Table 2**
Indigenous mallee mammals (excluding bats) of Mildura, Victoria.
Sources: Strahan (1995), Bennett et al. (2006).

| Species | Common name | Family | Body mass (kg) | Locomotion | Diet | Activity |
|---|---|---|---|---|---|---|
| *Tachyglossus aculeatus* | Spiny echidna | Tachyglossidae | 2–7 | Large ground | Insectivore | Nocturnal |
| *Ornithorhynchus anatinus* | Platypus | Ornithorynchidae | 1.0–2.2 | Aquatic | Omnivore | Diurnal |
| *Lasiorhinus latifrons* | Southern hairy-nosed wombat | Vombatiformes | 19–32 | Large ground | Grazer | Nocturnal |
| *Antechinus flavipes* | Yellow-footed antechinus | Dasyuridae | 0.02–0.08 | Scansorial | Insectivore | Nocturnal |
| *Dasyurus geoffroii* | Western quoll | Dasyuridae | 0.6–2.2 | Scansorial | Carnivore | Nocturnal |
| *Dasyurus maculatus* | Spot-tailed quoll | Dasyuridae | 4–7 | Scansorial | Carnivore | Nocturnal |
| *Ningaui yvonneae* | Mallee ningaui | Dasyuridae | 0.004–0.01 | Small ground | Insectivore | Nocturnal |
| *Phascogale calura* | Red-tailed phascogale | Dasyuridae | 0.04–0.07 | Small ground | Insectivore | Nocturnal |
| *Planigale gilesi* | Paucident planigale | Dasyuridae | 0.005–0.016 | Scansorial | Omnivore | Nocturnal |
| *Planigale tenuirostris* | Narrow-nosed planigale | Dasyuridae | 0.004–0.009 | Scansorial | Omnivore | Nocturnal |
| *Sminthopsis crassicaudata* | Fat-tailed dunnart | Dasyuridae | 0.01–0.03 | Small ground | Insectivore | Nocturnal |
| *Sminthopsis murina* | Slender-tailed dunnart | Dasyuridae | 0.01–0.03 | Small ground | Insectivore | Nocturnal |
| *Chaeropus ecaudatus* | Common dunnart | Peramelidae | 0.2 | Small ground | Insectivore | Nocturnal |
| *Isodon* af. *I. auratus* | Short-nosed bandicoot | Peramelidae | 0.25–0.67 | Small ground | Omnivore | Nocturnal |
| *Macrotis lagotis* | Bilby | Peramelidae | 1.0–2.5 | Large ground | Omnivore | Nocturnal |
| *Perameles bougainville* | Western barred bandicoot | Peramelidae | 0.18–0.29 | Small ground | Omnivore | Nocturnal |
| *Perameles gunni* | Eastern barred bandicoot | Peramelidae | 0.5–1.45 | Large ground | Omnivore | Nocturnal |
| *Phascolarctos cinereus* | Koala | Phascolarctidae | 7–15 | Arboreal | Browser | Diurnal |
| *Petaurus breviceps* | Sugar glider | Phalangerida | 0.1–0.2 | Aerial | Omnivore | Nocturnal |
| *Petaurus norfolcensis* | Squirrel glider | Phalangerida | 0.2–0.3 | Aerial | Omnivore | Nocturnal |
| *Trichosurus vulpecula* | Common brushtail possum | Phalangerida | 1.5–4.5 | Arboreal | Omnivore | Nocturnal |
| *Cercarcetus concinnus* | Western pygmy mouse | Burramyidae | 0.008–0.02 | Arboreal | Insectivore | Nocturnal |
| *Cercartetus lepidus* | Little pygmy mouse | Burramyidae | 0.006–0.008 | Arboreal | Insectivore | Nocturnal |
| *Pseudocheirus peregrinus* | Common ringtail possum | Pseudocheiridae | 0.7–1.1 | Arboreal | Browser | Nocturnal |
| *Acrobates pygmaeus* | Feathertail glider | Acrobatidae | 0.01–0.04 | Aerial | Omnivore | Nocturnal |
| *Bettongia leseur* | Burrowing bettong | Potoroidae | 1.5 | Large ground | Fungivore | Nocturnal |
| *Bettongia penicillata* | Brush-tailed bettong | Potoroidae | 1.3–1.6 | Large ground | Fungivore | Nocturnal |
| *Lagorchestes leporides* | Eastern hare wallaby | Macropoidea | 1–10 kg | Ground | Browser | Diurnal |
| *Macropus fuliginosus* | Western gray kangaroo | Macropodidae | 3–53.5 | Large ground | Grazer | Diurnal |
| *Macropus greyi* | Toolache wallaby | Macropodidae | 10–45 | Large ground | Grazer | Diurnal |
| *Macropus robustus* | Common wallaroo | Macropodidae | 6–47 | Large ground | Grazer | Diurnal |
| *Macropus rufogriseus* | Red-necked wallaby | Macropodidae | 15–27 | Large ground | Grazer | Diurnal |
| *Macropus rufus* | Red kangaroo | Macropodidae | 17–85 | Large ground | Grazer | Diurnal |
| *Onychogalea fraenata* | Bridled nailtail wallaby | Macropodidae | 4–8 | Large ground | Grazer | Diurnal |
| *Onychogalea lunata* | Crescent nailtail wallaby | Macropodidae | 3.5 | Large ground | Grazer | Diurnal |
| *Wallabia bicolor* | Black wallaby | Macropodidae | 10.3–20.5 | Large ground | Browser | Diurnal |
| *Hydromys apicalis* | Water rat | Muridae | 0.34–1.27 | Aquatic | Carnivore | Diurnal |
| *Leporillus apicalis* | Lesser stick-nest rat | Muridae | 0.15 | Small ground | Browser | Nocturnal |
| *Leporillus conditor* | Greater stick-nest rat | Muridae | 0.18–0.45 | Small ground | Browser | Nocturnal |
| *Notomys mitchelli* | Mitchell's hopping mouse | Muridae | 0.04–0.06 | Small ground | Frugivore | Nocturnal |
| *Pseudomys apodemoides* | Silky mouse | Muridae | 0.016–0.022 | Small ground | Frugivore | Nocturnal |
| *Pseudomys bolami* | Bolam's mouse | Muridae | 0.01–0.21 | Small ground | Frugivore | Nocturnal |
| *Pseudomys desertor* | Desert mouse | Muridae | 0.015–0.035 | Small ground | Frugivore | Nocturnal |

## 2.3. Mammals

The native fauna of mallee vegetation includes a variety of marsupials and monotremes of small size, insectivorous to frugivorous diet, and nocturnal activity patterns (Tables 1–2). Unusual for such dry climates is the high proportion of arboreal and aerial mammals: the latter including gliders (Table 2), as well as 16 species of bats (Bennett et al., 2006). Also distinctive are fungivores, such as bettongs (*Bettongia leseur*), which exhume and consume native truffles (Maser et al., 2009).

## 2.4. Other animals

The invertebrate fauna of mallee is dominated by ants, unlike grasshopper and termite dominance of Australian grasslands and rainforest (Greenslade and Greenslade, 1989: Shorrocks, 2007). Of

**Table 3**
Mallee, woodland and shrubland study sites in New South Wales, Australia.

| Location | Coordinates | MAP (mm) | Plant height (m±2σ) | Maximum plant height (m) | Soil A horizon thickness (cm) | Soil Bk depth (cm) | Dominant species | Formation |
|---|---|---|---|---|---|---|---|---|
| Gunbar | S33.95894° E145.12595° | 203 | 0.3±0.3 | 1.42 | 16 | 16 | Saltbush (*Sclerolaena tricuspis*) | Shrubland |
| Booligal | S34.03244° E144.82653° | 204 | 1.01±0.6 | 1.54 | 17 | 21 | Nitre goosefoot (*Chenopodium nitrarium*) | Shrubland |
| Lake Mungo | S33.74500° E143.08167° | 226 | 0.3±0.2 | 0.52 | 9 | 23 | Bluebush (*Maireana pyramidata*) | Shrubland |
| Damara | S34.15419° E143.32983° | 274 | 7.4±2.9 | 10.7 | 30 | 35 | Yellow mallet (*Eucalyptus incrassata*) | Mallee |
| Goolgowi | S34.00914° E145.66322° | 299 | 11.1±5.0 | 16.1 | 27 | 34 | White cypress pine (*Callitris columellaris*) | Woodland |
| Balranald | S34.55142° E143.58503° | 322 | 7.5±3.0 | 11.24 | 12 | 37 | Red mallet (*Eucalyptus socialis*) | Mallee |
| Maude | S34.46547° E144.32517° | 364 | 10.3±4.2 | 13.9 | 30 | 37 | Black box (*Eucalyptus largiflorens*) | Woodland |
| Back Creek | S33.86613° E147.35642° | 476 | 15.7±2.8 | 19.8 | 23 | 65 | Belah (*Casuarina cristata*) | Woodland |
| Narrandera | S34.75156° E146.50253° | 483 | 14.7±5.2 | 21.1 | 17 | 52 | Yellow box (*Eucalyptus melliodora*) | Woodland |
| Bland Creek | S33.76181° E147.51970° | 507 | 13.9±6.4 | 20.9 | 32 | 60 | Apple-top box (*Eucalyptus bridgesiana*) | Woodland |
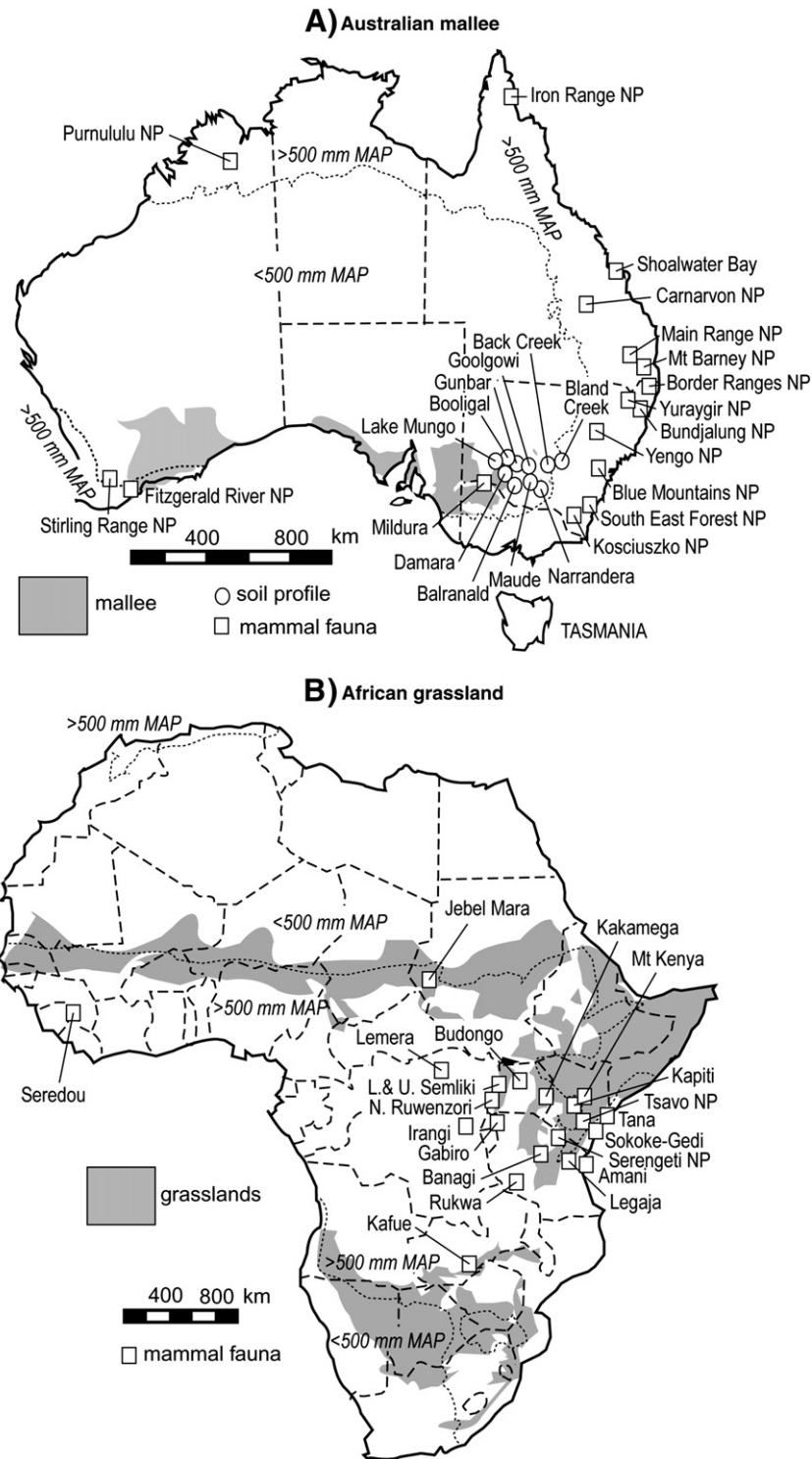
**Fig. 1.** Distribution of mallee in Australia (A: from Hill, 1989) and grassland in Africa (B: from White, 1983), with locations of soil profiles studied in Australia (open circles) and modern mammal faunas studied in Australia (A) and Africa (B).

