Reconstructing incomplete fossil reptilian skulls where much of the skull is missing: a preliminary investigation using ratios and rhynchocephalians.

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Introduction

The fossil record is notoriously incomplete; many fossil taxa are known from only a scarce few bones and complete skulls are a rarity. Reconstructing a skull where most of the material is missing is normally left to the interpretation of the researcher and is therefore susceptible to human bias, especially if the taxon has few or no living relatives. Rhynchocephalians (a group of lizard-like reptiles) are represented in the fossil record throughout the Mesozoic, but today are represented by a single living species, and much of their fossil material is very incomplete. Here, in this preliminary pilot study, we investigate the use of ratios of linear measurements of the skulls of rhynchocephalians as a means of predicting the dimensions of markedly incomplete rhynchocephalian skull material.

Summary

- Significant correlation was found between a number of linear ratios for the skulls of rhynchocephalians (Fig. 1, 2, 3), demonstrating there is some predictability in skull shape based on these measurements. However, the linear models generally show only moderate R^2 values, demonstrating there is fair amount of variance in the data.
- In a test case on *Sphenodon* (Fig. 4), we found that rhynchocephalian skull shape is reasonably predictable based on our linear models.
- It's best to use complete skulls where possible, but comparisons with closely related taxa can plug gaps in reconstructions.
- In future work, we need to make such numerical comparisons for other clades before we can assume similar relationships exist outside of Rhynchocephalia.

Methods

We took linear measurements to calculate the ratios for 14 variables (Fig. 1, 2) from the skulls and cranial material of 22 rhynchocephalian taxa where, at minimum, images of the complete maxilla or dentary were available in the literature. Measurements were taken as ratios to eliminate scaling as a factor. The 14 variable sets were then examined to identify and eliminate outliers, and check for normality in their distribution in SPSS v. 26 (IBM Corporation). The skulls for the aquatic *Pleurosaurus* (e.g. Dupret 2004) were excluded due to their unusually elongated morphology. The 14 variables were then tested for significant correlation using Pearson's correlation in RStudio v. 4.0.2 (R Core Team), and linear prediction models were then taken as the line of best fit in Excel (Microsoft Office).

Pearson's Correlation Coefficient (r)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1														
2														
3	-0.7													
4														
5			-0.67											
6				0.84										
7	0.55	0.6		0.76		0.56								
8				-0.64		-0.63								
9					0.75									
10				0.6										
11						0.77	0.82	-0.57		0.77				
12						0.79	0.82	-0.57		0.79				
13						0.83	0.81	-0.64		0.83				
14	0.74		-0.75											

***p*-value**

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1														
2														
3	0.003													
4														
5			0.008											
6				<0.001										
7	0.033	0.019		0.001		0.028								
8				0.004		0.006								
9					<0.001									
10				<0.001										
11						<0.001	<0.001	0.013		<0.001				
12						<0.001	<0.001	0.018		<0.001				
13						<0.001	<0.001	0.005		<0.001				
14	<0.001		<0.001											

1	Skull width by length (where width is measured a jugal/maxillary joint)	8	Pre-orbital by post-orbital length of skull
2	Skull height by length (where height is measured at the coronoid region)	9	Length of retroarticular compared to total mandible length
3	Skull height by width	10	Pre-coronoid length by post-coronoid length of mandible (up to the articular joint)
4	Height of coronoid process divided by length of complete mandible	11	Height of coronoid process by length of mandible (up to the articular joint)
5	Outlever (articular joint to retroarticular) by length of inlever (dentary to articular joint)	12	Height of coronoid process by length of dentary
6	Pre coronoid length by post coronoid length of mandible	13	Height of coronoid process by length of pre coronoid region of dentary
7	Maxillary height by maxillary length	14	Orbit length by total skull length

Figure 1: Matrix of the Pearson's correlation coefficients (top) and the corresponding significant *p*-values (bottom) for the analyses of the ratio variables. Cells highlighted in green are significant values, grey cells are non-significant, red cells are non-independent values, and black cells are replicates.

