

On the origin, evolution and phylogeny of giraffes *Giraffa camelopardalis*

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The origin, phylogeny, and evolution of modern giraffes (*Giraffa camelopardalis*) is obscure. We review here the literature and conclude that the proximate ancestors of modern giraffes probably evolved in southern central Europe about 8 million years ago (Mya). These ancestors appear to have arisen from the gelocid ancestral assemblage of 20–25 Mya via the family Palaeomerycidae. From the palaeomerycids arose the Antilocaprinae (Pronghorns) via the subfamily Dromomerycinae, and two subfamilies of giraffids, the Climacoceratidae and Canthumerycidae. The terminal genus of the Climacoceratid line was the now extinct massive giraffid *Sivatherium* sp. The Canthumerycids gave rise to the okapi and giraffes via the intermediate forms of *Giraffokeryx*, *Palaeotragus* sp. (of which the okapi is the extant form), *Samotherium* sp. and *Bohlinia* sp. all of which are extinct. Stimulated by climate change, progeny of *Bohlinia* entered China and north India, evolved into typical *Giraffa* species and became extinct there about 4 Mya. Similarly, following their preferred habitat, African *Giraffa* entered Africa via Ethiopia about 7 Mya. Here, seemingly unaffected by the climate changes occurring to the east and causing extinction of its Asian counterparts, *Giraffa* radiated into several sequential and coeval species culminating with the evolution of *G. camelopardalis* in East Africa from where it dispersed to its modern range. Fossils of *G. camelopardalis* appear about 1 Mya in East Africa.

The underlying stimulus for *Giraffa* evolution seems to have been the vegetation change that began about 8 Mya, from the prevalent forest (C3) biome to a savannah/woodland/shrub (C4) biome. *Giraffa*'s success as a genus is attributed to its great height and unique coat markings. Its height is a consequence of elongation of all seven cervical vertebrae and of the lower more than the upper limb bones. Advantages conferred by its height include protection from predation, increased vigilance, and in males sexual dominance and access to nutrients. Its coat colourings are highly heritable and provide protection from predation by camouflage, especially in the young. As giraffe are unable to sweat and pant, the patches may also act as thermal windows and may have an important thermoregulatory function.

INTRODUCTION

One of the more enduring folklore tales about modern giraffes is that they defy Darwinian “long continued” gradualistic evolution, appearing in the African Pleistocene as if they had no ancestors, having been created by an act of God as a monument to biological structural engineering. In Lankester's (1908) words, “It is altogether exceptional, novel, and specialised”.

Thus Hitching (1982) could say “There are no intermediate forms showing a three-quarter length giraffe neck”, and “What little evidence there is, is consistent with Gould-Eldredge's punctuated equilibria . . . that evolution may develop rapidly (producing) the ‘sudden’ appearance of modern giraffe”. Thus over “a period of thousands of generations a series of mutations accumulated producing stronger branchial arches, greater musculature and a bigger heart. Although of no selective advantage for these at the time, they became fixed by a process of gene fixation in a small population, so that if a mutation for long neck subsequently occurred the support systems for it would be in place”.

Hitching was writing in 1982 when there was considerable fossil evidence of giraffe prehistory, but it was incomplete and difficult to construe. Hitching's idea was however much later supported by Gould (1996) himself. Referring to giraffes, he said that “ancestral species are relatively short-necked and the spotty evidence gives no insight into how the long necked modern species arose”.

We set out here an alternative conclusion that arises from a review of the palaeontological and biochemical evidence of giraffe prehistory, and show that a history of intermediate forms does exist. Of the approximately 20–30 ancestral species, only three survived into relatively modern times and only two are extant. Thus it is not only their origin that is in need of illumination, but also how modern giraffes have survived against the odds. Their survival is usually attributed to their great height and unique markings. We have therefore also reviewed the evolutionary biology and physiology of these to assess their contribution to the survival of giraffes.

GIRAFFE PALAEOLOGY AND EVOLUTIONARY BIOCHEMISTRY

Palaeontological research directed towards the understanding of the evolution of giraffes began several years before Darwin & Wallace (1858) announced their discoveries. It seems to have been initiated as early as 1838 by Cautley. He found an elongated third cervical vertebra in the Siwalik deposits of Pakistan (see Figure 10) and attributed it to a giraffe species. This and other fossils were subsequently described by Falconer & Cautley in 1843. They anticipated, and wishfully hoped for the demise of, the modern folklore of giraffe evolution before it had arisen:

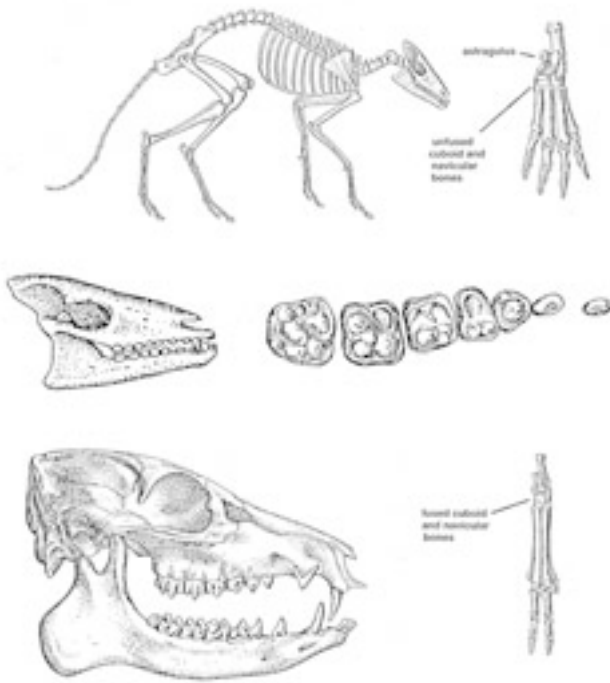


Figure 1. (Upper) Skeleton of *Diacodexus*. Note that the astragalus articulates with the tibia above and the separate cuboid and navicular bones below. The shape limits movement to the vertical plane. Note also the absence of a diastema and the bunodont teeth. (Lower) Skull and ankle of *Hypertragulus*. Note the developing diastema, fusion of the cuboid and navicular bones, and reduction in the number of metatarsals. Teeth are still bunodont. From Carroll (1988).

“The Giraffe has hitherto been confined, like the human race, to a single species, and has occupied an isolated position in the order to which it belongs . . . it may be expected that, when the ossiferous beds of Asia and Africa are better known, other intermediate forms will be found, filling up the wide interval which now separates the giraffe from the antlered ruminants, its nearest allies in the order . . .”

Two giraffids are extant. *Okapia johnstoni*, first brought to the attention of modern science by Sclater (1901) Lankester (1901) and, in 1902 by its discoverer Johnston. An inhabitant of the Ituri forest refuge in Zaire, its future and likely survival must be at best tenuous given the current political instability of this region. The other extant species is *Giraffa camelopardalis* Linnaeus, the familiar modern African giraffe. Both are eutherian (placental) mammals of the Class Mammalia, the Superorder Ungulata, Order Artiodactyla, and most significantly, the Suborder Ruminantia (Pecora). Their origins thus lie in the origins of artiodactyl ruminants. The evolutionary line from the first ruminant to modern giraffe is, however, tortuous and far from obvious, but there is general agreement amongst the main interpreters of the palaeontological and biochemical evidence (Kraus & Miyamoto, 1991; Allard *et al.*, 1992; Hassanin & Douzery, 1999; Webb & Taylor, 1980; Carroll, 1988; Janis & Scott, 1988; Gentry & Hooker, 1988; Scott & Janis, 1993; Gentry, 1994; Irwin *et al.*, 1991) that ruminant origins can be traced back to an artiodactyl fauna that had its origins in the late Palaeocene and became recognisable in the early Eocene some 50 million years ago (Mya).

In geological time the gap between the first artiodactyls and pecorans is large, perhaps 30–35 My long. The filling of this

“great and formative void” (Carroll, 1988) begins with a divergence of artiodactyls from perissodactyls and cetaceans which, from analysis of the evolution of the cytochrome *b* gene (Irwin *et al.*, 1991, Figure 8), occurred 40–60 Mya. The oldest known fossil artiodactyl assemblage is the Dichobunidae. The only complete skeleton of an animal from this group is that of a rabbit-sized forest dwelling animal called *Diacodexus* (Figure 1). *Diacodexus* lived in the Holarctic of Pangea (Figure 2), a part of the then land mass comprising regions now known as North America, Europe and Asia. Its fossils have been dated to the early Eocene of 60–55 Mya. What made this creature unique and clearly an artiodactyl was its astragalus, a part of its ankle. Its astragalus (Figure 1) limited the movements of its foot to the vertical plane, articulating with the tibia above and the cuboid and navicular bones below, and conferring improved running and leaping. Its movements were assisted by elongated metapodials, and transfer of most weight-bearing to the third and fourth digits.

Diacodexus also had the archetypical mammalian complement of teeth:

$$I^{3/3} C^{1/1} P^{4/4} M^{3/3} = 44.$$

Most significantly the molars (M) were low-crowned (brachydont), and had knob-shaped cusps (bunodont) (Figure 1). The bovid dental formula is:

$$I^{0/4} C^{0/0} P^{3/3} M^{3/3} = 32.$$

and that of giraffes is:

$$I^{0/3} C^{0/1} P^{3/3} M^{3/3} = 32.$$

and they are higher crowned (more hypsodont) and the molar cusps more crescent shaped (selenodont) in these two groups. Thus during the long evolution of ruminants tooth number and character were to change.

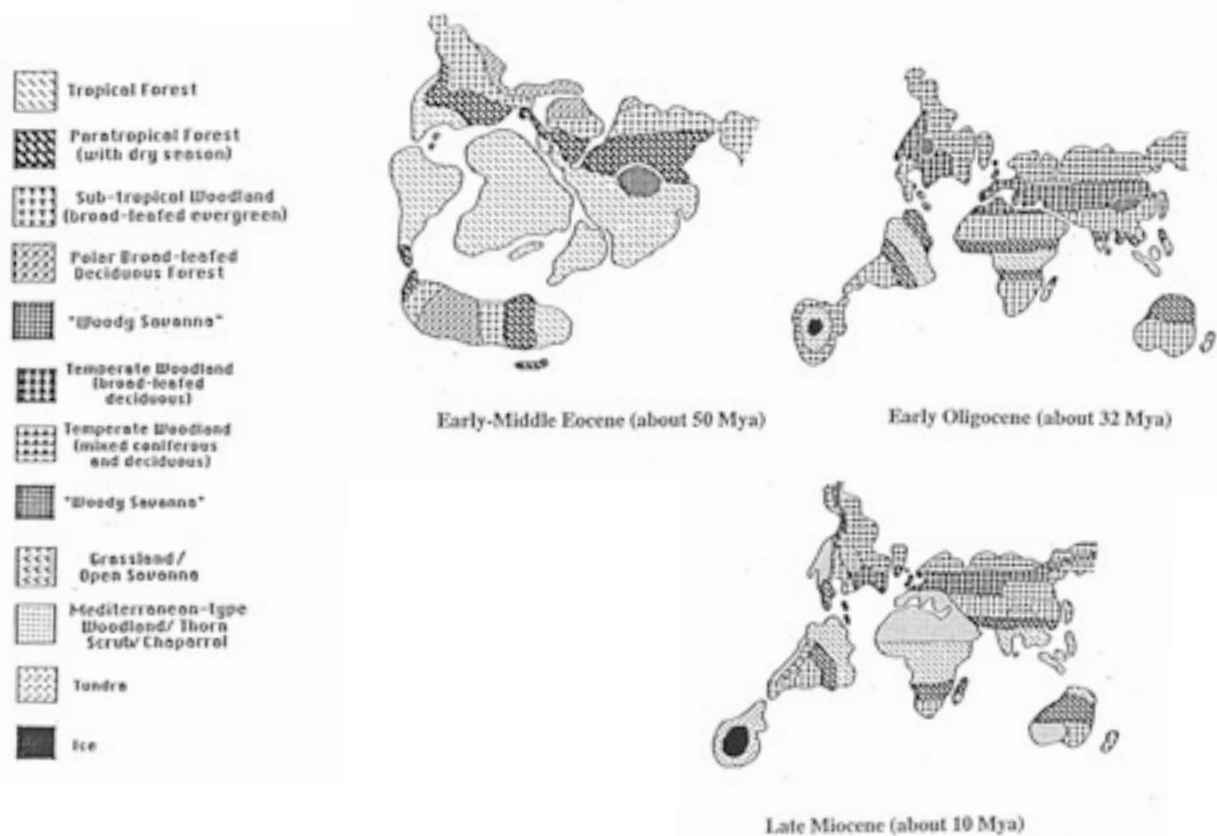
Tooth anatomy is important. Teeth are unpalatable and incredibly hard. They are therefore rarely eaten by scavengers, are resistant to the effects of erosion over time, and are often the only fossil remnants available on which to identify a species. Justification for use of such a tiny fragment of an animal to deduce a life history is that, although tooth morphology is far from constant and evolves, it is highly hereditary. Thus Lydekker (1891), who as far as we know said it earliest and best, at least in relation to giraffes:

“... (species) are severally distinguished by the characters of their molar teeth, and that, although the teeth of one group may approximate more-or-less closely to that of another, we do not find any instances where one member of a group possesses teeth of a totally different type from those of the other representatives of the same group. These facts strongly indicate that when we meet with fossil remnants having molar teeth of the very peculiar type met with in the giraffe, we shall be justified in considering that there must be a certain amount of relationship between the owners of such teeth.”

While Lydekker emphasised giraffe molar morphology as important, Singer & Bone (1960) much later determined that the most diagnostic tooth in giraffes was the lower canine, which in giraffes is bilobed. This feature is now the generally accepted synapomorphy of the Giraffidae (Hamilton, 1978).

Tooth morphology is also important from another aspect. Changes in morphology especially in the shape of the molar cusps, and in the number, position and slope of anterior teeth, especially of incisors, are highly correlated with the nature of

Figure 2. Change in land mass shape and vegetation between the early Eocene and late Miocene. Note that at the time of appearance of *Giraffa* ancestors 10 Mya, Eurasia and north Africa were linked to central southern Europe and the vegetation had become sub-tropical or temperate woodland and Mediterranean-type woodland/thorn scrub. From Janis (1993).



the diet and the anatomy and physiology of the gastrointestinal tract. Thus, in noting the primitive nature of *Diacodex* teeth, it can be deduced that Dichobunidae were omnivorous and had a simple intestinal tract. The corollary is that their initial evolutionary success lay not in any dietary adaptation, the adaptation most characteristic of modern ruminants, but rather in their improved mobility.

