

# Habitat preference of mosasaurs indicated by rare earth element (REE) content of fossils from the Upper Cretaceous marine deposits of Alabama, New Jersey, and South Dakota (USA)

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## Abstract

Knowledge of habitat segregation of mosasaurs has been based on lithology and faunal assemblages associated with fossil remains of mosasaurs and stable isotopes ( $\delta^{13}\text{C}$ ). These approaches have sometimes provided equivocal or insufficient information and, therefore, the preference of habitat by different mosasaur taxa is still suboptimally constrained. The present study is focused on the analysis of rare earth element (REE) ratios of mosasaur fossils from the Upper Cretaceous formations of western Alabama, USA. Results of the REE analysis are used to infer the relative paleobathymetry associated with the mosasaur specimens and then to determine if certain taxonomic groups showed a preference for a particular water depth. Comparisons are then made with mosasaur specimens reported in the literature from other regions of North America from different depositional environments. Results indicate that *Mosasaurus*, *Platecarpus* and *Plioplatecarpus* may have preferred more restricted habitats based on water depth whereas *Tylosaurus* and *Clidastes* favoured a wider range of environments. Results also suggest that *Plioplatecarpus* lived in a shallower environment than its *Platecarpus* predecessor. Although the results of this study are encouraging, caution must be exercised before drawing any final conclusions due to the small sample size of most of the taxa analysed.

**Keywords:** biogeochemistry, carbonate, habitat segregation, paleobathymetry, paleoecology

## Introduction

Mosasaurs are a widespread and diverse group of marine reptiles that inhabited the world's oceans during the Late Cretaceous. Fossils of these animals have been found on all continents, including Antarctica (Martin et al., 2002), suggesting that they were well adapted to a number of different environments. Differences in tooth morphology show that some groups of mosasaurs specialised in specific prey items (Martin & Bjork, 1987; Massare, 1987; Schulp, 2005; Martin & Fox, 2007). Because of this wide geographic distribution and specialised diet of some taxonomic groups, certain mosasaurs may have had restricted ecological or environmental ranges based on the habitat requirements of their prey.

Previous attempts at identifying the habitat segregation of mosasaurs have been based on lithology, microfossil

assemblages (Russell, 1967; Bryan, 1992; Kiernan, 2002) or macrofaunal associations (Lingham-Soliar, 1995; Manning, 2007). In some cases these methods do not agree, suggesting that the factors involved in determining habitat preference are probably more complex than any single method can reveal.

Applications of biogeochemistry in habitat determination have included research into stable carbon isotopes in tooth enamel and other skeletal material. These studies have shown that  $\delta^{13}\text{C}$  values in structural carbon typically become more depleted with distance of foraging habitat from shore (Clementz & Koch, 2001; Robbins et al., 2008; Robbins, 2010; Schulp et al., 2013; Strganac et al., 2014). These studies further concluded that this method for determining foraging habitat is complicated by biological factors such as respiratory mode, diving habits, body size and diet, in addition to other factors such as latitude, geologic age and the level of

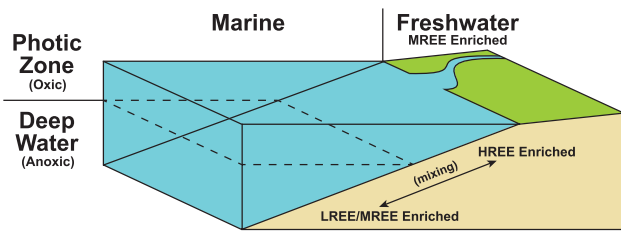


Fig. 1. Simplified diagram of natural water environments and the regions of relative REE enrichment based on studies by Patrick et al. (2004, 2007). A gradient from HREE-enriched shallow water to LREE/MREE-enriched deep water in marine environments is the result of mixing by oxic and anoxic waters. Freshwater rivers and some estuarine systems are often MREE/LREE enriched.

$\delta^{13}\text{C}$  at the base of the food chain, which also impact  $\delta^{13}\text{C}$  signatures.

Patrick et al. (2004, 2007) demonstrated that certain rare earth element (REE) signatures may be used as a proxy for

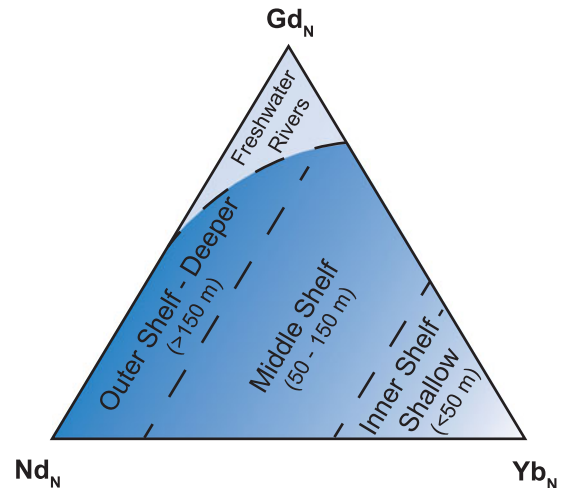


Fig. 3. Correlation of shelfal marine and freshwater river/estuarine environments with LREE/MREE/HREE ratios based on research by Patrick et al. (2007), Hanczaryk (2002) and Haq et al. (1987) (see Fig. 2).

