Mammals as palaeoecological indicators

Peter ANDREWS

Accepted for publication: 20 Oct. 1994

ANDREWS P. 1995. Mammals as palaeoecological indicators. Acta zool. cracov., **38**(1): 59-72.

Abstract. The study of palaeoecology aims to reconstruct past ecologies with a view to understanding evolutionary and biogeographic change. There are many sources of information leading to palaeoecological reconstructions, but in this paper I will be concerned with the use of mammals as palaeoecological indicators. Methods of varying complexity can be used to interpret palaeoecology from the evidence of mammalian faunas. There is no right way or wrong way to do this, only the most appropriate for the particular case, whether it be complex or simple. Most methods rely on the comparative method, i.e. comparisons of past faunas with those living today. Taxonomic comparisons are the most common in palaeontology, with inferences on palaeoecology being made on the basis of relationships of fossil with living taxa. There is growing emphasis also on morphological comparisons, whereby functional morphologies of fossil animals can be interpreted by reference to those of living animals, with the ecological consequences of the morphologies inferred from these. Total species diversity of fossil faunas can also provide limited ecological information, and the diversity may also be analysed by single ecological parameters such as size distributions of faunas. Finally, ecological diversities may be analysed by univariate statistics or combined in multivariate functions to provide more complete information on the structure of whole communities, and these analyses may also be manipulated by rarefaction to simulate particular taphonomic biases in fossil faunas or to attempt to reconstruct past communities that have no living counterpart today.

Key words: Ecosystem, palaeoecology, taxonomy, adaptation, size, multivariate analysis, species diversity, ecological diversity.

Peter ANDREWS, Natural History Museum, Cromwell Road, London SW7 5BD, England.

I. INTRODUCTION

The aim of palaeoecology is to provide the context in which evolutionary changes occur. Evolutionary change over time takes place in a changing world, and it may be asked of any speciation event whether it is the result of changing environment or due to some other factor. Darwinian thought tends to link speciation with environmental change, and although non-adaptive or random events also play a part, I am assuming that this link is valid. The first stages in the analysis of the evolution of a set of organisms entails phylogenetic hypotheses based on character distributions. The identification of character changes through a phylogeny, however, provides no information about the historical processes underlying such changes, only that they have occurred (GANS 1989). Analysis of historical processes requires an understanding of the interactions between fossil organisms and their environment, i.e. their past ecology. The study of palaeoecology is thus complementary to the study of systematics of animal and plant life.

Ecology can be defined as the totality of interactions between organisms and their environment (ODUM 1983). Palaeoecology can therefore be defined as the inferred interactions between past organisms and their then-existing environment. The environment consists of a physical aspect, weather, atmosphere, source rock for soil, etc; and a biological aspect, the interactions between the living species making up the biotic community occupying a given area. The community in relation to environment is denoted as an ecosystem, with community used in the sense of all living populations, both animal and plant, occupying one time and one place. Palaeocommunities are beyond our skill to reconstruct in their entirety, because so many of the populations making up past communities are not preserved in the fossil record as a result of taphonomic bias. What we seek to do in palaeoecological reconstruction, therefore, is to make inferences about past ecosystems by using certain parts of past communities as markers, assuming them to be representative of the communities as a whole. This assumption underlies all attempts at palaeoecological reconstruction, and at present there is no way around it, nor likely to be as far as we can see at present. Methods of analysis vary according to the size and nature of the palaeocommunity available for investigation. Simple methods are easier and quicker to apply, but they inevitably omit greater or less parts of the palaeoecological evidence and may give misleading results; complex methods are difficult and often cumbersome to apply, but since they draw on greater variety of information they are likely to provide deeper insights into past ecologies.

Past ecosystems are interpreted by comparison with present-day ones, but it must be recognized at the outset that past ecosystems do not necessarily have present-day counterparts and the proper understanding of these requires more sophisticated methods of analysis. Simple taxonomic comparisons between fossil animals and their supposed living counterparts may not be sufficient to interpret past ecosystems that differ from those of the present day, and the same may be true also of comparisons of functional morphology and ecological diversity. The question to be asked here is whether or not it is safe to assume comparability in ecosystems, and if there is any reason to believe not, these methods can at best only provide a partial insight into the nature of past ecosystems. To go further it is necessary to introduce simulated variations into present-day communities in order to increase levels of similarity with the fossil communities, and this will be attempted here by rarefaction.

II. TAXONOMIC ANALYSIS

Comparisons of the taxonomic composition of mammalian faunas with those living today are one of the commonest methods of palaeoecological analysis. Such comparisons may be quantified in statistically elegant ways, but they all have the problem that the ecological affinities of extinct species, or even extant species living in earlier times, are essentially unknown, so that ecological inferences drawn from them may be incorrect.

