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Diet of ancient Egyptians inferred from stable isotope systematics

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ABSTRACT

Carbon, nitrogen and sulfur stable isotope compositions were measured in hard and soft tissues from Egyptian mummies of humans and animals in order to track the diet of ancient Egyptians from 5500 to 1500 years B.P. The carbon isotope ratios of bone apatite ($\delta^{13}C_{bo} = -14.3 \pm 0.9‰$) and hair protein ($\delta^{13}C_h = -19.9‰$) are compatible with a diet based almost exclusively on C3-derived food (proportion of C4 < 10%). Less negative carbon isotope ratios of enamel ($\delta^{13}C_{en} = -11.6 \pm 0.7‰$) relative to bones from the same mummies could be the result of differences in the chemical microenvironment in which mineralization occurred, as well as of differences in diet between children and adults, in particular through the consumption of milk or millet gruel during infancy and childhood. High values of nitrogen isotope ratios for hair protein ($\delta^{15}N_h = 9.1‰–15.5‰$) are ascribed to aridity rather than fish consumption because the $\delta^{34}S$ values of human hair are lower than those measured in Nile perch scales. Except for Coptic mummies, the constancy of $\delta^{13}C_{bo}$ and $\delta^{13}C_{en}$ over a duration of ~3000 years is striking considering the various political, technological, and cultural changes that impacted the Egyptian civilization during this time interval.

1. Introduction

Ancient Egypt stands out as one of the first great civilizations that emerged at the end of the Neolithic period (6000 B.P.) and is particularly renowned for its exceptional longevity. Throughout its long history, ancient Egypt alternated between periods of stability and prosperity, and troubled times resulting from episodes of war or severe drought. The central government was overthrown and restored several times, and the shape of the Egyptian territory itself was modified through military conquests or defeats. Not all of these political events directly influenced the day-to-day life of the population, but they facilitated innovation through adaptation or assimilation of foreign customs and technologies, resulting in cultural and economic evolution over the centuries. This intrinsic evolution of ancient Egypt is expected to have had consequences such as major changes in life expectancy and culinary habits. The diet of ancient Egyptians reflects how they were utilizing natural resources, whether through trade or living only on what they themselves could produce, with both strategies having different outcomes for their environment. For example, food and timber trade between ancient Egypt and distant countries (Gardiner, 1961; Trigger et al., 1983) is known well before the establishment of the spice and silk routes between Europe and South-East Asia during the Middle Ages. Variation in diet also testifies to progressive agricultural practices through the development of new tools and irrigation techniques such as the shaduf, which appeared during the New Kingdom (3300 B.P.; Butzer, 1976).

Current knowledge of the diet of ancient Egyptians arises from two major sources of information. Figurative depictions exhibit the food products that were known to ancient Egyptians and also reveal how they were processing cereals and fruits into bread, beer, and wine (Alcock, 2006). These portrayals are, however, often biased because they mostly represent the food consumed by higher social classes, who could afford paying artists to commit costly festive meals to perpetuity. They are further difficult to interpret because translation of names of ingredients often is ambiguous and

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probably not exhaustive. Food and cooking recipes also can be deduced from the analysis of food remains preserved in either graves or middens (David, 2007; Samuel, 2000; van Neer et al., 2004) or at habitation sites (Bagnall, 2006; Redding, 1984; Smith, 2003; Wetterstrom, 1984). Beyond the identification of food products, their average proportion in the daily diet of ancient Egyptians is a key parameter remaining difficult to estimate. Large consumption of gritted bread is certain because of the notable common dental wear in human remains (Gamza and Irish, 2012; Leek, 1972). As for other food sources such as vegetables, fish or meat, only indirect inferences can be made by considering the salaries paid in kind to pyramid workers and craftsmen from the King's valley. These indicate that ancient Egyptians consumed large amounts of cereals through bread and beer, and also ate vegetables (e.g. onions, lettuce) and legumes (e.g. peas, fenugreek, lentils). Meat is not mentioned and probably represented a very small portion of the diet, except for the wealthiest people. For the working classes, animal proteins were rare and came from dairy foods, fowl, and fish.

The stable isotope analysis of human tissues can provide complementary information on the diet of ancient Egyptians, with the possibility of estimating the relative proportions of plants and animal proteins of terrestrial or aquatic origin. With this purpose in mind we measured the carbon isotope compositions of human bone apatite ($\delta^{13}C_{bo}$), enamel apatite ($\delta^{13}C_{en}$) and hair ($\delta^{13}C_{h}$) in order to quantify the relative proportions of C3- and C4-derived foods in the diet of ancient Egyptians and how this diet evolved from the Predynastic Period (~5500 B.P.) to Byzantine Egypt (~1500 B.P.). Along with the carbon, nitrogen and sulfur isotope compositions of soft tissues (feathers, scales, and hair) of various animal samples (fish, birds, and mammals), we also analyzed $\delta^{34}S_{h}$ and $\delta^{15}N_{h}$ of human hair samples to evaluate how animal protein and freshwater food may have contributed to the diet of ancient Egyptians.

2. Stable isotope ratios and their potential for recording dietary patterns

The use of $^{13}C/^{12}C$ ratios in diet reconstruction is based on the distinction between different pathways of carbon fixation in plants (Bender, 1971; O'Leary, 1988; Smith and Epstein, 1971). The C3-plant group is by far the most diverse and comprises the majority of vegetables, cereals, and fruits, while C4-plants are rare, and limited to millet and sorghum in Africa. C3-plants strongly discriminate against ^{13}C during photosynthesis, and these plants therefore are markedly depleted in ^{13}C relative to atmospheric carbon dioxide. Discrimination against ^{13}C is less pronounced for C4-plants resulting in higher $\delta^{13}C$ values compared to C3-plants. White et al. (1999) found that C3- and C4-plants cultivated at Asyut have present-day $\delta^{13}C$ of about −26.5‰ and −11.65‰, respectively. These values have to be corrected for the recent burning of fossil fuels that over the last decades has led to a decrease of 1.5‰ of the atmospheric $\delta^{13}C$ value (Marino and McElroy, 1991; White et al., 1999). Thus, the mean reference values for C3- and C4-plants during Ancient Egyptian times are, respectively, −25‰ and −10‰. When plants are consumed, carbon is incorporated into body tissues and in this manner the isotopic composition of the food is transferred to the tissues all the while undergoing isotopic fractionation the magnitude of which depends on the tissue in question.

The nitrogen isotope composition of human and animal bone collagen is controlled by the food that is consumed, and is enriched, on average, by +3‰ to +5‰ compared to the diet (Schwarcz and Schoeninger, 1991). This isotopic enrichment of body protein is caused by the excretion in urine of ^{15}N-depleted glutamine derived from ammonia (Balter et al., 2006). Aquatic resources, especially marine food sources, are markedly ^{15}N-enriched compared to terrestrial foods (Schwarcz, 1991). Nitrogen isotopes ratios, however, are also linearly correlated in a wide range of plants and animals with the amount of rainfall (Cormie et al., 1994; Gröcke et al., 1997; Heaton et al., 1986; Schwarcz et al., 1999; Sealy et al., 1987). The ^{15}N-enrichment of plants in arid environments is the consequence of ^{15}N-enrichment of the soil driven by ammonia evaporation, which is ^{15}N-depleted compared to nitrates, ammonium, and organic compounds present in the soil (Schwarcz et al., 1999). In the case of animals, increasing $\delta^{15}N$ observed with increasing aridity is due to the consumption of ^{15}N-enriched foods and to the physiological adaptation to drought by the excretion of concentrated urine (Ambrose and DeNiro, 1986). Finally, nitrogen isotope compositions may also reflect partly the health status of a given individual. During times of severe nutritional stress, high $\delta^{15}N$ values are expected in tissues as a result of preferential deamination of ^{14}N-aminoacids to provide sugar for energy (Katzenberg and Lovell, 1999) and subsequent elimination of the ^{14}N-enriched nitrogen in urine. For bone pathologies with bone modification or remodeling, increase in $\delta^{15}N$ has been measured only in lesions, not in distant bone (Olsen, 2013). Lastly, pregnant women have lower $\delta^{15}N$ hair values (−1.1 to −0.3‰) because of nitrogen retention (Fuller et al., 2004).