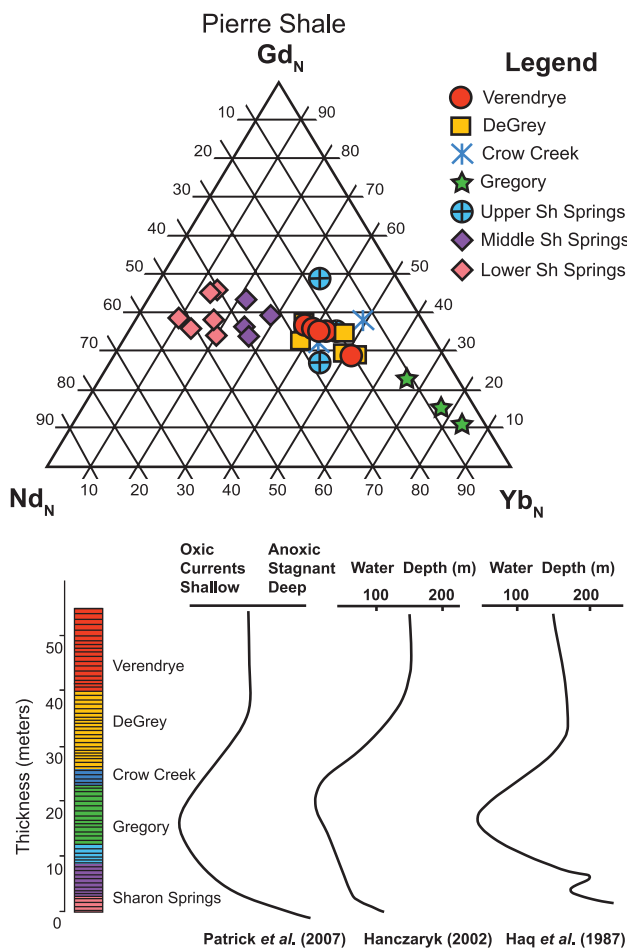


Fig. 2. Ternary diagram of normalised REE ratios of mosasaur fossils from South Dakota by geologic formation (top) and corresponding sea level curve developed by Patrick et al. (2007) compared to previous studies (bottom). Representative LREE, MREE and HREE in ternary diagram are neodymium ( $\text{Nd}_N$ ), gadolinium ( $\text{Gd}_N$ ) and ytterbium ( $\text{Yb}_N$ ), respectively. Shallow environments plot toward the  $\text{Yb}_N$  vertex whereas deeper environments plot away from the  $\text{Yb}_N$  vertex. (Figures adapted from Patrick et al., 2007.)

determining relative bathymetry during early diagenesis of fossils. Their study examined the REE content of labile sediments, pore waters and natural waters in several present-day marine environments. Representative light, medium and heavy rare earth elements (LREE, MREE, HREE) were selected from their data and plotted on ternary diagrams by percentage relative to each other. The results of their analysis showed that shallow water marine environments were relatively enriched in HREE whereas deeper water marine environments were depleted in HREE and enriched in LREE/MREE. Freshwater rivers and some estuaries tend to be relatively enriched in MREE/LREE (Patrick et al., 2007), but none of the geologic units in the present study are believed to represent these types of depositional environments (Mancini et al., 1995; Staron et al., 2001; Parris et al., 2007). The explanation for these observed enrichments was that ‘HREE enrichment is due to enhanced solubility of HREE in relatively high pH and alkaline seawater, produced by preferential HREE carbonate complexing, and sorption of LREE by HFO [hydrrous ferric oxide] and tests of planktonic organisms’ (Patrick et al., 2007, p. 75). The LREE/MREE enrichment of deeper ocean water is attributed to the release of these elements by dissolving planktonic tests and other particles in deep water environments. The region between the shallow and deep water depth showed a gradient from HREE to LREE/MREE due to mixing of shallower oxic and deeper anoxic seawaters. In the ternary diagrams, proximity to the HREE vertex was the best indicator of relative bathymetry. A simplified diagram of the different environments and the regions of relative REE enrichment can be seen in Fig. 1.

Following this interpretation of REE data these authors then analysed mosasaur fossils from the Pierre Shale Group of South Dakota to determine if LREE/MREE/HREE content could be used as a proxy for determining paleobathymetry of marine geologic formations at the time of deposition. The analysed mosasaur fossils were divided by the geologic unit from which they were

recovered and their normalised LREE/MREE/HREE ratios were plotted on a ternary diagram. The plotted results were then used to develop a relative sea-level curve for the Pierre Shale Group formations. This interpreted sea-level curve compared well with previous interpretations of water depth developed using traditional stratigraphic methods (Fig. 2).

The present study employs the same principles of LREE/MREE/HREE distribution in marine environments, but categorises the results by mosasaur genera rather than geological units. Mosasaur preference for water of a certain depth range should be reflected in the REE signature that was acquired during the early diagenesis of their skeletal remains. It should be emphasised that depth range does not necessarily equate to proximity to shore as sea floor gradient in different locations may vary and shallow water structures such as carbonate platforms or submerged sea mounts may be located well offshore.

The REE ratios of mosasaurs from the Pierre Shale reported by Patrick et al. (2007) were combined with the paleobathymetry estimates for the Pierre Shale Group determined by Haq et al. (1987) and Hanczaryk (2002) in Fig. 2 to produce a ternary diagram with divisions based on approximate continental shelf depths (Fig. 3). This combined ternary diagram was used to

determine the preferred habitats of mosasaur genera in this analysis.

