Systematic palaeontology (vertebrate palaeontology)

Biogeographic relationships of African carnivoran faunas, 7–1.2 Ma

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Abstract

This study analyses the carnivore component of African fossil faunas from three time slices: 7–5 Ma, 4–3 Ma, and 2.5–1.2 Ma, using cluster analysis and principal coordinate analysis (PCO) of presence/absence data on genera. The faunas mostly cluster by time slice, with the exception of Laetoli (Tanzania) and Ahl al Oughlam (Morocco), which differ from all other faunas. The separation during the Late Miocene of a Chado–Libyan bioprovince from the remainder of Africa is supported. No such distinctions are present in the other time slices. Taxonomic distance is not generally correlated with geographic distance, though if Langebaanweg is removed from the 7–5 Ma time slice, the correlation at that time is significant. Comparison of these paleontological results with phylogeographic studies of modern species leads to some general comments on the analytic power of the fossil record with regard to interregional migrations. ***To cite this article: L. Werdelin, C. R. Palevol 7 (2008).***

Résumé

Relations biogéographiques entre les faunes africaines de carnivores, 7–1,2 Ma. Cette étude analyse la composante carnivore des faunes fossiles africaines de trois périodes, 7–5 Ma, 4–3 Ma et 2,5–1,2 Ma, en utilisant l'analyse cluster et l'analyse en coordonnées principales des données d'absence/présence des genres. Les faunes se regroupent essentiellement par période temporelle, à l'exception de Laetoli (Tanzanie) et Ahl al Oughlam (Maroc) qui diffèrent de toutes les autres faunes. La séparation, au cours du Miocène supérieur, d'une bioprovince Tchadolibyenne du reste de l'Afrique est corroborée. De telles distinctions n'apparaissent pas au cours des autres périodes. La distance taxonomique n'est généralement pas corrélée à la distance géographique bien que, si l'on retire Langebaanweg de la période 7–5 Ma, cette corrélation soit alors significative. La comparaison de ces résultats paléontologiques avec les études phylogéographiques d'espèces modernes conduit à des commentaires généraux sur le pouvoir analytique de l'enregistrement fossile en ce qui concerne les migrations inter-régionales. ***Pour citer cet article : L. Werdelin, C. R. Palevol 7 (2008).***

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1. Introduction

Modern-day Africa is divided into a large number of ecoregions as well as smaller units [9]. These regions are predictably correlated with climatic regimes and their biota is adapted to local circumstance, or as closely as it can be given the rate and amplitude of climate change in the past few million years. This is necessarily also true of the past, and much effort has gone into reconstructing local environments through study of their fauna and flora [1]. However, the vast majority of these studies have focused on single localities or basins [8,12,32,33]. Relatively little work has been done on interregional differences in faunas and environments, i.e., the interregional biogeography of Africa. What work has been done in this respect has, for the most part, either been done with a view to comparing regions of Africa with extra-African regions [3,4,28], or has dealt with the biogeography of a single taxon or small group of closely related taxa (most notably the hominins). Few studies have considered the biogeography of entire biota or trophic levels within biota to see how this could inform the study of interregional migration patterns and the causes behind them, though exceptions do exist [14].

A notable exception is Reed and Lockwood [34], who looked at exactly this, examining at biogeographic patterns in modern and fossil herbivores to find correlations between geographic distance, taxonomic similarity and ecological similarity. In this study I will carry out a similar analysis of the carnivore faunas of a number of African fossil mammal localities and relate geographic and taxonomic distance (ecological distance will not be considered here).

2. Material and methods

This study is based on the carnivoran constituent of the mammal faunas of Africa between 7 and 1.2 Ma (henceforth just called "faunas"). It focuses on three time slices: 7–5 Ma, 4–3 Ma, and 2.5–1.4 Ma. These time slices are of special significance. The first, 7–5 Ma, encompasses the time of origin of the first bipedal hominids, and therefore, so current thinking goes, the first members of our lineage, the hominins. The second time slice, 4–3 Ma, is the time of greatest species richness among African carnivorans [44]. The third time slice, 2.5–1.2 Ma, includes the origin of *Homo* at or near 2.5 Ma, the origin of the modern human body plan with *H. ergaster/erectus*, at or near 1.8 Ma, and the first time our lineage left Africa, some time after 1.8 Ma. All three time slices include faunas from North, East, and South Africa (except the 4–3 Ma time slice, for which no suitable North African fauna exists). The study uses genera rather than species as its analytical level. This is not desirable, but is unfortunately necessary, as many carnivoran remains are too fragmentary to identify to the species level, and species lists therefore often include large numbers of "Genus sp.," which would not be helpful in the present case, unless it could be demonstrated conclusively that "Genus sp." from one site is the same or different from "Genus sp." from another site, something that is only occasionally possible. Faunas with fewer than five genera have been excluded. This is a small number in itself, but has to be weighed against the value of having more faunas included in the analyses.

Two main statistical methods are used. One is paired-group (UPGMA) clustering [37] with the Raup–Crick similarity measure, which has been found to be especially useful for paleontological data [31]. It weights data on the basis of frequency, so that widespread taxa do not have a disproportionate effect on the results, and also does not disproportionately favor unique taxa, as many similarity indices do. Only one cluster analysis, of all faunas together, was carried out.

