Journal of South American Earth Sciences 79 (2017) 364–376

Contents lists available at ScienceDirect

Journal of South American Earth Sciences

journal homepage: www.elsevier.com/locate/jsames

First record of lobed trace fossils in Brazil's Upper Cretaceous paleosols: Rhizoliths or evidence of insects and their social behavior?

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ARTICLE INFO

Article history:
Received 7 June 2017
Received in revised form
17 August 2017
Accepted 19 August 2017
Available online 24 August 2017

Keywords:
Continental ichnology
Social insects
Marília Formation
Maastrichtian
Rhizoliths

ABSTRACT

This is the first report of trace fossils potentially associated with insect social behavior in sandy and well-drained paleosols of the Upper Cretaceous continental sequence of Brazil. The trace fossils consist of dozens of lobed and vertical structures cemented by $CaCO_3$ and preserved mainly in full relief in paleosols of the Marilia Formation (Bauru Basin) in the state of Minas Gerais. The described ichnofossils are predominantly vertical, up to 2 m long, and are composed of horizontal lobed structures connected by vertical tunnel-like structures that intersect in the center and at the edges. The lobed structures range from 3 to 15 cm long and 2–6 cm thick. Two different hypotheses are analyzed to explain the origin of the trace fossils; the less probable one is that the structures are laminar calcretes associated with rhizoliths and rhizoconcretions. The hypothesis involving social insects was considered because the trace fossils described herein partially resemble a modern ant nest and the ichnofossil *Daimoniobarax.* The micromorphological analysis of the lobed and tunnel-like structures indicates modifications of the walls, such as the presence of inorganic fluidized linings, dark linings and oriented grains, supporting the hypothesis that they are chambers and shafts. The architecture and size of the reported nests suggest the possibility that social insect colonies existed during the Maastrichtian and are direct evidence of the social behavior and reproductive strategies of the Cretaceous pedofauna.

1. Introduction

From a paleobiological point of view, trace fossils are direct evidence of the ethology of organisms from the past and are physical evidence of behavioral evolution, in addition to indicating the minimum age for the emergence of certain behaviors and adaptive structures, such specialized roots (Buatois and Mángano, 2011; Genise et al., 2016; Genise, 2017). This is very relevant, especially considering social insects, whose traces are rarely fossilized under conditions that reflect their social organization.

In this sense, paleosols provide us with a rare opportunity to study the reproduction strategies and diversification, as well the organization of social insects over time. They preserve the subterranean architecture of the nests and these fossil nests may be evidence of eusocial behavior available to study back in time (Genise, 2017).

The structures described in this work show great similarity to the ichnotaxon *Daimoniobarax* related to ant activity (Smith et al., 2011). Among arthropods, ants (Hymenoptera, Formicidae) present an evolutionary history of great success, occupy several niches and are fundamental to the maintenance of different ecosystems (Hölldobler and Wilson, 1990; Ward, 2006). Such success is directly related to eusociality, thus an understanding of this behavior over time is essential to comprehend how ants came to dominate terrestrial ecosystems from the mid-Cretaceous to the present (Hölldobler and Wilson, 2009; Ward, 2006; Barden and Grimaldi, 2016).

Although records indicate that the oldest ants appeared in the fossil record 100 million years ago (LaPolla et al., 2013), ichnological records associated with ant activity are scarce, being reliably recorded from the Lower Paleogene (Table 1). For older periods, nests described as having social insects as their tracemakers often lack the macromorphological and microstructural features

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http://dx.doi.org/10.1016/j.jsames.2017.08.016
0895-9811/

Table 1
Ichnofossils associated with ant activity from the Paleogene to the Quaternary. The ichnofossils described for the Cretaceous may be associated with other social insects, but may also indicate eusocial behavior.

Ant nest trace fossil records				
Age	Formation name (age)	Locality	Ichnofossils	Source
Quaternary	Sopas Formation (Late Pleistocene)	Uruguay	Daimoniobarax	Verde et al. (2016)
Neogene	Ogalla Formation (Pliocene)	Kansas, USA	*Daimoniobarax*	Smith et al. (2011)
	Pawnee Creek Formation (Miocene)	Colorado, USA	*Parowanichnus*	Hembree and Hasiotis (2008)
	San Andres Formation (Plio-Pleistocene)	Buenos Aires, Argentina	*Barberichnus*	Laza (1995)
	Cerro Azul Formation (Miocene)	La Pampa Province, Argentina	*Attaichnus*	Laza (1982)
Paleogene	Maız Gordo Formation (Lower Paleogene)	Argentina	*Krausichnus*	Genise et al. (2016)
	Asencio Formation (Paleogene/Early Eocene)	Uruguay	*Krausichnus*	Verde et al. (2016)
	Claron Formation (Paleocene-Eocene)	Markagunt Plateau, Utah	*Parowanichnus*	Bown et al. (1997)
Cretaceous	Chubut Group	Patagonia, Argentina	–	Genise et al. (2010a,b)
	Kaiparowits Formation	Utah, USA	*Socialites tumulus*	Roberts and Tapanila (2006)

necessary for ichnotaxonomic identification and classification.