## Methods and materials

Fossil mosasaur specimens that had been identified to the genus level were selected with permission from the collections of the Alabama Museum of Natural History (ALMNH) (Table 1). These specimens were recovered from a number of different localities in Alabama, with samples representing all outcropping Late Cretaceous marine formations in the central and western regions of the state (Fig. 4).

The mosasaur specimens from Alabama were processed using methods adopted from Patrick et al. (2004) and Staron et al. (2001). Approximately 0.5 g of fossil material was removed from larger specimens using a Dremel® rotary tool equipped with diamond drill bits. Drill bits were cleansed with dilute trace metal grade nitric acid (HNO<sub>3</sub>) and rinsed with deionised water between samples to prevent cross-contamination. Sampling was restricted to the cortical region of the bone to reduce possible contamination or dilution of REE signatures by infilling matrix located in the trabecular bone.

Table 1. List of mosasaur specimens sampled from the Alabama Museum of Natural History (ALMNH) collections

Taxon	ALMNH number	Description	Locality
<b>Eutaw Formation, Tombigbee Sand Member</b>			
<i>Tylosaurus</i> sp.	PV 1994.0001.0021	Premaxilla	Catoma Creek, Montgomery Co.
<i>Platecarpus tympaniticus</i>	PV 1993.0002.0132	Maxilla fragment	APe-3, Perry Co.
<i>Tylosaurus</i> sp.	PV 2005.0006.0253	Vertebra	Montgomery Co.
<b>Mooreville Formation, Lower Unnamed Member</b>			
<i>Tylosaurus</i> sp.	PV 1985.0019	Partial skeleton	Newbern, Perry Co.
<i>Tylosaurus proriger</i>	PV 1985.0022	Partial skeleton	West Greene, Greene Co.
<i>Clidastes</i> sp.	PV 1985.0048.0001	Vertebra	West Greene, Greene Co.
<i>Clidastes</i> sp.	PV 2005.0006.0007	Vertebra	Dallas Co.
<i>Platecarpus</i> sp.	PV 1993.0013.0001	Partial skeleton	AHl-6, Hale Co.
<i>Clidastes</i> sp.	PV 2005.0006.0068	Partial skeleton	Harrell Station, Dallas Co.
<i>Clidastes</i> sp.	PV 2005.0005.0072	Partial skeleton	West Greene, Greene Co.
<i>Clidastes</i> sp.	PV 1993.0012.0001	Bone fragment	Gainesville, Greene Co.
<b>Mooreville Formation, Arcola Limestone Member</b>			
<i>Clidastes</i> sp.	PV 2005.0006.0058	Squamosal	Boligee, Greene Co.
<b>Demopolis Formation, Lower Unnamed Member</b>			
<i>Platecarpus</i> cf. <i>P.somenensis</i>	PV 2005.0006.0008	Partial skeleton	Greene, Co.
<i>Mosasaurus</i> sp.	PV 2005.0006.0074	Partial skeleton	Greene, Co.
<b>Ripley Formation</b>			
<i>Mosasaurus hoffmanni</i>	PV 1990.0003	Partial skeleton	ALn-3, Sandy Ridge, Lowndes Co.
<b>Prairie Bluff Formation</b>			
<i>Mosasaurus hoffmanni</i>	PV 1988. 0018	Partial skelton	ALn-7, Braggs, Lowndes Co.
<i>Mosasaurus hoffmanni</i>	PV 1991.0013.0002	Maxilla fragment	ALn-7, Braggs, Lowndes Co.
<i>Plioplatecarpus</i> sp.	PV 1991.0032.0001	Vertebra	Ft. Deposit, Butler Co.

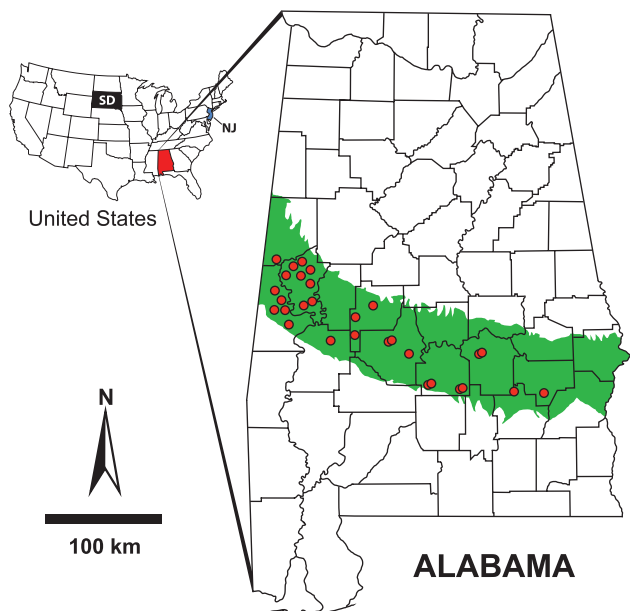


Fig. 4. Map of Alabama, USA, showing the region of outcropping Late Cretaceous marine formations (green area) and the collection localities of mosasaur fossils analysed in this study (red circles). Previously published REE data for mosasaur fossils from South Dakota (SD) and New Jersey (NJ) were also used.