As a complement to the cluster analysis, principal coordinate analysis (PCO) was used [46] for both all faunas together and for faunas of each time slice separately. PCO is an ordination technique capable of handling presence/absence data, producing a series of orthogonal coordinate axes based on a selected similarity measure. Here, I have used two different distance measures. Most distance measures tend to weight unique occurrences (in this case taxa unique to a locality) heavily. In a situation like the present one, where the sample sizes are very uneven, this will tend to affect the analyses unduly, such that in the 4–3 Ma time slice, for example, Laetoli, with its many taxa will tend to be placed far apart from the other localities simply because a large fauna will necessarily include many unique taxa (Table 1). To address this problem, I have in the PCO analyses of individual time slices used the Dice index of similarity as the distance measure. The Dice index upweights shared taxon occurrences at the expense of unique ones, and has been shown in simulation studies [2,25] to produce the best results among a number of similar indices. The Raup–Crick index, used in the cluster analysis, does not produce useful results when applied in the PCO. In the analysis of all data I have used the Euclidean distance as the distance measure of choice, for two reasons. First, there are fewer unique taxa if all localities

Table 1

The faunas included in the present study along with the number of genera of carnivoran present and the source of the taxonomic information used. For the number and percentage of unique taxa, the first number is in relation to other faunas of that time slice while the values in parentheses are in relation to all faunas of all time slices.

Tableau 1

Faunes incluses dans cette étude, avec le nombre de genres de carnivores présents et la source de l'information taxonomique utilisée. Pour le nombre et le pourcentage des taxons propres à une faune, le premier chiffre est relatif aux autres faunes de la période de temps concernée, tandis que les chiffres entre parenthèses sont relatifs à l'ensemble des faunes toutes périodes temporelles confondues.

Fauna	Number of genera/unique genera/% unique genera	Source
7–5 Ma time slice		
Lothagam: Upper Nawata	9/1(1)/11.1(11.1)	[41]
Lukeino Fm.	10/1(0)/10.0(0)	[26]
Toros-Menalla	13/7(3)/53.8(23.1)	Several, summarized by S. Peigné (pers. comm., 2008)
Sahabi	7/2(2)/28.6(28.6)	[22,35,45]
Lemudong'o	10/1(0)/10.0(0)	[23], personal observations (unpublished)
Adu-Asa Fm/Sagantole Fm.	12/0(0)/0(0)	[19]
Langebaanweg	16/1(0)/6.3(0)	Personal observations (unpublished)
4–3 Ma time slice		
Allia Bay	5/0(0)/0(0)	Personal observations (unpublished)
Laetolil Beds, upper unit	22/8(1)/36.4(4.5)	[42]
South Turkwell	5/0(0)/0(0)	[43]
Shungura Fm, Mb. B	9/0(0)/0(0)	Personal observations (unpublished)
Koobi Fora Fm., Tulu Bor Mb.	5/0(0)/0(0)	Personal observations (unpublished)
Nachukui Fm., lower Lomekwi Mb.	6/0(0)/0(0)	Personal observations (unpublished)
Usno Fm.	9/0(0)/0(0)	Personal observations (unpublished)
Woranso-Mille study area, Ethiopia	12/1(0)/8.3(0)	Personal observations (unpublished)
Hadar	12/1(0)/8.3(0)	Personal observations (unpublished)
Makapansgat, Mbs 3–4	11/2(1)/18.2(9.1)	[40], personal observations (unpublished)
2.5–1.4 Ma time slice		
Shungura Fm., Mb. D–F	9/2(0)/22.2(0)	Personal observations (unpublished)
Shungura Fm., Mb. G	9/1(1)/11.1(11.1)	Personal observations (unpublished)
Koobi Fora Fm., Upper Burgi Mb.	11/2(0)/22.2(0)	Personal observations (unpublished)
Koobi Fora Fm., KBS Mb.	10/1(1)/10.0(10.0)	Personal observations (unpublished)
Koobi Fora Fm., Okote Mb.	6/1(0)/16.7(0)	Personal observations (unpublished)
Olduvai, Bed I	13/6(0)/46.2(0)	[29,30], personal observations (unpublished)
Olduvai, Bed II	8/1(1)/12.5(1)	[29,30], personal observations (unpublished)
Ahl al Oughlam	21/12(4)/57.1(19.0)	[16], personal observations (unpublished)
Kromdraai, Mb. A	14/3(1)/21.4(7.7)	[40]

are considered, not just those within time slices. Second, over longer time spans, rare or unique taxa can be important to distinguish between stratigraphically discrete units as is, in fact, the case here. Thus, in this situation, downweighting rare or unique taxa is counterproductive. A minimum spanning tree (MST) connecting all localities in the space of the first two coordinates in each analysis of the individual time slices was calculated. The branch lengths of the MST were used to compare with geographic distances between the localities by means of a rank correlation test to investigate to which extent physical proximity dominates the similarity patterns.

Statistical analyses were carried out using PAST, version 1.82 [20], available for download free from: http://folk.uio.no/ohammer/past/.