170 species of mallee lizards and frogs, 101 are small and hide in cracks, 42 are fossorial, 19 scansorial and 8 arboreal (Cogger, 1989). The mallee bird fauna is diverse (92 resident species of 292 observed including migrants and waterbirds: Emison and Bren, 1989), and includes two large ground birds. First, the mallee fowl (*Leipoa ocellata*), 0.6 m long and 1.5–2.5 kg in weight, forms large (1 m deep, 1.8 m diameter, 0.5 m high) fermentative incubation mounds in the soil (Frith, 1962). Second, the emu (*Dromaius*

*novohollandiae*) is 1.5–1.9 m tall and weighs 18–48 kg (Davies, 2003).
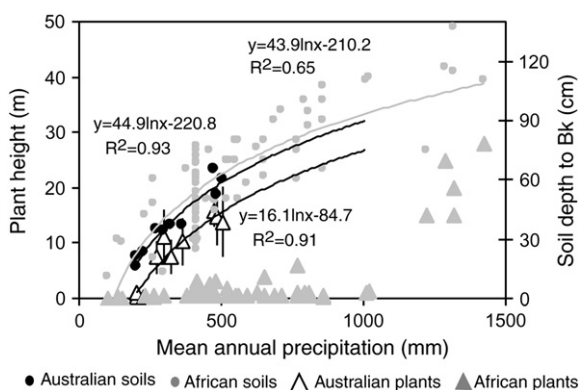
## 3. Materials and methods

This research included separate data compilations for modern and fossil soils and mammals, with modern data used to derive climofunctions for use with fossil data.
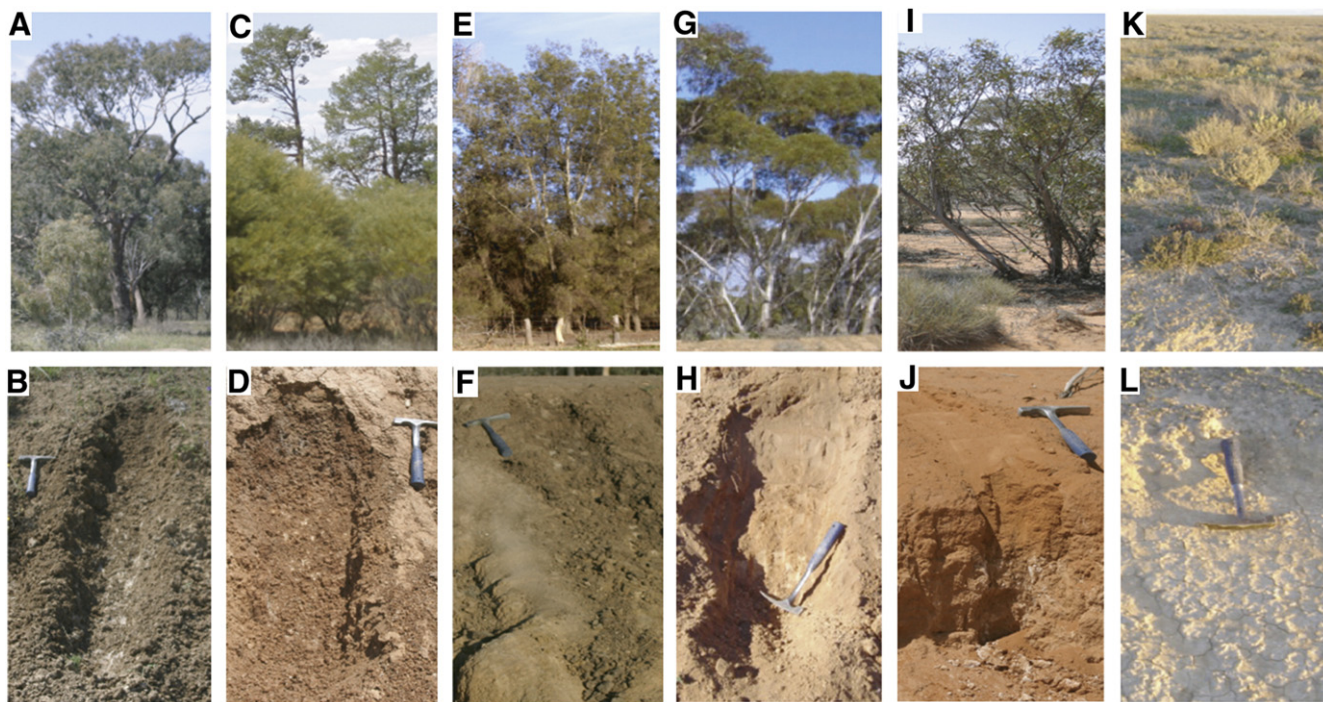
**Fig. 2.** Studied soil profiles and vegetation in western New South Wales; A–B, box woodland in Bland Creek; C–D, white cypress woodland near Goolgowi; E–F, belah woodland in Back Creek; G–H, mallee woodland near Balranald; I–J, mallee shrubland near Damara; K–L, desert shrubland at Mungo Lake. Scales for soils are hammer with handle 25 cm long, and heights and other details of vegetation are in Table 3.

### 3.1. Soils

Fieldwork for this study included study of soil profiles, measurement of vegetation stature and identification of living plants in southwestern New South Wales, Australia (Table 3). Heights of 100 of the tallest plants were measured using a laser rangefinder (Opti-logic model 100LHA). Soils at each station were examined by digging in existing road cuts and waterhole banks. Graphic sections of the soils (Fig. 4A–J) were measured with a milliner's tape, tested for acid reaction with dilute hydrochloric acid and fresh colors taken with a Munsell color chart. The depth to carbonate nodules (Bk horizon) and height of mallee vegetation in New South Wales are shown in Fig. 3, which also shows for comparison, African data on depth to carbonate nodules and plant height (both culled from a global database of Retallack, 2005).

### 3.2. Paleosols

Pedological data also are presented here for Eocene and Cretaceous paleosols (Fig. 4K–M): Luluta pedotype (5.4 m in section of Retallack, 1998) of the Sand Creek facies (Bown, 1979) of the Willwood Formation (early Eocene) in Sand Creek 6 miles east of Worland, Wyoming (Fig. 4K: N43.999035° W107.845628°), Zizi pedotype (6.6 m in section of Retallack, 1998) in the Elk Creek facies of the Willwood Formation (early Eocene) in Elk Creek 10 miles northwest of Worland, Wyoming (Fig. 4L: N44.078963° W108.130487°), and Ainka pedotype in the Mussentuchit Member of the Cedar Mountain Formation (mid-Cretaceous) high (171 m in section of Retallack, 2009a) on the eastern ridge of Little Cedar Mountain km north east of Castle Dale, Utah (Fig. 4M: N39.19456° W110.80373°). These are representative of 2468 moderately developed paleosols from 40 different sites for Permian to Eocene rocks of Utah and surrounding states documented by Retallack (2009a).

### 3.3. Modern mammals

My Australian mammal compilation aimed to assign species in modern local assemblages to ecological categories comparable with those used by Andrews et al. (1979) for an African compilation of local mammal faunas of comparable diversity. As in that study, bats were not included because they are rarely fossilized along with other mammals. Species lists for nature preserves and national parks were obtained from various printed sources (Schodde et al., 1992; Woinarski, 1992; Thomson-Dans et al., 1993; Chapman, 1995; McCarthy et al., 2004; Bennett et al., 2006) and government-maintained websites (http://wildlifeatlas.nationalparks.nsw.gov.au, accessed June 22, 2009; http://www.epa.qld.gov.au, accessed June 3, 2009). Taxonomic category, sizes, diets, and locomotion for each Australian taxon were from Strahan (1995). A total of 71 local faunas were considered for this study, but only 16 of those had 30 or more taxa (Fig. 1, see Background dataset for online publication Table 4),
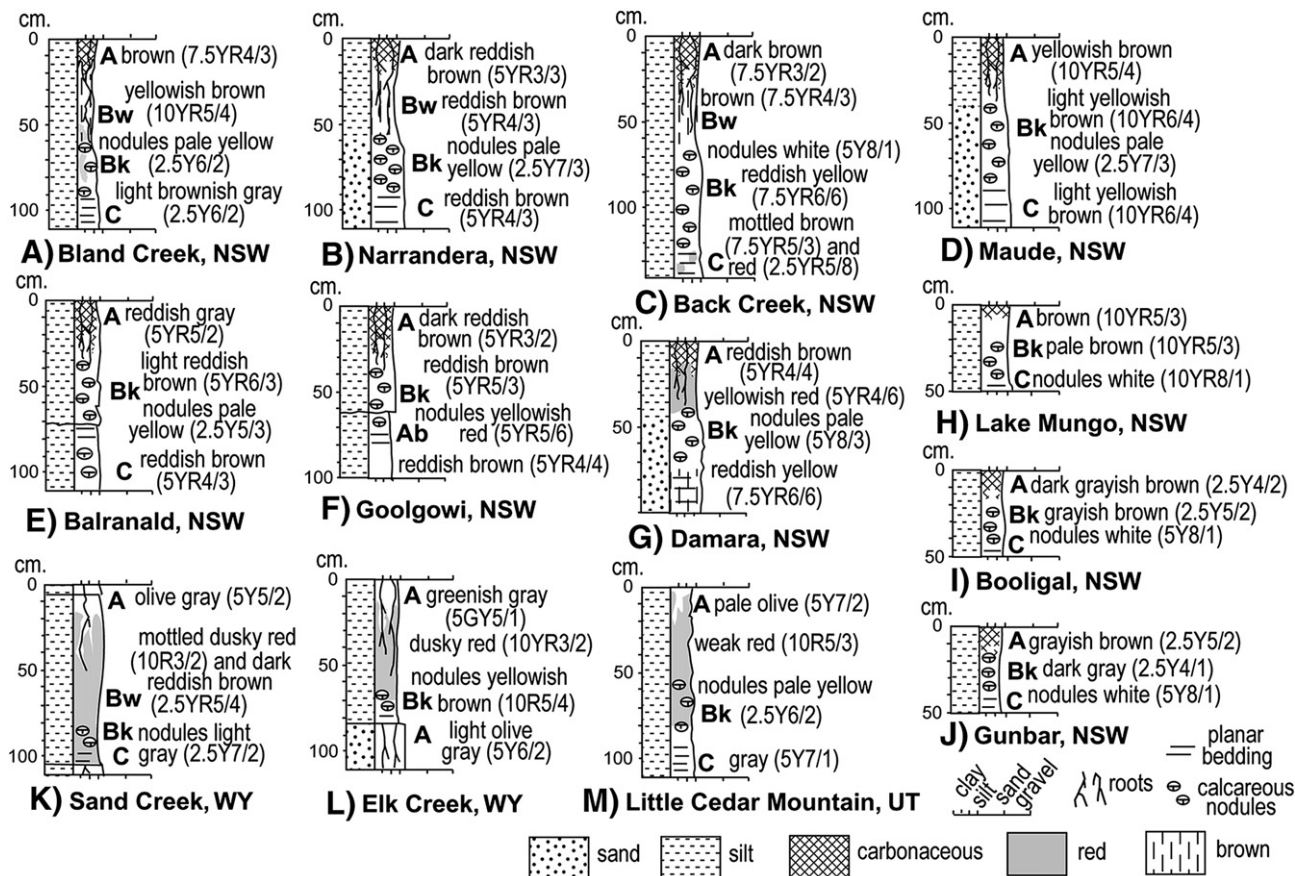


