Estudios Geol., 54: 209-230 (1998)

CLIMATE AND EVOLUTION: IMPLICATIONS OF SOME EXTINCTION PATTERNS IN AFRICAN AND EUROPEAN MACHAIRODONTINE CATS OF THE PLIO-PLEISTOCENE

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ABSTRACT

Recent discussions of correlations between global climatic change and evolution of the African Plio-Pleistocene biota have revealed apparent discrepancies between the timing and significance of events recorded in different data sets. The most notable differences have occurred in relation to a major shift in the ratio of marine oxygen isotopes by 2.5 myr and claims for a causally related transition in the biota. Vegetational changes recorded in palaeosol stable isotope values suggest that the major increase in more open vegetation occurs later ~ 1.7 myr. We investigate the problem with particular reference to events at 1.7 myr and the African extinctions of machairodont cats that take place in their aftermath, since extinctions of such eurytopic taxa are likely to mark significant changes in conditions. We compare the pattern of such extinctions with those of similar or identical taxa in Eurasia and the New World, and suggest that a major environmental change is clearly indicated in each case. It is likely that the African vegetational changes recorded ~ 1.7 myr represent a terrestrial response to global climatic changes recorded in marine core records ~ 1.9 myr.

Key words: *Climate, evolution, Plio-Pleistocene, machairodont cats, extinctions, Africa, Europe.*

RESUMEN

Estudios recientes sobre las correlaciones entre cambios climáticos globales y la evolución de la biota del Plio-Pleistoceno Africano han revelado aparentes discrepancias entre las fechas y la significación de eventos registrados en distintas fuentes. Las diferencias más notables se refieren a un importante cambio en la proporción de isótopos de oxígeno marinos hace 2,5 millones de años, y a la posibilidad de una transición biótica relacionada causalmente con dicho cambio. Cambios en la vegetación detectados a través de los valores de isótopos estables en los paleosuelos sugieren que el principal cambio hacia una vegetación más abierta ocurrió más tarde, hace 1,7 millones de años. Nosotros estudiamos el problema refiriéndonos en particular a los eventos de hace 1,7 millones de años, y a la extinción en Africa de los félidos con dientes de sable que se produce poco después, puesto que las extinciones de taxones euritópicos como éstos probablemente señala cambios significativos en las condiciones ambientales. Nosotros comparamos el patrón de dichas extinciones con los de taxones semejantes o idénticos, en Eurasia y América, y sugerimos que en cada caso hay claros indicios de importantes cambios ambientales. Es probable que los cambios en la vegetación de Africa registrados hace 1,7 millones de años representen una respuesta en el medio terrestre a los cambios climáticos globales reflejados en el registro marino hace 1,9 millones de años.

Palabras clave: *Clima; evolución; Plio-Pleistoceno; macairodontinos; extinciones; Africa; Europa.*

Introduction

At a recent meeting held in Malawi[1] to assess the relationships between aspects of African biogeography, climate change, and early hominid evolution, considerable discussion took place about the role of climate in evolution and the time scale of any significant environmental and biotic changes

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[1] Wenner-Gren conference «African Biogeography, Climate Change, and Early Hominid Evolution», october 25-november 2, 1995, Salima, Malawi.

(Sikes and Wood, 1996). Several previous investigations, centred on the evolution of the larger African terrestrial Mammalia (Vrba, 1985a, 1985b, 1988, 1994, 1995a, 1995b; Turner 1995b; Turner and Wood, 1993a), have argued that a significant and causal relationship exists between a major step in global cooling seen in the deep-sea core record, often referred to as the 2.5 Myr event (Shackleton, 1995), and Late Pliocene evolutionary events in diverse mammalian lineages. These evolutionary events are considered to have been mediated through habitat changes, themselves inferred in large part from palynological data as summarised most recently by Bonnefille (1995). A parallel study by Pickford and Morales (1994) has confirmed the appearance of a faunal turnover pulse in East Africa at 2.5 ± 0.5 Myr.

However, several investigators concerned with more localised patterns of eastern African vegetational change indicated by palaeosol stable carbon isotopes (Cerling, 1992; Cerlin *et al.*, 1988, Kingston *et al.*, 1994; Sikes, 1994, 1995, 1996, in press) have pointed out that the kinds of vegetational changes often considered to have resulted from this climatic step, such as a decrease in the proportion of wooded cover, are not actually seen in their data until close to 1.7 Myr, when a dramatic increase in C4 grasslands is recorded. This later date for major, environmentally determined changes in biotic communities receives apparent support from the work of Kappelman *et al.* (1997), who argue that functional analyses of bovid postcranial elements point to a post-2.0 myr age for adaptations to more open habitats. In contrast, Spencer (1997) has used analyses of bovid feeding apparatus to argue that, while secondary grasslands did indeed exist in eastern Africa by 2.0 myr, the adaptations to such habitats exhibited by a range of taxa are by then well-established and indicative of a longer history. Both may be accommodated in the conclusion by Behrensmeyer *et al.* (1997) that significant faunal changes in the Turkana Basin began after 2.5 myr and continued through to 1.8 myr. A further twist is given to the problem by the records of aeolian dust from marine sediment cores collected off west and east Africa and Arabia (deMenocal, 1995; deMenocal and Bloemendal, 1995), which indicate substantial periodic alterations in African vegetational cover and provide evidence for increases in arid conditions on the continent at both 2.5 and 1.7 myr. Further support for the notion that such increases in aeolian dust are driven by globally-important mechanisms is provided by recent evidence for multiple episodes of aridity in the Kalahari sand sea during the last glaciation (Stokes *et al.*, 1997) and for episodes of aridity in Africa during previous glacial phases (deMenocal *et al.*, 1993).

Clearly, the terrestrial and marine records cannot offer precise equivalence. One of the evident strengths of the marine record is its relative continuity, a situation attained by terrestrial sediments in only limited and special circumstances (Kukla and Cílek, 1996), while local and regional tectonic events may serve to blur the signature of more global changes. We may therefore expect to see some differences in the two sets of data. But such apparently significant discrepancies raise a number of questions. If a series of major events in the African biota do indeed cluster around the 2.5 myr climatic event or occur in its immediate aftermath, then what is the wider significance of the 1.7 myr event? Was it a global phenomenon in its own right? What, if anything, happens in the rest of the biota in concert with vegetational changes at 1.7 myr, or may be reasonably linked to such changes? An obvious point to note in the context of human evolution, for example, would be that the earliest record of *Homo erectusler-gaster* falls close in time to such changes, as pointed out by deMenocal (1995): is that simply coincidental? Ironically, at least one previous examination of this period in human evolution has rejected any link to climatic events, largely on the grounds that there was «no dramatic global climatic oscillation signal» (White, 1995, 378). However, a diametrically opposite view has been expressed by Reed (1997), who sees a major expansion of grazing mammals at about 1.8 myr coincident with expansion of secondary grasslands and increased seasonality as suggested by deMenocal (1995) and Cerling (1992) and the demise of the paranthropine hominins.

In an effort to understand the wider significance of this event at the Pliocene-Pleistocene boundary in Africa[2], and to seek some resolution of the differences in interpretation stemming from different research perspectives, we focus attention on the pattern of final extinction of a particular group of species, the cats of the subfamily Machairodontinae, often commonly referred to as the sabretooths. We do this for two main reasons. First, because although extintion has probably been the fate of most organisms that have ever lived, it seems intuitively likely that extinctions of such catholic, eurytopic species as the large felid members of the Carnivora are likely to mark significant changes in conditions, and in Africa such extinctions fall in the period close after 1.7 myr. This latter point was highligh-

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[2] The lower boundary of the Pleistocene is taken as 1.8 Ma based on the Vrica marine section in Calabria (Berggren *et al.*, 1985 and as modified in Van Coevering, 1997a).

ted by one of us several years ago (Turner, 1990) although its potential significance was not appreciated at the time in part because it was then thought that the extinction of one sabretoothed cat, *Megantereon cultridens,* occurred much later, after 1.0 myr. Second, because we have first-hand information about a further, broadly similar pattern of machairodontine extinction later in time in the very different setting of Middle Pleistocene Europe (Turner, 1992a, 1992b, 1995a, 1995c, 1995d), a data set that can be used to examine the situation in Africa in a comparative manner. We consider these patterns of extinction against the background of global and regional change, and in doing so draw particular attention to the evidence for a global-scale event in the deep-sea core data close to 1.9 myr that may have a major bearing on the issue.

The machairodont cats of the African and European Plio-Pleistocene

In popular portrayal, the machairodontine cats are often equated with the dinosaurs as an example of maladaptation or over specialisation, as bizarre animals unable to fit in and thus somehow the architects of their own extinction. In reality, just like the dinosaurs, they were a highly successful group if we judge by their longevity in the fossil record and their considerable diversity (figure 1), and by the fact that the sabretoothed plan has been followed by several other, variously more distantly related groups such as the pseudo-felids of the family Nimravidae and the marsupial sabretooth, *Thylacosmilus,* of South America (Caroll, 1988; Turner and Antón, 1997; Werdelin and Turner, 1996b).

