

Microbial mediation in invertebrate trace fossil preservation in Sousa Basin (Early Cretaceous), Brazil



Ismar de Souza Carvalho ^{a,*}, Leonardo Borghi ^a, Antonio Carlos Sequeira Fernandes ^b

^a Universidade Federal do Rio de Janeiro, Instituto de Geociências, Departamento de Geologia, Av. Athos da Silveira Ramos, 274, Cidade Universitária (Ilha do Fundão), 21.941-916, Rio de Janeiro, RJ, Brazil

^b Universidade Federal do Rio de Janeiro, Museu Nacional, Departamento de Geologia e Paleontologia, Rio de Janeiro, RJ, Brazil

ARTICLE INFO

Article history:

Received 22 May 2015

Received in revised form

13 June 2016

Accepted in revised form 17 June 2016

Available online 21 June 2016

Keywords:

Biofilms

Microbial mats

Invertebrate trace fossils

Sousa Basin

Cretaceous

ABSTRACT

Well-preserved invertebrate and vertebrate trace fossils commonly occur in reddish, fine to very fine-grained sandstone and mudstone bedsets of the Antenor Navarro and Sousa formations in the Sousa Basin, referring to an Early Cretaceous pull-apart basin in northeastern Brazil, related to the South Atlantic opening. Palaeoenvironments are understood as oxidizing terrestrial (alluvial fans and meandering rivers with extensive floodplains or perennial flooded areas), under hot and humid palaeoclimates punctuated by drought episodes. The ichnodiversity is low but trace fossils are abundant in the invertebrate ichnoassemblages analyzed in this paper. The ichnoassemblages are composed mainly of shallow endostratal traces. Repichnia and Fodinichnia behaviours are represented by *Aulichnites* isp., *Palaeophycus* isp., *?Arenicolites* isp., *Planolites* isp., *Taenidium* isp. and *Phycodes* isp. and are a taphonomic challenge in terms of their production and preservation, particularly considering its palaeoenvironment. Field observations and collected samples reveal common presence of microbially induced sedimentary structures associated to these traces. Biofilms and thin microbial mats seem to produce the adequate conditions of nutrient supply, moisture and substrate biostabilization to allow trace makers' survival and taphonomically enhance the preservation of the invertebrate trace fossils in an unstable and even sometimes inhospitable environment.

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1. Introduction

The preservation of invertebrate continental trace fossils has not been extensively evaluated, particularly the ones occurring in oxidizing, ephemeral, high to moderate energy fluvial and lacustrine systems. Usually, such trace fossil preservation is considered to be controlled by grain size, sediment consistency and humidity of the substrate, but not by its biosedimentological aspects. However, [Fernández and Pazos \(2013\)](#) showed that biostabilization by microbial mats and biofilms also play an important role in the preservation of such traces.

The Sousa Basin is well-known by its terrestrial trace fossils ([Leonardi, 1989](#); [Carvalho and Leonardi, 1992](#); [Carvalho, 2004](#)), along with exquisitely preserved primary sedimentary structures (such as ripple marks, raindrop imprints and mudcracks). [Carvalho et al. \(2013\)](#) stressed the importance of microbial mats and biofilms

for enhancing the preservation potential of vertebrate trace fossils (footprints and dinosaur tracks) at this basin.

Biofilms, as a way of substrate stabilisation, may entrap sedimentary grains by the interwoven cyanobacterial filaments, also protected by the mucous-rich cyanobacterial cover (EPS – Exopolysaccharide) against flowage frictional forces; or by its sealing through denser biofilm or microbial mat ([Noffke et al., 2001](#)).

This study describes epistratal invertebrate trace fossils in the Sousa Basin and points out to the role of biofilms or microbial mats in their preservation.

2. The Sousa Basin

Throughout most of the Early Cretaceous, South America was still connected to Africa as part of Gondwana. At that time in northeastern Brazil, an area of hundreds of square kilometers, with ephemeral to perennial rivers and shallow lakes constituted common palaeoenvironments.

The Sousa Basin ([Fig. 1](#)) is part of a wide sedimentary basin complex in the Borborema Province ([Matos, 1992](#); [Medeiros, 2008](#)),

* Corresponding author. Tel.: +55 21 3938 9405.

E-mail address: ismar@geologia.ufrj.br (I.S. Carvalho).

also known as the “interior basins of Northeast Brazil” (Ponte, 1992), which are pull-apart basins (Matos, 1992) originated during the breakup of Gondwana in the Early Cretaceous (Françolin and Cobbold, 1994; Mabesoone, 1994; Valença et al., 2003; Castro et al., 2007). Roesner et al. (2011) revealed Devonian strata in subsurface (well drillings), which can be understood as an unknown remnant Palaeozoic basin and as part of its basement.

Along the faulted borders of these pull-apart basins, deposition consisted of alluvial fan systems and distally characterised braided fluvial lithofacies (Mabesoone et al., 1979). In the central region of the basins, meandering fluvial systems were established with a wide floodplain laterally associated with perennial to temporary lakes (Fig. 2).

The lithofacies, sedimentary structures and stratal geometries of the Antenor Navarro (lower) and Rio Piranhas (upper) formations are interpreted as fan-delta, alluvial fan and braided fluvial palaeoenvironments (Fig. 3). In the Sousa Formation, the reddish laminated mudstones, which are thinly interbedded with siltstones and very fine cross-laminated sandstones in extensive tabular beds, are interpreted as floodplains with ponds and swampy areas. These pass laterally and stratigraphical upwardly into reddish mudstones interpreted as lacustrine (perennial/temporary) palaeoenvironments (Leonardi, 1989; Machado et al., 1990; Carvalho and Leonardi, 1992; Garcia and Wilbert, 1994; Da Rosa and Garcia, 2000). These Early Cretaceous rocks are strong reddish coloured, typical sediments in oxidizing terrestrial environments.

3. Sedimentary palaeoenvironments and stratigraphy

The main lithologies in the Sousa Basin are terrigenous clastics, including breccias and conglomerates, sandstones, siltstones, mudstones, marls and shales grouped into three lithostratigraphic units: Antenor Navarro, Sousa, and Rio Piranhas formations, all belonging to the Rio do Peixe Group and reaching a thickness of up to 2870 m (Mabesoone, 1972; Mabesoone and Campanha, 1973).

