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Dinosaur bones: fossils or pseudomorphs? The pitfalls of physiology reconstruction from apatitic fossils

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Abstract

A prerequisite to any attempt to reconstruct thermophysiology of ancient animals through analysis of stable isotopes of oxygen is the assumption that apatitic fossils are isotopically unaltered parts of their original skeletons. We suggest that sufficient evidence is available to seriously question this assumption. Because living bones contain about 1/3 by weight of organic matrix, mass balance considerations show that at least half of an apatitic fossil must be new material added post mortem. Furthermore, living apatitic skeletons contain almost no rare earth elements and uranium, whereas apatitic fossils bear high concentrations of these elements. Additionally we found that while in living fish correlation between $\delta^{18}O$ of oxygen in the phosphate and that in the carbonate of apatite is poor, these two values are linearly correlated in fossil fish. This suggests diagenetic recrystallization has taken place. Perfect preservation of micro-textures such as Haversian canals does not prove the pristine condition of a fossil; some of the most beautifully preserved fossils are highly silicified. Most apatitic fossils probably are pseudomorphs replacing original skeletal elements. Whereas distribution of stable isotopes of oxygen in fossils might provide information about their burial environment, it could be misleading in attempts to interpret the organisms' physiology This cautionary note is supported by the similarity of $\delta^{18}O_p$ in bones of coexisting fossil fish, dinosaurs, and various other reptiles at different latitudes. The overlap of predicted $\delta^{18}O_p$ values in fish and mammals living in contact with the same environmental water also weakens the hope that ectotherms can be distinguished from endotherms by the isotopic composition of oxygen in their bones and teeth.

Keywords: Vertebrata; bones; biomineralization; fossilization; diagenesis; oxygen isotopes; dinosaurs

1. Introduction

For more than three decades measurement of the distribution of stable isotopes of oxygen in biogenic skeletons has served as a powerful tool for both estimation of paleo-environments of past oceans and lakes (Epstein et al., 1951; Shackleton and Kennett, 1975; Savin, 1977; Talbot, 1990) as well as attempts to distinguish between organisms living in marine as opposed to fresh water (Keith et al., 1964). Most of these studies used calcium carbonate secreting organisms (mollusks, foraminifera) as the recording medium. Increasing application of the isotopic analysis of oxygen in the phosphate of apatites (Longinelli, 1965; Longinelli and Nuti, 1973; Kolodny et al., 1983) extended

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the range of problems which can be studied by measurement of $\delta^{18}O$ in biogenic solids. These analyses have the advantage of making use of a material that apparently is more resistant to post-depositional alteration than carbonate. This results from the fact that exchange between phosphate oxygen and water oxygen is extremely slow in inorganic conditions, but it is very rapid in enzyme catalyzed reactions (Tudge, 1960; Kolodny et al., 1983). Its stability not only suggested $\delta^{18}O$ in phosphate ($\delta^{18}O_p$) as an "ideal geochemical recorder" (Kolodny et al., 1983)—recording accurately during a skeleton building organism's life and preserving the signal well after the organism's death—but also opened the possibility of using $\delta^{18}O_p$ for obtaining information about the physiology of endothermic ("warm-blooded") organisms. (see review in Lifson and McClintock, 1966).

This approach to the use of stable isotopes of oxygen has its origin in the studies of Lifson and coworkers in the early days of isotope chemistry. Analysis of apatitic skeletal remains as an indicator of an animal's drinking water has been suggested by Longinelli and Peretti Padalino (1983), as well as by the Jerusalem group (Luz et al., 1984; Luz and Kolodny, 1985). The latter group showed experimentally the excellent correlation between controlled drinking water and bone composition in laboratory rats. They were able to suggest a simple box model of oxygen fluxes in and out of a mammal's body, explaining this correlation to a first approximation. This rather simple model was later improved by Luz et al. (1990), Ayliffe and Chivas (1990) and recently by Bryant and Froelich (1995). It is not surprising that demonstration of a relationship between $\delta^{18}O_p$ and an animal's physiology led to the hope that $\delta^{18}O_p$ of fossil bones and teeth might hold the key to reconstruction of the thermal physiology of extinct animals. Also, it is not surprising that the first problem to be approached from this angle was an attempt to decipher the thermal physiology of dinosaurs and solve the "cold-blooded – warm-blooded" dilemma of these exciting giants.