Approximately 100 mg of powder per sample were dissolved with 3 ml of trace metal grade nitric acid (10%) and diluted with 7 ml of deionised water, and subsequently filtered through a 0.2  $\mu\text{m}$  fibreglass medium prior to chemical analysis to remove any undissolved particles.

Prepared solutions were diluted by a factor of 100 before analysis with a Perkin Elmer Elan 6000® inductively coupled plasma mass spectrometer (ICP-MS). The ICP-MS was calibrated prior to analysis using ICP-MS Multi-element Standard manufactured by High Purity Standards whereas Claritas PPT Multi-element Standard manufactured by Spex Chemical was used as the quality control standard during testing. Each sample was analysed 20 times and automated analytical software processed the results. Analytical error for most specimens was within  $\pm 5\%$  of certified values, and results are reported in parts per million (ppm) (Table 2). Resulting values were normalised with the North American Shale Composite (NASC) (Gromet et al., 1984) (Table 3).

Additional REE data was acquired from published reports of mosasaur specimens from the Pierre Shale of South Dakota (Patrick et al., 2004) and the Navesink and lower Hornerstown formations of New Jersey (Staron et al., 2001). Of the previously reported data, only mosasaur specimens that could be identified to genus level were used in the present study.

Rigorous statistical analysis of the data in this study was not performed because most of the taxonomic groups are represented by a very small sample size. It is believed that statistical analysis would not produce any meaningful results

beyond what can be observed in the ternary diagrams for each taxon. This is a preliminary study of a potential method for habitat determination that will require analysis of a much larger sample size in order to prove its value.

## Analyses and results

Normalised neodymium ( $\text{Nd}_N$ ), gadolinium ( $\text{Gd}_N$ ) and ytterbium ( $\text{Yb}_N$ ) values were used as respective LREE/MREE/HREE representatives. These particular REEs were selected to allow better comparison with previous studies and because their quantities are least altered by their chemical properties (Patrick et al., 2004). The  $\text{Nd}_N$ ,  $\text{Gd}_N$  and  $\text{Yb}_N$  quantities were summed and plotted on ternary diagrams by percentage of total. Other LREE/MREE/HREE combinations were tested but the ternary diagram patterns did not differ greatly from the REE representatives selected.

The resulting LREE/MREE/HREE ternary diagram patterns for the analysis are presented in Fig. 5. The REE pattern for *Tylosaurus* (Fig. 5) is the most widely dispersed of the five genera analysed in this study, with results ranging from deep water environments to moderately shallow water depths (Fig. 3). *Tylosaurus* also has the largest sample size of the taxonomic groups analysed in the study ( $N = 15$ ).

The data points for *Clidastes* (Fig. 5) ( $N = 6$ ) are as unconstrained as those of *Tylosaurus*, but they are arranged in a linear pattern directed toward the  $\text{Yb}_N$  vertex in the range of intermediate or moderate water depth. No other taxonomic group in this study has a linear pattern to this degree.

The REE pattern for *Mosasaurus* (Fig. 5) displays the tightest cluster of data points ( $N = 6$ ) of the taxonomic groups analysed. This cluster is located in the range of deeper, outer-shelf marine environments.

*Platecarpus* and *Plioplatecarpus* (Fig. 5) are relatively well constrained, but the sample size for *Platecarpus* is exceptionally small (*Platecarpus*  $N = 3$ ; *Plioplatecarpus*  $N = 6$ ). The *Platecarpus* grouping is positioned in a deeper water portion of the ternary diagram than *Plioplatecarpus*.

## Discussion and conclusions

The basic premise of the analysis presented here is that the majority of individuals within a vertebrate taxonomic group die and are buried in the environment in which they lived. In a marine environment, some individuals, especially those with high body fat content in very shallow water (Reisdorf et al., 2012), may become buoyant with *post mortem* decompositional gasses and be transported by water or air currents to exotic locations well away from their typical habitat before burial. However, these 'bloat and float' individuals are here assumed to be exceptional rather than the standard and most specimens are preserved in or near their preferred habitat (Reisdorf et al., 2012; Mateus et al., 2013).

Table 2. Rare earth element (REE) content (in parts per million, ppm) of mosasaur specimens from Alabama