3. Results

3.1. General characterization of the faunas

The faunas used in this paper are listed in Table 1. The numbers show that Toros-Menalla and Sahabi have many unique genera, presumably a function of their relatively isolated geographic position, as will be discussed below. What is most interesting about these numbers is that most faunas with many unique genera in their time slice have these numbers drastically reduced when all time slices are considered. Thus, Laetoli has 36.4% unique genera within its time slice but only 4.5% when all faunas are taken into consideration. This is a reflection of the fact that many genera have their first appearance datum (FAD) at Laetoli, in its turn probably an effect of
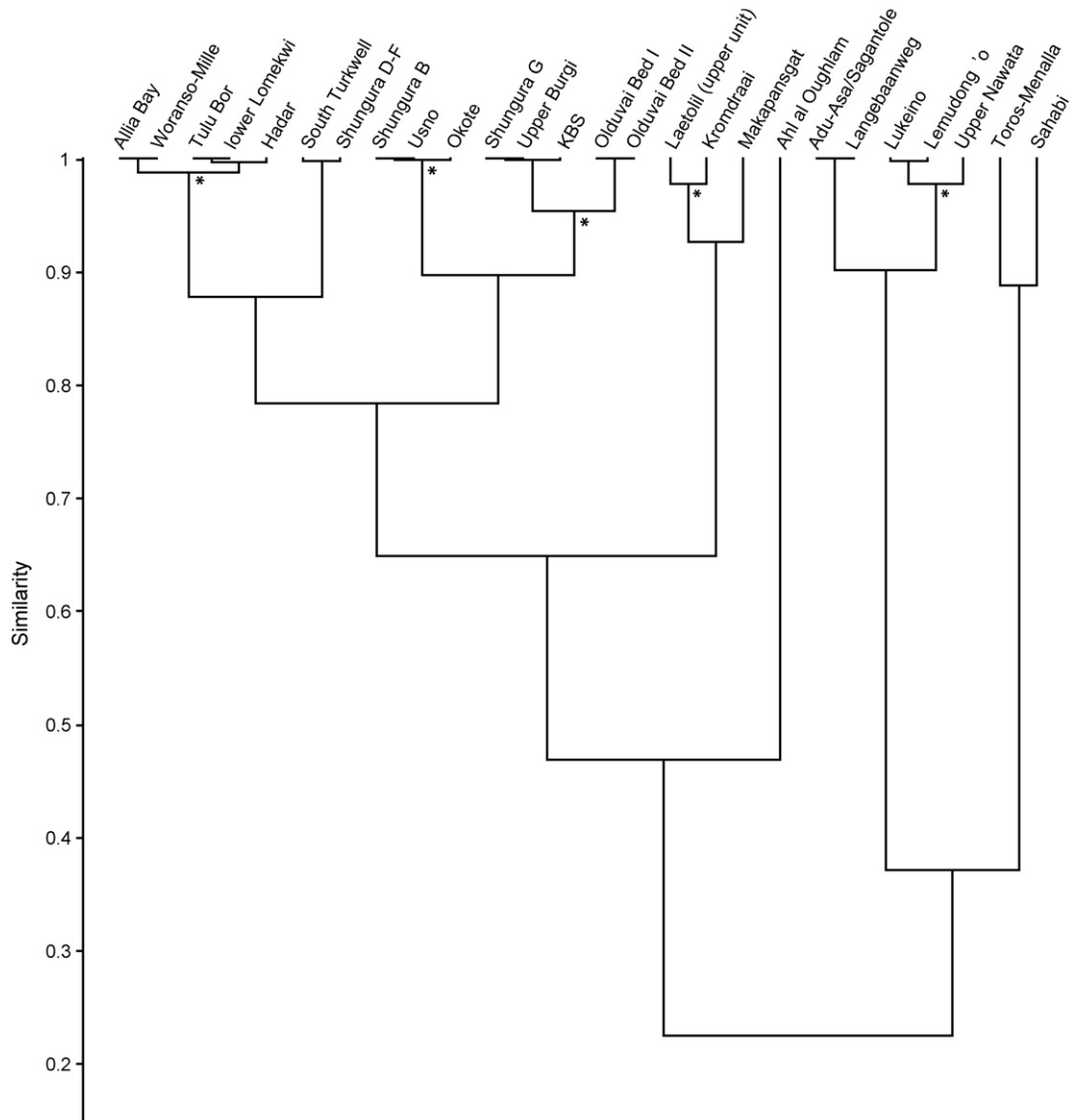
Fig. 1. Phenogram showing the results of the cluster analysis using the Raup–Crick method on faunas of all time slices. Bifurcations denoted by asterisks are not significant (nor are, of course, bifurcations above these).

Fig. 1. Phénogramme montrant les résultats de l'analyse cluster utilisant la méthode Raup-Crick sur les faunes de l'ensemble des périodes de temps. Les bifurcations indiquées par des astérisques ne sont pas significatives (comme ne le sont pas, bien sûr, les bifurcations situées au-dessus).

the unique environmental conditions at Laetoli [42,44]. A similar situation applies to Olduvai, Bed I, but in this case the uniqueness is likely to be because Olduvai is the only substantial fauna in its time slice to have been collected through excavation and sieving.

3.2. All time slices, joint analysis

The first analysis is a cluster analysis of all localities from all time slices. The results are shown in Fig. 1. Six major clusters were found. The first split is

between faunas of the 7–5 Ma time slice and other faunas. The former is subsequently split into two groups, one uniting Toros-Menalla with Sahabi and one uniting the remaining faunas of the 7–5 Ma time slice. The next split separates Ahl al Oughlam from the faunas of the 4–3 Ma and 2.5–1.2 Ma time slices. Moving up the tree, the next split separates Laetoli and the two South African faunas Makapansgat and Kromdraai from the East African faunas of the 4–3 Ma and 2.5–1.2 Ma time slices. The two South African faunas do not cluster together—Kromdraai clusters with Laetoli rather than

with Makapansgat, although this split is not statistically significant.

The subsequent split is between East African faunas of the 4–3 Ma and 2.5–1.2 Ma time slices, except that the younger Shungura D–F clusters with the 4–3 Ma time slice and the older Shungura B and Usno with the 2.5–1.2 Ma time slice. The latter time slice is further split into a cluster uniting the two Olduvai members with two Koobi Fora members and Shungura G, while the other cluster unites the Okote Mb. of Koobi Fora with the Omo faunas Shungura B and Usno. In the 4–3 Ma cluster, South Turkwell is united with Shungura D–F and these are well separated from the other faunas of the time slice, which are very similar to each other.

The first two coordinates of the PCO of all faunas together are plotted in Fig. 2. Here we can see the influence of unique taxa on the results, as Laetoli and Ahl al Oughlam, two faunas with many unique taxa relative to other faunas in their time slice, are placed in relative isolation at the top of the diagram. However, ignoring these two faunas, the remaining faunas are neatly clustered by time slice, except that Usno falls among the 2.5–1.2 Ma time slice faunas.