The Antenor Navarro Formation is the basal lithostratigraphic unit in the Sousa Basin, overlaying a disconformity of unnamed Devonian rocks (Roesner et al., 2011), and overlaid conformably in a gradational lithostratigraphic contact with the Sousa Formation. Its thickness in outcrops is around 100 m. Lithologically the unit is characterised typically by coarse arkoses and conglomeratic lithic sandstones with trough-cross beddings, whose palaeocurrents point to the South and Southeast (Lima Filho, 2002). Trace fossils occur in more fine-grained sediments (e.g. Serrote do Letreiro

locality, here described for invertebrate trace fossils), and the overall palaeoenvironment is understood as braided rivers in distal alluvial fans.

The deposits of the Sousa Formation typically crop out expressively in the centre of the basin, where conformably overlays the Antenor Navarro Formation, with a mean thickness of around 800 m. Lithologically, the deposits are characterised mostly by reddish and greenish/grayish microclastics (mudstones, calciferous mudstones or “marls”). This succession is interbedded with fine to coarse-grained, immature sandstone beds (some of them calciferous). These deposits frequently show horizontal- and cross-laminations, symmetrical and asymmetrical ripple marks, mud-cracks, raindrop imprints and convolute laminations. The Sousa Formation is the most fossiliferous unit of the Sousa Basin (six localities herein described for invertebrate trace fossils), and the palaeoenvironment is understood as a perennial shallow lake, and in some instances, as an ephemeral lake transitioning to a fluvial floodplain (Carvalho and Leonardi, 1992).

Deposits of the Rio Piranhas Formation crop out at the southern border of the Sousa Basin, being characterised mostly by poorly to very poorly sorted, immature, very coarse-grained sandstones (arkoses and lithic sandstones) and conglomerates, deposited in alluvial fans related to the tectonic activity of the Malta Fault; their thickness is estimated in 300 m in outcrops and palaeocurrents pointing to the North (Lima Filho, 2002). This unity is devoided of fossils, and is located at the top of the lithostratigraphic column.

In terms of depositional systems, these three lithostratigraphic units seem to be part of a tract of alluvial fan–fluvial–lacustrine facies, deposited in the Sousa Basin during Berriasian–early Barremian times. Supported by the lithofacies and palaeocurrent data, alluvial fans must have operated from both, northern and southern borders (Antenor Navarro and Rio Piranhas formations). There are coarse-grained clastics that become finer towards the basin's centre (Antenor Navarro Formation). Braided rivers distally pass the basin through meandering channels and shallow lakes (Sousa Formation). Climatic fluctuations during the depositional history of the basin would be responsible for drought episodes of variable duration in a more humid overall context. This is evident by the immaturity of the sands of the Antenor Navarro and Rio Piranhas formations, and the presence of mudcracks, raindrop imprints and calciferous mudstones in the Sousa Formation. In this complex taphonomic setting, trace fossil preservation is enhanced towards the centre of the basin, in lower energy depositional facies, where moisture is more constant, thus allowing biofilms and microbial mats to easily proliferate.

4. Palaeontology

The existence of a diverse vertebrate ichnofauna, consisting of footprints and tracks of theropods, sauropods and ornithopods is one of the most striking aspects of the Sousa Basin. Invertebrate trace fossils such as trails and burrows produced by arthropods, molluscs and annelids are also common (Carvalho, 2004). Despite the strong reddish colour, typical of sediments in oxidising terrestrial palaeoenvironments, thin beds of greenish shales, mudstones, and siltstones marls are also present, thus allowing body fossils. These fossils are ostracods, conchostracans, plant fragments, palynomorphs, and fish scales. The large-sized conchostracan *Palaeolimnadiopsis reali* (up to 3.5 cm in length), which has been described from some lacustrine facies of Sousa Basin, refers to optimum ecological conditions for these species. Conchostracans lived in alkaline ephemeral lakes, with a large amount of nutrients including ions such as calcium and phosphorus (Carvalho, 1993, 2000a, 2004). A warm and wet palaeoclimate was pointed out by Carvalho et al. (2013), based on the palynological assemblage, a

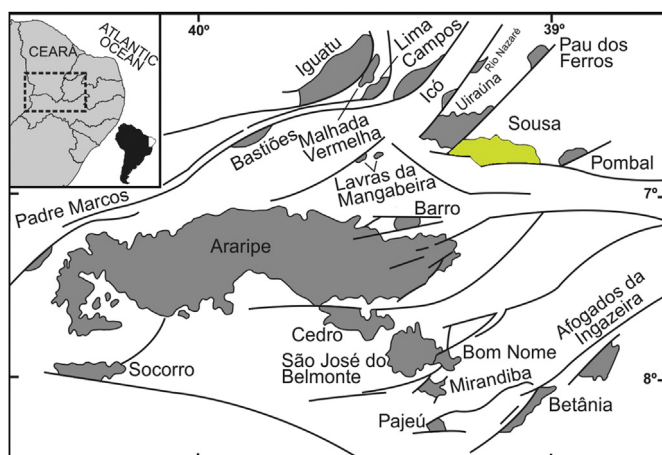


Fig. 1. Distribution of the Cretaceous basins of Northeastern Brazil in the context of Borborema Province and location area of the Sousa Basin.