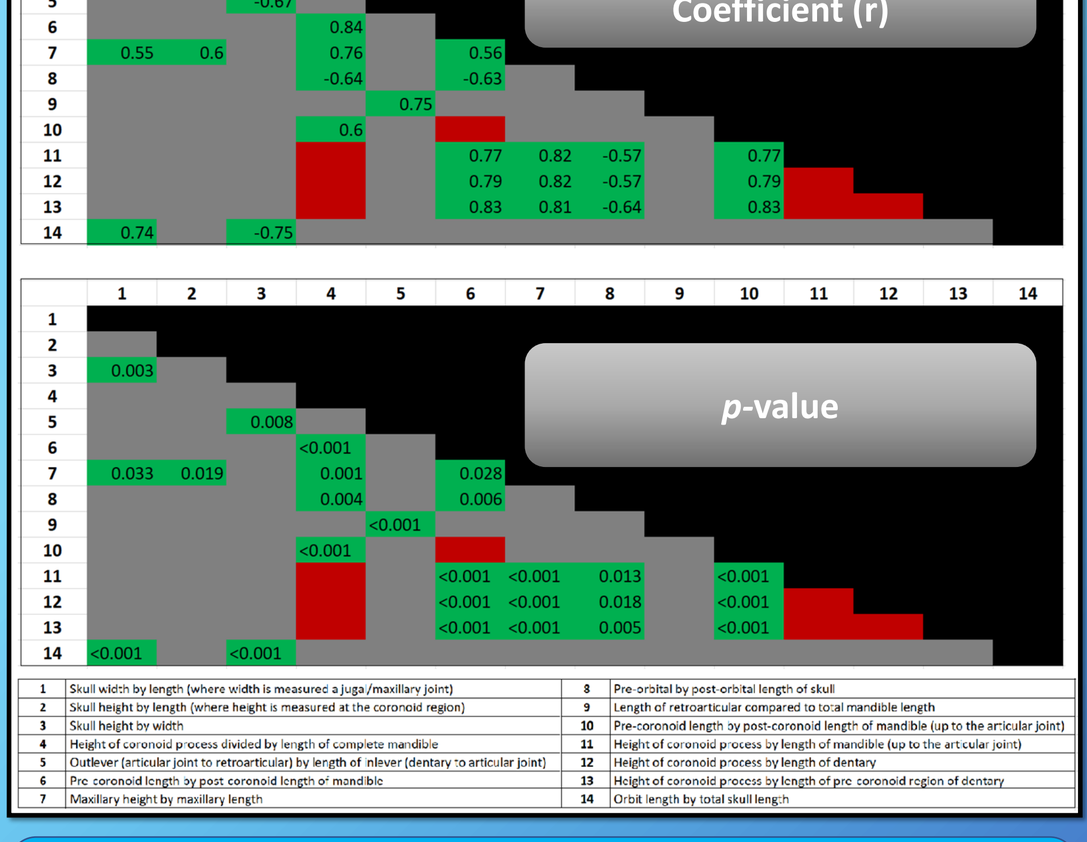
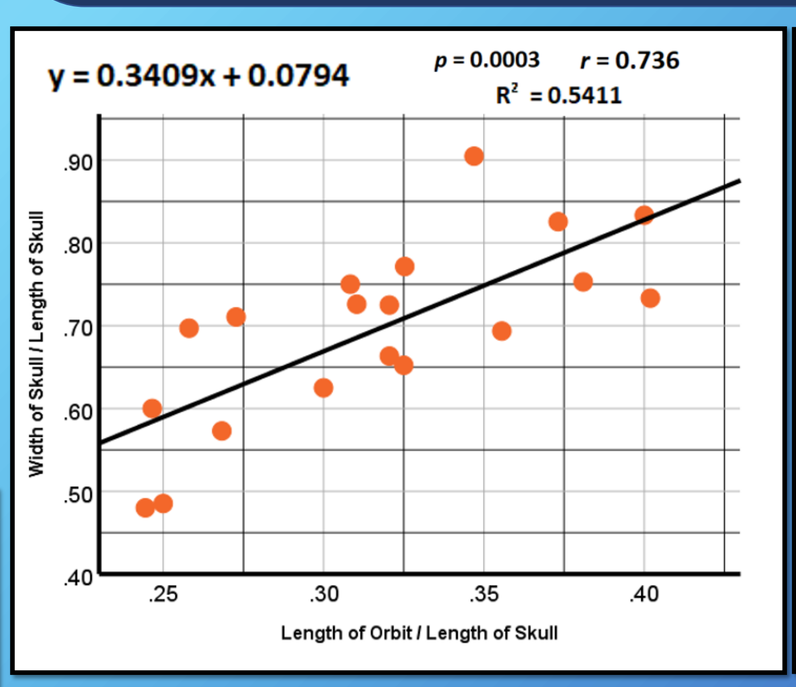


Figure 2: The linear measurements used for calculating the ratio variables, demonstrated here on the skull of *Sphenodon punctatus* (skull available online, Maisano 2001).



