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Mechanical and chemical alterations of skeletal tissues in a recent Saharian accumulation of faeces from *Vulpes rueppelli* (*Carnivora, Mammalia*)

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Abstract. A collection of modern sand-fox *Vulpes rueppelli* faeces from the Egyptian desert has been analysed using the taphonomic method. These excrements come from Bir Tarfawi, an uninhabited oasis in the Saharan desert. Representation, fragmentation, abrasion as well as chemical content of the preserved skeletal and dental elements of vertebrates have been analysed by various techniques (calculation of representation and fragmentation percentages, percentages of molars and incisors digested, SEM & EDS analyses). The results show the action of canid digestive tract and that stomach juices greatly alter not only the structures of bones and teeth but also their chemical composition. The first phase of digestion plays an important role in the fossilisation processes by inducing major pre-diagenetic biases. The contribution of small-sized Carnivora to bone accumulations in fossil sites must be exceptional and fortuitous.

Key words: taphonomy, bones, *Vulpes rueppelli*, Egypt.

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I. INTRODUCTION

The complex processes involved in the fossilisation of recent assemblages of terrestrial vertebrates are still poorly understood. It is asserted that such primary concentrations of modern bones as owl pellets or carnivora faeces (coprocoenosis: MELLET 1974), represent an initial condition leading to the formation of fossil accumulations (ANDREWS 1990).

Studying such modern assemblages of microvertebrates from the taphonomical point of view is a recent method. It has been suggested that common methodology should be used for modern and fossil assemblages. However, before trying to reconstruct the origin of fossil sites, it is necessary to develop the study of modern concentrations.

It is well known that microvertebrate sites provide valuable data on stratigraphy, paleogeography, and systematics. Moreover, they can also be used to reconstruct the past climatic environment, diet of preys and predators or diagenetic processes. Exact knowledge of the origin of a fossil bone accumulation is of great interest because during the initial stages of concentration (i.e. preburial and burial phases), some biases may occur in taxonomical, mechanical and chemical preservation (DAUPHIN et al. 1989; DENYS 1985; KOWALSKI 1990). These biases should be taken into account in further interpretations of the site, and they probably play a role in the future evolution of the assemblage during diagenetic processes (DAUPHIN & DENYS in press).

There is general agreement that most fossil microvertebrate asemblages are due to primary accumulations of avian pellets. Therefore the few available taphonomic studies have been concentrated on recent owl pellets. The data on other bone collectors are rare, while it has been shown that carnivores, ants or porcupines can be important agents giving rise to primary concentrations.

The presence of a large collection of faeces of *Vulpes rueppelli* in the Institute of Systematics and Evolution of Animals (Polish Academy of Sciences) in Cracow inclined us to undertake this study.

Many studies have been devoted to the preservation of bones in pellets assemblages (ANDREWS 1990; BRAIN 1981; DENYS 1985; DENYS & MAHBOUBI 1992; DODSON & WEXLAR 1979; HOFFMAN 1988; KORTH 1979; KUSMER 1990; MAYHEW 1977; RACZYŃSKI & RUPRECHT 1974). Some of them deal rather with representation, others with fragmentation. Macro- and microscopic aspects of remains are also described, as is their chemical content. Most of the authors attempted to define the criteria for identifying each type of modern coprocoenosies, but this approach clearly puts in evidence the difficulty in distinguishing between predators involved. It appears that at least 14 parameters (qualitative and quantitative) were required to recognize the species of the predator and to distinguish different assemblages (ANDREWS 1990). This method based mostly on counting the preserved skeletal elements and examination of breakages and digestion patterns is relatively tedious. But, one of the results of these studies, is the possibility of applying the same method for both modern and fossil microvertebrate assemblages, even if in the latter case it requires further improvements (DENYS subm. msct).

Few studies of mammalian predator faeces assemblages have been made to this end (ANDREWS & NESBIT-EVANS 1983; ANDREWS 1990). It was generally asserted that the preservation of bones in carnivora faeces is very limited owing to the heavy action of stomach juices. However, in some cases besides owl pellets, the excrements of carnivores represent important preliminary phase of concentration of small mammals remains in modern environment (ANDREWS 1990). ANDREWS (1990) analysed remains derived from *Canis latrans* and *Vulpes vulpes* from Europe, but the data are very limited.

With the development of methods for chemical investigation, more authors tried to characterize each skeletal tissue (i.e. bone, enamel, dentine). It is well known that bone, dentine and enamel have different compositions; the mean H_2O content of bone is about 32%, 22% for organic matter and 46% for mineral phase. The proportions are respectively 13.2%, 17.5% and 69.3% in dentine; they are 2.3% (H_2O), 1.7% (organic matter) and 96% (mineral phase) in enamel. Moreover, the chemical composition differs between these hard tissues. The data on bones are numerous, but they are often based on captive or laboratory animals. The current opinion is that the chemical composition of hard tissues is partly dependent on diet. Captive and laboratory animals have a special diet, so they can hardly be used as reference. Therefore, we have established new references for the chemical composition of fresh killed wild rodents using the punctual analytic method (DAUPHIN & DENYS 1988).

The chemical composition of recent rodent bones and teeth are summarized in Table I. The highest contents of Ca and P are in enamel, the lowest in molar dentine. The incisor and molar enamels are rich in Cl and Na. The incisor dentine is characterized by a very high content of Mg (higher than 1%). The Ca/P weight ratio varies from 1.59 (incisor dentine) to 1.83 (bone and molar enamel) (Table II). According to the weight ratio 100Sr/Ca (referred to as Sr/Ca further in the text), recent rodents are herbivorous animals if the data from SILLEN (1981) are used. In this respect the molar enamel is on the boundary between herbivores and carnivores (Table II). According to the data published by BYRNE & PARRIS (1987), the 100 Mg/Ca weight ratio is about 1.603 in deer bone and 0.852 in

Table I

Chemical content of fresh recent bones and teeth (in ppm). m: average, s: standard deviation, mi: minimum, M: maximum, IE: incisor enamel, ID: incisor dentine, ME: molar enamel, MD: molar dentine