A considerable variety of machairodontine felid taxa were present from the Late Miocene until the earliest Pleistocene in Africa. The genus *Machairodus* has been identified in Mio-Pliocene deposits at Lothagam (Leakey *et al.,* 1996), Sahabi (Howell, 1987) and Langebaanweg (Hendey, 1974), while a skull from the Tunisian site of Ain Brimba referred to *Machairodus africanus* has been recovered from deposits thought to date between 3.5 and 2.0 Ma (Petter and Howell, 1987). Work clearly needs to be done on the affinities of much of this material. However, we are mainly concerned here with three genera: *Dinofelis, Homotherium* [generally considered a descendant of *Machairodus* (Turner and Antón, 1997)] and *Megantereon,* shown here in figure 1 to illustrate life appearance and comparative sizes.

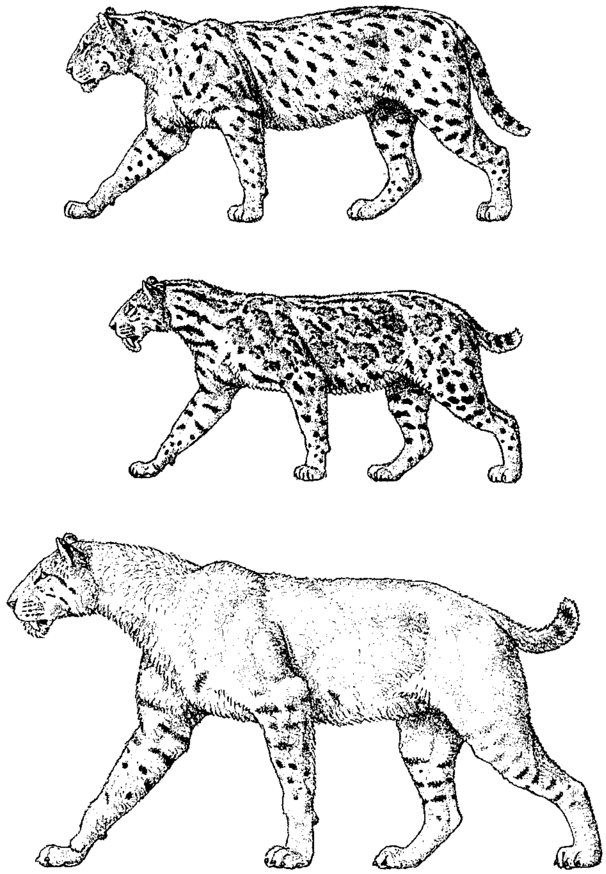

Fig. 1.—Life appearance and size comparison of *Dinofelis barlowi* (top), *Megantereon cultridens* (centre) and *Homotherium latidens* (bottom). All drawn to scale, with a typical height at shoulder of 110 cm for *Homotherium.* Specific coat patterns are unknown but typical of those seen across the range of living felids. For details of reconstrution methods see discussions given by Turner and Antón (1997).

The machairodont specialisations of *Dinofelis* are much less pronounced than in the other two genera, and its morphology is in many ways intermediate between felines and typical machairodonts (figs. 1 and 2). This intermediate morphology has been the cause of contrasting classifications of *Dinofelis* and related genera (such as *Metailurus*), usually called the metailurines. For instance, Crusafont and Aguirre (1972) gave subfamilial rank to the metailurines, while Hendey (1974) included *Dinofelis* and all metailurines within the subfamily Felinae, and Harrison (1983) included them within the Machairodontinae. Beaumont (1964) originally placed the metailurines among the felines but later (Beaumont, 1978), he emphasized their incipient machairodont traits, and removed them from the feline radiation in his proposed phylogeny. Following the latter view, Turner and Antón (1997) included the Metailurini as a tribe in the subfamily Machairodontinae, but obviously further work is neccesary to clarify the position of the metailurines within the felid radiation.

In Africa, *Dinofelis* is first recorded at Lothagam (Leakey *et al.*, 1996) and is then found at Langebaanweg (Hendey, 1974). The specific affinity of the latter material is unclear but it has been suggested that it is probably *Dinofelis barlowi* (Turner, 1990); Cooke (1991, 19) noted the similarities but suggested that 'the differences appear to warrant' specific separation. The more derived *Dinofelis piveteaui* is known from Kromdraai A at close to 1.7 myr, all animals perhaps the size of a large modern jaguar, *Panthera onca*. Significantly, the genus *Dinofelis* is only known from the lowermost Member 1 at Swartkrans (Brain, 1981), where most if not all of the deposits are likely to post-date Kromdraai A, with a probable date of around 1.8-1.5 myr (Brain, 1993; Turner, 1993). The postcranial skeleton has never been well described, although material from Langebaanweg associated with dental remains (Hendey, 1974; Turner, unpublished data) suggests a powerfully-built animal. Lewis (1997), has argued for comparatively robust forelimbs and gracile hindlimbs in material currently still under study. In eastern Africa, *Dinofelis* is last recorded in the Okote Member of the Koobi Fora Formation, around 1.5 myr (Harris *et al.*, 1988); unpublished material listed as *Dinofelis barlowi* by Pickford (1986) is present at Kanam East, but the date is currently unclear (Vrba, 1995b).

Homotherium latidens, a larger animal rivalling male lions, *Panthera leo*, in size, first appears at Langebaanweg (Hendey, 1974), and is a relatively frequent find in East African deposits until its last appearance again in the Okote Member close to 1.5 myr (Leakey, 1976; Howell and Petter, 1976; Harris, *et al.*, 1988). It is rare in the Transvaal caves, but occurs at Makapansgat, Members 4 and 5 at Sterkfontein and at Kromdraai A. *Homotherium* is remarkable for the relative length of its front limbs (Ballesio, 1963), giving it an apparently awkward posture, but for all that it too was a powerful animal in which the limb length may have provided considerable leverage (Kurtén and Anderson, 1980; Turner and Antón, 1997). Material under study from the Spanish Lower Pleistocene locality of Incarcal (Antón and Galobart, in prep) is showing increasing evidence of cursorial adaptation in this species. The claws are mostly small, and it is now apparent that the single large claw identified in association with the relatively complete skeleton from Sénèze in the Auvergne by Ballesio (1963) may actually have been a phalanx of the first anterior digit, the dewclaw. The bones of the forelimb are long and relatively slender, and in general we may therefore say that *H. latidens* was more cursorially adapted, less individually strong and less well-equipped for ambush hunting than a lion, a conclusion also reached by Lewis (1977).

Megantereon cultridens, an animal often considered similar in size and overall build to a large jaguar (Schaub, 1925), was in fact highly variable in size, with smaller animals more the size of a leopard, *Panthera pardus*, and by implication rather sexually dimorphic (Turner, 1987). It is first clearly recorded in the Usno Member of the Omo deposits in East Africa, perhaps in Member B of the Shungura Formation (Howell and Petter, 1976; Turner, 1987), and then fairly regularly in the later Shungura members until its last record there in Member G. The latest record in eastern Africa is once more in the Okote Member of the Koobi Fora formation close to 1.5 myr (Harris *et al.*, 1988). In South Africa it is recorded from Kromdraai A, Kromdraai B, Swartkrans and Sterkfontein, although it is unknown at Makapansgat (Turner, 1986, 1987, 1993). Its appearance in Member 3 at Swartkrans was originally taken as evidence for appearance post 1.0 myr (Turner, 1990), but there is now thought to be no compelling evidence for placing Member 3 significantly later than Member 1 at around 1.8-1.5 myr (Brain, 1993). Material from Elandsfontein in Cape Province has no clear date, but the deposits there are a considerable palimpsest derived from hyaena dens and certainly include earliest Pleistocene taxa (Hendey, 1974).

In Europe, *Machairodus* is mainly known from deposits of Vallesian and Turolian (late Miocene) age, while *Dinofelis* is first recorded in the latest Miocene (Morales and Aguirre, 1976) and then is found throughout the Lower Pliocene (Hemmer, 1965). *Homotherium latidens* was present throughout most of the Pliocene and much of the Pleistocene before its last records at sites such as Westbury-sub-Mendip in England and Mosbach in Germany at close to 0.5 myr (Turner, 1992b, 1995c, 1995d, in press a). *Megantereon cultridens* is also known from at least the mid-Pliocene onwards, and is last recorded at the German locality of Untermassfeld in deposits of Jaramillo age (Turner, 1987; Turner, 1995d).

In each of these Old World continents the machairodontine cats in general, and many individual species in particular, were therefore long-established members of the fauna by the end of the Pliocene (table 1). They witnessed the origin and/or incursion of the conical toothed cats of the still extant subfamilies Pantherinae (species such as the lion, *Panthe-*

ra leo, the leopard, *Panthera pardus*) and the Acinonychinae (the cheetahs of the genus *Acinonyx*), and overlapped in time with them to varying extents (Turner, 1990, 1992b, 1995d; Pickford and Morales, 1994). As we show below, they survived when much of the rest of the larger mammal fauna around them was changing, and it is difficult to avoid the conclusion that the eventual extinctions of the machairodonts required changes in conditions that differed significantly from those occurring during their membership of their respective large carnivore guilds.

