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C. R. Palevol 3 (2004) 583–590

COMPTES RENDUS PALEVOL

General Palaeontology (Palaeobiochemistry)

Diagenetic trends of dental tissues

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Received 6 October 2003; accepted after revision 12 July 2004

Written on invitation of the Editorial Board

Available online 16 September 2004

Abstract

Dentine and enamel from mammal teeth of modern fresh samples, regurgitated pellets, carnivore faeces and fossil samples have been studied from a variety of locations in terms of their microstructure and chemical composition. Enamel is more durable than dentine during fossilisation, and consequently is less altered in terms of its composition. Statistical analyses of the data show that contents of several elements differ between enamel and dentine; that fossil teeth are generally depleted in Mg and Na, and enriched in Fe and Sr relative to modern samples, and that the different fossil sites can be discriminated. ***To cite this article: Y. Dauphin, C.T. Williams, C. R. Palevol 3 (2004).***

Résumé

La structure et la composition chimique de la dentine et de l'émail de dents actuelles et fossiles de mammifères d'origines et d'âges variés ont été examinées. Les dents actuelles sont fraîches, ou extraites de pelotes de régurgitation et de fèces de carnivores. L'émail est souvent moins altéré que la dentine, mais n'est pas dépourvu de modifications diagénétiques. Une analyse statistique montre que les dents fossiles sont généralement appauvries en Mg et Na, mais enrichies en Fe et Sr. Les caractéristiques et les amplitudes des altérations dépendent des sites fossiles. ***Pour citer cet article : Y. Dauphin, C.T. Williams, C. R. Palevol 3 (2004).***

Keywords: Enamel; Dentine; Mammals; Microstructure; Chemical composition; Diagenesis

Mots clés : Émail ; Dentine ; Mammifères ; Microstructures ; Composition chimique ; Diagenèse

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1631-0683/$ - see front matter
doi:10.1016/j.crpv.2004.07.007

Version française abrégée

1. Introduction

Les dents de vertébrés ont des formes variées, mais sont généralement composées de deux couches minéralisées. Toutefois, malgré une minéralogie commune (apatite), ces tissus dentaires ont des structures et des compositions différentes [3,23], qui sont le reflet de la systématique et de l'environnement. Les dents fossiles sont donc utilisées à des fins systématiques, paléoenvironnementales et de datation. Cependant, le contrôle de la qualité de la préservation est souvent limité à un examen de la minéralogie, et les biais induits par des modifications de structure et de composition sont encore peu connus. Dans cette étude, nous comparons les structures et les compositions chimiques de dents de mammifères d'origines géographiques et d'âges géologiques différents, pour tenter d'estimer les variations à divers stades de la fossilisation.

2. Matériel et méthodes

Des dents actuelles et fossiles de mammifères ont été utilisées [8,10–15]. Les microstructures ont été étudiées au microscope électronique à balayage. La composition chimique élémentaire a été analysée sur deux microsondes électroniques (WDS, NHM, London; EDS, UPS, Orsay [16]). Pour les analyses statistiques, les compositions chimiques de plusieurs dents ont été moyennées, pour chaque type de tissu, et pour chaque origine. Quatre origines ont été définies: tissus frais, pelotes de régurgitation, fèces de carnivores, fossiles. Plus de 200 dents ont été prises en compte pour une analyse multivariée en composantes principales, basée sur 10 éléments chimiques.

3. Résultats

La dentine des dents récentes a des tubules à section arrondie (Fig. 1a). La surface de l'émail montre la structure prismatique avec des motifs variés selon les taxons (Fig. 1b). Les dents extraites de pelotes de régurgitation récentes montrent des états d'altération divers, qu'il s'agisse de la dentine (Fig. 1c), ou de l'émail (Fig. 1d, e). Les variations sont plus grandes dans les tissus fossiles. Les tubules de la dentine peuvent être remplis de dépôts secondaires (Fig. 1f). L'aspect de l'émail est également irrégulier (Fig. 1g–i).