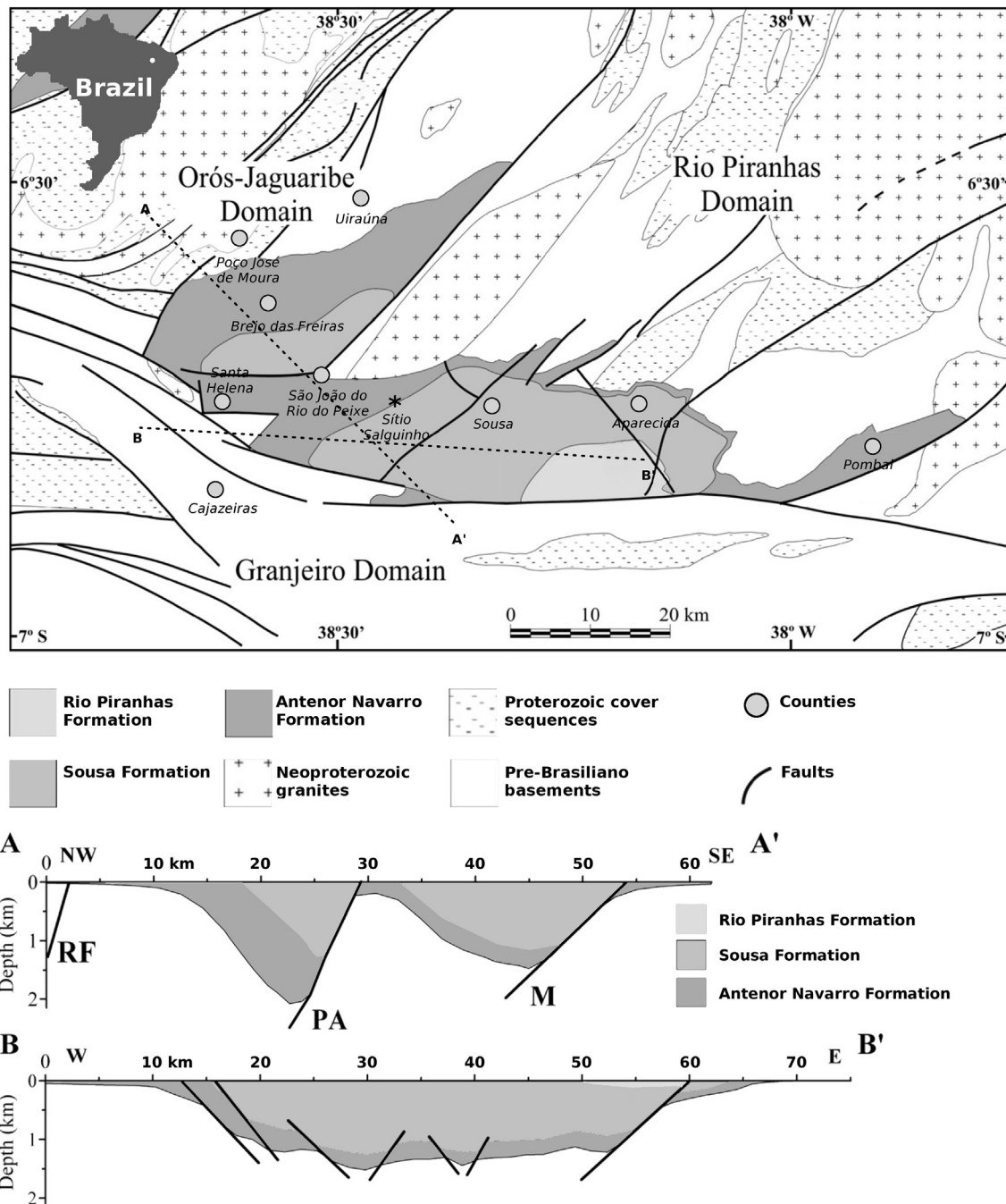


Fig. 2. Geological framework of the Rio do Peixe Basins and geological sections (A–A' and B–B') through Brejo das Freiras and Sousa basins (modified from Castro et al., 2007). Studied localities belonging to Sousa County.

characteristic of the Rio da Serra (Berriasian–Hauterivian) and Aratu (lower Barremian) local stages (Lima and Coelho, 1987; Regali, 1990).

The invertebrate trace fossil assemblage is preserved in deposits of the Sousa and Antenor Navarro formations (Carvalho, 1989; Siqueira et al., 2011).

5. Ichnotaxonomy

The invertebrate trace fossils were mostly identified in the field and, when possible in hand specimens based only by their ichnogenus level and their ethological classification (Bromley, 1996).

?Arenicolites Salter, 1857

?Arenicolites isp.

(Fig. 4A)

Specimens. Several specimens recorded in one slab, MN 5.616–I, housed in the Palaeontological Collection, Museu Nacional, Federal University of Rio de Janeiro.

Description. Paired circular structures observed in the bedding plane of the same slab. The circular structures present variable diameters between 3 and 5 mm. Although about 12 paired structures can be observed in the slab, was not possible to see the tubes of the circular structures in cross section.



Fig. 3. The stratigraphic succession of Antenor Navarro Formation (Serrote do Letreiro, Sousa Basin) is characterized by successive tabular bodies of conglomeratic sandstones, coarse sandstones and centimetric levels of fine sandstones and siltstones.

Remarks. *Arenicolites* is interpreted as a dwelling burrow of oligochaete worms (Bromley and Asgaard, 1979) or insects (Rindsberg and Kopaska-Merkel, 2005) in continental environments. Rindsberg and Kopaska-Merkel (2005) recognized four ichnospecies of *Arenicolites*, but the lack of a cross section of the paired structures doesn't allow the accurate identification of the ichnospecies of *Arenicolites*. This ichnogenus is only known at four Brazilian Mesozoic continental lithostratigraphical units: Sanga do Cabral and Caturrita formations (Triassic of the Paraná Basin; Netto, 1989, 2000; Netto et al., 1994; Gandini et al., 2004), Sousa Formation (Lower Cretaceous of the Sousa Basin; Carvalho, 1989) and Adamantina Formation (Late Cretaceous of the Bauru Basin; Fernandes and Carvalho, 2006).

Stratigraphy. Sousa Formation, Berriasian–early Barremian.

Location. Pedregulho locality, Sousa County, Paraíba State, Brazil (06°45'22.6" S/38°20'56.7" W).

Aulichnites Fenton and Fenton, 1937

Aulichnites isp.

(Fig. 4B–4D)

Specimens. Eight specimens associated with *Taenidium barretti* recorded in the same slab, MN 5613-I (Fig. 4B, C); one specimen associated with several unidentified bioturbations in the same slab, MN 5617-I (Fig. 4D), housed in the Palaeontological Collection, Museu Nacional, Federal University of Rio de Janeiro.

Description. Unbranched, straight to slight sinuous bilobate trails with a narrow median furrow. Trails of the MN 5613-I sample with 0.8–1.0 cm width, and 1.5 cm length. Trails of the MN 5617-I with 0.7 cm width, and 2.5 cm length.

Remarks. *Aulichnites* is interpreted as crawling traces of gastropods or other animals of similar locomotion habit (Howard and Frey, 1984). This ichnogenus is only known in Brazil's marine sediments of Vila Maria and Rio Bonito formations (Silurian and Permian of the Paraná Basin; Netto, 1994, 2000; Moreira and Borghi, 1999) and Inajá Formation (Devonian of the Jatobá Basin; Muniz, 1979). This is the first register data in an Early Cretaceous non-marine lithostratigraphic formation in Brazil.

