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Are the dinosauromorph femora from the Upper Triassic of Hayden Quarry (New Mexico) three stages in a growth series of a single taxon?

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ABSTRACT

The lagerpetid *Dromomeron romeri* and the theropod *Tawa hallae* are two dinosauromorphs from the Norian (Upper Triassic) of the Chinle Formation, situated in New Mexico, USA. However, a recent study suggests the inclusion of the holotype of *D. romeri* (GR 218) and paratype (GR 155) and referred (GR 235) specimens of *T. hallae* in an ontogenetic series of a single species. The specimens GR 218 and GR 155 include just an isolated femur, while GR235 includes femora, pelvis and tail. The inclusion of the specimens in an unique ontogenetic series relies on the putative immature condition and plastic deformation of the specimen GR 218. However, as observed here, the disparity between the femora of *D. romeri* and *T. hallae* is considerably higher than those expected from the ontogenetic variance in dinosauromorphs. In addition, *D. romeri* shares an unique suite of traits with *Dromomeron gigas*, a species known from a mature specimen. Therefore, the high disparity between *D. romeri* and *T. hallae*, lack of traits shared solely between the three femora, and a suite of traits shared between *D. romeri* and *D. gigas*, precludes the inclusion of the three femora from Hayden Quarry in a growth series of a single taxon.

Key words: Chinle Formation, Dinosauria, Dinosauriformes, Lagerpetidae, Norian, ontogeny.

INTRODUCTION

The Hayden Quarry (HQ) fossiliferous locality is situated in New Mexico, USA. This locality is dated as Norian in age and is in the lower portion of the Petrified Forest Member of the Upper Triassic Chinle Formation (Irmis et al. 2007). The HQ has yielded an impressive fossil record of early dinosaurs and dinosaur relatives (Irmis et al. 2007, Nesbitt et al. 2009a), including the lagerpetid *Dromomeron romeri* (Irmis et al. 2007) and the theropod *Tawa hallae* (Nesbitt et al. 2009a). However, Bennett (2015) suggests the inclusion of the holotype of *D. romeri* (specimen GR 218) and paratype (GR 155) and referred (GR 235) specimens of *T. hallae* in an ontogenetic series of a single species. The specimens GR 218 and GR 155 are composed by one isolated femora each, while GR235 includes femora, pelvis and tail (Nesbitt et al. 2009a).

According to Bennett (2015), several morphological traces of GR 218 are related to incomplete ossification and plastic deformation,

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leading to taxonomic misidentifications. Indeed, several studies have demonstrated the influence of ontogeny on the femoral anatomy of dinosauromorphs (e.g. Nesbitt et al. 2009b, Piechowski et al. 2014, Griffin and Nesbitt 2016). However, there are features on the holotype of *D. romeri* that casts doubt on the inclusion of the specimen in an ontogenetic series with the other two femora. In addition, Bennett (2015) does not suggest any morphological features shared solely by the three femora (GR 218, GR 155, GR 235) among dinosauromophs. Therefore, in order to evaluate the validity of Bennett's proposal, the disparity between the femora of *D. romeri* and *T. hallae* is compared with those produced from ontogenetic variance in other dinosauromorphs. In addition, some comments are included following recent discoveries regarding lagerpetids.

INSTITUTIONAL ABBREVIATIONS

GR, Ruth Hall Museum of Paleontology, Ghost Ranch, New Mexico, USA; **PVSJ**, Instituto y Museo de Ciencias Naturales, San Juan, Argentina; **TMM**, Vertebrate Paleontology Laboratory, Texas, USA; **WTAMU**, West Texas A&M University, Texas, USA; **ZPAL**, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