L'émail présente de fortes teneurs en Na et Cl, alors que la dentine est riche en Mg, S et Sr (Fig. 2A). La forte teneur en Mg de la dentine des incisives est liée à leur croissance continue [9]. La répartition des teneurs par origine est plus complexe (Fig. 2B). Les tissus frais et ceux des fèces montrent des teneurs en Na, Mn, S, K, Mn et Cl similaires. Les dents fossiles et des pelotes sont appauvries en Mg et Na, alors que les fossiles sont enrichis en Fe et Sr. Les éléments majeurs sont également différents (Fig. 2C et D). L'axe 1 de l'analyse en composantes principales représente 36,1%, et l'axe 2 19,9% de la variabilité totale. L'axe 1 est déterminé par les fortes teneurs en P, Ca, Cl et S, l'axe 2 par les teneurs en Fe, Mg et K. Le graphe sur lequel les individus sont groupés par tissu montre que la dentine est riche en Sr, Mg et S, alors que l'émail est riche en P, Ca et Cl (Fig. 2E). Les divers types de croissance de la dentine entraînent une forte variation de Mg. La zone figurant l'émail est plus petite, les teneurs n'étant pas dépendantes du type de croissance. Lorsque les individus sont groupés par origine, les dents actuelles sont riches en P, Ca, Cl, Mg et S, et pauvres en Mn et Sr (Fig. 2F). Les dents extraites des fèces sont presque incluses dans les dents fraîches. Les dents fossiles montrent les plus grandes variations, notamment à cause des fortes teneurs en Sr de certains sites d'Olduvai.

4. Conclusion et discussion

4.1. Variabilité des échantillons étudiés

L'émail, au contraire de la dentine, est un tissu compact, peu riche en matrice organique. Les modifications sont donc plus visibles dans la dentine : élargissement des tubules, remplissages secondaires, etc. Évaluer sa composition chimique exacte sans inclure les dépôts exogènes est difficile, même avec des méthodes d'analyse localisée. Les fossiles ont des origines diverses [10,12–14]. En dépit des regroupements effectués et de la diversité des sites, la dentine et l'émail semblent avoir conservé leurs caractéristiques majeures. Cependant, un examen détaillé montre que la dentine subit plus que l'émail les influences du sédiment enrobant. La grande variété des sites fossiles est clairement mise en évidence par l'analyse statistique. La majorité des tissus fossiles est enrichie en Ca, le comportement de P étant moins régulier. La conservation n'est pas homogène dans un site donné (Fig. 1c) et il n'y a pas de corrélation directe entre la qualité de la conservation et l'âge géologique.

4.2. Autres exemples, autres paramètres

De nombreuses recherches ont eu lieu sur les teneurs en Sr pour la reconstitution des régimes alimentaires des fossiles, et les résultats semblent incohérents [2,28]. De plus, des études récentes sur des échantillons actuels ont montré la complexité des facteurs intervenant dans la régulation des teneurs en Sr [4,19,20]. Cette complexité, associée à une connaissance encore médiocre des facteurs diagénétiques, complique les interprétations paléobiologiques et les datations basées sur les compositions chimiques [22]. La structure et la composition chimique ne sont pas les seuls critères d'évaluation de l'état des dents. Dans certains cas, le contenu en matrice organique décroît dans la dentine fossile, et la cristallinité augmente [21]. Ces résultats ne sont pas généralisables [26], mais une augmentation des teneurs en carbonates semble fréquente [25]. Quant aux données sur les modifications de la composition des matrices organiques fossiles, elles demeurent rares [17,18]. Les dents de reptiles, composées d'émail et de dentine, sont abondantes au cours des âges géologiques. L'émail est fin et le plus souvent dépourvu de prismes. Peu de données sont disponibles, mais la variabilité semble similaire à celle des dents de mammifères [1,6,7]. Quant aux dents de poissons, les terres rares y sont parfois utilisées comme *proxies* [5,24,27].

La forme des dents permettant une identification taxonomique précise et donnant des informations sur le régime alimentaire de l'animal, les dents sont moins disponibles pour les analyses dites « destructrices ». Ces données chimiques et physiques sont plus abondantes sur les os, qui servent également de support à la mise au point de nouvelles méthodes. Ainsi, il est encore prématuré de vouloir prédire la diagenèse à partir de « lois », mais l'étude de chaque nouveau cas permet une progression dans l'affranchissement des biais d'interprétation.