		Na	Mg	Cl	S	Fe	Zn	Sr	K	Mn	P	Ca
BONE	m	**3784**	**4181**	**629**	**2179**	**790**	**1091**	**456**	**564**	**279**	**141578**	**259512**
	s	951	769	141	742	759	516	311	464	332	10519	18896
	mi	2100	2760	450	1100	117	200	172	60	0	126600	240200
	M	5547	5150	913	3290	2917	2150	1130	1513	904	163000	304600
IE	m	**7311**	**1438**	**3974**	**65**	**561**	**966**	**401**	**384**	**2**	**189846**	**340741**
	s	604	206	900	77	67	404	209	330	5	17944	30753
	mi	6790	1290	2711	0	467	630	114	200	0	166033	299456
	M	8156	1742	4783	175	610	1510	611	878	9	205650	366500
ID	m	**4941**	**13442**	**583**	**1244**	**533**	**1234**	**1219**	**1074**	**883**	**162602**	**257906**
	s	1405	2096	146	336	117	554	1159	1089	119	18498	37740
	mi	3420	11260	400	690	450	670	178	93	0	141379	205364
	M	7080	16786	733	1550	730	2090	3200	2678	267	179800	291900
ME	m	**6471**	**3225**	**2077**	**465**	**605**	**1659**	**284**	**378**	**99**	**156344**	**287030**
	s	1086	3011	481	475	141	694	133	300	104	26497	62362
	mi	5030	1030	1690	10	500	1120	140	0	0	128736	219300
	M	7490	7440	2780	1020	810	2670	450	660	236	190900	350000
MD	m	**4243**	**2359**	**704**	**1488**	**541**	**1122**	**552**	**774**	**123**	**124986**	**213732**
	s	263	1266	225	1103	175	413	199	565	156	55721	117875
	mi	3900	1064	450	322	283	700	355	200	0	65645	88909
	M	4483	3920	922	2436	670	1642	809	1308	345	179400	328000

Table II

Weight ratios of hard tissues in fresh wild recent (REC) and Bir Tarfawi rodents (BIR). Sr/Ca is 100Sr/Ca, as Mg/Ca, Zn/Ca and Na/Ca. Same abbreviations as in Table I

		Ca/P	Sr/Ca	Mg/Ca	Zn/Ca	Na/Ca
	BONE	1.833	0.176	1.611	0.420	1.458
R	IE	1.795	0.118	0.422	0.283	2.146
E	ID	1.586	0.473	5.212	0.478	1.916
C	ME	1.836	0.099	1.124	0.578	2.254
	MD	1.710	0.258	1.104	0.525	1.985
	BONE	1.951	0.342	1.331	0.325	2.171
B	IE	1.827	0.200	0.395	0.303	2.498
I	ID	1.625	0.185	5.772	0.335	2.944
R	ME	1.768	0.083	0.339	0.036	2.240
	MD	1.797	0.071	1.181	0.298	2.034

cat bone. Our data on rodent bones indicate, as expected, a herbivorous diet. This is also true of the 100 Na/Ca weight ratio, while the 100 Zn/Ca weight ratio is lower than the data published previously.

These new approaches to fresh bones have also been extended to the skeletal elements extracted from owl pellets or from fossil accumulations (DAUPHIN et al. 1989, DAUPHIN & DENYS in press). The presented studies have been undertaken to characterize the changes in the bone and other skeletal tissue contents resulting from digestion or from fossilisation. If the chemical effects on the bone composition resulting from digestion by owls are now known (DAUPHIN et al. 1989), that is not yet the case as regards mammalian predators.

II. MATERIAL AND METHODS

A. Material

Fresh recent rodent specimens originated from France: *Rattus rattus*, *Mus musculus*, *Apodemus sylvaticus*, *Arvicola terrestris* and from Tanzania : *Arvicanthis* sp. Four molars, 5 incisors (one devoid of enamel) and 11 bones were used for chemical analyses. All the animals used were collected in wildlife environment. This sample was prepared with animals from different geographical regions and different taxonomic groups to eliminate some problems related to the diet or local geochemical variability.

The scats from which the material studied here originated were collected in an uninhabited oasis in the southern part of Egyptian Western desert (22°55' N, 28°53' E) by one of us (K. KOWALSKI). This region is very arid with scarce vegetation. 634 scats of

the sand fox *Vulpes rueppelli*, collected on the surface were prepared and sorted under water. The faunal composition was given by KOWALSKI (1988, Table I, p. 91). Vertebrates were present in more than 67% of faeces. Lizards were rare, while snakes and birds were more common. Insects were also present. The only rodents in the material studied was *Gerbillus gerbillus* (KOWALSKI 1988). 7 bones, 3 molars and 3 incisors of the last species have been analysed with EDS system.

B. Methods

The contents of the carnivora faeces were studied by the method described by DAUPHIN & DENYS (1988), DAUPHIN et al. (1989) and ANDREWS (1990).

a. Preservation and fragmentation

The degree of preservation and fragmentation of skeletal elements were calculated on

$$PR = \frac{Observed\ frequency}{Theoretical\ frequency} \times MNI$$

the basis of two indices, the percentage of representation (PR) and the percentage of fragmentation (PF), and were compared with other assemblages.

MNI : minimal number of individuals found in the assemblage.

Observed frequency (OF): relative frequency of each skeletal element found in the assemblage studied.

Theoretical frequency: calculated number of the specimen of each bone found as a function of MNI. For example, on the assumption that all the bones of each individual are present in the fecal accumulation, we should find for one individual: 1 skull, 2 mandibles, maxillaries, femora, humeri, tali, calcanea, ulnae, tibia-fibulae, radii, scapulae, pelves), 1 sacrum, 4 incisors, 12 molars, 54 vertebrae, 24 metapodials, 54 phalanges, 24 ribs. PR is obtained by averaging PR calculated for each skeletal element.

The fragmentation percentage is the ratio of unbroken bones to the total number of bones found.

b. Digestion

Other criteria are used to determine the degree of digestion in a coprocoenosis. They are the degree of digestion of incisors and molars (ANDREWS, 1990) and the degree of digestion of some long bones, both determined by macroscopic and microscopic observations (ANDREWS 1990; DENYS 1985). The SEM observations have been performed on the JEOL SEM 6300 F (URA 327 C.N.R.S., Université de Montpellier 2).

c. Chemical analyses

The punctual analytic method was used for comparison between recent and fossil rodents: scanning electron probe X-ray emission micro-analysis (Energy Dispersive Spectrometry or EDS). It allowed us to analyse hard tissue, avoiding sediment contamination.

Analyses were made with a Link microprobe (URA 723 C.N.R.S., Université Paris 11 - Orsay), using the AN 10000 program. This method is nondestructive, and the positions of the points analysed in relation to the structural features are precisely known. This is necessary because of the small size of rodent teeth, and the vicinity of enamel and dentin. The concentrations of P, Ca, Na, Mg, Cl, S, Fe, Zn, Sr, K and Mn were counted. The beam diameter is 100 or 200 nm, the voltage is 15 Kv, the reference element is cobalt.