Proximity to the sea or consumption of marine food can be detected by measuring the sulfur isotope composition of collagen or hair. Oceanic sulfate has $\delta^{34}S$ of +21‰, which is reflected in the composition of marine primary producers with $\delta^{34}S$ values ranging from +17‰ to +21‰ (Privat et al., 2007). Continental plants from a wide range of regions have $\delta^{34}S$ ranging from +2‰ to +6‰ because they assimilate sulfur from a large variety of sources (Peterson and Fry, 1987). Freshwater plants generally have $\delta^{34}S$ close to the value of dissolved sulfate (Trust and Fry, 1992). However, the $\delta^{34}S$ values of both rooted estuarine plants and benthic plankton can be as low as −17‰ owing to the absorption of ^{34}S-depleted sulfate that derives from the sulfide produced by bacteria living in anoxic sediments (Fry, 2008). Because there is no fractionation of sulfur isotopes between diet and consumers (Peterson and Fry, 1987), $\delta^{34}S$ of hair fibers and bones can provide direct evidence of consumption of marine (Macko et al., 1999) or freshwater (Privat et al., 2007) food within a given population.

Bone and enamel are the most commonly studied types of tissue for the purpose of paleodiet reconstructions because they are the most abundant remains and generally are more resistant to degradation than soft tissues. Carbon isotope compositions of the structural carbonate in bone and enamel apatite reflect the total diet consumed by vertebrates (Ambrose and Norr, 1993; Kellner and Schoeninger, 2007; Tieszen and Fagre, 1993). It is of particular interest that enamel $\delta^{13}C_{en}$ records the diet during childhood (Dupras and Tocheri, 2007) and can be compared to bone $\delta^{13}C_{bo}$, which reflects the diet of an individual during the last years of life (White et al., 2004). Comparison of $\delta^{13}C$ for different teeth from a given individual further allows for the identification of changes in diet during childhood, especially the timing of weaning (Dupras and Tocheri, 2007; Wright and Schwarcz, 1998, 1999).

Carbon, nitrogen, and sulfur isotope ratios measured in hair fibers provide complementary dietary information (Macko et al., 1999; O'Connell et al., 2001). Hair fibers consist mainly of proteins and their stable isotope compositions closely reflect the composition of dietary proteins (Tieszen and Fagre, 1993, Schoeller et al., 1986), except potentially in the case of low protein intake (Schwarcz, 2000). In particular, the carbon isotope composition of hair is enriched by +1.5‰ to +3‰ compared to the protein of the diet (Nakamura et al., 1982; Schoeller et al., 1986; Katzenberg and Krouse, 1989). Hair contains on average more sulfur than does collagen (4–5%,

Richards et al., 2003, instead of 0.5%, Privat et al., 2007), thus favoring hair for the analysis of sulfur isotopes. Hair grows by about 1 cm per month (O'Connell and Hedges, 1999), hence the strands of hair collected here, always shorter than 10 cm (see Section 3), reflect the diet of the last year (or months) of life of each individual.

3. Material and analytical methods

Samples of human hair, enamel, and bone were collected from Egyptian mummified heads and Predynastic individuals kept in the Musée des Confluences, Lyon, France, as well as from Coptic mummies preserved in the Musée Testut-Latarjet d'Anatomie, Lyon, France. The mummies originate from different localities in the Egyptian Nile Valley (Table 1; Fig. 1). The age and sex of the mummies are unknown. However the collection of dynastic heads was previously studied by Herzberg and Perrot (1983) who estimated that the majority of the population was less than 40 years old. They likely corresponded to Egyptians belonging to the middle class. Among these mummies, only those labeled with locality and a clear designation to a specific period of the Egyptian history were sampled for the present isotopic study (Table 1). The selected mummies were in variable states of preservation with a few heads having retained hair and skin, while most had only skulls preserved. In the former case, access to teeth and bones was limited and, therefore, data for both soft and hard tissues from a single individual remain exceptional. A macroscopic examination was done before each sampling to check for the absence of pathological lesions and remodeling of the bones. Bone samples were obtained by sawing and/or tearing apart bone fragments with pliers. In a few cases bone fragments that were already detached were used. Samples of hair consisted of locks of a few centimeters (always shorter than 10 cm) cut close to the skull.

Table 1
Carbon isotope compositions of apatite carbonate in enamel ($\delta^{13}C_{en}$) and bone ($\delta^{13}C_{bo}$) of Egyptian mummies. (*) Age label probably erroneous considering the cemetery ages at these localities: at Khozan, cemetery age is Naqada (5850–4800 B.P., Hendrickx, 2010) and for Deir-el-Medineh, the village is Ramessid (18th–20th dynasties, 3500–3000 B.P., Valbelle, 1985). (#) Mummies radiocarbon dated by Richardin et al. (2013) to the Byzantine Period (n° 1343: 1385 ± 30 B.P. and n° 1448: 1525 ± 30 B.P.). (J): juvenile human.