At its simplest level, the taxonomic identity of past organisms is assessed, and by comparison with similar and/or related organisms in present day habitats, inferences are made as to past habitats. This method may be applied to one or a selected number of taxa, as has commonly been the case in the past, or it may be applied to a significant section of the total assemblage. Analysis of pollen (BONNEFILLE 1976; CADMAN & RAYNER 1989; HARRISON & HARRISON 1989) or macro-plant remains (AXELROD 1950; COLLINSON 1983) provide direct evidence on the vegetation present at many fossil sites, but these are rarely preserved at the same levels as mammals, so that degrees of association cannot be tested. It may also be the case that even though the species composition of the flora is known, the structure of the vegetation may still be ambiguous, especially if there is some indication that the pollen comes from many different habitats and is spread over thousands of years.

The taxonomic analysis of the mammalian faunas remains the most widespread form of palaeoecological analysis. AVERY (1987, 1990, 1991) has applied taxonomic analysis to good effect on small mammal associations from Pleistocene and Holocene sites in South Africa, and she has related differences in taxonomic composition of successive faunas to differences in vegetation and thence to differences in climate. AVERY has not, however, investigated the taphonomy of her cave assemblages, beyond the statement that they were probably derived from the prey assemblages of an unknown predator, and the fact that different predators have different hunting strategies, resulting in different prey assemblages, must raise questions about the validity of her palaeoecologic and/or climatic inferences. I have also recently used taxonomic analysis to show change through time in an English middle Pleistocene cave sequence (ANDREWS 1990a), and by taking account of differential taphonomic effects on the fauna I was able to correlate ecological and climatic change with changes in taxonomic composition in the mammalian faunas. At the bottom of the sequence was a warm temperate fauna; and this was succeeded by a fauna which was taphonomically distinct but which had similar ecological indications. Above these were two levels with cold faunas, while above these was a return to warm temperate conditions in two more levels. At the top of the sequence was a return to cold conditions again, even colder than the previous cold stage. The duration of these climatic fluctuations could not be determined, because there was no evidence available on sedimentation rate, but systematic studies on the small mammals show that the whole sequence of warm-coldwarm-very cold fits within the end stages of the Cromerian interglacial (CURRANT in press).

III. MORPHOLOGIC ANALYSIS

Characters in living mammals may be observed to serve particular functions, and when the same characters are present in fossil mammals it may be assumed that the same function was present in the fossils. An index was devised by VRBA (1980) comparing the proportions of bovid tribes in fossil faunas. At first sight this might appear to be a taxonomic scheme, but in fact the choice of tribes shows it to be morphologic. Alcelaphines and antelopines are compared with tragelaphines and reduncines, the first two tribes containing almost entirely grazing species with hypsodont teeth, the second two containing mainly browsing species with brachydont teeth. The index of one to the other separates grazers from browsers, and this indicates vegetation differences between grassland and woodland with possible climatic inferences as well. Up to a point this index works very well, for there is a major dichotomy between grazing and browsing bovids in Africa today, but since some of the bovid species are migratory, and in the course of their annual migration they pass through, and often die in, many different ecosystems, it is possible for misleading results to ensue.

Another example of morphologic-based analyses is based on the study of postcranial morphology. KAPPELMAN (1991) has studied features of the bovid hind limb and has demonstrated a functional linkage between several femoral characters and habitat type. For example, cursorial species that live in open habitats have a laterally expanded femoral head adaptive for running fast, whereas forest bovids have a more spherical head giving greater ranges of movement for leaping. VAN VALKENBURGH (1987) has distinguished between locomotor function in climbing, digging and running (cursorial) carnivores, and she has found that certain osteological indices are good predictors of locomotor behaviour in living carnivores. For example, arboreal carnivores have more strongly curved claws, shorter metatarsals and longer proximal phalanges than do terrestrial species.

A third type of morphologic-based analysis is based on dietary differences seen in the teeth. There are many examples of this. JANIS has shown that the degree of hypsodonty of the molars of bovids is strongly related to habitat (JANIS 1988). Ungulates feeding at ground level in open habitats are significantly more hypsodont (regardless of food preference) than ungulates living in closed habitats. Crown complexity has also been shown to be equally important in herbivores (SCHMIDT-KITTLER 1984; JANIS 1988; JANIS & FORTELIUS 1988). Thick enamel may be related to food that is abrasive, but brittle rather than tough so that blades are not needed for its comminution (KAY 1975; JANIS & FORTELIUS 1988). Bilophodonty is necessary for very tough foods (JANIS & FORTELIUS 1988).