MATERIALS AND METHODS

The disparity between *D. romeri* and *T. hallae* femora was calculated from the morphological data matrix of Martínez et al. (2016), which is a modified version of the data matrix presented by Nesbitt (2011). The data matrix of Martínez et al. (2016) includes 293 morphological characters, among them, 27 are femoral characters. The percentage of codification differences of femoral characters was quantified and compared to disparity between small and large individuals of *Dromomeron gregorii* (Nesbitt et al. 2009) and *Silesaurus opolensis* (Dzik 2003). The femoral ontogeny of both species was studied by Nesbitt et al. (2009b) and Piechowski et al. (2014), respectively. Therefore, the polarization of small individuals of both species follows these studies and the external morphology of TMM-31100-764 and TMM-31100-1234 to *D. gregorii* and ZPAL AbIII/457L to *S. opolensis*. The codifications for the specimens are in the Table I.

RESULTS AND DISCUSSION

The polarization of femoral characters of small and large individuals of *D. gregorii* in the data matrix of Martínez et al. (2016) reveals a total of 16% of difference between them (Fig. 1b). This corresponds to 4 of the 25 comparable characters. The polarization of small and large individuals of *S. opolensis* results in 13% of difference (3 of the 23 comparable characters) (Fig. 1c). On the other hand, the comparison between the femora of *D. romeri* and *T. hallae* is significantly higher, revealing a total of 65% of difference (Fig. 1a). Such percentage corresponds to 17 of the 26 comparable characters. This represents about four times the difference from the ontogenetic series of *D. gregorii*. Therefore, the disparity between *D. romeri* and *T. hallae* is considerably higher than those expected from the ontogenetic variance in dinosauromorphs. Even if the morphology of the femoral head of GR 218 is a taphonomic artifact (Bennett 2015), other femoral portions are quite distinct from *T. hallae*, especially the distal end (Fig. 2).

The 98 mm long femur of *D. romeri* (GR 218) is ascribed to an immature individual by Bennett (2015) due the incompletely ossified epiphyses. Indeed, the close related taxa are larger than GR 218, for instance, *D. gregorii* reaches 127 mm in length, while *Dromomeron gigas* (Martínez et al. 2016) has approximately 190 mm (PVSJ 898). According to Bennett (2015), the ontogenetic state of the distal end of GR 218 explains various differences from other better ossified dinosauromorph femora that

TABLE I
Codification for the specimens evaluated in the disparity quantification of the 27 femoral characters of Martínez et al. (2016).

Character number	*T. hallae*	*D. romeri*	*D. gregorii* (large)	*D. gregorii* (small)	*S. opolensis* (large)	*S. opolensis* (small)
203	2	1	1	1	1	1
204	0	1	1	1	2	0
205	0	1	1	0	0	0
206	0	0	0	0	1	1
207	2	0	0	0	1	1
208	2	1	1	1	1	1
209	0	1	?	?	0	0
210	1	0	0	0	2	1
211	1	0	1	0	1	1
212	0	0	0	0	1	1
213	0	1	1	1	0	0
214	0	0	1	0	1	0
215	1	1	1	1	0	0
216	2	0	0	0	1	1
217	1	2	0	0	0	0
218	0	?	0	0	0	0
219	0	0	0	0	0	0
220	1	1	1	1	1	1
221	1	1	1	1	0	0
222	1	1	1	?	1	?
223	0	0	0	0	1	1
224	0	1	1	1	0	0
225	0	1	1	1	0	0
226	0	1	1	1	0	0
291	0	1	0	0	0	0
292	0	1	0	0	0	0
293	0	1	1	0	0	0

were cited as diagnostic characters to *D. romeri* by Irmis et al. (2007). However, the recently described 190 mm long femur of *D. gigas* shares these peculiar differences and has no indicative of immaturity. On the contrary, *D. gigas* is the largest lagerpetid ever found and also bears several muscle scars (Martínez et al. 2016), an indicative of maturity (Griffin and Nesbitt 2016). Indeed, as pointed by Martínez et al. (2016), *D. gigas* and *D. romeri* share an unique suite of traits, including a sharp ridge on the craniomedial end of the femur (Fig. 2a-c) and a lateral tuberosity on the craniolateral of the distal end of the femur. Until the description of *D. gigas*, these features were restricted to *D. romeri*. The another factor erected by Bennett (2015) as responsible by the form of GR 218 is plastic deformation. However, Sarigül (2016) described a fragmentary right femur (WTAMU-V-8301 - Fig. 2d) referred to *D. romeri* which shares the same morphology of GR 218. Thus, GR 218, WTAMU-V-8301, and