In the middle Eocene the early artiodactyls underwent extensive adaptive radiation that resulted in twenty or more families of which one, ultimately, was to lead to the Ruminantia (Carroll, 1988). Changes associated with this radiation included clear signs of adaptation to herbivory. These were the higher crowned teeth (hypsodonty) and broader molars with crescent-shaped (selenodont) cusps mentioned earlier, and a lengthened diastema in the skull (Figure 3). These characteristics are those of modern ruminants especially browsers. The teeth and associated changes to the intestinal tract allow the processing of fruits, leaves, and flowers of shrubs to obtain access to plant cell contents (Hofmann, 1989), rather than access to the nutrients in the cell wall. The lengthened skull, apart from providing space to house an enlarged and more prehensile tongue, also provided the anatomical substrate for an enlarged nasal mucosal surface, an adaptation that facilitates olfaction and temperature regulation. The elongation of the muzzle also produced a gap behind the incisors and between the canine and anterior premolar teeth. Lower incisors became procumbent, an evolutionary change that improved the cropping of vegetation. With later loss of the upper incisors, possibly because tooth loss occurs at the junctions of bones (Tobias, 1955) (in this case between the two premaxillae and between the premaxilla-maxilla junctions) it would become easier for the tongue to project. Similarly and at about the same time the lower canines evolved to resemble incisors.

Hypertragulidae

The earliest assemblage of animals whose fossil record suggests that they had begun the changes that would lead to ruminants and ultimately to modern giraffes, is the hypertragulids. These were, like the Dichobunidae, small forest-dwellers feeding on a low fibre, non-abrasive diet rather like their living descendants the tragulids (chevrotains, *Hyemoschus aquaticus* and mouse deer, *Tragulus* spp.) do today. They lived in what is now North America and the divergence that gave rise to them occurred about 40 Mya.

The hypertragulids were characterised, like higher ruminants today, but unlike *Diacodex*, by a fusion between the cuboid and navicular bones of the ankle into the cubo-navicular bone (Figure 1). In the forelimb their radius and ulna were fused proximally as were the tibia and fibula of the hindlimb. In addition, their medial metacarpal and metatarsal bones had begun the process of fusion, while the lateral metapodials had regressed in size, more so in the hindlimb (where only four toes were present) than in the forelimb which retained all five toes.

Leptomerycidae

By some 10 My later, about 35 Mya, a group of later ancestral ruminants that differed sufficiently to be grouped in a family had emerged from the hypertragulid assemblage. This family was the Leptomerycidae. Leptomerycids had an astragalus whose proximal and distal parts formed a straight line. The magnum and trapezoid bones in the elbow had fused rather like the earlier cubo-navicular fusion of the ankle. The radius and ulna of the forelimb, and tibia and fibula of the hindlimb, fused

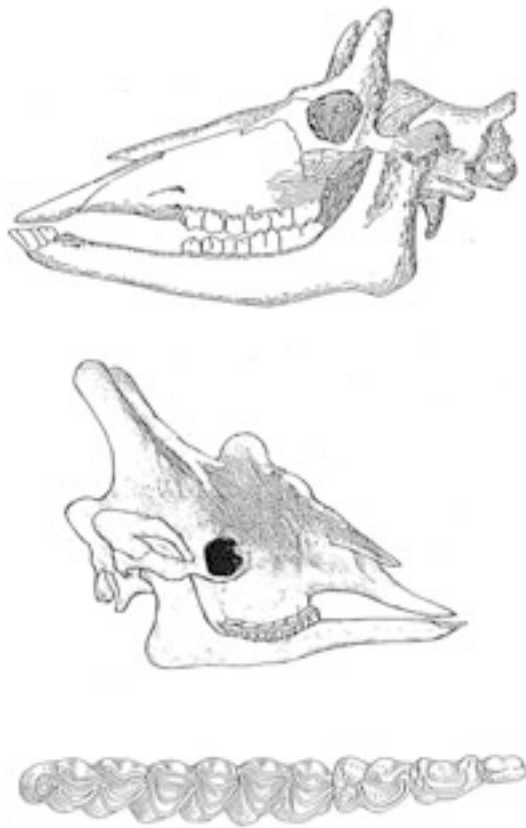


Figure 3. (Upper) Skull of *Samotherium*. Note the Giraffid-like ossicones, the elongated muzzle, the large diastema, and bi-lobed lower canine. (From Bohlin, 1926). (Lower) Skull of *G. camelopardalis* redrawn from Dagg & Foster, 1976, and the right lower cheek teeth of *Okapia*. From Churcher (1978). Note the selenodont molar cusps.

proximally in the hypertragulids had by now fused distally as well. These fusions were accompanied by fusion of the IIIrd and IVth metapodials, and further regression of the lateral ones. These changes in the distal parts of the limbs were essential precursors for the later limb elongation that is characteristic of ruminants, especially giraffes, because they provide the strength to support increases in length.

Leptomerycids also show another important development: the odontoid process of their second cervical (axis) vertebra is elongated and spout shaped, changes which increase neck stability, allow it to rotate about its long axis, and herald the increasing importance of the neck as a tool.

It is clear from these adaptations that the evolutionary pressures favouring particular characters were changing. The early development of the first artiodactyls and then the hypertragulids was dominated by adaptations that improved locomotion and possibly thermoregulation. After the hypertragulids changes occurred that improved feeding. This change in emphasis can be attributed to a dramatic change in climate (Figure 4). In the first 10 My of artiodactyl evolution the ambient temperature was hot, and precipitation high. These conditions lasted until separation of the Pangean landmass initiated a fall in temperature. Australia separated from Antarctica, and Greenland from Norway. Separation initiated cooling by establishing cold sea currents between the separating masses, the Antarctic icecap developed and sea levels fell (Janis, 1993). The rate of cooling was accelerated by the Asia-India collision that occurred about 40 Mya, throwing up the Alps and Himalayas (Janis, 1993) and producing the Tibetan plateau (Raymo & Ruddiman, 1992),

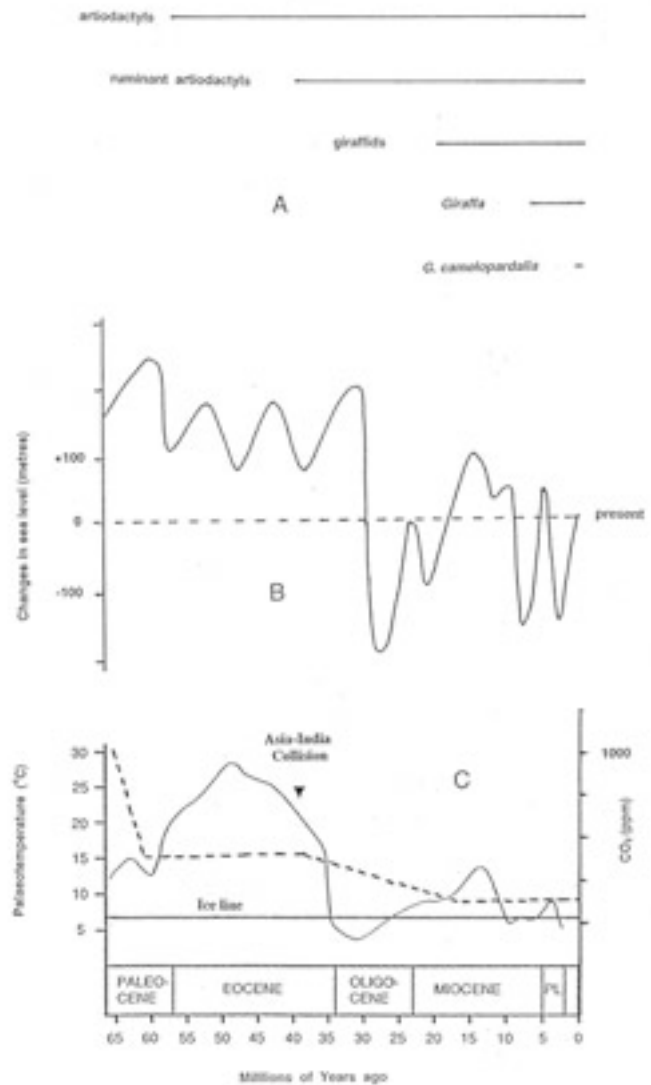


Figure 4. Correlation of the emergence of artiodactyls and *Giraffa* (A) with changes in sea level (B) and average ambient temperature (C). In B the dotted line represents current sea level and the solid line changes in sea level. In (C) the dotted line is CO₂ (ppm) and the solid line is temperature. Current CO₂ concentration is about 350 ppm compared to the 260 ppm that prevailed from the early Miocene mini-warm to the pre-industrial era. Redrawn from Janis (1993); Cerling *et al.* (1998); Hendey (1982); Kerr (1980); Raymo & Ruddiman (1992).

events that rearranged airflow currents and effectively divided the world climates into north and south (Figure 5). A more arid world was a further consequence.

Changes to vegetation followed (Figure 2). Forests shrank and savannah-woodlands expanded, and for a period of some 10 My there was consolidation and conservation of faunal characters rather than the flexible experimentation that had characterised previous eras. This period of consolidation, which began about 35 Mya, was the Oligocene.

Towards the end of the Oligocene it is possible to recognise new characters in artiodactyls that had survived the “deep freeze” (Janis, 1993) of climate change. The family of fossil artiodactyls that arose out of the Leptomerycidae and showed these characters was the Gelocidae. Gelocids appear in the fossil record of 25 Mya and are a key group in the evolution of the Pecoran families.

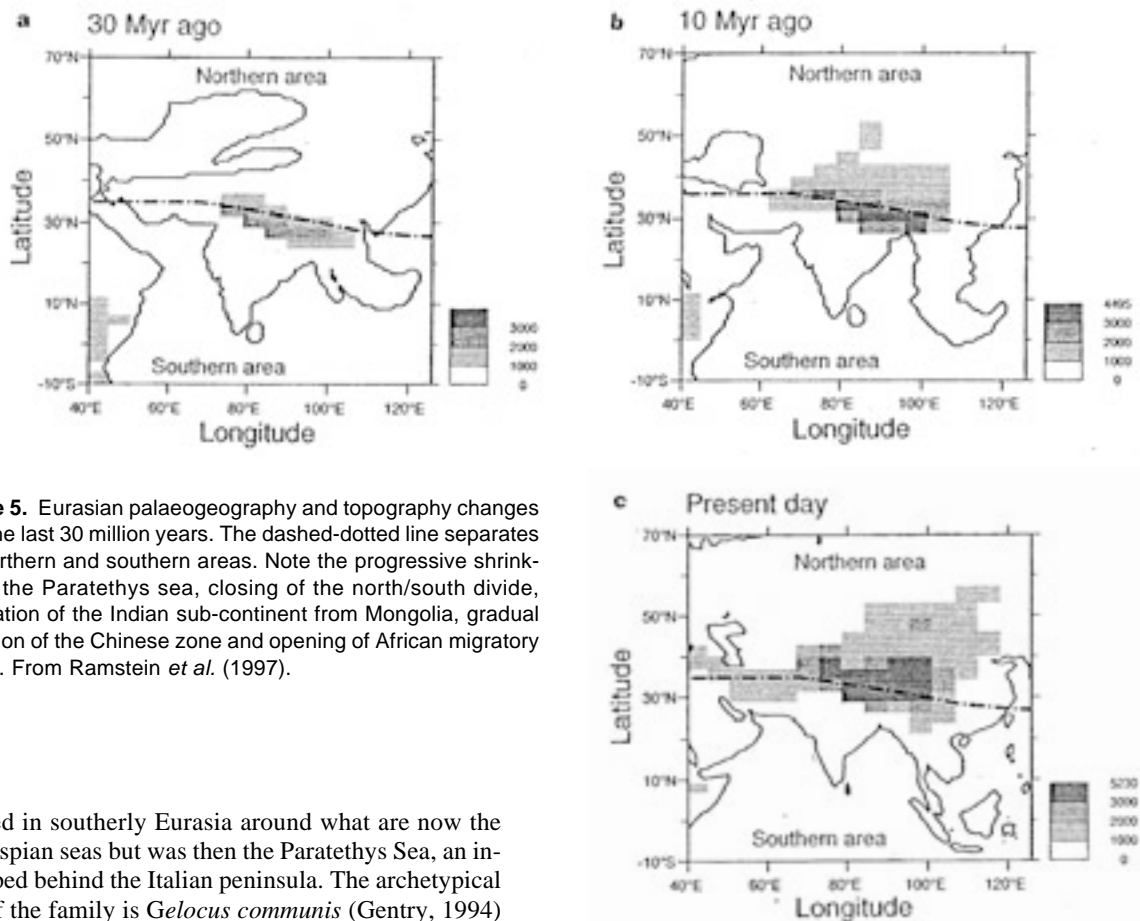


Figure 5. Eurasian palaeogeography and topography changes over the last 30 million years. The dashed-dotted line separates the northern and southern areas. Note the progressive shrinking of the Paratethys sea, closing of the north/south divide, separation of the Indian sub-continent from Mongolia, gradual elevation of the Chinese zone and opening of African migratory routes. From Ramstein *et al.* (1997).

Gelocidae

Gelocids lived in southerly Eurasia around what are now the Black and Caspian seas but was then the Paratethys Sea, an inland sea trapped behind the Italian peninsula. The archetypical fossil form of the family is *Gelocus communis* (Gentry, 1994) the “first fully progressive artiodactyl” (Carroll, 1988). *Gelocus* is characterised by increased selenodonty of molar cusps, showing its high reliance on plant material for its nutrients, and suggesting that gastrointestinal adaptations to herbivory had become a main evolutionary pressure. *Gelocus* also had elongated principal metapodials and a compact and parallel-sided astragalus, which illustrate the increasing role of speed and agility in the lives of artiodactyls. It was the first artiodactyl to exploit the stability of the limb format to increase limb length. It must have looked and functioned much like a modern gazelle.

The key importance of the gelocids is not only that they were the first and highly successful artiodactyl. They also mark the beginning of the first of two evolutionary radiations that produced the pecorans. From the gelocid genetic pool came all of modern artiodactyl ruminants – the Cervidae (Old World deer), Bovidae (Capriinae and Antelopiinae), Giraffidae (okapi and giraffe), Antilocapriinae (pronghorn antelope, *Antilocapra americana*), and Moschidae (musk deer, *Moschus* spp.).

The appearance of distinct families of pecoran ruminants in the fossil record occurred at about 18–21 Mya, which means that they started evolving from their ancestral stock much earlier. From analysis of the evolution of the cytochrome *b* gene (Irwin *et al.*, 1991), and from DNA sequence analysis (Kraus & Miyamoto, 1991; Allard *et al.*, 1992), and known rates of mutation, the time of this earlier radiation can be established with some accuracy. The data suggest that the pecoran radiation, and divergence of the pecoran families occurred over a 5 My period between 28 and 23 Mya. The period of 28–23 Mya coincides with a rising average ambient temperature (Figure 4) and a rising sea level, which would have increased precipitation and allowed an abundant flora to flourish (Janis, 1993). Subsequent post-divergence evolution would then have allowed the five distinct families to appear in the early Miocene fossil strata of 18 to 21 Mya.