Deciphering dinosaur thermophysiology by isotopic criteria was attempted by Barric, Showers and their coworkers (Barrick et al., 1992; Showers et al., 1992; Barrick and Showers, 1994). Their results caused considerable excitement (Kerr, 1992; Morell, 1994; Anonymous, 1994). In several reports the senior authors of this paper were quoted as expressing their skepticism about these findings. The purpose of this paper is to present the available evidence relevant to an assessment of our ability to distinguish endothermic from ectothermic dinosaurs by isotopic methods. We present our argument stressing two essential points: (a) an examination of the possibility of a hypothetical difference in $\delta^{18}O_p$ between endotherms and ectotherms (b) a consideration of the evidence that whatever the differences between living bones—biological apatite—of endotherms and ectotherms might have been, the isotopic composition of fossil bones is not a reflection of these but rather of burial environments.

1.1. "Cold-blooded" vs. "warm-blooded" organisms

The isotopic composition of oxygen in the phosphate of biogenic apatite ($\delta^{18}O_p$) is related to the temperature of deposition of the solid (t) and the isotopic composition of the water from which it is deposited ($\delta^{18}O_w$) (Longinelli and Nuti, 1973):

$$t(^{\circ}C) = 111.4 - 4.3(\delta^{18}O_p - \delta^{18}O_w) \quad (1)$$

In $\delta^{18}O_p - \delta^{18}O_w$ space, Eq. (1) will plot as a set of parallel isotherms with a slope of unity and intercepts of $(25.9 - 0.24t)$. (Fig. 1). When considering these values it must be noted that not all combinations of $\delta^{18}O_p - \delta^{18}O_w - t$ are permitted: it is rather unlikely that one will observe a combination of very ^{18}O depleted water and high temperatures of deposition just as it is unlikely that high $\delta^{18}O_w$ values will exist in very cold waters. This results from the close correlation between the isotopic composition of meteoric water and air temperature (Dansgaard, 1964).

Luz and Kolodny (1985) have demonstrated that Eq. (1) holds true for both mammals and fish. The important difference between the two groups is that in fish $\delta^{18}O$ of the body fluids is similar to that of ambient water resulting from rapid H_2O exchange across the gill membranes. The situation in mammals is different. Here respiratory gas exchange takes place in lungs and water

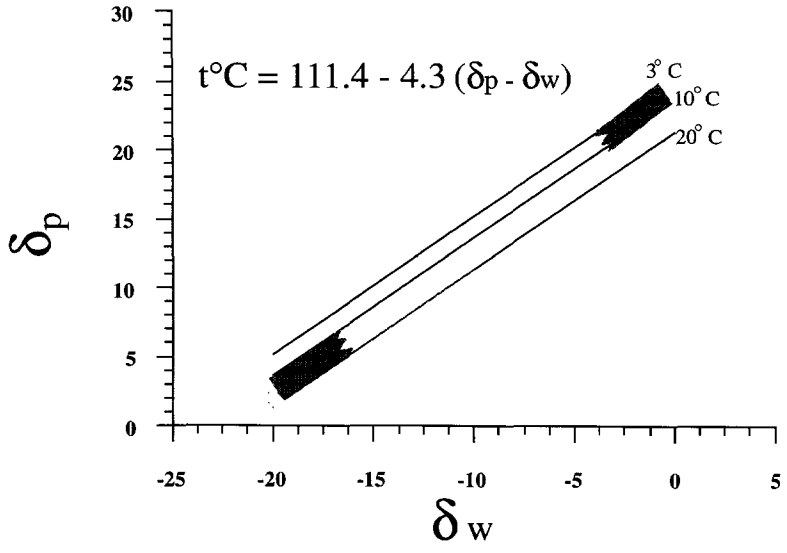

Fig. 1. $\delta^{18}O_p$ of fish bones versus the isotopic composition of the water in which they live ($\delta^{18}O_w$), at three temperatures (3°C, 10°C, 20°C). The hatched areas mark unlikely combinations of temperature and environmental water composition.

exchange is limited to active uptake in drinking and in food ingestion, and to water excretion. In this case water turnover in the body is much slower. The isotopic composition of mammal body water ($\delta^{18}O_{bw}$) depends on that of the intake water ($\delta^{18}O_w$) as well as on metabolic water and respiratory CO_2 (Luz et al., 1984; Luz and Kolodny, 1985, 1989).

