# Oxygen isotope evidence for semi-aquatic habits among spinosaurid theropods

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## ABSTRACT

**Spinosaurs 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 spinosaurs, 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 crocodilians and turtles, we conclude that spinosaurs had semiaquatic lifestyles, i.e., they spent a large part of their daily time in water, like extant crocodilians or hippopotamuses. This result sheds light on niche partitioning between large predatory dinosaurs, since spinosaurs 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 extremely tall neural spines on the dorsal vertebrae and peculiar, more or less conical and unserrated teeth (Stromer, 1915). Since then, spinosaurid remains have been reported from the Cretaceous of various parts of the world, including Africa (Bouaziz et al., 1988; Buffetaut, 1989; Sereno et al., 1998; Stromer, 1915; Taquet and Russell, 1998), Europe (Charig and Milner, 1986; Ruiz-Omeñaca et al., 2005), South America (Kellner and Campos, 1996; Medeiros, 2006; Sues et al., 2002), and Asia (Buffetaut and Ingavat, 1986; Buffetaut et al., 2008; Hasegawa et al., 2003); the oldest representatives are from the Late Jurassic of Africa (Buffetaut, 2008). That spinosaurids probably had dietary adaptations and lifestyles that were unusual for theropods was first suggested on the basis of fragmentary 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 peculiarly constructed skull, with narrow and elongate jaws, somewhat reminiscent of longirostrine crocodilians (Rayfield et al., 2007); this suggested piscivorous habits, a hypothesis strengthened by stomach contents including partially 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 hypothesis of spinosaurs as "crocodile mimics" (Holtz, 1998) has been widely accepted. However, their postcranial anatomy differs relatively little from that of usual 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 ($\delta^{18}O_p$) from biogenic apatites can be used to assess possible aquatic habits in spinosaurid dinosaurs. At the global scale, variations in the $\delta^{18}O$ values of homeothermic vertebrate (such as mammals or theropod dinosaurs; Amiot et al., 2006; Barrick and Showers, 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; Luz et al., 1984). For example, physiological adaptations to specific habitat use (aquatic, semiaquatic, or terrestrial) affect the $\delta^{18}O_{bw}$ value by controlling the magnitude of the oxygen fluxes involved in body input and output, some of them being associated with oxygen isotopic fractionations (Bryant and Froelich, 1995; Kohn, 1996; Luz and Kolodny, 1985). From living and fossil communities of mammals and reptiles, it has been observed that differences in mean $\delta^{18}O_p$ values between coexisting aquatic or semiaquatic vertebrates and terrestrial forms are related to their habitat use, aquatic or semiaquatic vertebrates having $\delta^{18}O_p$ values significantly lower than the values of coexisting terrestrial animals (Amiot et al., 2006; Bocherens et al., 1996; Cerling et al., 2008; Clementz et al., 2008; Fricke and Rogers, 2000) (Fig. 1).

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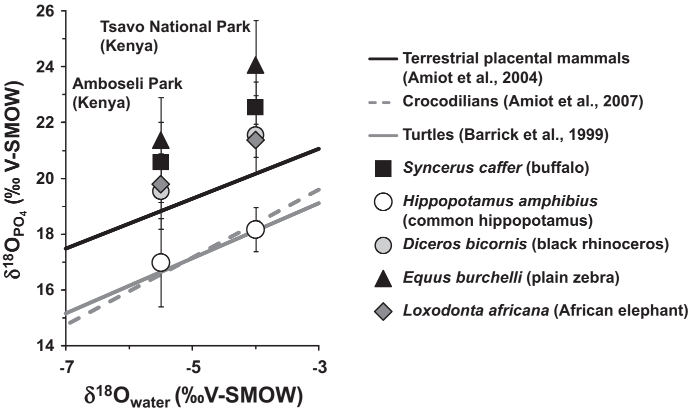

**Figure 1. Mean oxygen isotope compositions of apatites versus drinking waters of mammals from two Kenyan parks showing difference in $\delta^{18}O_p$ values between semiaquatic hippopotamuses and terrestrial herbivorous mammals (error bars are ±1σ). V-SMOW—Vienna standard mean ocean water. Phosphate-water fractionation lines of terrestrial placental mammals, semiaquatic turtles, and crocodilians are displayed for comparison. Estimate of $\delta^{18}O$ value of water at Amboseli Park was arbitrarily chosen and explained in GSA Data Repository material (see footnote 1).**

