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Pliocene large-mammal assemblages from northern Chad: sampling and ecological structure

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Abstract Numerous Pliocene large-mammal assemblages have been discovered in Chad over the last decade. They offer a unique opportunity to understand the settings in which important chapters of Hominid evolution took place in Central Africa. However, it is crucial to first investigate both sampling and taxonomic homogeneity for these Chadian assemblages because they occur over large sectors in a sandy desert that offers virtually no stratigraphic section. Using cluster analysis and ordination techniques, we show that the three Pliocene sectors from Chad are homogeneous and adequate sampling units. Previous stable isotope analyses on these assemblages have indicated that the environment became richer in C₄ plants between approximately 5.3 and 3.5–3 Ma. To test whether this environmental change has affected the structure of palaeo-communities, we assigned body mass, trophic and locomotor eco-variables to mammal species from the three sectors. Statistical analysis shows that the overall ecological structure of the assemblages is not linked with the opening of the plant cover, and eco-variables show no temporal trend from the oldest sector to the youngest. For example, there is no significant change in the relative diversity of grazing and browsing taxa, although mixed feeders are less diversified in the youngest sector than in the preceding one. This pattern apparently does not result from

potential biases such as methodological artefacts or taphonomic imprint. Instead, it seems that local heterogeneous environmental factors have played a major role in shaping the ecological spectrum of Chadian mammal palaeo-communities during the Pliocene.

Introduction

In the last decade, fieldwork conducted by the Mission Paléoanthropologique Franco-Tchadienne (MPFT) in the Djurab Desert, northern Chad, has led to the discovery of several hundred Miocene–Pliocene vertebrate sites [4–7]. Our purpose here is to study the Pliocene sites that are distributed within three biochronologically dated fossiliferous sectors: Kossom Bougoudi (KB, ~5.3 Ma, i.e. close to the Miocene–Pliocene boundary), Kollé (KL, 5–4 Ma) and Koro-Toro (KT, 3.5–3.0 Ma). The main stratigraphic and taphonomic features of the sectors are given in Brunet and MPFT [3] and Düringer et al. [10]. The KT sector is particularly significant because it has yielded the first australopithecine found west of the Rift Valley [4].

The location, age and richness of these Pliocene assemblages offer a unique opportunity to investigate the settings in which important chapters of Hominid evolution took place. However, several issues must be addressed before the Chadian assemblages can be compared with other African faunas: what is the quality of the sampling? What can be considered as adequate sampling units for palaeo-ecological investigations? Do these assemblages show any significant ecological change through time?

These questions are particularly relevant in the case of the Chadian fossils for several reasons. First, the geological context of the localities in the Djurab erg is markedly different from that in most contemporaneous African sites: stratigraphic sections are rare and seldom thicker than a few metres, geomorphological landmarks are scarce, and site accessibility varies substantially over a single year due to permanent dune movements and intense deflation.

Second, the fossil sectors were defined on two main criteria: geographic location and presence of biochronolog-

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ically informative taxa. However, within a given sector, such taxa or association of taxa are not found at all sites. Also, Geraads et al. [11] noticed that the distribution of bovids could be very heterogeneous among KT sites, suggestive of a mosaic landscape.

Third, stable isotope analyses indicated that the environment became richer in C_4 plants from KB to KT, implying an opening of the plant cover in Chad during the Pliocene [17]. Yet, the response of mammal communities to these environmental changes remains to be explored.

We analysed the mammalian assemblages from the Pliocene sectors KB, KL and KT to test for sampling adequacy, to define adequate sampling units and to investigate possible changes in community structure.

Materials and methods

Here, we use the terms “site” and “locality” interchangeably, and their denomination represent the name of their fossiliferous sector and their order of discovery (e.g. KL09 was the ninth site identified in the Kollé sector). Fossils from a single site are the result of one or several years of collecting that we refer to as collections. Note that each collection represents several field missions (typically three) over a single year. Small mammals (<1,000 g) were removed from the data set because of their uneven preservation and sampling. The full data set is based on updated faunal lists that concern 64 taxa distributed over 18 localities (Electronic Supplementary Material, S1).

Faunal distinction across localities was explored using the unweighted pair group method with arithmetic averages (UPGMA) hierarchical agglomerative cluster algorithm on matrices containing faunal similarity indices based either on abundance data (Spearman rho) or on presence/absence data (Jaccard, Simpson and Raup–Crick indices). Only sites with at least ten specimens were retained for this analysis. The results were compared with those of an ordination method. For the latter, we selected the non-metric multidimensional scaling (NMDS) technique applied to a Spearman rho similarity matrix. Methodological details can be found in Raup and Crick [15] and Legendre and Legendre [14]. Computations were performed with *PAST* 1.30 [12]. Abundance data correspond to the number

of specimens identified at the lowest possible taxonomic level, and specimens that unequivocally belong to a single individual are counted only once.