3.3. 7–5 Ma time slice

The results of the PCO with its MST are shown in Fig. 3A. This figure shows Langebaanweg as a hub from which nearly all other faunas radiate. This suggests that Langebaanweg may have a disproportionate influence on the analyses. To investigate this I reran the analysis without Langebaanweg. The MST, but not the PCO itself, differs considerably in the analysis without Langebaanweg, as shown in Fig. 3B. The position of the faunas in the PCO with and without Langebaanweg is almost the same, showing that Langebaanweg in fact does not influence the results of the PCO. It's presence in the analysis changes the MST, however. The MST for the analysis without Langebaanweg shows Lemudong'o linking to Lukeino, Upper Nawata and Adu-Asa, with the latter then linking to Sahabi, and that locality to Toros-Menalla. As can be seen from Fig. 4, which places the MST on a map of Africa, this result almost perfectly mirrors geography. The correlation between the MST distances and geographic distances is just barely significant (Kendall's $\tau = 0.8$, $p[uncorr] = 0.0500$). Only one rank differs—the distances between Adu-Asa/Sagantole–Sahabi and Sahabi–Toros-Menalla being reversed.
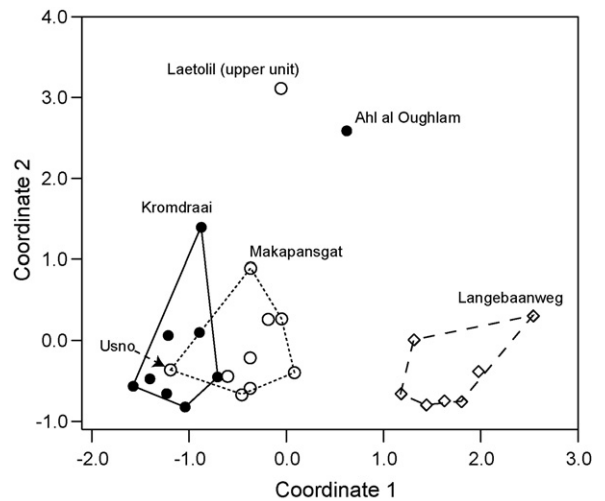

Fig. 2. Diagram showing the first two coordinate axes of the PCO of faunas of all time slices. Coordinate 1 has the eigenvalue 34.71 (18.80% variation explained), coordinate 2 the eigenvalue 25.11 (13.60% variation explained). Laetoli and Ahl al Oughlam are very different from the other faunas, probably as a result of their many unique taxa. The faunas of the different time slices are shown with their convex bounding boxes: dashed line: 7–5 Ma; dotted line: 4–3 Ma; solid line: 2.5–1.2 Ma. Apart from the position of Usno (and the cases of Laetoli and Ahl al Oughlam) there is no overlap between time slices. In each case, the South African locality (specified by name in the diagram) is the most distant, creating a peak in the bounding box.

Fig. 2. Diagramme montrant les deux premiers axes de coordonnées de l'analyse en coordonnées principales des faunes de toutes les périodes de temps. La coordonnée 1 a une valeur propre de 34,71 (18,80 % de la variation totale exprimée) et la coordonnée 2 une valeur propre de 25,11 (13,60 % de la variation totale exprimée). Laetoli et Ahl al Oughlam sont très différentes des autres faunes, ce qui est probablement dû à leurs nombreux taxons propres. Les faunes des différentes périodes de temps sont montrées dans des boîtes englobantes convexes : ligne tiretée : 7–5 Ma ; ligne pointillée : 4–3 Ma ; ligne continue : 2,5–1,2 Ma. En dehors de la position d'Usno (et des cas de Laetoli et Ahl al Oughlam), il n'y a aucun recouvrement entre les périodes temporelles. Dans chacune, la localité sud-africaine (indiquée nominalement sur le diagramme) est la plus distante, créant un pic dans la boîte englobante.

3.4. 4–3 Ma time slice

The result of the PCO analysis of the 4–3 Ma time slice faunas is shown in Fig. 5, along with its MST. The complex nature of the MST on this diagram is because the calculation of the MST takes into account all dimensions in the data, not just the two that are shown on the PCO plot. Also, the "crossroads" at Usno is because the line from Woranso-Mille to Laetoli happens to pass directly through the point for Usno (thus, Usno does not link Woranso-Mille and Laetoli). The results show that Laetoli and Makapansgat are close together, the two northern Turkana Basin faunas sit in a space of their
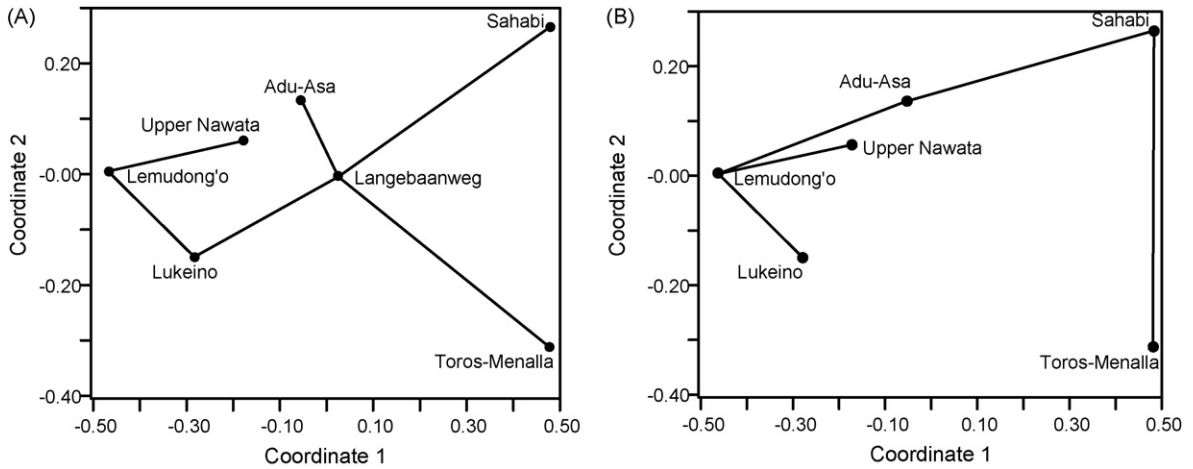
Fig. 3. A. Diagram showing the first two coordinate axes of the PCO of the 7–5 Ma time slice faunas. Coordinate 1 has the eigenvalue 0.790 (61.26% variation explained), coordinate 2 the eigenvalue 0.212 (16.41% variation explained). B. Diagram showing the first two coordinate axes of the PCO of the 7–5 Ma time slice faunas with Langebaanweg removed. Coordinate 1 has the eigenvalue 0.790 (62.53% variation explained), coordinate 2 the eigenvalue 0.212 (16.77% variation explained).