Taxon	ALMNH number	La	Ce	Pr	Nd	Sm	Eu	Gd	Tb	Dy	Ho	Er	Tm	Yb	Lu	ΣREE
<i>Clidastes</i> sp.	PV 1985.0048.0001	54.54	72.92	7.53	28.17	4.71	1.07	5.03	0.73	5.27	1.18	3.86	0.56	4.07	0.67	190.32
<i>Clidastes</i> sp.	PV 2005.0006.0007	305.34	364.00	36.66	129.69	19.60	4.85	22.19	3.37	23.70	5.38	16.29	2.18	13.21	1.83	948.30
<i>Clidastes</i> sp.	PV 2005.0006.0068	467.22	726.24	82.73	304.57	50.66	12.00	53.90	8.31	55.88	11.74	33.70	4.30	23.88	3.16	1838.28
<i>Clidastes</i> sp.	PV 2005.0005.0072	86.33	171.21	18.39	69.78	12.56	2.98	11.46	1.66	10.50	2.02	5.69	0.72	4.53	0.63	398.49
<i>Clidastes</i> sp.	PV 1993.0012.0001	507.07	853.55	98.63	366.02	60.65	13.45	58.29	8.80	56.54	11.37	31.79	4.03	22.53	3.03	2095.75
<i>Clidastes</i> sp.	PV 2005.0006.0058	29.16	36.12	3.94	14.62	2.44	0.54	2.74	0.41	3.19	0.74	2.55	0.36	2.84	0.43	100.10
<i>Mosasaurus hoffmanni</i>	PV 1991.0013.0002	29.29	60.81	6.83	27.01	4.79	1.18	4.45	0.66	4.37	0.90	2.63	0.34	2.17	0.30	145.73
<i>Mosasaurus hoffmanni</i>	PV 1990.0003	77.88	129.64	11.75	44.14	7.06	1.94	7.85	1.18	8.16	1.81	5.50	0.78	5.05	0.77	303.50
<i>Mosasaurus hoffmanni</i>	PV 1988. 0018	118.00	208.75	21.53	86.32	13.93	3.79	14.88	2.13	13.84	2.83	7.90	0.99	5.71	0.81	501.41
<i>Mosasaurus</i> sp.	PV 2005.0006.0074	146.22	229.07	27.11	106.29	19.49	4.75	19.48	2.81	18.29	3.72	10.95	1.45	8.90	1.27	599.81
<i>Platecarpus</i> cf. <i>P.somenensis</i>	PV 2005.0006.0008	471.13	846.59	94.45	340.56	55.37	13.20	50.78	7.35	44.82	8.60	23.49	3.04	17.55	2.44	1979.37
<i>Platecarpus</i> sp.	PV 1993.0013.0001	419.23	676.25	69.40	256.61	41.09	10.43	44.30	6.61	44.11	9.33	27.03	3.53	20.72	2.91	1631.53
<i>Platecarpus tympaniticus</i>	PV 1993.0002.0132	118.54	194.61	22.30	85.80	15.04	3.61	15.12	2.14	13.86	2.81	8.09	1.02	6.53	0.99	490.47
<i>Plioplatecarpus</i> sp.	PV 1991.0032.0001	123.91	156.41	15.51	58.90	8.48	2.40	10.12	1.50	10.96	2.64	8.55	1.23	8.11	1.28	410.01
<i>Tylosaurus proriger</i>	PV 1985.0022	338.64	567.47	59.28	223.51	36.25	9.85	39.19	5.65	36.73	7.38	20.30	2.52	14.06	1.93	1362.76
<i>Tylosaurus</i> sp.	PV 1994.0001.0021	76.54	103.91	9.94	37.77	6.42	1.66	6.48	0.98	6.77	1.45	4.60	0.64	4.57	0.71	262.45
<i>Tylosaurus</i> sp.	PV 2005.0006.0253	162.67	226.85	22.63	83.27	14.11	3.73	13.56	2.00	13.36	2.79	8.41	1.18	7.66	1.13	563.36
<i>Tylosaurus</i> sp.	PV 1985.0019	233.01	216.86	17.40	57.83	6.81	1.35	9.29	1.36	11.04	3.05	11.07	1.69	11.98	1.98	584.73

Table 3. Normalised REE values ( $REE_{sample}/NASC$ ) of mosasaur specimens from Alabama (North American Shale Composite values from Gromet et al., 1984)

Taxon	ALMNH number	La	Ce	Pr	Nd	Sm	Eu	Gd	Tb	Dy	Ho	Er	Tm	Yb	Lu
<i>Clidastes</i> sp.	PV 1985.0048.0001	1.75	1.09	0.98	1.03	0.84	0.90	1.03	0.86	1.26	1.16	1.36	1.17	1.33	1.46
<i>Clidastes</i> sp.	PV 2005.0006.0007	9.82	5.46	4.76	4.73	3.51	4.11	4.53	3.97	5.68	5.27	5.73	4.54	4.32	3.98
<i>Clidastes</i> sp.	PV 2005.0006.0068	15.02	10.89	10.74	11.12	9.06	10.17	11.00	9.78	13.40	11.51	11.87	8.96	7.80	6.86
<i>Clidastes</i> sp.	PV 2005.0005.0072	2.78	2.57	2.39	2.55	2.25	2.52	2.34	1.96	2.52	1.98	2.00	1.51	1.48	1.38
<i>Clidastes</i> sp.	PV 1993.0012.0001	16.30	12.80	12.81	13.36	10.85	11.40	11.90	10.35	13.56	11.14	11.19	8.39	7.36	6.59
<i>Clidastes</i> sp.	PV 2005.0006.0058	0.94	0.54	0.51	0.53	0.44	0.46	0.56	0.48	0.77	0.72	0.90	0.75	0.93	0.94
<i>Mosasaurus hoffmanni</i>	PV 1991.0013.0002	0.94	0.91	0.89	0.99	0.86	1.00	0.91	0.78	1.05	0.88	0.92	0.71	0.71	0.66
<i>Mosasaurus hoffmanni</i>	PV 1990.0003	2.50	1.94	1.53	1.61	1.26	1.65	1.60	1.38	1.96	1.77	1.94	1.62	1.65	1.67
<i>Mosasaurus hoffmanni</i>	PV 1988.0018	3.79	3.13	2.80	3.15	2.49	3.21	3.04	2.50	3.32	2.77	2.78	2.07	1.87	1.76
<i>Mosasaurus</i> sp.	PV 2005.0006.0074	4.70	3.43	3.52	3.88	3.49	4.02	3.98	3.30	4.39	3.65	3.85	3.02	2.91	2.76
<i>Platecarpus</i> cf. <i>P.somenensis</i>	PV 2005.0006.0008	15.15	12.69	12.27	12.43	9.91	11.19	10.36	8.65	10.75	8.43	8.27	6.33	5.73	5.31
<i>Platecarpus</i> sp.	PV 1993.0013.0001	13.48	10.14	9.01	9.37	7.35	8.84	9.04	7.77	10.58	9.14	9.52	7.34	6.77	6.33
<i>Platecarpus tympaniticus</i>	PV 1993.0002.0132	3.81	2.92	2.90	3.13	2.69	3.06	3.09	2.51	3.32	2.75	2.85	2.13	2.14	2.15
<i>Plioplatecarpus</i> sp.	PV 1991.0032.0001	3.98	2.35	2.01	2.15	1.52	2.03	2.07	1.76	2.63	2.59	3.01	2.57	2.65	2.77
<i>Tylosaurus proriger</i>	PV 1985.0022	10.89	8.51	7.70	8.16	6.48	8.35	8.00	6.64	8.81	7.24	7.15	5.26	4.59	4.19
<i>Tylosaurus</i> sp.	PV 1994.0001.0021	2.46	1.56	1.29	1.38	1.15	1.40	1.32	1.15	1.62	1.43	1.62	1.34	1.49	1.55
<i>Tylosaurus</i> sp.	PV 2005.0006.0253	5.23	3.40	2.94	3.04	2.52	3.16	2.77	2.36	3.20	2.74	2.96	2.46	2.50	2.45
<i>Tylosaurus</i> sp.	PV 1985.0019	7.49	3.25	2.26	2.11	1.22	1.15	1.90	1.60	2.65	2.99	3.90	3.51	3.91	4.30
	NASC values (ppm)	31.1	66.7	7.7	27.4	5.59	1.18	4.9	0.85	4.17	1.02	2.84	0.48	3.06	0.46