Assemblages from the three fossiliferous sectors were also compared after assigning taxonomic, trophic, locomotor and body mass attributes to their mammalian members based on anatomy, geochemistry and tooth-wear patterns (S2, S3). Eco-variable categories were taken from Kovarovic et al. [13]. Analyses were made both on all assemblages and on those containing at least seven taxa. To test whether assemblages differ significantly in their relative ecological structure, we used the analysis of similarity (ANOSIM) technique based on rank-ordered Bray–Curtis similarities [9], as well as cluster confidence intervals [8] computed using *SpeciesCI* 3.0 [2]. These two techniques contrast the variation between clusters with variation within clusters due to sampling error and distributional patchiness.

Results

We first explored the quality of sampling by computing the proportion of taxa that is new in the successive collections of each site. Only sites with at least three collections were analysed. The taxa composing the core of the assemblages are captured after the third collection in most localities (Fig. 1). Clearly, the discovery of rare taxa is still expected in later collections. In KT for example, the “rebounds” of two curves after they reach 0% are due to the recovery of a single taxon (known from a single specimen), and for which specimens identified at the family level were already found in preceding collections.

Cluster analyses reveal that assemblages from a same sector group together, and that KB and KL assemblages are closer relative to those of KT (Fig. 2a). These observations agree with a sectorial partition, and they remain virtually unchanged even when data matrices are analysed with the genus as the minimum taxonomic category. However, there is some degree of intra-sector variability because several subsets of assemblages are often connected by relatively long branches. These sites were intensively sampled (up to six collections), and their faunas contain several rare taxa.

The NMDS scatter plot reveals a pattern very similar to that in the cluster analyses (Fig. 2b). Furthermore, if one

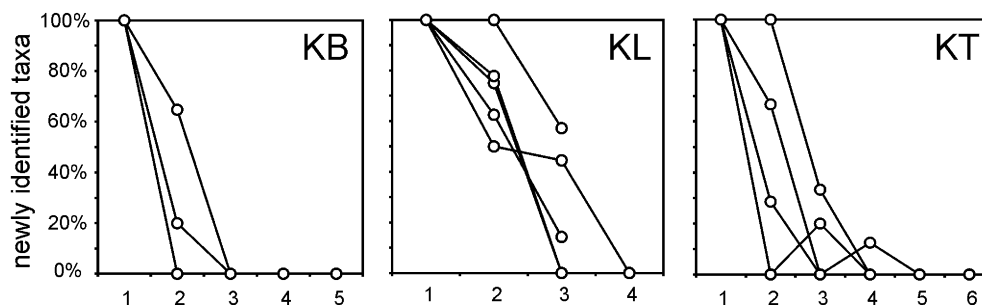


Fig. 1 Sampling of the Pliocene sites KB, KL and KT sectors, Djurab erg, northern Chad. The graphs give the proportion of newly identified mammal taxa in the successive collections of each site (x-axis). For most localities, sampling is satisfactory after three col-

lections. Two sites from the KL sector seemed to be undersampled, but their early collections contained much fewer specimens and taxa than later ones