Gentry & Hooker (1988) suggested that a subfamily of the Gelocidae, the Palaeomerycidae were the ruminant ancestral stock. In a later analysis Gentry revised this proposal and suggested that the ancestral gelocid from which both deer and the palaeomerycids arose was *Dremotherium*, that the bovinds and giraffids were closely related, and arose from an ancestral grouping that included the genus *Teruelia* (the giraffid ancestor) and *Walangia* (the bovid ancestor) (Figure 6A). This analysis fits the timing suggested by the biochemical data.

An alternative scheme developed by Matthew (1929), and Colbert (1935a) and refined by Stirton (1944), is summarised in Figure 6B. This scheme suggests that the palaeomerycids were the ancestral stock. If so, the palaeomerycids must have been evolving 23–20 Mya during the early Miocene warming (Figure 4). Divergence of pecorans from their ancestral stock can only have begun after 20 Mya, and the DNA evidence and the fossil record indicates that the pecoran families were clearly established by then. A palaeomerycid origin for all pecorans therefore seems unlikely.

A third possibility is that pecorans arose from both the gelocid and palaeomerycid assemblages (Figure 6B). One reason for concluding this is that the ancestors of Giraffidae appear in the fossil record after the appearance of the cervids, at about the time of the bovid radiation of 18 Mya (Allard *et al.*, 1992, Gentry, 1994). This temporal association suggested to Gentry (1994) that giraffids arose from, and are closely related to, the Bovids. This is unlikely. There is abundant evidence that suggests that giraffids share a common origin with cervids and not with bovinds. Anatomical evidence for this conclusion lies in the similarities of their teeth (e.g. Colbert, 1936b), which differ markedly from those of ancestral bovinds (Figure 7), and the similarities between the structure of their “horns”. The horns

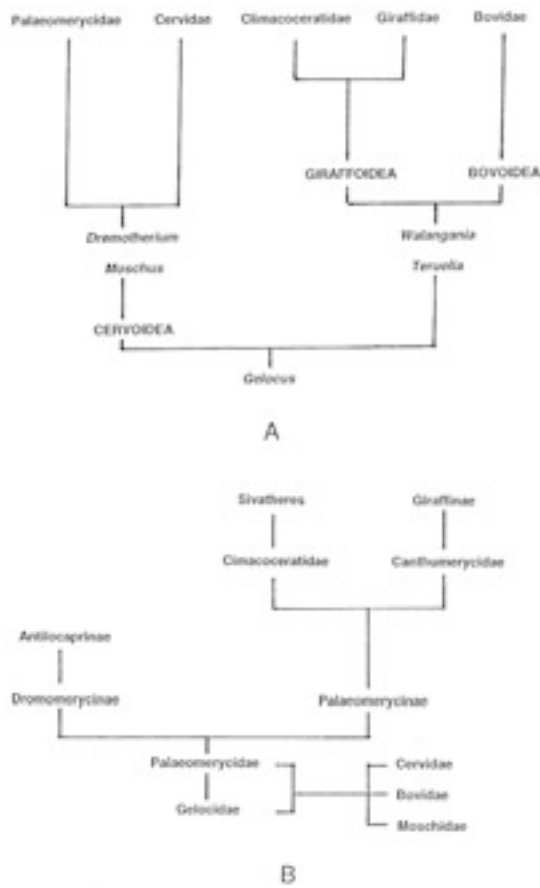


Figure 6. A. Relationships of families of Old World Pecora according to Gentry (1994). **B.** A possible phylogeny of giraffe based on Matthew (1929), Colbert (1935a), and Stirton (1944).



Figure 8. Phylogenetic relationships of 20 mammalian genera determined from analysis of cytochrome b genes. The cladogram is consistent with an initial radiation of placental mammals about 80 Mya, a divergence between chevrotains and other pecorans at 45 Mya, and radiation within the pecorans about 20–25 Mya. Note that giraffes and deer are grouped together. From Irwin *et al.* (1991).

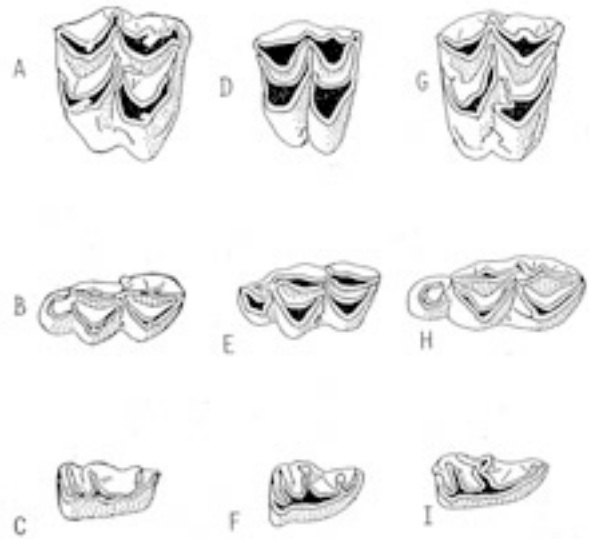


Figure 7. Occlusal views of the right cheek teeth of the primitive Giraffid *Canthumeryx* (A, B, C), the primitive bovid *Eotragus* (D, E, F) and the primitive cervid *Dicrocerus* (G, H, I). Top rows are M2s, middle rows are M3s and bottom rows are P4s. Note the Cervid and Giraffid similarity. Redrawn from Gentry (1994).

differ in that cervid antlers are deciduous while those of giraffids and bovids are not. They differ also in their anatomical origins. Cervid antlers and bovid horns are an outgrowth of bone base while giraffe horns develop from an epithelial cartilaginous growth point (Lankester, 1907), which subsequently ossifies and fuses with the skull. This difference in origin of giraffid horns is captured in the name “ossicone” (Lankester, 1907).

A close relationship between giraffids and cervids is also supported by giraffe hair slope patterns, which are more similar to those of cervids than of other ungulates (Kidd, 1900). Ridewood (1901) also reported that the hairs of giraffes and okapi are similar and differ from those of antelope. However the most convincing evidence is biochemical. Analysis of cytochrome *b* gene evolution (Irwin *et al.*, 1991, Figure 8), pancreatic ribonuclease primary structure (Beintema *et al.*, 1979), DNA sequence analysis (Kraus & Miyamoto, 1991; Allard *et al.*, 1992), and K-casein gene phylogeny (Cronin *et al.*, 1996) all show that giraffids are more closely related to cervids than they are to bovids, and confirm their phylogenetic affinities.

Drawing these observations together, a reasonable conclusion is that the *Gelocus* assemblage gave origin to the Bovidae (including the Antilopiinae and Capriinae) via a *Gelocus-Walangia* ancestral line. The Old World deer (the Cervidae) and the Palaeomerycidae assemblage evolved via a *Gelocus-Dremotherium* line. The Palaeomerycidae were the origin of New World deer (the Antilocapridae) and the Giraffidae via two sub-families, the Dromomerycinae and the Palaeomerycinae (Stirton, 1944) (Figure 6B). Dromomerycids evolved into the New World deer, and made their way to temperate North America to survive there as pronghorn “antelope”.

The Palaeomerycinae were the origin of the Giraffidae. It is possible that the Palaeomerycine *Teruelia*, a hornless gelocid about the size of a small gazelle the only fossil form of which has been found in Spain (Agusti & Moya Sola, 1991) was the earliest ancestral giraffid. If so, from *Teruelian* stock two families of giraffids arose: the Climacoceratidae and the Canthumerycidae.

Figure 9. Reconstructions of Sivather species.
A. *Climacoceras* from Hende (1982);
B. *Prolibytherium magnieri* from Churcher (1978);
C. *Sivatherium giganteum* from Savage & Long (1986);
D. *Sivatherium maurusium* from Churcher (1978).



Climacoceratidae

The most important and so far the most primitive known climacoceratid is *Climacoceras africanus* (Figure 9A) first described by MacInnes (1936) from fossils found at Koboko Island in the Kavirondo Gulf of Lake Victoria. MacInnes called it the “fossil deer” of Africa saying it was the size of a roe deer, *Capreolus capreolus*.

Climacoceras must have been remarkably successful. It lived in large herds (Hende, 1982) and was widespread throughout Africa. Fossils of other climacoceratid species have been found at Fort Ternan in Kenya (*C. gentryi*) (Gentry, 1970), a fossil deposit dated with some accuracy to 14 Mya (Churcher, 1970), at Arrisdrift in Namibia (Hende, 1978), a deposit dated to about 17 Mya (Gentry, 1994), and at Nyakach (= Nyanza, Kenya) dated to 15 Mya (Thomas, 1984). The Arrisdrift climacoceratid was about 20% larger than either the Koboko or Fort Ternan species. It lived in a forested riverine habitat and could have been a regional variant isolated from its eastern and northern African relatives by the southern African river systems (Hende, 1978). All three species have features that link them to giraffids generally and their sister group the Canthumerycidae specifically. However, although having features that indicate their closeness to giraffes they are not on the lineage that leads to modern giraffes. It is more likely that *Climacoceras* gave rise to a sister group of *Giraffa*, the Sivatheriinae.

Sivatheres were as big as elephants, *Loxodonta africana*, massive and heavily built, short-legged, short-necked, with large and ornamented horns (Figure 9C, D). They were bulk grazers/browsers. Their centre of origin was Asia of the early Miocene, and they evolved via *Prolibytherium magnieri* (Figure 9B) into two persistent and successful forms. The first was *Sivatherium giganteum*, the terminal Asian form (Figure 9C), which became extinct in the early Pleistocene, and *S. maurusium*, which was widespread in Africa. *S. maurusium* survived perhaps until 3500BP in north Africa (Colbert, 1936a).

Canthumerycidae

The earliest known giraffine ancestor is *Canthumeryx sirtensis*. The fossil deposit in which this fossil was found, was discovered by Arambourg (1959, 1963). It lies near Gebel Zelten about 200 miles south of Tunis in Libya, now in desert but at the time that *Canthumeryx* lived there it was a flourishing alluvial/flood plain/savannah/river basin habitat (Hamilton, 1973). The fossil fauna of Gebel Zelten is typical of early Burdigalian or late Aquitanian age that establishes it as 20 to 25 Mya (Hamilton, 1973), although other methods of dating place it an age of 15 to 17 Mya (Gentry, 1994), and 14.3 to 18.0 Mya (Morales *et al.*, 1987).

Canthumeryx was first described by Hamilton in 1973, and he named it *Zarafa zelteni*, an evocative name that recalls the Arab origins of the word from which the name for the genus *Giraffa* is derived. In a later analysis of the fossil and others, Hamilton (1978) renamed *Zarafa*. The name change arose because of a prior description he had given to a fossil skeleton of a similar form found in Kenya and to which *Zarafa* in the order of things had to be referred. *Zarafa zelteni* thus became *Canthumeryx sirtensis* after the Greek mythological character Canthus who had been sent to Libya to meet his fate.

Canthumeryx was a medium sized, slender antelope about the same size as a fallow deer *Dama dama* (Hamilton, 1973, 1978). Crucially it had the characteristic bilobed giraffoid lower canines. Hamilton (1978) further suggested that the utility of this feature was that it facilitated stripping of foliage from browse. Its limb length can be calculated to have been about 85–100 cm long, and its shoulder height would therefore have been about 1.5 m. It had unbranched (simple) horns that projected



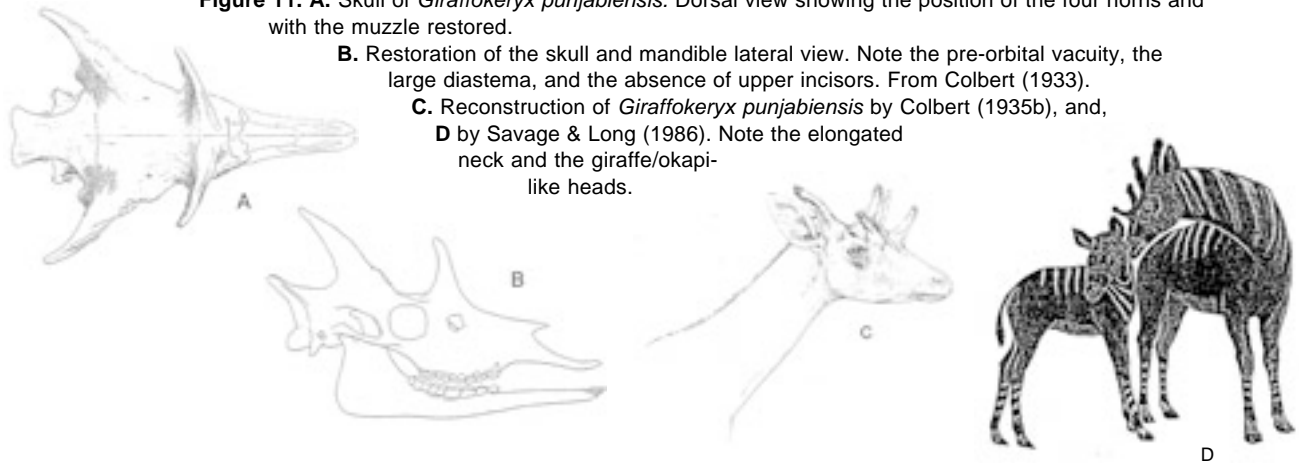
Figure 10. **A.** Reconstruction of *Canthumeryx sirtensis* from Churcher (1978);
B. Map showing the relationship between the East African fossil sites and the Siwalik deposits. The peri-Caspian Sea area is equidistant from both. From Morgan *et al.* (1994).

Figure 11. A. Skull of *Giraffokeryx punjabiensis*. Dorsal view showing the position of the four horns and with the muzzle restored.

B. Restoration of the skull and mandible lateral view. Note the pre-orbital vacuity, the large diastema, and the absence of upper incisors. From Colbert (1933).

C. Reconstruction of *Giraffokeryx punjabiensis* by Colbert (1935b), and,

D by Savage & Long (1986). Note the elongated neck and the giraffe/okapi-like heads.



sharply laterally and lay almost horizontally from a position above its orbits (Figure 10A). Its skull was wide and had large occipital condyles (which articulate with the first (atlas) vertebra), but the atlas was not elongated having a length to width ratio of 1.03 *cf.* that of a giraffe of 1.17. Like its gelocid ancestor it seems to have been very similar to a lightly built, medium sized, slender-limbed, but in this case, a not very agile gazelle.

Related and later species have been discovered throughout the middle east, in Iraq and Saudi Arabia and Greece, and these species existed over a period 18–15 Mya. The species that are similar to *Canthumeryx* are *Injanatherium*, which flourished in the mid-Miocene in Saudi Arabia and in the late Miocene in Iraq (Morales *et al.*, 1987), and *Georgiomeryx* from Greece (De Bonis *et al.*, 1997). *Georgiomeryx* was a direct descendant of *Canthumeryx*, had flattened supra-orbital horns, and its fossils have been dated to 15.16 to 16.03 Mya (De Bonis *et al.*, 1997). *Injanatherium*, significantly, had two pairs of horns and its later age and distribution of its fossils suggest that it occupied a more easterly, Asian, part of the central southern European biome, while *Georgiomeryx* had migrated more westwards.