Data can be obtained in the form of spectra (Fig. 1). Because of the high ratio of Ca and P, other bands are flattened. So the computer gives data as the ratio of contents. About 10 points were analysed in the tissue of a specimen. The values of these ten points were averaged to give one mean for the tissue and one for the specimen.

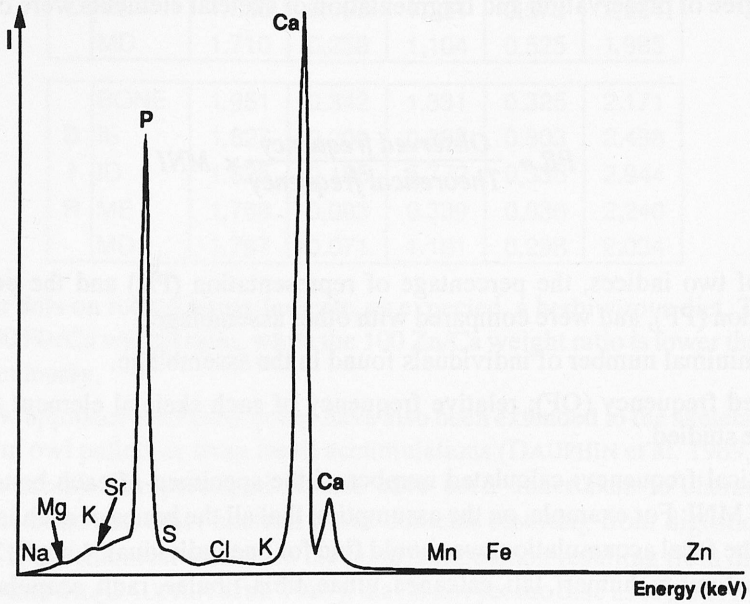


Fig. 1. X-Ray spectrum with K lines, but without Sr (L lines) from a rodent bone from Bir Tarfawi. I: Intensity.

A multivariate analysis was performed with the principal component analysis, based on correlation matrix (STATITCF program). Bone, dentine and enamel from Bir Tarfawi scats represent 19 specimens, whereas in the fresh recent rodent material 34 specimens are represented. Variables are represented by 11 chemical elements.

IV. RESULTS

A. Skeleton preservation

The preservation of the rodent skeletal elements recovered from the Bir Tarfawi scats is characterized by a very small number of bones and still smaller of identifiable bones. Nearly all skeletal elements of vertebrates were represented, except for braincase bones.

There is no scapula. The representation of bones is given in Table III. NMI (calculated on the basis of the number of left maxillaries) is 4 individuals. In some scats only isolated molars were found. The mean percentage representation is 26.3% (N = 15), against 27.3% when isolated incisors and molars are included (N = 17). Some skeletal elements are still joined together and there is a complete distal paw and 4 connected vertebrae.

The degree of fragmentation is high and there is no intact bone. The patterns of breakages are given in Fig. 2 and Plates IV-VI. Many of the bones are broken to such a degree that they are not identifiable, showing angular sharp ends. Only the proximal femur heads remain intact, but no other parts of the articular zone. The distal end of the femur

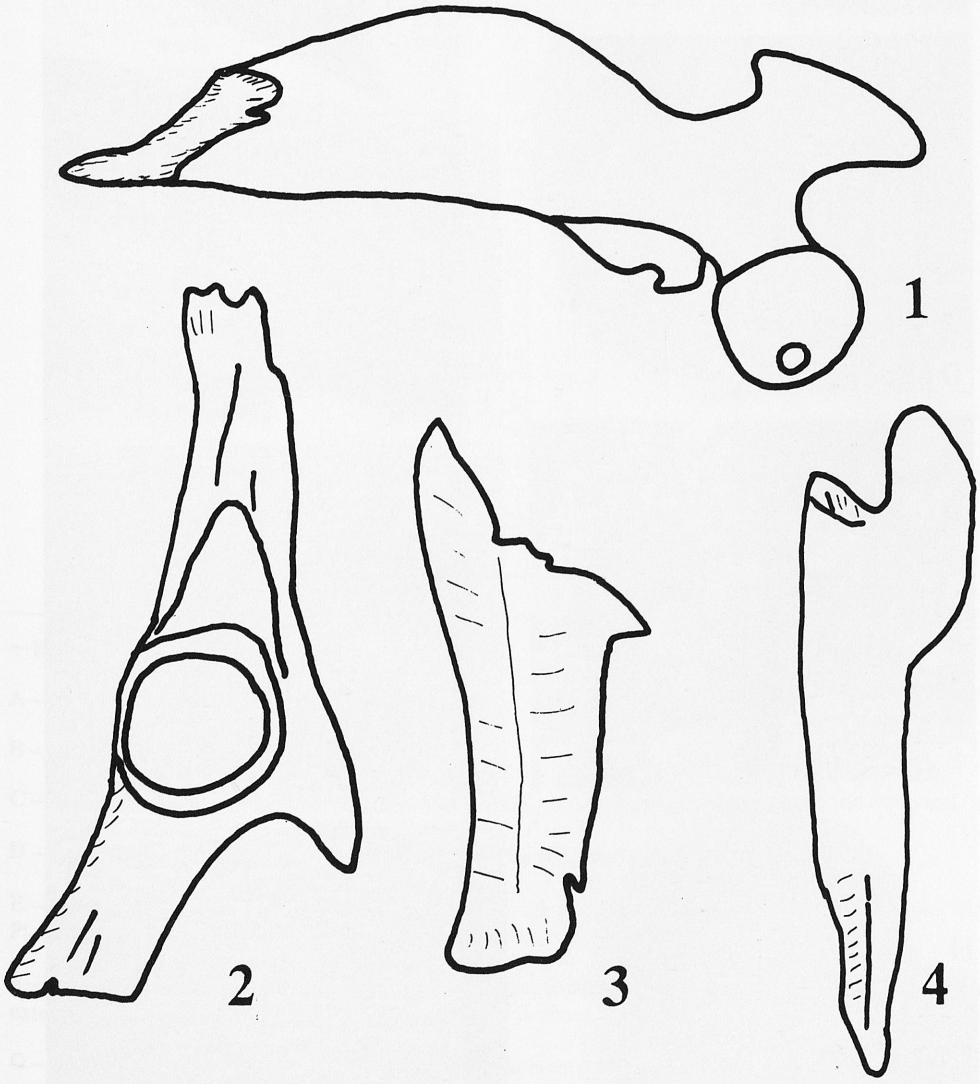


Fig. 2. A view of the bone breakages in scats of *Vulpes rueppelli*. 1 – proximal shaft of a femur (x10), 2 – pelvis fragment with acetabulum (x10), 3, 4 – unidentifiable bone fragments showing characteristic breakages.

