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Original article

Biogenic control on the origin of a vertebrate monotypic accumulation from the Late Triassic of southern Brazil☆

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ABSTRACT

This study is a taphonomic investigation of a new Late Triassic monotypic association from the *Hyperodapedon* Assemblage Zone (Santa Maria Formation, southern Brazil). All skeletal elements belong to the traversodontid cynodont *Exaeretodon*, representing a minimum of four individuals from different ontogenetic stages. Biogenic traces are identifiable on some elements, such as invertebrate scavenging traces, vertebrate bite marks, and evidence of trampling which was probably responsible for accelerating the disarticulation of upper postcanine teeth and for fracturing a skull and a lower jaw. We classify this accumulation as generated by extrinsic biogenic action (predation/necrophagy and possibly trampling) due to the following reasons: (i) random spatial orientation of the elements enclosed into the matrix; (ii) absence of hydraulic equivalence among the specimens and presence of mudstone lenses in close association with the fossils; (iii) presence of nearly all Voorhies' groups; (iv) association of a large number of cranial elements presenting different stages of disarticulation; and (v) presence of biogenic traces. Both disarticulation patterns and invertebrate scavenging traces indicate that the bones remained exposed for some time before burial. During this time of exposure, carnivore vertebrates also scavenged on some nutritive and transportable postcranial elements. We suggest an ecteniniid cynodont as a potential modifier agent (predation/necrophagy) of this particular monotypic accumulation of synapsids.

1. Introduction

Sedimentary strata from the Santa Maria Formation (Middle/Upper Triassic of southern Brazil) provide a rich and important vertebrate fossil fauna (Langer et al., 2007). Although well studied in taxonomic terms, their vertebrate accumulations still need detailed taphonomic and paleoecological investigations (Holz and Barberena, 1989; Bertoni-Machado et al., 2008). Among the already published taphonomic investigations, those by Holz and Barberena (1994), Holz and Schultz (1998), Holz and Souto-Ribeiro (2000), Reichel et al. (2005), Bertoni-Machado and Holz (2006), Bertoni-Machado et al. (2008), and França et al. (2011) marked the beginning of vertebrate taphonomy in Brazil, shedding light on the genesis of fossil accumulations from the Santa Maria Fm. Furthermore, these analyses unveiled the fossilization processes that altered the quality of this important fossiliferous Triassic unit.

The Santa Maria Fm. yields some monotypic fossil accumulations whose taphonomy was recently investigated. Bertoni-Machado et al. (2008) evaluated a Ladinian monotypic occurrence of the genus *Massetognathus* and ascribed its genesis to the bone sorting produced by predators/scavengers. França et al. (2011) analyzed the origin of a rauisuchid monotypic concentration from Ladinian strata of the Santa Maria Fm. and interpreted it as the result of short-distance hydraulic transport. Other cases still under study involve recently found associations of juvenile individuals ascribed to the dicynodont *Dinodontosaurus* (Ugalde et al., 2014). Here, we report a new monotypic concentration of vertebrates from the Santa Maria Fm. We performed a taphonomic analysis in order to track the possible factors that controlled its genesis and to provide paleontological information on this particular concentration of fossil vertebrates.

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2. Geological setting

The rocks from the Santa Maria Fm. (*sensu* Andreis et al., 1980) belong to the Gondwana II Supersequence of the Paraná Basin as erected by Milani (1997). The fossiliferous locality from where this particular vertebrate accumulation was recovered is known as "Janner" outcrop (29°39′10.89″ S, 53°17′34.20″ W), located about 2 km from the Agudo town, central region of the Rio Grande do Sul State, southern Brazil (Cabreira et al., 2011; Fig. 1). Zerfass et al. (2003) divided the Triassic Ladinian-Raethian interval from Rio Grande do Sul in three depositional sequences: Santa Maria 1 (Ladinian), Santa Maria 2 (Carnian-Norian), and Santa Maria 3 (Raethian). The "Janner" outcrop belongs to the Santa Maria 2 Sequence (= Candelária Sequence of Horn et al., 2014), which comprises non-laminated to finely laminated reddish mudstones with some sandy inclusions (Zerfass et al., 2003). Fonseca (1999) interpreted these deposits as a fluvial system with channels that range from stable to sinuous, where the siltstones represent floodplains and the sandy lenses characterize fluvial channels. The present material comes from about 8 m high from the reddish mudstone of the outcrop basis (Fig. 2), whereas in the upper levels the strata are composed of massive sandstones in which no fossil vertebrate has been reported so far.