While *Canthumeryx* and its relations clearly are at the base of the *Giraffa* line, they existed 10 to 15 My before the first appearance of *Giraffa* and clearly did not have a giraffe-like shape. They also appear to have become extinct towards the early middle Miocene about 14 or 15 Mya. The 7 to 8 My gap between them and the appearance of the first undoubted giraffes has to be filled, therefore, by some or other ancestor. It is filled first by *Giraffokeryx*.

Giraffokeryx

Giraffokeryx (keryx = herald) is a key species. It has all the attributes of a giraffe ancestor and occupies the right evolutionary position. Its features straddle its Palaeomerycine antecedents on the one hand and the Palaeotraginae assemblage that seems to have arisen from them. *Giraffokeryx* was first identified by Pilgrim (1911) from a number of teeth and mandibles he found in the lower Siwalik (“Chinji”) deposits of India/Pakistan, a deposit dated to 12–15 Mya by Simons *et al.* (1971), and about 10 Mya by Matthew (1929). The most complete description of *Giraffokeryx* is that of Colbert (1933), which he later summarised (Colbert, 1935b), from specimens including a skull in the American Museum of Natural History. It was a medium sized member of the Giraffidae distinguished by its two pairs of horn cores (ossicones) (Figure 11A).

Reconstructions of it differ. Colbert (1935a) concluded from his analysis of its fossils that it had an elongated neck and drew it as a small giraffe (Figure 11C). Another reconstruction by Savage & Long (1986) shows it looking more like an okapi, but

nevertheless with a clearly elongated neck (Figure 11D). Its resemblance to okapi is not fortuitous. In all probability the okapi, which Joleaud (1937) and Colbert (1938) called a “living fossil”, is a persistent, little changed palaeotragine that has survived by occupying a forest refuge niche unchallenged by other species.

Palaeotraginae

The Palaeotraginae, it can be surmised, arose in the mid-Miocene, African-Arabian faunal realm as a radiation from their ancestral Canthumerycid assemblage. This radiation coincided with the boviniae-antilopinae radiation that DNA analysis suggested lasted for 7 My between 23 Mya and 16–17 Mya (Allard *et al.*, 1992), but which analysis of the evolution of the cytochrome *b* gene indicated took place a little later between 15 and 12 Mya (Hassanin & Douzery, 1999). The Palaeotraginae comprise three genera, *Giraffokeryx*, and two others *Palaeotragus* and *Samotherium*.

Palaeotragus sp. were medium sized giraffids having limbs and neck slightly elongated, usually with a single pair of horns that were sexually dimorphic. Their skull was elongated and broadened, especially between the horns (Forsyth Major, 1891), but did not contain the sinuses so characteristic of later *Giraffa*. They ranged from East Africa (Churcher, 1970) to Mongolia (Colbert, 1936b), immense distances apart.

Churcher (1970) described the earliest palaeotragine from fossils recovered from the Fort Ternan (and also Muruorot and Rusinga), a deposit dated at 14 Mya (Retallack *et al.*, 1990), and named it *Palaeotragus primaevus*. At Fort Ternan this species was so common that it could be described from 243 specimens. It had gracile long limbs, and we can conclude it was a powerful runner and leaper. Its dental formula (Churcher, 1970) was:

$$I^{0/3} \quad C^{0/1} \quad P^{3/3} \quad M^{3/3} = 32.$$

which is the same as *Giraffa*. The lower canine was bilobed. Its teeth were however primitive being slim, not broadened, and brachyodont. It depended almost completely on browse for food and water (Cerling *et al.*, 1991, 1997). The shape of its muzzle was similar to okapi and giraffes (Solounias & Moelleken, 1993), and its teeth show microwear patterns of pits and scratches, which are determined by food, similar to those found in modern giraffes (Cerling *et al.*, 1997). Churcher (1970), following the assumptions of the time, regarded *P. primaevus* as an offshoot of the Asian palaeotragine stock that had reached Africa by migrating across the Suez isthmus as sea levels fell between 23 and 16 Mya (Figure 4). Both Hamilton (1978) and Gentry (1994) regarded *P. primaevus* as being close to or iden-



Figure 12. A. Heintz's proposal for the migration of Palaeotraginae from north Africa. Note that *Zarafa zelteni* is *Canthumeryx sirtensis*, and *P. primaevus*, *Giraffokeryx*, and *P. tungurensis* are probably identical species. See text for additional discussion. From Heintz (1975). B. A cave painting from Algeria of *Helladotherium*. From Joleaud (1937).

tical to *Giraffokeryx punjabiensis*, and this linkage provides the continuum between *Giraffokeryx*, which was becoming extinct, and the palaeotragine assemblage that filled the niche created.

The subsequent discovery of numerous other palaeotragine fossils led Heintz (1975) to propose that palaeotragines migrated from a north African centre of origin well before the appearance of *Hipparion* sp. in the fossil record (i.e. at least 12 Mya), into eastern Eurasia (Mongolia), central Europe (Greece, Turkey, Crimea, Iraq), western Europe (Spain, Portugal), Africa and India, but not temperate northern Europe. The fossil records described by Crusafont-Pairo (1952) in Spain, Arambourg (1963) in North Africa, Heintz (1975) in north Africa and Greece, Churcher (1970) in East Africa, Pilgrim (1911), Matthew (1929), Bohlin (1926, 1935), and Colbert (1935b) in the Pakistan Siwalik deposit, Pilgrim (1934) and Colbert (1936b) in Mongolia, and Ciric & Thenius (1959) in Yugoslavia, all support this hypothesis.

Eurasian paleotragines did not have *Giraffa*-like morphology and are completely unrelated to *Giraffa* (Gentry, 1994). They form an independent lineage and assemblage of animals that are a sister group to the paleotragines that would ultimately produce modern giraffes. In Africa two *Palaeotragus* sp. are thought to have existed: *P. primaevus* and *P. germaini*. *P. germaini*, a paleotragine first described by Arambourg (1959) and known from Moroccan, Algerian and Tunisian fossil deposits of the late Miocene and therefore later than *P. primaevus* (*Giraffokeryx*), was of large size and resembled *Giraffa* in its elongate neck and limbs. The evolutionary line of these species could be *Canthumeryx* > *Injanatherium* > *Giraffokeryx*/*P. primaevus* > *P. germaini*.

The corollary of this conclusion is that the Palaeotraginae are a descendant assemblage of the Canthumerycidae, that *Giraffokeryx* is a primitive palaeotragine and that it is also an intermediate form between the Canthumerycidae and the later Palaeotraginae. Therefore the paleotragines are an ancestral group, and *Giraffokeryx* an ancestral species, to *Giraffa*. If so, then overlapping and sequential time scales, and the presence of a genetic propensity to generate *Giraffa*-like features, can be expected in the palaeotragine fauna. These features can be seen in the third palaeotragine genus, *Samotherium*.

Samotheres

Samotheres are large, progressive palaeotragines that differ generally from *Palaeotragus* sp. by being of much larger size,

and having longer faces (Churcher, 1978) with a typical giraffe profile (Figure 3). Their horns were supraorbital and thus placed further forward than they are in giraffes. The skull roof was broadened and inflated by "pneumatic cavities" (Forsyth Major, 1891). Well-developed cranial sinuses are a characteristic of living giraffes and serve to enlarge the skull without adding mass, an important prerequisite for neck elongation. An increase in size of frontal sinuses also forces ossicones away from their primitive position over the eyes towards the skull midline (Colbert, 1938). Sinuses are absent in *Palaeotragus* and therefore in the *Samotheres* represent an evolved and developed feature. In addition their teeth are hypsodont as they are in giraffes, but other teeth features resemble those of *Palaeotragus* and show the close relationship between them (Hamilton, 1978).

Palaeotragus sp. appear to have become extinct around 9–10 Mya and the *Samotheres* became the dominant palaeotragines in the late Miocene/ early Pliocene (9–5 Mya) (Gentry, 1994; Churcher, 1970) occupying the niche vacated by the extinction of *Palaeotragus* sp. *Samotheres*, therefore, follow *Palaeotragus* chronologically, and this together with their features, is convincing evidence of an ancestor–descendent relationship. Several *Samotheres* species have been described. They are likely to be variations or subspecies suggestive of geographical reproductive isolation but not necessarily physiological reproductive isolation. Just three species seem to be sufficiently distinct to warrant separation. These are *S. africanum*, *S. boissieri* (= *S. sinense* = *S. tafeli*, from Samos and China) and *S. neumayri* (that resembles *S. sinense* (Hamilton, 1978)), an early Pliocene form (Churcher, 1970) from Iraq and China.

S. africanum

Eurasian *Samotheres* did not have the morphology that suggests they were the ancestors of *Giraffa*, and in any case do not seem to have left any descendants. On the other hand *S. africanum* did have the morphology, but the origin of *S. africanum* is less clear than is the origin of the Eurasian *Samotheres*.

A possible intermediate form between the palaeotragines and the African *Samotheres* is *Helladotherium*, which was first described by Forsyth Major and Lydekker (1891) from fossils found in Greece and in the Siwalik. A cave painting (Joleaud, 1937) of *Helladotherium* (Figure 12B) which makes it look like a large hornless *Giraffokeryx* or okapi, makes this conclusion plausible.

A more likely origin of *S. africanum* is *P. germani*. Harris (1987b) noted that the skeleton of *P. germani* had the same dimensions as that of *S. africanum* and differed only in that *S. africanum* had larger ossicones. Therefore, he concluded, that *P. germani* was *S. africanum* or at least an antecedent to it. *S. africanum* fossils have been recovered from Algeria, Tunisia, and Egypt, and possibly Kenya (Churcher 1970). Its giraffe-like features and chronological age make it a logical antecedent of the *Giraffa* lineage.

Bohlinia

A fossil form that could have evolved from *S. africanum*, occupied the right chronological niche, and had the appropriate progressive giraffe-like morphology, was *Bohlinia attica*, and it can be regarded as the immediate ancestor of giraffes. Geraads (1986) put it thus: “*Bohlinia attica* does not seem to possess any apomorphic characters in the *Giraffa* assemblage and it constitutes then an acceptable ancestor”. Early fossils found of *Bohlinia* were so similar to both extant and fossil giraffes that, when they were discovered, they were classified as *Giraffa attica* by Gaudry and Lartet (Forsyth Major, 1891). Bohlin (1926) made a more complete description from fossils he found in Pikermi in Greece about 100 miles southwest of Athens as the crow flies. The Pikermi fossil deposit is 7–9 My old (Agusti *et al.*, 1999), so the chronology of *Bohlinia* is correct. Bohlin originally called the fossil species *Orasius* (derived from a corruption of the latinised form *Oraflus* for giraffe), but Matthew (1929) who agreed that it was a giraffine suggested that it be called *Bohlinia*, which later Simpson (1945) did and entrenched the name.

The pre-eminent status of *Bohlinia* as an intermediate form between its palaeotragine-samothere ancestors and *Giraffa* can be judged from its many common traits with *Giraffa*, particularly their long legs and neck, similar ossicones, the characteristic bilobed lower canine, and selenodont rugose molars. Harris (1976c) remarked that, although it was smaller than early African *Giraffa* (e.g. *G. gracilis*), *Bohlinia* resembled them closely.

The evolutionary experiment that *Bohlinia* inherited from *P. germani*/*S. africanum* was evidently successful, and had clearly not required Hitching’s “series of accumulated modifications over thousands of generations” (Hitching, 1982). It gave rise over the next few millions of years to a relatively rapid adaptive radiation, and emergence of the genus *Giraffa*. The earliest of these radiations followed a south-easterly migration into Indo-Asia and produced four or five Asian *Giraffa* sp., and a large Chinese form, *Honanotherium* sp. (Bohlin 1926). Later radiations were by a south-westerly migration into Ethiopia, and even further southwards into Africa, where at least five African species evolved. Of these 10 or so species just one has survived.

Indo-Asian Giraffa

If *Bohlinia* was the ancestor and it or its descendents migrated to India it did this first in the late Miocene early Pliocene, the time when the first *Giraffa* species, *G. priscilla*, evolved. The fossils of this species are very limited. The species was founded by Pilgrim (1911) on left upper 2nd and 3rd molars, a fragment of a mandible and a right upper molar. No postcranial skeleton is known.

G. punjabiensis

A second Asian species was *G. punjabiensis* which, according to Harris (1991), is the oldest known and unmistakable *Giraffa*. It is dated to 7.1–7.3 Mya or the late middle Pliocene. *G. punja-*

biensis had features similar to those of *Bohlinia*, but is regarded as being an advanced form closely related to modern giraffes (Harris, 1976c) and generically distinct from *Bohlinia*, especially with respect to its brachyodont, less selenodont but rugose molars. It was smaller than the early African *Giraffa*, and was the ancestor of the later Asian *Giraffa*. It was extinct by the end of the Pliocene.

G. sivalensis

The descendent of *G. punjabiensis* and the climax of the Indo-Asian line was *G. sivalensis*. It was first described by Falconer & Cautley (1843–1844), had an early Pleistocene age (Churcher, 1978), and was thus chronologically sequential to *G. punjabiensis*. Falconer & Cautley found two fossils remnants that they could attribute to giraffe, but thought that they were from separate species. One fossil came from an immature individual and Falconer & Cautley summarised its anatomy thus:

“... a true well-marked species of giraffe closely resembling the existing species in form, but one-third less in height, and with a neck proportionately more slender.”

The second fossil they said was “... all but indistinguishable from ... the Nubian giraffe”.

Pilgrim (1911) classified both as *G. sivalensis*.

In body size it was larger than extant giraffes and its teeth, although larger than those of *G. punjabiensis*, were smaller than those of extant giraffes. It was extinct by the mid-Pleistocene.

AFRICAN LINEAGE

Modern African giraffes were well known to the Khoisan as far south as Graaff Reinet. They were also known to the Egyptians in the far north from times of earliest antiquity, although by then restricted to north Africa below 15 °N latitude i.e. the head of the Nile (Laufer, 1928). The first formal observation of extant giraffes in southern Africa was made on 28th November 1663 (Godee Molsbergen in Bigalke, 1951) about 120 miles south of the Gariep (formerly Orange) River in Namaqualand. It was not known more southerly than that and indeed even then seems to have been migrating northwards as by 1761 “there does not seem to be any evidence of the occurrence of this animal south of the Orange River” (Sclater, 1900). Of course exploration of the eastern regions of southern Africa in what is now Mpumalanga and KwaZulu-Natal would have revealed an abundance of them.