The same situation applies to all animals that use lungs for gas exchange (modern reptiles and birds for example). The extent to which $\delta^{18}O_{bw}$ will deviate from $\delta^{18}O_w$, depends on the ratio of the metabolic rate and body water turnover. Bryant and Froelich (1995) recently demonstrated the rather complicated relationship between these factors and $\delta^{18}O_{bw}$. In general at low metabolic rate $\delta^{18}O_{bw}$ of air breathing organisms will be close to $\delta^{18}O_w$. As the metabolic rate increases with respect to water turnover $\delta^{18}O_{bw}$ will usually become greater than $\delta^{18}O_w$. A number of factors account for this phenomenon: (1) Preformed water in food is expected to be enriched in ^{18}O because of evaporation isotope effects in plants. (2) Metabolic water and metabolic CO_2 (CO_2 and body water exchange oxygen very rapidly) contain oxygen of atmospheric origin. The isotopic ratio of atmospheric oxygen is constant—($\delta^{18}O =$ 23.5‰ vs. SMOW) and is always more enriched in ^{18}O than any meteoric water; (3) Water vapor lost in respiration is depleted in ^{18}O with respect to body water, so the latter must become enriched in ^{18}O as more and more water vapor is lost in respiration. Exhaled CO_2 is enriched in ^{18}O with respect to body water, and will thus tend to deplete the heavy isotope in body water. This effect, however is over balanced by the other factors mentioned.

Enrichment of ^{18}O in body water over that of meteoric water is greater when $\delta^{18}O_w$ is low because of the constant composition of atmospheric oxygen. As $\delta^{18}O_w$ decreases the effect of mixing ^{18}O enriched oxygen of constant composition must be greater. It follows that the effects of metabolic rates will be greater at high latitudes (low $\delta^{18}O_w$). This has been demonstrated experimentally by Luz et al. (1984) and by Luz and Kolodny (1985).

In mammals $\delta^{18}O_p$ (the isotopic composition of bone phosphate) is greater than $\delta^{18}O_{bw}$ by about 18‰ (Luz and Kolodny, 1985). This is the enrichment expected from Eq. (1). The relationship in this case of $\delta^{18}O_p$ vs. $\delta^{18}O_w$ is a simple function of the $\delta^{18}O_{bw}$ vs. $\delta^{18}O_w$ relationship and vice versa. The situation in reptiles may be more complicated

because the $\delta^{18}O_p - \delta^{18}O_{bw}$ offset is not constant and depends on the variable reptile body temperature. This last statement need to be qualified, because $\delta^{18}O_p$ depends on the temperature at which bone material is being laid down, and not on the average body temperature. In fact our preliminary data (unpublished) suggest that reptile bones are formed at a rather narrow temperature range, one that is much smaller than the overall ambient temperature variation. This may indicate some behavior strategy of regulating body temperature, at least as far as bone formation is concerned. If this conclusion holds true it would cast a serious doubt on the value of bone isotopic composition as an indicator of endothermy of dinosaurs. If reptiles do not regulate their body temperature at the time of bone formation, their $\delta^{18}O_p$ will be greater than in mammals having the same $\delta^{18}O_{bw}$ (assuming ambient temperature is lower than the mammal's body temperature).

