Using linear measurements to diagnose the ecological realm of *Spinosaurus* (#91634)

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Using linear measurements to diagnose the ecological realm of *Spinosaurus*

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Much of the ecological discourse surrounding the polarising theropod *Spinosaurus* has centred on qualitative discussions. Using a multivariate data analytical approach on size-adjusted linear measurements of the skull, we examine patterns in skull shape across a range of sauropsid clades, across three ecological realms (terrestrial, semi-aquatic, and aquatic) utilising cluster analyses to identify emergent properties of the data. Results revealed terrestrial ecologies to be significantly distinct from both semi- and fully aquatic ecologies, the latter two were not significantly different. Spinosaurids plotted away from theropods in morphospace and close to marine taxa and wading birds. The position of nares and the degree of rostral elongation had the greatest effect on categorisation. Unsupervised clustering resulted in two distinct groups rather than three, indicating that habitat categorisation do not adequately explain skull morphological variance, suggestive of division based on feeding on aquatic versus terrestrial food items.

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Abstract:

Much of the ecological discourse surrounding the polarising theropod *Spinosaurus* has centred on qualitative discussions. Using a multivariate data analytical approach on size-adjusted linear measurements of the skull, we examine patterns in skull shape across a range of sauropsid clades, across three ecological realms (terrestrial, semi-aquatic, and aquatic) utilising cluster analyses to identify emergent properties of the data. Results revealed terrestrial ecologies to be significantly distinct from both semi- and fully aquatic ecologies, the latter two were not significantly different. Spinosaurids plotted away from theropods in morphospace and close to marine taxa and wading birds. The position of nares and the degree of rostral elongation had the greatest effect on categorisation. Unsupervised clustering resulted in two distinct groups rather than three, indicating that habitat categorisation do not adequately explain skull morphological variance, suggestive of division based on feeding on aquatic versus terrestrial food items.

Introduction:

The enigmatic theropod *Spinosaurus aegyptiacus* (Stromer, 1915) is putatively considered semi-aquatic to some capacity (Aureliano *et al.,* 2018; Henderson, 2018; Ibrahim *et al.,* 2020; Fabbri et al., 2022; Sereno et al., 2022). This is supported by morphological (Ibrahim et al., 2014; Beevor et al., 2021), geographical (Bertin, 2010; Benyoucef et al., 2015), and isotopic (Amiot et al., 2010) evidence. Of specific interest are cranial adaptations to piscivory (itself indicative of aquatic affinities) observed in *Spinosaurus*; conical, interlocking dentition, posteriorly retracted nares, lateral skull compression, and raised orbit position (Ibrahim et al., 2014; Arden et al., 2019; Hone and Holtz, 2021). Partial piscivory has been widely presumed for spinosaurids (Charig and Milner, 1997; Allain et al., 2012; Sales and Schultz, 2017; Fabbri et al., 2022a). Spinosaurine spinosaurids show fewer, larger teeth with fluting in place of serrations compared to baryonychine spinosaurids, (Sereno et al., 1998; Sales and Schultz, 2017; Hone and Holtz, 2021), which have been proposed as adaptations to a diet including hard-bodied prey (Massare, 1987; Hone and Holtz, 2021). Alternatively, this dentition could be an adaptation to withstand greater bite forces generated by greater body size compared to baryonychine spinosaurids (Sakamoto, 2022), similar selection pressures were suggested by Sereno et al. (2022).

Within the *Spinosaurus* literature, definitions of ‘semi-aquatic’ can be varied. We define a ‘semi-aquatic’ animal to refer to those that utilise aquatic environments for a significant proportion of their nutritional resources and/or spend a significant proportion of time within bodies of water but retain terrestrial locomotory capabilities. However, a more specific diagnosis of the habitat use of *Spinosaurus* would be advantageous, as there is no consensus thus far (Ibrahim et al., 2014; Hone and Holtz, 2021; Fabbri et al., 2022; Sereno et al., 2022). Most recent research broadly addresses one of two competing hypotheses: the ‘underwater pursuit predator’ hypothesis (Ibrahim *et al.,* 2020) and the ‘shallow water wading' hypothesis (Hone and Holtz, 2021). The former paints *Spinosaurus* as specialised in actively chasing down prey whilst submerged in the water column, propelled by tail and trunk (Ibrahim et al., 2020). In contrast, the latter hypothesis describes a hunting mode wherein the majority of the animal remains above the waterline, except for portions of the limbs and rostrum, suggesting stork-like feeding behaviours (Paul, 1988; Hone and Holtz, 2017; Arden et al., 2019).