Plate IV

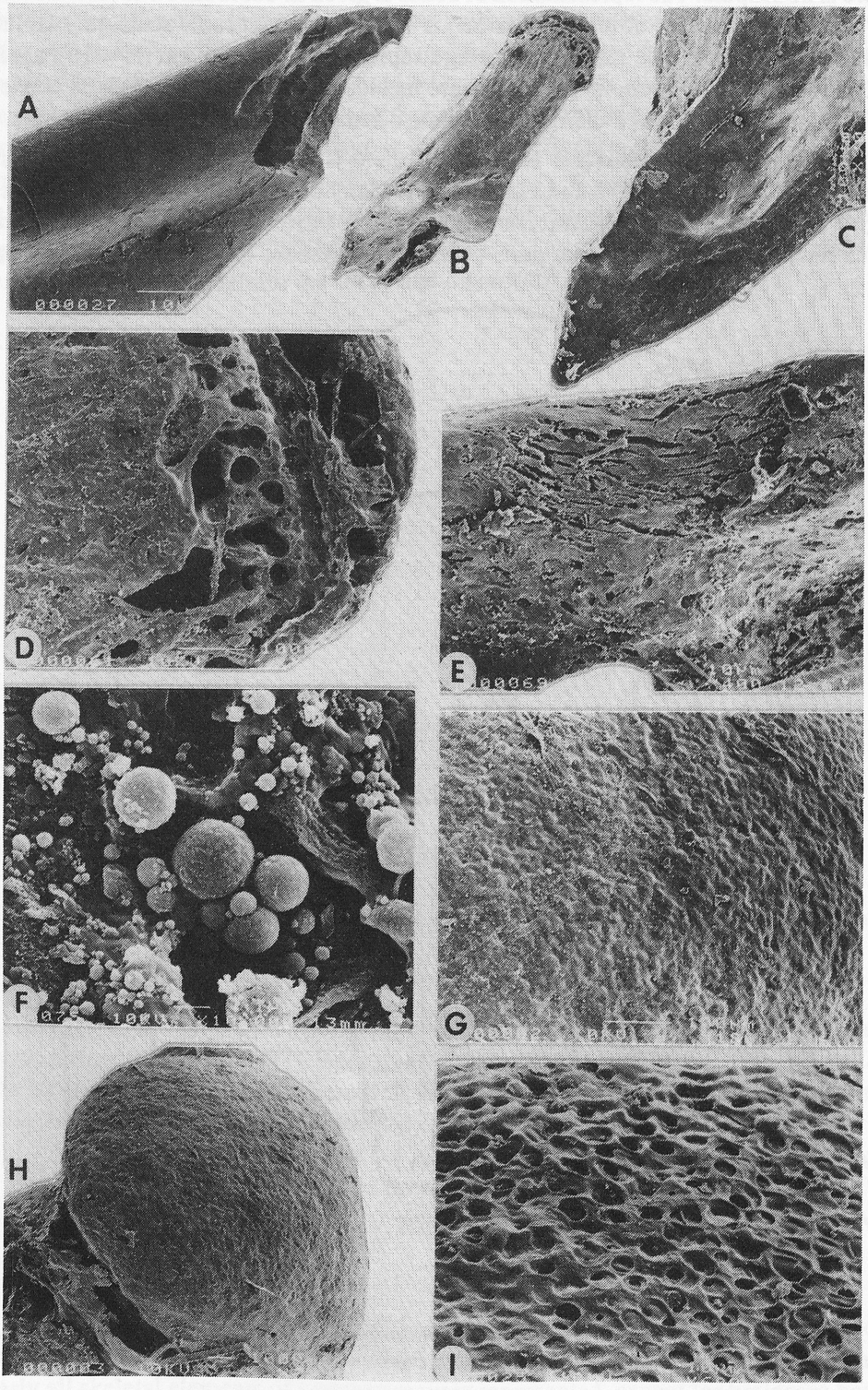


Table III

Observed frequencies of skeletal elements and average representation percentages for the Bir Tarfawi *Vulpes rueppelli* scat assemblages. Comparison with other canid assemblages after ANDREWS & NESBIT-EVANS (1983). MNI: minimal number of individuals. OF: observed frequency, PR: percentage representation.

	Vulpes rueppelli		*Canis latrans*		*Vulpes vulpes*		*Alopex lagopus*	
Skeletal element	OF	PR	OF	PR	OF	PR	OF	PR
Mandibles	5	62.5	13	92.8	4	50	6	100
Maxilla	7	87.5	8	57.1	2	25	5	83.3
Incisors	8	50	16	57.1	10	68.8	0	0
Molars	10	20.3	25	29.8	15	31.3	12	33.3
Femur	4	50	14	100	8	100	1	16.6
Tibia	1	12.5	12	85.7	5	62.5	2	33.3
Pelvis	4	50	6	42	2	25	0	0
Calcaneus	2	25	2	14.3	2	25	0	0
Talus	1	12.5	1	7.2	1	12.5	2	33.3
Humerus	4	50	14	100	6	75	3	50
Radius	1	12.5	10	71.4	2	25	1	16.6
Ulna	2	25	9	64.3	3	37.5	1	16.6
Scapula	0	0	2	14.3	1	12.5	0	0
Ribs	3	1.6	13	8.4	8	8.3	5	7.5
Vertebrae	19	4.4	57	25.4	30	23.4	26	27.1
Metapodials	3	1.9	36	25.7	23	28.9	18	30
Phalanges	0	0	66	15.7	48	20	53	29.4
Number of bones	**59**		**2015**		**938**		**186**	
MNI	**4**		**7**		**4**		**3**	
Number of scats	**634**		**27**		**24**		**10**	
Relative average PR		**24.45**		**47.3**		**37.1**		**28**

←Plate IV

A – Broken proximal end of a femur shaft (× 18).

B – General view of a calcaneum (× 15).

C – Aspect of a fracture in the shaft of a *Gerbillus gerbillus* femur showing smoothed bone and sharp end (× 54).

D – Detail of proximal articular surface of a calcaneum with heavy perforations (× 100).

E – Detail of *Gerbillus gerbillus* mandibule bone much alterated under the roots of M_1 (general view in Plate V G) (× 250).