Stratigraphy. Sousa Formation, Berriasian–early Barremian.

Location. Fazenda Piau locality A, Sousa County, Paraíba State, Brazil (06°44'24.9" S/38°19'54.9" W).

Phycodes Richter, 1850

Phycodes isp.

(Fig. 4E)

Specimen. Field observation.

Description. Comb-like branching sinuous trails forming bunches with highly complex meanders. Some trails cluster or seem to plunge at very shallow depths, what resembles the arthropycid ichnogenus *Phycodes*.

Remarks. This ichnogenus is only known in Brazil's marine sediments of Santa Bárbara Formation/Serra dos Lanceiros Aloformation (Precambrian–Cambrian of the Camaquã Basin; Martini da Rosa, 1999; Netto, 2000; Netto and Martini da Rosa, 2001) and Passa Dois Group (Permian of the Paraná Basin; Fairchild et al., 2001). This is the first registered data in an Early Cretaceous non-marine lithostratigraphic formation in Brazil. Annelids are the potential tracemakers.

Stratigraphy. Antenor Navarro Formation, Berriasian–Hauterivian.

Location. Serrote do Letreiro locality, Sousa County, Paraíba State, Brazil (06°41'36.89" S/38°18'29.72" W).

Palaeophycus Hall, 1847

Palaeophycus tubularis Hall, 1847

(Fig. 4F)

Specimens. Several specimens recorded in three slabs, MN 5612-I, associated with intense bioturbation, housed in the Palaeontological Collection, Museu Nacional, Federal University of Rio de Janeiro.

Description. Unbranched and slightly curved, cylindrical burrows, with diameters between 4 mm and 10 mm. Burrow fill identical to the host rock. There is no wall space between the burrow fill and the host rock, and the surfaces of the burrow fill are rugose.

Remarks. There are five recognized ichnospecies of *Palaeophycus* (see Pemberton and Frey, 1982; Fernandes and Carvalho, 2006):

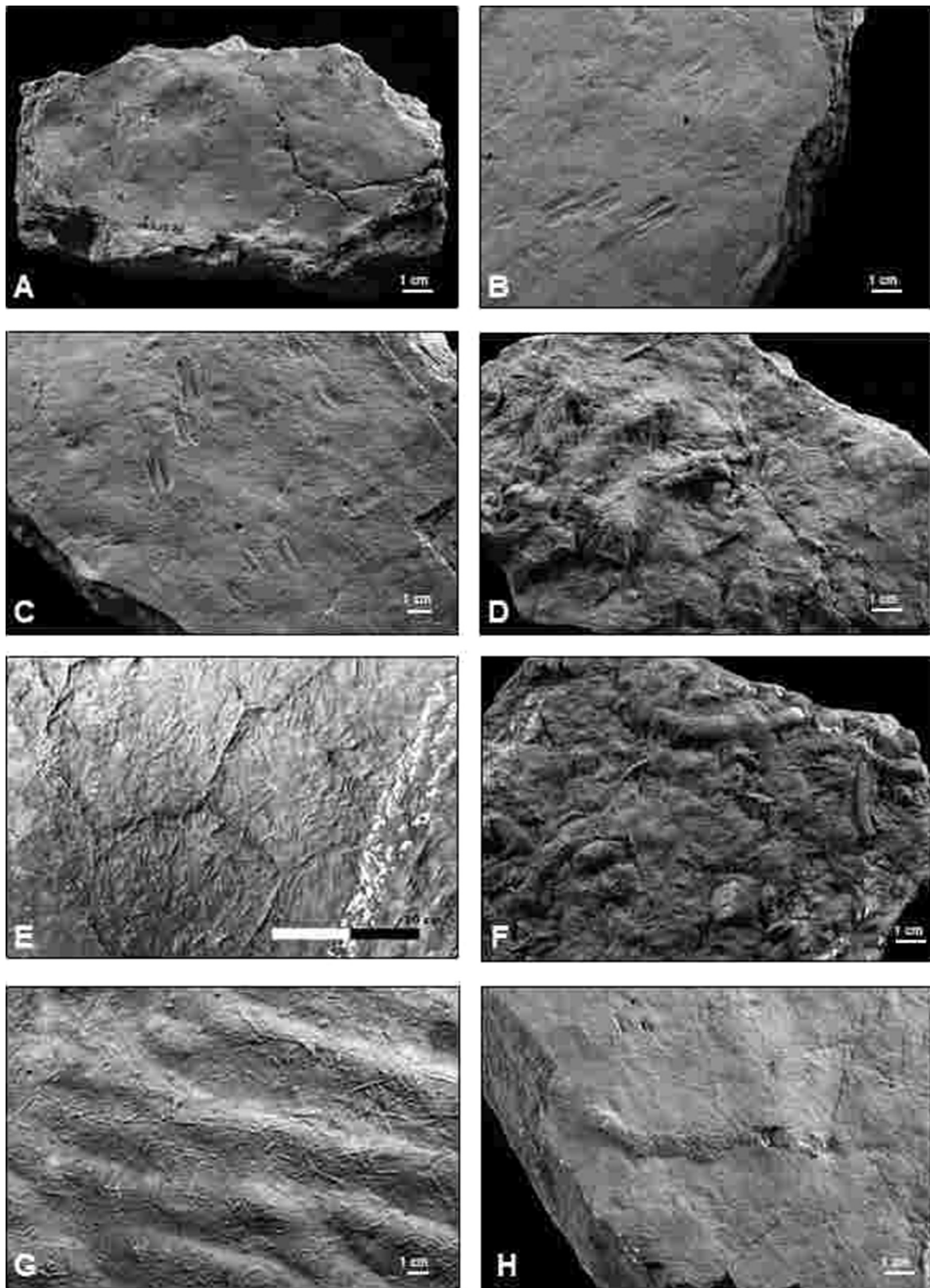


Fig. 4. Ichnofossils from the Sousa Basin. A. *?Arenicolites* isp., MN 5616-I. B. and C. *Aulichnites* isp., MN 5613-I. D. *Aulichnites* isp., MN 5617-I. E. *Phycodes* isp., photo in loco. F. *Palaeophycus tubularis*, MN 5612-I. G. *Planolites* isp., MN 5624-I. H. *Taenidium barretti*, MN 5613-I.