Of course any examination of the timetable of those extinctions must face the problem that last appearance datums (LADs), like first appearance datums (FADs), will be subject to biasing errors, a point usefully discussed in some detail by Vrba (1995a), b) and by Pickford and Morales (1994). [The recent article by Behrensmeyer *et al.* (1997) faces this problem in its effort to refute the «turnover pulse» hypothesis of evolution in African faunas in response to late Pliocene climatic change based on material from the Turkana Basin; effectively they come to the same conclusions as Vrba after a lengthy discussion of how to deal with appearance datums but still claim to have rejected the hypothesis]. In Europe the Middle Pleistocene extinction of the machairodonts is by now well attested by the sheer quantity of later deposits from which they are consistently absent. In Africa the picture is less clear, and it is possible that well-dated specimens later than our presently observed LAD of ~ 1.5 Myr will appear, just as any synthesis of palaeontological data will be overtaken by events. For this reason we have shown the last appearances as *E*?, to mark the residual uncertainty over precise times of extinctions. However, the pattern as we presently see it strongly suggests to us that the machairodonts were not significant components of the Pleistocene large predator guild in Africa, a conclusion paralleled at least for East Africa by Pickford and Morales (1994). It is difficult, as has been said elsewhere (Turner, 1990) to know exactly how much to make of relative abundances of various carnivore taxa in the African fossil record when the numbers are so absolutely small in many instances and the vagaries of the fossilisation process are hard to estimate. Absence from the fossil record is always hard to evaluate —indeed the appearance of members of the extant African Carnivora is extremely patchy after their first record in any given region. But by around 1.5 myr the modern species have been around for some time and the fauna in general is taking on a more modern aspect. In these circumstances, when we look at the larger picture of change in the African Carnivora, it is the machairodont cats that go extinct. Moreover, the emphasis of our treatment of these extinctions here is to see them as the effects of changes in conditions, as something that occurs in the aftermath of climatic and vegetational change and their impact on prey structure and availability and not as some kind of «sudden death» event.

Aspects of machairodontine palaeoecology

Many discussions of the behaviour of the machairodont cats have appeared in the literature, and several may be found in the various references already cited. We are concerned here with one important aspect of behaviour, their prey capture and consumption abilities and techniques in comparison with those of living cats. Turner and Antón (1997) summarise numerous investigations and discuss prey capture, killing and consumption methods at length.

In broad outline, living big cats capture, kill and then eat, a three stage process but one in which a killing bite at the neck region, or a clamping of the muzzle, may be employed to induce suffocation *during* capture and despite any struggles of the prey (see, for example, the discussions about lions, leopards and cheetahs given by Schaller, 1972 and Bailey, 1993). In contrast, and despite significant differences between them in size and proportion, several inter-related features of anatomy must have both constrained and directed the hunting strategy and killing tactics of machairodonts in another direction. The over-riding impression of both *Dinofelis* and *Megantereon* is of a strong body with a short back, large claws and —especially in the case of *Megantereon*— long, sharp but inherently fragile canine teeth, animals built for capturing using a short rush and considerable strength to bring down and hold their prey before killing by some form of slashing bite. Attempting to clamp the muzzle would have meant the risk of biting into bone, and only with prey held essentially still could they have slashed or bitten into the neck in order to induce blood loss and shock or suffocation without risking damage to their slender canines as a result of striking bone or through torsion (Turner and Antón, 1997, fig. 4.24).

Homotherium differed from this body pattern, as we have stressed above. It too had a strong back, but its limbs were more slender, the front limb was more elongated and the claws appear to have been relatively smaller (Antón and Galobart, in prep). Such a body plan suggests a more cursorial lifestyle and hunting strategy (Turner and Antón, 1997), and would imply that some degree of group activity was perhaps employed to bring down and restrain prey.

In any event, a cursorial hunting strategy can only be deployed in relatively more open terrain, where larger group size may be needed to repel the inevitable attention of scavengers. The likelihood of group activity is strongly underlined in the case of the similarly proportioned American species *Homotherium serum*, known in some numbers at the Texas late Pleistocene site of Friesenhahn Cave in association with numerous remains of juvenile mammoths (Marean and Ehrhardt, 1995), a prey that most likely would require group hunting.

However, like *Megantereon*, *Homotherium* too possessed elongated and therefore dangerously fragile upper canines. Just how long these canines were in *Homotherium* and *Megantereon* may be seen in figure 2, although even such elongated teeth were surpassed by those of the American genus *Smilodon* (fig. 2). In short, none of these cats could have operated by killing in the same way as a lion or a leopard with the attendant risk of damage to its teeth. In the case of *Dinofelis*, the constrains would have been lesser, because their canines were not as

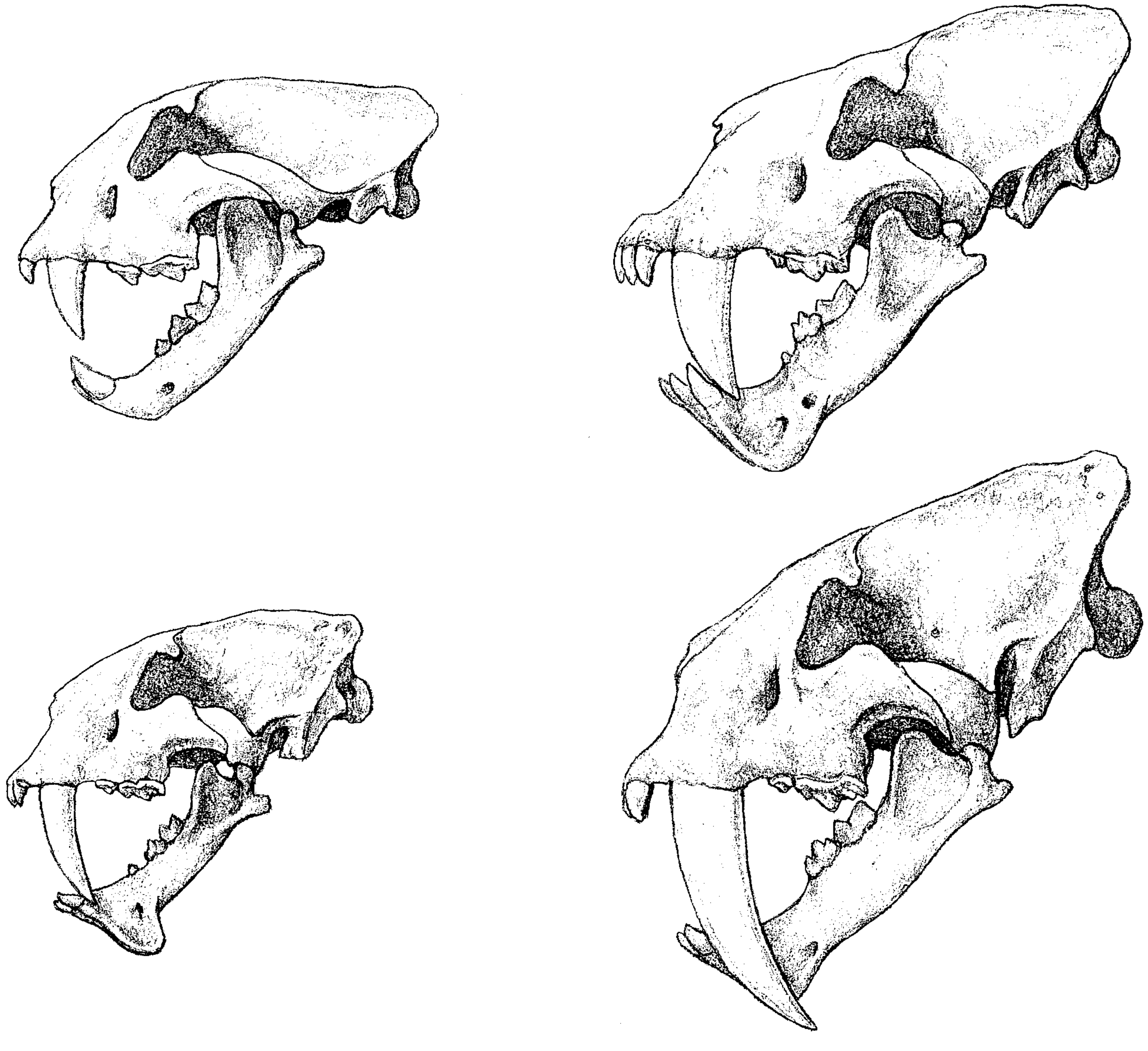

Fig. 2.—Crania and dentitions of machairodont felids to illustrate dental size and proportions. *Dinofelis* (top left); *Homotherium* (top right); *Megantereon* (bottom left); *Smilodon* (bottom right). All drawn to scale with body sizes of the first three as in figure 1.

long or laterally compressed, but a more careful approach to struggling prey than that seen in modern pantherines would be expected, especially in *D. pivetaui*. The most probable habitat for *Megantereon* and *Dinofelis* to hunt in would have been more closed vegetation, permitting a close stalk of a carefully selected prey animal followed by a short dash from cover and firm seizure. For *Homotherium*, group action in more open areas of vegetation would have achieved the same end, with larger prey subdued by weight of numbers.

Ecological Relationships Between Modern Larger Cats

We have stressed both the differences and the similarities between the extinct large cats and outlined some relevant aspects of their likely hunting and prey-capture and dispatching methods, but what of their interactions within the palaeoecosystem? Some insights into the ecology and inter-relationships of machairodont cats may be gained from a review of the relationships between different species of modern large cats and their interactions with other carnivores.