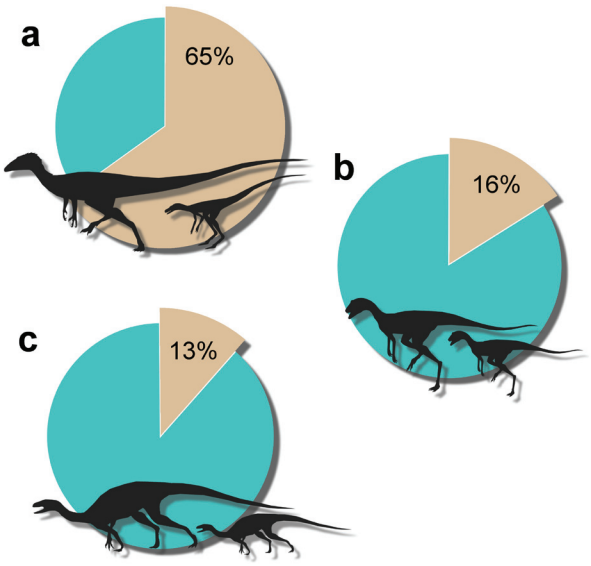

Figure 1 - Percentage of codification differences of femoral characters. **a**, difference between *Dromomeron romeri* and *Tawa hallae*; **b**, difference between small and large specimens of *Dromomeron gregorii*; **c**, difference between small and large specimens of *Silesaurus opolensis*.

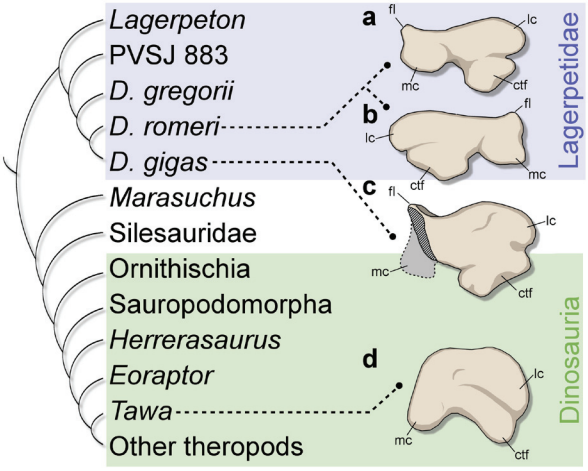

Figure 2 - Simplified phylogenetic relationships of basal dinosauromorphs based on a data set of Martínez et al. (2016) depicting position of lagerpetids and *Tawa hallae*. **a**, femur of GR 218 in distal view; **b**, femur of WTAMU-V-8301 in distal view; **c**, femur of PVSJ 898 in distal view; **d**, femur of GR 244 in distal view. Abbreviations: ctf, crista tibiofibularis; fl, flange; lc, lateral condyle; mc, medial condyle. Images not to scale.

PVSJ 898 shares a quite peculiar suite of traits, which suggests taphonomic deformation as an implausible hypothesis to explain the morphology of GR 218. Therefore, plastic deformation, as well as incomplete ossification, apparently have no significant effect on the shape of GR 218.

In conclusion, (i) the high disparity between *D. romeri* and *T. hallae*, (ii) lack of traits shared solely between the three femora (GR 218, GR 155, and GR 235), and (iii) a suite of traits shared between *D. romeri* and *D. gigas*, precludes the inclusion of the three femora from Hayden Quarry in a growth series of a single taxon.

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