P. tubularis Hall, 1847, *P. striatus* Hall, 1852, *P. heberti* (Saporta, 1872), *P. sulcatus* (Miller and Dyer, 1978) and *P. alternatus* Pemberton and Frey, 1982. As cited by Fernandes and Carvalho (2006), *P. tubularis* and *P. heberti*, are comprised by smooth and unornamented straight to slight curved burrows. *P. tubularis* is thinly lined up and *P. heberti* is composed by thick-lined cylindrical burrows. The specimens studied have mainly the features recognized in specimens of *P. tubulares*, probably thin-lined, with very thin walls that were not preserved in the samples. In non-marine environments, *Palaeophycus* is probably produced by insects, arthropods (Buatois and Mángano, 1993) and very small worms. *Palaeophycus* is only known from two other Brazilian Mesozoic continental lithostratigraphical units: Cariri Formation (?Early Cretaceous of the Araripe Basin; Fernandes et al., 2002) and Adamantina Formation (Late Cretaceous of the Bauru Basin; Fernandes and Carvalho, 2006).

Stratigraphy. Sousa Formation, Berriasian–early Barremian.

Location. Fazenda Piau locality A, Sousa County, Paraíba State, Brazil (06°44'24.9" S/38°19'54.9" W).

Planolites Nicholson, 1873

Planolites isp.

(Fig. 4G)

Specimens. Several specimens associated with ripple marks in six slabs, MN 5624-I, housed in the Palaeontological Collection, Museu Nacional, Federal University of Rio de Janeiro.

Description. Cylindrical unlined and unbranched forms in full reliefs lacking distinct walls, straight or slightly curved, with 1 mm wide and variable length of up to 6 cm. The infilling is structureless and doesn't differ from the surrounding sediment.

Remarks. The slabs are intensely bioturbated and the burrows are randomly distributed in the crests and the wave-ripple troughs. These may be connected with the accumulation of organic matter by all the sediment, being the main food source for the tracemakers. Tracemakers of *Planolites*, in continental environments, are probably polygenetic in origin and may be produced by arthropods, including insects (Gradzinski and Uchman, 1994). *Planolites* is known in several marine lithostratigraphic units in Brazil from the Precambrian-Cambrian to Cretaceous (Fernandes et al., 2002; Netto et al., 2007). This is the first registered data in an Early Cretaceous non-marine lithostratigraphic formation in Brazil.

Stratigraphy. Sousa Formation, Berriasian–early Barremian.

Location. Fazenda Piau locality B, Sousa County, Paraíba State, Brazil (06°44'24.7" S/38°19'54.8" W).

Taenidium Heer, 1877

Taenidium barretti (Bradshaw, 1981)

(Fig. 4H)

Specimen. One specimen associated with eight of *Aulichnites* in the same slab, MN 5613-I, housed in the Palaeontological Collection, Museu Nacional, Federal University of Rio de Janeiro.

Description. A slight sinuous and cylindrical unlined burrow with very thin back-fill of meniscus-shaped packets at one extremity of the burrow. The trace has an average diameter of 6 mm, apparently constant in the specimen, with a length of 7.5 cm.

Remarks. *Taenidium barretti* differs from other ichnospecies of *Taenidium* by its more curved and thin menisci, variable diameter, and more sinuous burrows (Fernandes and Carvalho, 2006), being these, the characteristics of the specimen studied. In non-marine sediments, *Taenidium* is probably produced by insect larvae or other arthropods, and is a typical component of the Scoyenia Ichnofacies (Buatois et al., 2002). *Taenidium* is also known at other Brazilian Mesozoic continental lithostratigraphical units: Sanga do Cabral Formation (Triassic, with *T. serpentinum* Heer, 1877; Netto et al., 1994) and Botucatu Formation (Early Cretaceous, with *T. serpentinum* and *T. satanassi* D'Alessandro and Bromley, 1987;

Fernandes et al., 1990), both formations of the Paraná Basin; Araripe Formation (Early Cretaceous of the Araripe Basin; Carvalho, 1989; Fernandes et al., 1998); Antenor Navarro and Sousa formations (Early Cretaceous of the Sousa Basin; Fernandes and Carvalho, 2001); and Adamantina Formation (Late Cretaceous of the Bauru Basin, with *T. barretti*; Fernandes and Carvalho, 2006).

Location. Fazenda Piau locality A, Sousa County, Paraíba State, Brazil (06°44'24.9" S/38°19'54.9" W).

6. Palaeoenvironmental interpretation of the invertebrate trace fossils

Antenor Navarro Formation – *Taenidium barretti* may be attributed to worm-like soft-bodied invertebrates (Oligochaeta annelids) or arthropods (particularly hemipters, coleopterans and arachnids), which actively rework the usually wet and semi-consolidated continental sediments. The annelids can bioturbate lake bottom sediments or humid subaerial substrates. Insects rework the sediment at lakeshores and riverbanks, as well as the dryer deposits far from waterbodies (Smith and Hein, 1971; Chamberlain, 1975; Laza, 1982; Brussaard and Runia, 1984; Melchor et al., 2012). *Taenidium barretti* is considered not only a feeding trace, but also has been interpreted as a locomotion structure (Graham and Pollard, 1982). When worm-like organisms move within the sediment, they may ingest fine-grained material to obtain the necessary nutrients for their metabolism, forming burrows with internal meniscoid structures due to sediment backfilling (Heinberg, 1974). The menisci of *Taenidium*, as a feeding structure, would result from two kind of sediments – one similar to the matrix, corresponding to undigested sediment; and the other, a more fine-grained of coprolitic origin, caused from faecal backfilling by organisms such as annelids (Heinberg, 1974; D'Alessandro and Bromley, 1987; Buatois and Mángano, 1996). The locomotion of arthropods that actively burrow could also create menisci through sediment displacement, however without coprolitic sediment production by simple mechanical grain sorting (Smith et al., 2008; Counts and Hasiotis, 2009).

Phycodes isp. traces occur in the same very fine-grained sandstones as *Taenidium barretti* – thinly interbedded with mudstones and mudcracks, which not only cross-cut, but also are crossed-cut by the traces. These feeding traces are developed suggestively before and during the early drying episodes of the substrate.

The ichnological assemblages of *Taenidium barretti* and *Phycodes* isp. from the Antenor Navarro Formation are monoichnospecific, both belonging to the Scoyenia ichnofacies.