Fig. 3. A. Diagramme montrant les deux premiers axes de coordonnées de l'analyse en coordonnées principales des faunes de la période 7–5 Ma. La coordonnée 1 a une valeur propre de 0,790 (61,26 % de la variation exprimée), la coordonnée 2 une valeur propre de 0,212 (16,41 % de la variation exprimée). B. Diagramme montrant les deux premiers axes de coordonnées de l'analyse en coordonnées principales des faunes de la période 7–5 Ma, sans Langebaanweg. La coordonée 1 a une valeur propre de 0,790 (62,53 % de la variation exprimée), la coordonnée 2 une valeur propre de 0,212 (16,77 % de la variation exprimée).
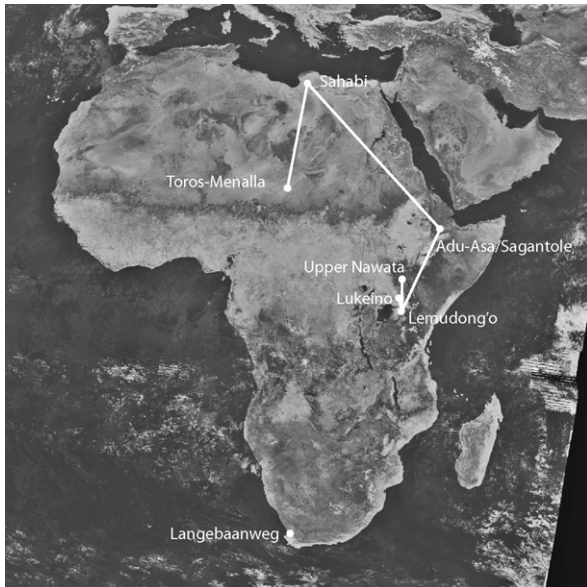

Fig. 4. The minimum spanning tree from Fig. 3B drawn on a map of Africa. The distances are not those of the MST, but are correlated with them (rank correlation; Kendall's $\tau = 0.8$, $p[uncorr] = 0.0500$).

Fig. 4. Arbre maximal minimal tiré de la Fig. 3B, dessiné sur une carte de l'Afrique. Les distances ne sont pas celles de cet arbre mais y sont corrélées (corrélation de rang ; τ de Kendall = 0,8, p [non corr.] = 0,0500).
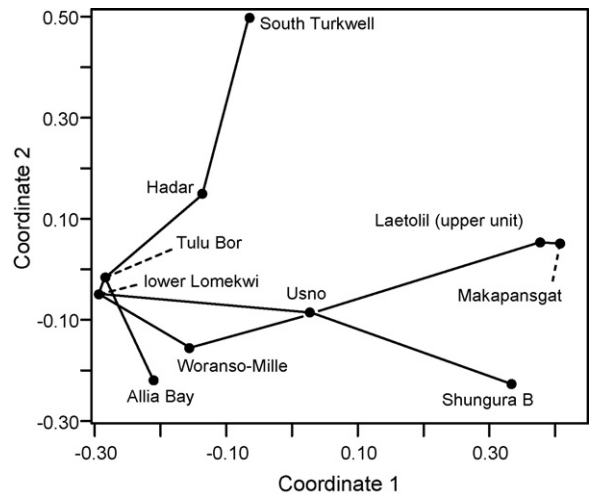

Fig. 5. Diagram showing the first two coordinate axes of the PCO of the 4–3 Ma time slice faunas. Coordinate 1 has the eigenvalue 0.680 (36.30% variation explained), coordinate 2 the eigenvalue 0.410 (21.87% variation explained).

Fig. 5. Diagramme montrant les deux premiers axes de coordonnées de l'analyse en coordonnées principales des faunes de la période 4–3 Ma. La coordonnée 1 a une valeur propre de 0,680 (36,30 % de la variation exprimée), la coordonnée 2 une valeur propre de 0,410 (21,87 % de la variation exprimée).
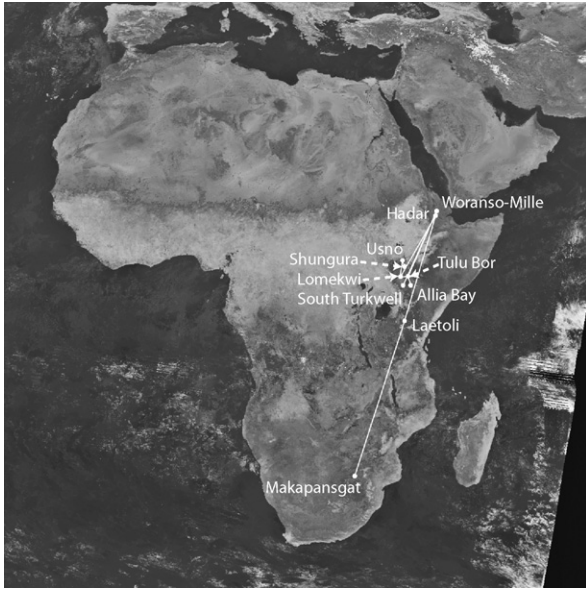
Fig. 6. The minimum spanning tree from Fig. 5 drawn on a map of Africa. In this case the distances are not correlated with those of the MST (rank correlation; Kendall's $\tau = 0$, $p[uncorr] = 1$).