Observations of $\delta^{18}O_p$ vs. $\delta^{18}O_w$ often show simple systematic relationships (Longinelli, 1984; Ayliffe and Chivas, 1990; Luz et al., 1990). Usually data points plot in linear patterns with a slope less than 1, and the trends are different than those of fish. These slopes appear to be species dependent, approaching unity at large body sizes (lower metabolism compared to water turnover). On Fig. 2 we plot the relationships for two hypothetical mammals, a small one (WB-1) with a $\delta^{18}O_p - \delta^{18}O_w$ slope of 0.6 and a large one (WB-2) with a slope of 0.9. As discussed above, reptile $\delta^{18}O_p$ values will fall on similar trends as mammals but may have greater ^{18}O enrichment. In Fig. 3 we overlay the curves of Fig. 2 on those of Fig. 1. It is evident that there is almost no area in $\delta^{18}O_p - \delta^{18}O_w$ space which discriminates clearly between fish on one hand, and mammals and reptiles on the other hand. For any $\delta^{18}O_w$ and environmentally reasonable temperatures $\delta^{18}O_p$ overlap for fish, mammals and reptiles of biologically reasonable physiological nature. The only exception may be at low $\delta^{18}O_w$ where small mammals and reptiles may have greater $\delta^{18}O_p$ than fish. Indeed fresh water fish from Israel have $\delta^{18}O_p$ in the range of 15.4–19.6‰, quite similar to the range of human teeth from Israel. Likewise a fish from Lake Inari (Finland) yielded $\delta^{18}O_p$ of 11.1‰, while human teeth from the same area yielded values of 11.9–13.6‰ (Kolodny et al., 1983; Levinson et al., 1987). Thus it appears that there is a low probability of distinguishing a fossil endotherm from one derived from an ectotherm solely on the evidence of the isotopic composition of the oxygen in its bones or teeth.

1.2. Living vs. fossil bones and teeth

In this study we analyzed a recent vertebrate faunal assemblage from the Jordan Valley, that included a bony fish (teleost), a turtle and a crocodile. In addition five terrestrial vertebrate faunas from the Early Cretaceous to latest Cretaceous were analyzed. The paleolatitudes of these assemblages extend from 30°N to 77°N. Paleolatitudes were taken from the literature (Smith et al., 1973; Brouwers et al., 1987) or determined with the computer program Terra Mobilis! (Denham and Scotese, 1987). The various assemblages contained one or more dinosaurs, and two contained pterosaurs. Bony fish, sharks, turtles and crocodiles also were present. All analyses were performed according to the methods used in Jerusalem at the time (Shemesh et al., 1988). For most samples that involved using $BiPO_4$ as the phosphate purifying phase, for a few Ag_3PO_4 was used. No systematic differences were detected between the two procedures.

Table 1 presents a summary of the analytical results. The major feature evident from the table is the similarity of oxygen isotopic compositions of the different taxa from any given locality, and the close correlation between paleolatitude (or latitude) and $\delta^{18}O_p$. This is most strikingly demonstrated in the Maastrichtian faunas. The Alaskan (paleolatitude 77°N) hadrosaurs yielded $\delta^{18}O_p$ between 5.4 and 7.5‰, with a single specimen showing 9.9‰. A teleost vertebra from the same formation yielded $\delta^{18}O_p$ of 8.0‰. Compare these data to those from the intermediate latitude (46°N) Lance Fm. Wyoming, fauna in which all fossils range between 12.0 and 14.9‰, and the paleosubtropical (32°N) Javelina Formation, Texas, in which bony fish, reptile, pterosaur, ceratopsian, and hadrosaur fossils, all show values of 16.6–19.3‰. No systematic difference between fish, reptiles and dinosaurs can be detected in the values