Individual	Species	Locality	Period	Archaeological age (BP) (year BP)			Sample	$\delta^{13}C_{bo}$	Sample	$\delta^{13}C_{en}$	$\Delta^{13}C_{en\text{-}bo}$
90002402	Human	Roda	PR	~6000	–	5000	Cranial bone	−14.41			
90001252	Human	Roda	PR	~6000	–	5000	Bone	−14.03			
30000334	Human	Khozan	4th *	5850	–	4800			Upper left premolar (PM2)	−11.42	
30000318	Human	Khozan	4th *	5850	–	4800	Occipital condyle	−14.23			
30000327	Human	Khozan	4th *	5850	–	4800	Cranial bone	−14.04			
30000331	Human	Khozan	4th *	5850	–	4800	Cranial bone	−11.50			
30000323	Human	Hypogee Elephantine	12th	3935	–	3723	Occipital bone	−14.02			
30000308	Human	Deir el Medineh	12th *	3500	–	3000	Right lateral pterygoid process	−13.82	Lower right incisor	−11.96	1.86
30000305	Human	Deir el Medineh	12th *	3500	–	3000			Incisor or canine	−11.98	
30000232	Human	Gournah	18th	3500	–	3245			Upper incisor	−13.20	
30000233	Human	Gournah	18th	3500	–	3245			Lower left molar (M1)	−12.22	
30000291	Human	Gournah	18th	3500	–	3245	Cranial bone	−14.29			
30000292	Human	Gournah	18th	3500	–	3245	Cranial bone	−13.84			
30000238	Human	Gournah	18th	3500	–	3245	Cranial bone	−14.54			
30000239	Human	Gournah	18th	3500	–	3245			Tooth fragment from the mandible	−11.94	
30000249	Human	Gournah	18th	3500	–	3245			Upper right premolar (PM1)	−11.20	
30000242	Human	Gournah	26th	2614	–	2475			Upper molar (M3)	−10.94	
30000241	Human	Gournah	26th	2614	–	2475	Right temporal styloid process	−14.57	Upper canine	−12.03	2.54
30000248	Human	Gournah	26th	2614	–	2475	Right lateral pterygoid plate	−13.97	Upper right molar (M3)	−11.24	2.73
30000157	Human	Gournah	26th	2614	–	2475	Cranial bone	−13.64			
30000158	Human	Gournah	26th	2614	–	2475	Lateral pterygoid plate	−13.40	Tooth fragment	−11.74	1.66
30000158	Human	Gournah	26th	2614	–	2475	Lateral pterygoid plate	−13.40	Lower left premolar (PM2)	−11.37	2.03
30000159	Human	Gournah	26th	2614	–	2475			Lower left premolar (PM1)	−10.92	
30000159	Human	Gournah	26th	2614	–	2475			Lower left premolar (PM2)	−10.74	
30000160	Human	Gournah	26th	2614	–	2475	Lateral pterygoid plate	−13.63	Lower left canine	−12.20	1.43
30000160	Human	Gournah	26th	2614	–	2475	Lateral pterygoid plate	−13.63	Lower left premolar (PM1)	−11.42	2.21
30000118	Human	Gournah	PT	2282	–	1980	Cranial bone	−13.92			
30000196	Human	Gournah	PT	2282	–	1980	Right temporal styloid process	−13.56	Upper left molar (M2)	−10.98	2.59
30000169	Human	Gournah	PT	2282	–	1980	Supraorbital ridge	−13.25	Lower right premolar (PM1)	−11.32	1.92
30000197	Human	Gournah	PT	2282	–	1980	Cranial bone	−14.50	Upper left premolar (PM2)	−11.75	2.75
30000139	Human	Thebes	PT	2282	–	1980	Bone from the interior of the skull	−14.35			
30000161	Human	Thebes	PT	2282	–	1980	Temporal styloid process	−14.02	Upper left molar (M3)	−11.60	2.42
30000163	Human	Gournah	GR	2282	–	1555	Zygomatic arch	−14.80	Tooth fragment	−12.53	2.27
30000164	Human	Gournah	GR	2282	–	1555	Temporal styloid process	−14.71	Lower right molar (M3 ?)	−11.50	3.21
30000162	Human	Gournah	GR	2282	–	1555	Lateral pterygoid plate	−14.43	Lower left M1 or lower right M3	−10.81	3.62
30000172	Human	Gournah	GR	2282	–	1555	Left lateral pterygoid plate	−13.54			
90001855	Crocodile	Kom Ombo	GR	2282	–	1555			Teeth	−9.74	
90010267	Cat	Stabl-Antar	GR	2282	–	1555	Bone from the mandible	−15.15	Lower right carnassial (M1)	−12.47	2.68
90010266	Cat	Stabl-Antar	GR	2282	–	1555	Bone from the mandible	−15.41			
1448	Human	Antinopolis	CO#	~1300	–	~1950	Cranial bone close to the bregma	−15.11			
1343	Human	Antinopolis	CO#	~1300	–	~1950	Vertebral bone	−15.68			
n.a.	Human (J)	Antinopolis	CO	~1300	–	~1950	Left parietal bone	−15.45			
n.a.	Human (J)	Antinopolis	CO	~1300	–	~1950	Left part of the frontal	−15.62			
n.a.	Human	Antinopolis	CO	~1300	–	~1950	Cranial bone	−15.39			
n.a.	Human	Antinopolis	CO	~1300	–	~1950	Cranial bone	−15.55			
n.a.	Human	Antinopolis	CO	~1300	–	~1950	Cranial bone	−15.20			

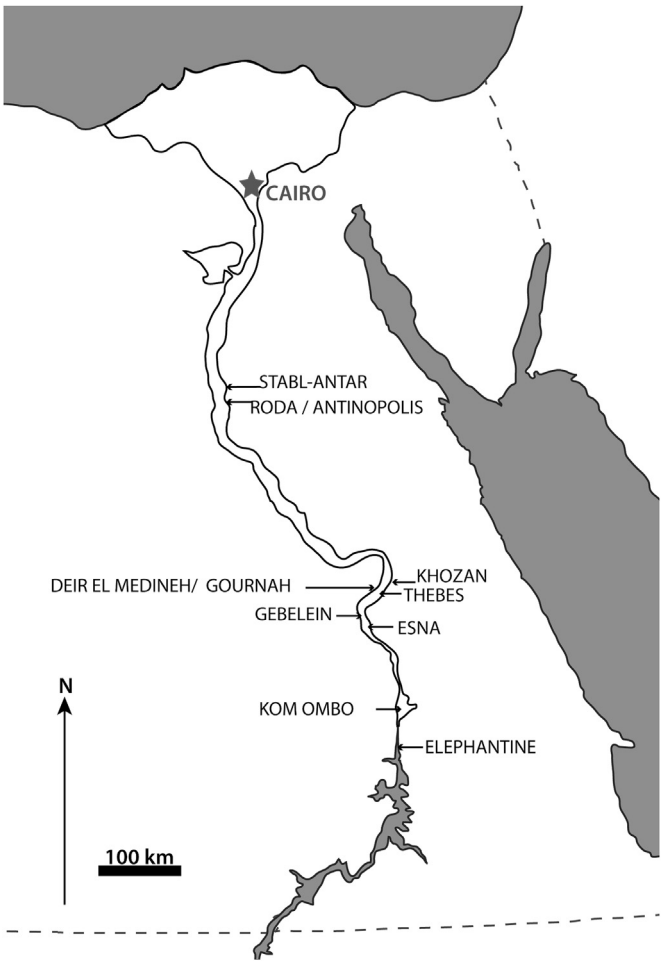

Fig. 1. Map of Egypt showing the localities of the mummies sampled in the present study.

Animal mummies from Egypt, kept in the Musée des Confluences, Lyon, France, were also sampled to explore the food chain and the potential food resources available to ancient Egyptians. The samples include scales from the Nile perch, hairs from cats, dogs, rodents, and gazelles, and bird feathers.

Bone samples were ground into powder in an agate mortar. Teeth were drilled using a diamond-head to produce enamel powder. Bone and enamel powders were pretreated using 10% hydrogen peroxide to remove organic matter (after Daux et al., 2008). After 1 h, the powders were rinsed three times with double deionized water and dried in an oven at 50 °C. Carbon isotope ratios were determined using a MultiPrep™ automated preparation system coupled to a dual-inlet Elementar™ Isoprime™ isotope ratio mass spectrometer. For each sample, two aliquots of 2–3 mg of apatite were reacted with anhydrous supersaturated phosphoric acid at 90 °C for 60 min. Isotopic compositions are reported in Table 1 using the delta notation in ‰ relative to the Vienna Pee Dee Belemnite (V-PDB). All sample measurements were adjusted to the international reference NIST NBS19 according to Werner and Brand (2001). The reproducibility of the carbon isotope measurements is 0.1‰ (2σ).

Human and animal hair samples were prepared following the first steps of the protocol of Richardin et al. (2011, 2013) prior to keratin extraction. For all individuals, about 10 mg of hair were immersed in ultrapure water and put in an ultrasonic bath to remove all solid contaminants. They were further cleaned with a mixture of dichloromethane:methanol (1:1, v/v), then twice with acetone in order to remove lipids. Between each step, samples were rinsed with doubled deionized water. The samples were then submitted to a standard acid-alkali-acid (AAA) treatment that attacked both exogenous carbonates and humic acids leaving about 5 mg of clean hair. The cleaning of two feather sub-samples (90010094b and 90001244b), using the same methodology as for hair, resulted in catastrophic weight loss during rinsing steps, and hence was abandoned prior to the AAA treatment. As a result, all feathers were analyzed without any chemical preparation. Scales were rinsed twice with deionized water and left to dry without acid leaching to remove carbonate salt. Decalcification of scales was found by Inamura et al. (2012) to be unnecessary for stable isotope analysis and, moreover, could affect nitrogen isotope ratios (Fincel et al., 2012). Due to the low sulfur content of fish scales compared to hair, several scales were pooled to constitute a 2–3 mg sample size suitable for the stable isotope analyses. For human hair samples, three replicates of ~450 μg of hair fibers were loaded into tin capsules, whereas for animal hair and feather samples, the triplicates weighed ~1 mg. The samples were combusted into an elemental analyser (VaryoPyroCube™) to produce nitrogen (N_2), carbon dioxide (CO_2) and sulfur dioxide (SO_2) gases. These gases were then carried by helium flow to an Isoprime™ mass spectrometer for the determination of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$. Laboratory reference materials calibrated against international standards were routinely measured along with the samples. Precisions for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ were ±0.05‰ (2σ), ±0.2‰ (2σ), and ±0.3‰ (2σ), respectively.