**Fig. 3.** Distribution of depth to carbonate nodular (Bk) horizon and plant height in the Australian soils studied here (Table 3), compared with depth to carbonate in African soils and heights of African vegetation (Retallack, 2005).

**Fig. 4.** Australian soils of dry woodland mallee and desert shrubland examined (A–J: Table 3), and early Eocene paleosols from the Willwood Formation, near Worland, Wyoming, U.S.A. (Retallack, 1998) and a Cretaceous (Albian) paleosol from the Mussentuchit Member, Cedar Mountain Formation, near Cedar Mountain, Utah, U.S.A. (Retallack, 2009a).

because of human alteration of Australian mammal faunas (McKenzie et al., 2007). Bandicoots (e.g. *Chaeropus ecaudatus*, *Isoodon macrourus*, *Perameles nasuta*) are the most vulnerable component of the Australian fauna to anthropogenic extinctions: most local faunas of less than 30 species lacked bandicoots. Mean annual precipitation for each fauna was obtained from an Australian government website (www.bom.gov. au accessed June 22, 2009).

*3.4. Fossil mammals*

My compilation of fossil mammal assemblages (Fig. 5) in Australia, Kenya and Rocky Mountain region of the western US (see Tables 5–7 in Background dataset for online publication) emphasized particular local faunas (alpha diversity) for comparability with the modern compilations of particular local faunas. Thus each fossil assemblage is from a small region (<1 km$^2$) at the same stratigraphic level. Online compilations such as the Paleobiology Database were a useful biblio-graphic tool for both taxa and taphonomic information, but this study used primary literature and cited sources. Most sites were calcareous paleosols or wetlands with disarticulated bones (Pickford, 1986; Retallack, 2009a; Metzger and Retallack, 2010), although some sites at Riversleigh are limestone fissure sites (Travouillon et al., 2009). The main criterion for inclusion was an adequate number of taxa. Lists of taxa per fossil fauna were compiled from primary liter-ature of Australia (Marshall, 1975; Merrilees, 1975; Hope, 1978; Rich, 1991; Long et al., 2002; Megirian et al., 2004; Travouillon et al., 2009), Kenya (Madden, 1972; Isaac, 1978; Savage and Willamson, 1978; Pickford and Andrews, 1981; Thomas, 1981; Hill et al., 1985, 2001; Pickford, 1986, 2000, 2001a, 2001b, 2007; Retallack, 1991a; Nakaya, 1994; Leakey et al., 1995; Retallack et al., 1995; Hill, 1996;

Behrensmeyer et al., 2002; Retallack et al., 2002; Leakey and Harris, 2003; Pickford and Kunimatsu, 2005; Pickford and Senut, 2005; Tsujikawa, 2005a,b; Ambrose et al., 2007; Peppe et al., 2009) and the United States (Douglass, 1903; MacDonald, 1949; Black, 1961; Munthe, 1988; Rasmussen, 1989; Emry, 1990; Stucky et al., 1990; Bown et al., 1994; Gunnell, 1994; McDonald et al., 1996; Prothero and Emry, 1996; Cross and Yi, 1997; Pinsof, 1998; Cifelli et al., 1999; Rasmussen et al., 1999; Reynolds and Lindsay, 1999; Turner and Peterson, 1999; Hill, 2001; Tabrum et al., 2001; Ackersten et al., 2002; Sankey, 2002; Foster, 2003; Gingerich, 2003; Kielan-Jaworowska et al., 2004; Eaton, 2006a,b; Barnosky et al., 2007; Retallack, 2007b).

The classification of Cretaceous mammals used here follows Kielan-Jaworowska et al. (2004). Cimolesta is used in the sense of McKenna and Bell (1997) for a pangolin clade including Palaeorcytidae, Cimolestidae, Apatemyidae, Stylinodontidae, Tillotheriidae, Wanglidae, Harpyodidae, Bemalambdidae, Pastoralodontidae, Titanoideidae, Pantolambdidae, Barylambdidae, Cyriacotheriidae, Pantolambdodon-tidae, Coryphodontidae, Pantolestidae, Paroxyclaenidae, Ptolemaiidae, Epoicotheriidae, Metacheiromyidae, Manidae, and Ernanodontidae. Cete, the whale order of McKenna and Bell (1997) includes the following terrestrial clades: Triisodontidea, Mesonychidae and Hap-alodectidae. Other orders of McKenna and Bell (1997) used here include Dinocerata (Uintatheriidae), Procreodi (Oxyclaenidae, Arctocyonidae), Condylarthra (Hyopsodontidae, Mioclaenidae, Phenacodontidae, Periptychidae, Peligrotheriidae, Didolodontidae) and Arctostylopida. Not included in this study were bats (Chiroptera and Dermoptera, in-cluding fossil Mixodectidae), because they are seldom found with other mammal fossils.

Geological ages of Kenyan fossil sites summarized by Pickford (1986), have been modified by Leakey and Harris (2003), Pickford
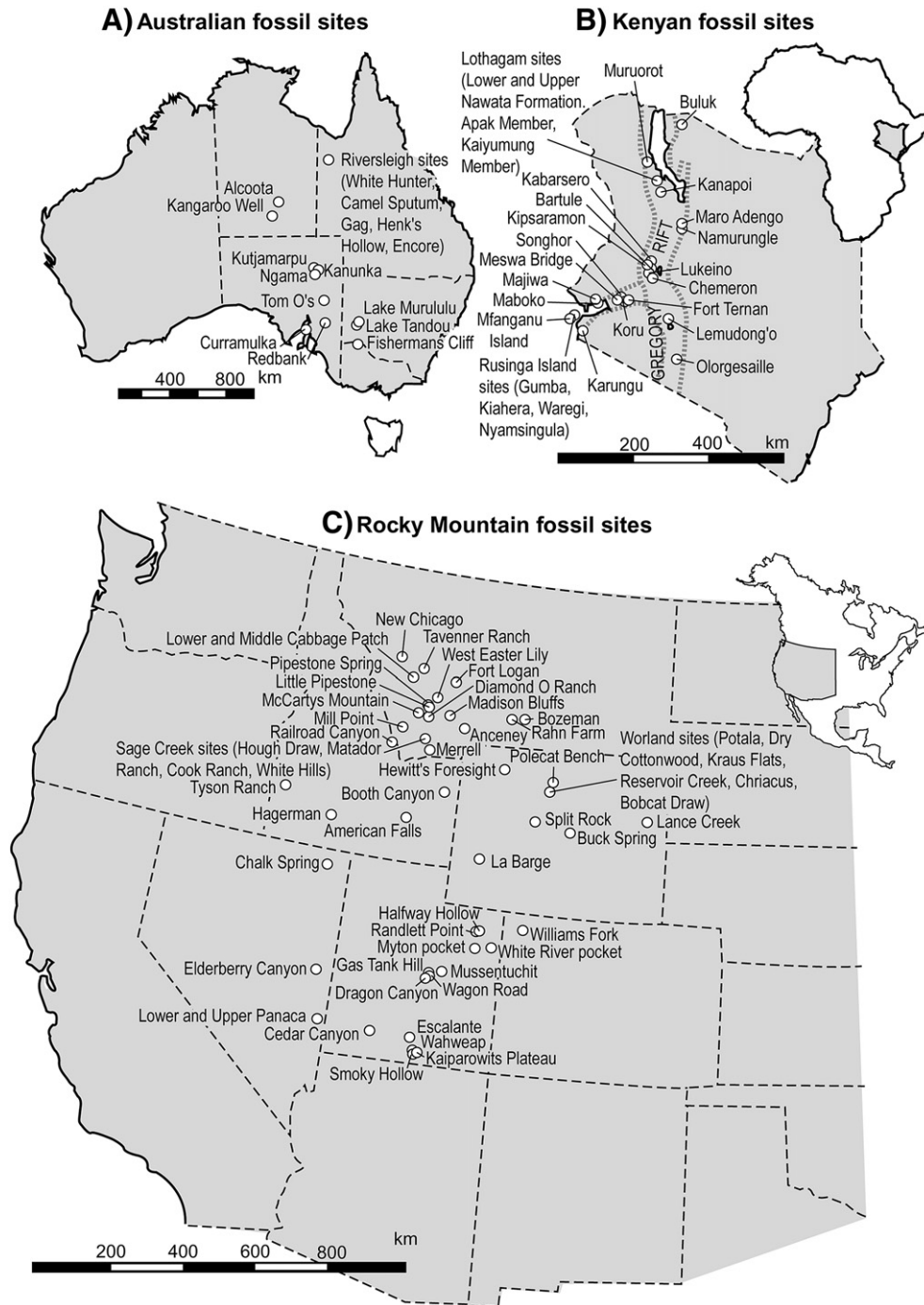
**Fig. 5.** Cenozoic and Mesozoic fossil sites studied in Australia (A), Kenya (B) and the Rocky Mountain region, U.S.A. (C).

et al. (2006), Ambrose et al. (2007), and Peppe et al. (2009). Ages of Australian sites are from Metzger and Retallack (2010) and of Rocky Mountain sites from Retallack (2007b, 2009a).

The sizes (in kg) of most Australian fossil mammals were taken from the estimates of Travouillon et al. (2009) and some African mammal sizes were from Silva and Downing (1995). Other Australian marsupial weights were estimated from fossil teeth and jaws using regressions of Myers (2001). Sizes of African and North American fossil mammals were calculated using regression equations of Damuth and McFadden (1990) based on molar length, Legendre (1988) using car-nassial area of carnivores, Hopkins (2008) based on toothrow length of rodents, and Hemmer (2007) based on molar area of primates.