Fig. 6. Arbre maximal minimal tiré de la Fig. 5, dessiné sur une carte de l'Afrique. Les distances ne sont pas corrélées avec celles de cet arbre (corrélation de rang ; τ de Kendall $= 0$, p [non corr.] $= 1$).
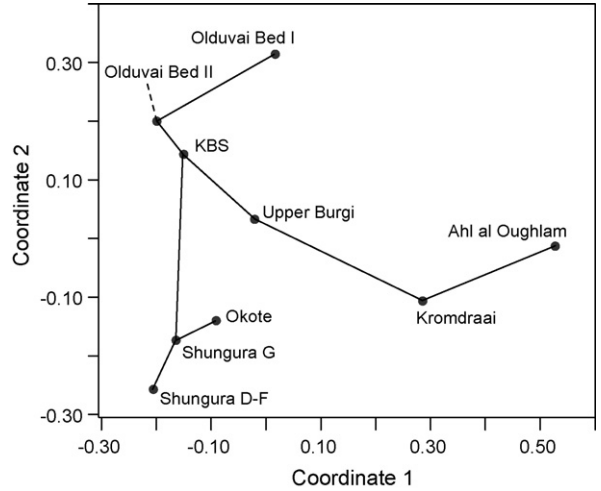

Fig. 7. Diagram showing the first two coordinate axes of the PCO of the 2.5–1.2 Ma time slice faunas. Coordinate 1 has the eigenvalue 0.500 (42.71% variation explained), coordinate 2 the eigenvalue 0.288 (24.59% variation explained).

Fig. 7. Diagramme montrant les deux premiers axes de coordonnées de l'analyse en coordonnées principales des faunes de la période 2,5–1,2 Ma. La coordonnée 1 a une valeur propre de 0,500 (42,71 % de la variation exprimée), la coordonnée 2 une valeur propre de 0,288 (24,59 % de la variation exprimée).

own, and there is a cluster of southern Turkana Basin and Afar region faunas that links through Hadar to South Turkwell, which is relatively distant. These results are broadly similar to those of the cluster analysis described earlier.

The MST is shown on a map of Africa in Fig. 6. It is clear from this map that the correlation between MST distance and geographic distance is much weaker than in Fig. 3 of the 7–5 Ma time slice. In fact, they can be considered completely uncorrelated (Kendall's $\tau = 0$, $p[uncorr] = 1$).

3.5. 2.5–1.2 Ma time slice

The PCO analysis and MST shown in Fig. 7 show that Ahl al Oughlam and Kromdraai are distant from the East African faunas, while within the latter the Okote is very close to the Shungura Fm. faunas. The two Olduvai faunas are linked, though the distance from Bed II to KBS is shorter than from Bed II to Bed I. KBS, on the other hand, links to both Bed II and to the Upper Burgi Mb. of Koobi Fora. Again, the results are broadly comparable to those of the cluster analysis.

Fig. 8 shows the MST for the 2.5–1.2 Ma time slice grafted on to the map of Africa. This clearly shows the longest geographic links connecting to Kromdraai. The correlation between MST distance
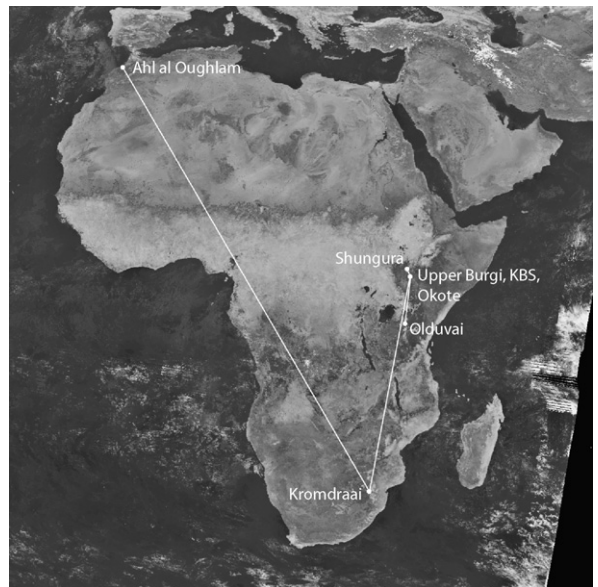

Fig. 8. The minimum spanning tree from Fig. 7 drawn on a map of Africa. The distances are not correlated with those of the MST (rank correlation; Kendallís $\tau = 0.1543$, $p[uncorr] = 0.593$).

Fig. 8. Arbre maximal minimal tiré de la Fig. 7, dessiné sur une carte de l'Afrique. Les distances ne sont pas corrélées avec celles de cet arbre (corrélation de rang ; τ de Kendall $= 0,1543$, p [non corr.] $= 0,593$).

and geographic distance is not significant (Kendall's $\tau = 0.1543$, $p(uncorr) = 0.593$).

4. Discussion

With only a few exceptions, the analyses of all faunas together align well with expectations (Figs. 1 and 2). Faunas from the same time slice group together with little overlap, with faunas from more distant localities being somewhat more distant in the analyses as well. The faunas from the 7–5 Ma time slice are separated into two groups at a high degree of significance. Since Toros-Menalla and Sahabi form one group and the East and South African faunas another, this result is in concordance with the proposed separation between a Chado–Libyan bioprovince and the remainder of Africa [24]. The split between Adu-Asa/Sagantole + Langebaanweg and the remaining 7–5 Ma time slice faunas may be stratigraphic, as the two former are the youngest of the localities in this time slice. Thus, they share, e.g., *Mellivora*, a taxon otherwise only found in younger faunas, whereas several of the other 7–5 Ma faunas (e.g., Upper Nawata, Toros-Menalla) instead have mellivorines that are more primitive than *Mellivora*.