According to the sedimentological data for the Antenor Navarro Formation, the strata from the Serrote do Letreiro site reveal a fluvial origin, during torrential floods in alluvial fans, close to the source areas (Mabesoone, 1994; Carvalho, 2000b). In high-energy fluvial channels, as observed in alluvial fans, fluctuations of the sedimentation and erosional rates result in an unfavourable environment for the formation and preservation of biogenic structures. Furthermore, the nutrients shortage prevents the sustenance of a diversified ichnofauna. At Serrote do Letreiro, the trace fossils attributed to invertebrate activities are found in fine-grained sediments, accumulated in low-energy conditions, on top of sandy bars and channel banks. These settings underwent fluctuations of water flow discharge and periodic interruptions in sedimentation when the sandy bars and the channel banks are exposed, thus forming overbanks (Carvalho, 1989).

Sousa Formation – The invertebrate ichnoassemblages from the Sousa Formation are found in a succession of strata characterized by siltstones and claystones, thinly interbedded with silty/clayey sandstone beds. Symmetrical (wave) and asymmetrical (current) ripples, mudcracks, and linsen to flaser beddings are

common physical structures. Convolute laminations are associated to sediment deformation due to intrastratal water overpressure produced by tetrapod footprints, which are abundant. Feeding (fodinichnia), crawling (repichnia), resting (cubichnia) and habitation (domichnia) structures are all represented in the invertebrate ichnoassemblage. Locally, the abundance of trace fossils in the Sousa Formation may suggest a high nutrient content in the environment, which would allow the sustenance of a considerable amount of benthic infauna and epifauna (Carvalho and Carvalho, 1990).

The ichnoassemblages of Sousa Formation are similar to others previously described in literature, such as those in the ancient fluvial deposits from the Fleming Fjord (Triassic, Greenland; Bromley and Asgaard, 1979), Diligencia (Miocene, California; Squires and Advocate, 1984) and Duchesne River (Eocene, Utah; D'Alessandro et al., 1987) formations, beyond extant fluvial ones (Ratcliffe and Fagerstrom, 1980). The Sousa Formation ichnoassemblages, however, seem to be particularly related to lentic conditions like shallow lakes or constantly flooded areas, resembling abandoned meanders, as interpreted by Leonardi (1989).

7. Taphonomic aspects of the invertebrate trace fossils: microbial role in the preservation

The knowledge about the structures formed by microbial mat activity and the amount of case studies that allow a better understanding of the role of microbial mats in the preservation of sedimentary features in sands and sandstones (macroclastics) is increasing in the literature since the seminal work of Noffke et al. (2001). However, those observations have been made particularly in the paralic and marine environments, ancient to extant (Borghini and Paula Freitas, 2010; Noffke, 2010; Buatois and Mángano, 2011a; Buatois et al., 2013). Nevertheless, the recognition of this role concerning to muds and mudstones (microclastics) and to terrestrial environments is still in progress (Schieber et al., 2007; Buatois and Mángano, 2011b; Noffke and Chafetz, 2012).

In the Sousa Basin, well-preserved vertebrate trace fossils produced in microclastics of ancient terrestrial environment during the Early Cretaceous were described by Carvalho et al. (2013), who stressed the taphonomic role of biofilms and microbial mats in the preservation of dinosaur tracks; but nothing has been discussed concerning the invertebrate traces.

