Rodent faunal lists in karstic and open-air sites of Africa: an attempt to evaluate predation and fossilisation biases on paleodiversity

Listas faunísticas de roedores en yacimientos karsticos y al aire libre de África: un intento para evaluar los sesgos de predación y fosilización sobre la paleodiversidad

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ABSTRACT

The recorded differences of rodent diversity between the Plio-Pleistocene faunas of East Africa and Transvaal (South Africa) are discussed. A comparison is made with recent predation assemblages processes in order to evaluate this factor. Differential preservation but also fossilisation processes and more especially site nature and sedimentation factors are also reviewed here and an attempt is made to evaluate their influence on paleodiversity.

Key-words: Rodents, Predation, Owl pellets, Africa, Caves, Open-air sites Plio-Pleistocene, Diversity

RESUMEN

Se analizan las diferencias de diversidad registradas en las asociaciones de roedores dentro de las faunas Plio-Pleistocenas de Africa Oriental y el

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Transvaal (Suráfrica). Con objeto de evaluar este factor se ha comparado estos resultados con los procesos en conjuntos de predadores actuales. Se ha considerado asimismo la acción de factores tales como la conservación diferencial, pero también otros, como los procesos de fosilización y, más especialmente, la acción de los procesos sedimentarios y la naturaleza del yacimiento, en un intento por evaluar su influencia sobre la paleodiversidad.

Palabras clave: Roedores, predación, egagrópilas de buhos, África, cuevas, yacimientos al aire libre, Plio-Pleistoceno, diversidad.

INTRODUCTION

Eastern and Southern African regions stand among the various regions having yielded a good small mammals record. Plio-Pleistocene rodent assemblages from both areas were compared for the first time by Denys (1990) and it was concluded, in the absence of any taphonomical study, that the fossil assemblages from these two regions were different from the modern ones and that South Africa had greater species diversity of species than East Africa during Plio-Pleistocene times. Attempts to explain such differences included some ecological and biogeographical reasons, among them, a greater diversity of habitats in South Africa, isolation of South Africa, the presence of the Rift Valley in East Africa and the absence of extinctions allowing rodents to survive the different climatical episods (Denys & Jaeger 1986, Denys 1990). Since then, different taphonomical studies have demonstrated that predation is the factor to control the concentration of small mammals in fossil sites (Andrews 1990, Fernández-Jalvo 1992, Sánchez *et al.*,1997, Laudet 1995). Andrews (1990), Kowalski (1990) have shown that the size of preys and predators are important sources of biases and on the diversity of owl pellet assemblages as well as the hunting habits and diet of the raptor, the season of accumulation of the remains. Other works have pointed the importance of fossilisation processes in explaining the diversity of species (Andrews 1990, Badgley *et al.* 1995, Dauphin *et al.*, 1994, Denys *et al.*, 1996). Finally, the importance of differential preservation processes as a bias factor of the faunal content has just begun to be evaluated (Andrews 1990, Denys *et al.*, 1996).

The purpose of this paper is to review and evaluate the processes by which taphonomic factors (i.e. predation and fossilization) affect diversity and some component of the faunal composition. For this purpose, a review of the diversity patterns of modern, fossil and predation assemblages of tropical Africa, has been carried out.

MATERIAL AND METHOD

East and South African modern assemblages have been compared (Fig.1). Faunal lists have been found in literature as well as from my own data (Denys 1990, in press, in prep. tables 1, 2, 3). The different predation assemblages (owl and diurnal raptors pellets or carnivora scats) have been selected for this study only when the predator has been correctly identified and has yielded a rather good sample of individuals. Special attention has been paid to the Gerbillinae and Murinae diversity which is considered a good taxon-free indicator of aridity versus humidity for African faunas (Jaeger 1976, Fernández-Jalvo *et al.* submitted). The modern data have been plotted following the general vegetation zones defined by White (1986). The faunal lists given from large surveys or coming from intensive trapping sessions have also been included and were selected as reference sample by Denys (1990).

RESULTS

The specific diversity of modern rodent faunas of Africa is still not well described. For this approach, the description can be done at the genus level. This is not a problem for a comparison with fossil faunas and owl pellet assemblages, where the presence of two species of the same genus in the same assemblage is unusual. The generic diversity patterns of each biogeographical region of Africa is summarized in table 1. Mean diversity ranges between 10 and 38. Members of the subfamily Gerbillinae range between 0 and 4 genera whilst Murinae range between 2 and 18. The average diversity is lower in northern savannas (Sahelo-Sudanian-Guinean, with 15,3 genera) than in southern savannas (Zambezian, with 25 genera). The highest generic diversity does not occur in the forest but in the Somali-Masai region, i.e.the transitional area between northern and southern savannas (Table 1). The rodent community of the Sahara is constituted by numerous Gerbillinae, well-adapted to desert life, and a very low amount of Murinae. In Sahel, both groups, Gerbillinae and Murinae, show roughly the same number of genera. The Sudanian zone has similar number of genera of Gerbillinae as the Sahel. Compared to the Sahel, there are 7 genera of the sub-family Murinae. The

Biogeographic zone	**Rodents**	**Gerbillinae**	**Murinae**
Sahara	10	4	2
Sahelian	10	4	4
Sudanian	17	4	8
Guinean	19	2	11
Forest	30	0	17
Montane forest	19	0	9
Regional mosaic of Lake Victoria	30	1	16
Somali-Masai	38	34	18
Zambezian	25	1	12
Highveld temperate grassland	16	1	5
Namib	13	3	4
Kalahari-SW arid	24	3	6
Cape	17	2	7
Trappings	–	–	–
Zambezian	–	–	–
Songo Monzambique	8	0	6
Kafue River (Zambia)	24	2	10
Itala (Natal	9	0	6
Nyika (Malawi)	9	0	5
Cape	–	–	–
Cedarberg	11	1	4
Swellendom	12	1	5
Highveld Transvaal	–	–	–
Nylsvley	11	2	3
Grassland 1	18	3	4
Grassland 2	21	3	6
Acacia Savanna	13	1	4
Bush 1	24	3	9
Bush 2	22	3	8
Bush 3	19	2	8
Mopane Savanna	23	2	8
Bush 4	19	1	8
Forest	23	1	10
SW arid	–	–	–
Sw arid Transvaal	9	2	2
Kalahari Gemsbock Nat. Par	16	3	5
Somali Masai	–	–	–
Omo river (Ethiopia)	16	5	7
Kerio river (Kenya)	11	4	3
Tana River (Kenya)	7	0	2
Foret montagne Serengeti	15	0	11
Bush Serengeti (Tanzania)	17	3	12
Afro-alpine grassland Serengeti	7	0	5
Nakuru (Kenya)	11	0	7
Mont Meru (Tanzania)	14	0	9
Dakawa (Tanzania	14	2	10