1. Introduction

Despite various external morphologies, teeth have the same overall structure and consist of an outer layer covering the crown of the tooth, a middle dentine layer that forms the core of the tooth and surrounds a pulp cavity. Both dentine and enamel are readily preserved during fossilization, being essentially calcium phosphate (apatite) in composition. However, despite a common mineralogy, dentine and enamel have different microstructures and compositions, the structure being characteristic to high-level taxa [23]. In dentine, the mineral component is approximately 70% (by weight) and the remaining organic matrix is rich in collagen. Mammal enamel consists of highly ordered microcrystals, arranged in prisms encompassing a range of complex patterns [3].

The structure, mineralogy, and compositions of dentine and enamel have been used in a variety of studies including phylogenetics, palaeoecology (palaeodiets) and dating. Often however, insufficient emphasis has been placed on the quality of preservation of the samples in such studies, and the potential impact of diagenetic changes is not well understood. For example, studies of prehistoric teeth from graves need to consider also the funeral methods used, and biases that may result from artificial burial. In this study, we compare the structure and compositions of dentine and enamel from mammal teeth of different ages and origins, in order to establish the effects of various stages during natural fossilization processes.

2. Material and methods

2.1. Material

A range of modern and fossil mammal teeth of varying size were analysed in this study. Modern teeth are fresh teeth, or extracted from pellet regurgitations, and sampled from localities in France, Morocco, Algeria and Tanzania [11]; teeth from carnivore faeces are from the Sahara desert [15], and fossil teeth are from various localities in Africa, including Olduvai (Tanzania), Sterkfontein (South Africa), Tighenif (Algeria), Malawi [8,12–14], and also from Quercy, France [10].

2.2. Chemical composition

Microstructures of the enamel and dentine were observed on fractures and etched surfaces using scanning electron microscopy. Microanalyses were performed on two separate electron microprobes (WDS, at NHM, London; EDS, at UPS, Orsay) [16].

2.3. Statistical analyses

For statistical analyses, the chemical compositions of several teeth were averaged for each tissue (i.e.

incisor dentine), so that one individual represents several teeth from different taxa. Four categories are defined: modern fresh samples (8 samples), teeth from regurgitation pellets (20), carnivore faeces (4), fossils (29). In total, more than 200 teeth have been analysed. Principal component analysis (PCA) was based on correlation matrices, so that the statistical weights of elements with high concentrations (P, Ca) were moderated within the software. For PCA, a total of 61 samples and 10 variables were used.

3. Results

3.1. Microstructures

In the modern fresh teeth studied, the dentine tubules are parallel with circular transverse sections (Fig. 1a). The outer surface of the enamel displays a variety of patterns dependant on the taxa (Fig. 1c). Each prism is distinct and is composed of elongated crystallites. Dentine in teeth extracted from modern regurgitation pellets shows some minor, but variable degrees of modifications, where in some cases the diameters of the tubules are not regular. In other samples, the tubules and their organic contents are locally well preserved (Fig. 1c). The degree of preservation of the enamel is also variable. In some samples, the arrangement and structure within the rods are well preserved (Fig. 1d), but have been clearly altered in other pellets, even from the same locality (Fig. 1e). The range and degree of variability of the state of preservation of the tissues is larger in fossil samples. The dentine tubules are often devoid of organic material, or are partly filled with secondary minerals (Fig. 1f). Similar inconsistencies in preservation can be observed in the enamel where crystallites and rods can be either well preserved (Fig. 1g), or partly destroyed (Fig. 1h). In larger teeth, the surface of the enamel is often eroded (Fig. 1i), but in cross section, the prism structure may be preserved.

Thus, the preservation of the structure of enamel and dentine, in both modern and fossil teeth, is variable.

3.2. Chemical composition

Enamel has higher Na and Cl contents in incisors and molars than dentine, whereas dentine has relatively higher Mg, S, and Sr contents (Fig. 2A). The higher content of Mg in dentine incisor is related to the growth mechanism in rodent and lagomorph teeth [9]. However, the average content of each element, as a function of origin is more complex (Fig. 2B). For Na, Mn, S, K, Mn, and Cl, fresh teeth and carnivores samples have similar profiles. Samples from pellets, and also from fossil teeth are strongly depleted in Mg and Na, and additionally, fossil teeth are generally enriched in Fe and Sr. From Fig. 2C, it can be seen that the major element contents, Ca and P, are different in the two tissues. The contents of major elements, P and Ca, also differ according to the origin of the teeth: Ca is relatively low in modern and pellet teeth, but high in carnivore and fossil teeth (Fig. 2D).