## MATERIALS AND METHODS

We used 109 new and 24 published (Amiot et al., 2006) $\delta^{18}O_p$ values of tooth enamel from spinosaurs, other theropods, crocodilians, and turtle shell bones (for the complete data table, see the GSA Data Repository[1]). These fossil remains were recovered from 12 Cretaceous fluvial or fluvio-deltaic localities ranging from the Hauterivian–Barremian to the early Cenomanian, and are situated on all continents where spinosaurids have been identified so far (Asia—Buffetaut and Ingavat, 1986; Buffetaut et al., 2008; Europe—Charig and Milner, 1986; Africa—Bouaziz et al., 1988; Buffetaut, 1989; South America—Medeiros, 2006; Fig. 2). For consistency (e.g., to avoid body size differences that may lead to variations in $\delta^{18}O_p$ value differences between spinosaurs and coexisting terrestrial theropods), we selected spinosaur and coexisting other theropod teeth of similar sizes. Samples were prepared and measured for their oxygen isotope compositions using a standard procedure (Lécuyer, 2004; Lécuyer et al., 2007; see the Data Repository). Differences in oxygen isotope compositions of fossil remains were tested for significance using a nonparametric Wilcoxon signed-rank test and a two-way ANOVA (analysis of variance; see the Data Repository).

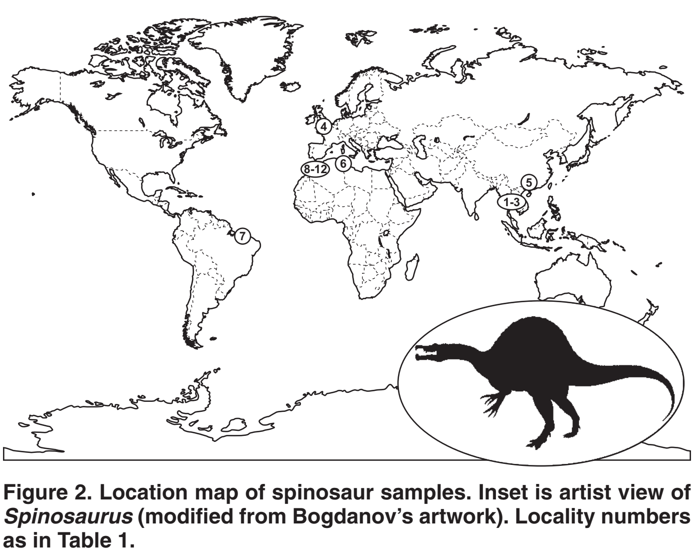

**Figure 2. Location map of spinosaur samples. Inset is artist view of *Spinosaurus* (modified from Bogdanov's artwork). Locality numbers as in Table 1.**

## RESULTS

The $\delta^{18}O_p$ values obtained for spinosaurids were compared with those of associated terrestrial theropods and semiaquatic crocodilians and turtles (Fig. 3). The entire data set reveals that the $\delta^{18}O_p$ values of spinosaurid dinosaurs are 1.3‰ lower than $\delta^{18}O_p$ values of other coexisting theropods (Wilcoxon signed rank, $n = 9$, $p = 0.02$), but not significantly different from $\delta^{18}O_p$ values of coexisting crocodilians (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, spinosaur values are either comparable to those of terrestrial theropods (location 12; Table 1) or extend from crocodilian and turtle values to terrestrial theropod values (locations 6, 8, and 11; Table 1).

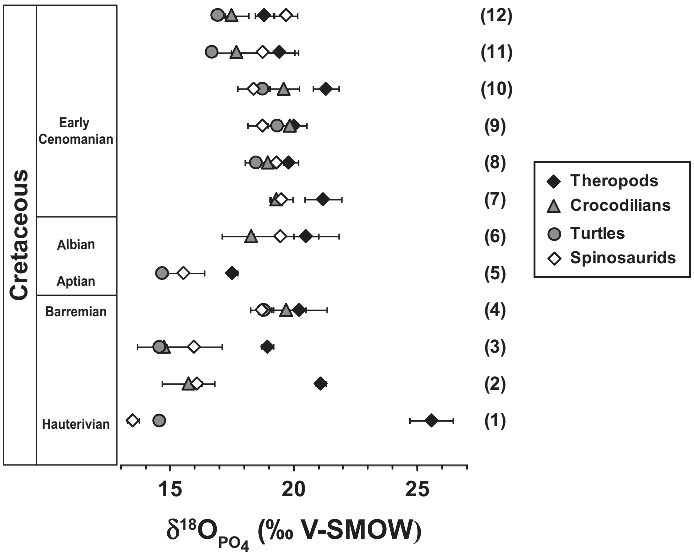

**Figure 3. Mean phosphate $\delta^{18}O$ values of skeletal apatite from spinosaurs, theropods, freshwater turtles, and crocodilians sorted by geological age, from Hauterivian–Barremian to early Cenomanian (error bars are ±1σ). V-SMOW—Vienna standard mean ocean water. Locality numbers as in Table 1.**

## DISCUSSION

Secondary precipitation of apatite and isotopic exchange during microbially mediated reactions may alter the primary composition of biogenic apatites (Blake et al., 1997; Zazzo et al., 2004a). However, apatite crystals that make up 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 (Kolodny et al., 1983; Lécuyer et al., 1999). Although no method is available to demonstrate definitely whether the oxygen isotope composition of fossil vertebrate phosphate was affected by diagenetic processes, several ways to assess the preservation state of the primary isotopic record have been proposed (Fricke and Rogers, 2000; Kolodny et al., 1996; Lécuyer et al., 2003; Pucéat et al., 2004; Zazzo et al., 2004b). Here, the main argument supporting the preservation of the original oxygen isotope