4. Results

The carbon isotope ratios measured in bone apatite ($\delta^{13}C_{bo}$) and enamel ($\delta^{13}C_{en}$) samples from the present study are listed in Table 1 and plotted in Fig. 2. The average bone $\delta^{13}C_{bo}$ value is -14.3 ± 0.9‰, which is identical within the quoted errors to Iacumin et al.'s (1996) value of -14.4 ± 0.5‰. The average enamel $\delta^{13}C_{en}$ value is -11.6 ± 0.6‰, again identical within the quoted errors to the average value of -11.8 ± 1.1‰ at Tombos, Nubia (Buzon and Bowen, 2010), and comparable to the average value of -12.2‰ ± 0.3‰ at Kellis cemetery, Egypt (Dupras and Tocheri, 2007).

Thus, the $\delta^{13}C_{en}$ values are on average 2.7‰ less negative than the $\delta^{13}C_{bo}$ values. When Coptic mummies are disregarded, the difference remains large (2.5‰) and statistically significant (Kruskal–Wallis test: $p < 10^{-5}$). Paired samples of tooth and bone from the same individual also show a large difference in their carbon isotope ratios (2.4‰, Student t-test: $p < 10^{-5}$). Moreover, statistically significant differences (Mann–Whitney–Wilcoxon test: $p < 10^{-3}$) exist between early-forming teeth (incisors, first molars, and canines) and later-forming teeth (premolars and second and third molars).

For an assessment of the variation of $\delta^{13}C_{en}$ with time, it was possible to apply statistical tests only to the time span ranging from the 18th dynasty (3500–3245 B.P.) to the Greco-Roman period (2282–1555 B.P.), which showed no significant evolutionary changes. In the case of $\delta^{13}C_{bo}$, statistical tests could be applied to the entire time span sampled, except for the 12th dynasty (3935–3723 B.P.), and they reveal an overall significant change (Kruskal–Wallis: $p = 0.002$; Fig. 2) controlled mostly by the lower values recorded in Coptic mummies. In detail, statistical differences exist only between Coptic mummies and mummies from the 26th dynasty (2614–2475 B.P.) and the Ptolemaic period (2282–1980 B.P.) ($p = 0.038$ and 0.017, respectively, Mann–Whitney test). Mummies from the Greco-Roman period (2282–1555 B.P.) are similar to mummies from both preceding and following periods. This lack of distinction must be taken into account by any proposed scenario.

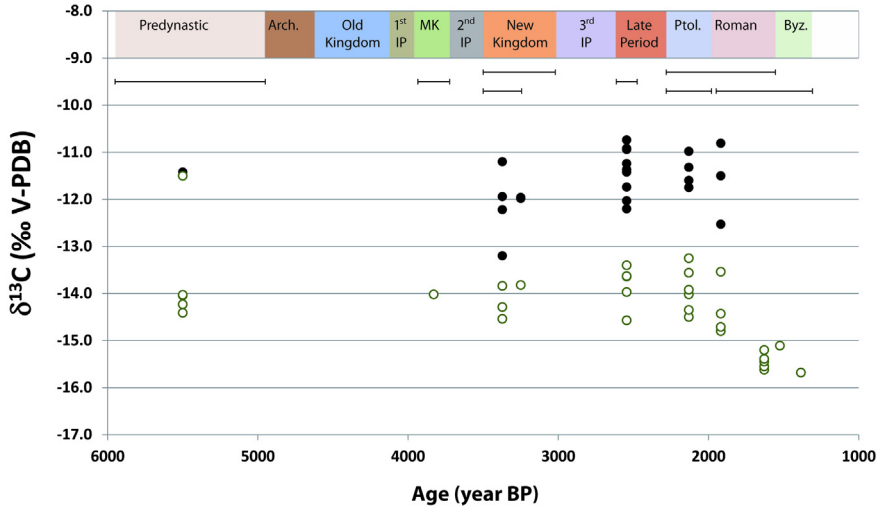

Fig. 2. $\delta^{13}C$ of apatite carbonate from enamel (solid circles) and bone (open circles) of ancient Egyptians. See Table 1 for mummy ages. Horizontal bars: duration of each period considered.

The carbon, nitrogen, and sulfur isotope compositions of hair are listed in Table 2. The $\delta^{13}C_h$ of hair ranges from −20.4‰ to −19.2‰ and, thus, is similar to the isotopic ratios measured for hair (in particular female hair) from the Kellis cemetery (Williams et al., 2011), and within the lower range of hair values from Nubians (Schwarcz and White, 2004). A Kruskal–Wallis test shows that $\delta^{13}C$ of hair fibers from Coptic mummies is significantly different from that of dynastic mummies (p-value = 0.038). The $\delta^{15}N$ values of hair fibers range from +9.1‰ to +15.5‰ and the $\delta^{34}S$ values range from +7.1‰ to +11.1‰.

Table 2
Carbon, nitrogen, and sulfur isotope compositions of hair from Egyptian human mummies, and of hair, scales, and feathers from animal mummies. (b) Sub-sample of feather cleaned with solvents (see text for details).

Individual	Species	Locality	Period	Sample	%C	%N	%S	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$	C/N	C/S
Human												
30000103	Human	Gournah	26th	Hair	49.6	15.0	4.9	−19.2	12.8	8.9	3.3	10.2
30000257	Human	Gournah	26th	Hair	49.6	14.4	4.5	−19.9	14.2	8.1	3.4	10.9
30000127	Human	Thebes	26th	Hair	46.7	14.8	5.1	−19.5	15.5	7.1	3.1	9.2
30000102	Human	Thebes	26th	Hair	47.8	14.6	5.0	−20.2	9.8	8.7	3.3	9.6
30000125	Human	Thebes	26th	Hair	47.9	14.6	5.0	−20.0	12.1	7.8	3.3	9.5
30000139	Human	Thebes	PT	Hair	48.0	15.7	4.7	−19.9	11.8	8.4	3.0	10.1
1448	Human	Antinopolis	CO	Hair	49.1	14.7	5.2	−20.4	9.1	10.6	3.3	9.5
1343	Human	Antinopolis	CO	Hair	47.3	14.1	4.9	−20.3	11.2	11.1	3.3	9.6
n.a.	Human	Antinopolis	CO	Hair	47.4	14.7	5.0	−20.1	10.8	9.6	3.2	9.5
Composite (2 or more fishes)												
90002164 and 90002659	Nile perch		*GR?*	Scales	28.8	7.7	0.9	−19.0	8.8	7.2	3.7	31.9
90002168 and 90002260	Nile perch		*GR?*	Scales	25.1	5.2	0.9	−18.6	11.3	9.8	4.8	27.7
90002180, 90002225 and 90002193	Nile perch		*GR?*	Scales	25.2	5.6	0.6	−18.9	10.4	10.2	4.5	42.1
90002196 and 90002258	Nile perch		*GR?*	Scales	28.7	7.9	0.7	−19.0	11.1	9.0	3.6	40.1
90002231 and 90002244	Nile perch		*GR?*	Scales	22.8	4.7	0.7	−19.4	11.2	10.7	4.9	34.5
90002248 and 90002241	Nile perch		*GR?*	Scales	25.6	8.2	0.7	−15.1	7.8	8.9	3.1	38.9
90001349, 90002241 and 90002269	Nile perch		*GR?*	Scales	22.3	6.0	0.7	−18.5	11.4	10.7	3.7	31.6
Single fish												
90002232	Nile perch		*GR?*	Scales	17.0	4.5	0.5	−19.1	11.1	9.1	3.8	31.4
90002238	Nile perch		*GR?*	Large scale	25.8	6.8	0.7	−19.9	10.9	9.3	3.8	37.7
90002167	Nile perch		*GR?*	Scales	27.9	6.5	0.7	−19.6	11.3	10.6	4.3	37.7
90001179	Nile perch	Esna	*GR?*	Large scale	32.7	6.9	0.5	−27.6	9.5	11.8	4.7	68.5
Mammals												
90002356	Cat			Hair	48.3	14.4	3.3	−20.6	13.0	8.8	3.4	14.7
90002644	Rodent (*Acomys*?)	Kom Ombo	*Roman?*	Hair	43.5	12.9	3.6	−22.1	4.3	9.7	3.4	12.1
90002286	Antelope			Hair	48.5	14.4	2.8	−20.7	11.8	12.5	3.4	17.3
90002280	Gazelle			Hair	47.8	13.4	2.4	−17.3	10.2	9.2	3.6	20.2
90001211	Dorcas gazelle	Kom Mereh	*Roman?*	Hair	32.6	8.8	1.6	−21.4	12.3	7.6	3.7	19.8
90010003	Gazelle	Kom Mereh	*Roman?*	Hair	48.1	14.0	2.7	−17.3	13.6	14.6	3.4	17.6
90001404	Dog	Asyut	GR	Hair	48.8	15.2	4.2	−19.7	13.3	7.7	3.2	11.7
90001403	Dog	Asyut	GR	Hair	45.1	14.3	4.4	−20.7	13.4	10.1	3.2	10.2
90002324	Dog	Asyut	GR	Hair	44.2	14.1	4.0	−19.7	12.1	8.5	3.1	11.1
Birds												
90002490	Ibis			Feather	53.2	9.0	1.9	−20.3	15.5	6.8	5.9	28.5
90002444	Goose?			Feather	47.3	13.9	3.1	−16.3	14.3	5.5	3.4	15.4
90010094	Bird of prey	Gizeh	*LP-PT?*	Feather	50.8	11.7	2.3	−19.0	12.8	11.1	4.3	21.9
90010094b	Bird of prey (b)	Gizeh	*LP-PT?*	Feather	48.0	14.5	2.3	−17.2	12.5	12.7	3.3	21.2
90001244	Nile goose	Gournah	*Ramessid?*	Feather	41.9	12.2	3.1	−19.4	15.0	6.9	3.4	13.6
90001244b	Nile goose (b)	Gournah	*Ramessid?*	Feather	47.3	14.2	2.5	−19.2	14.4	7.5	3.3	18.7