The shallow water wading hypothesis has received notable support in recent publications (Hone and Holtz, 2021; Sereno et al., 2022), though discussions remain ongoing (see (Fabbri et al., 2022a; Fabbri et al., 2022b)). Here, we expand on the work by Hone and Holtz (2021) to develop their quantitative approach to analysing cranial morphology in sauropsids across different ecological habitats. To this end, we aim to:

- Increase the number and diversity of taxa in the dataset utilised by Hone and Holtz (2021).
- Evaluate whether skull morphometrics reflect ecology.
- Categorise the habitat of *Spinosaurus* based on skull morphometrics.

Materials and methods:

99 taxa from 8 clades were examined and subdivided by known or inferred ecologies (terrestrial, semi-aquatic, or aquatic). Our dataset expanded upon that of Hone and Holtz (2021), increasing the number of representatives of examined clades and adding the families Ardeidae (herons) and Ciconiidae (storks), to allow morphological comparisons between *Spinosaurus* and these ecological analogues (wading birds) as proposed by Hone and Holtz (2021). Taxa were selected upon the availability of photographs (The Experimental Zoology Group of Wageningen University, 2022), 3D scans (The University of Texas at Austin, 2022), or reconstructions depicting the skull in dorsal and lateral orientations (Supplementary material).

[Figure 1]

Figure 1. Principal component analysis of 6 size-adjusted linear (Mosimann) variables in 95 representative taxa across 8 sauropsid clades (Squamata and Crurotarsi further divided based on ecology). **(a)** Distribution of taxa in morphospace of principle component (PC) 1 (48.06% of variance) and PC2 (30.10% of variance). Convex hulls delimit K-means (k=3) cluster groupings. Green markers indicate terrestrial ecology, light blue markers indicate a semi-aquatic ecology, dark blue markers represent a fully aquatic ecology, and orange and red represent unknown ecologies. Silhouettes of taxa highlight the naris (blue) and the orbit (green). **(b)** Measurements were taken from the skull in lateral view. Skull height (SH), skull length (SL), distance from naris to anterior margin (NA), distance from naris to dorsal margin (ND), and distance from orbit to dorsal margin (OD). Not pictured: skull width (taken from dorsal view). Modified from (Hone and Holtz 2021). **(c)** Comparison of skull morphology between *Spinosaurus sp.* (top, modified from (Ibrahim et al 2014)) and *Pliosaurus kevani* (bottom, modified from (Benson et al

2013)). *Allosaurus* and *Spinosaurus* by Tasman Dixon, *Varanus* by Steven Traver, *Goniopholis*, *Tylosaurus*, *Rhomaleosaurus*, and *Baryonyx* by Scott Hartman, and *Leptoptilos* by L. Shyamal.

For each taxon, 6 measurements were taken using ImageJ v. 1.53 (Abràmoff et al., 2004) (figure 1b) following Hone and Holtz (2021). Isometric scaling due to body size was accounted for by converting to Mosimann shape variables (Mosimann, 1970; Sakamoto and Ruta, 2012; Morales and Giannini, 2021). These values were log-transformed (Glazier, 2013), centred on 0 and scaled to unit variance.

Data analyses

All data and statistical analyses were conducted in PAST v. 4.03 (Hammer et al., 2001). A principal component analysis (PCA) was performed on the transformed shape data of 95 taxa (those with incomplete information were excluded). Taxa were grouped by clade and ecology. Permutational multivariate analyses of variance (PerMANOVA) were used to assess the overlap in morphospace between clades, and between ecologies. To determine the appropriate number and pattern of clustering in morphospace, we used both classical (unsupervised) and k-means (supervised) cluster analyses. We chose k=3 for k-means analysis to reflect the number of ecologies.

Results:

PC1 and PC2 together account for 78.16% of the variance in the data, with PC1 explaining 48.06% and PC2 explaining 30.10% respectively. A morphospace plot of PC1 against PC2 (figure 1a) reveals that an increase along PC1 is associated with an increase in skull size and a decrease in NA. Whereas increase along PC2 is associated with skull heights approximately equal to skull length, progressively deeper-set orbits (long OD) and nares (long ND), and increasing distance from the naris to the skull anterior margin (long NA) (supplementary material). Ecologies are scattered across morphospace, though an increase along PC1 appears to be associated with increasing terrestriality. When clades contain representatives from multiple ecologies (squamates and crurotarsans), members remain close in morphospace despite their assigned ecologies (figure 1a). Wading birds, spinosaurids, mosasaurs and plesiosaurs occupy the same region of morphospace, with *Spinosaurus* being most similar to *Pliosaurus kevani* (figure 1c).

