EVOLUTIONARY RELATIONSHIPS OF ATOPOSAURID CROCODYLIFORMS AND EVIDENCE FOR ALLOPATRIC SPECIATION DRIVING THEIR HIGH DIVERSITY IN THE LATE JURASSIC OF EUROPE

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1. INTRODUCTION

Atoposaurids comprise a clade of small-bodied terrestrial and semi-aquatic crocodyliforms. They were an important component of Late Jurassic and Early Cretaceous European ecosystems, with less common occurrences extending their known stratigraphic range from the Middle Jurassic to the end Cretaceous (Fig. 1). Despite a range of recent discoveries, there is currently little taxonomic consensus for atoposaurid inter-relationships. Most of these genera are multispecific, with *Theriosuchus* having five currently accepted species spanning some 80 million years. Several additional putative atoposaurid taxa, if valid, would extend their range into the Late Jurassic of Asia, and the Early Cretaceous of North America and Africa.

Figure 2. The newly re-ranked species, *Alligatorellus bavaricus* from the lower Tithonian of Germany [1].

Figure 1. Stratigraphic and geographic distribution of known and putative atoposaurid species. Modified from [1].

3. PHYLOGENETIC ANALYSIS

A new matrix was built comprising 7 outgroup and 13 ingroup taxa, and 352 characters. This dataset was analysed in TNT v. 1.1, resulting in 3 MPTs with a length of 654 steps. The strict consensus tree was timescaled in the R package *strap* using the 'equal' method (Fig. 5).

4. RESULTS

All *Theriosuchus* species form a clade including *Wannchampsus*, recently named as a paralligatorid [2]. This suggests that either *Wannchampsus* should be referred to *Theriosuchus*, or there is greater diversity within this clade. Irrespective, this provides evidence for an Early Cretaceous atoposaurid radiation into both North America and Asia. Both *Alligatorellus* and *Atoposaurus* species group together, strengthening our arguments for their validity as separate genera.

5. CONCLUSIONS AND FUTURE RESEARCH

These results confirm the monophyly of Atoposauridae, and suggest that a taxonomic revision of *Theriosuchus* is required. Future research will require comparison with other small neosuchians, including bernissartiids, and incorporation of other putative atoposaurids such as *Brillanceausuchus* and *Karatausuchus*. Inclusion of these taxa should help to confirm the position of Atoposauridae within Neosuchia and stabilise the within-group relationships.

2. LATE JURASSIC EUROPEAN DIVERSITY

Taxonomic revision of western European atoposaurids leads us to recognise the existence of three closely related and sympatric genera in the Late Jurassic French and German basins, including the newly re-ranked species *Alligatorellus bavaricus* ([1] Fig. 2). This provides evidence for allopatric speciation, possibly driven by fluctuating highstand sea levels (Fig. 3). A principal components analysis of key morphometric characteristics, combined with unique anatomical features and primary indicators of ontogenetic age, shows that these genera cannot be conclusively demonstrated to be part of the same growth series, as previously suggested (Fig. 4).

Figure 3. (A) Geographic distribution of Late Jurassic atoposaurid localities. 1: Cerin; 2: Kelheim; 3: Painten; 4: Solnhofen; 5: Guimarota; 6: Andrs; 7: Langenberg; 8: Uppen. (B) Approximate palaeogeographic distribution of Late Jurassic atoposaurids. Map reconstruction from Ron Blakey, Colorado Plateau Geosystems, Arizona USA (<http://cpgeosystems.com/paleomaps.html>). [1]

Figure 4. PCA plot for 6 primary measurements: skull length, skull width, orbit length, ulna length, femur length and tibia length. Modified from [1].

Figure 5. Time-calibrated strict consensus tree. Atoposauridae is marked by a red star.

[1] Tennant, J. P. and Mannion, P. D. (2014) Revision of the Late Jurassic crocodyliform *Alligatorellus*, and evidence for allopatric speciation driving high diversity in western European atoposaurids, *PeerJ*, **2**e599

[2] Adams, T. L. (2014) Small crocodyliform from the Lower Cretaceous (Late Aptian) of central Texas and its systematic relationship to the evolution of Eusuchia, *Journal of Paleontology*, **88**, 1031-1049