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[1] GSA Data Repository item 2010038, oxygen isotope compositions of vertebrate phosphates, oxygen isotope analysis of phosphate procedure, statistical analyses, and estimation of Amboseli National Park water $\delta^{18}O$ value, is available online at www.geosociety.org/pubs/ft2010.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

TABLE 1. AVERAGE $\delta^{18}O_P$ AND STANDARD DEVIATION VALUES OF THEROPODS, SPINOSAURS, CROCODILIANS, AND TURTLES FOR EACH LOCALITY

| | Spinosaurs | | | Theropods | | | Crocodilians | | | Turtles | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Loc. | 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 Hmaima (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 systematic offset observed between semiaquatic turtles and crocodilians and terrestrial theropods, the latter having significantly higher $\delta^{18}O_p$ values than coexisting crocodilians and turtles, whatever their age and geographical location (Wilcoxon signed rank, $n = 9$, $p < 0.01$). If early diagenetic processes had occurred, they would have homogenized $\delta^{18}O_p$ values of all vertebrate remains whatever the physiology and ecology of the corresponding taxa (Lécuyer et al., 2003). This observation is a strong argument supporting at least partial preservation of the original $\delta^{18}O_p$ values (Amiot et al., 2006; Fricke and Rogers, 2000). A diet-related difference as a possible explanation for $\delta^{18}O_p$ value offsets between spinosaurs and other coexisting theropods is highly unlikely, because there is direct fossil evidence indicating an opportunistic feeding behavior among spinosaurs, rather than strict ichthyophagy. Indeed, dinosaurs (Charig and Milner, 1997) and pterosaurs (Buffetaut et al., 2004) have been shown to be a part of the spinosaur diet either by scavenging (Buffetaut et al., 2004) or by predation (Kellner, 2004). Moreover, as opportunistic predators, coexisting crocodilians and spinosaurs most likely had similar diets, and the $\delta^{18}O_p$ values of crocodilians do not differ significantly from those of spinosaurs, despite their known semiaquatic lifestyle. Low $\delta^{18}O_p$ values of spinosaurs compared to other theropods can be interpreted as the result of differences between the oxygen isotope compositions of their body water. A semiaquatic behavior for spinosaurs would reduce daily aerial evapotranspiration, 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 fluids $^{18}O$ enrichment relative to drinking water in semiaquatic animals such as crocodilians or hippopotamuses is also the result of elevated water turnovers and water loss through urine or feces (Bentley and Schmidt-Nielsen, 1965; Clementz 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 theropods, and the similar values shared by spinosaurs and semiaquatic crocodilians and turtles. This interpretation is also supported by similar offsets observed between the $\delta^{18}O_p$ values of present-day herbivorous mammals (zebras, buffalos, elephants, and rhinoceroses) and those of coexisting hippopotamuses from two Kenyan national parks (Bocherens et al., 1996; Cerling et al., 2008; Fig. 1). Considering that compared animals have similar diets (both hippopotamuses and other coexisting herbivorous mammals feed on land plants [Boisserie et al., 2005], and spinosaurs were predators like coexisting crocodilians and other theropods) and thermoregulations (mammals and theropod dinosaurs are both considered as homeotherms; Amiot et al., 2006; Fricke and Rogers, 2000; Luck and Wright, 1959), the similar isotopic offsets observed between spinosaurs versus theropods and hippopotamuses versus terrestrial mammals is most likely related to analogous aquatic lifestyles.

The amphibious habits of spinosaurs, given their apparent lack of anatomical adaptation to aquatic habits, may have been a thermoregulatory strategy. Modern crocodilians and hippopotamuses submerge to regulate their body temperature (Noirard et al., 2008; Seebacher et al., 2003). Such a behavior among spinosaurid theropods is therefore conceivable. Niche partitioning to avoid competition for resources with other vertebrates is another hypothesis that may explain the semiaquatic lifestyle of most spinosaurs. Indeed, at all localities where they occur, spinosaur remains are found associated with those of other theropods of comparable size. Fish eating and an aquatic habitat may have been a way for most spinosaurs to reduce competition for food and territory with other large theropods, which had an unequivocal 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 fish catching in jaw elongation and tooth morphology. As shown by fossils from many African Cretaceous localities, spinosaurs apparently coexisted and competed for food resources with both other large theropods on land and large or giant crocodilians in rivers and lakes. These peculiar trophic conditions with multiple top predators may have forced some African spinosaurs to have a more opportunistic habitat use by alternating aquatic and terrestrial life.

Stable oxygen isotopes unambiguously show for the first time that some dinosaurs, i.e., the spinosaurid theropods, used freshwater environments more as a living habitat than just as temporary hunting (or fishing) 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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