The carbon, nitrogen, and sulfur isotope compositions of animal samples (feathers, scales, and hair fibers) are listed in Table 2. The $\delta^{13}C$ values of fish scales cluster around −19‰, except for two fish specimens (90002241, 90001179). The $\delta^{13}C$ values of mammal hairs lie between −21.4‰ and −17.3‰, a range slightly lower than that defined by bird feathers ($-20.3‰ < \delta^{13}C < -16.3$). Nitrogen isotope ratios are lowest for rodents (+4.3‰), while the highest values were measured on feathers of ibises and geese (+14.3 to +15.5‰), with the value for a prey bird also being relatively high (+12.5‰). Intermediate $\delta^{15}N$ is recorded in fish scales (+7.8‰ to +11.4‰), as well as in the hairs of a cat, a few dogs, and gazelles (+10.2‰ to +13.4‰). The range of sulfur isotope compositions of fishes is more restricted (+7.2‰ to +11.8‰) than that observed for mammals (+7.6‰ to +14.6‰), while water birds have low $\delta^{34}S$ (+5.5‰ to +7.5‰) compared with the analyzed prey bird (+11.1‰).

5. Discussion

5.1. Preservation of tissue stable isotope compositions

The most common diagenetic processes that can alter the carbon isotope compositions of bone and enamel are the chemical and isotopic exchanges of carbonate ions with groundwater and soil water after burial and the dissolution and recrystallization of mineralized tissues (Wright and Schwarcz, 1996). These processes are particularly enhanced in the presence of fluids and under microbially-mediated conditions (Zazzo et al., 2004). The dry conditions prevailing in Egypt therefore minimize the risk of post-mortem modification of the original carbon isotope ratios. Moreover, burial within a coffin or sarcophagus limits chemical interactions between tissues and surrounding sediment. These assumptions are strengthened by the comparison between the isotopic composition of oxygen in carbonate and phosphate of mummies (Touzeau et al., 2013), which show good preservation of the oxygen isotope compositions of apatite carbonate.

Hair is resistant to chemical degradation because it is composed of hydrophobic proteins (Bertrand, 2002). The hair sampled here from Egyptian mummies was partly covered by particles of organic matter, which were successfully removed through the successive acid-alkali-acid baths. The carbon, nitrogen, and sulfur contents of the sampled mummy hair fibers are similar to those of present-day humans (C = 49.9%, N = 15.3%, and S = 5.1%; Bertrand, 2002), indicating preservation of the stable isotope compositions.

5.2. Geographic origin of food sources and dietary evolution

Local food production in ancient Egypt, from cereals to animals, is extensively documented by both archeological and literary sources (Alcock, 2006; Butzer, 1976; Samuel, 2000). The fertility of the Nile valley not only satisfied the needs of the relatively small Egyptian population but often produced excess cereal and textile that could be traded for wood, silver, copper, and spices, which were resources that Egypt lacked (David, 2007). Although food importation on a regular basis, with the exception of spices, has not been documented so far for ancient Egypt, trade with foreign countries allowed the introduction of new food resources that subsequently became farmed in Egypt. The local origin of food is also attested to by $^{87}Sr/^{86}Sr$ of enamel and bone from mummies of ancient Egyptians (Touzeau et al., 2013). Except for a single individual considered a potential migrant, $^{87}Sr/^{86}Sr$ is remarkably uniform, ranging from 0.7076 to 0.7082 (Touzeau et al., 2013), and similar to the Nile River sedimentary composition (Krom et al., 2002), indicating that ancient Egyptians were consuming food produced exclusively within the Nile Valley. Bone and enamel $\delta^{13}C$ values likewise remain constant throughout the studied period (Fig. 2). Only Coptic mummies have apatite carbonate and hair $\delta^{13}C$ values slightly lower than other mummies. Such constant carbon isotope compositions suggest that ancient Egyptians had a relatively basic diet with a restricted number of food items.

5.3. The $\delta^{13}C$ record of weaning

On average milk is ^{13}C-depleted compared to the mother's body (Jenkins et al., 2001) because it contains high levels of lipids, which are ^{13}C-depleted compared to carbohydrates and proteins in plants and animals (DeNiro and Epstein, 1977; Tieszen and Fagre, 1993). Once breast-feeding has stopped, teeth (premolars and second and third molars) start recording higher $\delta^{13}C$ values in accordance with a diet approaching that of adults. While increases in $\delta^{13}C$ values of about +0.7‰ have been reported in the literature (Wright and Schwarcz, 1998, 1999; Dupras and Tocheri, 2007), our data reveal comparably heavy isotope enrichment with $\delta^{13}C$ values of −12.2‰ for early-forming teeth (first molars M1, incisors I, and canines C) against −11.3‰ for later-forming teeth (PM, M2, and M3). Calling for consumption of ^{13}C-enriched weaning foods (Dupras et al., 2001; Dupras and Tocheri, 2007; Wright and Schwarcz, 1998, 1999) is unnecessary to explain the observed carbon isotope shift, and, therefore, the most straightforward explanation of reduced milk intake is favored here.