Once buried in marine sediment, the preserved skeletal remains begin to assimilate REEs located in the surrounding labile sediment and pore waters during the early stages of diagenesis (Trueman & Benton, 1997; Trueman, 1999). Patrick et al. (2004, 2007) showed that REEs are fractionated to a certain degree in marine and freshwater environments due to the chemical properties of the individual REEs and the environmental conditions that are present in water of various depths. Because the ratios of LREE/MREE/HREE tend to be relatively uniform in marine sediments deposited in water of a given depth, and because most individuals of a taxonomic group are buried in the environment in which they lived, the LREE/MREE/HREE ratios of mosasaur fossils should also be uniform if their preferred habitat was restricted to water of the same depth.

In Fig. 6, two ternary diagrams illustrate the different hypothetical REE ratio patterns that would result if a given mosasaur taxon had a preferred habitat based on water depth (A) or was widely distributed with no preference of water depth (B). In diagram A, the majority of specimens are clustered tightly together, which represents the preferred habitat for this taxon, whereas only a few outliers represent 'bloat and float' carcasses or unusual individuals who ventured outside of the preferred habitat. In diagram B, there is no central core where the majority of specimens are clustered, suggesting that this taxon did not have a preferred habitat and was able to acquire food in multiple environments.

The REE ratios of taxa analysed in this study suggest that some mosasaur genera may have preferred a specific range of water depth whereas others appeared to be widely distributed with no preference of water depth. In Fig. 5, the specimens in the *Tylosaurus* diagram are not confined to a specific cluster and are widely distributed, which suggests they had the most variation in habitat of any genus in this analysis. This is not surprising considering that *Tylosaurus* did not possess specialised teeth or other derived morphological features that would limit it to a specific type of prey or environment. Martin and Bjork (1987) documented one *Tylosaurus* specimen from South Dakota with the remains of a shark, fish, turtle, marine bird and a smaller mosasaur in the gastric region of its abdomen. The ability to thrive on a variety of prey items such as this would probably not have limited *Tylosaurus* to any specific marine environment. Although many of the *Tylosaurus* specimens in this study are identified as *Tylosaurus* sp. (including all of the specimens from South Dakota), it is likely that the majority of these specimens are *T. proriger* based on the stratigraphic range of this species (Everhart, 2005). The  $\delta^{13}C$  signatures in *Tylosaurus* tooth enamel possess a wide range of values, suggesting that they fed in a variety of habitats (Robbins, 2010), which agrees with the dispersed REE pattern for the genus in the ternary diagram.

The ternary diagram for *Clidastes* (Fig. 5) shows a peculiar linear pattern for the REE ratios in the specimens analysed. Although there is no clearly defined cluster signifying the

