

Oxygen isotope evidence for semi-aquatic habits among spinosaurid theropods

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ABSTRACT

Spinosaurids were large theropod dinosaurs showing peculiar specializations, including somewhat crocodile-like elongate jaws and conical teeth. Their biology has been much discussed, and a piscivorous diet has been suggested on the basis of jaw as well as tooth morphology and stomach contents. Although fish eating has been considered plausible, an aquatic or semiaquatic lifestyle has seldom been suggested because of the apparent lack of corresponding adaptations in the postcranial skeleton of spinosaurids, which on the whole is reminiscent of that of other large terrestrial theropods. On the basis of the oxygen isotopic composition of their phosphatic remains compared with those of coexisting terrestrial theropod dinosaurs and semiaquatic crocodylians and turtles, we conclude that spinosaurids had semiaquatic lifestyles, i.e., they spent a large part of their daily time in water, like extant crocodylians or hippopotamuses. This result sheds light on niche partitioning between large predatory dinosaurs, since spinosaurids coexisted with other large theropods such as carcharodontosaurids or tyrannosaurids. The likely ichthyophagy and aquatic habits of spinosaurids may have allowed them to coexist with other large theropods by reducing competition for food and territory.

INTRODUCTION

The theropod family Spinosauridae was erected for *Spinosaurus aegyptiacus*, from the Cenomanian of Egypt, characterized by several unusual spines on the dorsal vertebrae and peculiar, more or less conical and unserrated teeth (Sereno, 1915). Since then, spinosaurid remains have been reported from the Cretaceous of various parts of the world, including Africa (Bouček et al., 1988; Buffetaut, 1989; Sereno et al., 1998; Sereno, 1915; Taquet and Russell, 1998), Europe (Charig and Milner, 1986; R6i-Omeaca et al., 2005), South America (Kellner and Campos, 1996; Medeiros, 2006; S6es et al., 2002), and Asia (Buffetaut and Inga, 1986; Buffetaut et al., 2008; Hasegawa et al., 2003);

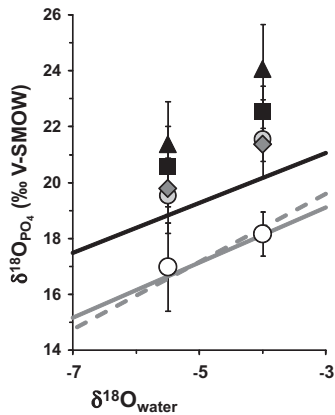
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the oldest representatives are from the Late Cretaceous of Africa (Buffetaut, 2008). The spinosaurids probably had dietary adaptations and lifestyles that have been suggested for theropods as well as suggested on the basis of fragments of material from Africa (Taquet, 1984). The discovery of a fairly complete spinosaurid skeleton from the Wealden of southern England, described as *Baryonyx walkeri*, revealed a peculiar constellation of features, including narrow and elongated jaws, some that have reminiscent of longirostrine crocodylians (R6i-Omeaca et al., 2007); his suggested piscivorous habits, a hypohistid stomach contents including partial digested fish scales (Charig and Milner, 1997). However, direct evidence concerning spinosaurid diet is inconclusive since it appears that they also fed on dinosaurs (Charig and Milner, 1997) and pterosaurs (Buffetaut et al., 2004). Nevertheless, because of the above-mentioned convergences in jaw and tooth shape, the hypohistid spinosaurids as crocodile mimics (Holmes, 1998) has been widely accepted. However, their postcranial anatomy differs relatively little from that of large, bipedal theropods, and is not particularly suggestive of aquatic habits. As evidence based on morphology and stomach contents remains equivocal, we have applied stable isotope geochemistry to this question.

Oxygen isotope compositions of phosphate ($\delta^{18}\text{O}_p$) from biogenic apatites can be used to assess possible aquatic habits in spinosaurid dinosaurs. At the global scale, variations in the $\delta^{18}\text{O}$ values of homeothermic vertebrates (such as mammals or theropod dinosaurs; Amiot et al., 2006; Barrick and Shivers, 1994; Fricke and Rogers, 2000) phosphate and body water are mainly controlled by variations in the compositions of drinking and food water, as well as by differences in physiology and ecology (Longinelli, 1984; Lu et al., 1984). For example, physiological adaptations to specific habitats (aquatic, semiaquatic, or terrestrial) affect the $\delta^{18}\text{O}_p$ values by controlling the magnitude of the oxygen isotope in body water and water, some of them being associated with oxygen isotope fractionations (Brannen and Froelich, 1995; Kohn, 1996; Lu and Kolodn, 1985). From living and fossil communities of mammals and reptiles, it has been observed that differences in mean $\delta^{18}\text{O}_p$ values between coexisting aquatic or semiaquatic vertebrates and terrestrial forms are related to their habitat, aquatic or semiaquatic vertebrates having $\delta^{18}\text{O}_p$ values significantly lower than the values of coexisting terrestrial animals (Amiot et al., 2006; Bocherens et al., 1996; Cerling et al., 2008; Clemens et al., 2008; Fricke and Rogers, 2000) (Fig. 1).