Locomotion was inferred from skeletal proportions and modern relatives (Rose, 1990; Strahan, 1995; Janis, 2008), and diets inter-preted from tooth morphology, wear and isotopic composition (Janis et al., 1998, 2008; Long et al., 2002; Leakey and Harris, 2003; Kielan-Jaworowska et al., 2004). Multituberculates and Australian macropoids with plagiaulacid premolars longer than molars are here considered fungivores (Retallack, 2010a), because of the observed diet of living potoroos and bettongs with this distinctive tooth type (Lee and Cockburn, 1985; Seebeck et al., 1989). Fungivores thus include the following multituberculate families: Eobataaridae, Plagiaulacidae, Ptilodontoidea, Eucosmodontidae, and Arginbaataridae. Other multi-tuberculates with $P_4$ shorter than $M_x$ are here interpreted as omnivores:

Allodontidae, Paulchoffatidae, Cimolomyidae, Taeniolabidoidea, and Djadochtatheroidea. Additional evidence for gritty diet and wide gape around large food items has been presented for fossil multituberculates by Krause (1982) and for fossil kangaroos by Flannery (2004). A spreadsheet with all specific interpretations and literature sources can be downloaded from my website http://pages.uoregon.edu/dogsci/doku.php?id=directory/faculty/greg/about.

## 3.5. Climofunctions

Categories for each fossil assemblage were converted to percentages for comparison of variation in proportion to different categories through time. All possible relationships between faunal proportions and mean annual precipitation at the modern sites in Africa and Australia were explored initially using linear regression (Table 8 in Background dataset for online publication). Those with the highest coefficient of determination in linear regression were then further investigated by curve fitting to find the most significant climofunctions. These predictive equations of paleoprecipitation from fossil mammalian faunal proportions could then be compared with estimates of paleoprecipitation calculated from depth to calcareous nodules (Bk horizon) in paleosols (Retallack, 2005) for the same regions of Kenya (Retallack, 2007a), Australia (Metzger and Retallack, 2010) and North America (Retallack, 2007b, 2009a).

## 4. Modern mammal variation with climate

Proportional variation in different ecological categories along a rainfall gradient in Africa (Fig. 6) and Australia (Fig. 7) is modest over the whole range of mean annual precipitation from 1500 to 2500 mm. Africa differs from Australia however in showing two distinct segments: steeper variation in mammalian faunal composition is found between 500 and 1000 mm mean annual precipitation than under higher precipitation.

### 4.1. Taxa

The obvious difference between African and Australian faunas is dominance of African mammals by ruminants (Artiodactyla) and Australia by kangaroos (Macropodidae, which is within Phalangerida but here kept separate from other "Phalangerida pars"). The drier the climate and more open the vegetation, the more diverse are these higher taxa (Background dataset for online publication Table 4).

Both Artiodactyla and Macropodidae are cursorial (suited to running), compared with other mammals (Bakker, 1983; McGowan et al., 2008). Nevertheless, paws and springing hop (saltatorial locomotion) of kangaroos is a fundamentally different form of locomotion than later evolved hooves and gallop of artiodactyls. African grasslands are softened by spreading turf of grasses with buried rhizomes and modular growth adapted to abuse by herds of hard hooves (Shorrocks, 2007). In contrast, Australian woodlands are, and presumably were, silty, sandy, or rocky with scattered plant obstacles, including shed limbs and bark of mainly woody plants (McKenzie et al., 2004). These comparisons support the notion that paws are an ancestral condition that evolved in woodlands, whereas hooves are derived grassland adaptations (Bakker, 1983).

### 4.2. Size classes

Small mammals dominate the specific diversity of both African and Australian mammal faunas. In dry climates (mean annual precipitation 500–1500 mm) the representation of small mammals declines in Africa, but not in Australia. Australia is quite different from Africa in lacking elephant to zebra sized mammals (>180 kg). Even in the category of pig to gazelle sized animals (45–180 kg), and baboon to dog sized species (1–45 kg), Australia is less diverse (Figs. 6B, 7B).
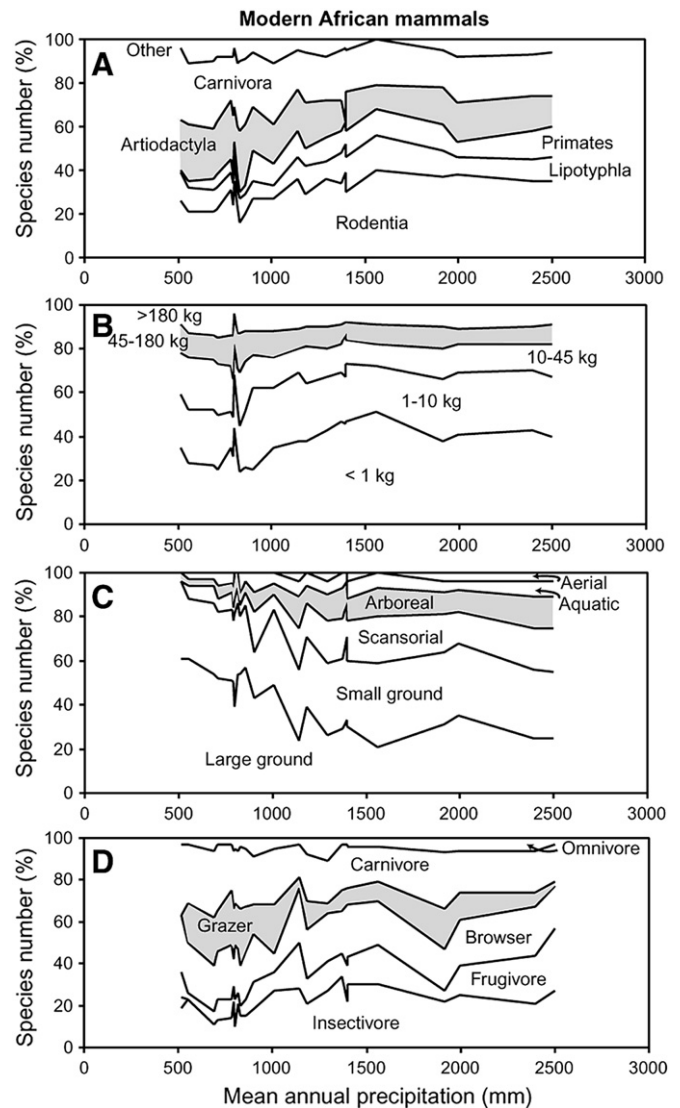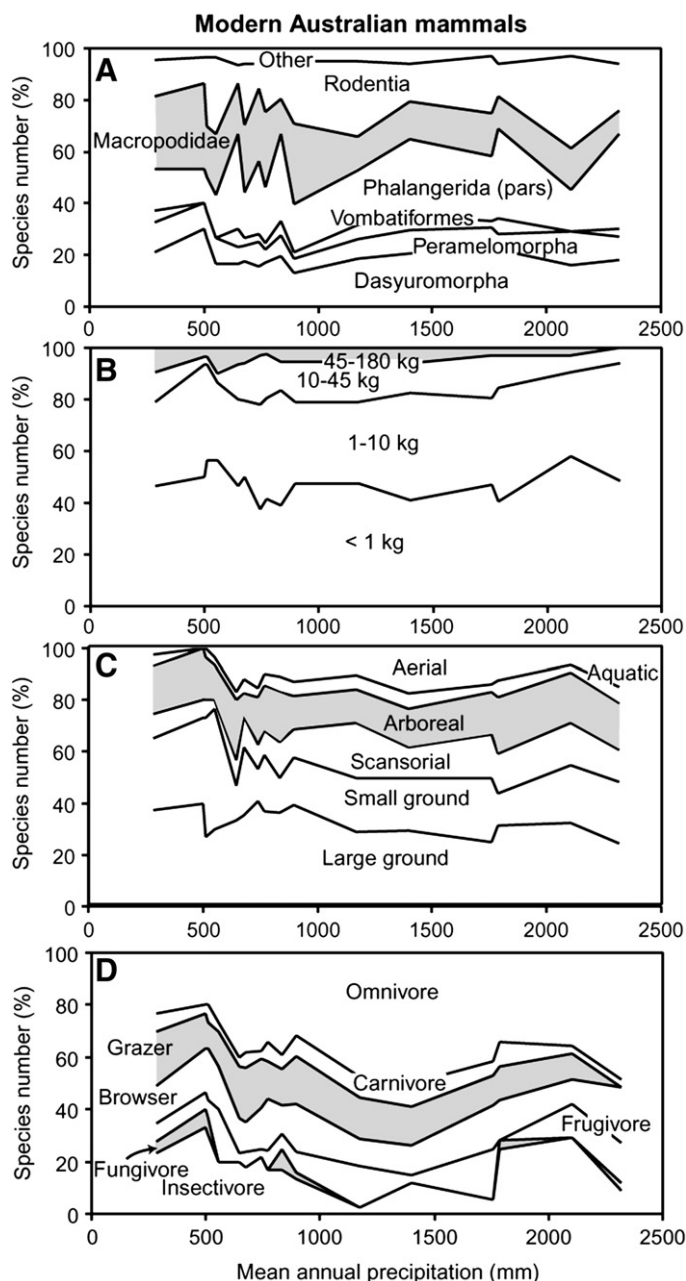


Fig. 6. Percent species of mammals in categories of higher taxa (A), size (B), locomotion (C) and diet (D) along a precipitation gradient of the studied faunas of Africa (Fig. 1). Data is from Andrews et al. (1979).

The lack of large (>180 kg) mammals in Australia is due to Pleistocene (ca. 45 Ka) extinction of megafauna, including bunyips (Diprotodon optatum) and large flightless birds (Genyornis newtoni: Murray and Vickers-Rich, 2004). This extinction is commonly blamed on immigrant aboriginals and their "fire-stick farming" (Barnosky et al., 2004; Miller et al., 2005). Like elephants in Africa today, extinct Australian megafauna roamed through most Australian climatic zones (Hope, 1978; Prideaux et al., 2007; Turney et al., 2008; Forbes et al., 2010). The greater decline of mouse-sized mammals (<1 kg) in dry climates (500–1500 mm mean annual precipitation) of Africa may be due to the predatory pressure of eagles and falcons there. Heavily grazed and trampled African grasslands afford little cover and food for small mammals compared with mallee woodland and saltbush deserts of Australia.

### 4.3. Locomotion

The steep decline in aerial, arboreal and scansorial mammals in Africa toward dry regions (500–1500 mm mean annual precipitation) is quite different from the pattern in Australia (Figs. 6C, 7C). Aerial mammals glide from tree to tree, arboreal mammals live all their

**Fig. 7.** Percent species of mammals in categories of higher taxa (A), size (B), locomotion (C) and diet (D) along a precipitation gradient of the studied faunas of Australia (Fig. 1). Data is from Table 4 (see also data online at http://pages.uoregon.edu/dogsci/doku. php?id=directory/faculty/greg/about).

lives in trees, and scansorial mammals take to trees with facility, but also forage widely on the ground (Andrews et al., 1979).

Aerial, arboreal and scansorial locomotory categories are all dependent on trees, so that changing proportions mirror the open parkland vegetation structure of African grasslands compared with the low woodland structure of Australian mallee (Fig. 3). Continuity of canopy may be a key variable in maintaining viable populations of aerial and arboreal mammals, although some, such as African bush babies (*Galago senegalensis*), persist even in open wooded grass-lands (Coe, 1985). Small size is also necessary for aridland arboreal mammals, because trees are small with thin and flexible branches in dry regions.

### 4.4. Diet

A striking difference between Africa and Australia is the high proportion of omnivores in Australia (Figs. 6D, 7D). Obligate fungivores are found in Australia, but unrecorded in Africa.

