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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).***

Keywords: Carnivora; Africa; Miocene; Pliocene; Pleistocene; Phylogeography; Migration

Mots clés : Carnivora ; Afrique ; Miocène ; Pliocène ; Pléistocène ; Phylogéographie ; Migration

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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