The first principal axis of the PCA contains 36.1% of the total variance, whereas axis 2 represents 19.9%. The first principal component corresponds to higher P, Ca, Cl, and S values. In the second principal component the samples correspond to higher Fe, Mg and K. Two plots were obtained from the PCA: in the first one, the samples were arranged according to the tissue type (Fig. 2E); and in the second, they were arranged according to their origin (Fig. 2F).

The first plot (Fig. 2E) shows that the dentine has higher Sr, Mg, and S contents, whereas the enamel is higher in P, Ca, and Cl. In incisor dentine, the range of variation is high, because of the different growth modes in these teeth. Continuously formed hypsodont molars with high Mg contents are also present in the samples. Dentine from both incisor and molar teeth has high S contents. The variation in the enamel is smaller than that of dentine, and additionally the growth mode is not sensitive to elements such as Mg. Thus, although this graph allows us to compare the tissues, they do not explain the origin of some observed large variations (e.g. Sr) from the fossil samples collected at Olduvai, Tanzania.

The second plot (Fig. 2F) shows that both the fresh and pellet teeth have higher P, Ca, Cl, Mg and S contents, and lower Mn and Sr contents, but with a large overlap between these two categories. Teeth extracted from carnivore faeces have lower P, Ca, and Cl concentrations. The range of variation observed for the fossil teeth is the largest of the four categories, with pellet and fresh teeth being most similar.