Quantitative analyses of tooth wear have also proved valuable in reconstructing diets in fossil mammals. Early work measured gross differences between grazers and browsers (WALKER et al. 1978), but increasingly refined microscopy has led to greater distinctions being made, in particular relating to frugivory and the differences between robust and gracile australopithecines (GORDON 1982; GRINE 1986; KAY 1985; TEAFORD 1988; KAY & GRINE 1988). In the future we may have whole faunas with microwear analysed for all the species, and when that is done the dietary spectrum obtained will provide more precise palaeoecological reconstructions that we can achieve at present.

Dietary distinctions may also be made with non-dental evidence. The structure of the stomach is highly diagnostic of mammalian groups such as the ruminants and the cercopithecoid monkeys, in which the stomach is structually adapted to utilise distinct types of food (HOFMAN 1968). Unfortunately, such evidence is not generally available from the fossil record. On the other hand, the shape of the premaxilla in large herbivores has been shown to be related to diet (SOLOUNIAS et al. 1988). Browsing species have

narrow, pointed premaxillae and therefore narrow mouths, which enable them to select individual leaves when feeding, while the square premaxillae of grazers are more suited to the mowing operation necessary for the ingestion of large quantities of low quality grass. SOLOUNIAS et al. (1988) have shown that a fossil giraffe was a grazing species rather than a browser, as most are today.

One qualification that must be made of function-based analyses is that pre- or post-adaptation may change the function without changing the morphology. For example, the thick enamel found on all species of *Sivapithecus* (MARTIN 1985) was considered to indicate a diet of tough but brittle food (KAY 1981), but when the microwear was examined (TEAFORD & WALKER 1984) a diet of soft objects was indicated. The specimens of *Sivapithecus* examined came from late Miocene deposits, but further work on the microwear of a middle Miocene thick enamelled hominoid, *Griphopithecus alpani* from Pasalar (ANDREWS & MARTIN 1991; KING 1992) showed that it had the expected pattern of hard object microwear. It is probable that there was a dietary change in the course of the evolution of *Sivapithecus* but without any reduction in enamel thickness. In this event, thick enamel was a heritage character in *Sivapithecus* giving a misleading adaptive message.

IV. SPECIES DIVERSITY

The taxonomic and morphologic analyses just described are nearly always restricted to one part of the mammalian fauna. This may be because evidence is limited to those parts of the faunas, or because the worker's field of study is so limited. The methods that follow, however, use the entire mammalian fauna, and the simplest way of analysis is to count the species. Harsh environments have lower numbers of species than more equable and complex environments, but the relationship between climate, vegetation and mammalian species diversity is not a simple one, and a simple count of species numbers is not a reliable measure of ecology. When interpreting palaeoecology, there are the additional taphonomic biases that may increase diversity as a result of faunal mixing or time-averaging, or decrease it as a result of species loss.

Species diversity has two components: species richness, or heterogeneity, and species abundance, or equitability. The former can be considered simply by the numbers of species in different faunas or habitats, or by calculating diversity indices which take into account sample size. The latter can be estimated by plotting frequency distributions, but it can be more productive to test goodness of fit to different distribution models. Species richness is measured by the number of species in a given area, known as \pm -diversity. For example, the Miocene fauna from Pasalar has a total of 52 species, and the taphonomy of the site indicates that the great majority of the fossils were derived from a single source over a restricted period of time (ANDREWS 1995). Some species were found to have been selected against (ANDREWS & ERSOY 1990), so that the number 52 is actually an underestimate of the original number living on the ground in the Miocene. This number is greater than is found today in any temperate ecosystem or in open grassland under any climatic regime, and it can therefore be taken to indicate the presence of relatively equable conditions at Pasalar, subtropical to tropical climate with some form of woodland.

Palaeoecological analyses have often been restricted to species distributions (FLEMING 1973; NEL 1975; ANDREWS et al. 1979), but there is no reason why they cannot be applied to relative abundances of species. The difficulty with this is that data are often not available for fossil faunas, or, if they are, they are unreliable because of taphonomic modifications. Prey selection by predators, for example, or size selection by transport may modify the species composition of fossil assemblages to varying degrees, but the impact of these taphonomic processes on species numbers is of far greater extent. Species abundance distributions summarize all the information in a community, either in a single number (number of species) or index (diversity index), or in graphical form such as a rank abundance plot or frequency distribution. Diversity indices generally reflect either the dominance or evenness of faunas, i.e. the extent to which they are dominated by one or a few species. Distributions of species abundances have been calculated for the Pasalar fauna (Fig. 1). This shows the distribution of abundance classes along the horizontal axis with the numbers of species in each class on the vertical axis. Compared with this is the expected line computed on the basis of a log-series distribution (MAGURRAN 1988), and the two lines tested for difference by chi-squared show no significant difference between them (ANDREWS in preparation). Log-series distributions characterize environmental