5.4. Differences between enamel and bone $\delta^{13}C$ values

Enamel $\delta^{13}C_{en}$ values are significantly higher than those of $\delta^{13}C_{bo}$, whether as a whole (+2.7‰) or on the scale of individuals (+2.4‰). This difference may reflect either true differences in diet at different periods of life, i.e. consumption of specific foods during childhood, or differences arising from isotopic fractionation during tissue mineralization. As mentioned above, breast-feeding should lead to lower $\delta^{13}C$ values in enamel than in bone because of the ^{13}C-depletion of milk. Thus, the "weaning effect" cannot account for the observed positive offset ($\Delta_{en\text{-}bo} > 0$), which, additionally, is larger in its absolute value than what would be expected from weaning (~2.5‰ instead of ~0.7‰). Positive enamel-bone isotopic offsets were previously observed in a controlled-feeding study of animals (Warinner and Tuross, 2009). Given that pigs have a digestive tract similar to that of humans, as well as a comparable omnivorous diet, this animal is considered a good 'model', or proxy, for investigating past human nutritional habits (Patterson et al., 2008). Warinner and Tuross (2009) demonstrated that pig canines are ^{13}C-enriched by 2‰ compared to humerus bones formed at the same time. Thus the carbon isotope fractionation between blood bicarbonate and bone seems to be different from that between blood bicarbonate and enamel. The difference observed for Egyptian mummies may be ascribed partly to this tissue-related difference in carbon isotope fractionation, partly to a change in diet between the periods of tooth and bone growth. Biologically, such tissue-related offset could be due to differences in the microenvironment of enamel formation and bone renewal (Warinner and Tuross, 2009) and could result from distinct mechanisms of pH buffering between the two types of tissue (Smith et al., 2005). Smith et al. (2005) proposed that ameloblasts counteract local acidic conditions by releasing bicarbonate ions into enamel layers. Pasteris et al. (2004) pointed out that bone apatite is not hydroxylated as opposed to enamel hydroxyapatite, and also proposed that this chemical difference has a biological significance for bone remodeling. Other differences between the two tissues are structural, with bone apatite crystals

being on average ten times smaller and less atomically ordered than enamel hydroxyapatite (Pasteris et al., 2004).

5.5. Assessment of dietary C3/C4 proportions

Sorghum and millet, the two C4-cereals common in Africa, are rare in the archaeological record from Egypt. For the Roman Period, they are known at Kom el-Nana (Middle Egypt, Smith, 2003), Berenike (Red Sea Coast, Cappers, 1999), in the Dakhleh oasis (Dupras et al., 2001), and at Qasr Ibrim in Egyptian Nubia (Clapham and Rowley-Conwy, 2007). Their presence indicates that these plants were known to the Egyptians at least from the Roman period, but their rarity in the assemblages compared to emmer wheat, free-threshing wheat, and barley indicates that they were probably not consumed in significant proportions, except at Qasr Ibrim, located at the Sudanese border, where sorghum became the most common cereal from the Meroitic period onwards (Clapham and Rowley-Conwy, 2007).

Two tissue-specific equations determined on the carbon isotope compositions of enamel and bone carbonate were used to estimate the original diet composition ($\delta^{13}C_d$) of ancient Egyptians (Fig. 3). Both are based on experimental data from pigs, considered, as discussed in Section 5.4, as an experimental model close to humans and used because of the absence – for obvious ethical reasons – of similar control-feeding studies in humans. The 'enamel equation' (1) was determined by combining data from Passey et al. (2005) and Warinner and Tuross (2009). In these two studies, the authors verified that the sampled teeth were fully formed during the period of consumption of the controlled diet.

$$\delta^{13}C_d = 1.18(\pm 0.08) \times \delta^{13}C_{en} - 11.53(\pm 0.68) \quad R^2 = 0.98;\ n = 7 \tag{1}$$

The 'bone equation' (2) was calculated using data from Howland et al. (2003) and Warinner and Tuross (2009). In both cases, the controlled diet was provided during a period of intensive growth of the pig, and, therefore, the percentage of remaining bone anterior to the controlled diet is small. However, the duration of the experiment was shorter in the study of Warinner and Tuross (2009) than in that carried out by Howland et al. (2003). Consequently, a remnant of the original bone composition ($\delta^{13}C = -8‰$) may have persisted in the former study, thereby explaining its slightly higher $\delta^{13}C_{bo}$ values compared to those of the Howland et al. (2003) study.

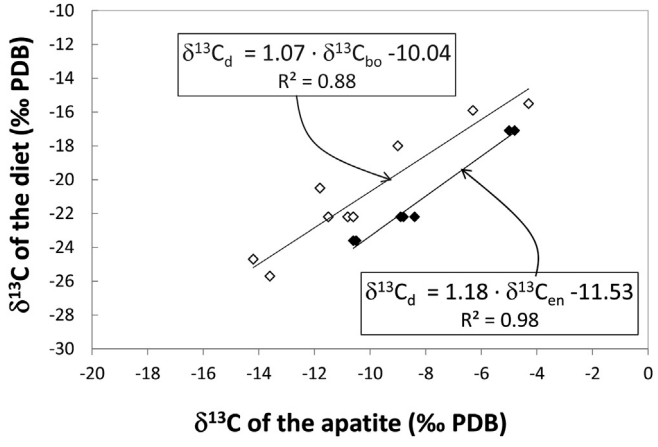

Fig. 3. Relationships between the carbon isotope composition of the diet ($\delta^{13}C_d$) and apatite carbonate for the two mineralized tissues (enamel: solid diamonds; bone: open diamonds). Data come from controlled diet studies on pigs (Howland et al., 2003; Passey et al., 2005; Warinner and Tuross, 2009).

$$\delta^{13}C_d = 1.07(\pm 0.13) \times \delta^{13}C_{bo} - 10.04(\pm 1.39) \quad R^2 = 0.88;\ n = 11 \tag{2}$$

Using average enamel and bone $\delta^{13}C$ values of, respectively, −11.6‰ and −14.3‰ in equations (1) and (2), the calculated $\delta^{13}C_d$ of food are −25.2‰ and −25.3‰, respectively, which are essentially identical. Both calculated $\delta^{13}C_d$ values compare well with the global average carbon isotope composition of −25.5‰ for C3-plants published by O'Leary (1988) after correction for fossil fuel release in the atmosphere (Fig. 4). If we consider the end-members of −25‰ for C3-plants and −10‰ for C4-plants in Egypt, as proposed by White et al. (1999), it can be concluded that the C4 contribution to the diet is close to zero taking into account the uncertainties associated with both equations (1) and (2) and the $\delta^{13}C$ values of the end-members (Fig. 4).

The observed offset between the enamel and bone $\delta^{13}C$ calls for caution before any attempt at comparing diets between different populations. In the context of the present study, we note that, on the one hand, bone $\delta^{13}C$ values are similar to those measured by Iacumin et al. (1996) in the Nile valley, and, on the other hand, enamel $\delta^{13}C$ values are similar to those measured by Dupras and Tocheri (2007) at the Dakhleh Oasis (Fig. 5). This observation indicates that the diet of ancient Egyptians at both sites was similar and poor in C4-foods compared to the diet of ancient Nubians (Schwarcz and White, 2004). It is possible that the small C4-component of the Egyptian diet (Williams et al., 2011) resulted from the consumption of animals raised with C4 fodder (Dupras et al., 2001; Dupras and Tocheri, 2007).