main features of the rodent community of tropical and montane forest are the absence of Gerbillinae and a very high diversity of Murinae. The taxonomic diversity in the lake Victoria mosaic region, is peculiarly high (30 genera). Yet, this region has still not been well-studied and it will probably reveal a higher specific diversity. In the Zambezian savanna region, there is only one genus of Gerbillinae versus 12 genera of Murinae. The temperate Highveld grassland region is markedly impoverished compared to the Zambezian region (1 Gerbillinae for 5 Murinae). The Cape Province fauna is not very different from the Zambezian savannas with 2 Gerbillinae and 7 Murinae. The Namib and SW arid have 3 Gerbillinae for 4 to 6 Murinae. The faunal diversity and the Gerbillinae/Murinae ratio values are shown in table 1 for

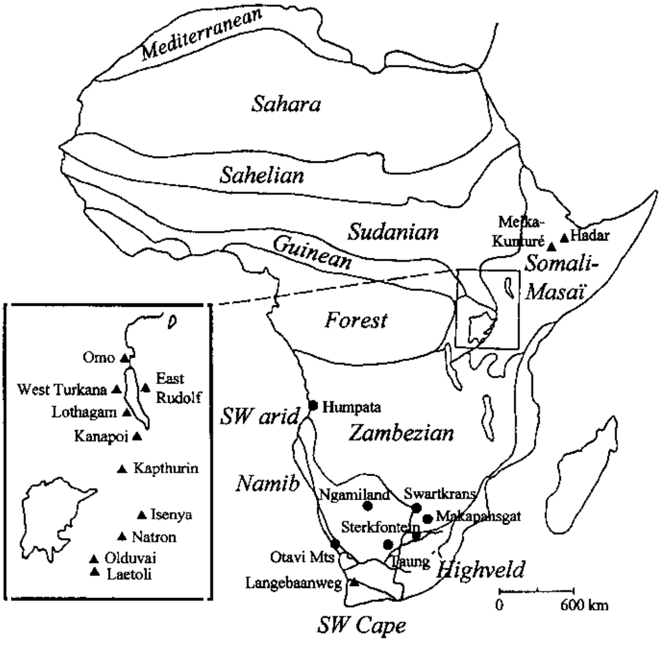

Fig. 1.–Main vegetation zones of Africa (after White 1983) and position of the main Plio-Pleistocene sites of East and South Africa. Cave sites. Open-air sites: Triangle.
Fig. 1.–Principales zonas de vegetación de África (según White, 1983) y posición de los principales yacimientos Plio-Pleistocenos de África Oriental y de Suráfrica. Yacimientos de cuevas: circulo; Yacimientos al aire libre: Triángulo.

Table 1.–Rodent diversity in modern vegetation zones of Africa and from different ecological surveys (after Denys 1990, *in prep.*, for references).
Tabla 1.–Diversidad presentada por los roedores en las distintas zonas de vegetación actuales de Africa y en diferentes reservas ecológicas (según Denys 1990, *in prep.*, para las referencias).

East Africa (Somali-masai	Age, Ma	MNI	Total	Rodents	Gerb.	Mur.
site						
Ibole	5		4	4	0	2
Hadar	3	165	10	10	1	5
Laetolil Beds	3,7	217	26	11	2	2
Omo B	3	85	26	13	1	7
Omo C	2,5	44	10	9	0	5
Upper Ndolanya beds	2,8	53	13	7	1	2
OMOF	2	69	19	13	2	6
OMOG	1,8	16	13	10	1	5
Oldavai Lower Bed I	1,8	111	16	14	1	9
Oldavai upper Bed I	1,7	429	18	15	2	7
Oldavai lower Bed II	1,1	–	10	10	1	6
Oldavai upper Bed II	1	–	4	4	1	1
Natron	1,7	14	12	7	0	4
East Turkana	1,6	15	14	9	1	5
Isenya	0,8	50	16	11	1	5
Olduvai Bed IV	0,8	–	11	11	1	6
Masek Beds	0,6	–	4	4	1	2
Kapthurin	0,3	–	5	5	0	1
Melka Kunturé	1	–	6	6	0	3
Ngaloba Beds Laetoli	0,12	–	7	7	1	3
South Africa	–	–	–	–	–	–
Zambezian	–	–	–	–	–	–
Humpata 2	1,3	–	11	11	1	5
Highveld	–	–	–	–	–	–
Makapansgat EXQRM	3,7	2708	35	17	1	8
Makapansgat MRCIS	3,7	1418	32	19	1	8
Makapansgat MLWD	3,7	291	20	15	0	9
Sterkfontein type site	3	3551	33	18	1	7
Sterkfontein Extension	1,7	–	16	16	0	9
Swartkrans	1,5	–	20	16	1	8
Kromdraai B	1,5	1350	31	20	1	7
Kromdraai A	1,5	371	19	16	2	7
Sw arid+Namib	–	–	–	–	–	–
Wondewerk	0,1	–	16	16	3	5
Jägersquelle	2	–	21	16	3	4
Nosib	2	–	19	14	1	5
Ngamiland	3	–	16	11	2	3
Taung	1,5	–	17	17	2	5
Cape	–	–	–	–	–	–
Langebaanweg QSM	5	843	14	14	1	4
Langebaanweg PPM 3AN	5	779	13	13	1	4
Langebaanweg PPM 3AS	5	565	13	13	1	4
Klasies River Mouth	0,1	–	35	15	2	7

different trapping studies. Of course the faunal diversity values of the trapping sites are lower than the general values obtained in the studied regions. This is also true for Murinae and Gerbillinae.