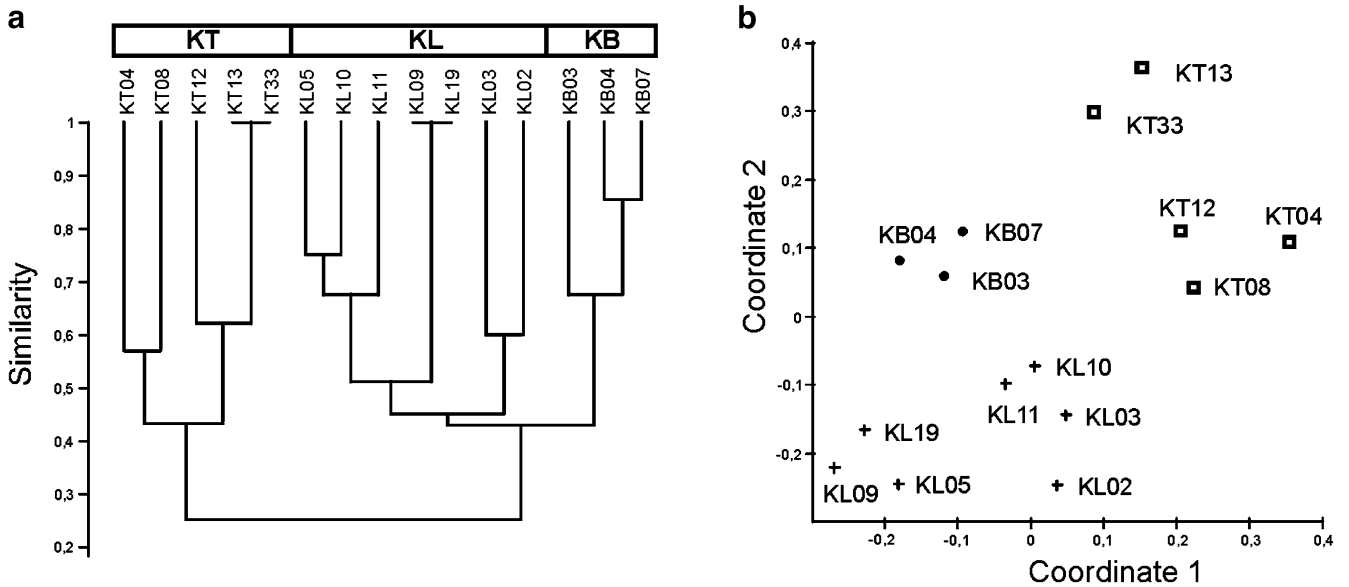


Fig. 2 a Dendrogram obtained after a Q-mode UPGMA cluster analysis based on the Simpson index. Assemblages from a same sector (KB, KL and KT) cluster together, although intra-sector similarity is variable. Other similarity indices (Spearman rho, Dice and

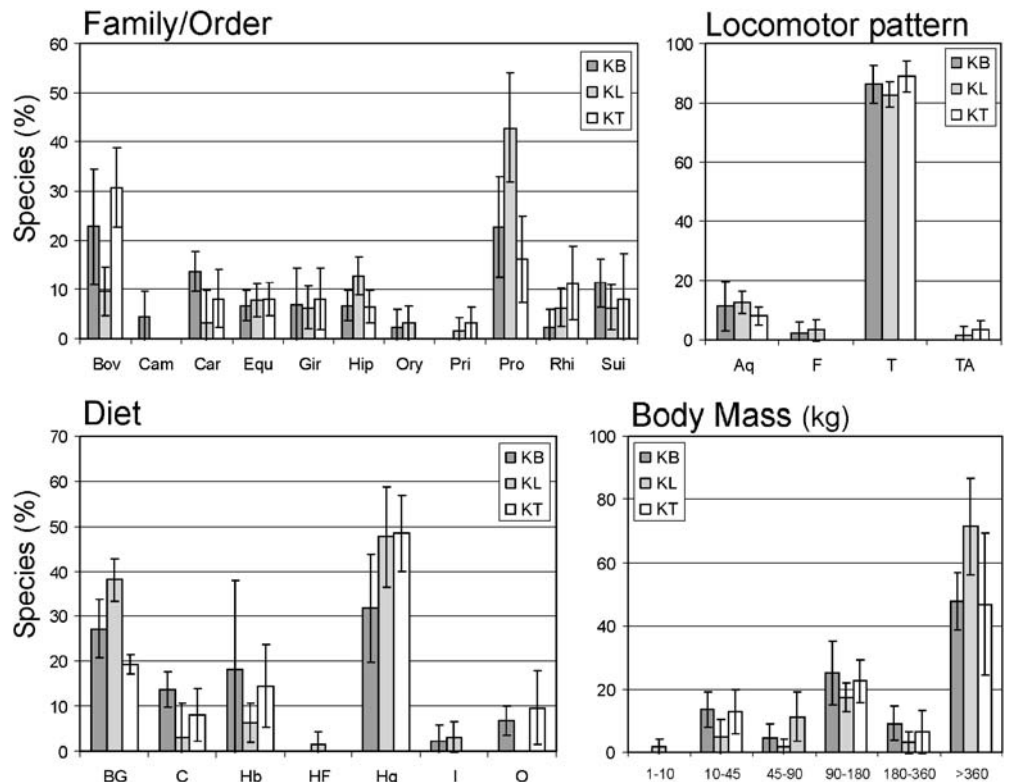
Raup/Crick) yield similar sectorial groupings. b Two-dimensional NMDS ordination of the Spearman rho matrix for the same assemblages, revealing a pattern similar to that in the cluster analysis. Final stress value is 19.28%

regards the assemblages of a same sector as replicate samples, the overall difference in taxonomy across sectors is found to be significant with the ANOSIM permutation test ($R=0.542, p<0.001$).