The hair $\delta^{13}C$ values measured in ancient Egyptians are plotted in Fig. 5, along with isotopic values taken from the literature (Supplementary material). After correction for carbon dioxide release of anthropogenic origin, $\delta^{13}C$ values are similar or slightly lower than those measured in hair fibers of present-day Europeans (Macko et al., 1999) and Asians (Thompson et al., 2010), who are consuming low amounts of C4 foods (<10%). Thus the information derived from hair is coherent with information derived from apatite carbonate. The hair $\delta^{13}C$ value of dynastic mummies also is similar to the mean annual $\delta^{13}C$ value measured in hair at the Dakhleh Oasis (Williams et al., 2011) and in Egyptian mummies from Gizeh and the Kharga oasis (Thompson et al., 2005). This

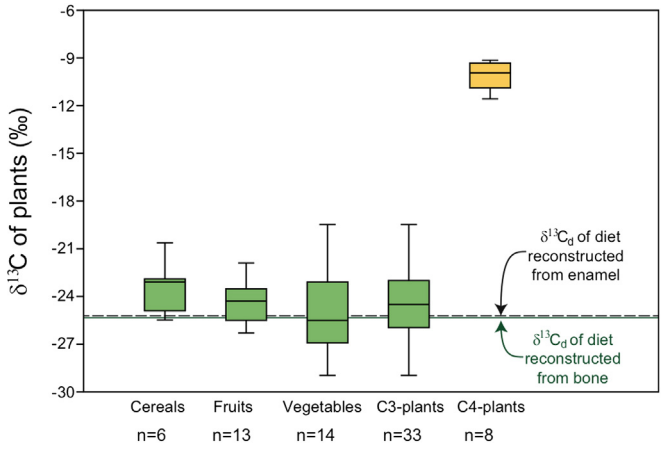

Fig. 4. $\delta^{13}C$ of the diet estimated from bone and enamel (horizontal lines) and box plot of the $\delta^{13}C$ of Egyptian plants from the literature (Dupras et al., 2001; Iacumin et al., 1998; Macko et al., 1999; White and Schwarcz, 1994). Modern plants have been corrected for anthropogenic CO_2 release. Green boxes: C3-plants; yellow box: C4-plants. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

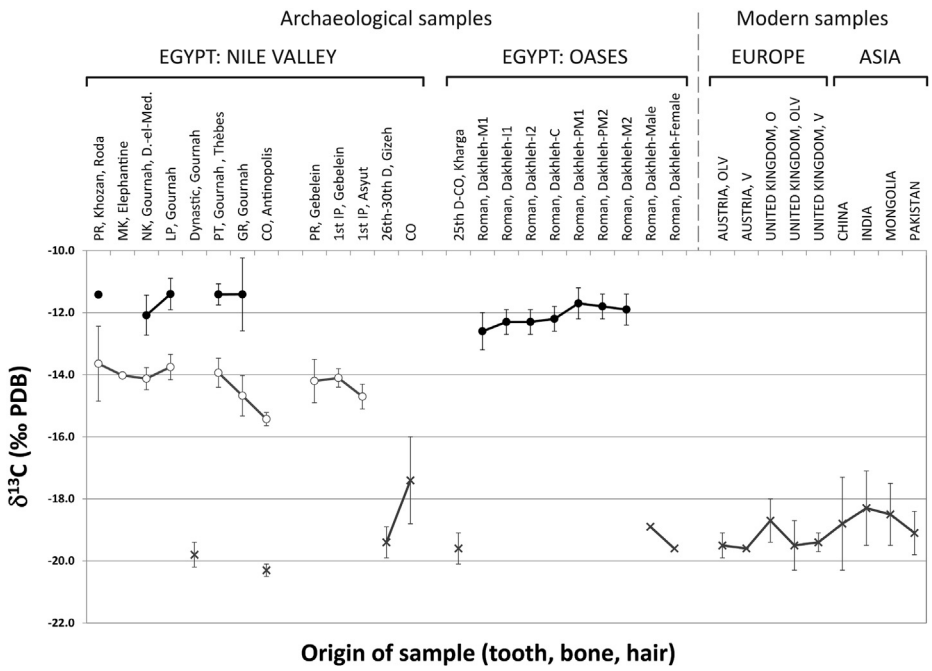

Fig. 5. $\delta^{13}C$ of hair and apatite carbonate from ancient Egyptians compiled from this study and the literature (Iacumin et al., 1996; Thompson et al., 2005; Macko et al., 1999; Dupras and Tocheri, 2007; Williams et al., 2011), as well as comparison with data for modern individuals (anthropogenic CO_2-corrected after Macko et al., 1999; Thompson et al., 2010). Solid circles: enamel; open circles: bone; crosses: hair. O: omnivore; OLV: ovo-lacto-vegetarian, V: vegan.

observation suggests a relative homogeneity in the amount of C4 food consumed from the Nile Valley to the oases despite the different agricultural practices between the two environments. The slightly lower $\delta^{13}C$ values of apatite carbonate from Coptic mummies could be explained by preferential consumption of leaf vegetables since they are ^{13}C-depleted compared to the whole plant (O'Leary, 1988). Another source of ^{13}C-depleted carbon is plant oil due to kinetic fractionation promoted by the pyruvate dehydrogenase complex during lipid biosynthesis (DeNiro and Epstein, 1977). For example, Prowse et al. (2005) proposed that elderly people who lived in Isola Sacra (Roman period; 1st to 3rd centuries A.D., ~1700 B.P.) consumed large amounts of olive oil and wine because their $\delta^{13}C_{bo}$ is lower than that of other adults. Introduction of olive oil in Egypt during the Roman period (Alcock, 2006) hence may explain the slightly lower $\delta^{13}C$ values observed in Coptic mummies.

5.6. Estimation of the consumption of animal products

The $\delta^{13}C_h$ value of hair is higher by +1.5 to +3‰ relative to the $\delta^{13}C$ values of dietary protein. Consequently, the $\delta^{13}C$ value of dietary protein of ancient Egyptians has been deduced from their average $\delta^{13}C_h$ hair value of −19.9‰ by subtracting 2.25 ± 0.75‰. The dietary carbon isotope composition of ancient Egyptians is the result of simple mass balance between two end-members, which are plants and animal protein. Plant protein should be slightly ^{13}C-enriched (+0.9‰, Schoeller et al., 1986) compared to the total plant and is thus fixed at −24‰. The average $\delta^{13}C$ value of animal muscle was estimated using keratin and collagen data from Egyptian (Dupras et al., 2001; Thompson et al., 2005) and Nubia animal remains (Iacumin et al., 1998; Thompson et al., 2008). Collagen $\delta^{13}C$ values were converted into muscle values by subtracting 2‰ (Tykot, 2006) and modern values were corrected by +1.5‰ for anthropogenic carbon dioxide release, leading to an average $\delta^{13}C$ value of animal muscle of −18 ± 3‰. This average value represents, however, only an approximate estimate of the animal products actually consumed by Egyptians of the Nile valley for the following reasons: 1) it is most likely biased towards large mammals (cow, goat, sheep), with only rare fish and birds; 2) mammals from Nubia and oases probably consumed more C4 fodder than mammals from the Nile valley; 3) dairy products have lower $\delta^{13}C$ values than meat. Considering these various potential biases, the true average $\delta^{13}C$ value of consumed animal products may have been closer to −20‰. Using the calculated average $\delta^{13}C$ value of −18 ± 3‰, mass balance calculations indicate that animal protein represents 29 ± 19% of protein in the diet. This proportion is similar to that of 32% observed in present-day ovo-lacto-vegetarians (Petzke et al., 2005) and lower than the average of 64% of present-day omnivores (Petzke et al., 2005). Assuming the lower estimate of −20‰ for animal products in the diet of ancient Egyptians, the proportion of animal protein may have reached 50%. On the basis of available present-day data, a proportion of animal protein in the diet of ancient Egyptians close to 30% seems to be the most robust interpretation, implying that ancient Egyptians most likely consumed less protein of animal origin than do modern humans.

The nitrogen isotope ratios measured in human hair fibers vary from +9.1‰ to +15.5‰, which are similar to $\delta^{15}N$ measured at Kerma, Nubia (Thompson et al., 2008) and in Egypt (Macko et al., 1999; Thompson et al., 2005), but higher than $\delta^{15}N$ documented for omnivorous modern Europeans and North Americans (~9.5‰, Macko et al., 1999; Thompson et al., 2010), as well as Asians (~8.5‰; Thompson et al., 2010). Such differences may arise from a variety of causes, including consumption of aquatic animals, increase in the $\delta^{15}N$ baseline of the environment owing to aridity, or modified nitrogen metabolism caused by pregnancy, illness, or nutritional stress (Katzenberg and Lovell, 1999; Olsen, 2013).