These dietary differences could be a study bias, because the African data are based on traditional concepts of the diet of Lipotyphla and other small mammals as insectivores (Andrews et al., 1979). Australian data are based on more recent observations of diets compiled by Strahan (1995), who notes that many Australian small mammals previously regarded as insectivores take a wide variety of small food items including plants, mollusks, seeds, fruits, frogs and lizards. Even combining omnivores and insectivores, there are still proportionally more in Australia than Africa.

The preference of potoroos and bettongs for truffles has been documented by direct observation and analysis of feces (Lee and Cockburn, 1985; Seebeck et al., 1989), and is unlikely to have been overlooked in Africa. Most truffles are associated with woody plants as mycorrhizae (Flannery, 2004; Maser et al., 2009), so this difference may reflect the dominance of woody plants in Australian aridlands, compared with grasses in Africa. Truffle-eating macropoids all contain plagiaulacid premolars, which are more elongate than molars ($P_4 > M_x$) in truffle specialists than facultative truffle eaters (Retallack, 2010b). The grooved blade of the plagiaulacid premolar is well suited to slicing large truffles, because its steep sides shed attached grit, rather than occluding on these hard particles.

## 5. Mammalian climofunctions

Regressions were fit to chosen ecological categories versus mean annual precipitation (Fig. 8). Regressions between percentage specific diversity of ecological categories and mean annual precipitation are more significant for Africa than Australia. A similar discontinuity at about 1000 mm mean annual precipitation to that found here has also been demonstrated for gamma diversity of modern faunas in southern Africa (Andrews and O'Brien, 2000) and North America (Badgley and Fox, 2000).
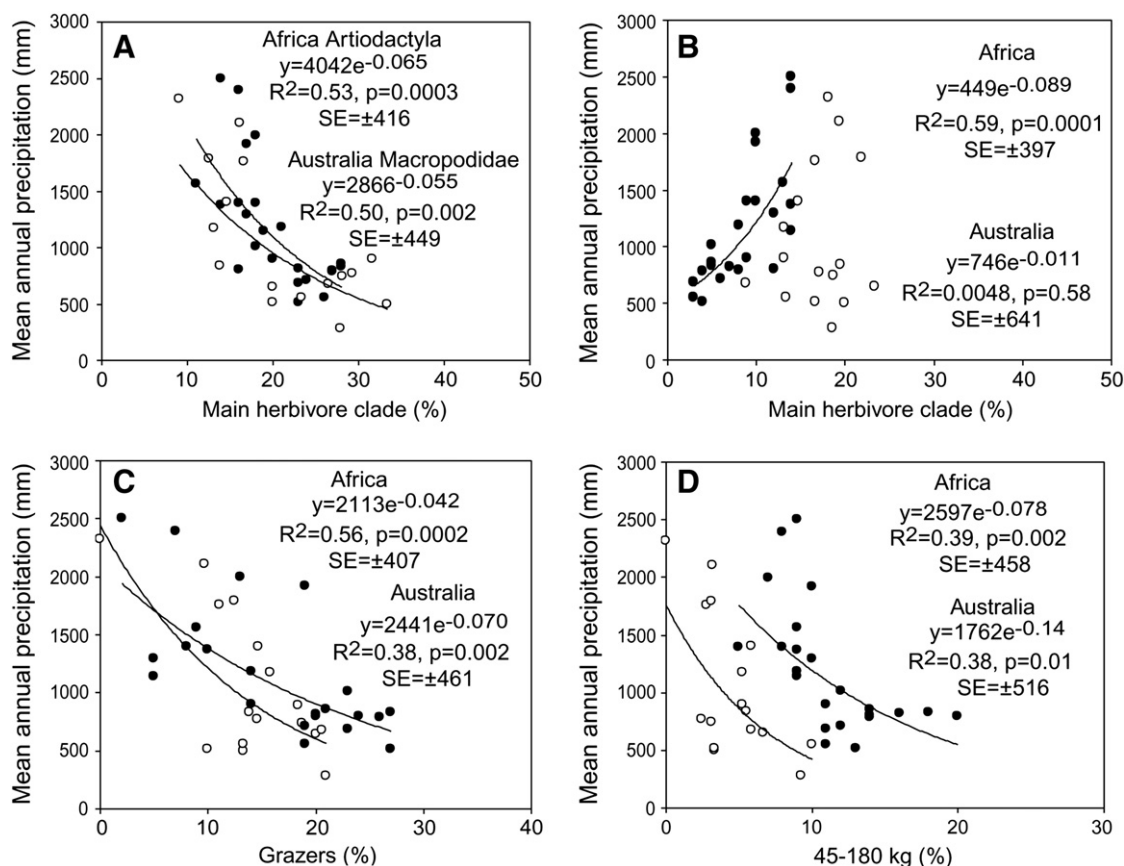
### 5.1. Main herbivore clade

The proportion of species of Artiodactyla in Africa and of Macropodidae in Australia both increase in drier climates, in data clouds that are overlapping (Fig. 8A). Both relationships are statistically significant (F test p<0.05) but their standard errors are broad, comparable with a similar relationship devised by Reed (1998) between percent rodent species and mean annual precipitation in Africa.

This result supports the notion of kangaroos as ecological vicars of antelope (Freudenberger et al., 1989; Springer et al., 1997; Flannery, 2004). Bunch grasses are uncommon in mallee vegetation, where the ground is either bare or covered with bark and sclerophyll leaves. Grasses are restricted to local glades or parks on clayey depressions or flanking creeks. The supple limbs of mallee trees are not difficult to push through, but these as well as ground obstacles of fallen branches, sheets of bark and narrow erosional rills make running difficult and dangerous. The stature of mallee trees becomes smaller in drier climates (Fig. 3) until the point where shrubs can be passed in a bound by kangaroos, and easily negotiated by emus.

### 5.2. 45–180 kg size

Pig to gazelle sized species are a greater proportion of faunas in dry climates in both Africa and Australia, but there are fewer animals of this size class everywhere in Australia (Fig. 8D). These relationships are significant (F test p<0.05), but have high standard error.

**A** Africa Artiodactyla
$y=4042e^{-0.065}$
$R^2=0.53$, $p=0.0003$
$SE=\pm416$

Australia Macropodidae
$y=2866-0.055$
$R^2=0.50$, $p=0.002$
$SE=\pm449$

*Mean annual precipitation (mm)* vs *Main herbivore clade (%)*

**B** Africa
$y=449e^{-0.089}$
$R^2=0.59$, $p=0.0001$
$SE=\pm397$

Australia
$y=746e^{-0.011}$
$R^2=0.0048$, $p=0.58$
$SE=\pm641$

*Mean annual precipitation (mm)* vs *Main herbivore clade (%)*

**C** Africa
$y=2113e^{-0.042}$
$R^2=0.56$, $p=0.0002$
$SE=\pm407$

Australia
$y=2441e^{-0.070}$
$R^2=0.38$, $p=0.002$
$SE=\pm461$

*Mean annual precipitation (mm)* vs *Grazers (%)*

**D** Africa
$y=2597e^{-0.078}$
$R^2=0.39$, $p=0.002$
$SE=\pm458$

Australia
$y=1762e^{-0.14}$
$R^2=0.38$, $p=0.01$
$SE=\pm516$

*Mean annual precipitation (mm)* vs *45-180 kg (%)*

**Fig. 8.** Paleoprecipitation predictive equations derived from modern mammal faunas of Australia (open circles) and Africa (closed circles) using percent Artiodactyla or Macropodidae (A), percent arboreal species (B), percent grazers (C) and percent taxa 45–180 kg (D).

Australian megafaunal extinctions are a part of the reason for this discrepancy between African and Australian sizes (Barnosky et al., 2004; Miller et al., 2005), but do not explain why there are more large animals in more arid regions. Although pigs and wombats thrive in closely wooded settings, antelopes and kangaroos avoid the branches of trees and seek open spaces for running escape. The proportion of these moderately large animals increases at the point where vegetation becomes more open, and this is different for each continent: around the 1000 mm isohyet in the grasslands of Africa and around the 500 mm isohyet in the mallee of Australia (Fig. 3). Cenograms show few mammals between 0.1 and 1 kg size in Australian deserts (drier than shown in Fig. 3), or between 0.5 and 8 kg in African grasslands (500–1000 mm in Fig. 3), but no gaps in mallee or rainforest mammal size distributions (Travouillon and Legendre, 2009).

### 5.3. Arboreal

The proportion of arboreal species declines in dry regions of Africa, but there is no change in the proportion of arboreal species with precipitation in Australia (Fig. 8B). Only the relationship for African faunas is statistically significant ($p<0.05$).

These results may reflect the very different vegetation structures of Australia and Africa. In Australia, tree canopy declines in stature continuously from the 2500 mm to the 300 mm isohyet (Eq. (1)). In Africa, also trees become smaller in semi-arid climates (Fig. 3). However, African trees are widely spaced in wooded grasslands between the 1000 and 300 mm isohyet (Shorrocks, 2007). Many arboreal and gliding mammals cannot tolerate such wide spacing of trees (Coe, 1985).

### 5.4. Grazers

The proportion of grazing species increases in drier regions in both Australia and Africa (Fig. 8C). Both these relationships are significant, and their data clouds overlap.

Comparable proportions of grazers in Australia and Africa are surprising considering the much lower availability of grass in Australian mallee compared with African grassland. Mallee presents a monotonous cover, but open glades have seasonal bunch grasses on clayey depressions, sand dunes and creek banks (Cheal and Parkes, 1989). Grazing kangaroos have lower basal metabolic rates and are more flexible in diet than grazing ungulates, and also can abort fetuses to survive water and food shortages (Strahan, 1995; Flannery, 2004).

## 6. Paleoecological records

Variation through time of ecological categories of fossil mammals is available since the late Oligocene in Kenya (Fig. 9) and Australia (Fig. 10), but since the Cretaceous in the north American Rocky Mountains, where the Cretaceous–Tertiary mass extinction is a marked discontinuity (Fig. 11).

### 6.1. Taxa

Mammals in the fossil record of the Rocky Mountains (Fig. 11A) are more like those of Kenya (Fig. 9A) in artiodactyl-rodent dominance, than like indigenous fauna of Australia (Fig. 10A). Artiodactyl-rodent dominance of specific diversity extends back the base of the available record in Kenya (23.5 Ma), but in the Rocky Mountains back to basal Eocene (55.8 Ma). Macropodidae dominance of Australian specific diversity

extends back to the base of the available record in the late Oligocene (25 Ma). Artiodactyls expanded dramatically in diversity at 17 Ma in the Rocky Mountains (Fig. 11A) and Kenya (Fig. 9A), but comparable expansion of Macropodidae was delayed until 2 Ma in Australia (Fig. 10A). The Cretaceous–Tertiary boundary was a fundamental reorganization of Rocky Mountain mammal faunas, with marsupials (Didelphimorpha) and other archaic orders (Aegialodonta, Cimolesta, Multituberculata, "Symmetrodonta" and Eutriconodonta) never to regain their former prominence.