Further evidence that giraffes found the African habitat congenial is provided by Lydekker (1904) who reported the results of 20 years of arduous and unrepeatable data collection that had the aim of classifying *G. camelopardalis* by variations in skin markings, ossicones, and geographical distributions. He was able to distinguish 11 subspecies: *G. typica* (Ethiopia), *G. antiquorum* (Sudan), *G. peralta* (Nigeria), *G. reticulata* (Somalia), *G. cottoni* (Uganda), *G. tippelskirchi* (Kenya), *G. rothschildi* (Baringo), *G. congolensis* (Congo), *G. angolensis* (Angola), *G. wardi* (Transvaal, South Africa) and *G. capensis* (Cape Province, South Africa). These, except for *G. peralta*, with their distributions, are shown in Figures 13 and 14. All these subspecies interbreed easily and successfully, their geographical distributions are not as distinct as Lydekker suggested, and their skeletal remains are identical (Singer & Bone, 1960). Thus they are now known to be regional or geographical polymorphisms and are no longer recognised as valid subspecies (Singer & Bone, 1960; Skinner & Smithers, 1990). All are *G. camelopardalis*. They are nevertheless important as they illustrate the

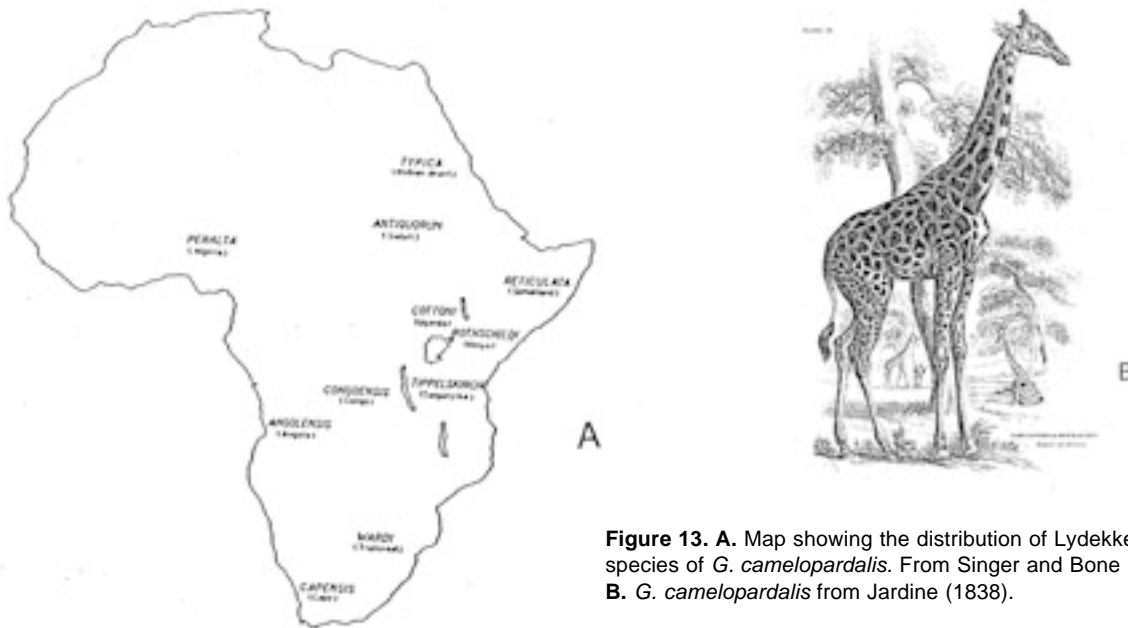


Figure 13. A. Map showing the distribution of Lydekker's sub-species of *G. camelopardalis*. From Singer and Bone (1960). B. *G. camelopardalis* from Jardine (1838).

wide distribution of the genus in Africa as well as an ability to produce variants suited to local conditions.

There can be no doubt therefore that the habitat of Africa was highly suited to *Giraffa* anatomy and physiology. Their ancestor–descendant sequence is confused however. This is not because intermediate forms do not exist. For example it is clear from the literature that five species (*G. gracilis*, *G. pygmaea*, *G. stillei*, *G. jumae*, *G. camelopardalis*) may have existed either sequentially or in parallel, but it is how these forms evolved and are related that is unresolved.

Harris (1976b) noted that three of these species coexisted in the Pliocene/Pleistocene of East Africa, separable in size and by shape and orientation of ossicones. The largest of these was *G. jumae*, followed by *G. gracilis*, with the smallest being *G. pygmaea*, which at the time he regarded as being synonymous with *G. stillei*. The presence of three apparently coeval giraffes could be attributed to a rapid evolution and radiation on reaching sub-saharan Africa. A second bovine-antelope radiation was occurring at about 6 or 7 Mya (Hassanin & Douzery, 1999) which suggests that environmental conditions were highly favourable for ruminant radiation and speciation.

In an attempt to condense a mass of information Harris (1991) wrote, referring to an earlier observation he had made (Harris, 1976a), that:

“The earliest undoubted record of giraffes from subsaharan Africa is from the Quartoze Sand Member of the Varswater Formation at Langebaanweg in South Africa, whose age, based on fossil evidence, appears to be early Pliocene.”

The species Harris was referring to is *G. jumae*, and Hendeby's analysis of the age of the Langebaanweg deposit indicated that it was 4.5 My old (Hendeby, 1981). Harris's conclusion does not, therefore, fit all the evidence, especially the chronology. For example, if the first appearance of *G. jumae* was at the Cape at 4.5 Mya, and the first appearance of a smaller species, *G. gracilis*, is at 3.9 My in East Africa, then the origins of these two species are obscure and they cannot both derive from *Bohlinia* of 7–9 Mya. This gap would be too large. Nor can their presence be by migration from Asia as the separation of Africa from Arabia by the Red Sea occurred at 3.5 to 4 Mya (Hsiu *et al.*, 1977), even if a migration route was open from Asia to Arabia,

which is unlikely (see Figure 9). Moreover, Pickford (1975) and Churcher (1978) report the presence of Giraffinae (although these finds remain undescribed and uncertain (Harris, 1991)) at Lukeino (= Baringo in Kenya) at around 6 Mya, and these too cannot be reconciled with an appearance of *G. jumae* and *G. gracilis* around 4 Mya.

It seems that to make any sense of the existing data, it must be assumed that the history of *Giraffa* in Africa started about 7 Mya with an arrival in Ethiopia across the Arabian-African land bridge. This conclusion is rendered necessary by the presence of a *Giraffa* in the northern Kenya Rift valley in a fossil deposit dated to 7.0–5.4 Mya (Pickford, 1975). This ancestor may have been a derivative of one of the Asian *Giraffa*, in particular the contemporary *G. punjabiensis*, that entered Africa by migration. Kurten (1957), for example, showed that “an unchecked spread of some 1000 km in a century would seem a moderate estimate for most larger mammals”, thus both the chronology and the time scale, required for such a migration are right. However, the absence of a migratory route makes it unlikely. Moreover, the anatomy of *G. punjabiensis* is different and more advanced than that of African *Giraffa*, so Churcher (1978) regarded *G. punjabiensis* as similar but not in the same lineage.

G. gracilis

If migration of an Asian form is unlikely, the alternative solution is that the African *Giraffa* arose from Pliocene *Bohlinia*. Constructing a lineage on this basis, the earliest African species of *Giraffa* is usually regarded as being *G. gracilis*, which has at various times been synonymised with *G. stillei* and *G. pygmaea*. *G. gracilis* morphology was similar in many respects to that of *Bohlinia*. It is a late Miocene to early Pleistocene species with a range restricted to East Africa (Harris, 1976c; Hamilton, 1978). It is abundant in the Laetoli deposits of Kenya dated at 5–2 Mya (Harris, 1987a). It is also present at East Rudolph (Harris, 1976b) another Pliocene/Pleistocene site, in the Serengeti (Harris, 1976c) and at Olduvai (Leakey, 1965) but not with any certainty in other parts of Africa. The East African Pliocene therefore probably represents the climax of *Giraffa* as a species in Africa.

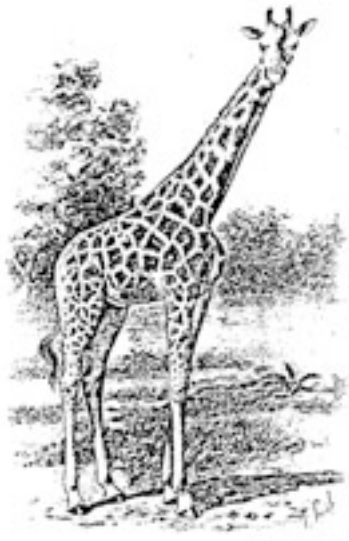
Some fossils of *G. gracilis* were, from the elongation of its



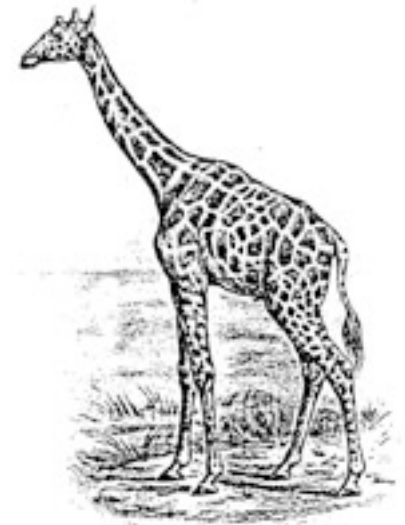
Giraffa Camelopardalis Antelopum. ♂ Ju.



Giraffa Camelopardalis Anguicoma. ♂



Giraffa Camelopardalis Typica. ♂ Ju.



Mala Cingis Giraffa. (From the type specimens in the Torrioni Museum.)



Fig. 1.
Retinoides Giraffa.
From a photograph of Carl Reppert.



Giraffa Camelopardalis Polakowskii. ♂



Heads of (1) *Giraffa Camelopardalis Cottoni* and (2) G.C. Ward.



Giraffa Camelopardalis Gemma. ♂

Figure 14. Lydekker's (1904) drawings of sub-species of *G. camelopardalis*. Note the subtle differences in coat markings and horn number and orientation.

limbs and neck, of comparable stature to *G. camelopardalis* (Arambourg, 1947), but they suggest that *G. gracilis* was more lightly built than *G. camelopardalis* or *G. jumae*. It was larger than *G. pygmaea* and *Bohlinia* (Harris, 1976c), and smaller than modern female giraffes. Its feet were relatively small having a footprint the size of an eland, *Tragelaphus oryx* (Harris, 1987a) (Figure 15). This conclusion was reached when, having noted fossilised footprints in the Laetoli ash bed, Mary Leakey asked a local tracker what might have made the spoor. The answer given was “eland” and, based on this observation and assuming that the tracks were made by an adult, *G. gracilis* must have been about half the size of *G. camelopardalis*. The dimensions of its fossils vary however, which suggests that it increased in height over time.

G. stillei

G. gracilis may have been preceded by an Ethiopian (Omo) form identified by Arambourg (1947) in a fossil deposit of Pliocene/Pleistocene age and now known to be 3.8 to 1.8 My old (Harris, 1976c). If so, the earliest fossil of this migrant so far recovered is aged at 3.3 to 2.7 Mya (Harris, 1976c), which is too recent for it to be considered an ancestor to *G. gracilis*. It was found in association with a larger *Giraffa* probably *G. jumae*. This Omo fossil is assumed to be *G. stillei* and is regarded as a separate species on account of its small size. Harris (1976c) has argued convincingly however that *G. gracilis* and *G. stillei* are synonymous. Except for more rugose enamel and possibly a smaller size of *G. stillei* the two cannot be separated on fossil evidence. A similar fossil was discovered at Lake Baringo in Kenya suggesting a southward movement from the Ethiopian highlands. Thus a possible scenario is that *G. stillei* was a descendent of *Bohlinia* that evolved on entry into Africa, increased its size in the favourable ecological niche of East Africa, and resulted in the evolution of *G. gracilis*. If this fossil is a progenitor of the African *Giraffa* lineage, earlier fossils of it remain to be recovered.

G. pygmaea

An even smaller form is *G. pygmaea*. *G. pygmaea* is a Pleistocene form although a rare one, at least at Lake Rudolph (Harris, 1976b, 1976c). Harris implies that Arambourg's Omo specimen of 3.5 Mya could be *G. pygmaea*, and that if this was the case a lineage of *G. pygmaea* > *G. stillei* > *G. gracilis* was possible. Thus he at first synonymised the three (Harris, 1987a) but later separated *G. pygmaea* from the other two (Harris, 1991). He separated them because *G. pygmaea*, *G. gracilis*, and *G. stillei* appear to have been coeval for many millions of years, and ancestral–descendent forms cannot also be coeval. This anomaly forces the conclusion that, while *G. stillei* may have been ancestral to *G. gracilis*, later fossils of *G. stillei* are confusions of *G. gracilis* rather than evidence that they were contemporary. On the other hand, it seems reasonable to conclude that *G. pygmaea* was a contemporary smaller variant occupying a niche habitat that allowed it to evolve into a subspecies. This niche habitat according to Harris (1991), based on Pellew's (1983a) analyses of giraffe feeding ecology, was valley bottom, riverine woodland, while *G. gracilis* (and presumably *G. stillei*) was a ridge top *Acacia* woodland feeder. Competition with bovid browsers such as eland might have led to the mid-Pleistocene extinction of *G. pygmaea* and an increase in size of *G. gracilis*, such that ultimately its fossils were indistinguishable from those of *G. camelopardalis* and *G. jumae*.

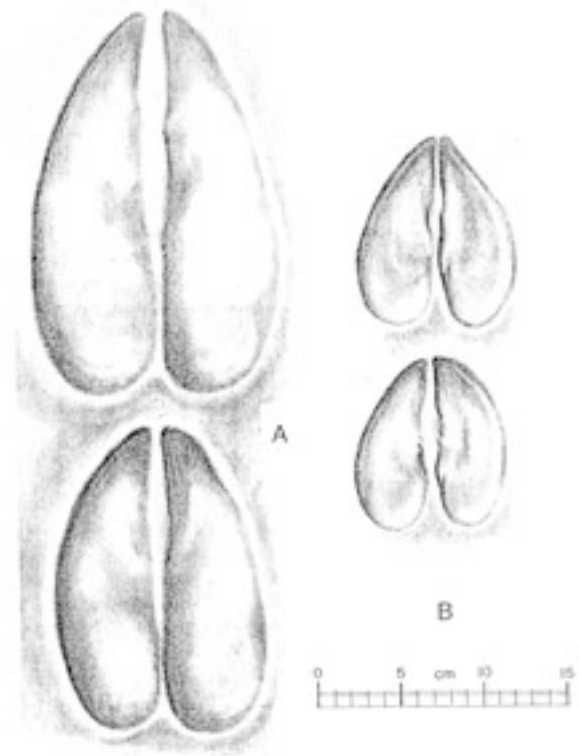


Figure 15. Comparative sizes of footprints of, **A.** *G. camelopardalis* and, **B.** eland (*Tragelaphus oryx*). From Skinner & Smithers (1990).