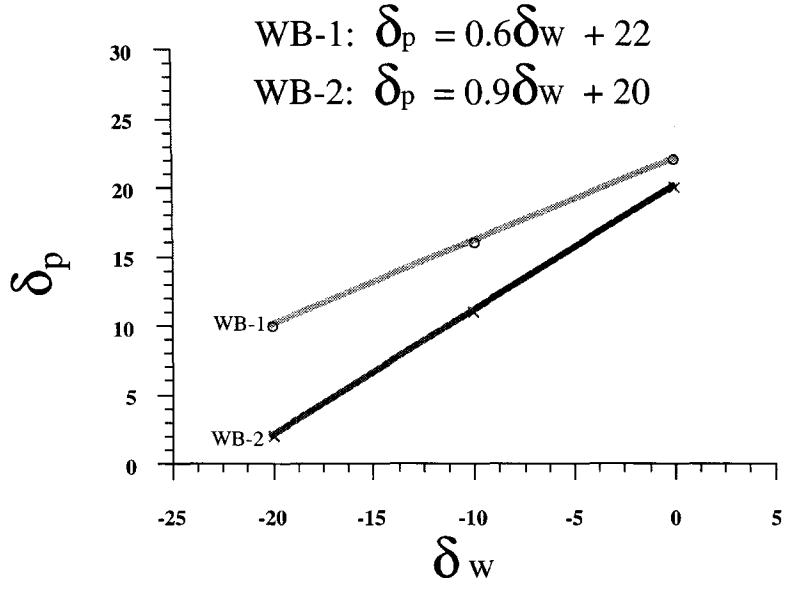

Fig. 2. $\delta^{18}O_p$ versus $\delta^{18}O_w$ in two "hypothetical mammals" as representing arbitrary endotherms. To demonstrate the likely range of compositions a low slope (0.6) representing a small mammal, and a slope close to unity representing a large body were selected.

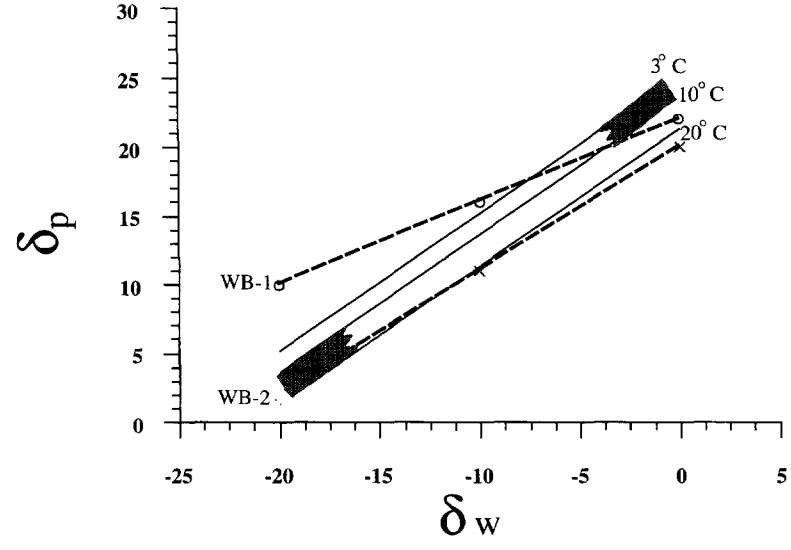

Fig. 3. A combination of Figs. 1 and 2. Note that for most of the range of $\delta^{18}O_w$, there are no values which discriminate between cold-blooded and warm-blooded organisms.

presented in Table 1. Obviously, one explanation for the observed pattern is the relationship outlined above, namely that the different taxa had original isotopic compositions which were dominated by the composition of the water which they drank or in which they lived. Such an explanation gains limited support from the similarity of $\delta^{18}O_p$ in recent fish, turtle, and crocodilian specimens from the Jordan Valley. An alternative explanation may be that the similarity between taxa reflects condi-

Table 1
Isotopic composition of oxygen in the phosphate ($\delta^{18}O_p$) of dinosaurs, fish and reptiles from the same locality

	Jordan V., Israel	Javelina Fm., Texas	Aguja Fm., Texas	Weald, Is. of Wight	Lance Fm., Wyoming	Prince Creek Fm., Alaska
Age	Recent	Maast.	Campan.	Neocom.	Maast.	Maast.
Paleolatitude	32N	32N	32N	31N	46N	77N
Taxon						
shark			16.3			
bony fish	15.2	19.3		18.5	12.0	8.0
turtle	15.4	17.8	18.4	18.7	12.9	
crocodile	15.3		17.7		12.8	
pterosaur		16.6			14.9	
carnosaur			17.3		14.0	
ceratopsians		16.7	17.2		14.4	
hadrosaurs		18.5			13.5	5.4–7.5; 9.9[a]
Iguanodon				19.3		
Hypsilophodon				19.0		
ankylosaur			16.6			