Cretaceous–Tertiary (66 Ma) mammal community reorganization is best explained by mass extinction (Sloan et al., 1986; Archibald, 1996), which also terminated dinosaurs on land and ammonites at sea (Schulte et al., 2010). This was also a time of $CO_2$ greenhouse, as revealed by stomatal index of fossil *Ginkgo* and from increased paleoclimatic warmth and humidity evident in paleosol chemical weathering (Retallack, 2009a). Other greenhouse spikes are recognized from similar data on
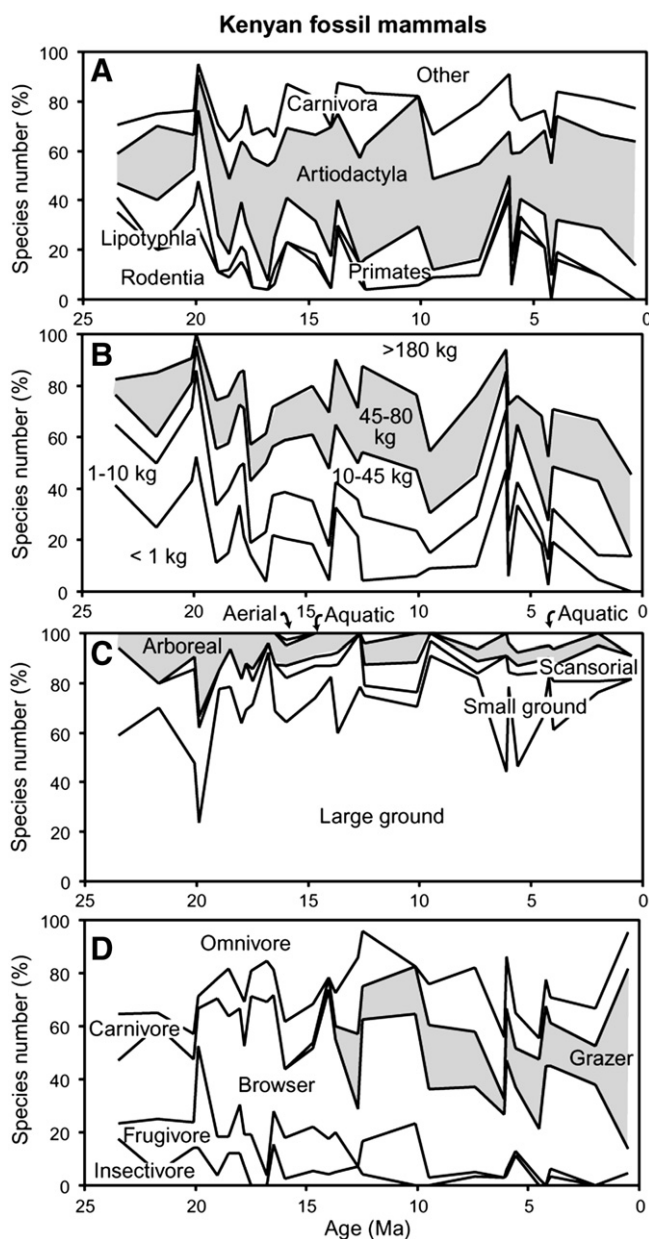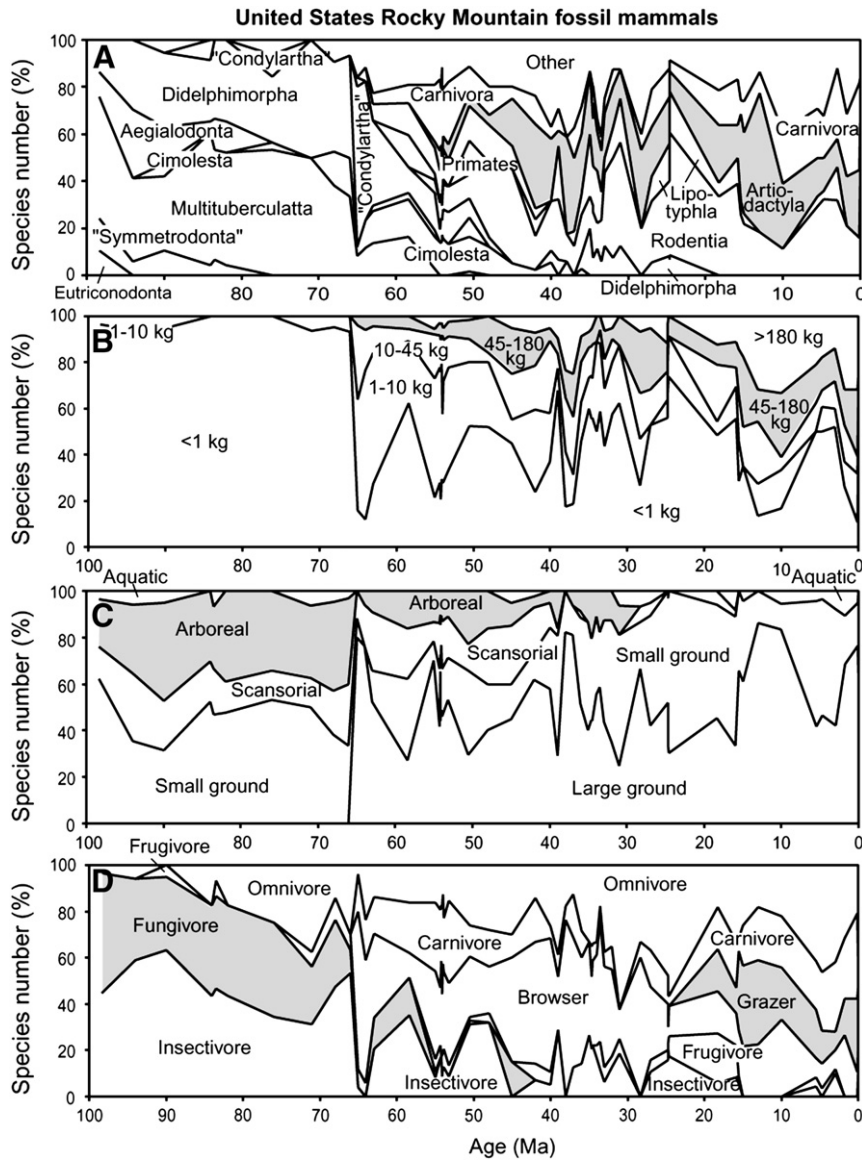


Fig. 9. African mammalian paleocommunity variation through time in taxa (A), size (B), locomotion (C) and diet (D). Data is online at http://pages.uoregon.edu/dogsci/doku.php?id=directory/faculty/greg/about.
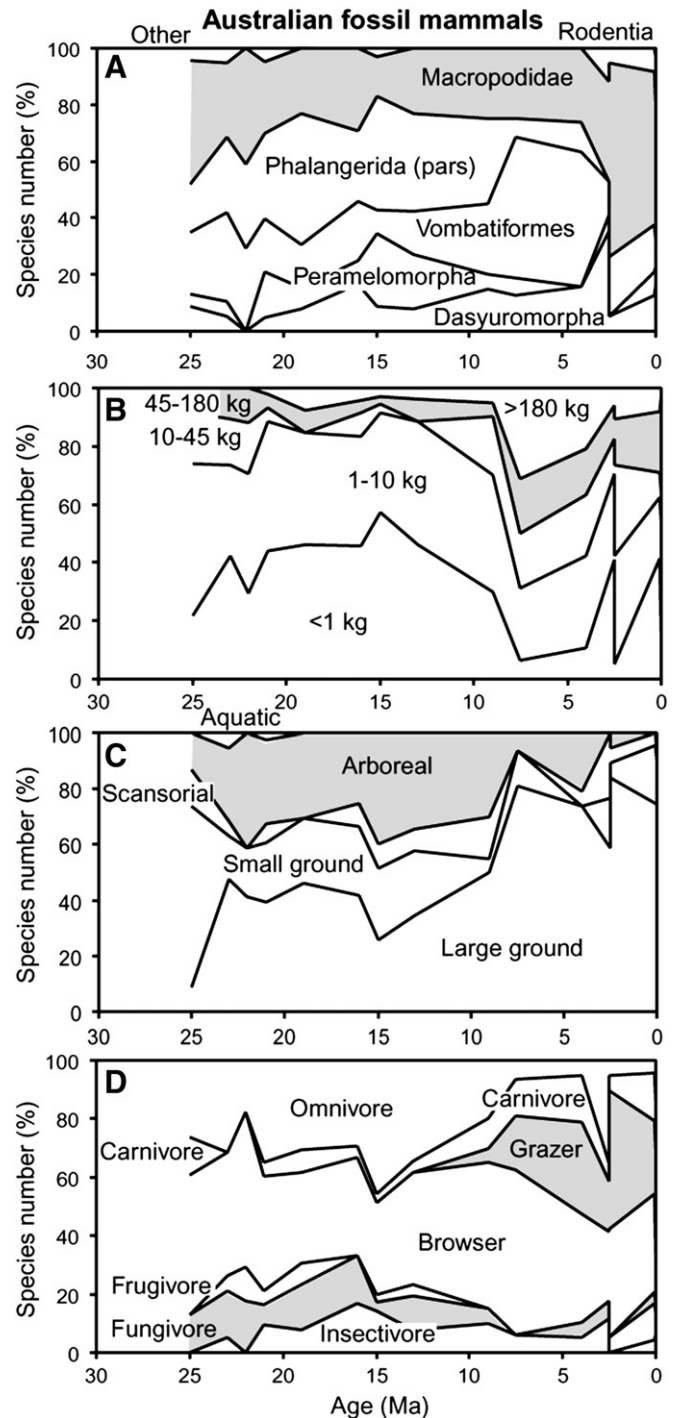


Fig. 10. Australian mammalian paleocommunity variation through time in taxa (A), size (B), locomotion (C) and diet (D). Data is online at http://pages.uoregon.edu/dogsci/doku.php?id=directory/faculty/greg/about.

the spread of lateritic and bauxitic paleosols at 55, 49, 39, 35, 30, 19 and 16 Ma (Retallack, 2008a, 2009a,b, 2010a), and these greenhouse events are indicated by marine alkenone proxies, despite marine-nutrient calibration problems (Pagani, 2002; Pagani et al., 2011). These greenhouse and associated paleoclimatic spikes contributed to marked swings in mammalian community composition (Figs. 9–11).

The 17 Ma rise of artiodactyl diversity and 2 Ma diversification of Macropodidae have been attributed to the advent and spread of grassland ecosystems (Flannery, 2004; Janis, 2008). Independent evidence of sod grasslands at this time comes from paleosols at Karungu

**Fig. 11.** North American Rocky Mountain mammalian paleocommunity variation through time in taxa (A), size (B), locomotion (C) and diet (D). Data is online at http://pages. uoregon.edu/dogsci/doku.php?id=directory/faculty/greg/about.

(Forbes et al., 2004) and Maboko, Kenya (Retallack et al., 2002), and Railroad Canyon, Idaho (Retallack, 2009b), Bone Creek, Oregon, and Agate, Nebraska (Retallack, 2007b). Such paleosols have not yet been found in Australia (Metzger and Retallack, 2010), but there was a pronounced rise in abundance of pollen of daisies (Asteraceae) and grasses (Poaceae) at about 2.5 Ma in western New South Wales (Martin, 1989). Phytolith assemblages of Montana–Idaho have been interpreted by Strömberg (2005) as evidence for an abrupt change from forest to open grassland during the earliest Miocene (23 Ma), and thus as evidence for delayed evolutionary response of artiodactyls to vegetation change. However, paleosols at 22 Ma and earlier in Oregon, Montana and Nebraska are shallow calcareous soils like those of desert shrublands (Retallack, 2007b). The "forest" phytoliths of Strömberg (2005) are similar to those in modern and Pleistocene phytolith assemblages attributed to sagebrush and other desert shrubs (Blinnikov et al., 2002; Blinnikov, 2005). The rise of artiodactyls was thus not cued to clearing of forest, but sod thickening by grasses which displaced shrubs and trees in semi-arid to subhumid regions (Retallack, 2007b).