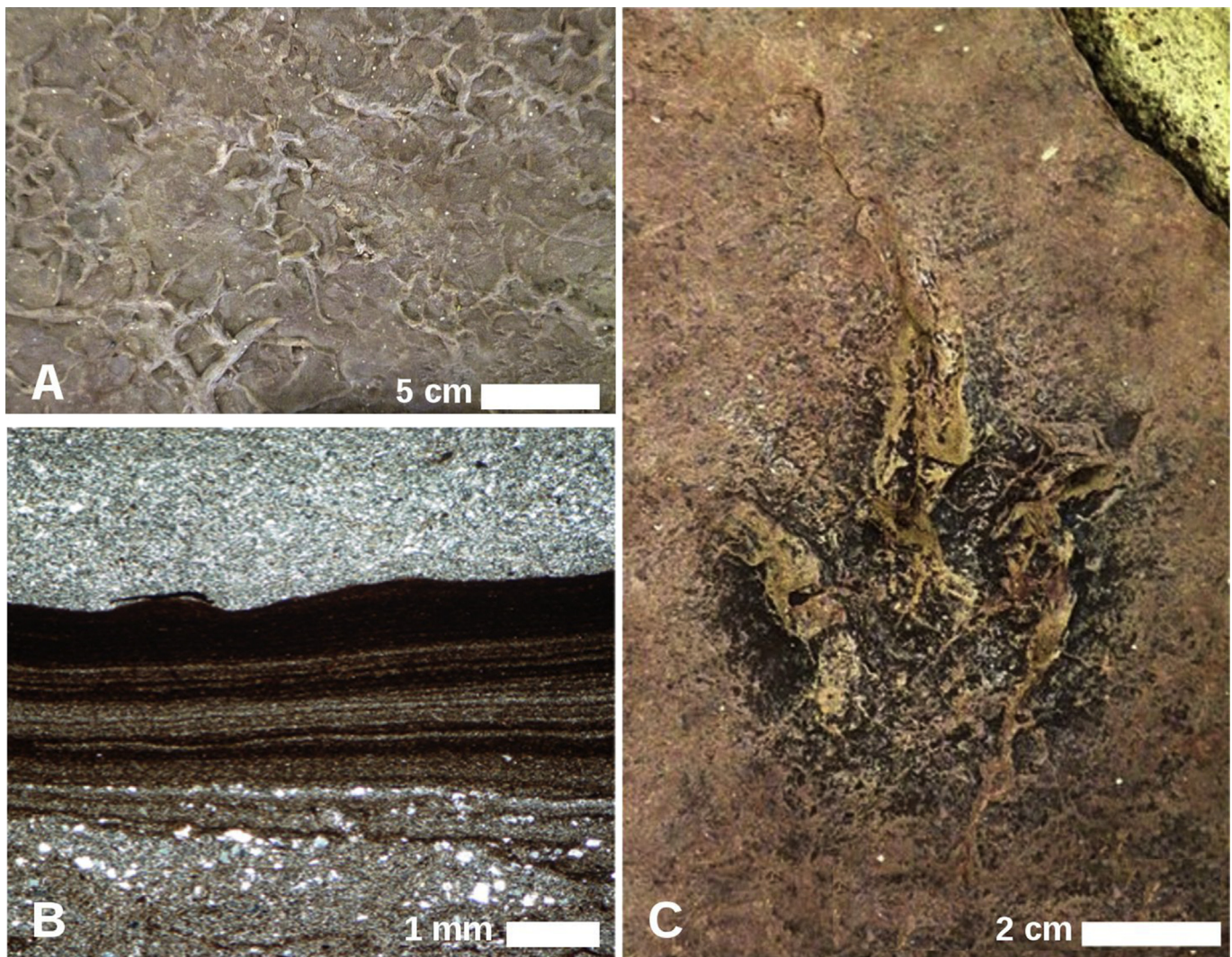


Fig. 5. A. Periodic interruptions in sedimentation when sandy bars of river channels are exposed allowing bioturbation. Small cracks in fine sandstones of Anterior Navarro Formation probably related to elephant skin structures (Serrote do Letreiro locality). B. Photomicrograph of very thin microbialaminations overlain by very fine sandstones, softly deformed by loading (crossed polarizers, Sousa Formation). Observe the mat fragment (chip). C. Corrugated structures superimposed to a coelurosauri form footprint (Fazenda Piau locality A, Sousa Formation), interpreted as elephant skin, a microbially induced sedimentary structure.

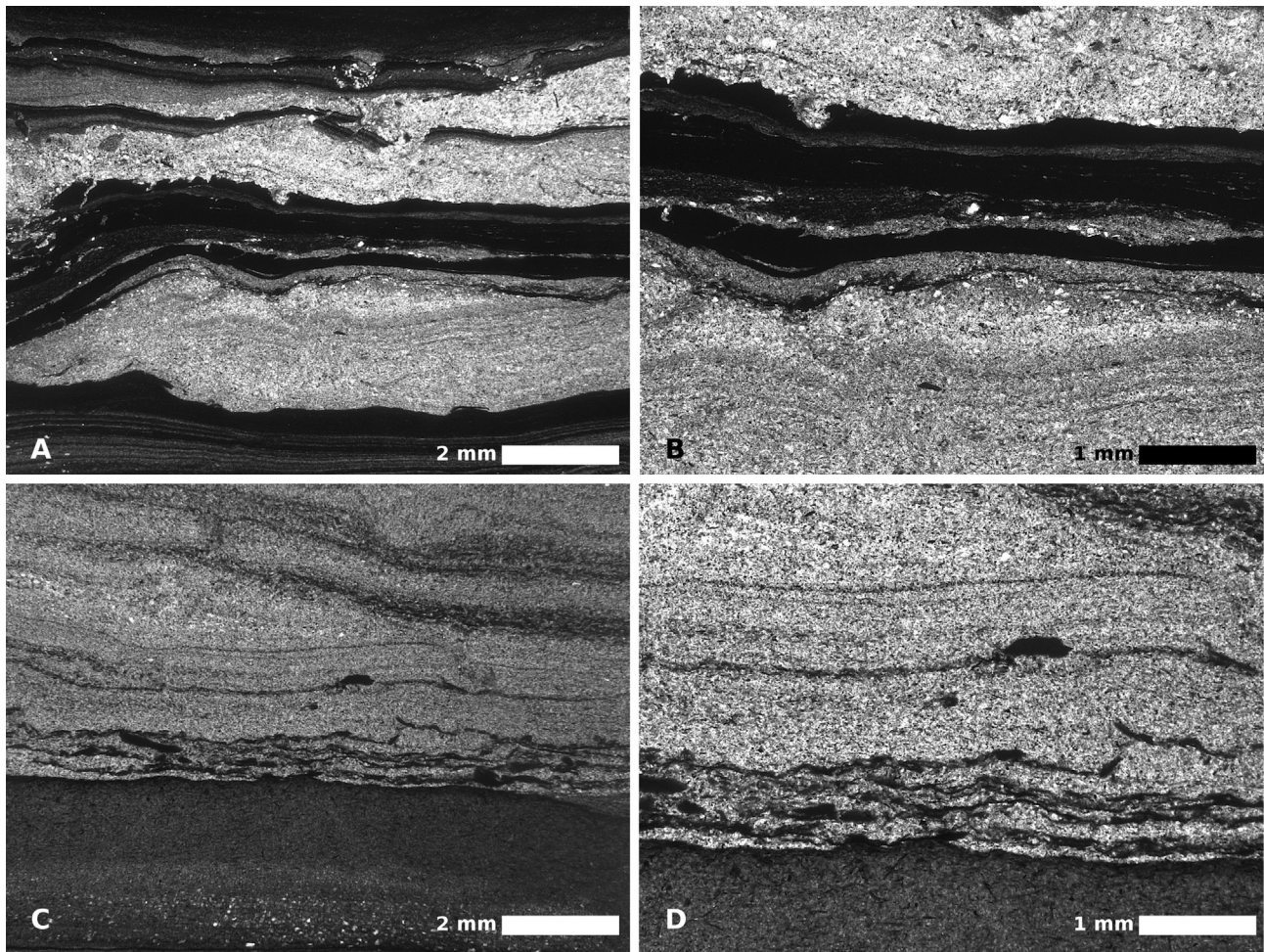


Fig. 6. A. Photomicrograph of very thin microbiolaminations (darker laminae), interpreted as biofilms and algal mats, disrupted in the upper part by hydrodynamic processes, represented by rippled siltstones (parallel polarisers, Sousa Formation). Observe the subtle load structure and the erosive nature at the top of the algal mat, enlarged in the photomicrograph (B). C. Photomicrograph of thin microbiolaminations (parallel polarizers Sousa Formation), showing imprinting structures and fragments of biofilms (mat chips), enlarged in the photomicrograph (D).

Cohesiveness of the substrate and its eventual consolidation by early lithification was explained by the existence of microbial mats in the case of vertebrate trace fossils preservation (Carvalho et al., 2013). This may have also occurred for the invertebrate trace fossils, in association with those traces. Alkaline waters would account for carbonate precipitation and early lithification, as supported by the conchostracofauna (Carvalho and Carvalho, 1990), and the presence of calciferous mudstones and marls.