The health status of the individuals studied here is largely unknown because most of them are preserved only as skulls and also because of the osteological paradox: severe infections may not be visible in bones. However, it is highly unlikely that all the individuals analyzed in this study were either pregnant and/or sick at the time of their death, keeping in mind that they all have high nitrogen isotope ratios. Furthermore, only a chronic disease, which

would not provoke a rapid death, could have modified the nitrogen isotope ratios in hair. Olsen (2013) and Linderholm and Kjellström (2011) compared the collagen nitrogen isotope ratios for individuals that were healthy and affected by chronic diseases: for arthrosis, periostitis, osteomyelitis, and leprosies, the nitrogen isotope ratios (aside from lesions) were not significantly different. Even for lesions, only small changes in the $\delta^{15}N$ values were detected, ranging from 0.5 to 2‰ (Olsen, 2013), similar to those caused by pregnancy (Fuller et al., 2004, 2005), which in both cases are not sufficient to explain the observed ^{15}N enrichment in the hair of mummies.

A strong influence of aridity on animal $\delta^{15}N$ values is attested to by $\delta^{15}N$ values of +13.6‰ for gazelles and antelopes, which are strict herbivores (Fig. 6b). Aridity also affects the nitrogen isotope composition of goats, cattle, and sheep from Egypt and Nubia (Iacumin et al., 1998; Dupras et al., 2001; Thompson et al., 2005, 2008, Fig. 6a), as well as certain plants (Macko et al., 1999, Fig. 6b). This strong influence of aridity hinders a rigorous assessment of the importance of aquatic resources in the diet of ancient Egyptians using $\delta^{15}N$ values alone. Sulfur isotope compositions of soft tissues may help remove the ambiguity between the respective contributions of aridity and food resources to the aquatic origin of the nitrogen isotope signatures of animals submitted to hydric stress.

Marine resources have sulfur isotope compositions markedly distinct from continental resources. In contrast, freshwater products are more ambiguous. Before attempting any paleodiet reconstruction, local fishes and other aquatic vertebrates therefore must be measured for their sulfur isotope compositions (Privat et al., 2007). The $\delta^{15}N$ and $\delta^{34}S$ values of mummified animals, including fishes, are reported in Fig. 6b, together with the isotope compositions of Egyptian plants (Macko et al., 1999). Nile perches have $\delta^{34}S$ values ranging from +7‰ to +12‰ and $\delta^{15}N$ values ranging from +8‰ to +11‰. Consequently, humans who consume a significant proportion of fish should have $\delta^{34}S$ around +10‰ and $\delta^{15}N$ values of at least +13‰ according to the 'trophic level effect' combined with the environmental hydric stress. Only Coptic mummies have $\delta^{34}S$ values compatible with fish consumption, although this observation is inconsistent with their relatively low $\delta^{15}N$. It cannot be excluded that the high $\delta^{34}S$ of hair fibers from ancient Egyptians results from the consumption of freshwater plants, crayfish, or fish low in the aquatic food chain compared to perches, which belong to the top predators of the Nile river (Mkumbo and Ligtvoet, 1992). Another hypothesis would be the presence of locally ^{34}S-enriched terrestrial plants. Moderately high $\delta^{34}S$ values (+10–11‰) have been reported for cultivated plants in the United States of America (Richards et al., 2003), and could also exist in Egypt given that the high-sulfur coals from northeastern Egypt have $\delta^{34}S$ ranging from +1‰ to +15.4‰ (Baioumy, 2010). Since other Egyptian mummies have $\delta^{34}S$ values that compare well with those of ibises, it cannot be ruled out that some Egyptians fed on freshwater products (crayfish and small fishes) that were also part of the diet of the ibis.

6. Conclusions

Carbon isotope ratios were measured in enamel, bone, and hair of ancient Egyptians. A significant offset (+2.5‰) is observed between the $\delta^{13}C$ values of teeth and bones that cannot be ascribed to the weaning effect. Following Warinner and Tuross (2009), this isotopic offset rather may be caused by differences in mineralization conditions of the two types of tissue. Using tissue-specific equations, the $\delta^{13}C$ value of the reconstructed diet is comparable and close to the average value of C3-plants (−25‰). $\delta^{13}C$ values of hair from ancient Egyptians also suggest that C4-derived foods were rare in the diet (<10%), a result consistent with previous studies (Iacumin et al., 1996; Thompson et al., 2005).

Carbon isotope ratios in mineralized tissues are constant throughout the studied period, indicating a preference for C3-derived food throughout the investigated time span. This is a

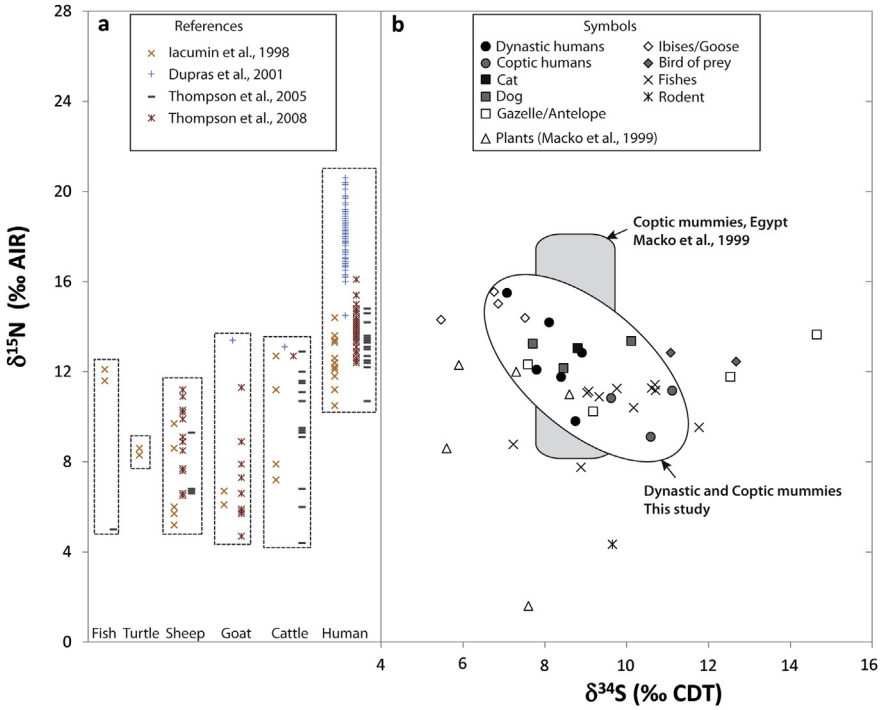

Fig. 6. a: Nitrogen isotope compositions of humans and animals from Egypt and Sudan (Iacumin et al., 1998; Dupras et al., 2001; Thompson et al., 2005, 2008). b: Nitrogen and sulfur isotope compositions of humans, plants, and animals from ancient Egypt (this study, Macko et al., 1999).

surprising result given that C4 plants are better suited to arid environments, and that the climate became increasingly arid during this period (Touzeau et al., 2013). Coptic mummies have $\delta^{13}C$ values slightly lower than other mummies, possibly as a result of the introduction of olive oil during the Roman Period.

Assessing the consumption of animal products is difficult because the $\delta^{15}N$ of soft tissues, such as hair, is controlled by parameters other than diet, and in particular by the prevailing hydric stress. Using the carbon isotope ratios of mummy hairs, the contribution of animal protein to the total dietary protein was estimated here at 29 ± 19%, corresponding to an ovo-lacto-vegetarian diet. Taking into account potential biases in the diet reconstruction, the proportion of protein of animal origin may have reached 50%. Both estimates are lower than the average value of 64% characterizing modern omnivorous Europeans (Petzke et al., 2005). Sulfur isotope ratios of mummy hairs further indicate that freshwater fish, such as the Nile perch, was not consumed in significant proportions.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jas.2014.03.005.

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