MATERIALS AND METHODS

We used 109 new and 24 published (Amio et al., 2006) $\delta^{18}\text{O}_p$ values of tooth enamel from spinosaurids, other theropods, crocodylians, and turtle shell bones (for the complete data table, see the GSA Data Repository¹). These fossil remains were recovered from 12 Cretaceous localities ranging from the Hauteriviian Barremian of the early Cenomanian, and are situated on all continents where spinosaurids have been identified so far (Asia: Buffe et al., 1986; Buffe et al., 2008; Europe: Charig and Milner, 1986; Africa: Buffe et al., 1988; Buffe et al., 1989; South America: Medeiros, 2006; Fig. 2). For consistency (e.g., to avoid body size differences that may lead to variations in $\delta^{18}\text{O}_p$ value differences between spinosaurids and coexisting theropods),

heropods), we selected spinosaurid and coexisting other theropod teeth of similar sizes. Samples were prepared and measured for their oxygen isotope compositions using a standard procedure (Lüder, 2004; Lüder et al., 2007; see the Data Repository¹). Differences in oxygen isotope compositions of fossil remains were tested for significant differences using a nonparametric Wilcoxon signed-rank test and a two-way ANOVA (analysis of variance; see the Data Repository¹).

RESULTS

The $\delta^{18}\text{O}_p$ values obtained for spinosaurids were compared with those of associated terrestrial theropods and semiaquatic crocodylians and turtles (Fig. 3). The entire data set reveals that the $\delta^{18}\text{O}_p$ values of spinosaurid dinosaurs are 1.3‰ lower than $\delta^{18}\text{O}_p$ values of other coexisting theropods (Wilcoxon signed rank, $n = 9$, $p = 0.02$), but no significant difference from $\delta^{18}\text{O}_p$ values of coexisting crocodylians (Wilcoxon signed rank, $n = 9$, $p = 0.515$) and turtles (Wilcoxon signed rank, $n = 6$, $p = 0.345$). In some Moroccan and Tunisian localities, however, spinosaurid values are either comparable to those of terrestrial theropods (locality 12; Table 1) or extend from crocodylian and turtle values of terrestrial theropod values (localities 6, 8, and 11; Table 1).

DISCUSSION

Secondary precipitation of apatite and isotopic exchange during microbial-mediated reactions may alter the primary composition of biogenic apatites (Blake et al., 1997; Zazzo et al., 2004a). However, apatite crystals in tooth enamel are large and densely packed, and isotopic exchange under inorganic conditions has little effect on the oxygen isotope composition of phosphates, even at geological time scales (Kolodner et al., 1983; Lüder et al., 1999). Although no method is available to demonstrate the heretofore oxygen isotope composition of fossil terrestrial phosphate as affected by diagenetic processes, several ways to assess the preservation status of the primary isotopic record have been proposed (Fricke and Rogers, 2000; Kolodner et al., 1996; Lüder et al., 2003; Hockley et al., 2004; Zazzo et al., 2004b). Here, the main argument supporting the preservation of the original oxygen isotope

TABLE 1. AVERAGE $\delta^{18}\text{O}_p$ AND STANDARD DEVIATION VALUES OF THEROPODS, SPINOSAURS, CROCODYLIANS, AND TURTLES FOR EACH LOCALITY

Loc.	Spinosaurs			Theropods			Crocodilians			Turtles		
	N	Mean	St. dev.	N	Mean	St. dev.	N	Mean	St. dev.	N	Mean	St. dev.
12	6	19.7	0.5	4	18.8	0.4	3	17.5	0.7	2	17.0	0.3
11	7	18.8	1.3	6	19.4	0.8	3	17.7	0.9	1	16.7	—
10	5	18.4	0.7	4	21.3	0.5	2	19.6	0.6	2	18.8	0.1
9	4	18.7	0.6	2	20.0	0.1	2	19.9	0.7	2	19.3	0.4
8	3	19.3	0.3	3	19.8	0.4	3	19.0	0.3	3	18.5	0.4
7	8	19.5	0.5	3	21.2	0.8	3	19.3	0.2	—	—	—
6	3	19.5	2.4	3	20.5	0.5	2	18.3	0.1	—	—	—
5	2	15.6	0.8	3	17.5	0.2	—	—	—	1	14.7	—
4	4	18.7	0.5	5	20.2	1.1	9	19.7	0.8	2	18.8	0.2
3	3	16.0	1.1	2	18.9	0.2	2	14.8	1.1	—	—	—
2	1	16.1	—	1	21.1	—	2	15.8	1.1	—	—	—
1	2	13.5	0.2	3	25.6	0.9	—	—	—	2	14.6	0.1

Note: Dashes indicate no data, or not applicable. Loc.—locality numbers: 1—Phu Wiang1 (Thailand); 2—Khok Kong (Thailand); 3—Phu Phok (Thailand); 4—Isle of Wight (England); 5—Liu Bang Cun (China); 6—Bateun El Hmama (Tunisia); 7—Laje do Coringa (Brazil); 8—Jebel al Qabla (Morocco); 9—Takemout (Morocco); 10—Chaaft (Morocco); 11—Khetitila Srhira (Morocco); 12—Bou Laalou (Morocco). N—number; St. dev.—standard deviation.