One relevant point to consider is the ecological separation of, and hierarchical relationship between, lion-sized and leopard-sized cats. In areas where the modern tiger, *Panthera tigris,* and the leopard are sympatric, vegetational cover is a key factor enabling the species to co-exist (Seidensticker, 1976). In areas of high cover, prey species weighing between 25 and 50 kg are relatively abundant, and can be quickly consumed by the leopard before competitors arrive or more easily transported and hidden or carried into a tree. In areas with sparse cover, the leopard finds it difficult to avoid encounters with the bigger cat, which steals carcasses and will even kill the smaller animal. In such cases, the leopard becomes scarcer or simply disappears. In contrast, in areas where the tiger is absent, such as Sri Lanka, the leopard ventures into open areas in pursuit of larger prey, even in broad daylight (Muckenhirn and Eisenberg, 1973).

In Africa, in areas where the lion and leopard are sympatric, the latter again seeks refuge in wooded areas, particularly in gallery forests (Schaller, 1972; Bailey, 1993). However, the leopard can also thrive in relatively dry, open environments such as the Kalahari Desert (Mills, 1990), and the factors that influence hunting success, including the extent of cover, appear to be the same in both species (Bailey, 1993). Nevertheless, lions are able to overcome the disadvantages of hunting in sparsely covered areas by means of group action (Stander and Albon, 1993).

The preference for woodland shown by the leopard in Africa is thus again seen to be largely a way of avoiding competition, improved by its ability to take relatively large carcasses up into the branches of trees (Mills and Biggs, 1993). The preference of lions for more open terrain appears to reflect two major factors. First, the availability of more concentrated biomass in such areas, and secondly the sheer physical dominance of the lion over other carnivores. This latter factor allows it to defend both carcasses and its own life in the high visibility conditions of the grasslands (Sunquist and Sunquist, 1989; Packer, 1986). We may thus expect that extinct cats of lion size, such as *Homotherium,* would have been similarly dominant over leopard to jaguar sized species such as *Dinofelis* and *Megantereon,* and the presence of the larger taxon associated with one or both of the others at a fossil locality would suggest the presence of enough cover in a mosaic of vegetation for the smaller species to avoid encounters with the larger. The fact that competitive exclusion among large carnivores is a process mediated by vegetational cover is demonstrated by recent studies of the ecology of wild dogs, *Lycaon pictus* (Creel & Creel, 1996; Gorman *et al.*, 1998). Wild dogs can decline or dissapear in areas with high density of lions and spotted hyenas and where high visibility makes carcass detection easier for potential kleptoparasites. In areas of more dense cover, even if lions and hyenas are abundant, wild dogs fare better because their kills remain undetected for longer. One can easily imagine that the gracile hunting hyenas of the genus *Chasmaporthetes* would also be subject to kleptoparasitism from stronger hyenids like *Pachycrocuta,* and *Homotherium* would be subject to carcass stealing by lions. In both cases, a reasonable amount of cover, like that seen today in Kruger Park or in Selous game reserve (Creel & Creel, 1996), would make life easier for the weaker predators.

The complex and shifting nature of the relationship between habitat and predator activity is underlined by correlations between dry season rainfall, resident prey biomass and lion populations in the Serengeti discussed by Hanby and Bygott (1979). It is clear that even for modern carnivores such as the lion and spotted hyaena, well adapted for life on the plains, a decrease in dry season rainfall forces a decrease in population. This decrease stems in large part from the increased proportion of migrating species among the ungulate biomass, which produces an increase in competition for a decreasing resource in the form of resident ungulates. This competition appears to operate largely between members of the same species, but has implications for inter-species relationships, particularly in the more crowded predator guilds that existed in the past. We return to the issue of crowding in predator guilds below.

Plio-Pleistocene Events in Africa and Europe

Three categories of information seem most relevant to an understanding of events around 1.7 myr in the context of the present discussion. First, the global and more regional pattern of changes in the environment over the relevant time span and its effect on the vegetation. Recent work on the vegetational record of the last 125 kyr in North America (Whitlock and Bartlein, 1997) points to a very strong correlation between climatic variations and vegetational change over that period, one for which crucially important accurate dating is now available. As Guiot (1997, 27) has put it in commenting on the results offered by Whitlock and Bartlein, «The message here is that we need first to understand the climatic forcings *before* being able to interpret terrestrial data, and that these forcings cannot be discovered independently in the terrestrial cores» (emphasis added). Second, the overall pattern of changes in the larger carnivore guilds of each region. Third, the pattern of changes in the ungulate faunas of the two regions, and in particular the changes involving those ungulates likely to have made up the prey spectrum of the larger carnivores.

Environmental Change

The global picture

Oxygen isotopic analyses of the Plio-Pleistocene ocean core data show a global trend towards lower temperatures with stepwise increases in cooling (Shackleton, 1995; Shackleton *et al.*, 1984; Prentice and Denton, 1988; Ruddiman and Raymo, 1988; Denton, in press). The most recent compilation is that given by Shackleton (1995, fig. 17.1-3), which provides a useful summary of the trend and the steps, although because that figure is produced in three sections a clearer picture is actually given by figure 6 of Pisias *et al.* (1995) shown here as figure 3. There is substantial agreement (Denton, in press; Shackleton, 1995) that one of the most important of the stepwise changes is that culminating at 2.5 myr, often referred to as the 2.5 myr event, with a shift to dominance of the 41 kyr astronomical cycle. This is clearly seen in figure 3, as both the mean and the isotopically most heavy points of the curve move inexorably downwards from around 3.5 myr (point 1) to reach a new plateau after stage 100 at around 2.5 myr (point 2). The period just after 2.5 myr sees the first major northern hemisphere glacial event of the Plio-Pleistocene marked by ice-rafting of debris in the northern oceans (Shackleton, 1995; Shackleton *et al.*, 1984). The global nature of this event is indicated by loess deposition in China (Kukla, 1987; Kukla and Cílek, 1996), palynological indicators of increasing cold in the Andes (Hooghiemstra, 1986) and palynological, lithostratigraphic and cryoturbic indicators from the Netherlands in conjunction with palynological evidence from correlated deposits in the Mediterranean (De Jong, 1988; Zagwijn, 1992b; Zagwijn and Suc, 1984).

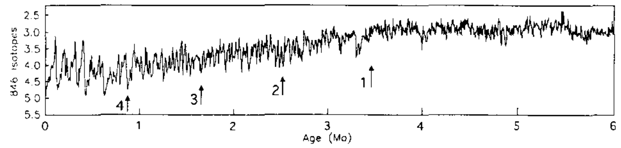

Fig. 3.—Modified stable isotope curve for Pacific benthonic foraminifera with points 1-4 added. Increasing isotopic values indicate colder conditions. For discussion see text. After Pisias *et al.*, 1995. figure 6.

A second major event often identified as second only in significance to that at 2.5 myr (Denton, in press; Shackleton, 1995) is recorded at isotopic stage 24 close to 0.9 myr (figure 3, point 4), with the shift to dominance of the 100 kyr astronomical cycle and the intensification of Northern Hemisphere glaciation (Ruddiman and Raymo, 1988; De Jong, 1988; Zagwijn, 1992a, 1992b). However, between these two, it appears evident from figure 3 that a third major step may be seen beginning at around 1.9 myr with the isotopically heavy excursion of stage 70 (point 3), when a lower plateau still is attained and maintained until the further marked shift of the 0.9 myr event. We have so far been unable to locate any assessment of the significance of this intermediate step in commentaries on the isotope curve, although Van Couvering (1997b, xv) makes clear reference to a «major climatic downturn» at or about 1.8 myr, but logic would suggest and intensification of conditions produced by the 2.5 myr event since both the mean and the isotopically heaviest points have once more fallen.

Africa

In Africa, the effects of these global changes have been reported in the period close to 2.5 myr, although they have clearly been affected by volcanic eruption, rifting and faulting (Partridge *et al.*, 1995). Palynological evidence from the Omo (Shungura) and from Hadar points to increasing cold and aridity in the eastern part of the continent at ca 2.5 Ma and to the spread of grasslands (Bonnefille, 1995; Bonnefille and Vincens, 1985; Bonnefille *et al.*, 1987), an interpretation supported by the evidence of small mammals in the Omo Shungura deposits (Wesselman, 1984). Deep-sea cores from the South Atlantic point to the presence of sediments apparently derived from increasingly arid terrestrial environments of western Africa during the same period (Janecek and Ruddiman, 1987), a finding supported most recently by the work of deMenocal (1995; deMenocal and Bloemendal, 1995).

However, palynological analyses have also suggested a second marked phase of grassland increase by around 1.7 myr in both the Turkana Basin and at Olduvai (Bonnefille, 1995; Bonnefille, *et al.*, 1987). More recently, analyses of palaeosol stable carbon isotopes used to reconstruct proportions of C3 and C4 biomass at sampled localities, and thus the extent of closed versus open landscapes since the Miocene (Cerling, 1992; Cerling *et al.*, 1988; Kingston *et al.*, 1994, Sikes, 1994, 1995, 1996, in press) have thrown further light on this patterning. These latter results between them show *no* major steps in the transformation of the vegetation around 2.5 myr, although Cerling (1992, 244) does record a shift towards C4 plants in the Upper Ndolanya Beds at Laetoli, but several of them cite evidence for an increased proportion of C4 grasses around 1.7 myr and for consistent appearance of modern vegetational structure only after 1.0 myr (Sikes, in press, table 1). Some of the best evidence for the shift at 1.7 myr is seen in the sequence of palaeosols at Olduvai Gorge (Sikes, 1994, 1995, 1996). Moreover, evidence from stable oxygen isotope values at the same localities, key indicators of local rainfall and temperature, also show evidence of relatively stable climatic conditions until 1.8 myr (Sikes, in press).