[a]The values 5.4–7.5‰ were obtained from eight fragments of *Edmontosaurus* quarried from the Liscomb bonebed; the higher value was obtained from a fragment from the original Liscomb collection that probably was collected on the surface below the bonebed (Davies, 1987). The value for bony fish was obtained from a specimen found at a microvertebrate locality probably somewhat lower stratigraphically (note Clemens and Nelms, 1993, and Clemens, 1994). Locality data are on file at the Museum of the University of Alaska (Fairbanks) and the University of California Museum of Paleontology (Berkeley).
The material from both the Aguja and Javelina formations came from the Big Bend National Park, Texas (Lehman, 1987; Busbey and Lehman, 1989).

tions of burial rather than conditions of life. This explanation casts doubt upon a principal assumption made in paleotemperature determinations, namely that the isotopic composition of the skeleton acquired by the organism during its life is preserved in its fossilized remains. We list below our reasons for doubting the validity of this assumption:

(1) Practically all apatitic fossils consist of carbonate–fluor apatite(CFA) as the major mineral phase in contrast to the biological apatite (BA) in which fluorine concentration is negligible, which is the building phase of apatitic components in bones and teeth of living organisms. As in most mineral transformations at low temperatures there is every reason to believe that this diagenetic transition from BA to CFA occurs by dissolution—reprecipitation. Tuross et al. (1989) noted that within 11 years of the death of a wildebeest, the average length as well as width/thickness of apatite crystals in its bones increased significantly. In a somewhat different context, diagenetic alteration of apatites has been advocated by McArthur and Herczeg (1990). Considerable effort was devoted to the examination of Fourier Transform infrared (FTIR) spectra of CFA (Showers et al., 1992), in order to prove their pristine condition. Still the point which must be born in mind is that the original phase was not CFA.

(2) As pointed out by Glimcher and coworkers (e.g. Kim et al., 1995) because only about 2/3 by weight of a living bone is composed of biological apatite, and the specific gravity of organic matter is lower than that of apatite by about a factor of 2, in a "totally mineralized" fossil about 2/3 of the apatite in the specimen must be new material added post mortem. A dramatic demonstration of this phenomenon has recently been observed by Bryant (1995), who compared living and fossil horse teeth which had not erupted from the mandible at time of death. He observed that unerupted enamel of living horses is not fully mineralized, while teeth of fossil horses at a similar stage of development are fully mineralized and composed of CFA. Bryant concludes that the fossilized enamel must be a diagenetic product.

(3) Living bones and teeth have extremely low concentrations of heavy metals; but their fossil counterparts are enriched in those metals. Thus rare earth elements REE are in ppb levels in living skeletal elements (Arrhenius et al., 1957; Bernat, 1975; Shaw and Wasserburg, 1985). The concentrations of REE in apatitic fossils are higher than in any other sedimentary mineral; it is 5–6 orders of magnitude higher than in seawater. Based on mass balance considerations, Grandjean et al. (1987) and Grandjean and Albarède (1989) have shown that REE must have been introduced into fish debris during very early diagenesis via a carrier phase (probably biogenic particulates such as zooplankton fecal pellets and oxihydroxides). Similar relationships were observed for U concentrations (Arrhenius et al., 1957; Bernat, 1975). Xu and Schwartz (1994) have shown recently that lead is absorbed by hydroxylapatite from an aqueous solution, the process consisting of hydroxyapatite dissolution and reprecipitation of a Pb-rich apatite.

Similarly, fresh water fish have less than 100 ppm Sr in their apatitic skeletal elements, while many of their fossil counterparts have thousands of ppm of Sr (Schmitz et al., 1991). It has been noted that $^{87}Sr/^{86}Sr$ ratios in marine fish debris are very often higher than expected from the $^{87}Sr/^{86}Sr$ seawater curve (Kolodny and Luz, 1992).