### 6.2. Size

Size distribution back in time varies dramatically in the Rocky Mountains (Fig. 11B), Kenya (Fig. 9B: see also Nieto et al., 2005) and Australia (Fig. 10B), with a profound mammalian size increase following the Cretaceous–Tertiary boundary in the Rocky Mountains. Cretaceous mammals of the Rocky Mountains are dominated by small mammals (<1 kg), but small mammal spikes are found subsequently. At the other end of the spectrum, horse to elephant sized animals (>180 kg) were found back as far as the useful record (23.5 Ma) in Kenya, but 55 Ma in the Rocky Mountains and 21 Ma in Australia. Megaherbivores were diverse back to the beginning of the Kenyan record (23.5 Ma), but did not diversify until 42 Ma in the Rocky Mountains and 7.5 Ma in Australia.

Rapid evolutionary radiation of large mammals following mass extinction at the Cretaceous–Tertiary boundary explains changing size proportions at 66 Ma (Sloan et al., 1986; Archibald, 1996). The later advent of megaherbivores in the Rocky Mountains than Kenya, reflects a well documented immigration of tropical Eurasian mammals

at the end of the Paleocene (Gingerich, 2003), when a global green-house spike enabled high latitude dispersal (Retallack, 2009a). Other greenhouse events (Retallack, 2009a) introduced rhinos to North America at 39 Ma (Lucas, 1992) and elephants at 19 Ma (Prothero and Dold, 2008). Some endemic North American lineages evolved large size independently (Alroy, 1998), and Australian megaherbivores evolved in isolation (Murray and Vickers-Rich, 2004). This had conse-quences for vegetation, because megaherbivores create open country by systematic destruction of trees and other vegetation (Owen-Smith, 1988).

### 6.3. Locomotion

Ground mammals, small and large, dominate the fossil records of Kenya, Rocky Mountains and Australia (Figs. 9C, 10C, 11C). Arboreal mammals have low proportional diversity in Kenya back to the base of the useful record (23.5 Ma), in the Rocky Mountains back to the Cretaceous–Tertiary boundary (66 Ma), and in Australia since late Pliocene (2.5 Ma). Arboreal mammals have been missing in Rocky Mountains fossil localities since the mid-Oligocene (30 Ma). In con-trast arboreal mammals were diverse during the late Cretaceous and Paleogene (30–100 Ma) in the Rocky Mountains and during the Neogene (2.5–25 Ma) in Australia.

The dominance of ground rather than arboreal mammals is com-patible with the taphonomic nature of most of the fossil localities: fragmentary jaws and teeth in highly calcareous paleosols (Bown, 1979; Retallack, 1991a, 1998). The shallow horizons of calcareous nodules in these paleosols are evidence of dry climates (<1000 mm mean annual precipitation) and open vegetation (Retallack, 2005). There are strong taphonomic biases against preservation of arboreal mammals of forest ecosystems, because forest soils are non-calcareous and bones are dissolved in them (Retallack, 1998). Non-calcareous forest paleosols are known from Kenya (Retallack, 1991a), Australia (Retallack, 2008a) and the Rocky Mountains (Retallack, 2007b), but none preserve adequate fossil mammal assemblages. Thus the arboreal mammals preserved in these assemblages were from lowland semi-arid to subhumid soils, more wooded than is the case in dry Kenyan rift valleys, and intermontane valleys of the Rocky Mountains today.

### 6.4. Diet

The most striking change in diet of the three regions is the advent (18.3, 14.7, 9 Ma) and then expansion (15.5, 12.7, 7.5 Ma) of grazers in Rocky Mountains, Kenya, and Australia, respectively (Figs. 9D, 10D, 11D). In each region, the past 2.5 Ma has seen expansion of grazer diversity. Fungivores have been diverse in Australia back to the beginning of its useful fossil record (25 Ma). Fungivorous multi-tuberculates were diverse during the Cretaceous in the Rocky Moun-tains, but persisted in reduced diversity from the earliest Paleocene to middle Eocene (66–45 Ma). The earliest fossil mammals with grazing wear in North America were late Hemingfordian (17 Ma) parahippine horses, probably immigrant to the Rocky Mountains from *Parahippus leonensis* in Florida (MacFadden et al., 1991; Janis, 2008; Mihlbachler et al., 2011). The earliest likely grazers of Kenya were hypsodontine bovids found at Maboko (14.7 Ma), and these were probably Eurasian immigrants (Gentry, 1970).

The persistence of fungivores in Australia, but decline in the Rocky Mountains and absence from Kenya can be explained by the fact that truffles preferred by fungivores are mycorrhizae of mesic conifers and angiosperms, and not known from grasslands and sagebrush (Maser et al., 2009). During the Neogene in Kenya and the Rocky Mountains, truffle-rich low woodlands may have been replaced in comparable climatic belts by truffle-poor grasslands.

Short-term spikes of browser diversity at 66, 55, 49, 39, 35, 30, 19 and 16 Ma (Figs. 9–11) correspond with short-term climatic perturbations of high $CO_2$ and warm-wet paleoclimate attributed to volcanic eruptions and bolide impacts (Retallack, 2009a). These events are all seen in the Rocky Mountain record (Fig. 11D), but some also are apparent from re-cords of lower temporal resolution from Kenya (Fig. 9D) and Australia (Fig. 10D). These were times of regional expansion, productivity, and di-versification of woodland communities, as revealed by paleosol distribu-tion, depth to Bk, and diversity (Retallack, 2007a, 2009a; Metzger and Retallack, 2010). High productivity and $CO_2$ levels postulated as explana-tion for the last of these browser diversity spikes (Janis et al., 2000) have been documented from paleosols of that age (16 Ma) in Railroad Canyon, Idaho (Retallack, 2009b).

## 7. Paleoclimatic records

Paleoclimatic implications of fossil mammal faunas can now be assessed using mammalian climofunctions of Fig. 8, by comparison with independent estimates of mean annual precipitation from the depth to calcareous nodules (Bk horizon) in paleosols (Retallack, 2007a,b, 2009a; Metzger and Retallack, 2010). Paleoclimate inferred from paleosol records in Fig 12 is matched well by some mammalian climofunctions, but not others. Percent grazers, for example, fails to predict precipitation at various times in the Neogene before grazers appear, but just because this proxy goes off scale, does not mean that precipitation was that of rainforest. Other proxies indicate semiarid to subhumid climates at those times.

The paleosol records are from the same localities and regions as the fossil faunas (Fig. 5), unlike climatic records such as the isotopic composition of marine foraminifera, which is a proxy for both alpine and polar ice volume and ocean paleotemperature (Zachos et al., 2001). Studies of mammalian evolution that have used such isotopic records (Alroy et al., 2000; Barnosky, 2001; Prothero, 2004; Hopkins, 2007) have found little correspondence with mammal evolution. Marine isotopic records appear to be poor proxies for continental climates, and the particular record most often used (Zachos et al., 2001) has been statistically smoothed and is a regional composite of Southern Ocean data for the Paleogene and North Atlantic data for the Neogene, remote from the regions studied in this paper.

### 7.1. Australia

A record of mean annual precipitation in Australia of low temporal resolution (Fig. 12B) is lower throughout the record than estimates based on diversity of Australian Macropodidae and 45–180 kg mam-mals, but within error for those mammalian climofunctions (Fig. 8). Percent Australian grazers gives reasonable estimates of paleoclimate only back to 7.5 Ma, when grazers first appear at Alcoota.

Paleosols and the two mammalian climofunctions that can be applied throughout the record both agree that inland Australia had semi-arid to subhumid paleoclimates back 26 Ma, and endured basal Miocene aridity and a middle Miocene humid spike like other parts of the world (Fig. 12A, C). Although middle Miocene and earlier faunas of Australia have been compared with rainforest faunas (Travouillon et al., 2009), this is not supported by the data and analysis presented here.

### 7.2. Kenya

A paleoclimatic record of Kenya from paleosols (Fig. 12A) is well supported by the proportional diversity of African artiodactyls and mammals in the size range 45–180 kg, although these proxies fail before 19 Ma. Percent African grazers agree with other proxies only back to 12.7 Ma, which is 2 million years after the first grazers immi-grated to Africa (Gentry, 1970).

As for Australia, the failure of some proxies, such as percent grazers, to predict mean annual precipitation does not support the notion of middle to early Miocene rainforest in Kenya. None of the
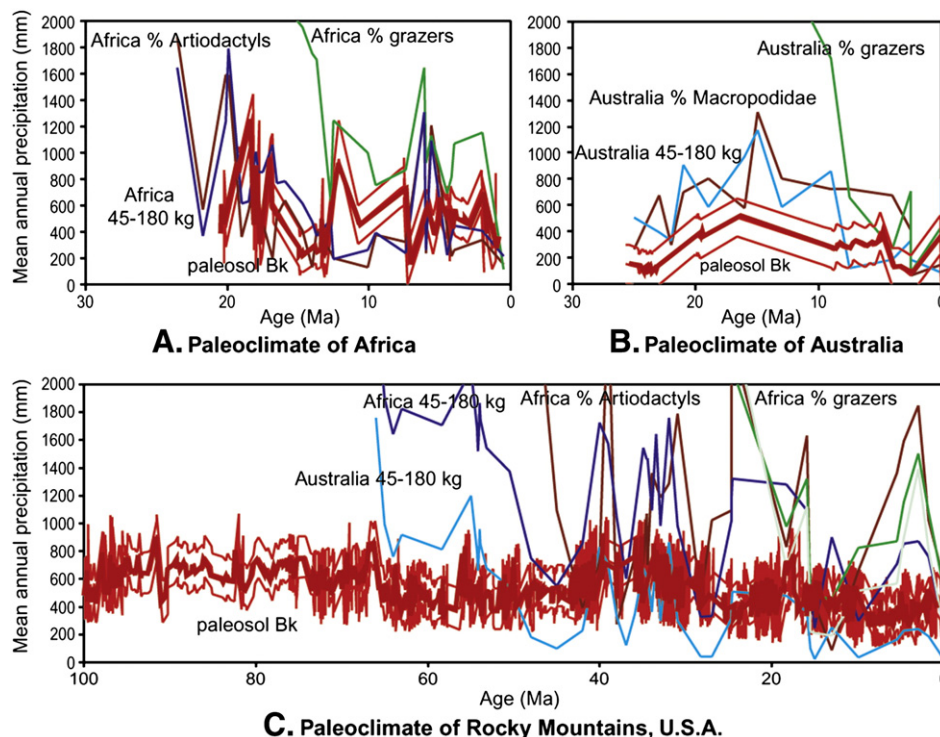
**Fig. 12.** Paleoprecipitation from depth to Bk of paleosols (heavy black line and flanking standard error) for Kenya (A: from Retallack, 2007a), inland Australia (B: from Metzger and Retallack, 2010), and Rocky Mountains, U.S.A (C: from Retallack, 2009a), compared with estimates based on fossil mammals (gray). Percent grazing species fails as an indicator before 12 Ma in Kenya, 7 Ma in Australia, and 20 Ma in Rocky Mountains. Other mammalian climofunctions work well for Kenya and Australia, but Australian percent mammals in the size range 45–180 kg is the best predictor for the Rocky Mountains back to 65 Ma.

estimated precipitation values reach those required for rainforest in Africa (at least 1750 mm: White, 1983), although rainforest has been used for vegetation of drier climates in Australia (Webb, 1968). Precipitation spikes at 8, 12, 16, and 18 Ma are comparable with those seen in North America (Fig. 12C). Thus rainforest postulated for early Miocene mammal faunas of Kenya (Andrews and Van Couvering, 1975; Andrews, 1992) is not supported by data and analysis presented here.