It is clear that the African palaeosol data is not reflecting the same pattern of events as either the marine oxygen isotope record or some of the other terrestrial indicators cited above, although the results do correlate with an increase in aeolian dust from the continent seen in ocean cores around 1.7 myr and thought to indicate a significant increase in aridity at that time (deMenocal, 1995; deMenocal and Bloemendal, 1995). Clearly questions of scale and sampling density will underlie at least part of this difference, but it is also likely that environments within Africa will have been affected by significant local events such as rifting and volcanism (Partridge, *et al.*, 1995) and that the signature of global changes will therefore have been altered because of localised effects on vegetational communities and the composition of meteoric water (Sikes, in press). If both oceanographic and terrestrial data are correct, and the evidence that they are is compelling, then one possible explanation for the differences in the timing of vegetational change is that only by 1.7 myr do local conditions in the localities sampled for palaeosol analysis begin to line up with those occurring on a global scale. One implication would be that the stepped changes in orbitally-induced conditions that produced the larger scale pattern by 2.5 myr had increased, or continued to increase, by 1.7 myr.

Europe

Both the 2.5 myr and 0.9 myr events are clearly seen in Europe, where for some time now it has been possible to match biotic and abiotic data from the Netherlands to the broad sequence seen in the ocean cores and to see the intensification of the glacial-interglacial cycles (Zagwijn, 1960, 1985, 1992a, 1992b, 1997; De Jong, 1988). Elements of the Pliocene forest vegetation, for instance, no longer appear in interglacial floras after the Praetiglian cold phase that began close to 2.3 myr, and tundra-like vegetational elements are first seen. Further intensification is particularly evident after 0.9 myr, and during the glacial periods that came to dominate over that time Europe was a region of treeless vegetation. The regeneration of the flora following each of the more intensive glaciations after 0.9 myr involved distinctly more succession in the immigration of forest species than is seen in earlier temperate phases of the Lower Pleistocene (Zagwijn, 1992b, 586), and appears to have involved dispersions into central and northern Europe from considerably greater distances (De Jong, 1988; Zagwijn, 1992a, figure 1).

Climatic changes close to 1.7 have been less readily apparent in the European record, although the Netherlands climate curve (Zagwijn, 1997, figure 16.1; De Jong, 1988, fig. 2) suggests that the beginning of the Eburonian cold stage may be correlated to the top of the Olduvai event. This point is reinforced by Kukla and Cílek (1996), who suggest a link between the Eburonian stage and one of their major Chinese loess units at close to 1.8 myr and thus to an uplift pulse in the Tibetan Plateau. More recently, Grichuk (1997) has shown that significant changes in the dendroflora of extra-tropical Eurasia occur at the level of the Olduvai palaeomagnetic event with the disappearance of all eastern Asiatic genera at an age close to 1.7 myr.

The Carnivore Guilds

Africa

The evolution of the Plio-Pleistocene larger carnivore guild in Africa has been discussed in detail (Turner, 1990), and the Hyaenidae have recently been entirely revised (Werdelin and Turner, 1996a). The currently known chronological distribution of the larger Felidae and Hyaenidae, based in large part on the discussions presented in those reviews, is shown in table 1. As may be seen, the African guild has changed markedly since the beninning of the Pliocene. By 3.5 myr most of the extant taxa were present in a rich carnivore fauna almost twice the size of that seen there today, and for the next two million years they appear to have coexisted with some of the more archaic elements of that fauna. Those archaic elements, including the machairodont cats of the genera *Homotherium, Megantereon* and *Dinofelis,* as well as the so-called hunting hyaenas of the genus *Chasmaporthetes* and the giant hyaena *Pachycrocuta,* only went extinct after 1.5 myr.

Clearly, the African guild as portrayed here in table 1 is a minimum statement of complexity. As we pointed out above it is difficult to use actual appearances and non-appearances at individual sites to draw any conclusions about relative abundance, and the difficulty of establishing true LADs and FADs is obvious. It is equally difficult to know precisely what to make of gaps in the appearance of taxa once they first occur in the record. The difficulties are compounded by inter-regional differences between faunas and faunal events in various parts of Africa, particularly between eastern and southern areas as previously discussed by Turner and Wood (1993b). It is also evident that continued taxonomic work will alter in some degree the nomenclature of the members of the large carnivore guild, although the structure is

Table 1.—**European and African Plio-Pleistocene Felidae and Hyaenidae. For details see Turner (1990, 1992a, 1992b, 1993, 1995a-d)**

Age Myr	3.0	2.5	2.0	1.5	1.0	0.5	0.0
EUROPE							
FELIDAE							
Acinonyx pardinensis	—	—	—	—	—	—	
Panthera gombaszoegensis				—	—	—	
Panthera leo						—	—
Panthera pardus						—	—
Homotherium latidens	—	—	—	—	—	— **E?**	
Megantereon cultridens	—	—	—	—	**E?**		
HYAENIDAE							
Pliocrocuta perrieri	—	—	—		—	—	
Pachycrocuta brevirostris				—	—	—	
Chasmaporthetes lunensis	—	—	—				
Crocuta crocuta						—	—
AFRICA							
FELIDAE							
Machairodus africanus	—	*? ? ? ?*					
Dinofelis barlowi	—	—	—	**E?**			
Dinofelis piveteaui	—	—	—	**E?**			
Megantereon cultridens	—	—	—	**E?**			
Homotherium latidens	—	—	—	**E?**			
Panthera leo	—	—	—	—	—	—	—
Panthera pardus	—	—	—	—	—	—	—
Acinonyx jubatus	—	—	—	—	—	—	—
HYAENIDAE							
Pachycrocuta brevirostis	—	—	—				
Chasmaporthetes nitidula	—	—	—				
Chasmaporthetes silberbergi	—	—	—				
Crocuta crocuta	—	—	—	—	—	—	—
Parahyaena brunnea		—	—	—	—	—	—
Hyaena hyaena	—	—	—	—	—	—	—

E? Marks extinctions of Machairodontinae. / Señala las extinciones de Machairodontinae.

likely to prove more robust. But here we are concerned with a larger-scale synthesis taking Africa (essentially eastern and southern regions) as a whole, one for which the scheme of table 1 seems to us adequate.

The later Pliocene African guild of larger carnivores appears almost crowded by modern standards, and equates to what Harris (1993) has termed a greater guild «depth», Such depth, according to her analysis, is a sign of environmental stability over the period —as seen from the viewpoint of the guild members— with resources plentiful and predictable. But any such deepening would produce a surfeit of «redundant» taxa that might dissappear should conditions change and alter the availability of those resources.

Europe

Several recent discussions have served to outline the details of the evolution of the European larger carnivore guild (Turner, 1992a, 1992b, 1995a, 1995c, 1995d, in press b, Turner and Antón, 1996). The currently known mid Pliocene-Pleistocene distributions of the Felidae and Hyaenidae based on those discussions are shown here in table 1.

There is no evident pattern of change in the guild at 2.5 myr, and the picture is one of essential stability until around 1.6 myr. The flesh-eating component of the guild consisted of the machairodont cats *Homotherium latidens* and *Megantereon cultridens*, animals with little bone-destroying ability, together with the gracile hunting hyaena, *Chasmaporthetes lunensis* and the large European cheetah, *Acinonyx pardinensis*. The bone-destroying role until that time, in the absence of any significant canids, was held by the large hyaenid *Pliocrocuta perrieri*.

The change at 1.6 Ma witnessed the local extinction of *Chasmaporthetes lunensis* and *Pliocrocuta perrieri* (although the latter re-appeared in Europe in the Middle Pleistocene) and several important first appearances. These included the European jaguar, *Panthera gombaszoegensis*, and the gigantic hyaenid *Pachycrocuta brevirostris* which «took over» the role of large, bone destroying hyaena in place of *P. perrieri*. The canids were for the first time represented by larger taxa in the form of *Canis arnensis*, *C. mosbachensis* and *C. falconeri*, leading Azzaroli (1983) to term this the «wolf» event. This initial change was reinforced by around 0.9 Ma by the first European appearances of the living species *Panthera leo*, *Panthera pardus* and *Crocuta crocuta*, incursions that were part of the changes in the fauna that characterised the «end-Villafranchian event» of Azzaroli (1983).

Several features of the distribution in time stand out. First is the change at 1.6 myr, during which a considerable turnover of the large carnivore guild takes place. However, this turnover has little apparent effect on the two machairodont cats of Europe, which continue to share the felid section of the guild with the cheetah and the newly arrived jaguar. At present the timing of the local extinction of *Megantereon* is unclear; it was still active at Untermassfeld in Germany at close to 1.0 myr, and how close its true extinction fell to that of *Homotherium* is unknown. Unfortunately, it is never a significant proportion of the assemblage at any one locality, and its known distribution is extremely patchy. The second point of note is the massive increase in overall taxon numbers at the end of Lower Pleistocene and during the early half of the Middle Pleistocene, with the co-occurrence of many of the older species alongside the modern taxa. This situation finds its closest parallel in the structure of the African guild between 3.5 and 1.5 myr, with a similar guild «depth» in the sense employed by Harris (1993) and with a similar appearance of crowding. The third is the change at around 0.5 Ma, with the final demise of what were then the older members of the guild, such as *H. latidens*, *P. gombaszoegensis* and *A. pardinensis* along with *Pliocrocuta perrieri*, *Pachycrocuta brevirostris* and various dogs, leaving a European community broadly similar in membership *and structure* to that of East Africa today (table 1). In other words, Europe and Africa share a similar pattern of overlap and eventual replacement in guild membership and structure, but with a different time scale.