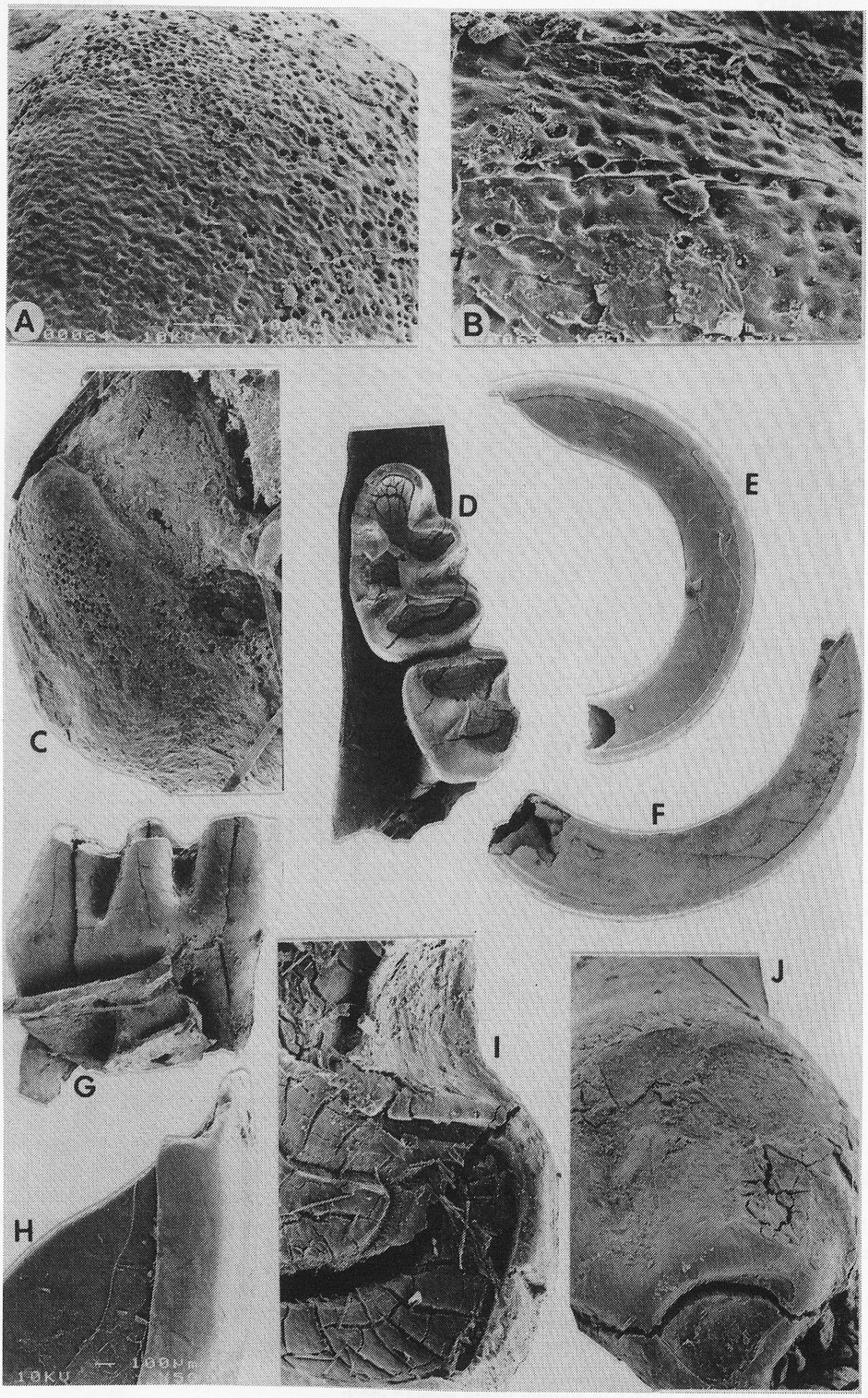
F – Spheric particles of unknown origin, varying in size, found all over on some bones and teeth; here on the external face of an isolated incisor; the largest sphere is about 2 μ in diameter (× 6 000).

G – Proximal head of a femur; detail of the cancellous bone (× 100).

H – General view of the previous femur head, showing no significant signs of alteration (× 40).

I – Detail of the articular surface of another femur head (× 360).

Plate V



is usually missing, and the shaft shows a very angular sharp end (Fig. 2, Plate IV A). On the mandible, the teeth are preserved but the bone is corroded very much (Plate IV E, VI G). No complete mandible or maxilla have been found. Pelves are broken, only the acetabulum zone subsists (Fig. 2). The proximal and a distal part of humeri, and a proximal ulna are present, but none of these rodent bones is complete. On the other hand, there is an intact bird humerus.

B. Digestion

Incisor digestion: most of the examined incisors from Bir Tarfawi show signs of corrosion. The isolated incisors show a white transparent enamel, dentine being generally brown. A lower *Gerbillus gerbillus* incisor shows a longitudinal crack on the external face (Plate VI E). The boundary between enamel and dentine is altered very much compared with fresh incisors (Plate V E, F, H). It is generally depressed and pits caused by dissolution can be observed (Plate VI F-H). On maxillary fragments with incisors, there are also traces of dentine and enamel dissolution on the visible part of the incisor.

Molar digestion: molars of *Gerbillus gerbillus* show different stages of alteration. The main characteristics were an abundance of cracks (Plate V A-D, G, I, J), and in some cases the in situ destruction of parts of the molars, specially the posterior cingulum of M_1 and M_2. Most of the teeth were literally embedded in small hair remains, and recovered with small irregular round particules of unknown origin (Plate IV F). The enamel around the

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←Plate V

A – Femur head showing a few signs of alteration (× 36).

B – Detail of articular crest of calcaneum (Plate IV D) (× 360).

C – Detail of femur articular surface (× 54).

D – Left *Gerbillus gerbillus* mandible with M_{1-2}; general view showing heavy digestion, many cracs in both longitudinal and transverse directions, dentine melted and collapsed, enamel collapsed in some parts (× 18).

E – General view of a *Gerbillus gerbillus* isolated incisor showing relatively few alterations except for the contrast between enamel and dentine layers (× 7).

F – General view of another isolated *Gerbillus gerbillus* incisor damaged a both ends with the begining of dentine dissolution on the dentine-enamel boundary but relatively few signs of digestion (× 12).