(4) The relationship between the isotopic composition of oxygen in the phosphate of apatite ($\delta^{18}O_p$) and the isotopic composition of oxygen in the carbonate of CFA ($\delta^{18}O_c$), also points to a recrystallization of apatite in the fossilization process (Kolodny and Luz, 1991). In the bones of living fish there is no correlation between $\delta^{18}O_p$ and $\delta^{18}O_c$; on the other hand these two variables are well correlated linearly in phosphorites. In this regard fossil fish illustrate an intermediate condition between living fish and phosphorites that might be the result of recrystallization in the presence of meteoric water (Kolodny and Luz, 1991).

It was on the basis of reasoning such as outlined above that we made the possibly extreme statement (Kolodny and Luz, 1991) that *every fossil fish is a CFA pseudomorph of an originally BA fishbone.* If this is the case then the time and environment of replacement are of crucial importance in analyzing the geochemical (frequently isotopic) signals recorded in the CFA.

Apatite recrystallization, as indicated by the introduction of the heavy metals into the CFA lattice probably occurs rather early in the fossil's history. Bernat (1975) suggested that the introduction of U may occur within the first ten thousand years after the death of an organism. In addition the microscopic textures of fossil bones are proof of their very early replacement. The excellent preservation of very fine original structures (e.g. Haversian canals) indicate that CFA was crystallized before these structures were destroyed. Pseudomorphism, more explicitly diagenetic dissolution–precipitation of a phosphatic phase might be of no consequence as far as the oxygen isotopic record is concerned, if dissolution took place in a purely "inorganic" environment. As impressively proven by the analytical technique that ends in $BiPO_4$ precipitation, several steps of dissolution and re-precipitation of phosphatic compounds do not alter $\delta^{18}O_p$. There is however ample indication (Soudry and Champetier, 1983; Lucas and Prevot, 1985) that in natural processes of apatite dissolution and precipitation very often are enzymatically (bacterially) mediated and the $\delta^{18}O_p$ re-set during replacement by CFA.

Time of replacement is a crucial factor in the signal recorded in a fossil. In most cases organisms die and are buried in environments similar to those in which they lived. Marine organisms normally will be buried in marine sediments, terrestrial organisms in rocks of lacustrine, alluvial or pedogenic character. If fossilization, including replacement of BA by CFA, occurs early enough, there is a high probability that the recorded signal ($\delta^{18}O_w$, temperature) will be similar to that recorded in the skeleton of the living organism. Exceptions to this generalization may occur in oscillating schizohaline environments, in which marine organisms may be buried in fresh water deposits and vice versa (see Kolodny and Luz, 1991).

The occurrence of early diagenetic pseudomorphosis can completely invalidate any attempt to reconstruct the physiology of an organism from its fossilized remains. To cite our previous examples, if a fresh water fish is buried in a locally

formed fresh water sediment, both $\delta^{18}O_w$ and temperature of burial will not differ markedly from the environment in which the fish lived. In contrast, if the body of a mammal is buried and its skeleton undergoes recrystallization in the same fresh water environment, the $\delta^{18}O_p$ of the fossil will not reflect the isotopic composition of the mammal's body water. It will be similar to that of the fossilized bones of a fish buried in similar conditions.

Recently, Barrick and his coworkers (Barrick et al., 1992; Showers et al., 1992; Barrick and Showers, 1994) suggested that isotopic evidence from dinosaur bones provides strong proof for the endothermic nature of these fossil giants. Their main argument is that living endotherms have isotopically ($\delta^{18}O_p$) uniform skeletons; intrabone $\delta^{18}O_p$ differences are small. Comparison of $\Delta\delta_p$ (the difference between $\delta^{18}O_p$ of trunk bones and extremities) in dinosaurian fossils (*Tyrannosaurus rex*) led them to conclude that the dinosaurs were homeotherms "with less than 4°C of variability in body temperature". We suggest here that the validity of their conclusion may be questioned because homogeneity in isotope signatures might well have been acquired post mortem.