A one-way PerMANOVA by clade, reveals that all aquatic taxa and semi-aquatic crurotarsans did not occupy significantly different ($p > 0.05$) regions of morphospace. Spinosaurids (excluding *Spinosaurus*) did not show significant differences from any other clade. Storks and herons, terrestrial and semi-aquatic squamates, and semi-aquatic and aquatic crurotarsans could not be differentiated from each other. Non-spinosaurid theropods were distinct from all clades except semi-aquatic squamates and spinosaurids. Likewise, semi-aquatic crurotarsans were distinct from all non-aquatic, non-spinosaurid taxa. A one-way PerMANOVA of the same data grouped by ecology showed all terrestrial ecology pairs as significantly different ($p < 0.001$) but aquatic and semi-aquatic ecologies could not be differentiated.

[Figure 2]

Figure 2. Morphospace plot of principal component scores as in figure 1, showing instead unsupervised cluster analysis groupings.

Supervised clustering using k-means (k=3) cluster analysis did not yield clusters according to the three habitat categories (figure 1a). Cluster 1 is characterised by narrow skulls, elongate rostra, and substantial nares to anterior margin distances (larger NA). Cluster 2 is also associated with rostral elongation but is distinguished from Cluster 1 by anterodorsally elevated nares (smaller OD and NA). Cluster 3 contains all other terrestrial taxa. High PC 1 scores indicate the absence of rostral elongation.

Unsupervised cluster analysis on the other hand produced two clusters (figure 2). Cluster A is formed of taxa with elongate skulls and long nares to anterior margin distances. Taxa in this cluster are all either aquatic (plesiosaurs and mosasaurs) or semi-aquatic (phytosaurs (Crurotarsi) and aves). Cluster B contains taxa with short nares to anterior margin distances, this includes all terrestrial taxa, semi-aquatic squamates, and non-phytosaur crurotarsans.

Discussion

The discrepancy between the number of clusters produced by supervised (figure 1a) and unsupervised (figure 2) cluster analyses demonstrates that the a priori categorisation (K=3) based on the three habitats is not supported by our linear morphometric data. Cluster membership did not correspond to specified ecology (terrestrial, semi-aquatic, or aquatic) in both analyses. Taken together, this indicates that ecomorphologies associated with habitat are not emergent properties of our dataset. Instead, unsupervised cluster membership (figure 2) appears to be largely determined by the distance from the nares to the anterior margin, which dictates the relative rostral length often interpreted as adaptations for foraging in water, either semi- or fully submerged. Thus, separation in morphospace may be influenced by factors such as diet (feeding ecology, i.e., what they are eating irrespective of where they live) and to a lesser extent phylogeny (Melstrom et al., 2021).

Members of cluster A (aves, plesiosaurs, mosasaurs, spinosaurids, and phytosaurs) (figure 2) demonstrate elongate skulls via elongation of the skeletal elements rostral to the naris, i.e., the maxilla-premaxilla complex. This distinguishes them from those with elongate skulls in Cluster B (i.e., non-phytosaurian crurotarsans), which achieve elongation of the rostrum via increasing the length of the nasal-maxilla complex (supplementary material). These two morphotypes attain the same outcome in terms of elongation of the rostrum (e.g., increased reach), but differ in which part of the rostrum is elongated relative to the nares, anterior (Clade A) or posterior (Clade B).

While it is difficult to address the sources of natural selection that differentiate the two evolutionary pathways to rostral elongation as we have not directly tested this here, it is possible to discuss the implications of phylogeny. Across all theropods examined (both spinosaurids and non-spinosaurids), the relative positions of the naris and orbit to the nasal remain constant (supplementary material). Interestingly, the rostral elongation in *Spinosaurus* is achieved via the lengthening of the skeletal elements anterior to the naris, thus maintaining the theropod configuration of the naris and orbit positions relative to the nasal. This feature is more prominent in *Spinosaurus* even compared to its closest relatives, the baryonychine spinosaurids (figure 1a, 1c). On the other hand, birds (avian theropods) ancestrally display elongation in the maxilla-premaxilla complex (Bhullar et al., 2015), despite their highly diverse feeding ecology, most of which being non-aquatic. Taken together, this indicates that theropods tend to elongate their rostra by extending the maxilla-premaxilla complex rather than the maxilla-nasal complex.