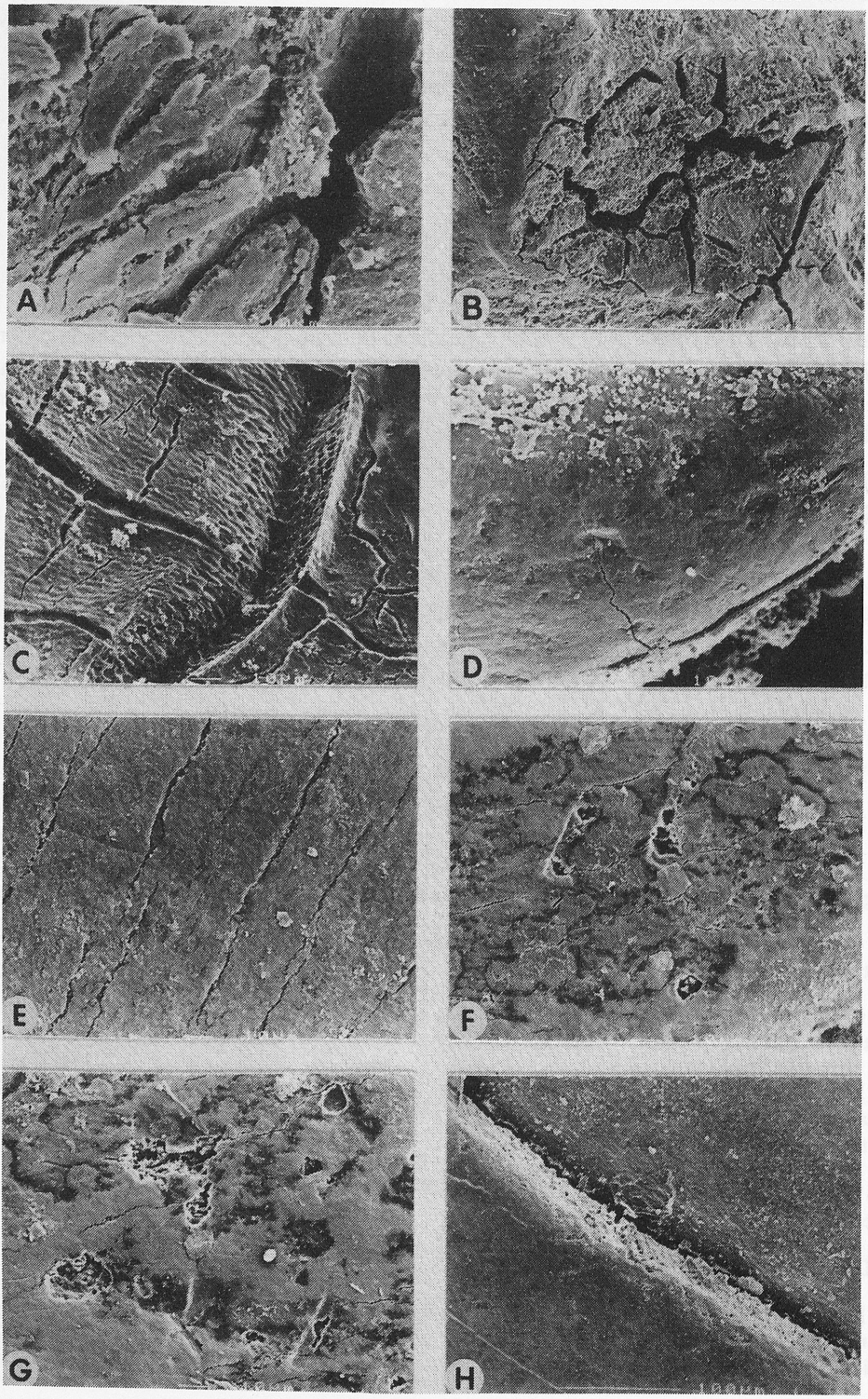
G – Lateral view of *Gerbillus gerbillus* mandible with M_1 internal side; the mandibular bone is much altered (detail in Plate IV E), the enamel is smooth and does not show signs of digestion, the same is true of the roots, but the fractures are numerous and severe (× 24).

H – Tip of a *Gerbillus gerbillus* incisor, showing a depression between dentine and enamel and moderate digestion (× 30).

I – Detail of the distal part of M_2 showing severe corrosion and cracks of enamel and dentine (× 108).

J – Detail of the prelobe of a *Gerbillus gerbillus* M^1, showing a transverse crack on the enamel-dentine boundary, this crack being continued laterally on the anterocone flanks . The anterior flank of this cusp shows distinct signs of alteration, illustrated in next photos (× 72).

Plate VI



cusps is smooth, except for small areas, generally situated at the boundary of the two tissues, where the structure is exposed. Entire layers of enamel can be removed, while in some specimens the dentine appears to be dissolved and collapsed (Plate V Fig. I).

On 13 maxillary and mandibular fragments with molars in situ, only one specimen shows well preserved, white and bright dentine, without traces of digestion. Five specimens show the enamel and dentine slightly affected, but the still white dentine shows light signs of dissolution. In 7 specimens, the dentine is very deeply dissolved and takes on a brown color, while the enamel can collapse. It is dissolved punctually, but can be well preserved in some parts of the same molar.

Bone digestion: mandibles and maxillary bones are corroded very much, especially at the boundaries with alveolar regions (Plate IV E, V G). They show signs of intense digestion, like longitudinal cracks, zones of deep holes sometimes displaying the roots of the molars, or of the incisors. The fracture zones are not rounded and show sharp, angularly foliated layers of cancellous bone.

The calcanea and talii also show signs of intense digestion, with relatively deep holes on the articular surfaces (Plate IV B, D). The femur head is slightly corroded and the surface of the cancellous bone does not show signs of deep intense abrasion (Plate IV H). At higher magnification, the surface of the cancellous bone seems to have been polished (Plate IV G, I, Plate V A-C). The shaft of the femur, as well as the region of fracture look quite smooth. The same was observed in the proximal humerus. The bone abrasion differs from scat to scat.

C. Chemical preservation

Fig. 1 shows a typical spectrum obtained for a compact bone of a Bir Tarfawi rodent. The high ratio of Ca (2 main bands) and P flattens the other bands (Sr, Mg...). The chemical content in bones and teeth is given in Table IV.

←Plate VI

A – Enamel desquamation on the border of the anterocone of the *Gerbillus gerbillus* M^1 (detail of Plate V J) (× 780).

B – Detail of the prelobe of the *Gerbillus gerbillus* M^1 showing mosaic cracks of the enamel (× 840).

C – Surface of the dentine of M_2 (detail of Plate V D and I) showing the exposed structure and numerous cracks (× 480).

D – Enamel border of an anterior cusp of *Gerbillus gerbillus* M_2, showing some small pits in a rather smooth and unaltered enamel (× 720).

E – Surface of a *Gerbillus gerbillus* incisor with longitudinal cracks without visible structure underneath (× 480).

F – Detail of the alterations on the surface of an isolated *Gerbillus gerbillus* incisor (× 480).

G – Round pits on alterated surface of the same isolated incisor as in previous photo (× 510).