The Table 2 shows the generic and specific diversity of the fossil small mammal assemblages and when known, the MNI (Denys in prep). The diversity is greater in South Africa than in East Africa. In East Africa, the number of rodent species ranges from 4 to 15, while in South Africa it ranges from 11 to 20. Comparing the particular groups in East Africa the number of species of Gerbillinae ranges from 0 to 2 while Murinae range from 1 to 9. In South Africa, the recorded values are 0 to 3 Gerbillinae against 3 to 9 Murinae.

Concerning the owl pellet assemblages, the rodent diversity has been compiled from different sets of data in Africa (Tables 3 & 4) according to the raptor categories described by Andrews (1990). *Tyto alba* belongs to the predation category 1. No taphonomic information is available for *Tyto capensis* which has been provisionaly placed in category 1. For *Tyto alba*, the rodent species richness varies from 3 to 15 and the diversity increases with the MNI. The diversity of the total small mammals is much higher due to the fact that *Tyto alba* usually has other small mammals like bats and insectivores in its diet (Vernon 1972) (Table 3). According to Delany & Delany (1986), *Tyto capensis* hunts in grasslands unlike *Tyto alba*. For a smaller number of samples, *Tyto capensis* shows a slightly higher average values than *Tyto alba* of specific numbers of diversity for total small mammals and rodents (Fig. 2, 3). The prey-spectrum is larger for *Tyto alba* compared to *Tyto capensis*. This could be due only to the sample size, which is greater in *Tyto alba* than in *T. capensis* (Fig. 2). In *Tyto alba* and *Tyto capensis*, the average values for Gerbillinae and Murinae are different, *T. alba* taking more Gerbillinae and less Murinae than *T. capensis* (Fig. 4, Tables 3 & 4).

According to Andrews (1990) and Fernández-Jalvo (1996), *Bubo lacteus* and *Bubo africanus* belong to category 2 and *Bubo bubo* to category 3. The available data concerning the different species of *Bubo* (Table. 4), are still too scarce to be reliable. This could be due to the relative smaller size of samples, as it can be seen that the range of the preys, especially for non-rodents, is wider in *Bubo* than in *Tyto alba*. This may be related with the

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Table 2.–Total small mammal and rodent diversity of the Plio-Pleistocene fossil faunas of East and South Africa (after Denys 1990, Denys *in prep.*), Gerb., Gerbillinae, Mur., Murinae.

Tabla 2.–Diversidad total presentada por los pequeños mamíferos y los roedores en las faunas fósiles del Plio-Pleistoceno de África Oriental y Suráfrica (según Denys, 1990, *in prep.*), Gerb.: Gerbilinae; Mur:, Murinae.

Category 1	Author	Country	Site	MNI	Species Total	Rodents	Gerb.	Mur.	Region
Tyto alba	Laurie 1971	Tanzania	Oloserian	338	13	9	0	6	Somali-Masai
			Masai kopjes	785	11	8	0	6	Somali-Masai
			Simba kopje	106	6	5	1	2	Somali-Masai
Tyto alba	Vernon 1972	Cape provincie	Loc. 6	340	13	9	2	3	Cape
		Cape provincie	Loc. 7	219	6	4	1	3	Cape
			Loc. 9	152	7	7	1	3	Cape
			Loc. 11	119	11	9	1	3	Cape
Tyto alba	Avery 1992	Cape	ABKB	460	14	9	2	2	Cape
			BTY	529	13	9	2	2	Cape
			GBKA	789	17	11	2	3	Cape
			GBKB	2770	16	10	2	3	Cape
Tyto alba	Vernon 1972	S. W. Africa	Loc. 13	431	5	5	2	3	SW Africa
			Loc. 12	82	5	4	2	1	SW Africa
		Natal	Loc. 1	233	6	5	0	3	Coastal forest
			Loc. 2	481	6	6	0	5	Coastal forest
			Loc. 3	130	5	4	0	3	Coastal forest
			Loc. 5	146	9	5	0	2	Coastal forest
Tyto alba	Vernon 1972	Transvaal	Loc. 21	1240	18	12	1	5	Highveld
			Loc. 22	427	14	10	1	4	Highveld
			Loc. 23	644	19	12	1	5	Highveld
			Loc. 24	278	16	9	1	4	Highveld
			Loc. 25	891	16	12	2	5	Highveld
			Loc. 26	162	13	11	1	5	Highveld
			Loc. 27	120	10	7	1	2	Highveld
			Loc. 28	230	9	6	1	2	Highveld
Tyto alba	Stein 1984	Zimbabwe	Bulawayo	377	11	9	1	5	Zambezian
Tyto alba	Happold & Happold 1986	Malawi	Matope	911	18	15	1	10	Zambezian
		Malawi	Lunzu	350	13	10	1	6	Zambezian
Tyto alba	Demeter 1978	Nigeria	Samaru	54	8	6	1	4	Guinean
Tyto alba	Winterbottom 1966	Namibia	Etosha	35	9	8	3	3	SW Africa
Tyto alba	Dean 1973	Transvaal	Warmbaths	655	14	9	1	4	Highveld
Tyto alba	Dean 1975	SW Africa	Friedenthal	203	10	8	3	3	SW Africa
Tyto alba	Dean 1975	SW Africa	Gochas	1133	13	8	3	4	SW Africa
Tyto alba	Dean 1975	North Cape	Kingston	538	16	12	3	4	Cape
Tyto alba	Denys 1985	Botswana	Okavangos	85	9	7	1	2	SW arid
	Brain 1981	South Africa	Swartkrans			7	1	3	Highveld
Tyto alba	Levinson 1985	Transvaal	Makapansgat			11	1	6	Highveld
Tyto alba	Denys unpub.	Namibia	Naukluft park	81	3	3	1	1	Namib
Tyto alba	Ba et al. in prep.	Senegal	Crocodile	199	9	6	2	3	Sudanian
Tyto alba	Ba et al. in prep.	Senegal	P. commander	126	7	4	2	2	Sudanian
Tyto alba	St Girons 1973	Maroc	Bouznika	255	6	5	1	4	Mediterranean
Tyto alba	Bruderer 1966	Mauritanie	Chott Boul	70	10	9	5	3	Sahelian