The Ungulates

Africa

In terms of both sheer taxon numbers and fine detail, perhaps the most important studies of African ungulate have been presented by Vrba (1982, 1985b, 1995b) for the Bovidae. As a major component of the faunas of Africa, they are also likely to have been among the most important prey species sought by all of the predators. However, it is now apparent that much useful information about both evolutionary pattern and process may also be gained from consideration of other ungulate and non-ungulate lineages, as most recently summarised by Turner (1995b; Turner and Wood, 1993a).

A major turnover event in the Bovidae identified by Vrba (1995b) at close to 2.5 myr, involving speciation events, immigrations of antilopine and caprine taxa and extinctions, is supported by the evidence of contemporaneous events across several diverse lineages. This event appears to have involved adaptations to more open conditions, including a shift in the importance of more open country, *larger* bovids. These may have been somewhat faster-moving, or at least more efficient in their locomotion, adaptations that may be linked to increases in foraging range. As pointed out in the introductory section, analyses of postcranial characters may suggest that some of the locomotory changes took place slightly later (Kappelman, *et al.*, 1997), although independent investigations of bovid feeding mechanisms tend to support arguments for environmentally induced turnover in the period prior to 2.0 myr (Spencer, 1997). These changes in the structure of the bovid guild would have impinged on the members of the carnivore guild, although until now it has not been clear precisely how and to what extent they may have been a factor in extinctions (Turner, 1990). However, Vrba (1995b) has given further attention to events in the Bovidae around 1.7 myr, much closer in time to the final appearances of the machairodont cats. Evidence of changes in the Bovidae provided by Vrba (1995b, fig. 7) shows immigrations of yet more open country groups entering the record after 2.0 myr, most notably as yet undetermined species of Ovibovini and Caprini in various horizons at West Turkana and in Shungura Member H.

A second ungulate group that deserves greater consideration than it has hitherto been given as a component of the prey spectrum is the Suidae. Famous —perhaps notorious— for their taxonomic complexity and role in underlining dating problems (Harris and White, 1979; Cooke and Wilkinson, 1978; Cooke, 1985), the pigs were an extremely diverse part of the Plio-Pleistocene fauna of Africa before being reduced to the three extant taxa. Their potential as palaeohabitat indicators has been recognised in recent years (Bishop, 1994), but what of their food potential to a predator? Schaller (1972) noted that warthog may figure largely in the diet of lions in areas where other prey are scarce. There is considerable change in the suid fauna of the later Pliocene in Africa between 2.0 and 1.6 myr —what White (1995, 375) refers to as «the most dramatic faunal turnover»— with *Notochoerus euilus* and *N. scotti* going extinct, the appearance of *Kolpochoerus majus*, the extinction of *Metridiochoerus andrewsi* and the appearance of *M. modestus*, *M hopwoodi*, and *M. compactus* (Bishop, 1994, in prep.; White, 1995). Members of the genus *Notochoerus* were huge animals, with adults up to perhaps 450 kg in weight and the stature of lion and a probable preference for more open habitats, while later members of the species *Metridiochoerus andrewsi* were

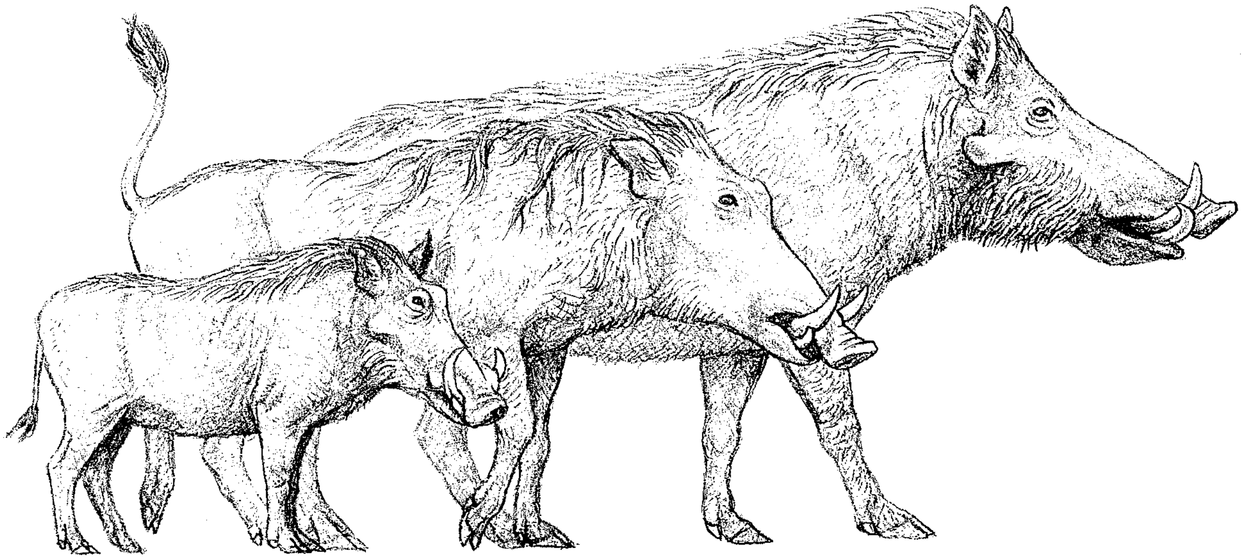

Fig. 4.—Size comparisons between extinct and extant Suidae. *Phacochoerus aethiopicus*, the living warthog (left); *Metridiochoerus andrewsi* (centre); *Notochoerus euilus* (right). Typical height of male *P. aethiopicus* at shoulder 65-85 cm (Haltenorth and Diller, 1980).

perhaps twice the size of a living warthog at 160 kg (Bishop, pers comm.); some likely comparative sizes are illustrated in figure 4. Adult notochoeres may well have been too large and aggressive for any of the Plio-Pleistocene cats, but the young of these, and indeed of all pigs, are likely to have been an attractive target, particularly before their tusks had begun to develope. Pigs today have generally high reproductive rates, and a constant supply of notochoer piglets would have been a valuable resource for any open country predator such as *Homotherium*. Moreover, piglets larger than those of extant pigs would have represented a better return on energy expended in capture. Taken as a whole, the Suidae represent too much food for the structural evolution of the family to have been without implications for the predators.

Europe

A turnover in the European fauna at around 2.5 myr has been recognised for some time (Azzaroli, 1983, 1995; Azzaroli *et al.*, 1988), with the replacement of a broadly warm, forest associated group of animals by more open-country taxa. At the same time, Azzaroli also argued that significant changes at the end of the Lower Pleistocene, post 0.9 myr, may be seen in the appearance of heavier bodied bovids of the genera *Bison* and *Bos*, which replace the more lightly-built members of the genus *Leptobos*, and the appearance of large-bodied cervids of the genus *Megaloceros*. It is now clear that the transition was a rather more drawn-out event than originally envisaged by Azzaroli (Agustí and Moyá, Solá, 1992; Sher, 1986, 1992; Turner, 1992b), but nevertheless it remains apparent that a turnover event occurred as part of larger-scale pattern of

Table 2.—**European Cervidae, Upper Pliocene-Recent. Time periods are shown as 500,000 yr intervals.**

Time period	3.0-2.5 Ma	2.5-2.0 Ma	2.0-1.5 Ma	1.5-1.0 Ma	1.0-0.5 Ma	0.5 Ma-present
Períodos de tiempo	3,0-2,5 Ma	2,5-2,0 Ma	2,0-1,5 Ma	1,5-1,0 Ma	1,0-0,5 Ma	0,5 Ma-presente
Pseudodama pardinensis	S-M					
Pseudodama rhenanus		S-M	S-M			
Pseudodama perolensis				S-M		
Pseudodama lyra	S-M	S-M				
Pseudodama nestii			S-M			
Pseudodama farnetensis				S-M		
Croizetoceros ramosus	S-M	S-M	S-M			
Cervus perrieri	M					
Arvernoceros ardei	M					
Procapreolus cusanus	S					
Eucladoceros falconeri		M				
Eucladoceros teguliensis			L			
Eucladoceros dicranios				M-L		
Eucladoceros tetraceros			M-L	M		
Megaceroides boldrini				L		
Megaceroides verticornis					L	
Megaceroides solilhacus					L	
Megaloceros savini					M-L	
Megaloceros giganteus						L
Alces gallicus				M		
Alces latifrons					L	
Alces alces *						L
Dama dama *					M	M
Cervus elaphus *						M-L
Capreolus capreolus *					S	S
Rangifer tarandus *						M

Size classes: S = small, M = medium, L = large, based on living European *Capreolus*, *Cervus* and *Alces* (Lister, 1988).
Taxonomy after Lister (1988), Azzaroli (1992) and Azzaroli and Mazza (1992, 1993).
* Living species.