Fig. 1. Numbers of species of the Pasalar mammal fauna are plotted against species abundances on a log2 scale ranging from the least abundant species on the left to the most abundant on the right. The rank abundances of the Pasalar data (solid bars) approximate to a log series distribution (MAGURRAN, 1988), and this has been tested by calculating goodness of fit to the expected distribution (open bars), using chi-squared. The log series index is given by 6=N(1-x)/x where N=total number of individuals and x is estimated from the iterative solution of S/N=(1-x)/x[-ln(1-x)] where S=total number of species the expected values from the model are given by $\alpha x, \alpha x^2/2, \alpha x^3/3...\alpha x^n/n$, and these are compared with the actual values of the Pasalar fauna grouped into 8 classes, giving a value for chi-squared of 5.83.

conditions with some extreme element either of climate or ecology, and this may also be inferred for the Pasalar palaeoecology, perhaps strong seasonality of climate.

Another aspect to species diversity that can be briefly mentioned is the turnover of species across space and time (PIMM & GITTLEMAN 1992). This is difficult to measure, but it may be of considerable importance in fossil faunas which accumulate over a period of time from a number of disparate sources: high turnover, which characterizes tropical wooded regimes, could theoretically lead to disproportionately high diversity levels for time-averaged faunas. Similarly, environmental heterogeneity would also produce high diversity, with possibly misleading conclusions if undetected. Levels of ó-diversity are also directly related to area (it has been predicted that diversity scales to (area)²⁵ (PRESTON 1962)). In his recent analysis of South American mammalian diversity patterns, MARES (1992) compared diversity levels in different habitat types. Tropical lowland forest actually contained fewer species than in dryland habitat types (434 species against 509), but in fact these figures indicate similar diversity levels since the areal extent of the dryland habitats is almost double that of lowland forest.

Estimates of species richness are also affected by sampling problems. It is a well known phenomenon that when taking samples of living biota, the larger the sample the higher will be the number of species present. This is equally true of fossils and of living biota. The most straightforward diversity indices are therefore based on some function of S/N, where S is the number of species and N is the sample size (see MAGURRAN 1988 and references therein).

V. SIZE DIVERSITY

Palaeoecological reconstructions of mammalian faunas have been based on cenograms (rank order distributions) by LEGENDRE (1986, 1987). Species are plotted in rank order, from small to large, and the steepness of the line and the presence of breaks in the continuum are taken to indicate different habitats. No attempt has been made to attribute these two factors to any ecological theory, although the former is clearly related to the species diversity (heterogeneity) of the fauna. As such, it is no more informative than the actual species number, which as has been noted above has limited ecological significance. The presence of the breaks in the size continuum has no immediately apparent relationship to habitat.

Size has also been the basis for multivariate analyses by DE BONIS et al. (1992). Size is one of the most easily measured ecologic variables in mammals, provided reliable regressions between tooth and/or postcranial size and body weight are available, but it is the one that I have found to have the least discriminating power. For instance, computing the distributions of three ecological variables for a sample of 23 modern African mammalian faunas using contingency tables (ANDREWS et al. 1979), highly significant differences were found for the dietary and spatial parameters (p=0.001) but no significant differences were found for the size analysis (P=0.1) between mammalian faunas from habitats as disparate as tropical forest and open grassland. Even the taxonomic analysis had a higher significance level than the size analysis (p=0.05). Thus, while size is easy to estimate for fossil species, it is the least informative ecological category and I am sceptical of conclusions based on size alone.

VI. TAXONOMIC DIVERSITY

Taxonomic distributions of entire mammalian faunas have been analysed by faunal resemblance indices (VAN COUVERING 1980) and at Order level (ANDREWS et al. 1979), with statistically significant differences between habitats. Weighted averages have also been used, as in the Habitat Spectra of VAN COUVERING (1980) and the Taxonomic Habitat Index of ANDREWS (1990a), but since these are based on degree of relationship of fossil species to living species of known ecology, they suffer from the same problems discussed above.