### 7.3. U.S. Rocky Mountains

A paleoclimatic record from paleosols in the Rocky Mountain states of Utah, Nevada and Montana (Retallack, 2009a) is matched well by the climofunction derived from proportional diversity of Australian mammals in the size range 45–180 kg, but only as far back as early Paleocene (65 Ma: Fig. 12C). Other mammalian climofunctions fail in intermittent spikes, and then fail completely further back than 48 Ma (African 45–180 kg), 45 Ma (African artiodactyls), and 18.3 Ma (African grazers).

The operational range of mammalian climofunctions is determined by their training sets (Fig. 8), so their application to the Rocky Mountain fossil record fails before evolution of suitable size ranges (65 Ma: Alroy, 1998) and immigration of artiodactyls (55 Ma: Gingerich, 2003) and grazers (17 Ma: MacFadden et al., 1991). The mammalian climofunctions also fail on several short-term (<1 Ma) climatic spikes. Some (but not all) of these spikes (66, 35, 8 Ma) correspond in time with impact events, evident from iridium anomalies, craters and [3]He anomalies (Alroy, 2003; Farley et al., 2006; Schulte et al., 2010). Other climatic spikes coincide with unusually large flood basalt eruptions such as the Deccan Traps (66 Ma), Antrim Volcanics (55 Ma) and Columbia River Basalts (16 Ma: Courtillot and Renne, 2003). These were perturbations to long term climatic cooling during the Cenozoic (Retallack et al., 2000; Retallack, 2001), which were recorded with varied intensity by different mammalian traits measured for this study.

### 8. Ancient mallee-like mammal communities?

The concordance of mean annual precipitation from a transfer function based on Australian mallee mammals and from paleosol depth to nodules in the Rocky Mountains (Fig. 12C) suggests size comparability of Paleogene fossil and modern mallee mammals. Cretaceous mammals of the Rocky Mountains were smaller again (Fig. 11B), but can also be considered in light of a mallee model. The mid-Cretaceous fauna of the Mussentuchit Member of central Utah (Kielan-Jaworowska et al., 2004) and the early Eocene fauna of the Willwood Formation of northern Wyoming (Rose, 1990; Bown et al., 1994) are especially instructive examples because the paleosols yielding these faunas have been described in detail (Bown, 1979; Retallack, 1998, 2009a; Kraus and Riggins, 2007). Apart from burial reddening and gleization expected in paleosols due to burial (Retallack, 1991b), paleosols of the Mussentuchit Member and Willwood Formation (Fig. 4K–M) are very similar to modern mallee soils of New South Wales (Fig. 4A–J).

### 8.1. Paleogene

Individual mammal assemblages from the early Eocene (53–55 Ma) Willwood Formation of Wyoming (Bown, et al., 1994) have no more than three species larger than 45 kg: a browsing cimolestid (*Coryphodon radians*) and condylarth (*Phenacodus primaevus*), and an omnivorous procreodid (*Anacodon ursidens*). Arboreal insectivorous, frugivorous and browsing primates were diverse, and many had the large orbits of nocturnal mammals (Bown and Rose, 1984; Janis et al., 2008). There were scansorial rodents and small carnivores, and modestly sized perissodactyls and artiodactyls lack cursorial limb structure (Bakker, 1983; Rose, 1990). The large ground bird *Gastornis giganteus* (formerly *Diatryma*) of the Willwood Formation has been considered predatory, but blunt beak and lack of talons now compare better with frugivorous large ground birds (Murray and Vickers-Rich, 2004).

Paleocene and Eocene mammal faunas of Wyoming, Montana and Utah have commonly been regarded as transitional between Mesozoic small mammals and large ungulates of the Asian immigrant White River chronofauna of the late Eocene (beginning 40 Ma: Alroy, 1998). The Paleocene and Eocene have been regarded as times of dramatic evolutionary radiation of mammals following dinosaur extinction (Maas and Krause, 1994), and this view is supported by fossil evidence for end-Cretaceous rise of crown-groups of Placentalia (Asher et al., 2005; Wible et al., 2007). Evidence from species-level molecular phylogeny of modern mammals found little effect of the end-Cretaceous extinctions, and identified two spikes in diversification rate at 93 and 19 Ma (Bininda-Emonds et al., 2007), related to rise of weedy angiosperms and grasslands respectively. My study similarly suggests that late Cretaceous and Paleocene–Eocene faunas were adapted to woody angiospermous vegetation of semi-arid to subhumid regions that was displaced by grassland ecosystems in the northern hemisphere, but not in Australia, where semi-arid low woodland lingers as mallee.

### 8.2. Mesozoic

The mammal fauna of the mid-Cretaceous (98 Ma) Mussentuchit Member of the Cedar Mountain Formation is represented by at least 28 small species of ground-dwelling fungivorous multituberculates, ground-dwelling insectivorus eutriconodonts, arboreal insectivorous aegialodonts and didelphomorphs, and one moderately large (1.8 kg), scansorial eutriconodont carnivore (Kielan-Jaworowska et al., 2004). Some of these creatures had monotreme or marsupial reproductive systems and physiologies (Lou, 2007). The same beds also yield fish, frogs, salamanders, turtles, lizards, snakes, crocodilians and a dinosaur fauna of graviportal sauropods and nodosaurs, and bipedal herbivores and carnivores (Cifelli et al., 1999).

## 9. Extinct woody plant communities

Extinct semi-arid to subhumid vegetation of Africa and North America may have had structural similarities with mallee, but the term mallee is inappropriate for such floristically different vegetation. Australian mallee *Eucalyptus* can be traced back to the middle Miocene from pollen records in New South Wales (Martin, 1989) and early Miocene from paleosols and megafossils in South Australia and Northern Territory (Metzger and Retallack, 2010). This fossil record reflects northward drift of Australia from cooler climates with lower evapotranspiration, higher effective humidity, and mixed conifer–angiosperm temperate woodland during the Eocene and Paleocene (Truswell and Harris, 1982; Retallack, 2008a). Climatic warming due to continental drift was partly undone by global climatic fluctuations including Plio-Pleistocene cooling (Metzger and Retallack, 2010). Unlike Australian mallee vegetation, comparable semi-arid woodlands of Africa and North America were supplanted by grassland ecosystems, and little is known of the floristic composition and other details of the extinct communities replaced by grasslands.

### 9.1. Africa

The extinct low woodland of semi-arid to subhumid regions of Africa has been called pori, from a Hadza word for bush (Retallack, 2007a), and the best available reference paleosol is the type Tek pedotype in the early Miocene (18 Ma) Hiwegi Formation on Rusinga Island Kenya (Retallack et al., 1995). The tuffaceous volcanic parent material of this paleosol would have been more fertile than quartzose mallee soils. This paleosol yielded common pits (mineralized endocarps) of hackberry (*Celtis rusingensis*), and the soil profile and associated roots and twigs are evidence that its vegetation had few spines and thorns, and moderate stature ($12 \pm 2.3$ m tall from Eq. (2)). Hackberry is evidence that this woodland was at least semideciduous. Other

paleosols (Okoto pedotype) in the Hiwegi Formation have a more diverse fossil flora of fruits and seeds, which grew in streamside galleries. The floristic affinities of fossils on Okoto paleosols are Zambezian, with legumes, palms and extant genera such as *Berchemia*, *Cnestis*, and *Lannea*. Somali–Masai wooded grassland taxa, such as *Acacia* or grasses (Collinson et al., 2009), appear at geologically younger sites of Maboko, Kaimagool and Fort Ternan (Wynn and Retallack, 2001; Retallack et al., 2002).

### 9.2. North America

The extinct low woodland of semi-arid to subhumid regions of North America is here termed cunhaka, from a Lakota Sioux word (cuᵗⁿhaka) for a "brush of bushes" (Buechel and Manhart, 1970). A suitable reference paleosol and fauna for this vegetation is the Zizi paleosol in the early Eocene (54 Ma) Willwood Formation near Powell, Wyoming (Winkler, 1983; Retallack, 1998). These paleosols had smectite clays from volcanic tuff more fertile than quartzose mallee soils. Also these paleosols yield endocarps of hackberry (*Celtis hatcheri*), indicating vegetation at least semideciduous. Their shallow Bk horizon (35 cm) indicates woodlands about 8 m tall (from Eq. (2)). Fossil plants from the Willwood Formation (Wilf, 2000; Wing et al., 2005) represent bald cypress swamps (in Histosols) and clayey paleosols (Alfisols) of the terminal Paleocene greenhouse warm–wet spike (Kraus and Riggins, 2007), when vegetation was distinct from the shallow-calcic Zizi and Luluta paleosols of the rest of the Willwood Formation (Retallack, 1998). Nevertheless, regional pollen floras of the Willwood Formation (Wing et al., 2005) and megafossils in lake beds of the middle Eocene Green River Formation (MacGinitie, 1969) are evidence for legumes, Juglandales and Betulales in Eocene cunhaka woodlands.

## 10. Conclusions

The small stature, common arboreal and nocturnal mammals of the Cretaceous and Paleogene are distinct from the range of ecomorphs common in grassland ecosystems. They are not necessarily evidence of rainforest communities, although there are cases of rainforest mammals preserved in volcaniclastic deposits (Eocene of Clarno: Hanson, 1996), sinkholes (Eocene of Messel: Schaal and Ziegler, 1992) and caves (Miocene of Riversleigh: Archer et al., 1991). In cases where mammals are preserved in calcareous paleosols (Bown, 1979; Retallack, 1991a), a more appropriate comparison of both paleosols and mammal faunas is with Australian mallee. Mallee-like mammal faunas and soils identified in this paper include the following: mid-Cretaceous (98 Ma) Mussentuchit Member of Cedar Mountain Formation in Utah (Fig. 4M: Cifelli et al., 1999; Retallack, 2009a), early Eocene (54 Ma) Willwood Formation in Wyoming (Fig. 4K–L: Bown, 1979; Bown et al., 1994; Retallack, 1998; Kraus and Riggins, 2007), early Miocene (18 Ma) Hiwegi Formation on Rusinga Island Kenya (Retallack et al., 1995; Peppe et al., 2009), and early Miocene (22 Ma) Ulta Formation near Kangaroo Well, Northern Territory, Australia, and middle Miocene (16 Ma) uppermost Etadunna Formation at Lake Palankarinna, South Australia (Metzger and Retallack, 2010). These were not rainforest mammal faunas, and do not demand extreme hydrological and paleoclimatic changes in the past compared with the present (Herold et al., 2011).

African and North American dry woodlands were ecologically comparable with Australian mallee, but floristically distinct, and so named pori and cunhaka woodlands, respectively, from indigenous languages for bush (Buechel and Manhart, 1970; Retallack, 2007b). Although the fossil flora of such communities is poorly preserved and thus incompletely known, deciduous hackberries and legumes of pori and cunhaka were distinct from evergreen *Eucalyptus* of mallee. Such floristic differences in part reflect different paleogeographic histories, but also the greater fertility of tuffaceous paleosols of pori

(Retallack, 1991a) and cunhaka (Retallack, 1998), compared with quartzose paleosols of mallee (Metzger and Retallack, 2010). Living mallee and extinct pori and cunhaka woodland played an important role in mammal evolution.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2012.05.009.

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