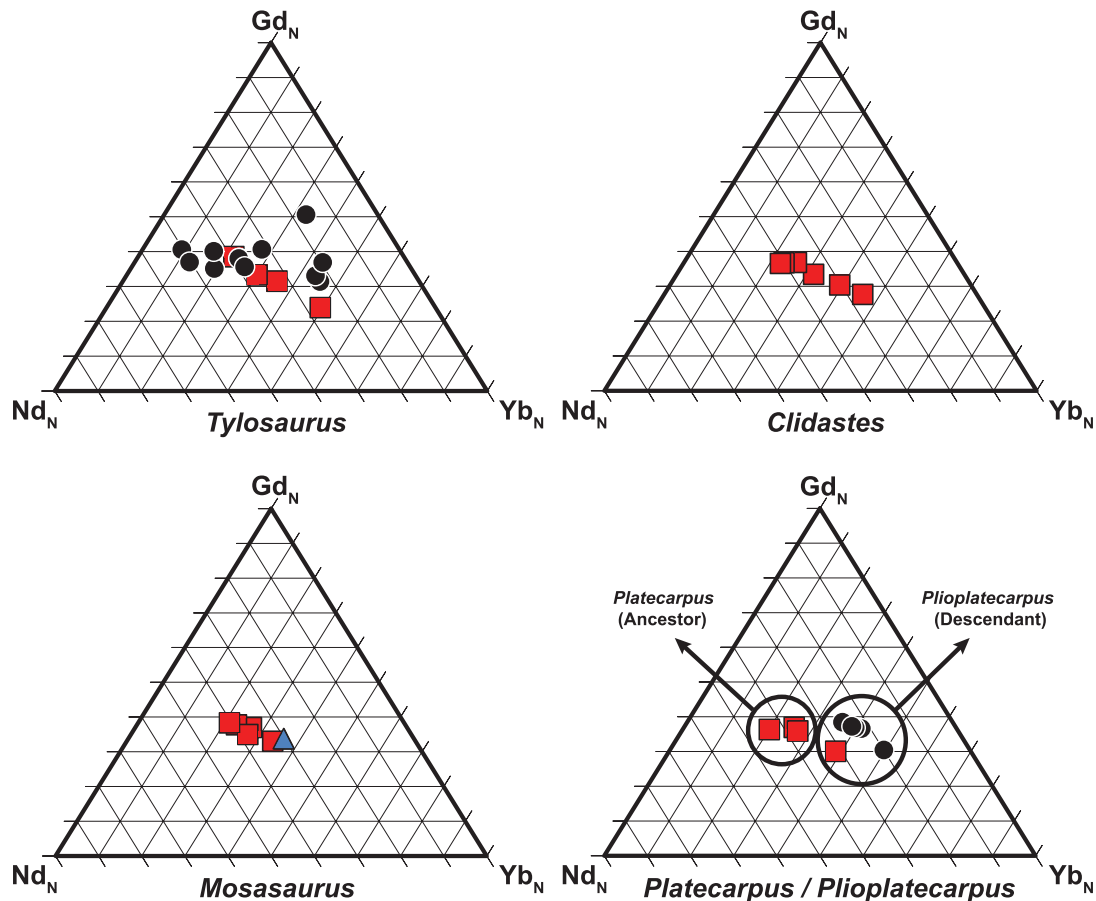


Fig. 5. Ternary diagrams of normalised REE ratios for *Tylosaurus*, *Clidastes*, *Mosasaurus*, *Platecarpus* and *Plioplatecarpus* from all areas of study. Red squares = Alabama, black circles = South Dakota, blue triangles = New Jersey. The dispersed pattern for *Tylosaurus* suggests that it did not have a preferred habitat whereas the compact pattern for *Mosasaurus* suggests that it may have preferred deeper, middle shelf marine environments. The intermediate pattern for *Clidastes* is inconclusive. The ancestral *Platecarpus* plots farther away from the  $Yb_N$  vertex than its descendant *Plioplatecarpus*, suggesting an evolutionary shift from deeper to more shallow water environments.

preference of a specific water depth, the linear shape may imply that *Clidastes* had a wider range of habitats, from middle to inner shelf environments. Additionally, the elongated shape of the pattern may suggest an intraspecific separation of individuals based on ontogeny, where juveniles live in separate environments from those of adults to avoid cannibalistic predation or so that the juveniles may obtain prey items more suitable for their smaller size. Of the *Clidastes* analysed in this study, the two samples plotting closest to the shallow water  $Yb_N$  vertex were taken from very large adult specimens whereas the four samples plotting further away from the  $Yb_N$  vertex, suggesting preference for deeper water, were taken from one juvenile and three subadult specimens. These findings are not in agreement with previous studies of  $\delta^{13}C$  values in tooth enamel of *Clidastes*, in which smaller individuals had higher values reflective of near-shore feeding and larger individuals had more negative values suggestive of feeding farther from the shore (Robbins et al., 2008; Robbins, 2010), although the findings of the present study may be influenced by the very low sample size ( $N = 6$ ). The linear REE pattern for

*Clidastes* in the present study may also be explained as an evolutionary shift in the genus from waters of one depth to another, given that the data were obtained from specimens over a relatively wide temporal span and not a single stratigraphic horizon. The results for *Clidastes* are currently inconclusive and will require additional analyses to define its habitat preference using additional analytical parameters.