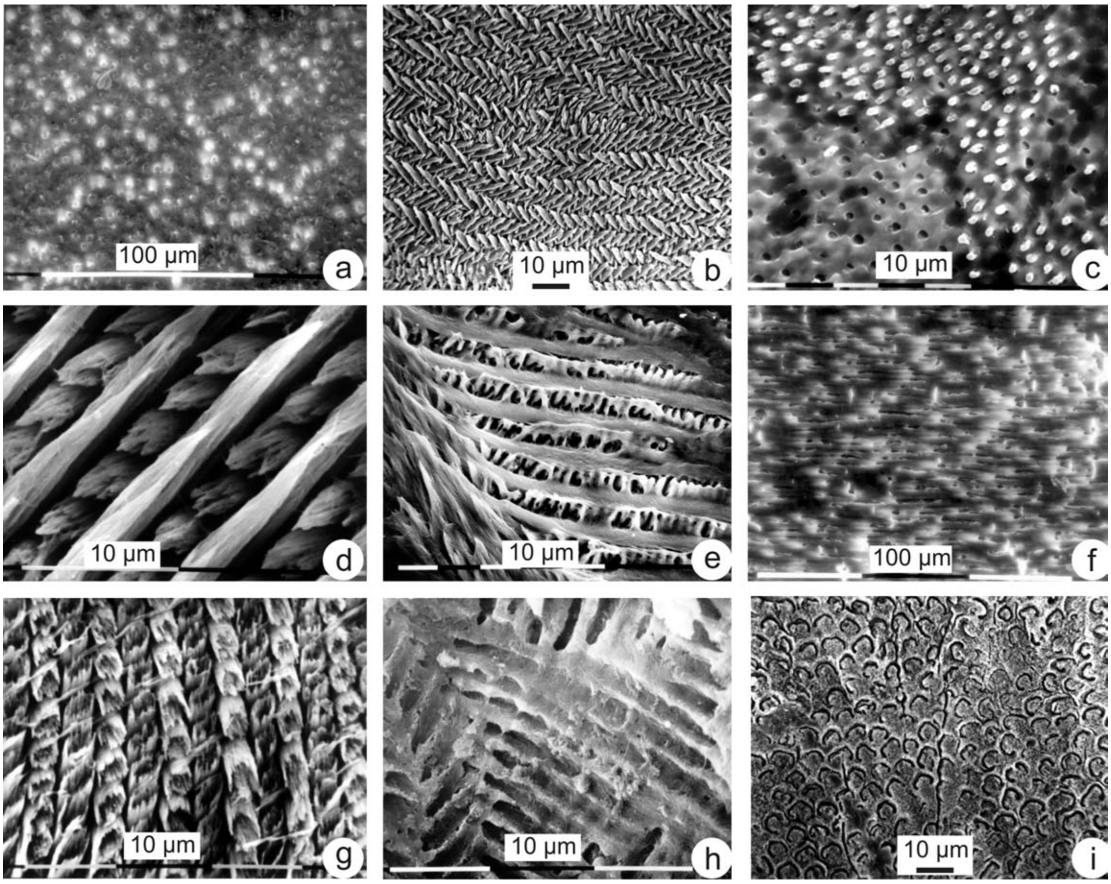

Fig. 1. Structure of the teeth. (**a**) Modern cervid incisor showing the tubular dentine. Etching employed 5% HCl for 15 sec. (**b**) Surface of a modern *Jaculus* showing the prismatic structure of the enamel. 5% HCl for 2 min. (**c**) Rodent dentine from a modern pellet (Tighenif, Algeria) showing empty and filled tubules. 5% formic acid for 45 s. (**d**) Rodent incisor from a modern pellet (Olduvai) showing the well preserved prismatic structure of the enamel. 5% formic acid for 15 s. (**e**) Rodent molar from a modern pellet (Olduvai) showing the altered prismatic structure of the enamel. 5% formic acid for 15 s. (**f**) Natural fracture in the dentine of a large mammal tooth (Malawi, Plio-Pleistocene) showing the tubules. (**g**) Rodent incisor from a fossil pellet (Tighenif) showing the well-preserved prismatic structure of the enamel. 5% formic acid for 2 min. (**h**) Natural surface of a rodent incisor from a fossil pellet (Tighenif) showing the altered prismatic structure of the enamel. (**i**) Enamel of *Numidotherium koholense* (Eocene, NW Africa) showing the keyhole pattern of the prisms.

Fig. 1. Structure des dents. (**a**) Dent d'un cervidé actuel montrant la dentine tubulaire. HCl 5%, 15 s. (**b**) Surface de l'émail d'un rongeur actuel (*Jaculus*) montrant sa structure prismatique. HCl 5%, 2 min. (**c**) Incisive de rongeur d'une pelote actuelle (Tighenif, Algérie) montrant des tubules vides et pleins. Acide formique 5%, 45 s. (**d**) Incisive de rongeur d'une pelote actuelle (Olduvai) montrant la structure prismatique intacte de l'émail. Acide formique 5%, 15 s. (**e**) Molaire de rongeur d'une pelote actuelle (Olduvai) montrant la structure prismatique de l'émail très altérée. Acide formique 5%, 15 s. (**f**) Fracture naturelle dans la dentine d'un grand mammifère fossile montrant les tubules (Malawi, Plio-Pléistocène). (**g**) Incisive de rongeur d'une pelote fossile (Tighenif) avec une structure prismatique de l'émail bien conservée. Acide formique 5%, 2 min. (**h**) Surface naturelle d'une incisive de rongeur d'une pelote fossile (Tighenif) montrant un émail altéré. (**i**) Surface d'une dent de *Numidotherium koholense* (Éocène, Nord-Ouest de l'Afrique) montrant le motif en « trous de serrure » de l'émail.

4. Conclusion and discussion

4.1. Variability of the preservation of the studied samples

Tooth enamel is compact, whereas dentine is relatively porous. Thus, dentine is more susceptible to diagenetic alteration than enamel. This alteration can lead to the tubules being sometimes enlarged by dissolution, or filled with sediment or with minerals precipitated from groundwaters during burial and subsequent fossilisation. The high organic content of the dentine is also a contributing factor as it is more easily destroyed