G. jumae/G. camelopardalis

Of all the *Giraffa*, the age of *G. jumae* is most uncertain. It could be as old as 6.5 My (Pickford, 1975). Churcher (1978), summarising information known at the time, said it was present in East and South Africa from late Miocene to mid-Pleistocene. Hendey (1982) and Harris (1976a, 1991) agree that it was found at the Langebaanweg fossil deposit in the far south of South Africa around 4.5 Mya. The Langebaanweg Varswater fossil deposits formed towards the end of the Mediterranean (Messinian) salinity crisis as the polar icecaps receded (Hendey, 1981). The drying up of the Mediterranean basin was caused by an expansion of the Antarctic icecap, which lowered sea levels and closed the access of the basin to the Atlantic. It has been dated to 6.6 to 5.2 Mya (Hsiu *et al.*, 1977) and it affected 2.5×10^6 km² of surrounding area. This area would have included north Africa and it seems reasonable to conclude that early giraffe entrants into Africa will have been affected by it. *G. jumae* must have reached Langebaanweg during it and perhaps as a consequence of it.

Leakey (1965) described its morphology on the basis of a skull and other fragments obtained from Rawe in Kenya. A second specimen found in 1963 was described by Leakey in 1970, and he concluded *G. jumae* was more heavily built than extant giraffes (Leakey, 1970).

Both *G. jumae* and *G. gracilis* appear to have become extinct about 1 Mya, the time that *G. camelopardalis* makes its appearance in the fossil record. Indisputable *G. camelopardalis* fossils occur for the first time at 1 Mya at West Turkana in East Africa (Harris, 1991). This simultaneous disappearance of two species in favour of one has several possible explanations. Harris (1987a) has suggested that as *G. jumae* is the same species it could have given rise to *G. camelopardalis* by evolution



Figure 16. A possible phylogeny of giraffes, correlated with age, based on our interpretation of the evidence reviewed.

and principally a reduction in its size. Alternatively a continued increase in size of *G. gracilis* would have achieved the same outcome. As *G. gracilis* has a morphology more closely related to *G. camelopardalis* than to *G. jumae* (Harris, 1976c), *G. gracilis* is the better origin. If *G. jumae* was sexually isolated from *G. gracilis* and/or *G. pygmaea*, then the disappearance from East Africa of *G. jumae* suggests that in the competitive environment of a numerically dominant and enlarging *G. gracilis* it, like *G. pygmaea*, became extinct. The changing climate between 8 and 6 Mya (Cerling *et al.*, 1998) that had induced the development of grasslands (see Figure 17), and made the African woodland savannah a habitat ideal for giraffes could, by this time, have restricted the feeding niches on which the three then extant *Giraffa* depended. If, on the other hand, *G. camelopardalis* is a smaller descendant of *G. jumae*, then it is *G. gracilis* that succumbed to competition. Finally if *G. jumae* was no more than a variant as suggested by Harris, then *G. camelopardalis* could also be a successful product of interbreeding between *G. jumae* and *G. gracilis*. Of the evolutionary possibilities, the best conclusion is that *G. camelopardalis* is derived from *G. gracilis* rather than *G. jumae*, and we can imagine that it developed as a successful variant at the expense of its competitors. A possible phylogeny of it is shown in Figure 16.

GIRAFFE EVOLUTIONARY BIOLOGY

Much of *Giraffa* history and evolution after *P. germaini*/*S. africanum* seems to have been influenced by changes in climate, and the habitat and vegetation changes that these brought. These changes seem to have begun about 10 Mya (Zhisheng *et al.*, 2001), with a second phase in the uplift of the Himalaya-Tibetan plateau, and retreat of the Paratethys sea, the great in-

land sea that formed behind the Italian Peninsula (Ramstein *et al.*, 1997) (Figure 5). Its retreat had as much influence on the central Asian climate as did the uplift of the Himalayas. North of the Himalayas there was an increase in the seasonality of the precipitation and the Tibetan plateau became drier. Summer and winter monsoons intensified. South of the Himalayas summer temperatures and precipitation increased. Tropical vegetation disappeared and was replaced by arid adapted plants and a savannah belt developed over eastern and northern Africa and western India (Janis, 1993; Ramstein *et al.*, 1997). Forests were replaced by dry biomes evolving towards small-leaved taxa and conifers. Sea floor spreading, silicate weathering, and sediment burial lowered atmospheric CO₂ concentrations (Raymo & Ruddiman, 1992). Although almost pure C₃ moist woodlands predominated (Cerling *et al.*, 1997, 1998), by 9.4 Mya in the Siwaliks of northern India under the effects of lower CO₂, grasses started to make their appearance (Morgan, 1994). The transition of the biome from C₃ shrubs to C₄ grasses began in earnest 8 Mya and took 1–1.5 My (Figure 17).

The transition was also associated with the emergence of the first of the true *Giraffa*, *G. punjabiensis* in Asia and the appearance of *Giraffa* in Africa. At the same time as vegetation change there was coastal upwelling of the Arabian Sea, and migratory routes from Europe to Asia and Africa opened (Ramstein *et al.*, 1997) allowing movement of giraffes. By 6 Mya C₄ plants dominated the Siwalik flora and the decline of *Giraffa* there began (Cerling *et al.*, 1998). Over the period of 6 Mya to 2.6 Mya monsoon variability increased, there was further uplift of the Himalayas, continental ice-sheets expanded and the world became colder (Zhisheng *et al.*, 2001). The change to an almost pure C₄ flora in Asia and China, the aridity and cold, caused the extinction of the Asian *Giraffa* by 4 Mya. In East Africa the early Miocene fauna was populated by forest adapted fauna. By the end of the Miocene open woodland had precipitated the bovidae-antelopinae radiation but, apart from increasing aridity, the changes were less severe and *Giraffa* survived.

What made *Giraffa* a relatively successful genus? Its most striking features are its elongated legs and neck, its distinctive coat markings, and a gentle, aloof disposition noted as long ago as 64 AD by Pliny the Elder (Pliny, 0064). It seems impossible to think that these attributes evolved independently of the vegetation and habitat changes to which it, its ancestors, and its antecedents were exposed. Its cryptic attributes are as numerous as they are remarkable. It has a unique cardiovascular system, a gastrointestinal tract suited to the needs of a concentrate selector, a range of thermoregulatory adaptations that are unique and a respiratory system adapted to its shape. The surface area of their footpads is enlarged to cope with their body mass. Another less obvious characteristic is inflation of the cranial roof by sinuses. These increase head volume without increasing its weight. A large head volume improves temperature regulation, olfaction and chewing. Heavy, rugose, brachydont, and selenodont molars provide a broader grinding surface for side-to-side mastication. An elongated muzzle and absent upper incisors house and facilitate extension of a prehensile tongue. Ossicones are more posterior than they are in either bovids or cervids and much reduced in size. Their eye orbits are telescopic and shifted posteriorly, which improves their field of vision. Compared to palaeotragines their mastoid bulla is small while their eye anatomy is better developed. This change in sensory emphasis correlates well with a change from a forest habitat (where hearing acuity is essential) to an open woodland habitat (where visual acuity is).

The adaptive advantages of most of these anatomical attributes are apparent but not unique. Their physiological adaptations are more unique in that, unlike those of most if not

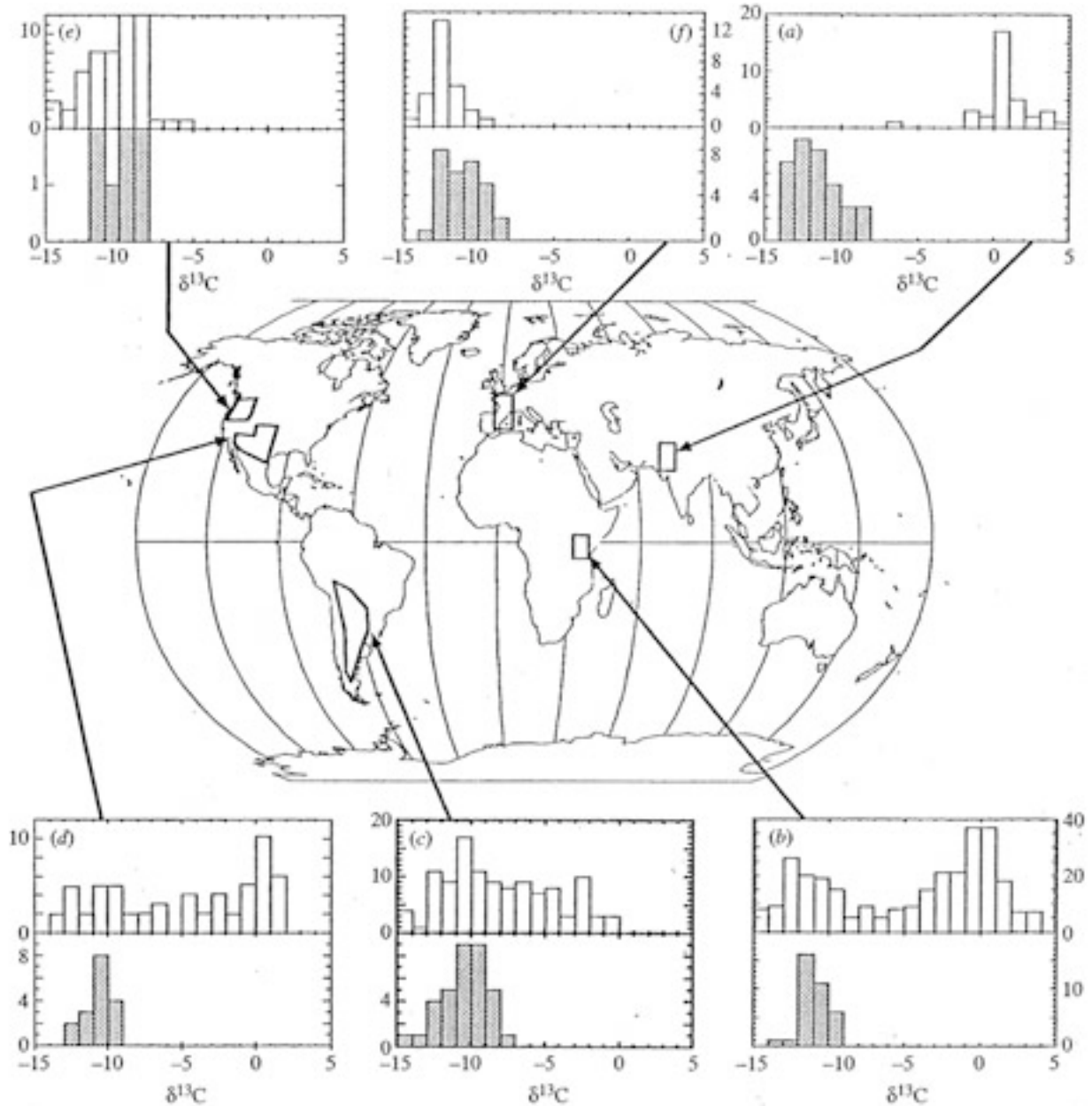


Figure 17. The emergence of C_4 (grassland) vegetation about 8 Mya. The upper half of each chart shows the isotope histogram after 6 Mya and which indicates a C_4 diet. The lower charts show the histograms of 8 Mya and which indicate a C_3 (shrub, dicotyledon) diet. Note that by 6 Mya the Siwalik vegetation was pure C_4 (Histogram a) while that in East Africa was mixed (Histogram b). Giraffes became extinct in Indo-Asia relatively soon after this vegetation change, while those in Africa flourished. From Cerling *et al.* (1998).

all other species, in giraffes they subserve the needs imposed by their anatomy rather than the needs imposed by their environment. Consequently despite their apparent success they can be expected to be sensitive to environmental change. In reviewing explanations for their survival we concentrate on the two features which seem to have characterised their evolution: their height and markings.

Height

Throughout the giraffid fossil record there is clear evidence of progressive limb and neck elongation. Limb and neck elongation began with the prerequisite structural changes seen in the Leptomerycids, but it is in the palaeotragines that giraffe-like limb and neck elongation seems to gain momentum. *Samotheres* and *Bohlinia* continued the elongation at a faster rate. The evolution of giraffes as a species over many millions of years is

therefore associated with a great increase in its height. Its height in turn is attributable to just two developments: elongation of the neck skeleton and elongation of the distal more than the proximal limb bones with disproportionate elongation of the metapodials. With respect to the rest of its skeleton relatively minor differences exist between it and, say, a large cervid (e.g. a reindeer *Rangifer tarandus*) or a similar sized bovid (e.g. buffalo, *Syncerus caffer*).

The elongation of the neck is a consequence of lengthening of the seven cervical vertebrae. In giraffes each of the neck vertebrae elongates about 30% more than can be predicted from the elongation during growth of other vertebrae (Slijper, 1946). The biological mechanism by which this differential growth is achieved, is unknown. Receptor density and affinity for hormonal regulators of growth will undoubtedly underlie it. Differential elongation is not, however, enough to explain the total increase in neck length. If 30% is added to each of the first six

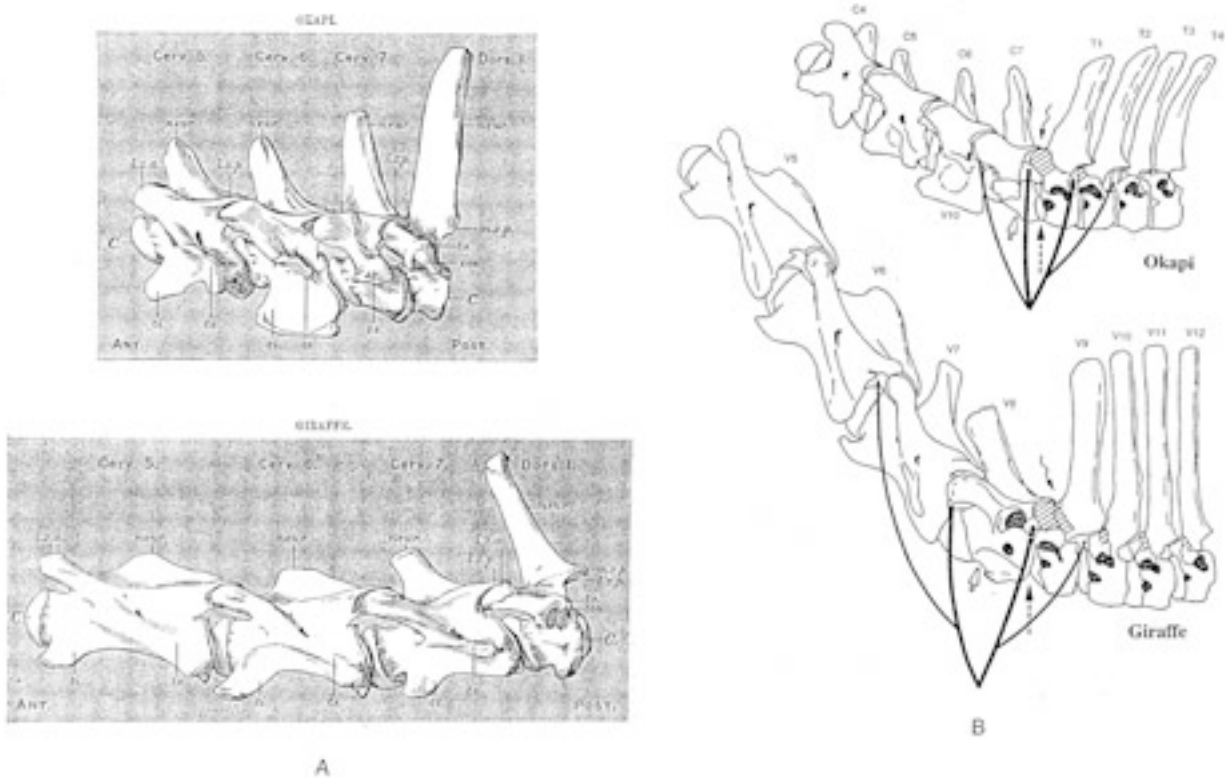


Figure 18. Comparison of the last cervical vertebrae and first thoracic vertebrae in giraffes and okapi. From Lankester (1908) **A**, and Solounias (1999). **B**. Note the relative elongation of each cervical vertebra in giraffe, the lack of bony prominences for muscle attachments, and the “cervicalisation” of T1. See text for discussion.

neck vertebrae (excluding the vertebra that forms the joint between the cervical (C) and thoracic (T) vertebrae) and if these lengths are then added together, calculated neck length is less than observed length.