The REE pattern for *Mosasaurus* is the most tightly clustered of the taxa in this study (Fig. 5) and most closely resembles the hypothetical pattern for specific habitat preference shown in Fig. 6. The data points for this genus are clumped in the area of outer middle shelf depth on the ternary diagram (Fig. 3), with a couple of outliers positioned in shallower water depths. Most of the individuals in this taxonomic group belong to *M. hoffmanni*, a large species of mosasaur with cranial adaptations for feeding on large prey (Lingham-Soliar, 1995; Mulder, 1999; Harrell & Martin, 2014). Bryan (1992) suggested that *M. hoffmanni* (= *M. 'maximus'*) lived in deep marine water based on his interpretation of the lithology of the Prairie Bluff Chalk in Alabama and taphonomy of ALMNH PV 1988.0018

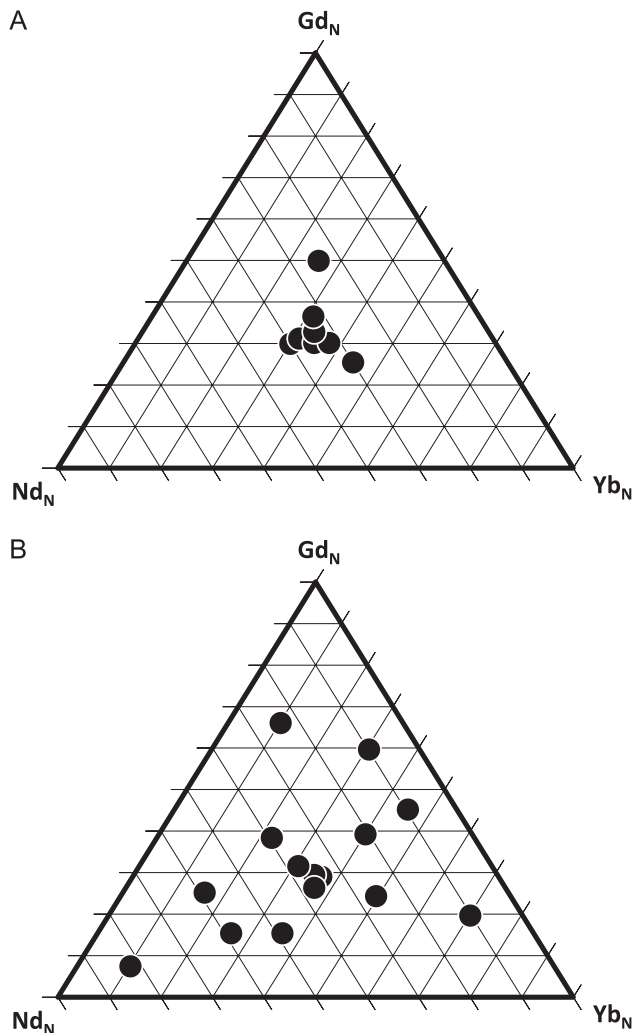


Fig. 6. Hypothetical ternary diagrams of normalised REE ratios showing expected distribution of data points if a given mosasaur genus had a preferred habitat based on water depth (A) or had no preferred habitat (B).

(see Table 1). Gallagher (2005) reported only *Mosasaurus* sp. from the Hornerstown Formation (Main Fossiliferous Layer) of New Jersey, a geologic unit that is interpreted as being a mid to outer shelf deposit (Staron et al., 2001). Lingham-Soliar (1995) and Manning (2007, as *M. 'maximus'*) believed *M. hoffmanni* to be from shallower middle to inner shelf depth using invertebrate and vertebrate faunal associations to determine paleobathymetry. Recent analysis of stable carbon isotopes in tooth enamel by Robbins (2010), Schulp et al. (2013) and Strganac et al. (2014) suggests that *Mosasaurus* may have fed in offshore/open ocean environments. The results of the present REE analysis for *M. hoffmanni* are in agreement with the interpretations of the carbon isotope studies.

The results for *Platecarpus* and *Plioplatecarpus* (Fig. 5) are combined on a single ternary diagram because of the probable ancestor–descendant relationship between the two genera (Holmes, 1996; Bell, 1997) and because their biostratigraphic ranges do not overlap (Russell, 1967). Although only three

*Platecarpus* specimens were analysed, their REE ratios plot close together in the deeper water, left side of the diagram. These three *Platecarpus* specimens were obtained from three different localities in Alabama, each representing a different geologic formation and age (Table 1). The more numerous *Plioplatecarpus* specimens also cluster relatively well, but on the shallower, right side of the diagram (Figs 5 and 3). This suggests an evolutionary shift from the older, deeper-water preferring *Platecarpus* ancestor to the younger, shallower-water preferring *Plioplatecarpus* descendant, although a high degree of uncertainty remains with only three *Platecarpus* specimens analysed. This shift in habitat preference may be partly due to a change in the prey preference of the two genera. The *Platecarpus* species analysed in this study have comparatively stout, conical marginal dentition and robust lower jaw whereas the *Plioplatecarpus* species analysed have slender, piercing marginal dentition and a more gracile lower jaw. Preserved gastric residues for *Platecarpus* include larger bony fish up to 1.2 m in length, whereas *Plioplatecarpus* has been found with the preserved remains of small, soft-bodied, belemnite cephalopods (Massare, 1987). Analysis of stable carbon isotopes in mosasaur tooth enamel shows a similar evolutionary shift in foraging habitat preference in *Platecarpus/Plioplatecarpus* (Robbins, 2010; Schulp et al., 2013), with *Platecarpus* feeding farther from shore than *Plioplatecarpus*, but distance from shore does not necessarily relate to water depth.

Although the number of specimens analysed in this study is not high, the results for most genera are consistent with the findings of previous researchers. Research on stable carbon isotopes performed by Robbins et al. (2008), Robbins (2010), Schulp et al. (2013) and Strganac et al. (2014) produced some results that are supported by the findings of the REE study presented here. Future research to improve the usefulness of REE analysis will include increasing the sample size for each taxon and grouping specimens at the species level, as well as additional data pertaining to the ontogeny of specimens and intraspecific chronostratigraphic variations.

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