VII. ECOLOGICAL DIVERSITY

Distributions of species diversities within ecological adaptations have been used as an alternative to taxonomic-based schemes (ANDREWS et al. 1979). Where fossil faunas are complete enough, it is possible to base inferences about palaeoecology on the diversity and structure of the whole mammalian community, not just on part. The mammalian communities recognized in this way are described not by their taxonomic content but by their levels of diversity and their ecological structure or ecological diversity. There are three aspects of mammalian populations which can be identified in fossil mammals and which relate to their ecological niche: their body size, the space they occupy, and their trophic level. The first may be estimated by regressions of tooth or limb size on body weights of known individuals (GINGERICH 1977; GINGERICH et al. 1982). The second is estimated on the basis of the limb proportions and function, which readily distinguish between fossorial, terrestrial, arboreal and aerial adaptations. The third is based on detailed anatomy of teeth and jaws, including data on tooth wear where available, and this enables broad divisions to be recognized between insectivorous, frugivorous and herbivorous adaptations. The spatial niche and trophic niche make up two of the three aspects of the niche identified by ODUM (1983), and body size is an important aspect of the third, the multi-dimensional niche, so that for any one mammal species, the combination of these three sources of information goes a long way towards distinguishing the ecological niche which it occupies and to which it may be more or less adapted. The combination of these data for all the mammals in a fossil mammalian community can therefore be taken to indicate the range of ecological niches occupied by that community, and hence to define the structure of the community.

There are several levels on which community ecology can be measured. Simple univariate or bivariate statistics may suffice for certain problems, but as questions become more complex, the data require greater statistical power to answer them (GAUCH 1989; SOUTHWOOD 1988). Community data are complex in themselves, but much of the information contained in the data consists of noise or redundant information, and the problem becomes one of separating this off from the usable information. This may be attempted using multivariate analysis, but it is then inevitably found that answers from multivariate methods require even more work to interpret, raising more complex questions in the process and leading to ever more refined methods of analysis.

66

The basis for my earlier work was a mixture of univariate and multivariate statistical methods (ANDREWS et al. 1979). For the most part, the data were presented in the form of univariate histograms depicting the proportional distribution of the species making up a fauna into the taxonomic, size, locomotor and dietary categories mentioned above. For a limited number of community types, representing a limited number of habitats, this is a powerful method, for it was found that communities from similar habitats did indeed have similar community structure (or ecological diversity), and communities from different habitats were conspicuously different. This was confirmed by highly significant (P=0.01) differences between different communities for two of the ecological parameters (see above).

The early work was concentrated on tropical African communities, but I have been working on extending the analyses to include a wider range of communities. The data base now extends to 83 localities with a world-wide distribution (excluding Australia), and the preliminary results of a principal coordinates analysis of these data are shown in Fig. 2. The distributions of individual communities are summarized by geographic regions and



Fig. 2. Principal Coordinates I and II for a series of 83 present-day mammal communities compared with fossil faunas from Miocene deposits at Pasalar, Turkey (PA) and Sansan, France (SA). The present-day communities have been grouped by geographic region and ecosystem since it has been found that these are the major factors by which the mammal communities group together. As.TRF = tropical rain forest from southeast Asia; Am.TRF = tropical rain forest from central America; Af.TRF = tropical rain forest from Africa; Af.DF = tropical deciduous (seasonal) forest from Africa; As.MF = subtropical monsoon (seasonal) forest from Asia; Eu.DF = deciduous mesophytic forest from temperate latitudes of Europe; Eu.TS = tundra and steppe from north-central Eurasia; EAf.SAV = woodland to grassland ecosystems in East Africa; SAf.SAV = woodland to grassland ecosystems in South Africa.

ecologic zones, with two fossil sites shown for comparison. There are two trends evident in these results: from bottom left to top right there is a trend from communities living in wet tropical forests in Asia and America to those living in dry tropical woodland savanna habitats in Africa; and from top left to bottom right there is a weaker trend from tropical to temperate climates. The two fossil faunas group with the subtropical forests and the impoverished African forests in the middle of the figure, so that as a result their position with regard to the two trends is ambiguous. This highlights a general problem with this form of analysis: it is difficult to identify the factors producing different combinations of communities and therefore to test their significance. Correspondence analysis has failed to produce any more definitive answer.

VIII. RAREFACTION

There are two problems common to all interpretations of palaeoecology. One is taphonomic bias which may so alter the composition of fossil faunas that they bear little or no relationship to the communities from which they originated. Taphonomic bias is omnipresent in fossil faunas, and the bias is often unknown in the absence of adequate collecting techniques. The second problem concerns the existence in the past of ecosystems different from any today with which they can be compared (VAN COUVERING 1980; ANDREWS 1992). Since we necessarily make use of the present in order to interpret the past, it follows that we need some method of identifying cases where ecosystems have evolved and straightforward comparisons cannot be made. The presence of unusual taxonomic or morphologic combinations of species may indicate some cases, although taphonomic bias would first have to be eliminated as a cause, but since these methods only provide at best a partial picture of past ecosystems it must remain uncertain whether the combinations observed are representative of the ecosystem as a whole or are artefacts of the fossil record.