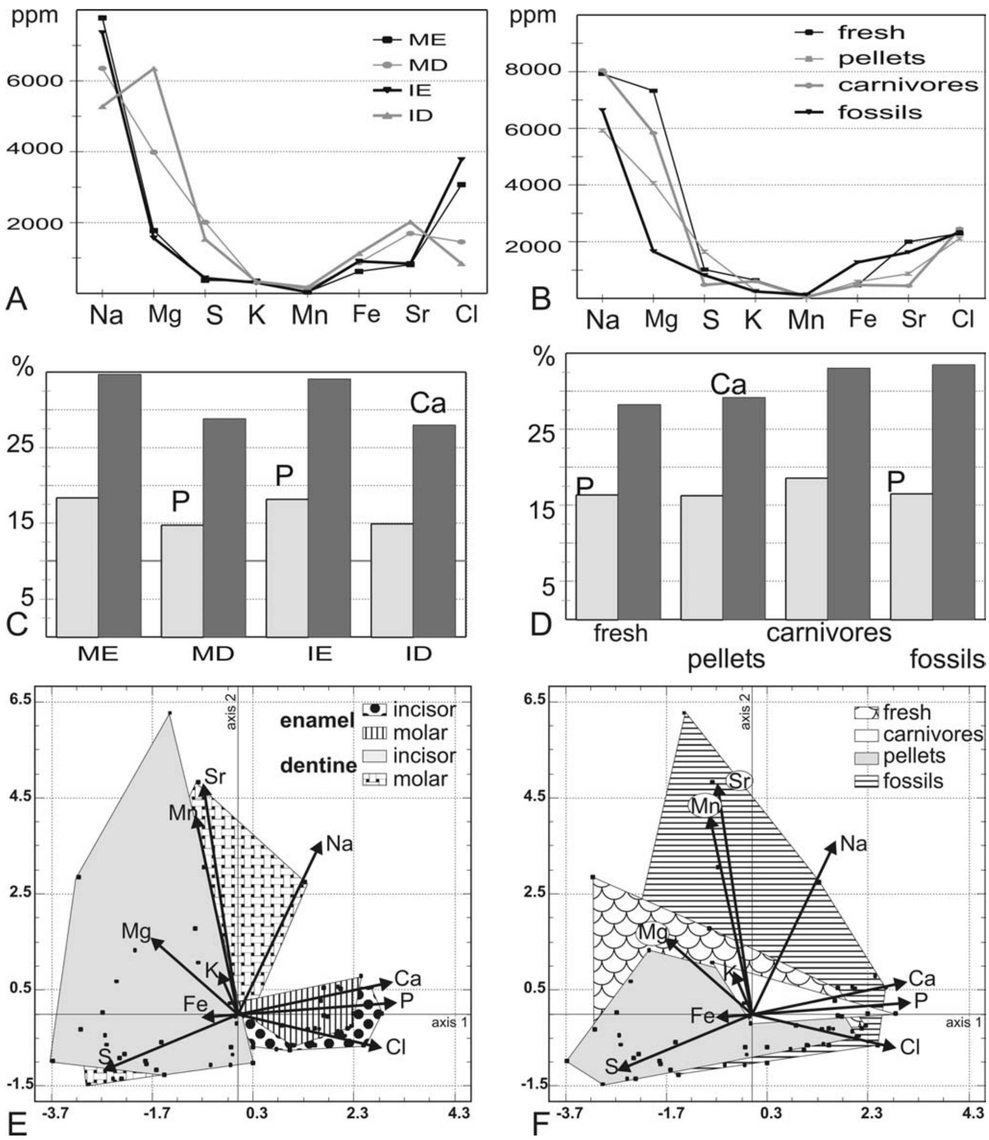

Fig. 2. Composition of the teeth. (**A**) Average contents in minor elements of the different tissues. (**B**) Average contents in minor elements according to the origin of the teeth. (**C**) Major element contents of the different tissues. (**D**) Major element contents according to the origin of the teeth. (**E, F**) Principal components analyses (PCA) based on chemical contents. (**E**) Samples are represented according to the tissue. (**F**) Samples are represented according to their origin. **ME**: molar enamel; **MD**: molar dentine; **IE**: incisor enamel; **ID**: incisor dentine. **fresh**: Modern fresh teeth; **pellets**: teeth extracted from various modern pellets regurgitation; **carnivores**: teeth extracted from modern *Vulpes* faeces; **fossils**: teeth from various fossil sites.

Fig. 2. Composition des dents. (**A**) Teneurs moyennes en éléments mineurs des différents tissus. (**B**) Teneurs moyennes en éléments mineurs selon l'origine des dents. (**C**) Teneurs moyennes en éléments majeurs des différents tissus. (**D**) Teneurs moyennes en éléments majeurs selon l'origine des dents. (**E–F**) Analyse multivariée en composantes principales (PCA) basée sur la composition chimique. (**F**) Individus groupés selon leur origine. **ME** : émail des molaires ; **MD** : dentine des molaires ; **IE** : émail des incisives ; **ID** : dentine des incisives. **fresh** : Dents récentes ; **pellets** : dents extraites de pelotes de régurgitation récentes ; **carnivores** : dents extraites des fèces de *Vulpes*, **fossils** : dents fossiles.

during diagenesis, and can lead to an increase in porosity and weaknesses in the structure.