Clases de tamaño: S = pequeño, M = mediano, L = grande, basado en el rango de tallas de *Capreolus*, *Cervus* y *Alces* (Lister, 1988).
Taxonomía ver Lister (1988), Azzaroli (1992) y Azzaroli and Mazza (1992, 1993).

Plio-Pleistocene ungulate dispersions, many of which originated in Asia (Sher, 1986, 1992).

We are used to thinking of Africa as the continent of faunal richness, but Europe prior to the extinctions at the end of the Pleistocene had its own remarkably rich and diverse array of larger mammals (Turner, 1992a), a fact to which the crowded, deepened nature of the carnivore guild during the central part of the Pleistocene partly owes its origins. Tables 2 and 3 show the distributions of size classes in European Cervidae and Bovidae over the past three million years, and the increased numbers of large taxa, may be clearly seen. By the Middle Pleistocene, if not slightly before, it is therefore clear that the size-bases structure of two major components of the prey fauna had changed considerably. Since prey size is a major determinant of hunting success (Pienaar, 1969; Schaller, 1972; Kruuk, 1972), such changes in size may not have been to the advantage of some of the large predators, particularly *Megantereon*. However, *Homotherium* may have found the changed emphasis on larger prey to its advantage if group hunting was possible. More meat is available on a larger carcass, while smaller species are usually more agile and difficult to capture without an expenditure of energy that makes killing them relatively inefficient (Schaller, 1972).

What is less obvious from tables 2 and 3 is the evidence for any pattern of change in the European ungulates at the beginning of the Pleistocene around 1.7 myr and coincident with the «wolf» event in the Carnivora. A limited turnover in the ungulate fauna appears to have been going on throughout the later Pliocene and Lower Pleistocene, but much of it appears to have involved changes within lineages. Although Azzaroli *et al.* (1988) suggested that the disappearance of *Gazella* and the proboscidean *Anancus*, and replacements among species of the bovid *Leptobos* and the cervids *Eucladoceros* and

Table 3.—**European Bovidae: Upper Pliocene-Recent. Time periods are shown as 500,000 yr intervals. For references see Turner (1992a)**

Time period	3.0-2.5 Ma	2.5-2.0 Ma	2.0-1.5 Ma	1.5-1.0 Ma	1.0-0.5 Ma	0.5 Ma-present
Períodos de tiempo	3,0-2,5 Ma	2,5-2,0 Ma	2,0-1,5 Ma	1,5-1,0 Ma	1,0-0,5 Ma	0,5 Ma-presente
Pliotragus ardeus	M	M				
Hesperidoceras merlae	S					
Gazella borbonica	S	S				
Gallogoral meneghini		S-M	S-M			
Gazellospira torticornis	S	S	S			
Leptobos stenometopon		M				
Leptobos merlai		M				
Leptobos etruscus			M-L	M-L		
Leptobos vallisarni				M		
Bison schoetensacki					L	
Bison priscus					L	L
Bos trocheros						L
Bos primigenius						L
Bubalus murrensis						L
Praeovibos priscus				M	M	
Ovibos moschatus					M	M
Megalovis latifrons			M			
Ovis musimon					S	S
Capra ibex *						S
Procamptoceras brivatense		S	S	S	S	
Rupicapra rupicapra *						S
Saiga tatarica *						S
Hemitragus bonali					M	M
Soergelia elizabethae					M-L	

Size classes: S = small, M = medium, L = large, based on ovicaprid - bison size range.
* Living species.

Clases de tamaño: S = pequeño, M = mediano, L = grande, basado en el rango de tallas entre ovicápridos y bisontes.
* Especie actual.

Pseudodama may be seen as an integral part of the wolf event, it is difficult to see any particular changes there that would have had any likely major impact on the machairodont cats.

Discussion

The final extinctions of the Plio-Pleistocene machairodont cats occurred at different times in Africa and Europe, but in each case two distinct sets of circumstances converged.

Stepped climatic change

The first was a major, *stepped* change in the climate producing a significant shift towards more open country as a predominant feature of the landscape. Whether the African example should be considered a two-stage step, with the second occurring at 1.9-1.7 myr, is perhaps open to question, but in any event we stress the *stepped* nature of that change for good reason. Such a step is particularly well-seen in the European case, where once the full system of glacial-interglacial cycles of the Pleistocene was underway after 1.0 myr it is clear that climate and the vegetation swung between marked extremes of closed and open conditions very different from those of the earlier part of the Pleistocene (Zagwijn, 1992a, 1992b). Any European taxon that found one extreme difficult may have found conditions ideal during the other, but long term success would have depended on coping with both. What might have been possible during earlier oscillations of climate before a *step* pushed the mean of the oscillation lower may well have been impossible afterwards.

The machairodonts were probably less well-equipped than the pantherine cats to cope with such extreme oscillations, although for different reasons in the case of each species. In Europe, a more open habitat would force the woodland-preferring *Megantereon* to face more encounters with larger animals like *Homotherium* and the lion, as well as the large, aggressive hyaenas of the genera *Pachycrocuta, Pliocrocuta* and perhaps even *Crocuta,* if the latter overlapped in time. These powerful scavengers would also take advantage of high visibility to locate and steal kills form the gracile hunting hyeaena *Chasmaporthetes.* In contrast, the more closed habitat of the interglacials would imply less biomass of grazing, herding ungulates, forcing the largest species of carnivores to compete for a diminished share of the prey. Such a scenario could explain the appearance of «dwarf» homotheres in the Middle Pleistocene of China (Kurtén and Anderson, 1980; Turner and Antón, 1997) —a response, perhaps, to shrinking resources. At the same time, the highly cursorial cheetah would find the increased cover a hindrance to its hunting methods.

In conditions that pushed the members of the large carnivore guild to an increased level of competition for resources, it is our impression that the modern, pantherine cats would have had a real advantage. The lion is able to survive in open habitats largely because of its social structure, but it retains very strong forelimbs and the highly propulsive hindquarters of an ambush hunter. In direct confrontation with a lion, *Homotherium* would have been at a distinct disadvantage because of its relatively weaker forelimbs, its smaller claws and fragile dentition. If forced to live in more forested conditions, the lion can readily operate as an ambush hunter, much like a tiger, a facility exemplified by the continued presence of the lion in all phases of the Middle and Upper Pleistocene of Europe. Lions also readily turn to hunting smaller prey in times of shortage (Viljoen, 1993), something likely to have been more difficult for the more specialised machairodonts. As for the leopard, it can readily exist on relatively small prey, and if faced by the threat of powerful scavengers can retreat with its prize into a tree. Such a feat is likely to have been more difficult for *Megantereon,* for all that it was undoubtedly a strong animal, since long and fragile canine teeth are not well suited to carrying heavy carcasses.

Changes in prey size and composition

The second circumstance was a change in both the taxonomic composition of the ungulate fauna and the size of many of the likely key prey species. Taxonomy alone may of course matter not in the slightest to a predator: two bovid species of broadly similar size, speed and behaviour, or for that matter a cervid and a bovid of equal similarity, might present broadly equivalent targets. But a change involving species with different characteristics and a increase in average sizes would inevitably have some effect. Faster and/or larger ungulates in somewhat more open terrain in Africa would have been rather awkward targets for animals like *Megantereon* and *Dinofelis* that probably needed to get close to their chosen prey and to subdue it by strength before they could begin the process of killing. To expend large amounts of energy on bringing down larger prey, only to be interrupted and driven off by competitors able to locate the kill in more open terrain, would have been a hard situation to cope with for species better adapted to hunting in more closed habitats. The major turnover in the Suidae after 2.0 myr is also likely to have altered the nature of predator-prey systems dramatically, and although the precise nature of such effects remains to be established we currently suspect that the loss of the young of the large bodied species *Notochoerus euilus* and *N. scotti* may have been a serious blow to *Homotherium* predation strategies. It is this very broad nature of the change in the ungulate fauna that may explain the demise of three machairodont taxa in Africa and two in Europe, since each may be assumed to have had its own degree of specialisation and might be expected to have reacted differently to changed circumstances. It is of course possible that a finer resolution will show a real separation between extinction times of *Dinofelis, Megantereon* and *Homotherium* in Africa, although all are still likely to fall within the period immediately after major climatic change and a shift in the structure of the ungulate population.

Of course if we can indeed see a processual link between extinction events in the machairodonts at the Plio-Pleistocene boundary in Africa and the later stages of the Lower Pleistocene in Europe, this raises the obvious and interesting question of what happens elsewhere. In Asia, the time scale of machairodont extinctions appears broadly similar to that of Europe, although *Megantereon* in that region appears to linger longer and to go extinct at broadly the same time as *Homotherium* (Turner, 1987). The interesting point here is that the Middle Pleistocene *Megantereon* from China was a particularly large variety, while *Homotherium,* as mentioned above, was represented by a dwarfed form (Turner and Antón, 1997). Each appears to have been attempting to «cope» with changing conditions by adapting its size, and it is probable that the forest refugia available in the south-eastern parts of Asia during the more arid episodes of the Pleistocene were the key to the longevity of *Megantereon* there. The fact that *Dinofelis* went extinct so much earlier in Eurasia than it did in Africa is also of interest, although beyond the scope of our present treatment.