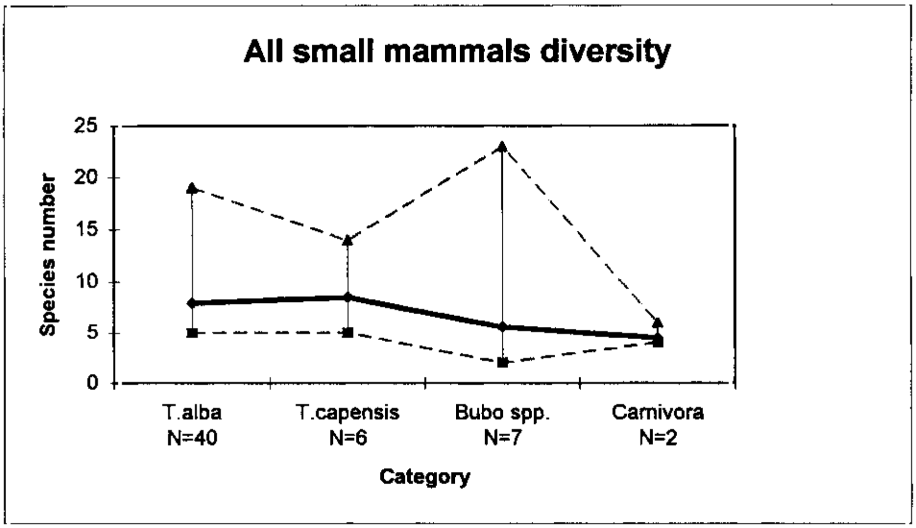

Fig. 2.–Total small mammals species numbers in different predation assemblages. Min: Minimum number of preys, Max.: maximum number of preys.
Fig. 2.–Número total de especies de pequeños mamíferos en diferentes conjuntos de predadores. Mín.: Número mínimo de presas, Máx.: Número máximo de presas.

larger size of the different species of *Bubo* spp (Fig. 2). Concerning this point, Andrews (1990) has remarked the opportunist diet of *Bubo lacteus* but with a preference for the gerbil *Tatera*. *Bubo africanus* is smaller than *B. lacteus* but has also an opportunist diet (Steyn, 1984).The number of species of Gerbillinae and Murinae are rather low for *Bubo spp.* compared to *Tyto spp* (Fig. 4).

Diurnal raptors and mammalian Carnivora are placed in categories 4 and 5. Their sample is low for Africa (Table 4). Some general remarks can be made: they have a low spectrum of preys (rodents and others) compared to categories 1 and 2 but also a lower MNI (Figs. 2, 3). By comparison, the number of Gerbillinae and Murinae is not so different from the two first categories of raptors (Fig. 3). The bulk of the diet of *Aquila verreauxii* is not formed by rodents (Boshoff *et al.*, 1991). Similarly, the scarce number of available pellets of *Falco tinnunculus* in Algeria yielded 2 Murinae, no Gerbillinae and a Crocidurinae (Denys & Mahboubi 1992).

Table 3.–Total small mammals and rodent diversity for predation assemblages of *T. alba*.
Tabla 3.–Diversidad total presentada por los pequeños mamíferos y los roedores en relación con los conjuntos de predadores de *T. alba*.

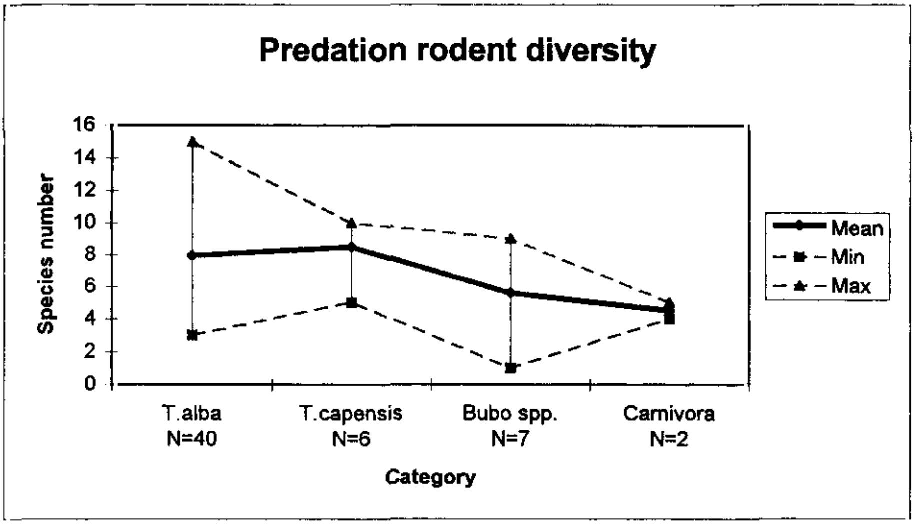

Fig. 3.–Rodent diversity in different predation assemblages. Min.: Minimum number of preys; Max.: maximum number of preys.

Fig. 3.–Diversidad de roedores en diferentes conjuntos de predadores. Min.: Número mínimo de presas; Max.: Número máximo de presas.

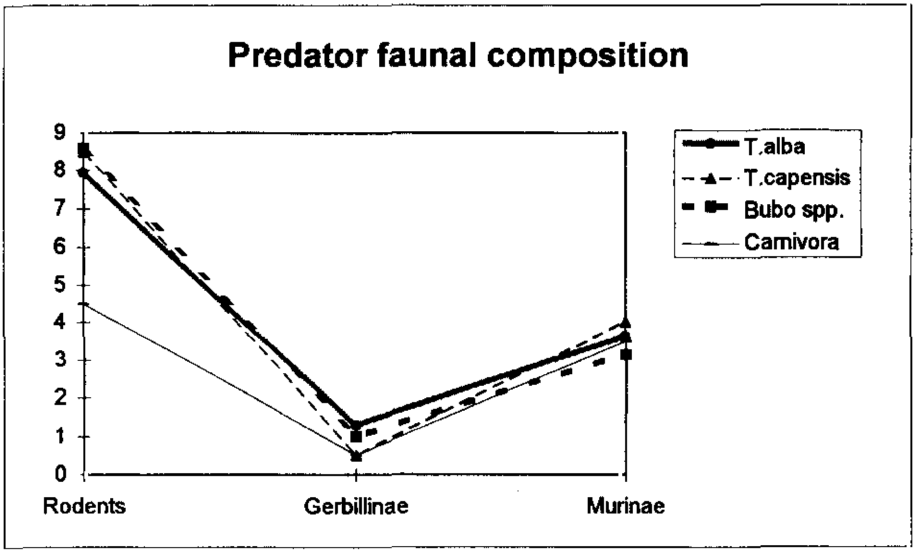

Fig. 4. Predation faunal composition on average for Gerbillinae and Murinae for modern assemblages.

