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 heropod famil Spinosa ridae as erec ed for *Spinosaurus aegyptiacus*, from he Cenomanian of Eg p , charac eri ed b e remel all ne ral spines on he dorsal er ebrae and pec liar, more or less conical and nserra ed ee h (S romer, 1915). Since hen, spinosa rid remains ha e been repor ed from he Cre aceo s of ario s par s of he orld, incl ding Africa (Bo a i e al., 1988; B ffe a , 1989; Sereno e al., 1998; S romer, 1915; Taq e and R ssell, 1998), E rope (Charig and Milner, 1986; R i -Ome aca e al., 2005), So h America (Kellner and Campos, 1996; Medeiros, 2006; S es e al., 2002), and Asia (B ffe a and Inga a , 1986; B ffe a e al., 2008; Hasega a e al., 2003); he oldes represen a i es are from he La e J rassic of Africa (B ffe a , 2008). Tha spinosa rids probabl had die ar adap a ions and lifes les ha ere n s al for heropods as rs s gges ed on he basis of fragmen ar ma erial from Africa (Taq e , 1984). The disco er of a fairl comple e spinosa rid skele on from he Wealden of so hern England, described as *Baryonyx walkeri*, re ealed a pec liarl cons r c ed sk ll, i h narro and elonga e ja s, some ha reminiscen of longiros rine crocodilians (Ra eld e al., 2007); his s gges ed pisci oro s habi s, a h po hesis s reng hened b s omach con en s incl ding par iall diges ed sh scales (Charig and Milner, 1997). Ho e er, direc e idence concerning spinosa rid die is inconcl si e since i appears ha he also fed on dinosa rs (Charig and Milner, 1997) and p erosa rs (B ffe a e al., 2004). Ne er heless, beca se of he abo e-men ioned con ergences in ja and oo h shape, he h po hesis of spinosa rs as crocodile mimics (Hol , 1998) has been idel accep ed. Ho e er, heir pos cranial ana om differs rela i el li le from ha of s al large, bipedal heropods, and is no par ic larl s gges i e of aq a ic habi s. As e idence based on morpholog and s omach con en s remains eq i ocal, e ha e applied s able iso ope geochemis r o his q es ion.

O gen iso ope composi ions of phospha e ($\delta^{18}O_p$) from biogenic apa i es can be sed o assess possible aq a ic habi s in spinosa rid dinosa rs. A he global scale, aria ions in he $\delta^{18}O$ al es of homeo hermic er ebra e (s ch as mammals or heropod dinosa rs; Amio e al., 2006; Barrick and Sho ers, 1994; Fricke and Rogers, 2000) phospha e and bod a er are mainl con rolled b aria ions in he composi ions of drinking and food a er, as ell as b differences in ph siolog and ecolog (Longinelli, 1984; L e al., 1984). For e ample, ph siological adap a ions o speci c habi a se (aq a ic, semiaq a ic, or erres rial) affec he $\delta^{18}O_{b}$ al e b con rolling he magni de of he o gen es in ol ed in bod inp and o p , some of hem being associa ed i h o gen iso opic frac iona ions (Br an and Froelich, 1995; Kohn, 1996; L and Kolodn , 1985). From li ing and fossil comm ni ies of mammals and repiles, i has been obser ed ha differences in mean $\delta^{18}O_p$ al es be een coe is ing aq a ic or semiaq a ic er ebra es and erres rial forms are rela ed o heir habi a se, aq a ic or semiaq a ic er ebra es ha ing $\delta^{18}O_p$ al es signi can l lo er han he al es of coe is ing erres rial animals (Amio e al., 2006; Bocherens e al., 1996; Cerling e al., 2008; Clemen e al., 2008; Fricke and Rogers, 2000) (Fig. 1).

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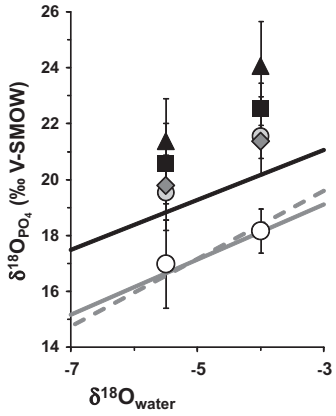

heropods), we selected spinosaur and coelurosing other heropod teeth of similar sizes. Samples were prepared and measured for their oxygen isotope compositions using a standard procedure (Lécuyer, 2004; Lécuyer et al., 2007; see the Data Repository). Differences in oxygen isotope compositions of fossil remains were tested for significance using a nonparametric Wilcoxon signed-rank tests and a Kruskal-Wallis ANOVA (analysis of variance; see the Data Repository).

MATERIALS AND METHODS

We used 109 new and 24 published (Amiot et al., 2006) $\delta^{18}O_p$ values of both enamel from spinosaurs, other heropods, crocodilians, and turtle shell bones (for the complete data table, see the GSA Data Repository[1]). These fossil remains were recovered from 12 Cretaceous continental or paleoenvironmentally 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., no allometric body size differences have major leading to variations in $\delta^{18}O_p$ value differences between spinosaurs and coelurosing terrestrial heropods), we selected spinosaur and coelurosing other heropod 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 tests and a Kruskal-Wallis ANOVA (analysis of variance; see the Data Repository).