Similar to dinosaur tracks, the invertebrate trace fossils in the Sousa Basin are not observed pervasively in all fine-grained strata of the Antenor Navarro and Sousa formations. In those strata, preservation is remarkable despite the context of a higher energy deposits in alluvial fans (Antenor Navarro Formation) or a lower energy in meandering rivers (Sousa Formation). Other peculiarities concerning the invertebrate trace fossil occurrences are the low ichnodiversity observed on the many sites; shallow tiers (positive and negative epichnia); a dense ichnofabric close to bedding surfaces prior to burial (surface constrained endichnia); and the common feeding and grazing habits (fodinichnia and repichnia). Such preservation aspects are in accordance to the understanding that trace fossils in fluvial/alluvial palaeoenvironments are commonly constrained to specific beds or bedding surfaces (Buatois and Mángano, 2004, 2007).

Field observations in all the aforementioned sites strongly suggest the presence of microbially induced sedimentary

structures allied to the invertebrate traces (see particularly Fig. 5 and Fig. 6). Evidences are diverse small pits, bumps and crinkles beyond short cracks that appear either as a bed surface background on which the trace fossils are produced, or also as overlapping the traces.

Phycodes isp. are typically associated to wrinkle structures at Serrote do Letreiro locality (Fig. 4E), which suggest a microbial mat protecting an annelid infauna living in a shallow tier, in soft-to firmground muddy substrate. Protection against desiccation should have occurred by delaying evaporation in the capillary vadose zone, in the uppermost muddy deposits accumulated in floodplains of the Antenor Navarro Formation, prior to desiccation. At last, desiccation occurs as shown by mudcracks that overprint the trace fossils and wrinkle structures. In this taphonomic window, microbial mats would not only promote sheltering for the ichnofauna, but also biostabilization of the substrate against quick drying out, and subsequent changes in the substrate consistency, what was registered as event beds or horizons.

Planolites isp., observed occurring preferentially on the crest of wave-ripple marks (Fig. 4G) at Fazenda Piau locality, suggest another taphonomic window, produced by the growth of microbial mats. In this particular case of mat levelling, the troughs of the ripples were preferably occupied by the mat, preventing from intense feeding action of small arthropods, which acted more freely on the crest of the ripples, where mats are slender. In

such case, mats would have been developed on the wave-ripples in subaqueous setting, after wave bottom reworking during continental storms (strong winds), which recycled and furnished nutrients to a peripheral, perennial/semi-perennial, shallow lake environment of the Sousa Formation. No exposure or desiccation feature is observed in relationship to this taphonomic context.

Elephant skin (Fig. 5A,C) structures also occur at Serrote do Letreiro locality, but in a diverse context than the *Phycodes* isp. ichnofauna. These microbially induced sedimentary structures seem to have been developed distinctively due to the phreatic waters reaching the uppermost sandy-muddy substrates, with an adequate nutrient input to have sustained a microbial mat cover on the top of sandy bars and channel banks in the Antenor Navarro Formation; however, trace fossils seem to have been preventing from occurring in such beds or horizons by the highly fluctuating water discharge, even allowing desiccation. Elephant skin structures also possess allied cracking and tearing off features (Fig. 5A), suggesting temporary watery conditions succeeded by drying out episodes.

Petrographically, can be observed very thin to thin microlaminations (Figs. 5B, 6), as well as fragmented biofilms and dispersed microbial filaments, which suggests the presence of ancient biofilms to slender microbial mats. Similar microbial mat features were also identified by Schieber et al. (2007) in muddy substrates from the Proterozoic Newland Formation, (Montana, USA) and the Kopela Shale (Pranhita-Godavari Basin, India).

Uchman et al. (2004) described, in the upper Oligocene deposits of the Lower Freshwater Molasse of Switzerland, a similar context of invertebrate trace fossils in mudstones with mudcracks and raindrop imprints interpreted as been deposited in ponds of fluvial braided floodplains, where insect larvae played an import role as tracemakers. Similarly, to what is interpreted in the Sousa Basin, muddy low-energy substrates would occur in both shallow subaqueous environments (humid phases) and subaerial desiccating ones (during prolonged wet seasons) in fluvial braided deposits. As Uchman et al. (2004) also suggests, microbial mats are very common in recent ponds, and can be the key for understanding the preservation of invertebrate trace fossils in such palaeoenvironments.

The role of these biofilms or microbial mats in subaerial environments can be twofold: source of nutrients to feed the infauna, and a moisture keeper for annelids and insect larvae. Furthermore, in a highly unstable subaerial environment concerning humidity and nutrient availability (i.e., distal alluvial fans and floodplains), biostabilization of the substrate fostered by such biofilms or microbial mats would enhance its preservation. As a result, this microenvironment sheltered by biofilms or microbial mats constitutes a taphonomic scenario in the Sousa Basin, encompassing the invertebrate trace fossils therein described.

8. Conclusions

The Sousa Basin shows well-preserved invertebrate and vertebrate trace fossils produced in microclastics of ancient terrestrial environments during the Early Cretaceous. Preservation of these traces in such palaeoenvironments would normally demand high sedimentation rates to prevent them from destruction (erosion), by substrate reworking due to successive floodings. Nevertheless, high sedimentation rates would have prevented the intense colonization of the substrate by the invertebrate trace fossil producers under discussion, mostly annelids and arthropods. The characteristic *Phycodes* isp. and *Planolites* isp. ichnoassemblages in the Antenor Navarro and Sousa formations showed a particular taphonomic relationship with microbially induced sedimentary structures, that provided particular environmental conditions for the colonization

of a soft to firm substrate, and subsequent burrow preservation. Early diagenesis, forming “hardgrounds”, is disregarded as a taphonomic possibility as no boring traces were observed. The delicate equilibrium between microbial mat development, sedimentation rates and the ichnofauna seems to be the key for the palaeoecological understanding of terrestrial (alluvial) palaeoenvironments. The multifunctional role of microbial mats appears as multiple taphonomic windows for both, the occurrence and the preservation of invertebrate trace fossils by biostabilization. Therefore, microbial mats are not the unique responsible for excellent preservation. Mud composition, moisture and cohesiveness also play their role.

Acknowledgements

Proper thanks are due to all who contributed with this study. Bruno Rafael Carvalho Santos and Amanda Goulart Rodrigues who produced the illustrations. The financial support was provided by Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (Faperj), Petrobras Human Resources Programme (PFRH-PB 218 Biossedimentologia) and the Conselho Nacional do Desenvolvimento Científico e Tecnológico (CNPq Proc. 301975/2009-4).

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