Fig. 4.–Composición faunística media de los predadores para las subfamilias Gerbillinae y Murinae en conjuntos actuales.

Category 1	Author	Country	Site	MNI	Species Total	Rodents	Gerb.	Mur.	Region
T. capensis	Vernon 1972	Transvaal	Loc. 37	69	14	10	1	4	Highveld
			Loc. 38	68	8	7	1	3	Highveld
T. capensis	Vernon 1972	Natal	Loc. 29	124	5	5	0	3	Coastal forest
			Loc. 30	80	10	7	0	5	Coastal forest
			Loc. 32	74	5	5	0	3	Coastal forest
T. capensis	Happold & Happold 1986	Malawi	Zomba plateau	147	8	7	0	4	Zambezian
Category 2									
Bubo lacteus	Andrews 1990*	Tanzania	Olduvai	58	4	4	3	1	Somali-Masai
Bubo lacteus	Andrews 1990*	Tanzania	Serengeti	42	2	1	1	0	Somali-Masai
B. africanus	F.-Jalvo et al. unpub	South Africa	Clarens nest	26	6	4	0	2	Highveld
B. africanus	F.-Jalvo et al. unpub	South Africa	Clarens pellets	34	7	7	0	4	Highveld
Buboafricanus	Demeter 1982	Ethiopia	Awash	1409	23	9	2	5	Somali-masai
Bubo africanus	Brain 1981	South Africa	Swartkrans			6	0	3	Higveld
Category 3									
Bubo b. ascalaphus	Denys et al in press	Algeria	Honaine	588	15	10	2	6	Mediterranean
Bubo b. ascalaphus	Denys et al in press	Algeria	Aflou	438	9	7	5	1	Hts Plateaux
Bubo b. ascalaphus	Denys et al in press	Algeria	Iglí	340	11	10	7	1	Sahara
Bubo b. ascalaphus	Denys et al in press	Algeria	Kerzaz	56	8	8	7	1	Sahara
Bubo b. ascalaphus	Denys et al in press	Algeria	Oued Meniet	130	7	7	6	1	Sahara
Categoris 4-5									
Ichneumia albicauda	Andrews 1990*	Kenya	Meswa	19	4	4	0	4	Somali-Masai
Ichneumia albicauda	Andrews 1990*	Kenya	Meswa	19	4	4	0	4	Somali-Masai
Bat-eared fox	Andrews 1990*	Kenya	Lainyamok	23	6	5	1	3	Somali-Masai
Vulpes rueppelli	Kowalski 1988	Egypt	Bir Tarfawi		1	1	1	0	Sahara
Aquila verreauxii	Boshoff et al., 1991	South Africa	Cape prov. net	3572	12	2	0	0	SW Cape
Aquila verreauxii	Boshoff et al., 1991	South Africa	Cape prov. nest	1236	14	5	0	0	Cape
Aquila verreauxii	Boshoff et al., 1991	South Africa	Cape prov. nest	608	11	3	1	0	Cape
Falco tinnunculus	Denys & Mahboubi	Algeria	Tighenif	8	3	2	0	2	Mediterranean
Indet. categories									
Asio abyssinicus	Yalden 1973	Ethiopia	Urgana valley	89	6	5	0	2	Somali-Masai
?indet.	Denys unpubl.	Burkina Faso	Oursi	173	11	7	4	3	Sudanian
?indet.	Denys unpubl.	Tanzanie	Peninj	52	7	7	1	5	Somali-Masai

Table 4.–Total small mammal and rodent diversity of Andrews (1990) predator categories 2 to 5. The *T. capensis* assemblages are noted? category I but no taphonomic study of digestion is yet available for this owl. Concerning some *Bubo spp.* and mammalian carnivora assemblages, I have completed the taxonomic determinations (noted with*) at the species level for rodents compared to the list of Andrews (1990).

Tabla 4.–Diversidad total presentada por los pequeños mamíferos y los roedores de las categorías de predadores 2 a 5 de Andrews (1990). Los conjuntos de *T. capensis* están señalados como? categoría I pero no existe aún un estudio tafonómico detallado de la digestión para esta forma de buho. En lo que respecta a algunas formas de *Bubo spp.* y conjuntos de mamíferos carnívoros se han completado las determinaciones taxonómicas (señaladas con un asterisco) a nivel de especie para los roedores, comparándolos con la lista presentada por Andrews (1990).

DISCUSSION

From these results, it seems clear that the average diversity reflected by predation assemblages is low compared to traps and to regional diversity. The recorded diversity in the fossil assemblages both in East and South Africa is higher than in the pellets but, of course, lower than in regional zones. But the fossil diversity is higher than or similar to that in trappings (Table 6).

Despite the Somali Masai region shows today a higher diversity than the Zambezian and highveld region, it is the contrary for the fossil assemblages from the same regions (Table 6). The same situation occurs for the *T. alba* assemblages but this might result from a sampling bias (only 3 samples known from East Africa against 10 in the highveld and 3 in the Zambezian region, see Table 3). The comparison of the MNI between Tanzania and Transvaal *T. alba* samples shows that the diversity is similar or higher in the highveld whilst the proportion of Murinae is higher in Tanzania and that of Gerbillinae lower. The diversity is also higher in South Africa for the faunas resulting from trappings, South Africa being better ecologically surveyed than East Africa.