RESULTS

The $\delta^{18}O_p$ values obtained for spinosaurids were compared with those of associated terrestrial heropods 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 coelurosing heropods (Wilcoxon signed rank, n = 9, p = 0.02), but not significantly different from $\delta^{18}O_p$ values of coelurosing 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 heropods (location 12; Table 1) or extend from crocodilian and turtle values to terrestrial heropod values (locations 6, 8, and 11; 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 definitively that the heritage oxygen isotope composition of fossil carbonate bioapatite phosphate was affected by diagenetic processes, several ways to assess the preservation status of primary isotopic records 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 arguments supporting the preservation of the original oxygen isotope

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.

composi ion is he s s ema ic offse obser ed be een semiaq a ic r les and crocodilians and erres rial heropods, he la er ha ing signi can l higher $\delta^{18}O_p$ al es han coe is ing crocodilians and r les, ha e er heir age and geographical loca ion (Wilco on signed rank, $n = 9$, $p < 0.01$). If earl diagene ic processes had occ rred, he o ld ha e homogeni ed $\delta^{18}O_p$ al es of all er ebra e remains ha e er he ph siolog and ecolog of he corresponding a a (L c er e al., 2003). This obser a ion is a s rong arg men s ppor ing a leas par ial preser a ion of he original $\delta^{18}O_p$ al es (Amio e al., 2006; Fricke and Rogers, 2000). A die -rela ed difference as a possible e plana ion for $\delta^{18}O_p$ al e offse s be een spinosa rs and o her coe is ing heropods is highl nlikel , beca se here is direc fossil e idence indica ing an oppor nis ic feeding beha ior among spinosa rs, ra her han s ric ich h ophag . Indeed, dinosa rs (Charig and Milner, 1997) and p erosa rs (B ffe a e al., 2004) ha e been sho n o be a par of he spinosa r die ei her b sca enging (B ffe a e al., 2004) or b preda ion (Kellner, 2004). Moreo er, as oppor nis ic preda ors, coe is ing crocodilians and spinosa rs mos likel had similar die s, and he $\delta^{18}O_p$ al es of crocodilians do no differ signi can l from hose of spinosa rs, despi e heir kno n semiaq a ic lifes le. Lo $\delta^{18}O_p$ al es of spinosa rs compared o o her heropods can be in erpre ed as he res l of differences be een he o gen iso ope composi ions of heir bod a er. A semiaq a ic beha ior for spinosa rs o ld red ce dail aerial e apo- ranspira ion, hich is kno n o be one of he signi can processes of ^{18}O enrichmen of bod a er rela i e o s rface a er (Kohn, 1996). Moreo er, lo bod ids ^{18}O enrichmen rela i e o drinking a er in semiaq a ic animals s ch as crocodilians or hippopo am ses is also he res l of ele a ed a er rno ers and a er loss hro gh rine or feces (Ben le and Schmid -Nielsen, 1965; Clemen e al., 2008). From hese considera ions, a semiaq a ic lifes le is he mos pla sible e plana ion for he o gen iso ope difference obser ed be een spinosa rs and o her coe - is ing heropods, and he similar al es shared b spinosa rs and semiaq a ic crocodilians and r les. This in erpre a ion is also s ppor ed b similar offse s obser ed be een he $\delta^{18}O_p$ al es of presen -da herbi o- ro s mammals (ebras, b ffalos, elephan s, and rhinoceroses) and hose of coe is ing hippopo am ses from o Ken an na ional parks (Bocherens e al., 1996; Cerling e al., 2008; Fig. 1). Considering ha compared animals ha e similar die s (bo h hippopo am ses and o her coe is ing herbi oro s mammals feed on land plan s [Boisserie e al., 2005], and spinosa rs ere preda ors like coe is ing crocodilians and o her heropods) and hermoreg la ions (mammals and heropod dinosa rs are bo h considered as homeo herms; Amio e al., 2006; Fricke and Rogers, 2000; L ck and Wrigh , 1959), he similar iso opic offse s obser ed be een spinosa rs ers s heropods and hippopo am ses ers s erres rial mammals is mos likel rela ed o analogo s aq a ic lifes les.

The amphibio s habi s of spinosa rs, gi en heir apparen lack of ana omical adap a ion o aq a ic habi s, ma ha e been a hermoreg la- or s ra eg . Modern crocodilians and hippopo am ses s bmerge o reg - la e heir bod empera re (Noirard e al., 2008; Seebacher e al., 2003). S ch a beha ior among spinosa rid heropods is herefore concei able. Niche par i ioning o a oid compe i ion for reso rces i h o her er e- bra es is ano her h po hesis ha ma e plain he semiaq a ic lifes le of mos spinosa rs. Indeed, a all locali ies here he occ r, spinosa r remains are fo nd associa ed i h hose of o her heropods of comparable si e. Fish ea ing and an aq a ic habi a ma ha e been a a for mos spinosa rs o red ce compe i ion for food and erri or i h o her large heropods, hich had an neq i ocal erres rial mode of life. This semiaq a ic o gen iso ope signa re is no clearl obser ed for *Spinosaurus* from T nisia and Morocco, e en ho gh his gen s possesses highl ad anced speciali a ions for sh ca ching in ja elonga ion and oo h morpholog . As sho n b fossils from man African Cre aceo s locali ies, spinosa rs apparen l coe is ed and compe ed for food reso rces i h bo h o her large heropods on land and large or gian crocodilians in ri ers and lakes. These pec liar rophic condi ions i h m l iple op preda ors ma ha e forced some African spinosa rs o ha e a more oppor nis ic habi a se b al erna ing aq a ic and erres rial life.

S able o gen iso opes nambig o sl sho for he rs ime ha some dinosa rs, i.e., he spinosa rid heropods, sed fresh a er en iron- men s more as a li ing habi a han j s as emporar h n ing (or sh- ing) gro nds. Dinosa rs ere h s a more ecologicall di erse gro p han pre io sl ho gh since a leas some of hem ere no res ric ed o er- res rial habi a s.

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