H – Detail of the dentine-enamel separation in an isolated incisor, showing a depression on the boundary between the two tissues and moderate digestion; the enamel has a bevelled border (× 200).

Table IV

Chemical content in Bir Tarfawi bones and teeth. Same abbreviations as in Table I

		Na	Mg	Cl	S	Fe	Zn	Sr	K	Mn	P	Ca
BONE	m	6553	4019	1395	1467	506	981	1030	280	121	154711	301866
	s	886	722	152	224	114	411	940	335	112	10425	27370
	mi	5050	3217	1192	1092	300	400	0	8	0	136150	252544
	M	7827	5350	1583	1756	633	1692	2917	1012	325	169120	338887
IE	m	9056	1431	4507	90	415	1100	725	292	26	198423	362459
	s	900	446	323	109	115	188	643	216	38	6308	17249
	mi	8138	923	4246	23	331	885	15	84	0	191308	345400
	M	9938	1761	4869	215	546	1231	1269	515	69	203331	379892
ID	m	8679	17016	724	492	482	987	545	697	64	181364	294790
	s	1170	2335	162	175	32	233	260	5	61	8616	11133
	mi	7353	14673	543	350	446	720	247	692	14	172027	285029
	M	9569	19343	853	687	507	1150	728	700	133	189008	306915
ME	m	8095	1190	3203	382	675	1250	293	565	67	187677	351358
	s	915	46	160	315	101	80	449	401	83	13445	15348
	mi	7070	1150	3040	60	560	1170	0	110	0	178430	341760
	M	8830	1240	3360	690	750	1330	810	865	160	203100	369060
MD	m	6369	3698	1405	938	309	932	223	863	45	174243	313068
	s	1587	952	1012	858	226	241	379	417	56	10687	26178
	mi	5075	2867	792	320	50	770	0	470	8	163536	293791
	M	8140	4736	2573	1918	467	1209	660	1300	110	184910	342870

The bones show a high Ca content (Table IV). Their Ca/P ratio is the highest. The bones have the highest contents of S, Sr and Mn and the lowest of Na, K and P. The enamel and dentine of incisors have a clearly different composition. The enamel is characterized by high contents of Na, Cl, P and Ca and low contents in Sr and Mn. The highest content of Mg occurs in dentine, whereas that of Cl and Ca is the lowest. The dentine shows the highest K content and its contents of Fe, Zn and Sr are the lowest. The highest contents of Fe and Zn and the lowest in Mg were found in the molar enamel. The molar and incisor enamel contain more Na and Cl than does their dentine. However, the Na/Cl ratio is different from that of NaCl. The molar and incisor enamel has higher contents of P and Ca that the dentines of these teeth. The dentine has a high Mg content. The Ca/P, Sr/Ca, Mg/Ca, Zn/Ca and Na/Ca ratios are presented in Table II. The Na/Ca ratios are similar in all the tissues studied, whereas Sr/Ca has a wide range. The Zn/Ca ratios are homogeneous, except in molar enamel.

V. DISCUSSION

A. Skeletal preservation

In the Bir Tarfawi assemblage of rodent bones, all skeletal elements are represented, except the braincase bones and the scapula. Taking into account the very small number of individuals estimated (MNI), the representation percentage is rather high compared with

other Canidae (ANDREWS & NESBIT-EVANS 1983). In earlier studies, the scapula was found in *Vulpes vulpes* and *Canis latrans* scats, but was absent in those of *Alopex lagopus*. The absence of connected posterior elements of the skull is general among carnivora assemblages, and is related to the ingestion mode of these predators.

The fragmentation patterns of the Bir Tarfawi assemblage are typical of carnivora digestion in showing angular ends of broken bones and molars broken in situ. The digestion of bones and teeth seems highly variable according to the predator, but *Vulpes rueppelli* digestion results in extreme corrosion of molars, and less extreme of incisors and bones. For *Otocyon*, ANDREWS & NESBIT-EVANS (1983) showed, as in Bir Tarfawi, the splitting of teeth and strong polishing of bones. They also noticed the occasional presence of articulated bones for *Canis latrans* and *Alopex lagopus*, but none for *Vulpes vulpes*. However, some of the cracks and splits of the Bir Tarfawi skeletal elements may result from a secondary weathering alteration. Faeces have probably been exposed to the action of the atmosphere for a long time in the dry climate of the Sahara, which may have caused supplementary alterations. At the present time, it is difficult to separate them from digestion effects.

B. Chemical preservation

Despite the small size of Bir Tarfawi samples, a t test has been calculated to compare them with the fresh recent rodent ones. These results are summarized in Table V. The differences between fresh and Bir Tarfawi bones are quite evident; they have 5 elements with a significant t test. Incisor dentine and molar enamel have 2 significant t tests, whereas molar dentine is similar. Na is the most discriminating chemical element: fresh and Bir Tarfawi bones, incisor enamel and dentine having a significant t test. Cl, S and P have also 2 significant t tests, Ca only one (Table V).

Table V

Results of the t-test between fresh wild recent rodents and Bir Tarfawi samples. S: significant difference, NS: non significant difference. Abbreviations as in Table I

	BONE	IE	ID	ME	MD
Na	***S***	***S***	***S***	NS	NS
Mg	NS	NS	NS	NS	NS
Cl	***S***	NS	NS	***S***	NS
S	***S***	NS	***S***	NS	NS
Fe	NS	NS	NS	NS	NS
Zn	NS	NS	NS	NS	NS
Sr	NS	NS	NS	NS	NS
K	NS	NS	NS	NS	NS
Mn	NS	NS	NS	NS	NS
P	***S***	NS	NS	***S***	NS
Ca	***S***	NS	NS	NS	NS

A principal component analysis shows that the first axis represents 33% of the total variance, the second axis 14.9%, the third one 11.9%. The specimens are sorted along axis 1 according to their contents of P, Ca and Na, opposed to S. They are sorted along axis 2 according to their contents of K, Mg and Na opposed to Fe (Fig. 3). They are sorted along axis 3 according to their contents of Mg and Sr. Except for fresh incisor enamel, the fresh tissues are grouped in the left part of graph axes 1-2 (Fig. 3), that is the low contents of P and Ca, and high content of S. The Bir Tarfawi specimens are in the high P and Ca content part of the graph. The fresh specimens are spread along axis 2, whereas those from Bir