1. INFLUENCE OF PREDATION ON DIVERSITY

The *Tyto alba* and *T. capensis* assemblages contain a very low ratio of representatives of Gerbilinae (Table 6). These values are equivalent to those recorded in modern South savanna faunas but lower than the values recorded in East and North savanna. The same values are also recorded for the representatives of Murinae, confirming a lower diversity spectrum of Murinae in the pellet assemblages of Tyto (Table 6). In the

Fossil Faunas	**Rodents**	**Gerbillinae**	**Murinae**
East Africa N = 16	5,5	0,5	2,5
South Africa N = 18	15,4	1,33	6,06
Modern Faunas			
East Africa	38	3	18
South Africa	25	2	7

Table.5.–Summary of the rodent diversity patterns in modern and fossil faunas.
Tabla 5.–Resumen de los modelos de diversidad presentados por los roedores en conjuntos de faunas actuales y fósiles.

Pellets		**Total diversity**	**Rodents**	**Gerbillinae**	**Murinae**
T. alba	Mean	10,9	7,95	1,29	3,63
N = 40	Min.-Max.	5 to 9	3 to 15	0 to 3	1 to 10
T. capensis	Mean	11	8,5	0,5	4
N = 6	Min.-Max.	5 to 14	5 to 10	0 to 1	3 to 5
Bubo spp.	Mean	8,6	5,57	1	3,14
N = 7	Min.-Max.	2 to 23	1 to 9	0 to 3	0 to 7
Carnivora		5	4,5	0,5	3,5
N = 2	Min.-Max.	4 to 6	4 to 5	0 to 1	3 to 4
Traps	Mean		10	0,5	4,5
South Africa	Min-Max		8 to 24	0 to 4	2 to 10
East Africa	Mean		13	2,5	8
	Min-Max		7 to 17	0 to 5	2 to 12
Regions	Mean		15,3	3,33	7,66
North Savannas	Min-Max		10 to 19	2 to 4	4 to 11
Somali-Masai			38	3	18
South Savannas	Mean		20,5	1	8,5
	Min-Max		16 to 25	1	5 to 10
SW arid + Namibia	Mean		18,5	3	5
	Min-Max		13 to 24	3	4 to 6
Cape			17	2	7
Fossil faunas					
South Africa all	Mean	21,41	15,39	1,33	6,06
N = 18	Min-Max	11 to 35	11 to 20	0 to 3	3 to 9
SW arid	Mean	17,8	14,8	2,2	4,4
N = 5	Min-Max	16 to 21	11 to 17	1 to 3	3 to 5
Highveld	Mean	25,8	15,4	0,88	7,9
N = 8	Min-Max	16 to 35	15-19	0-2	7 to 9
Cape	Mean	18,8	13,8	1,25	4,75
N = 4	Min-Max	13 to 35	13 to 15	1 to 2	4 to 7
East Africa all	Mean	12,2	5,5	0,5	2,5
N = 16	Min-Max	4 to 26	4 to 15	0 to 2	1 to 7
Caves	Mean	22,73	15,8	1,4	4,26
N = 15	Min-Max	11 to 35	11 to 20	0 to 3	1 to 9
Open-air	Mean	12,35	9,57	0,91	6,5
N = 22	Min-Max	4 to 26	4 to 15	0 to 2	5 to 9

Table 6.–Average, Minimum and Maximum values of total small mammals, rodents diversity for predators, trappings, modern and fossil faunas.
Tabla 6.–Valores máximo, mínimo y medio del total de mamíferos de pequeña talla, diversidad de roedores en relación con predadores, trampas, faunas actuales y fósiles.

fossil assemblages of East Africa the average ratio of Gerbillinae is placed between the values of *T. alba* and *T. capensis* while it is clearly below the values of *Bubo sp.* (Table 6). As a whole, fossil assemblages from South Africa show a higher average number of species of Murinae and Gerbilinae than those from East Africa (Table 5). The average number of fossil species of Gerbilinae from South Africa is roughly the same as in *T. alba* but the number of species of Murinae is higher. It should be noted that the intervals of variation of the prey number are equivalent. The number of species of Gerbillinae is higher in the fossil assemblages of South Africa than in the pellets of *Bubo sp.* (Table 6, Fig. 4). In turn, the remains of Murinae in the fossil assemblages from South Africa are more abundant than in the *T. alba* and *T. capensis* assemblages.

Bubo spp. from South Africa displays a slightly lower proportion of Murinae than the corresponding representatives from Kenya (Table 4). However, compared with the expected values, this proportion is very low. On what concerns the relative proportions of Gerbillinae, the values are identical in present day representatives of *Bubo sp.*, and fossil assemblages from South Africa, but they are lower in those from East Africa. In recent faunas, however, the values are inverted. Concerning the Murinae, their number in fossil assemblages from South Africa is slightly lower in average than in recent assemblages from the same region, but higher than the values obtained from recent assemblages of *Bubo spp.*

In summary, predation reduces diversity even in the case of a very opportunistic predator like *Bubo spp* or very rich owl pellet assemblages with high MNI. A lower diversity seems also to be the case in predator categories 3 to 4 compared to category 1, but this needs to be confirmed by larger samples. In the set of assemblages studied for Africa, the range of rodent prey species found in predation assemblages varies from 1 to 15 with a low average of 6,63 for all predators and 8,2 for the *Tyto spp.* assemblages. This decrease of diversity is less important in Gerbillinae than Murinae especially in the case of *Bubo spp.* which seems to predate selectively on gerbils. In the same way, it has also been shown (Andrews 1990) that prey selection and hunting habits of these owls can favor Gerbillinae compared to Murinae. The peculiarity of the South African fossil assemblages is their abundance in Murinae compared to East Africa, but also to predation assemblages. This, joined to the fact that all fossil assemblages show higher diversity than the recent owl pellet assemblages, reflects the greater importance of other factors than digestion and predation in controlling the fossil diversity.