An explanation for the anomaly is that giraffes have more than the typical number of mammalian cervical vertebrae (seven), a suggestion recently made by Solounias (1999). However, that giraffes have seven cervical vertebrae has been known for a long time (e.g. Owen, 1841), so Darwin (e.g. 1897) could say:

“The framework of bones being the same in the hand of man, wing of bat, fin of porpoise, and leg of horse, . . . the same number of vertebrae forming the neck of the giraffe and of the elephant . . . and innumerable other such facts, at once explain themselves on the theory of descent with slow and slight successive modifications.”

and Lankester (1908) in describing the bony anatomy of the neck of giraffe, agreed (Figure 18A).

Solounias (1999) challenged the usually accepted view that natural selection is constrained by prior anatomy, even in the case of giraffes, on the basis that, at least in part, the neck length can be attributed to the presence of an 8th cervical vertebra. Solounias’s suggestion is based on the idea that two major criteria and some minor criteria establish the identity of cervical or thoracic vertebrae, and the point of transition between them. The major criteria are the presence of an articulating rib and the origin of the four divisions (roots) of the brachial nerve plexus. Generally the brachial plexus results from the anastomosis of the ventral branches of the last three and first two thoracic nerves. Taking the okapi as the representative of the norm, Solounias noted that the four divisions arise from the intervertebral foramina between C6 and C7, C7 and T1, T1 and T2, and T2 and T3 with the most anterior division contributing as much

as the middle two (Figure 18B). In giraffes the contribution of the most anterior division is reduced giving the impression that the brachial plexus centre has shifted from the C7–T1 foramen to the T1–T2 foramen, and, therefore, that T1 is actually a C8.

If T1 is a C8 then it would not support a rib. However it does and so by definition this vertebra must be a T1. Its other morphological features suggest that as normally the role of articulation between the cervical and thoracic vertebrae is performed by C7 that C7 has become “dorsalised” (Lankester, 1908). In giraffes the role of articulation is taken over by T1 and Lankester concluded that it thus showed homeosis by having taken on the functions of C7 and, although he never said as much T1 had in effect become “cervicalised”. As a part of this modification the anterior division of the brachial plexus is reduced. Giraffes therefore have seven cervical vertebrae as indicated by Darwin and elongation of each has occurred.

Of course if the usual functions of C7, principally to constitute the articulating surface between cervical and thoracic vertebrae, have been taken over by T1 this leaves C7 to elongate and contribute to neck elongation. In this sense therefore the neck has an extra vertebra, but it has only seven cervical vertebrae like all other mammals except the sloth *Bradypus variegatus*. One morphological consequence of this rearrangement of the functions of the cervical vertebrae is that the point of the shoulder is pushed forward to produce the typical giraffe silhouette (Solounias, 1999).

Cervical vertebrae do not only lengthen. They also have to provide the infrastructure on which the ligaments and muscles that lift, rotate, extend, and flex the neck can insert. The origin of these muscles and the powerful elastic *ligamentum nuchae* that runs to the nuchal crest on the skull along the dorsal surface of the cervical vertebrae spines, are the spines of the thoracic vertebrae. To provide the necessary support the thoracic vertebrae spines are greatly elongated, a feature that creates the

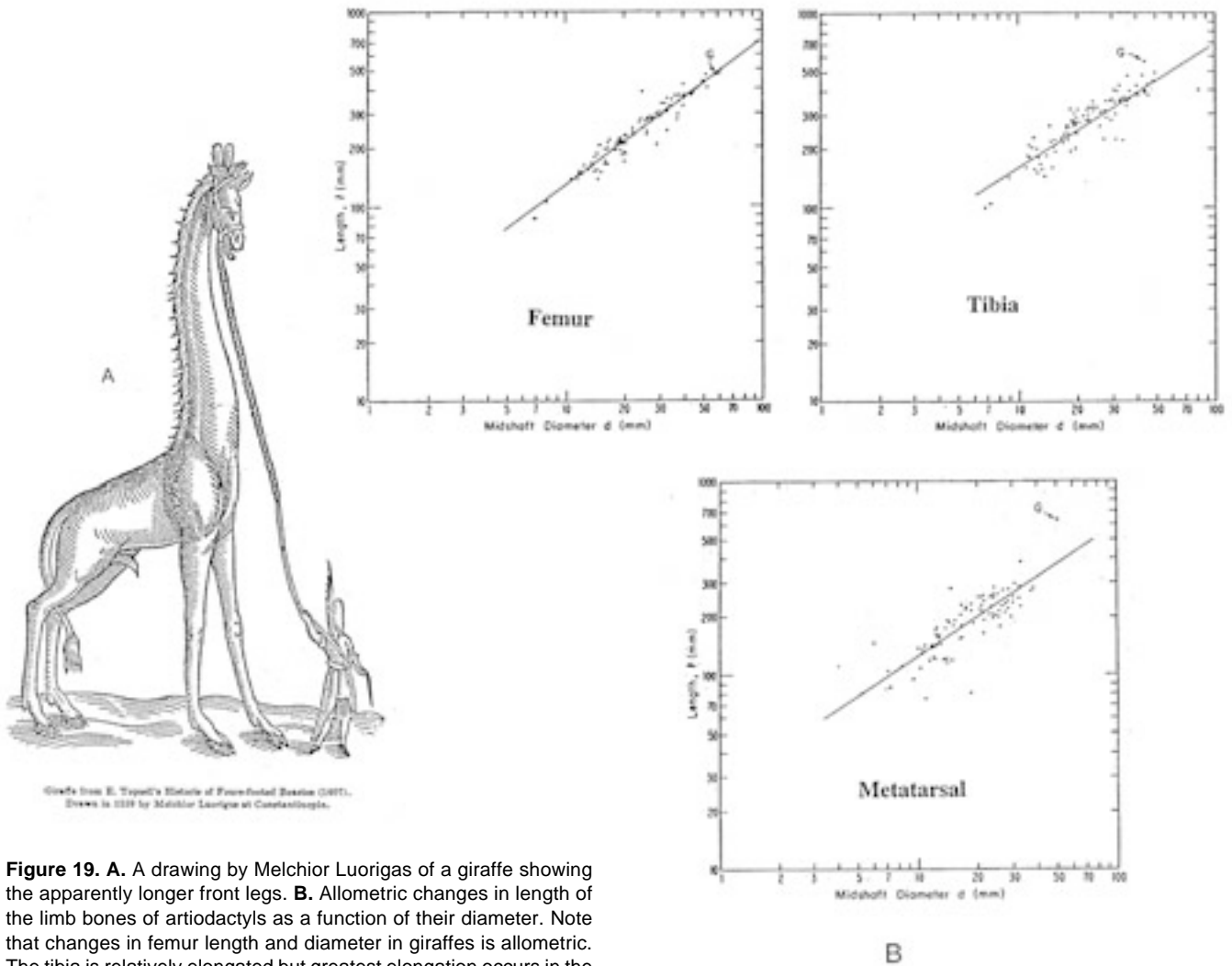


Figure 19. A. A drawing by Melchior Luorigas of a giraffe showing the apparently longer front legs. **B.** Allometric changes in length of the limb bones of artiodactyls as a function of their diameter. Note that changes in femur length and diameter in giraffes is allometric. The tibia is relatively elongated but greatest elongation occurs in the metatarsal. From McMahon (1975).

optical illusion that the front legs of giraffes are longer than the hindlegs. By a similar analogy it could be expected that the cervical vertebrae would also have higher spines and broader wings than those in the okapi. This is not the case however as Lankester (1908) first noted (Figure 18A). The conclusion must be that giraffe neck muscles do not contribute to its elevation or extension. Flexion will be produced by the main flexor muscles of the neck: the *rectus capitis ventralis*, *brachiocephalic* and *longissimus dorsi*. Extension it seems in modern giraffes as much as it was in its primitive ancestor, *Giraffokeryx*, is achieved more passively through the action of the elastic *ligamentum nuchae*. This arrangement makes ergonomic sense. If giraffes relied on muscle power to lift the neck and head and hold them elevated these muscles would quickly fatigue.

The effort required to manipulate the head and neck must nevertheless be considerable. One estimate is that the weight of the head and neck is 250 kg (Dagg & Foster, 1976). It might be greater if it were not minimised by several other adaptations. The first is the presence of cranial sinuses that add volume but not mass to the skull. Secondly there is reduction in size of the horns. Giraffe ancestors and relatives as we have seen had large and heavy cranial appendages. Modern giraffes have small and insignificant ossicones. In addition the absence of large bony structures on the cervical vertebrae to support neck muscles reduces their weight. Moreover, the neck vertebrae have a relatively low density and are lighter than most other bones in its skeleton (Table 1). While low-density vertebrae have this

advantage, a potential disadvantage is that their strength would be reduced. The problem of cervical vertebra strength (and thoracic vertebrae strength) must have been solved by clever structural engineering, although quite how this has been achieved has not been studied.

Elongation of the limbs is in a sense a more remarkable adaptation. Early depictions of giraffes suggested that the forelegs were far longer than the hindlimbs (Topsell, 1607) (Figure 19A) and, in this respect, they were similar to the okapi (Colbert, 1938). This elongation is, as we have seen, an illusion produced by elongation of the thoracic spines, and the length of fore- and hindlimbs is about the same.

Elongation of the limbs is however marked. It depended on the preliminary steps of fusion of the cubo-navicular bones of the hind limbs and the magnum and trapezoid bones of the front limbs, the modification of the astragalus to limit movements of the hind limb to the vertical plane, and fusion and reduction of the metacarpal and metatarsal bones. These developments provide the stability and strength for limb elongation, and were first expressed in the Leptomerycidae.

The relationship between the weight (W) able to be supported per unit of surface area (cm⁻²) and length is:

$$W \text{ (kg.cm}^{-2}\text{)} = k.L^{-2}$$

where “k” is a constant, “kg/cm²” a measure of body mass, and “L” is bone length (Cloudsley-Thompson, 1976). In other words

Table 1. Relative density of a giraffe skeleton.

Bone	Relative Density (%)
Cervical vertebrae	100
Thoracic vertebrae	98
Humerus	139
Radius/Ulna	150
Metacarpal	178

for an increasing body mass of an animal the legs must become shorter or their diameter wider. Conversely the greater the length of a limb the less the weight that can be carried by it unless cross-sectional area (strength) increases. Re-arranging this equation produces:

$$\text{kg.L}^2 = \text{k.cm}^2$$

Thus, if weight stays relatively constant, an increase in length is possible if cross-sectional area increases proportionately with length.

For giraffes however these relationships appear not to be true. McMahon (1975) determined the sites of elongation of the limbs, by plotting the relationship between length and diameter of the main bones of the hindlimbs of 70 specimens of different artiodactyls including giraffes (Figure 19B). Diameter can be taken as a measure of cross-sectional area and thus of strength. McMahon's plots show that the increase in femur length is allometric and predicted from the increase in size and mass of the animal. But the plots also show that in the tibia and metatarsal bones this relationship does not hold and the diameter does not increase as predicted. There is disproportionate elongation in both with most occurring in the metatarsals. Hamilton (1978) did a similar study that included several giraffids. He noted that relatively the metapodials of *Giraffa* are no longer or more slender than they are in other ruminants, but what is unique is that they are so slender in such a large animal. Geraads (1986) similarly confirmed the uniqueness of the limb morphology of the *Giraffa-Bohlinia* assemblage. The mechanical advantage of this arrangement is apparent. Elongation of the more distal limb bones (brachium, crus, and metapodials) and especially the metapodials, but not the more proximal limbs (humerus, femur) increases the mechanical advantage for locomotion by keeping the fulcrum (the elbow or knee) at the level of the trunk.

Giraffe limbs obviously are able to support their body mass, and thus the increase in length must be compensated for by an increase in strength independent of changes in diameter. One mechanism by which this could be achieved is if the lower limb bones are more mineralised and so have a higher density. We have made some very preliminary measurements of giraffe bone density and have calculated that if bone mass is a measure of calcification then about 80% of all skeletal calcium is in leg bones. The radius/ulna and metacarpal bone density is the highest of any bones (Table 1), which supports the idea that metapodial strength has been achieved by increased mineralisation of bones rather than an increase in diameter.

If the anatomical substrate for increased height can be analysed, the advantages that it might confer are less obvious. The cost of a long neck and limbs in terms of the many physiological adaptations needed to support them is high (e.g. Mitchell & Hattlingh, 1993; Mitchell & Skinner, 1993). Moreover the nutritional demands to support giraffe skeletal growth seem also to be high (Mitchell & Skinner, 2003). Giraffe reach their adult height of 4–5 m in 4–5 years (Dagg & Foster, 1976). During this time total body calcium increases about 10-fold from 2850 g to

Table 2. Giraffe calcium requirements.

	Male	Female
Adult body mass (kg) ¹	1174	792
% skeleton ¹	23.9	21.0
Mass of skeleton (kg)	280	166
% calcium in bone ²	13	13
g calcium in an adult	36 400	21 600
g/day required	20	12

¹ Hall-Martin *et al.* (1977)

² Langman (1978)

26 000 g (Table 2). This increase means that daily calcium absorption over the five-year period must average about 20 g (for comparison a human weighing 1/10 of a giraffe has a daily calcium requirement of 1/40). This quantity can only be obtained by almost complete dependence on legume browse, especially *Acacia* trees (Table 3) (Dougall *et al.*, 1964).

While dependence on leguminous browse seems essential, the idea that tallness enables exploitation of food sources that are beyond the reach of competitors such as bovids, is unlikely to be true. Pincher (1949) made one of the first objections to this hypothesis. He indicated that a Darwinian dearth severe, long-lasting enough, and/or frequent enough for natural selection to operate to produce a long neck, would cause the recurrent wastage of young giraffes, and would thus lead to extinction of the species rather than its evolution. Secondly, Pincher noted that the same dearths would have encouraged selection of other ungulates with long necks, and yet only giraffes achieved this distinction. Thirdly, males are on average a metre or more taller than females, which in turn are taller than their young. Dearths would place less tall members of the species at a permanent disadvantage, and extinction would be inevitable. His preferred explanation, following Colbert (1938), was that there had to be concomitant elongation of the neck as a response to increasing limb length, if giraffes were to be able to reach ground water. Quite why an increase in leg length might have been advantageous, he did not discuss.