That Shungura B and Usno group with the 2.5–1.2 Ma faunas while Shungura D–F groups with the 4–3 Ma faunas is almost certainly due to the presence at the former two localities of *Panthera* and *Acinonyx* (apart from Laetoli, the only two pre-2.5 Ma localities to have these taxa present) and their absence from Shungura D–F. In all likelihood this is a stochastic phenomenon, as these genera are always rare and could easily be missed if sample sizes are small. The grouping of Okote with Shungura G and Usno has more complex causes, probably related to the absence of taxa such as *Canis* from these faunas, but this is harder to verify.

The faunas placed in an intermediate position in Fig. 1 are a mixed group. Laetoli and Ahl al Oughlam are among the best sampled faunas and because of this share some taxa that might have been present in the less well sampled faunas, but have not been found due to sampling issues. The same reasoning may explain why Laetoli lies near the two Pliocene South African localities Makapansgat and Kromdraai. The later two, however, are distinct from similarly aged East African localities due to some distinct differences between East and South African faunas. Thus, e.g., *Vulpes* has been found in these two faunas but not at any East African Pio–Pleistocene site, though *Prototocyon/Otocyon* has [44]. *Vulpes* is also present at Ahl al Oughlam. The same situation pertains in the modern fauna, though *Vulpes pallida* maintains a

marginal presence in northern Ethiopia and Eritrea [36]. A phylogeographic study of this animal might indicate whether its current presence in eastern Africa is ancient or due to a recent range extension. The disjunct distribution of *Vulpes* today may thus be one of long standing. In addition, Kromdraai shares with Laetoli and Ahl al Oughlam *Nyctereutes* and *Viverra* (though if the record at Kromdraai really is *Viverra* is debatable). These genera are now extinct in Africa. Fig. 2 shows that these presences place Makapansgat and Kromdraai in the direction of Laetoli and Ahl al Oughlam along Coordinate 2, but that they are still closer to other faunas of their time slice in the PCO analysis.

In the PCO analysis of the 7–5 Ma time slice, Langebaanweg falls almost at the center of the diagram (Fig. 3A), though closest to Adu-Asa/Sagantole for reasons discussed above. This position of Langebaanweg is probably because it is a large fauna without any unique taxa, thus sharing "something with everybody." This interpretation is strengthened by the removal of Langebaanweg (Fig. 3B), which has almost no effect on the positions of the remaining faunas. In Fig. 4, placing the MST on a map, the Chado–Libyan bioprovince effect is distinct in the linking of Toros-Menalla with Sahabi rather than directly with East African faunas. Without Langebaanweg the MST is correlated with geographic distance, though adding Langebaanweg removes this correlation, showing that East and South Africa form part of the same bioprovince (at this level of analysis).

The results of the PCO analysis of the 4–3 Ma time slice (Figs. 5 and 6) are more complex. Coordinate 2 of Fig. 5 mostly serves to separate South Turkwell from the remaining faunas and can be ignored here except to note that this position seems mainly due to the absence from South Turkwell of a number of taxa that unite the other faunas (e.g., *Dinofelis*). As in the analysis of all time slices (Fig. 1), Laetoli and Makapansgat fall close together. Overall, however, Coordinate 1 separates those faunas, that in the overall analysis (Fig. 1) fall with the 2.5–1.1 Ma time slice fauna from the Okote (Usno and Shungura B from the northern Turkana Basin), from a combined group of southern Turkana Basin and Afar region faunas. Since these groupings do not follow geography, it makes sense that the MST does not either (Fig. 6), with the shortest distance in the MST (Laetoli–Makapansgat) being the longest distance on the map. It therefore does not appear that the area covered by the faunas of this time slice can be conveniently divided into provinces, although some taxa (such as *Vulpes*) are only found in South Africa. It is, however, of great interest that the faunas of the southern and northern Turkana Basin are not close to each other. This mirrors results

from other studies [34], though a hypothesis to explain the pattern has not yet been formulated.

The faunal positions in the PCO of the 2.5–1.2 Ma time slice are relatively closely correlated with geographic distance, though not significantly so (Figs. 6 and 7). The main exception is the placement of Okote close to the northern Turkana Basin faunas of the Shungura Fm., rather than with the other southern Turkana Basin faunas of the Upper Burgi and KBS Mbs. of the Koobi Fora Fm. This result is mainly due to the presence at Shungura D–F, Shungura G, and Okote of *Megantereon*. Since *Megantereon* is a rare taxon at the best of times, this may simply be a sampling issue, though Upper Burgi and KBS are faunas that are fairly well sampled compared to most in this time slice. Another possibility is that it represents a difference in habitat, as *Megantereon* is considered the large predator that would be most tied to closed habitats. However, studies of faunal and environmental change in the Omo mammal community of this time [5,6] do not support this notion. On the other hand, the analysis does not show any signal of the taphonomic break in Shungura Mb. G that is clearly in evidence in the bovids [5]. Nevertheless, even if the position of Okote is ignored as due to sampling, the (lack of) correlation between MST segment length and geographic distance does not change, suggesting that there are no discernible bioprovinces in this time slice either.

It is difficult to find comparisons with this study. Very few studies have compared the carnivoran faunas of South and East Africa [38,39]. These studies found no major differences between the two regions in their large carnivorans in the Plio–Pleistocene. At the generic level the results of the present study agree with Turner's, though at the species level, which was Turner's focal level, I find some differences not recorded by Turner, mainly due to expanded faunal lists in the past decade [44]. The smaller carnivorans are, of course, a different matter, but this study does not find any clear pattern to regional differences that would preclude South and East Africa being part of a broad carnivoran bioprovince.