Fossil sites are of course of various ages and burial regimes: Olduvai is a lake margin deposit with alternate layers of sediment and volcanic ashes [14], whereas Tighenif sediments are mainly composed of ferruginous sands [13]. In contrast, teeth from Quercy [10] and Sterkfontein [12] are embedded in indurated sediments. In the analysis of the four categories of modern and fossil teeth, the dentine and enamel have generally preserved their main characteristics. This appears to be in spite of the differences in the fossil sites. Previous detailed studies have shown that the composition of dentine in fossil samples is significantly more affected by the burial sediment than is the enamel: e.g., dentine from Tighenif is enriched in Fe, and dentine from Olduvai is enriched in Na and Sr, in each case relative to the enamel.

The different fossil sites are discriminated by the PCA graph, with the range of variations corresponding to axes 1 and 2 being the greatest of the 4 categories. Previous studies allow us to confirm that the high Sr and Na contents are from the Olduvai teeth [16]. In terms of the average compositions, fossil teeth have the highest P and Ca contents. However, detailed analysis indicates that the enrichment of Ca in enamel and dentine is relatively consistent, whereas P has a more variable behaviour.

The samples in this study display a large variation in the preservation of the dentine and enamel, and that this variation depends on several factors: principally the tissue type, the possible predation, and the burial environment. Some degree of variation can be present within a tooth at early stages of decay, as shown by the dentine in Fig. 1c. It should be noted that within any one fossil site, the degree of preservation itself might be variable. There is no observed direct correlation between the quality of the preservation and the age of the site in mammal dental tissues.

4.2. Other samples, other parameters

There have been many studies in bone and teeth relating to the concentration of Sr in these samples, because of its potential as a palaeodietary indicator element. In fossil samples, the results seem to be inconsistent [2,28]. However, as previously shown, the burial environment and enclosing sediment are important contributing factors [14]. Moreover, recent studies in modern bone and teeth samples [4,19,20] have highlighted the complex nature of the problem. Not only are the processes of incorporation of minor elements not well understood in modern samples, but also the changes resulting from digestion by a predator and fossilization processes are diverse. This biological diversity and post-mortem alterations can complicate the palaeobiological interpretations and dating techniques [22].

The structure and composition are not the only parameters indicative of the quality of the preservation. In large mammal teeth, it is relatively easy to separate mechanically the enamel and the dentine. Michel et al. [21] have shown that the organic matter content decreases in the fossil dentine, and that the crystallinity is lower in modern samples. No increase in the crystallinity has been observed in other sites [26], but an increase of the content of carbonate seems usual [25]. These data can be correlated with an observed increase in Ca in most fossil teeth. As for the changes in the composition of the organic matrices of the fossil enamel and dentine, detailed studies are rare. Of these, Fosse et al. [17] have deduced the persistence of collagen in fossil dentine, and Glimcher et al. [18] have studied the amino acid composition of enamel and dentine.

Reptile fossil teeth are also abundant within the geological record, these also being composed of orthodentine and enamel. There are fewer studies of reptile teeth than their mammal counterparts, and little data are available on their microstructure and chemical composition. Nevertheless, the variability in diagenetic changes appears to be similar to that for mammal tissues [1,6,7]. Some studies of fish teeth have used rare earth element concentrations to provide information on depositional palaeoenvironments [5,24,27].

Because the shape and morphology of a tooth provides important information in areas such as systematic and evolutionary studies, teeth (as samples) are less available for « destructive » chemical analyses. More data is available on bones, and palaeontologists prefer to experiment with new methods and techniques using bones, some of these being inappropriate for such purposes. Thus, it is too soon to draw specific conclusions about the diagenetic processes, but each case study provides useful information to avoid interpretative bias.

Acknowledgements

We thank Drs J.-J. Jaeger (USTL), K. Kowalsky (ISEA, Krakow), C. Denys (MNHN), B. Badré

(UMPC) and F. Schrenk (JWG Universität, Frankfurt), who provided some of the vertebrate specimens from their collections.

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