The fossil record from the "Janner" outcrop is remarkable due to the extreme abundance of the cynodont traversodontid *Exaeretodon*, easily exceeding the record of the rhynchosaur *Hyperodapedon* (Liparini et al., 2013). The predominance of *Exaeretodon* in comparison to *Hyperodapedon* chronologically places this outcrop in the upper portion of the *Hyperodapedon* Assemblage Zone (Langer et al., 2007), which allows the correlation of the "Janner" outcrop with the fossil fauna from the Ischigualasto Formation of northwest Argentina. Such biostratigraphic correlation suggests a late Carnian age to the "Janner" outcrop, based on the radioisotopic dating by Martinez et al. (2011) of the Ischigualasto Formation.

Besides *Hyperodapedon* and *Exaeretodon* genera, the "Janner" outcrop yielded the carnivorous cynodont *Trucidocynodon riograndensis* (Oliveira et al., 2010), the early dinosaur *Pampadromaeus barberenai* (Cabreira et al., 2011; Müller et al., 2015), and two indeterminate dinosauriforms (Müller et al., 2014; Pretto et al., 2015). Its fossil vertebrates are usually well preserved, allowing a detailed observation of their bone surface. Yet, some specimens display a certain degree of sedimentary compression. Disarticulation varies from isolated elements (Müller et al., 2014, 2015) to partially complete but disarticulated skeletons (Cabreira et al., 2011), and in rare cases completely articulated skeletons (Oliveira et al., 2010). Remains of different taxa in association were also reported, e.g., a partially articulated *Exaeretodon* together with a few dinosaur elements (Oliveira et al., 2007; R.T.M. pers. obs.).

3. Material and methods

The material consists of an association of bone elements from different individuals accumulated in a small area of about 1 m^2 (Fig. 3(A, C)). A single block of rock matrix concentrates most elements (Fig. 3(A)). Additionally, two isolated small skulls were recovered, given the difficulty to access the excavation point. The specimens were submitted to mechanical preparation with electric percussive tools, chisels, needles and paintbrushes, following May et al. (1994). Their exact position in the matrix was documented with photographs during both fieldwork and laboratorial preparation. The specimens are housed at the Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia (São João do

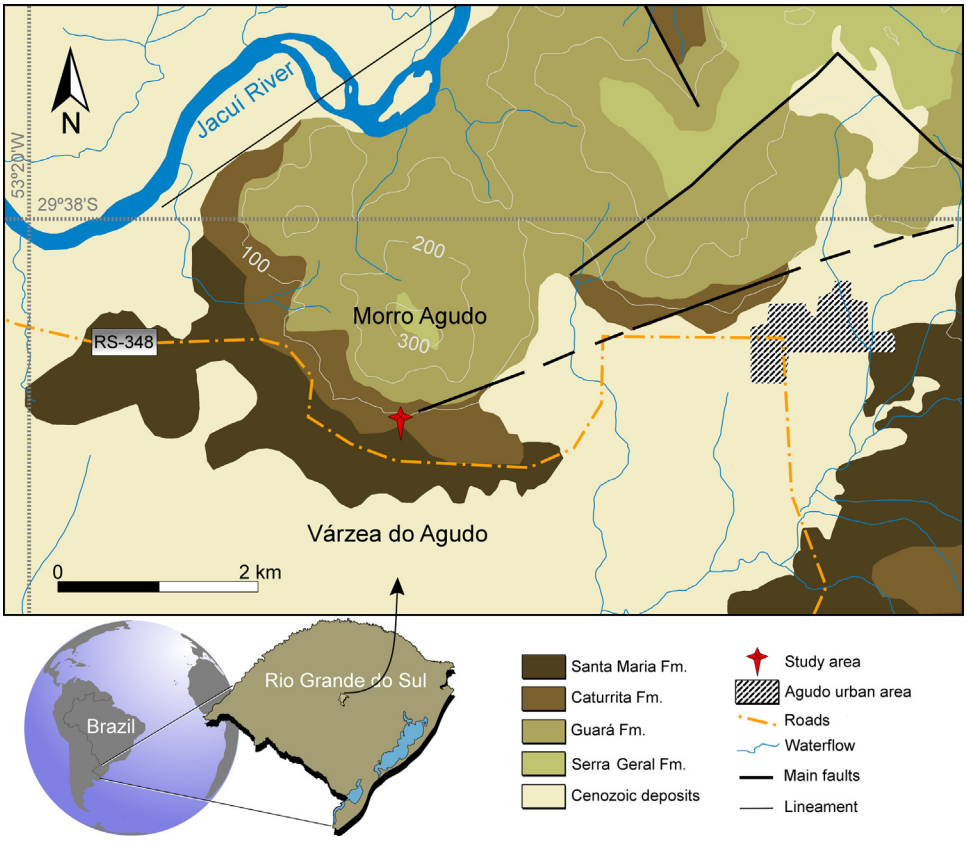

Fig. 1. Location map of the outcrop in southern Brazil. Modified from Zerfass et al., 2007.