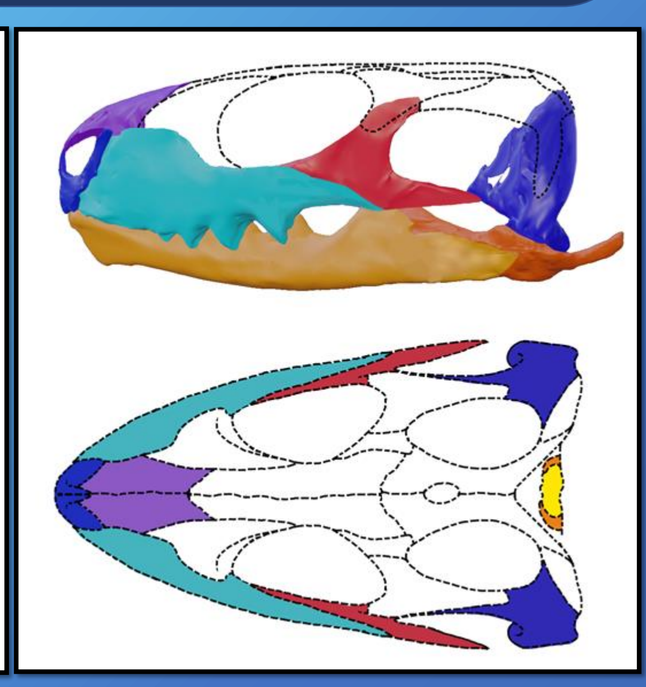
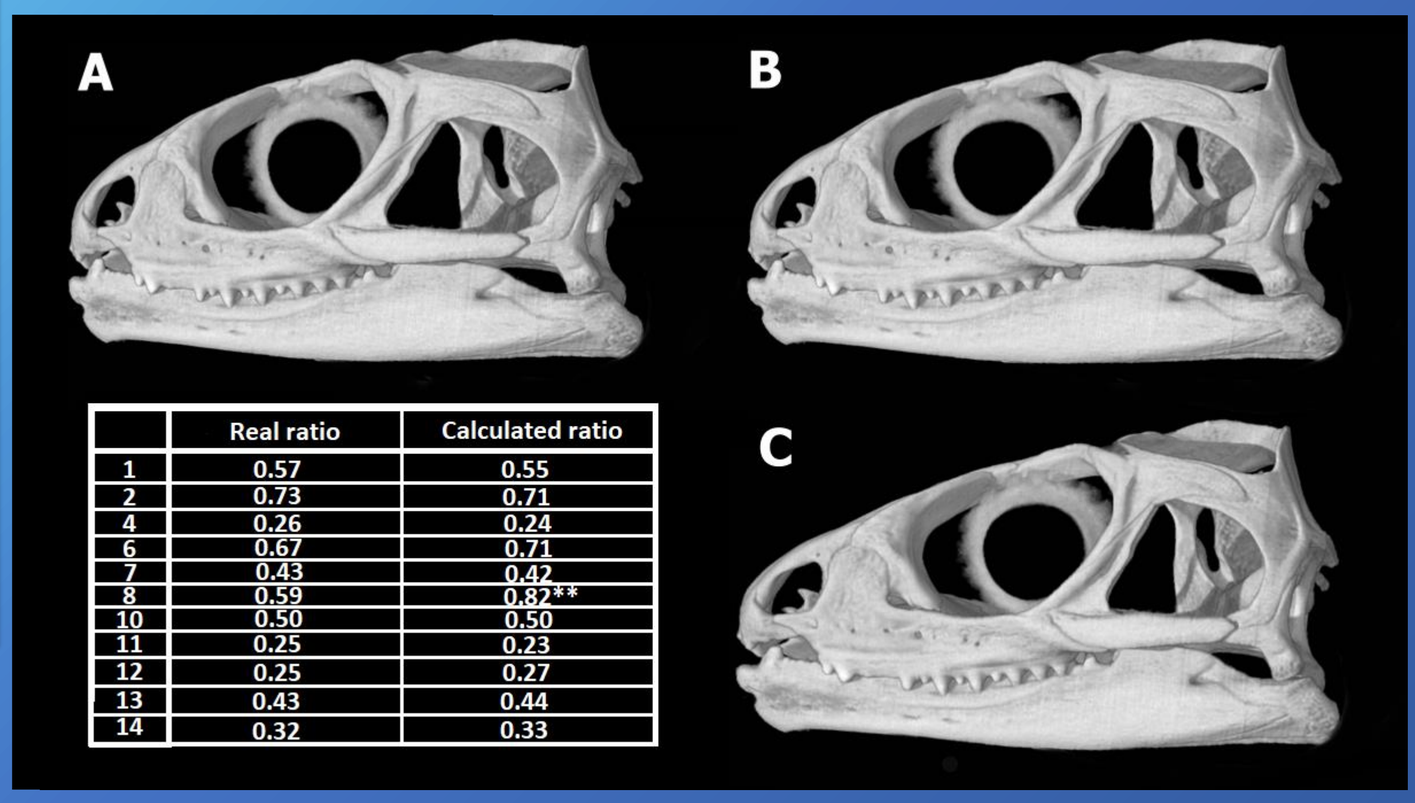