Present-day mammal communities all have certain attributes in common. Most of them have very similar size spectra, for instance, and any departure from this common pattern quickly becomes apparent. The size distribution of the Pasalar fauna, for example, shows a pattern distinct from any living community, with lower than expected numbers of very small mammal species (<100g). This could be because the Pasalar ecology was in some way different from any known today, but the high energy conditions peculiar to the Pasalar sediments suggest that the under-representation of the smallest species is taphonomic in origin. Distributions of locomotion and diet also have certain features in common in all modern mammal communities, and again departures from these can be identified, for example increased representation of herbivorous mammal species without corresponding increase in carnivore species. An example is shown here of percentage representation of carnivorous species compared with percentages of herbivorous grazing species (Fig. 3) for a world-wide series of 83 modern mammalian communities. A positive correlation is evident, with proportions of carnivorous species increasing with proportions of grazers, and with highest proportions in open ecosystems (tropical grassland and tundra) and lowest in tropical forests. Two fossil faunas are included in this analysis, from middle Miocene deposits of Sansan and Pasalar. The latter fits the predicted ecological reconstruction, which is that of subtropical seasonal forest (ANDREWS 1990b), and it would appear



Fig. 3. Distribution of percentage numbers of carnivorous species plotted against percentage numbers of grazing herbivorous species. The same series of 83 present-day mammal communities as shown in Fig. 2 are compared with fossil faunas from Miocene deposits at Pasalar, Turkey and Sansan, France. The present-day communities have been grouped in the same way as in Fig. 2: As.TRF = tropical rain forest from southeast Asia; Am.TRF = tropical rain forest from central America; Af.TRF = tropical rain forest from Africa; Af.DF = tropical deciduous (seasonal) forest from Africa; As.MF = subtropical monsoon (seasonal) forest from Asia; Eu.DF = deciduous mesophytic forest from temperate latitudes of Europe; Eu.TS = tundra and steppe from north-central Eurasia; EAf.SAV = woodland to grassland ecosystems in South Africa.

therefore that in this respect at least the Pasalar community is not distinguished from present-day ecosystems. The Sansan fauna, on the other hand, has higher than predicted proportions of carnivorous species, and lower proportions of grazers, so that it is grouped with the east Asian tropical forest communities from Burma to China. This may reflect a genuine similarity in community structure with these present-day communities or it may indicate a subtle change in community structure between Sansan and the present time.

It is possible to manipulate multivariate data to test possible variations in community structure, resulting either from taphonomic alteration or from genuine differences between past and present ecosystems. Euclidean distances have been used to construct comparative patterns of recent mammalian communities that have been altered in a variety of ways, e.g. progressive loss of small species, of arboreal species, of carnivorous species, and so on. By the process of rarefaction, recent faunas can be reduced in numbers of species to the size of fossil faunas. Comparisons can then be made between fossil and reduced recent faunas to obtain closest matches, either visually or statistically, producing either taphonomic conclusions about the fauna, more precise evidence on the palaeoecology of the fauna, or both. Fossil faunas that appear to be from mixed sources, or to represent habitats more complex than any present today, or different in some aspects of their community ecology, may also be simulated by combinations of living faunas.

Fig. 4 shows one of a series of simulations for one present-day mammal community compared with the analysis of the Pasalar fauna. This is one of 800 analyses based on taxon-free analysis of ecological data for 20 modern faunas from across the world. The modern community is from monsoon forests in central India at Kanha, and the Euclidean distances of this fauna from the distributions of 83 modern faunas are shown in figure 4. In this analysis, the Kanha mammal community has been altered by the elimination of 45% of the smallest species, so that only 55% of the species have been used in this analysis. The pattern of distances obtained for this size-biased sample from Kanha is shown compared with the distances of the Pasalar fossil fauna from the same data set of 83 modern communities, and the two patterns are closely similar. It should be noted that for neither community can its probable ecological structure be determined on the basis of Euclidean distances alone, for the 45% size-bias in the Kanha fauna has obscured its ecological structure, and taphonomic bias has done likewise for the Pasalar fauna. In both cases there are three sets of modern communities closest to the origin, Asian tropical rain forest, Asian subtropical monsoon forest and European temperate woodland. What is significant here is the similarities in distribution patterns between the two faunas (and the corresponding differences in pattern from all other modern communities analysed the same way -ANDREWS, in preparation). This leads to the two-fold conclusion that the Pasalar mammal community was probably derived from subtropical monsoonal forest similar to that seen



Fig. 4. A. Rarefaction analysis of a modern mammal community from subtropical monsoon (seasonal) forest from north-central India at Kanha. This is one of 40 analyses performed for this one community, and it shows the effect of reducing the species diversity to 55% of its original value (Kanha mammal community N = XX) by selectively eliminating small size mammals in the following proportions: dg – 50%, 100-500g – 75%, 500-1000g – 95%, and all other sizes 99%. This reduced community is then compared with 83 present-day mammal communities based on Euclidean distances calculated by proportions (dp) and absolute differences (da). B. Analysis of the Pasalar Miocene fauna (N = 52) performed in the same way as above, using the same method and comparative sample. today at Kanha, and that the community is biased through loss of some small species, a conclusion that had already been reached by analysis of taphonomy (ANDREWS & ERSOY 1990) and by univariate analysis of the size distribution of the Pasalar fauna (ANDREWS 1990b).