In the New World, final extinction of machairodont cats occurs on yet another time scale, and a very different pattern emerges. The taxa involved there are *Homotherium* and *Smilodon,* the latter (figs. 1 and 2) a possible descendant of *Megantereon* on that continent, but the New World extinctions are much later in time, falling right at the end of the Pleistocene (Kurtén and Anderson, 1980; Stuart, 1991; Beck, 1996). The New World machairodonts therefore managed to survive all the vicissitudes of the Plio-Pleistocene climatic shifts, together with the faunal changes at the beginning of the Irvingtonian and Rancho La Brean land mammal ages that broadly correlate in time with the 1.7 and 0.9 myr climatic steps (Kurtén and Anderson, 1980).

The New World example appears to fit poorly with the Old World pattern. On the face of things, it is difficult to argue that a step towards worsened climatic conditions in any way similar to those at 2.5, 1.9 or 0.9 occurred at the end of the Pleistocene. In many ways the environmental change at the end of the last glaciation appears to be no different from the other half dozen or so similar transitions now known to characterise the Middle and Upper Pleistocene as seen in figure 2. However, it is also true that the extinctions of the New World machairodonts when they did occur were as part of the most massive extermination of larger mammal taxa, a wholesale reduction in the fauna that removed not only other predator species such as the lion, the American cheetah-like *Miracinonyx* and the dire wolf, *Canis dirus* but also many prey taxa at all levels up to the family (Kurtén and Anderson, 1980, Appendix 2; Stuart, 1991). The level of redundancy in the carnivore guild, in other words, went further and deeper into the guild there than it did at any one time in Africa or Eurasia, where the machairodont extinctions left a still quite diverse array of large predators. But whatever the causal mechanism for the New World event in the Carnivora, the fact that so many prey taxa went was therefore itself the significant point. Indeed, given the extent of the reduction in prey, it may be more surprising that *any* predators managed to survive, perhaps reinforcing the arguments of Owen-Smith (1987) for the significant follow-on effect of the removal of megaherbivores as «keystone» taxa in any ecosystem. Such reductions in the larger taxa are likely to have had most effect on those species, such as the machairodonts, less able to switch to smaller prey.

It also now seems likely that the transition to the present interglacial was in reality quite different from earlier transitions, and may have been marked by considerably more stability. Lister and Sher (1995) have recently summarised some of the relevant data on this point, and stress the potentially disastrous effect of the change from the productive mosaic vegetation of the last glaciation tundra-steppe to the relatively low diversity and reduced productivity of the more zoned Holocene. Earlier interglacials, in contrast, were marked by higher levels of mosaicism, and thus were capable of providing refugia for grazing species of the tundra-steppe. Climatically induced collapse of the late Pleistocene ecosystem of North America is suggested by the results of the FAUNMAP Working Group published recently by Graham *et al.* (1996). It is worth stressing here that carnivores adapted to open environments are particularly likely to need refugia during forest-dominated intervals or other such crises. The case of the cheetah is an excellent example of an animal that appears to have nearly gone extinct in the recent past as a result of a population size «bottleneck», as indicated by the genetic uniformity it exhibits (O'Brien *et al.*, 1983). Such evident uniformity suggests an extreme range reduction, and, in a sense, extinction is nothing but the ultimate consequence of such a reduction.

When we considerer the wider implications of machairodont extinctions, we may ask how the discussion presented here bears on the question posed in the introduction about the likely causal relationship between events in the hominin record and vegetational changes in Africa at around 1.7 myr. We posed that original question in relation to the earliest record of *Homo erectus/ergaster*, but clearly much else was happening in the evolution of the hominins at or about that time as White (1995) has conveniently shown. In that discussion, White rejected any climatic effect on the pattern of hominin evolution just after 2.0 myr on the grounds that there was no dramatic climatic oscillation signal, and also rejected any suggestion that hominins and suids were «entrained to the same determining environments». Yet, as we have now seen, there is now both ample evidence of such a climatic event and a degree of parallel evolutionary change and turnover across a diversity of lineages that include hominins and suids sufficient to suggest a strong link to environmental determinants. So far as apparent conflicts between analyses of bovid dental versus postcranial elements are concerned, with the former pointing to changes between 3.0 and 2.0 myr (Vrba, 1995a, 1995b, Spencer, 1997, Turner, 1995b) and the latter apparently suggesting changes only after 2.0 myr (Kappelman *et al.*, 1997), one possible explanation is that the conflicting evidence actually falls into two categories. Limbbone morphology and proportions will bear more strictly upon the evolutionary history of the taxon, and may be constrained more by phylogenetic inertia while indicating a broadly similar habitat over that history. The form of the dentition itself is clearly genetically determined, and a steady state in dental parameters may also indicate both history and a broad similarity in habitat over time. However, the dentition, as part of the digestive system, is also likely to be forced to respond more rapidly to changing habitats, and we should therefore expect that bovid dentitions would show changes correlated with climatic shifts in advance of changes in the postcranial skeleton. The strongest argument in favour of the interpretation that the dental evidence reflects habitat changes prior to 2.0 myr is the fact that similar patterns are seen across so many diverse clades (Turner and Wood, 1993a, Turner, 1995b, in press c), ruling out the possibility that this is some form of artefact.

Foley (1994, in press), like White, has argued for what he sees as a generally poor correlation between climatic events and the pattern of hominin evolution, while stressing that such correlations as are seen seem to relate most strongly to extinctions, particularly in the period 1.91-1.61 myr. This conclusion is strongly supported by the investigation undertaken by Reed (1997), who stresses the pattern of extinction seen in the paranthropine hominins at this time. Indeed, and in particular to non-hominin specialists such as ourselves, it is at least as interesting to ask why animals such as the robust australopithecine taxa of the genus *Paranthropus* went extinct as it may be to consider the evolution of a particular lineage, the genus *Homo*, largely because we are ourselves its end product.

Conclusions

The extent of the end-Pleistocene New World reductions in the fauna are unparalleled in either Africa or Europe, despite the fact that a significant number of extinctions also occur in Europe at that time (Stuart, 1991). In the context of the present discussion the New World example, where extinctions cut deeper into the felid section of the guild in particular than they did in any single event elsewhere, serves to drive home the point that machairodont extinctions really seem to have required rather extraordinary circumstances to bring them about. The fact that these circumstances came together at different times in different continents merely serves to underline this point.

It is now becoming clear that evolutionary events do indeed happen in the rest of the African biota in concert with and in the aftermath of the vegetational changes around 1.7 myr, vegetational changes that are shown in the palaeosol record in particular and suggested very strongly by the palynological and ocean sediment data. By any objective standards we may therefore say that the event at 1.7 myr was certainly part of a global phenomenon, one marked by changes in the marine core record of oxygen isotope values at 1.9 myr that serve as the kind of background to the interpretation of terrestrial biotic events highlighted by Guiot (1997). The significance of this climatic event is underlined by events in the guild of larger carnivores in Africa, which lost three long-lived machairodont cat genera in its aftermath. The two smaller taxa, *Megantereon* and *Dinofelis*, were probably badly affected by a reduction in vegetational cover with a parallel change in the typical size and anti-predator response of the ungulate fauna, and by an increase in the frequency of encounters with large competitors such as *Homotherium,* lions and hyaena clans. *Homotherium* itself is in turn likely to have been badly hit by reductions in resident prey biomass in successive years of increased dry-season drought, circumstances that would have provoked increased competition between open terrain predators. *Homotherium,* together with the hyaenas *Pachycrocuta* and *Chasmaporthetes,* was the eventual loser, one of the «redundant» taxa as the depth of the guild, crowded by today's standards, reduced.

This pattern, albeit on a different time scale and with a different cast of species, is also seen in Eurasia and the Americas. However, what we can discern of the detail of the patterning in each case, combined with what we see in the modern setting, suggests that such environmental crises are likely to have had most impact on the «redundant» members of guilds that had become comparatively deep and crowded. For the two million years that they coexisted with extant members of the larger predator guild in Africa, a period of time virtually as long as that for which our own genus is recorded, the machairodont cats were evidently far from being redundant. They survived the climatic and habitat changes set in train at around 3.5 myr (fig. 3, point 1) and which by 2.5 myr were having a significant effect upon other components of the African biota, in particular the ungulates that made up the prey population. The extinction of the machairodonts therefore emphatically does not imply that earlier arguments for a climatically-induced turnover in the African fauna at 2.5 myr, or in its more immediate aftermath, are wrong. If the pattern seen in the isotopic signature of ocean sediments is correctly interpreted here, then the step at 1.9 myr (fig. 3, point 3) represented a *further* change in globally significant conditions, and only after that do circumstances appear to have impinged upon the large predator guild in a way that produced redundancies. However, the entire period between 2.5 and 1.5 myr in Africa should be seen as one in which a complex series of biotic changes took place, with the demise of the machairodont cats, together with some members of the Hyaenidae, as simply one of the final stages.

ACKNOWLEDGEMENTS

We thank Laura Bishop for discussions on evolutionary events in the Suidae and Nancy Sikes for discussions of the significance of the palaeosol evidence, but we accept full responsibility for interpretations presented. We also thank Jorge Morales for his useful comments on the manuscript.

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Recibido el 27 de julio de 1998.
Aceptado el 12 de noviembre de 1998.