Figure 3: Left, the linear model for the ratio variable "skull length by width (1)" vs. "orbit length relative to skull length (14)". Right, the reconstruction of the skull of *Clevosaurus sectumsemper* using these methods. Uncoloured elements are bones not known from the fossil record for this taxon.



	Real ratio	Calculated ratio
1	0.57	0.55
2	0.73	0.71
4	0.26	0.24
6	0.67	0.71
7	0.43	0.42
8	0.59	0.82**
10	0.50	0.50
11	0.25	0.23
12	0.25	0.27
13	0.43	0.44
14	0.32	0.33

Figure 4: Reconstruction methods applied to *Sphenodon punctatus*. (A) Original *Sphenodon* skull, (B) reconstruction based on linear models excluding variable 8, (C) incorrect reconstruction based on linear models including variable 8. **See results for possible explanation for variable 8.

Results and Discussion

Significant correlation was found between a number of the ratio variables (Fig. 1, 2), for example, there is positive correlation between variable 1 and 14 (Fig. 3); in other words, rhynchocephalians with wider skulls tend to have larger eyes. These linear ratios offer some predictability for cranial dimensions where much of the skull is missing (Fig. 3). However, there is also a lot of variance in the data (R^2 = 0.30-0.87), and the sample size is relatively small (n = 22). To help validate the linear models, we also calculated the cranial dimensions for *Sphenodon* (Fig. 4) using just the maxilla and dentary (as in *Clevosaurus sectumsemper*, Fig.3), and found that all calculated values in this case (excl. variable 8) were a close match, differing by no more than 0.04 from the real values. We believe that variable 8 is problematic because a longer snout it is linked to a relatively low coronoid process within the data-set, *Sphenodon* being unusual in that it possesses a relatively low coronoid process compared to most short-snouted rhynchocephalians. Future investigation into the application of these methods using extant true lizards (Squamata), for which there is the CT scans of hundreds of complete skulls freely available at sources such as Digimorph, DataDryad and MorphoBank, could prove fruitful. When using these linear models to calculate the measurements for a fossil taxon, we recommend that the bones are from the same specimen if possible, and to prioritise measurements calculated from models with higher R^2 values. Additionally, while it has not been tested yet, it is assumed that basing calculations on calculated values will become increasingly inaccurate, and it is best to rely on the primary calculations where possible.

References

1. DUPRET, V. 2004. The pleurosaurs: anatomy and phylogeny. *Revue de Paléobiologie, Genève*, 9: pp. 61-80.
2. MAISANO, J. 2001. "Sphenodon punctatus" (On-line), Digital Morphology. Accessed April 22, 2020 at http://digimorph.org/specimens/Sphenodon_punctatus/adult/.