Another complication is related to rhizoliths, which can show complex shapes (Cramer and Hawkins, 2009; Alonso-Zarza and Wright, 2010) similar to insect nests, roots or insect activities. Therefore, analyses of these structures must involve macro- and micromorphological characterizations and consider all possibilities for their origins.

Thus, despite the highlighted difficulties, the aims of this study are to (1) describe the morphology of the trace fossils, (2) discuss their paleoecological and paleoenvironmental significance, and (3) evaluate the probability of these ichnofossils being evidence of the social behavior of insects during the Cretaceous.

Therefore, the main objective this work is to describe and interpret the trace fossils present in the Marília Formation, since this material provides one of the rare opportunities in which such complex ichnofossils might be the first direct evidence of eusocial insect activity during the Upper Cretaceous in Brazil.

2. Geological setting

The trace fossils described here come from paleosols of the Marília Formation of Maastrichtian age (Cretaceous). They are located in the western portion of the state of Minas Gerais (MG), southeastern Brazil (Fig. 1A and B). These paleosols are part of the Bauru Basin, which originated after the fragmentation of the Gondwana paleocontinent and was filled during the Campanian-Maastrichtian (Batezelli, 2015).

More than 80% of the Marília Formation is constituted by paleosols developed in fluvial deposits interspersed with sandstones and conglomerates.

The depositional structures present are associated with river channels, lenticular sandbars, downstream accretion bars and floodplain elements, constituting amalgamated channel complexes interspersed with paleosols (Batezelli, 2015; Nascimento, 2017; Nascimento et al., 2017). Batezelli (2003); Batezelli (2015) interpreted this environment as an alluvial system dominated by braided rivers (*sensu* Stanistreet and McCarthy, 1993) that came from north/northeast to south/southwest from the Alto Paranaíba Uplift (SAP). The semi-arid climate of the Marília Formation is attested to by the occurrence of calcretes and clay minerals of the illite and palygorskite/sepiolite groups, suggesting a rainfall range between 500 and 1000 mm (Goudie, 1983; Wright and Tucker, 1991).

3. Materials and methods

The description of the ichnofossils and the included elaborations of sketches, drafts, and photographs for the documentation and dimensional characterization of the trace fossils were based on previous works by Bromley (1996), Smith et al. (2011) and Genise (2017). The morphological descriptions sought to emphasize the distribution, sizes, geometries, frequency, and orientation of the sedimentary facies, paleosols and other ichnological assemblages, as well as the superficial morphological characteristics, such as the cementation and filling of the chambers.

The systematic ichnology was based on the works of Bromley (1996) and Genise (2004, 2017) for the descriptions and identification of the ichnotaxobases, such as the shapes, types of walls, fillings and burrow system.

Micromorphological and microstructural analyses of trace fossils are necessary to identify the diagnostic characters related to soil modification. The description of thin sections thus followed the recommendations of Genise (2004, 2017) for the characterization of the chambers and shaft walls, as this is one of the main features used to identify tracemakers and to classify ichnofossils into ichnofamilies.

Paleosols were described as recommended by the Soil Survey Manual (Soil Survey Division Staff, 2014) and Retallack (2001), who emphasized the identification of horizons, color, presence of nodules, as well as bioturbation standards (rhizoliths and burrows). Micromorphological descriptions were performed with the help of a petrographic microscope following the methodology proposed by Stoops et al. (2010).

The major oxides present in the paleosol and trace fossils were determined by X-ray fluorescence spectrophotometry to quantify the percentage of CaO because one of the hypotheses of this work is that these trace fossils could be laminar calcretes with rhizoliths.

4. Results

The studied materials are preserved in a poorly developed paleosol composed of a massive C horizon inserted into a vertical section approximately 7 m high to the west of the city of Campina Verde at kilometer 159 of Highway BR-364 (Fig. 2A). Developed on fluvial deposits (sandstones and conglomerates), the paleosol profile is delimited by an erosive contact at the top (Fig. 2B and C), has reddish coloring (10R5/8) and ranges from 2 to 2.5 m thick. It is composed predominantly of quartz and subordinately by feldspar and mica grains. In thin section, the groundmass exhibits a chitonic c/f-related distribution (Fig. 3A), resulting in high porosity without any type of cementation. The fine fraction is made of speckled or undifferentiated b-fabric enveloping the grains or connecting them in the form of bridges (Fig. 3-B).

The b-fabric is composed of palygorskites (Fig. 3C and D), a common clay mineral in semi-arid modern environments (Khormali and Abtahi, 2003; Daoudi, 2004), where conditions of salinity and alkalinity promoted their formation *in situ* from the soil solution.