In contrast, Crurotarsi displays both pathways of rostral elongation in phytosaurs (Cluster A) and crocodyliforms (Cluster B), demonstrating less phylogenetic constraint across Crurotarsi as a whole, but distinct effects of phylogeny within Phytosauria and Crocodyliformes respectively, i.e., all phytosaurs are in Cluster A while all crocodyliforms are in Cluster B. The disparity in how rostral elongation is attained across Crurotarsi likely owes to it being a large and diverse clade, with phytosaurs being more basal, representing an older radiation, than crocodyliforms (Nesbitt, 2011). Regardless of what ecological selection pressures may be associated with rostral elongation, it is likely that members within clades consistently attain this trait.

In general, rostral elongation is viewed as an adaptation for both semi- and fully aquatic taxa feeding on aquatic prey. The associated increases in the out-lever distance (distance from jaw joint to bite point) results in greater relative jaw closing speed (Sakamoto, 2010; Ballell et al., 2019; Evans et al., 2019), which is a desirable trait when feeding on highly mobile aquatic prey (Massare, 1988; McCurry et al., 2017). However, species engaging with such a feeding ecology are subjected to the mechanical pressures of feeding in a dense fluid medium that restricts viable morphospace (Massare, 1988; Pierce et al., 2008). This combines with fewer modalities of feeding available to large-bodied marine organisms (Taylor, 1987) leading to convergence in skull shape (figure 2).

The observed rostral elongation may serve different purposes in the different clades represented in cluster A. In *Spinosaurus*, this may suggest further adaptation for a “stand-and-wait” predation strategy seen in herons and storks (Kushlan, 1976; Willard, 1977; Maheswaran and Rahmani, 2002). An increased distance between the tip of the rostrum and nares allows for a greater portion of the skull to remain submerged without restricting breathing, potentially increasing foraging efficiency as proposed under the ‘shallow water wading’ hypothesis (Hone and Holtz, 2021). In marine mosasaurs and pliosauroid plesiosaurs, rostral elongation is present but not as extreme, especially in plesiosauroid plesiosaurs (supplementary material). In these taxa, nares that are positioned closer to the dorsal margin of the head may have assisted with minimising the portion of the body exposed when surfacing for breath.

The variables investigated here -in particular, the position of the nares relative to the anterior margin of the skull- are largely able to discriminate between taxa that feed terrestrially and those that feed on aquatic prey (figure 1a, 2). However, due to similar biomechanical restrictions, taxa that feed on aquatic prey show substantial skull shape convergence with fully aquatic taxa which prevents definitive categorisation of taxa with uncertain ecology (such as *Spinosaurus*), based on linear measurement of the skull alone. Further investigations may wish to consider post-cranial data, phylogenetic analyses and dentition, as well as feeding guilds as a categorisation factor. The data we have gathered is not sufficient to completely evaluate the utility of size-adjusted linear measurements of the cranium, but functions as an exploratory study which provides a framework for future studies to develop this line of enquiry. Specifically, we emphasise the importance of comparing supervised and unsupervised clustering to assess if the former is appropriate.

Acknowledgements:

This research was funded by the University of Lincoln’s Undergraduate Researcher Opportunity Scheme (UROS).

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Figure 1

Principal component analysis of 6 size-adjusted linear (Mosimann) variables in 95 representative taxa across 8 sauropsid clades (Squamata and Crurotarsi further divided based on ecology).

(a) Distribution of taxa in morphospace of principle component (PC) 1 (48.06% of variance) and PC2 (30.10% of variance). Convex hulls delimit K-means (k=3) cluster groupings. Green markers indicate terrestrial ecology, light blue markers indicate a semi-aquatic ecology, dark blue markers represent a fully aquatic ecology, and orange and red represent unknown ecologies. Silhouettes of taxa highlight the naris (blue) and the orbit (green). **(b)** Measurements were taken from the skull in lateral view. Skull height (SH), skull length (SL), distance from naris to anterior margin (NA), distance from naris to dorsal margin (ND), and distance from orbit to dorsal margin (OD). Not pictured: skull width (taken from dorsal view). Modified from (Hone and Holtz 2021). **(c)** Comparison of skull morphology between *Spinosaurus sp.* (top, modified from (Ibrahim et al 2014)) and *Pliosaurus kevani* (bottom, modified from (Benson et al 2013)). *Allosaurus* and *Spinosaurus* by Tasman Dixon, *Varanus* by Steven Traver, *Goniopholis*, *Tylosaurus*, *Rhomaleosaurus*, and *Baryonyx* by Scott Hartman, and *Leptoptilos* by L. Shyamal.