Independently Hubert et al. (1996) reached recently similar conclusions concerning the effects of diagenesis on dinosaur bones from the Jurassic Morrison Formation. These authors review thoroughly evidence on crystal composition, size and shape, as well as heavy metal content of the fossil dinosaur bones. They reach the specific conclusion that "...the chemical composition of dinosaur-bone francolite... reflects the composition of the groundwater" and "...oxygen isotopic ratios ratios... may dominantly reflect groundwater temperature rather than dinosaur body temperature".

2. Selecting optimum fossils for isotopic analysis

From the foregoing discussion it is clear that isotopic analysis of most apatitic fossils probably will yield data on the post-mortem burial environment of the organism. In order to extract meaningful data on the physiology of the organism one must demonstrate that the material is indeed pristine, unaltered diagenetically. As general cautionary notes rather than a fixed set of rules, we offer the following observations that might help in recognizing vertebrate skeletal remains that are little altered or unaltered diagenetically.

Prefer enamel over bone. Numerous studies (e.g. Lee-Thorp and Van der Merwe, 1991; Ayliffe et al., 1992; Bryant, 1995) have repeatedly shown that signals recorded in tooth enamel are significantly better preserved than those obtained from tooth dentine, and are much better than the signals derived from bones. The difference probably stems in large part from the original higher degree of mineralization of enamel as compared to the other apatitic components, resulting in the frequent preservation of BA in Cenozoic fossil enamel.

Insist on preservation of micron-scale fine structure. Although this is a necessary condition for selection of a fossil for analysis, it is certainly not sufficient. Several years of SEM studies by the Bonn group have convinced us that enamel crystallites are morphologically extremely well preserved even in fossil enamel as old as Permian. Using transmission electron microscopy Zocco and Schwartz (1995) have compared dinosaur bones to those of a Pleistocene mammoth and a Recent crocodile. They show that although a large proportion of the small crystallites in the dinosaur bone seem pristine and "can be considered original", the bone also includes a large fraction of diagenetic crystals that formed after the death of the animal. Furthermore, the lack of chemical or mineralogical difference between the two kinds of crystals (both are CFA), may strongly suggest that both kinds were recrystallized after burial. The work of Hubert et al. (1996) demonstrates the detail of micron-scale structures of dinosaur bone that can be preserved during diagenesis of bone.

One should not confuse the detail of structural preservation, with the reliability of the chemical signals in the fossil. CFA pseudomorphs are not different in this sense, from replacement of organic structures by mineral phases completely unrelated to the original phase (CFA being a "cousin" phase of BA). Siliceous pseudomorphs of well preserved fine structures (shells, wood) are abundant in the record (e.g. Holdaway and Clayton, 1982; Stein, 1982; Maliva and Siever, 1988). It would never occur to one to analyze those for signals of life

conditions of the fossilized organisms. That ultrastructural preservation may be an unreliable indicator of biogeochemistry has been pointed out by Towe (1980). Also Banner and Kaufman (1994) have shown that extremely well preserved, non-luminescent brachiopods can be isotopically altered.

Avoid fossils with a close correlation of $\delta^{18}O_p - \delta^{18}O_c$. This criterion again is necessary but not sufficient. Wang and Cerling (1994) have shown how easily $\delta^{18}O_c$ of the carbonate in apatite can be altered. Hence the lack of correlation may be a secondary phenomenon, with only $\delta^{18}O_p$ carrying an early signal.

Require low levels of REE, Sr, U. Here too, mainly negative evidence is available. It seems very likely that all cases in which high levels of heavy metals in apatitic fossils were reported (e.g. enrichment of REE in dinosaur bones in Mongolian dinosaurs, Tauson et al., 1984) are examples of these elements being entrapped in CFA during recrystallization. We do not know of any examples of well preserved fossils which were low in these elements and were proved pristine by another criterion.

3. Conclusions

The major point of this communication is not that dinosaurs were *not* endotherms. Neither is it to demonstrate that the opposite is true. Our goal is to demonstrate that both the rules which govern $\delta^{18}O_p$ in invertebrates and mammals, and the conditions of diagenesis during formation of apatitic fossils, strongly limit our ability to arrive at such conclusions.

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