2. DIFFERENTIAL PRESERVATION AND DIVERSITY

As it has been shown, differential preservation of skeletal parts can favor the preservation (in terms of completeness of the skulls not in terms of diversity) of the most strongly built skulls of Gerbillinae and Dipodidae in *Bubo b. ascalaphus* pellets from Algeria (Denys *et al.*, 1996). Being more fragile, the skulls of Murinae may be more easily broken during the digestion processes (Denys, 1985) and hence offering less resistance to post-predation alterations processes which take place during burial and diagenesis. Studies of digestion traces on molars of Murinae and Gerbillinae show their better resistance to digestion attacks compared to the rootless evergrowing molars of Arvicolinae molars. Only a careful taphonomic analysis of the fossil assemblages will permit to evaluate this point in the present discussion. But, in general, post-predation and burial, diagenetical processes can be very destructive for bones and produce over-breakage patterns (Andrews, 1990) that make skull remains very rare and isolated teeth abundant (Sánchez *et al.*, 1997). One notable exception is the Laetoli Beds site in Tanzania where 10 nearly complete skulls of small rodents have been found. They belong to *Saccostomus* and *Heterocephalus* (Denys, 1986) but no skulls of Murinae or Gerbillinae have yet been found. *Saccostomus* is today rarely found in owl pellets assemblages as well as *Heterocephalus*. In that site, rapid burial has preserved here the most abundant, larger Muroidea and an exclusively fossorial rodent probably trapped in their burrows during the volcanisc ash falls rodents. Differential preservation result from intrinseque properties of bone structure and morphology and in fact this implies an increase in the range of larger, stronger elements (large Gerbils of Tatera group) versus smaller more fragile Murinae in the fossil assemblages. But, the nature of a site, its mode of formation as seen for the Laetoli Beds can be also important to explain the paleodiversity.

3. FOSSILIZATION AND DIVERSITY

Some observed anomalies in diversity can be explained by different factors, other than predation and differential preservation. These would mainly be: the different diversity pattern and the Murinae/Gerbillinae ratios of South African versus East African fossil assemblages compared respectively to modern diversity and pellet assemblages patterns. In fact, it should be noted that all East African sites correspond to «open-air» depo-

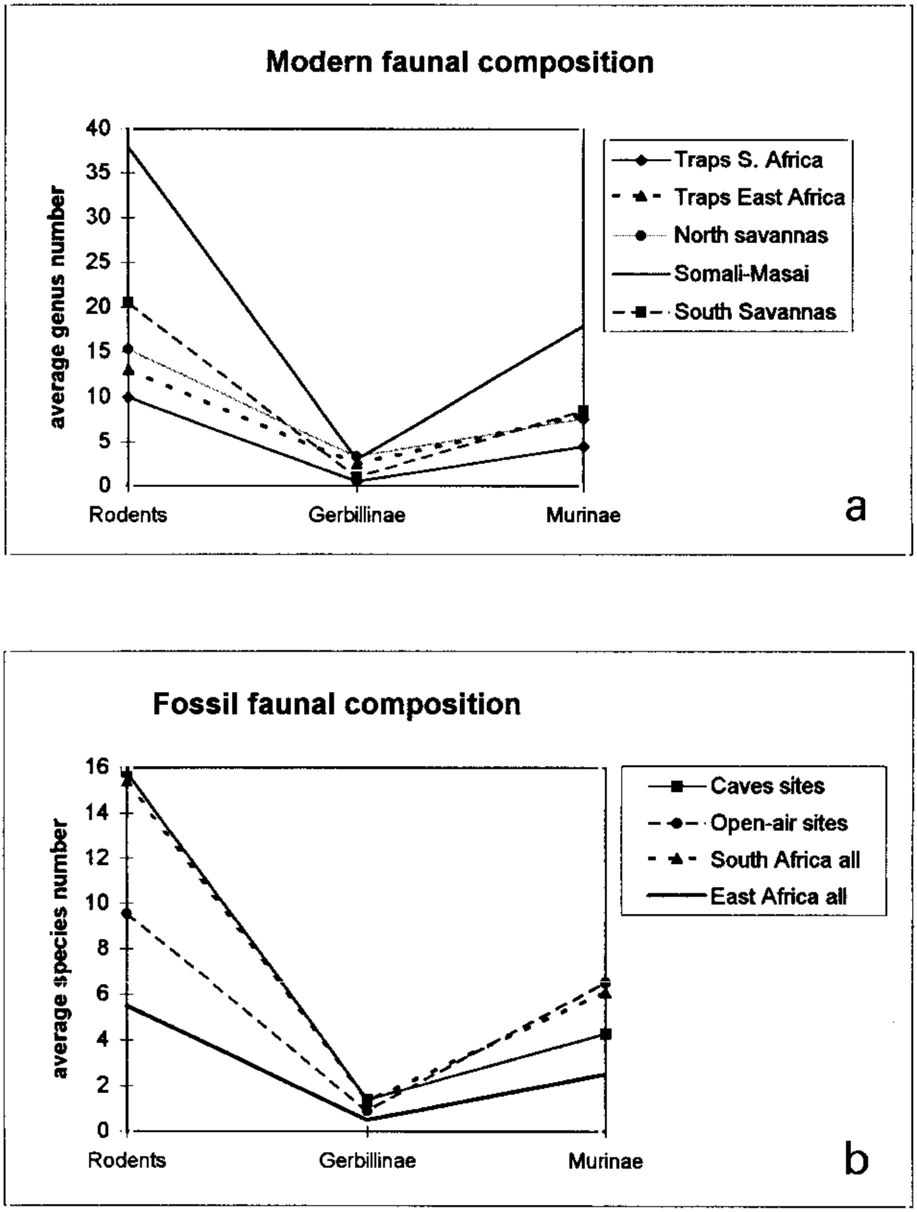

Fig. 5.–Faunal composition on average for Gerbillinae and Murinae for modern trappings and vegetation regions (5a) and for fossil faunas of East and South Africa (5b).
Fig. 5.–Composición faunística media de los predadores para las subfamilias Gerbillinae y Murinae en trampas actuales y regiones de vegetación (5a) y para conjuntos fósiles de África Oriental y Suráfrica (5b).

sits (lacustrine or fluviatile; terminology *sensu* Denys *et al.* in press) whilst most of South African sites are cave deposits with the only exception of Langebaanweg. We have plotted the recorded diversity values in these two different types of sites (Figs. 5a, 5b, 6). On figures 5b and 6, caves show a higher diversity than open-air sites. Representatives of Murinae are more abundant in open-air sites than in caves, whilst the Gerbillinae are more scarce in open-air sites. Cave sites present a higher diversity than predation assemblages. In open-air sites, in turn the values of diversity are much lower than in caves but closer to those of predation assemblages. In cave sites we nearly reach the level of the modern assemblages which is not at all the case in open-air sites. It is evident that cave sites yield generally a more abundant number of individuals (MNI; Table 2). But, even in the case of very abundant rodent-bearing and nicely preserved open-air sites such as Olduvai Bed I, the number of species is lower than for the Transvaal Australopithecine caves (Table 2).