For each assemblage, we tabulated the proportion of species assigned to the different eco-variable categories and to major family/order. If the opening of the plant cover through time has influenced the structure of faunal asso-

ciations, we expect to find the largest difference between the oldest and the youngest units (KB and KT). However, we found that in most situations, the large mammal assemblages of KB, KL and KT do not differ significantly in their structure (Fig. 3). Bovids and proboscideans are well represented, and correlatively, terrestrial, very heavy (above 360 kg) browsers–grazers/grazers predominate. According to 95% cluster confidence intervals, the only significant

Fig. 3 Relative frequency of large mammal species in orders/families and in ecological categories (locomotor pattern, diet, body mass) for assemblages in the KB, KL, and KT sectors. Error bars represent 95% cluster confidence intervals computed using the assemblages of each sector. Results are similar when only sites with at least seven taxa are included in the analysis. Ecological categories are from Kovarovic et al. [13]. Abbreviations: *Aq*, aquatic; *BG*, browser–grazer; *Bov*, Bovidae; *C*, carnivore; *Cam*, Camelidae; *Car*, Carnivora; *Equ*, Equidae; *F*, Fossorial; *Gir*, Giraffidae; *Hb*, browser; *HF*, herbivore–frugivore; *Hg*, grazer; *Hip*, Hippopotamidae; *I*, insectivore; *O*, omnivore; *Ory*, Orycteropodidae; *Pri*, Primates; *Pro*, Proboscidea; *Rhi*, Rhinocerotidae; *Sui*, Suidae; *T*, terrestrial; and *TA*, terrestrial–arboreal



differences are found between KL and KT assemblages. The former have significantly more browsers–grazers and proboscideans than KT assemblages, whereas the reverse is true for bovids (Fig. 3 and S3). Similarly, the global ANOSIM shows that the assemblages of the three sectors differ significantly only for diet ($R=0.406$, $p=0.0018$) and for family/order ($R=0.369$, $p=0.002$). When applied to each pair of sectors, this test reveals significant differences between KL and KT for both diet ($R=0.414$, $p=0.0028$) and family/order ($R=0.452$, $p=0.036$), and significant differences between KB and KL for family/order ($R=0.346$, $p=0.032$). There is no significant difference between KB and KT assemblages for any of the studied variables. The results are similar when only sites with at least seven taxa are retained in the analyses (S4, S5, S6).

Discussion

Several factors could blur the taxonomic distinction between the Pliocene sectors from Chad: absence of bio-chronologically informative taxa in some sites, frequent occurrences of long-ranging forms (e.g. *Giraffa jumae*, *Diceros bicornis*) and sampling error. We found that these factors are insufficient to mask sectorial identity, and the sectors are homogeneous and adequate sampling units. Individual sites from Chad can also be used as comparative units if they count at least three collections.

Stable isotope analyses have suggested an opening of the plant cover from KB to KT times, a result in accordance with the apparent increase in diversity and abundance of open-country grazers [10, 17]. However, we find that the overall ecological structure of large-mammal assemblages from Chad is independent from the regional change in vegetation through time. Several explanations can be invoked:

1. The categories used in our study are too broad to capture significant differences in assemblage structure. This seems improbable, however, because these categories have proven useful for discriminating different habitat types with extant and fossil mammal communities (e.g. [1]).
2. Recurrent taphonomic processes have homogenised the fossil assemblages. The three sectors had analogous depositional environments (ephemeral streams and lakeside), but the transport of vertebrate remains has been limited or absent [5]. It is very unlikely that similar fossil assemblages derive from significantly distinct communities in these conditions.
3. Palaeo-environments were heterogeneous, and other local factors have played a major role in shaping the ecological spectrum of mammal communities. Sedimentological and faunal evidence suggest that all three sectors corresponded to lakeside environments surrounded by a patchwork of gallery forest, wooded

savannah and open grassland [3, 4, 6]. This could explain the overall similarity in ecological structure, as well as the large-cluster confidence intervals due to intra-sectorial patchiness in the distribution of taxa. Also, the fact that KB/KL and KL/KT assemblages differ more ecologically than those from KB and KT (the oldest and the youngest units, respectively) suggests that local factors may have driven some aspects of community structure.

4. The overall ecological structure is resilient to environmental change. Migration, extinction and evolution have changed the species composition in the three sectors over time, but the ecological structure has remained globally similar. This pattern suggests some degree of structural continuity in mammal communities (different species playing a similar ecological role), at least in the three time slices concerned by our study. Rodríguez [16] proposed a model to explain structural continuity based on his observations on Pleistocene mammals from Atapuerca. He suggested that ecological emergent mechanisms can maintain community structure with minor changes during environmental perturbations. This model does not disagree with the Chadian assemblages, but further evidence is needed to support it.

Our study has defined sampling units and the main ecological properties of the Pliocene large-mammal assemblages from Chad. Future comparisons with other African assemblages will define inter-regional patterns, thus providing further information on the ecological and biogeographical context during important phases of Hominid evolution. In this perspective, much work is needed to characterise the influence of sampling, taphonomic imprint, and local vs regional palaeo-environmental factors.

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