Brownlee (1963) also concluded that preferential access to nutrients could not be the evolutionary stimulus for a long neck, and suggested that their shape conferred a thermoregulatory advantage usable by "young or old, male or female continuously and not merely in times of drought". Brownlee was referring to the fact that metabolic mass increases at a rate related to the cube of body dimensions while body surface area increases as the square of the dimensions. Thus long slender shapes increase surface area for heat loss without proportionately adding volume and metabolic mass. In addition, such a shape also enables giraffes to "achieve that size and tallness which confers greater ability to evade, or defend against, predators and to reach a source of food otherwise unavailable to them".

Nevertheless the persistent idea that giraffe height evolved because it confers a selective feeding advantage has some justification. For example, du Toit (1990) compared the preferred feeding heights of giraffes to those of a potential competitor, kudu (*Tragelaphus strepsiceros*). He found that, at least in the vegetation type of the central Kruger National Park (Tshokwane region), giraffes tended to feed at heights of 1.7 to 3.7 m with a preferred neck angle (with respect to the forelegs) of 90–135° (Figure 20). Giraffe bulls generally fed at a higher level than cows and the preferred neck angle of bulls was greater than 90° while that of cows was below 90°. Kudus, on the other hand, had a height preference of around a metre but a range of up to 2.0 m, and a preferred neck angle of 45–90°. They are thus com-

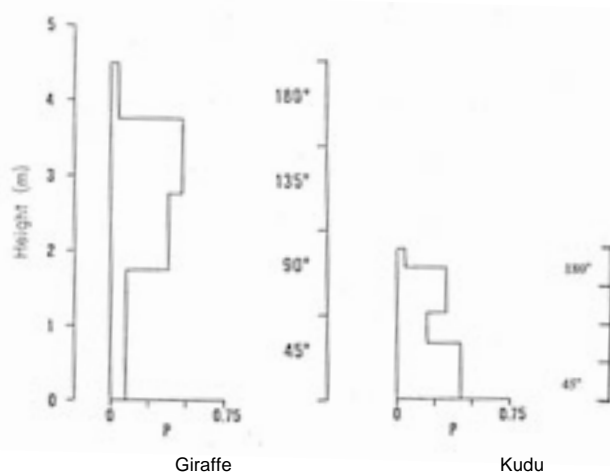
Table 3. Calcium and phosphate content of giraffe browse derived from Dougall *et al.* (1964).

Plant type	Ca %	PO ₄ %	Ca:P
Grass	0.42	0.23	1.8
All legumes	1.17	0.29	4.0
Giraffe legumes	1.42	0.20	7.1
Giraffe non-legumes	1.34	0.19	7.1

petitive with female (and young) if not male giraffes. Young & Isbell (1991) concluded that preferred feeding height is shoulder height i.e. 60% of maximum height and far below maximum possible feeding height. Feeding height varied according to the gender composition of groups. Females in female groups fed at 1.5 m, females in male groups at 2.5 m, and males in male groups at 3.0 m. At best therefore a long neck may confer intermittent advantage. In another study Leuthold & Leuthold (1972) found that in a different habitat (Tsavo National Park, Kenya), giraffes spend about half their feeding time browsing below a height of 2.0 m. In the Serengeti, giraffes spend almost all their feeding time browsing low *Grewia* bushes (Pellew, 1984). The question then is, if a height of 3.0 m is adequate to avoid nutrient competition why do giraffes grow to heights of 5 m? Dagg & Foster (1976) suggest the reason that when giraffes were evolving there were a number of high level browsers, including Sivatheres, competing for browse. This hypothesis is weak however because for many millions of years small giraffes were coeval with Sivatheres and larger giraffes and would not have been able to compete with them for nutrients.

The underlying theme of these studies is that current utility mirrors selective pressures. Although this is an unsubstantiated idea (Gould, 1996) it implies that in the evolutionary history of giraffes the tendency to elongate will have been produced by competition for preferred browse with the tallest winning. The implicit assumption is that browse abundance at the lower levels was insufficient for all competitors – which as shown above is not true given that young vulnerable giraffes then must compete maximally. The idea that a unique advantage for adults is an advantage for the species generally is an additional and questionable corollary. The studies also raise the obvious problems of how young giraffes and young trees ever grow into adults if there is competition for preferred browse and for browse at low height. The only reasonable answer to this paradox is that the volume of low level browse is far greater than is that of high level browse, and is abundant enough to provide browse for small as well as large giraffes, other browsers and allow for growth of the browse itself. In other words the presumptions of historical unavailability of browse and of browse bottlenecks as the selective pressures for neck and limb elongation, are highly doubtful and probably false.

As the feeding hypothesis is not robust another suggestion, analysed in depth by Simmons & Scheepers (1996), is that the alternative main driver of natural selection, sexual advantage, may be the reason for the long neck. In support of this idea is the relatively greater elongation of the neck vertebrae compared to thoracic and lumbar vertebrae. The frequently observed use of the neck as a weapon by males when defending a female in oestrus (Coe, 1967), and the dominance of large males over younger smaller ones in the competition for females (Pratt & Anderson, 1982) is additional evidence. If this is the case there will be sexual selection for a long neck, especially in males. Presumably if this is an autosomal mechanism, a consequence is that females would be genetically linked to the trait although having little need for it.

**Figure 20.** Proportions of feeding time (P) and corresponding neck angles at various heights of browse for giraffes and kudus. Redrawn from du Toit (1990).

None of these ideas provide a definitive explanation for the evolution of a long neck, a conclusion at odds with its uniqueness. Other examples of neck/limb elongation in camels *Camelus dromedarius*, llamas *Lama glama*, gerenuks *Litocranius walleri*, and ostriches *Struthio camelus* are rare and are not as dramatic as the giraffe, and do not seem to be associated exclusively with feeding. If a long neck had some general utility or advantage then its evolution, as in the case of flight, would have initiated an impressive radiation of forms and not the rather meagre array that exists and that the palaeontological evidence suggests. But even this conclusion is worrying because if a long neck has no utility then why has it survived? The costs are high in terms of the many physiological adaptations needed to support it and it seems to require dependence on protein and calcium rich browse.

Thus another suggestion, first mooted by Brownlee (1963) is that a long neck has survived because it has allowed evasion of predation: the good vision and height give giraffes an advantage over other animals by improving their vigilance. Dagg & Foster (1976) indicate that adult giraffes move to improve their view of a predator rather than try and rely on camouflage. Moreover their large size makes them a formidable physical opponent. As a result, although always vulnerable, giraffes are rarely killed by predators. Pienaar (1969) noted that fewer than 2.0% of all kills in the Kruger National Park were giraffes and that lions, *Panthera leo*, were the main predator. In one sense this ratio is not surprising as giraffes generally constitute about 2.0% of a fauna (Bourliere, 1963). However if they were an easy source of food presumably they would form a higher proportion of lion kills.

Coat colour patterns

The other main defence available to giraffe is their coat markings. There is no way of knowing when the markings so characteristic of modern giraffes evolved but it seems unlikely that the markings of Asian giraffes would have been the same as those of African forms. An Asian colouration similar to modern okapi seems highly probable if the habitat of the Asian giraffes was tropical and paratropical forest rather than Mediterranean woodland scrub/tropical forest/temperate woodland as it was in Africa (Figure 2).

While skin pigmentation is uniformly dark gray, coat markings are highly labile. Anecdotal reports of coat colours of

extant giraffes indicate that markings range from albino (Anon., 1971; Turner, 1969) and pure white (Butler, 1912; McDougall, 1939), through pale brown and unspotted (Arnold, 1940; Petzsch, 1950) or with a black band around the trunk (Blum, 1957), to black (Anon., 1923). These variations are consistent with the idea that coat colours are polymorphic, and also suggests that markings can be readily adapted to local conditions by natural selection to the extent, as we have seen, of being used to construct subspecies (Lydekker, 1904) (Figures 17–20). An apparent conclusion is that the markings contribute to camouflage, although this is counterintuitive as the large size of giraffes makes them inescapably conspicuous. However their coat markings break up the body outline especially when sunlight filters through trees and scrub, and they are difficult to see even when they are no more than a few metres away.

In this context one aspect of giraffe survival seems under-emphasised and this is that the survival of a species depends more on the survival of the young than on the survival of adults. There is no question that young giraffes are highly vulnerable to predation. In a three-year study, Foster & Dagg (1972) reported that in Nairobi National Park the mortality rate was about 75% in the first year of life, and highest during the first months of life. In a similar study but involving far fewer animals, Pellew (1983b) found that first year mortality in the Serengeti was about 60% and again that greatest mortality was in the first months of life. Estimated adult mortality in these protected environments was about 5–10% in the Serengeti (Pellew, 1983b) and about 10–15% in Nairobi (Foster & Dagg, 1972). In the latter case the population numbers were stable over the three-year period despite large movements of animals between the Park and the surrounding areas. In Pellew's study the population size was increasing at 5–6% per annum. An interpretation of these data is that population growth is related to calf mortality. High calf mortality is compounded, as in most large mammals, by slow reproduction rate. Gestation in giraffe is 457 days (Skinner & Smithers, 1990) and calving interval between about 550 days (Pellew, 1983b) and 650 days (Foster & Dagg, 1972).

Although high mortality of the young can be attributed to predation (Foster & Dagg, 1972), it can also be associated with a weak bond between cow and calf. Foster & Dagg (1972) reported for example that calves stayed with their mothers for about six weeks after birth and then start to drift away. In one case a month-old calf remained about two km from its mother for four days, and in another a two month-old calf was not seen with its mother for 29 months. On the other hand, Langman (1977) found a strong cow–calf relationship and noted that there would be very little benefit for giraffe calves to become independent at an early age. They would not have the height and body size that would protect them from predation until they were two years old. Langman showed however that giraffes can be regarded as a “hider” type of artiodactyl in which the cow hides her calf while she browses. Pratt & Anderson (1982) on the other hand, studying calf–cow relationships in Arusha National Park in Tanzania, found that “hiding” occurs infrequently but confirmed that a strong cow–calf bond exists up to the age of two years. This behaviour did not seem, however, to buffer high calf mortality.

All three studies raise the same question. Foster & Dagg (1972) could not link survival and mothering. If mothering does not ensure survival, how do calves survive? If hiding is an adaptation, how is hiding successful? It seems to us that the best explanation is that coat markings must provide excellent camouflage for young giraffes, a conclusion also reached by Langman (1977). For camouflage to be successful, coat markings must blend into the habitat. In this regard Trouessart (1908)

reported that the shape of patches correspond with the arrangement of *Acacia* branches, the colour of which and the angle of branching correlates with the interpatch coat markings. Moreover, if survival depends on being inconspicuous then there will be intense selection, in classic Darwinian fashion, for coat patterns that increase the chance of survival. This conclusion is underpinned by the high heritability of the shape, number, and area of markings (Dagg, 1968), and it would also explain the regional variations described by Lydekker (1904). We liken this phenomenon to the selection of black over white pepper-moths (*Biston betularia*) in the industrial north of England (Kettlewell, 1958, 1961), and believe that the survival of young giraffes, the prolonged survival of African giraffes compared to the Asian lineage, and Lydekker's regional “subspecies” can be attributed to it in whole or in part.

Coat patches, at least those in *G. camelopardalis*, also seem to have another function apart from camouflage that may contribute to survival. This function, first suggested by Skinner & Smithers (1990), is that patches “act as thermal windows through which giraffes dissipate heat”. Other megaherbivores, for example elephants, lose heat by slowly flapping their ears. Cetaceans use peripheral countercurrent heat exchangers. Giraffes are not known to sweat (although their skin contains sweat glands (Dimond & Montagna, 1976)), and are unable to pant (Hugh-Jones *et al.*, 1978), thus they do not seem to have available the main methods of heat loss. They may have the ability to regulate brain temperature (Mitchell & Skinner, 1993), but if they cannot pant or sweat how do they then lose heat?

Skinner's inference has its origin in an observation made by De Beaufort (1927) after he did an autopsy on a giraffe that died in Amsterdam Zoo in November 1926. De Beaufort noticed that large blood vessels in the skin formed polygonal patches on the skin surface and that numerous blood vessels branched off these and entered pigmented (patch) areas. Subsequent analysis of the anatomy and histology of this vasculature in patch and non-patch areas of the skin by Ackerman & Skinner (Ackerman, 1976) showed that beneath each patch is a deep subcutaneous plexus of vessels from which branches pass to a more superficial plexus. Inter-patch skin did not have this arrangement. This anatomy suggests that blood in deep plexus vessels, is supplied by the large vessels between each patch. From the deep plexus warm blood could be dispersed to the more superficial ones via anastomotic channels, and once there the heat could be dissipated. The converse is also possible. If the patches absorb radiant heat then during sunny but cold days warming of blood may occur. Measurement of skin temperature at the level of the deep and superficial plexuses confirms the idea of a thermal gradient (Mitchell & Skinner, 1993) and, as patches form a relatively large surface area of a skin already relatively large in relation to body mass, regulation of heat balance may be enhanced. It may be considered that this arrangement is really no different to that normally found in the skin of any animal. In all animals dilation of skin vessels is a well-established method of losing heat. However in giraffes the mechanism seems to combine camouflage and temperature regulation in a unique way, and it may well be that the sensitivity of the vessels and the capacity for heat loss may be different in giraffes.

It is impossible of course to make an estimate of the contribution patches make to survival either as camouflage or heat loss/gain, and in any case it would depend on the relative importance of them in the general pool of adaptations likely to enhance survival. As the survival of mammals seems to have depended more on being able to keep warm while ambient temperatures were falling during the critical Miocene phase of their evolution, a mechanism that enhances heat loss is counter-intuitive. However early mammals were small and an increase

in size requires different mechanisms to achieve heat balance.

Our analysis suggests that the evolution of modern giraffes from their forest-dwelling, okapi-like ancestors, has depended on and been stimulated by the emergence of a woodland scrub. This biome is rich in leguminous browse that provides the nutrients their skeletons require, and camouflage. In growing to a height of about two metres this food source is unavailable to most other browsers. It is a biome to which giraffes are adapted and to which they seem irretrievably bound. Whether this biome has other characteristics to make it congenial is unclear but there is a strong suggestion of co-evolution between it and giraffes. It is a biome however that is shrinking and with it so has the range of giraffes.

Finally it is worth emphasising that in trying to understand the relative contribution that each of giraffes' adaptations has made to their survival, no glib summary is possible. Darwin wrote in this connection:

“The preservation of each species can rarely be determined by any one advantage, but by the union of all, great and small.”

For giraffes, this seems particularly apt.

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