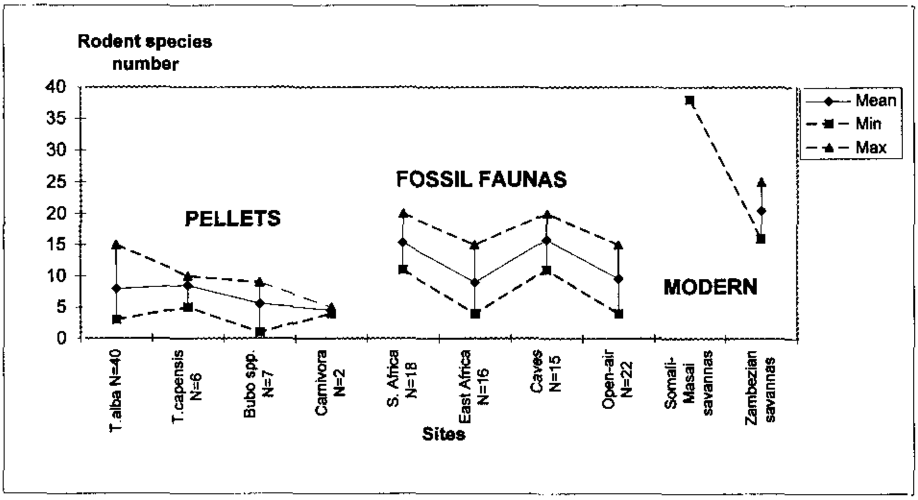

Fig. 6.–Relative comparison of the species number of rodent preys in pellets, fossil faunas and modern faunas.

Fig. 6.–Comparación relativa del número de especies de presas de roedores en egagrópilas, conjuntos fósiles y faunas actuales.

The processes of formation of caves and open-air sites are very different. Cave formation and sedimentary infill are rather complex processes implying different successive phases (Andrews, 1990; Brain, 1993; Fernández-Jalvo 1995, 1996). Evidence of transport by water occur frequently in caves and are responsible of reworking (Andrews, 1990, Cáceres *et al.*, 1996, Fernández-Jalvo, 1995, Laudet, 1995, Laudet *et al.*, 1996). Similarly, mixing of predator agents of bone accumulations can be more important in cave sites offering shelter for different animals (Baird, 1991). In caves, predators can relay through time in a same place. Also different types of owls and/or carnivora can occupy different parts of the cave, hence providing a supplementary increase of diversity. This mixture of predators (that can only be recognized after a careful taphonomic study) may lead to an increase in the species diversity in a site and could be an explanation for the higher diversity observed in South Africa. At Olduvai a taphonomic study has shown in level FLKN 5 a mixture of two predators. This corresponds to the highest diversity for all other East African sites (Table 2; Fernández-Jalvo *et al.*, in press). According to Badgley (1995), who found that certain taxa are predominant in some particular facies in the Siwaliks open-air sites, it follows that for a particular stratigraphic interval the taxonomic diversity should increase if a higher variety of sedimentary facies is sampled. Taking into account the facies diversity in East African open-air sites versus South African caves, we can see that in open air deposits of East Africa silty-clay (lacustrine sediment) and volcanic ashes are the only source of sediment where small mammal bones have been concentrated. In the caves of South Africa, however, sediments are more varied especially in those cave sections representing a complex filling history. For example, the stratigraphic sequences at Makapansgat cave comprises travertine deposits, calcified red mud, grey breccia, gravels, some bands with well-rounded pebbles, indicating sediment transport at some phases of the sedimentation in the cave and numerous lateral facies variations (Partridge 1979, Maguire *et al.*, 1985). At Langebaanweg, which is the only open-air site of South Africa, and despite some problems of lateral facies variation in the site, the total diversity of small mammals is very low compared to Transvaal cave sites (Denys, 1990).

To summarize, open-air sites clearly show lower diversity values compared to cave sites. This may be due to several factors, among which, time-averaging, reworking, cohabitation of predators, long duration of roosting and multi-sources of sediments transported from the surface, can be listed as the most relevant. Of course, time-averaging and reworking are also active in open-air sites, but the three other factors are suspected to be more efficient in caves.

CONCLUSION: FACTORS INFLUENCING DIVERSITY

Almost all South African fossil assemblages of karstic (cave) origin have yielded highly varied spectra of diversity compared to East African sites where rodents have been obtained in open-lacustrine sediments. From this work it is shown that the paleodiversity of small mammals depends basically on three parameters, namely predation bias (digestion, hunting habits, ingestion), differential preservation and fossilisation. Predation bias reduces in general the overall number of prey species, but the selectivity of a predator can lead to an overrepresentation of some taxa like Gerbillinae in *Bubo spp*. Ingestion-digestion biases can produce an overrepresentation of some taxa versus the others and favor the preferential preservation of more strongly built skulls like Gerbillinae or Dipodidae which biases not only the faunal lists but also some ecological indices (like, for instance, the Gerbillinae/Murinae ratio of Jaeger 1976). Finally, the fossilisation processes and especially time-averaging not only modify the initial community structure but can lead to an increase in diversity patterns by mixture of different predators and/or different levels. This case is clearly evident in the comparison of East African to South African sites. For palaeoecological interpretations, it is evident that cave sites reflect more diverse habitats and/or predators than open-air sites which would rather reflect more than one (at least two) predation assemblages. If the predator is an opportunist species the bias will be lower than in the case of a selective one. But, for cave sites the problems of transport and reworking are important and need to be taken in consideration by means of a careful taphonomic analyses prior to any palaeoecological interpretation. The fact that the Gerbillinae/Murinae ratio is biased by these three factors (hunting habits, differential preservation, fossilisation) has also palaeoecological consequences and only a careful taphonomical study *taxa per taxa* permits recognizing the modification of this ratio by differentiating the possible mixture of predators and of sources of the fossil material.

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