No previous studies have made comparisons between the carnivorans of North and East Africa, except on a locality-specific basis. However, this study agrees with studies on other groups, such as anthracotheres and hippos [24], that in the Late Miocene there is a distinct separation between a Chado–Libyan and an African bioprovince. No such distinction can be seen in the time of Ahl al Oughlam, which though it has a number of unique taxa nevertheless is typically African in faunal composition with only limited influences from Eurasia [16,17]. Thus, viewed at the million-year time scale and from the perspective of a carnivoran, post-Miocene Africa formed a single bioprovince, in distinction to the Late Miocene.

At shorter time scales the situation is different. A number of phylogeographic studies of medium-sized and large African mammals have been carried out in the past decade, including giraffe, *Giraffa camelopardalis* [7,21], hartebeest, *Alcelaphus bucelaphus* [13] and warthog, *Phacochoerus africanus* [27]. The majority of these studies have found a primary subdivision between a southern clade and a "northern" (mostly eastern, in some cases western + eastern) clade. Thus far, four carnivorans have been studied. In two smaller carnivores, the common genet, *Genetta genetta* [15] and white-tailed mongoose, *Ichneumia albicauda* [10] a north–south subdivision was found (in the case of *Genetta* preceded by a subdivision between a North African population and the sub-Saharan ones). In two larger carnivores, the wild dog, *Lycaon pictus* [18] and the lion, *Panthera leo* [11], on the other hand, there were no clear geographic subdivisions among the studied samples.

These phylogeographic results, which broadly speaking address processes occurring over the past 0.5–1 Ma, have generally been interpreted in terms of Pleistocene climatic fluctuations and concomitant changes to the environment such as expanding or contracting forest regions, grasslands, and deserts, suggest several things. The first is that in larger carnivorans gene flow between populations may be rapid enough to disrupt genetic isolating processes occurring over time frames of 10^5 years or less, although more species need to be studied to determine whether this is a general pattern or specific to wild dog and lion, two of the most mobile of extant carnivorans. Studies of medium-sized taxa such as jackals, *Canis* sp.; honey badger, *Mellivora capensis*; caracal, *Caracal caracal*, or serval, *Leptailurus serval* would indicate the limits of such a process. Second, smaller carnivorans such as genets and mongooses seem to retain the effects of Pleistocene climatic disruption in their genetic makeup, though again more species need to be examined.

Although the analysis above dealt with the movement of species within genera and the phylogeographic studies with the movement of subspecific units, useful insights can be gained from applying the information from the latter to the former. It must just be kept in mind that the time scale for the phylogeographies is on the order of 10^5 years while that of the paleontological data is on the order of 10^6 years. Combining the results suggests the following:

- similarities between East and South African faunas among the larger carnivorans at the generic or spe-

cific level are at present irrelevant to considerations of possible migration barriers between African subregions because any differences between regions in this faunal component is quickly erased by their dispersal abilities at time scales below current detection levels in the fossil record;

- cases where there are differences between these faunal components are of particular interest but must be studied on a case by case basis before they can be used to infer a general pattern;
- where there are such differences among larger carnivorans on a large scale (e.g., between the Chado–Libyan bioprovince and other African faunas as discussed above) this is evidence of barriers to dispersal and gene flow that persisted over time scales of 10^6 years and probably considerably more;
- similarities or differences between South and East African faunas among the smaller carnivorans are strong indications of disruption of gene flow (with attendant possibilities of local speciation and/or extinction) between regions at time scales of 10^5 years or less.

Such patterns have the potential of being observable in the fossil record. In fact, smaller carnivorans may be among the most informative of mammals in this regard, as they often have large species and genus ranges despite relatively limited dispersal abilities and many of them occupy a wide range of habitats. Indeed, some species, e.g., bat-eared fox, *Otocyon megalotis*; black-backed jackal, *Canis mesomelas* and aardwolf, *Proteles cristatus* have disjunct ranges in the present day. Species with large ranges that would be of considerable interest to study include sidestriped jackal, *Canis adustus*; slender mongoose, *Galerella sanguinea*; African civet, *Civettictis civetta*, and several species of *Genetta*. On the paleontological side, the phylogeographic results suggest that much more effort should be made to recover and study small carnivorans as among the groups that are the best interregional biogeographic indicators. That the potential exists to recover many more small carnivorans than at present is shown by faunas such as those of Laetoli and Olduvai which have large small carnivoran faunas [29,30,42].

It is of considerable interest that many of the large herbivores studied by phylogeographic means seem to generate phylogeographic signals on time scales similar to those of small carnivores. This surely reflects a fundamental difference between herbivores and large carnivores. The former are foodstuff specialists, but once the preferred food is present they have the ready means of consuming it. The latter are not specialists on the

particular foodstuff (meat is, after all, meat), but on the particular vehicle (animal) that the foodstuff comes in. Thus, unlike herbivores, it is obtaining the food that is the problem for a large carnivore, not the presence of the foodstuff *per se*. The latter perspective is evidently a larger-grained one and less of an impediment to migration than the former.

Hominins take something of an intermediate position in this respect. Given their broad dietary tolerances, at least after the appearance of the genus *Homo*, we can expect that their temporal scale matches that of the larger carnivorans, which means that the detail of hominin migrations would at the present level of resolution of the fossil record be invisible. Fortunately, resolution of the African Plio–Pleistocene fossil record is continually improving. When the scale of resolution goes significantly below 100,000 years, larger carnivorans may play a significant role in understanding biogeographic patterns at the regional scale and the details of hominin interregional migration patterns may become more amenable to study.

Acknowledgements

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