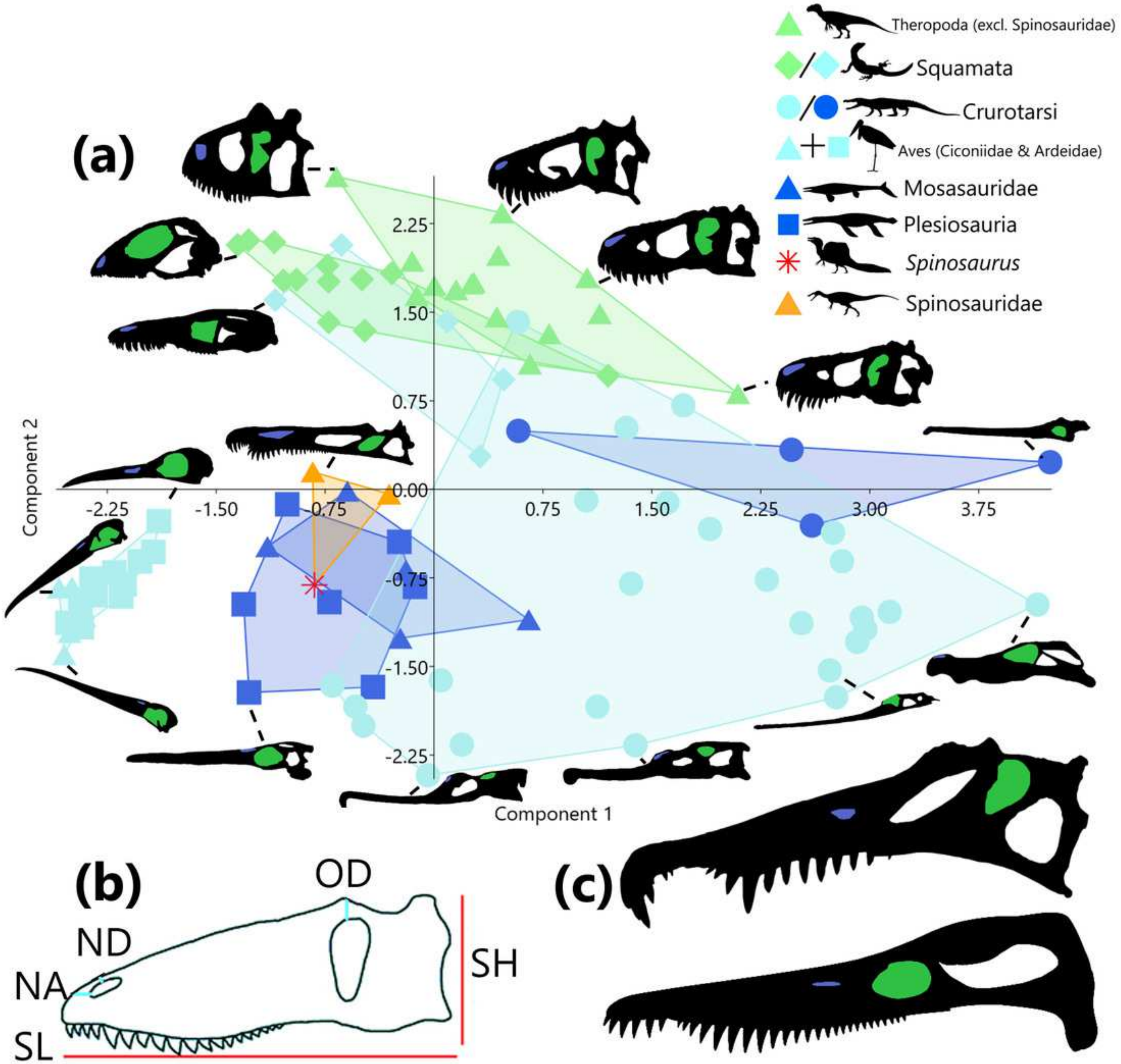
Theropoda (excl. Spinosauridae)
Squamata
Crurotarsi
Aves (Ciconiidae & Ardeidae)
Mosasauridae
Plesiosauria
Spinosaurus
Spinosauridae
(a)
Component 2
Component 1
2.25
1.50
0.75
0.00
-0.75
-1.50
-2.25
-2.25
-1.50
-0.75
0.75
1.50
2.25
3.00
3.75
(b)
OD
ND
NA
SH
SL
(c)

Figure 2

Morphospace plot of principal component scores as in figure 1, showing instead unsupervised cluster analysis groupings.