composition is the semi-aquatic offset observed between semiaquatic herbivores and crocodilians and terrestrial herbivores, the latter having significantly higher $\delta^{18}\text{O}_p$ values than coexisting crocodilians and herbivores, which have their age and geographical location (Wilcoxon signed rank, $n = 9$, $p < 0.01$). If early diagenetic processes had occurred, the $\delta^{18}\text{O}_p$ would have been homogenized $\delta^{18}\text{O}_p$ values of all herbivores remains have their petrological and ecological of the corresponding area (Lübbert et al., 2003). This observation is a strong argument supporting a least partial preservation of the original $\delta^{18}\text{O}_p$ values (Amio et al., 2006; Fricke and Rogers, 2000). A diet-related difference as a possible explanation for $\delta^{18}\text{O}_p$ value offsets between spinosaurs and other coexisting herbivores is highly unlikely, because here is direct fossil evidence indicating an opportunistic feeding behavior among spinosaurs, rather than strictly herbivorous. Indeed, dinosaurs (Charig and Milner, 1997) and pterosaurs (Böffe et al., 2004) have been shown to be a part of the spinosaur diet either by scavenging (Böffe et al., 2004) or by predation (Kellner, 2004). Moreover, as opportunistic predators, coexisting crocodilians and spinosaurs most likely had similar diets, and the $\delta^{18}\text{O}_p$ values of crocodilians do not differ significantly from those of spinosaurs, despite their known semiaquatic lifestyles. Low $\delta^{18}\text{O}_p$ values of spinosaurs compared to other herbivores can be interpreted as the result of differences between the oxygen isotope compositions of their bodies via a semiaquatic behavior for spinosaurs would reduce daily aerial evaporative transpiration, which is known to be one of the significant processes of ^{18}O enrichment of body water relative to surface water (Kohn, 1996). Moreover, low body ^{18}O enrichment relative to drinking water in semiaquatic animals such as crocodilians or hippopotamuses is also the result of elevated water intake and water loss through urine or feces (Benle and Schmid-Nielsen, 1965; Clemens et al., 2008). From these considerations, a semiaquatic lifestyle is the most plausible explanation for the oxygen isotope difference observed between spinosaurs and other coexisting herbivores, and the similar values shared by spinosaurs and semiaquatic crocodilians and herbivores. This interpretation is also supported by similar offsets observed between the $\delta^{18}\text{O}_p$ values of present-day herbivorous mammals (carnivores, ungulates, elephants, and rhinoceroses) and those of coexisting hippopotamuses from the Kenyan national parks (Bocherens et al., 1996; Cerling et al., 2008; Fig. 1). Considering the compared animals have similar diets (both hippopotamuses and other coexisting herbivorous mammals feed on land plant species [Boissier et al., 2005], and spinosaurs were predators like coexisting crocodilians and other herbivores) and

hermivorous animals (mammals and herbivorous dinosaurs are both considered as homeotherms; Amio et al., 2006; Fricke and Rogers, 2000; Lübbert and Wright, 1959), the similar isotopic offsets observed between spinosaurs versus herbivores and hippopotamuses versus terrestrial mammals is most likely related to analogous aquatic lifestyles.

The amphibious habits of spinosaurs, given their apparent lack of anatomical adaptations to aquatic habitats, may have been a hermivorous or strictly herbivorous. Modern crocodilians and hippopotamuses submerge to graze on their bottom vegetation (Noirard et al., 2008; Seebacher et al., 2003). Such a behavior among spinosaurid herbivores is therefore conceivable. Niche partitioning to avoid competition for resources within the herbivorous is another hypothesis that may explain the semiaquatic lifestyles of most spinosaurs. Indeed, at all localities where the ostracod, spinosaur remains are found associated with those of other herbivores of comparable size. Fish eating and an aquatic habit may have been advantageous for most spinosaurs to reduce competition for food and energy within the large herbivores, which had an omnivorous terrestrial mode of life. This semiaquatic oxygen isotope signature is not clearly observed for *Spinosaurus* from Tunisia and Morocco, even though this genus possesses highly advanced specializations for stretching in jaw elongation and oar morphology. As shown by fossils from many African Cretaceous localities, spinosaurs appear to be coexisting and competing for food resources within both the large herbivores on land and large or giant crocodilians in rivers and lakes. These petrological conditions within multiple predators may have forced some African spinosaurs to have a more opportunistic habitus by alternating aquatic and terrestrial life.

Sable oxygen isotope measurements show for the first time that some dinosaurs, i.e., the spinosaurid herbivores used fresh water even ironmen more as a living habit than just as an evaporative loss (or stretching) grounds. Dinosaurs were thus a more ecologically diverse group than previously thought since at least some of them were not restricted to terrestrial habitats.

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