A c k n o w l e d g e m e n t s . I am very grateful to Dr Jorge AGUSTÍ for inviting me to attend the workshop on the "Influence of Climate on faunal evolution in the Quaternary" at Sant Feliu des Guixols. I am also grateful the the European Science Foundation for financial support, and to Libby ANDREWS, Ann FORSTEN and Lars WERDELIN for reading and commenting on the text of this paper.

REFERENCES

ANDREWS P. 1990a. Owls, caves and fossils. Nat. Hist. Mus. publ., London, VIII + 231 pp.

- ANDREWS P. 1990b. Palaeoecology of the Miocene fauna from Pasalar, Turkey. Journal of Human Evolution, **19**: 569-582.
- ANDREWS P. 1992. Community structure in forest habitats. Journal of Human Evolution, 22: 423-438.

ANDREWS P. 1995. Time resolution of the Pasalar Miocene fauna. Journal of Human Evolution, 28.

- ANDREWS P., ERSOY A. 1990. Taphonomy of the Miocene bone accumulations at Pasalar, Turkey. Journal of Human Evolution, **19**: 379-396.
- ANDREWS P., LORD J. & EVANS E. M. N. 1979. Patterns of ecological diversity in fossil and modern mammalian faunas. Biological Journal of the Linnean Society, **11**: 177-205.
- ANDREWS P., MARTIN L. 1991. Hominoid dietary evolution. Philosoiphcal Transactions of the Royal Society of London, **334**: 199-209.
- AVERY D. M. 1987. Micromammalian evidence for natural vegetation and the introduction of farming during the Holocene in the Magaliesberg, Transvaal. South African Journal of Science, **83**: 221-225.
- AVERY D. M. 1990. Holocene climatic change in Southern Africa: the contribution of micromammals to its study. South African Journal of Science, **86**: 407-412.
- AVERY D. M. 1991. Micromammals, owls and vegetation change in the Eastern Cape Midlands, south Africa, during the last millennium. Journal of Arid Environments, **20**: 357-369.
- AXELROD D. I. 1950. Studies in late Tertiary paleobotany. Carnegie Institute Publications, Washington, 590.
- DE BONIS L., BOUVRAIN G., GERAADS D., KOUFOS G. 1992. Diversity and paleoecology of Greek late Miocene mammalian faunas. Palaeogeography Palaeoclimatology Palaeoecology, **91**: 99-121.
- BONNEFILLE R. 1976. Palaeoenvironmental implications of a pollen assemblage from the Koobi Fora Formation. Nature, **264**: 403-407.
- CADMAN A., RAYNER R. J. 1989. Climatic change and the appearance of *Australopithecus africanus* in the Makapansgat sediments. Journal of Human Evolution, **18**: 107-113.
- COLLINSON M. E. 1983. Fossil Plants of the London Clay. Palaeontological Association Field Guide, London.
- CURRANT A. in press. The small mammals from Westbury-sub-Mendip. In: P. ANDREWS C. STRINGER A. CURRANT and J. COOK, The Middle Pleistocene site at Westbury-sub-Mendip, Somerset. Natural History Museum Publications.
- FLEMING T. H. 1973. Numbers of mammal species in north and central American forest communities. Ecology, 54: 555-563.
- GANS C. 1989. Stages in the origin of vetebrates: analysis by means of scenarios. Biological Review, 64: 221-268.
- GAUCH H. G. 1989. Multivariate Analysis in Community Ecology. Cambridge: Cambridge University Press.
- GINGERICH P. D. 1977. Correlation of tooth size and body size in living hominoid primates, with a note on relative brain size in *Aegyptopithecus* and *Proconsul*. American Journal of Physical Anthropology, **47**: 395-398.
- GINGERICH P. D., SMITH B. H., ROSENBERG K. 1982. Allometric scaling in the dentition of Primates and prediction of body weight from tooth size in fossils. American Journal of Physical Anthropology, **58**: 81-100.
- GORDON K. D. 1982. A study of microwear on chimpanzee molars: implications for dental microwear analysis. American Journal of Physical Anthropology, **59**: 19-15.