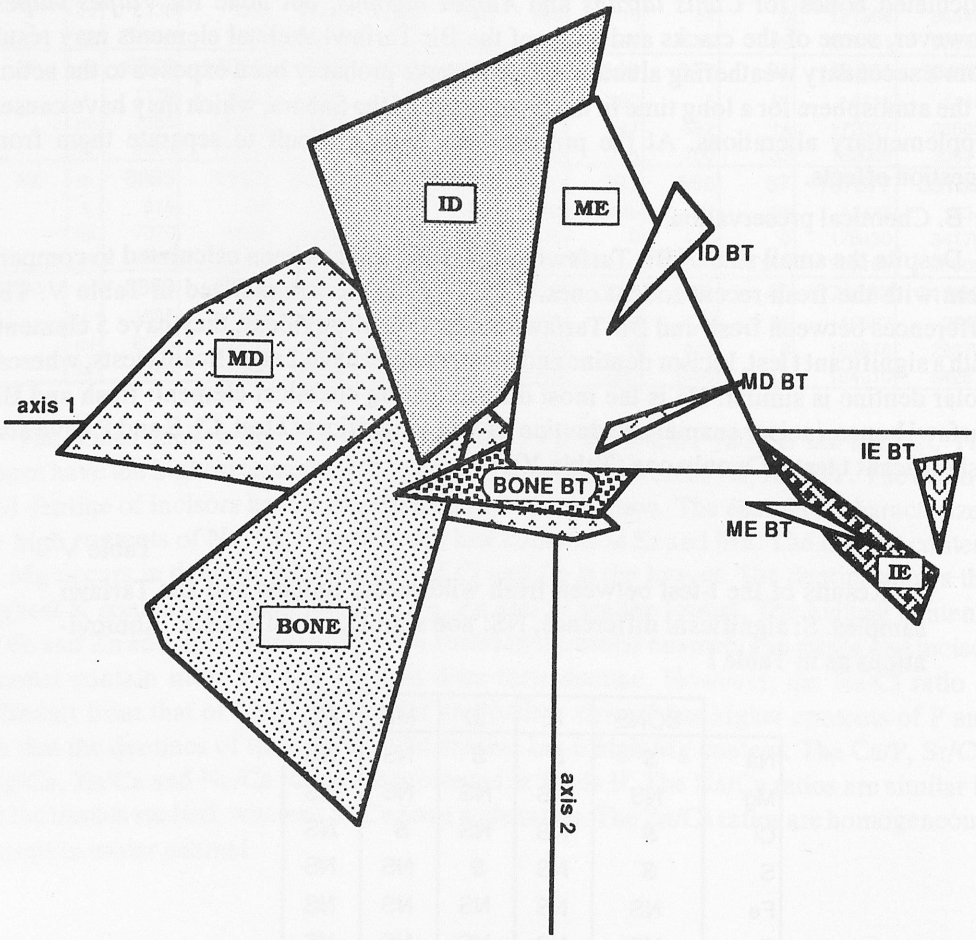


Fig. 3: Graph of individuals (Bir Tarfawi skeletal elements compared with fresh bones of wild rodents) obtained from PCA (correlation matrix data). Axis 1 (33%) represents the P, Ca and Na contents opposed to S; axis 2 (14.9%) represents the K, Mg and Na contents opposed to Fe. Bone BT: Bones from Bir Tarfawi; Bone: fresh bones of wild recent rodents; IE BT: incisor enamel from Bir Tarfawi; IE: fresh incisor of wild recent rodent enamel; ID BT: incisor dentine from Bir Tarfawi; ID: fresh incisor dentine of wild recent rodent; MD BT: molar dentine from Bir Tarfawi; MD: fresh molar dentine of wild recent rodent; ME BT: molar enamel from Bir Tarfawi; ME: fresh molar enamel of wild recent rodent.

Tarfawi are more concentrated (Fig. 3). Enamel shows the highest content among the fresh tissues and in the Bir Tarfawi sample. Only the fresh bones and the digested one have an overlap in their distribution (Fig. 3). The incisor dentine is clearly differentiated from other tissues in graph axes 2-3 owing to its high Mg content. The highest correlation coefficient is that for Ca and P (0.91); then P and S (r = –0.69). Others are lower than 0.57 in absolute values.

In the Bir Tarfawi samples, the Sr/Ca ratios are modified (Table II). However, they still fit into the variability of herbivorous animals. On the contrary, it has been shown that in the fossil assemblage of Tighenif (Algeria, Pleistocene) the bone Sr/Ca ratio (altered by diagenesis) indicates that rodents fit into the carnivorous animals values (DAUPHIN & DENYS, in press). According to the Sr/Ca ratios of other tissues, rodents are herbivorous. At this stage of the fossilisation process, the digestion by the predator does not induce major alterations.

VI. CONCLUSIONS

The macroscopic and microscopic characteristics of the bones accumulated by *Vulpes rueppelli* from Bir Tarfawi seem to correspond to the criteria given by ANDREWS (1990). So far, only 4 canid scat assemblages have been studied using such a methodology. There is not yet enough data to get statistical results, especially when individual variation in digestion depending on the age of preys and predators is considered. The differential conservation occurs in all the studied assemblages, especially in Bir Tarfawi, where enamel can be dissolved or preserved in the same tooth.

Chemical analyses confirm that digestion modifies skeletal element content. Chemical alterations are heterogeneous. The various ratios used for paleoenvironmental or diet reconstruction are also altered. Similar changes have been previously observed in owl pellet assemblages (DAUPHIN et al. 1989).

The importance of pre-diagenetic changes induced by the passage through the digestive tract of a predator is now confirmed and has to be taken into consideration in the study of microvertebrate assemblages. Even if the structure of skeletal tissues is still apparent, there are chemical changes which probably modify future changes in skeletal elements during further fossilisation processes. Early fragmentation and mechanical abrasion of bones and teeth are all factors influencing the future of the assemblages and their ability to fossilize.

The last question is to what degree such scat assemblages can contribute to the formation of fossil assemblages. Despite the high number of scats (634) collected in Bir Tarfawi, there are ony 59 identifiable mammalian bones and 18 isolated teeth of *Gerbillus gerbillus*. They are few compared with other canid scat assemblages. The bone proportions were, respectively, 2015 bones/27 scats for the coyote, 938 bones/24 scats for the red fox and 186 bones/10 scats for the artic fox (ANDREWS & NESBIT-EVANS 1983). The reason for such a low vertebrate share in the remains of Bir Tarfawi can also be explained by the very poor fauna of vertebrates in this small oasis with only a few species present (among them only one species of rodents; KOWALSKI 1988). The diet of the predator as a function of the environement should also be taken into consideration in interpreting differential preservation.

Despite the very characteristic traces left by digestion by carnivores, there are few probabilities that a fossil assemblage originates from such a coprocoenosis.

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