- GRINE F. E. 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. Journal of Human Evolution, **15**: 783-822.
- HARRISON T. S., HARRISON T. 1989. Palynology of the late Miocene Oreopithecus-bearing lignite from Baccinello, Italy. Palaeogeography, Palaeoclimatology, Palaeoecology, **76**: 45-65.
- HOFMAN R. R. 1968. Comparison of the rumen and omasum structure in East African game ruminants in relation to their feeding habits. Symposium of the Zoological Society of London, 21: 179-194.
- JANIS C. M. 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference. In: D. E. RUSSELL, J. P. SANTORO and D. SIGOGNEAU-RUSSELL (Eds) – Teeth Revisited. Mémoires du Museum national d'Histoire Naturelle, Paris, 53: 367-387.
- JANIS C. M., FORTELIUS M. 1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. Biological Reviews, **63**: 197-230.
- KAPPELMAN J. 1991. The environment of *Kenyapithecus* at Fort Ternan. Journal of Human Evolution, **20**: 95-129.
- KAY R. F. 1975. The functional adaptations of primate molar teeth. American Journal of Physical Anthropology, **43**: 195-216.
- KAY R. F. 1981. The nut-crackers a new theory of the adaptations of the Ramapithecinae. American Journal of Physical Anthropology, 55: 141-151.
- KAY R. F. 1985. Dental evidence for the diet of australopithecines. Annual Review of Anthropology, 14: 315-341.
- KAY R. F., GRINE F. E. 1989. Tooth morphology, wear and diet in *Australopithecus* and *Paranthropus* from southern Africa. In F. E. GRINE (Ed.) The Evolutionary History of the "Robust" Australopithecines. New York, Aldine de Gruyter, pp 427-447.
- KING T. 1992. Microwear Analysis of Fossil Hominoid Teeth from Pasalar, Turkey. Unpublished thesis, University of London.
- LEGENDRE S. 1986. Analysis of mammalian communities from the late Eocene and Oligocene of southern France. Palaeovertebrata, 16: 191-212.
- LEGENDRE S. 1987. Concordance entre paléontologie continentale et les évènements paléoceanographiques. Comptes Rendus de l'Academie des Sciences, Paris, **304**: 45-50.
- MAGURRAN A. E. 1988. Ecological Diversity and its Measurement. London, Croom Helm.
- MARES M. A. 1992. Neotropical mammals and the myth of Amazonian biodiversity. Science, 255: 976-979.
- MARTIN L. 1985. Significance of enamel thickness in hominoid evolution. Nature, 314: 260-263.
- NEL J. A. J. 1975. Species density and ecological diversity of South African mammal communities. South African Journal of Science, **71**: 168-170.
- ODUM E. P. 1983. Basic Ecology. Philadelphia, W. B. Saunders.
- PIMM S. L., GITTLEMAN J. L. 1992. Biological diversity: where is it? Science, 255: 940.
- PRESTON F. W. 1962. The canonical distribution of commonness and rarity. Ecology, 43: 185-215 and 410-432.
- SCHMIDT-KITTLER N. 1984. Pattern analysis of occlusal surfaces in hypsodont herbivores and its bearing on morpho-functional studies. Proc. Kon. Ned. Akad., 87: 543-480.
- SOLOUNIAS N., TEAFORD M., WALKER A. 1988. Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid. Paleobiology, 14: 287-300.
- SOUTHWOOD T. R. E. 1988. The concept and nature of the community. In: Organization of Communities, Past and Present. Blackwell, Oxford.
- TEAFORD M. F. 1988. Scanning electron microscope diagnosis of wear patterns versus artifacts on fossil teeth. Scanning Microscopy, 2: 1167-1175.
- TEAFORD M. F., WALKER A. C. 1984. Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*. American Journal of Physical Anthropology, 64: 191-200.
- VAN COUVERING J. A. H. 1980. Community Evolution in East Africa during the late Cenozoic. In: A. K. BEHRENSMEYER and A. HILL (Eds) Fossils in the Making, Chicago, University of Chicago Press, pp. 247-271.
- VAN VALKENBURGH B. 1987. Skeletal indicators of locomotor behaviour in living and extinct carnivores. Journal of Vertebrate Palaeontology, 7: 162-182.
- VRBA E. S. 1980. The significance of bovid remiains as indicators of environment and predation patterns. In: A. K. BEHRENSMEYER and A. HILL (Eds) – Fossils in the Making, Chicago, University of Chicago Press, pp. 247-271.
- WALKER A. C., HOECK H. N. & PEREZ L. 1978. Microwear of mammalian teeth as an indicator of diet. Science, 201: 908-910.