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Geological environments of dinosaur footprints in the intracratonic basins of northeast Brazil during the Early Cretaceous opening of the South Atlantic[1]

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The intracratonic basins of northeast Brazil are part of a Cretaceous rift system developed along pre-existing structural trends in the basement during the opening of the South Atlantic Ocean. Sedimentary basins such as those of Sousa, Uiraúna-Brejo das Freiras, Araripe, Cedro, Iguatu, Malhada Vermelha, Lima Campos and Icó contain a wide variety of vertebrate and invertebrate ichnofossils, and invertebrate, vertebrate and plant fossils, including palynomorphs. Among the clastic continental sediments of these basins, dinosaur footprints are the most abundant vertebrate remains. The dinosaurian ichnofaunas all have the same stratigraphic-time-palaeogeographical context, and represent parts of a widespread mega-tracksite. Similarities in the lithofacies of the deposits where the footprints occur reflect the same tectonic, climatic and sedimentary processes. The environmental setting was influenced by the initial development of the equatorial Atlantic seaway, with an endemic biota living nearby in ephemeral rivers and shallow lakes in a hot climate.

KEY WORDS: dinosaur footprints; northeast Brazilian basins; Early Cretaceous.

1. Introduction

The intracratonic basins of northeast Brazil are sites of Cretaceous sedimentation, whose origin and evolution were controlled by reactivation of pre-existing tectonic structures in the basement (Precambrian rocks) during the Jurassic and Cretaceous. This reactivation was closely related to the opening of the South Atlantic Ocean. Normal and transcurrent faults were the main structural style for the opening of grabens and half grabens in the central region of northeast Brazil during the Early Cretaceous. The basins lie in the western part of Paraíba, Rio Grande do Norte and Pernambuco states, and in the southern part of Ceará state, northeast Brazil (Figure 1). They have yielded a wide variety of vertebrate and invertebrate ichnofossils, as well as fossils of invertebrates, vertebrates and plants, including palynomorphs.

Dinosaur footprints are the most frequent palaeobiological traces in these basins. The best preserved ichnologic material comes from the Lower Cretaceous (Neocomian) of the Sousa and Uiraúna basins, also collectively known in the literature as the Rio do Peixe basins. The study of all of these Early Cretaceous footprints (Leonardi, 1989; Carvalho, 1989; Carvalho *et al.*, 1993a, b; 1994; Leonardi, 1994) demonstrates that, in spite of the paucity of skeletal remains, the dinosaur faunas of Brazil were abundant and diverse. Their study also permits inferences to be drawn about the palaeoenvironment in which these faunas lived during the early formation of the South Atlantic.

2. Environmental changes: origin of the Atlantic Proto-Ocean, migration of South America and climatic evolution

From the end of the Permian, sediment accumulation decreased in many Brazilian sedimentary basins, and was mainly restricted to portions of the Amazonas, Paraná and Parnaíba intracontinental basins. In the Jurassic the stability of the Brazilian Platform was broken. Intense tectonic activity related to the beginning of rupturing of the gondwanic crust along various Precambrian basement structural trends, created

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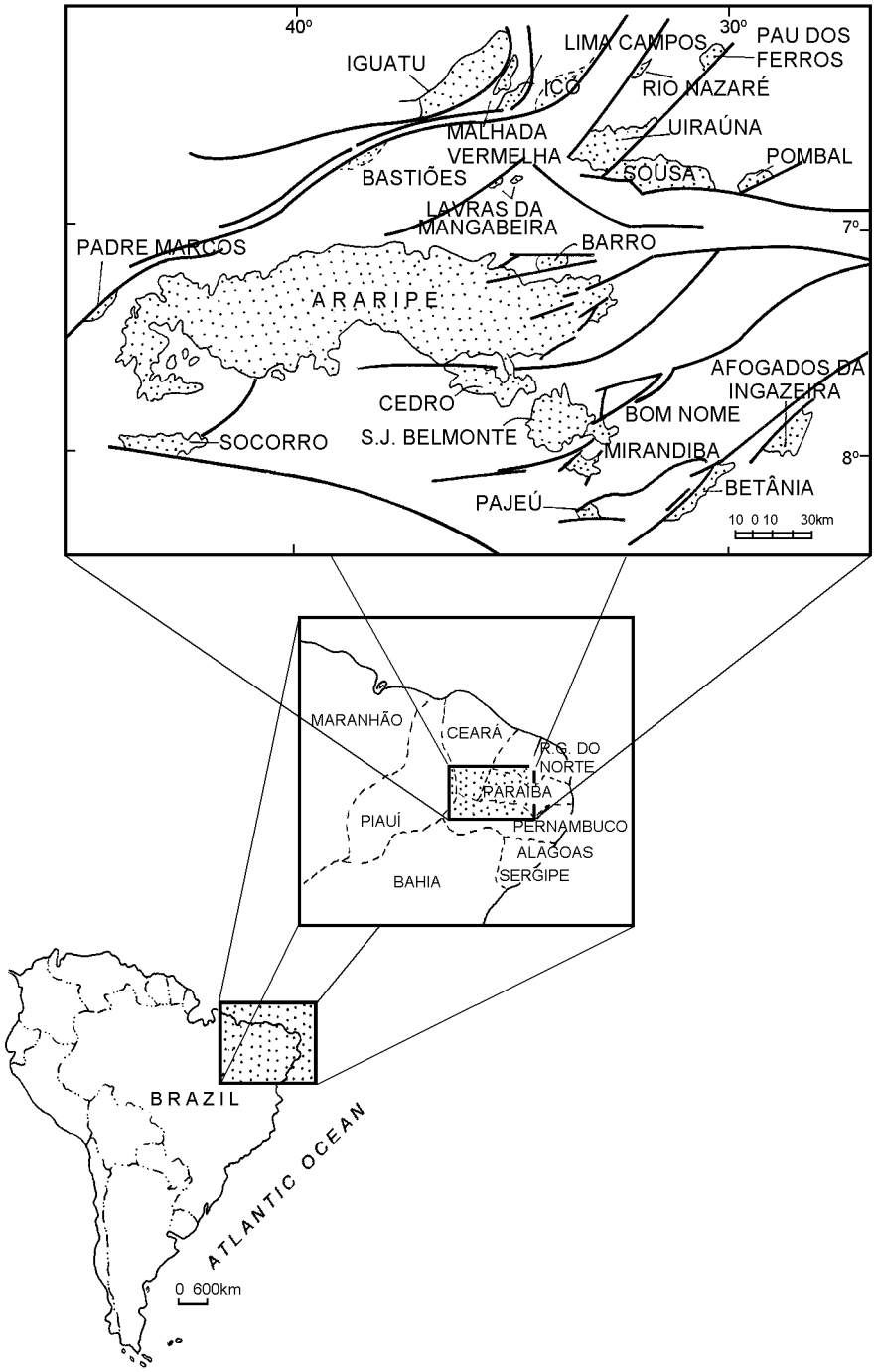

Figure 1. Map of the intracontinental basins of the Brazilian northeast.

many small sedimentary basins and led to rapid accumulation of continental sediment. Many of the individual half-grabens that resulted from this tectonism contained small lakes that captured the drainage network and had an eventual physical linkage (Machado Jr *et al.*, 1990). The lithofacies similarities between the deposits in different basins reflect similar tectonic, climatic and sedimentary processes.

According to Popoff (1988), at its beginning the South Atlantic was divided into three tectono-sedimentary domains: austral (southern); tropical (mid-latitude); and equatorial (northern). Their tectonic history was diachronous and did not coincide

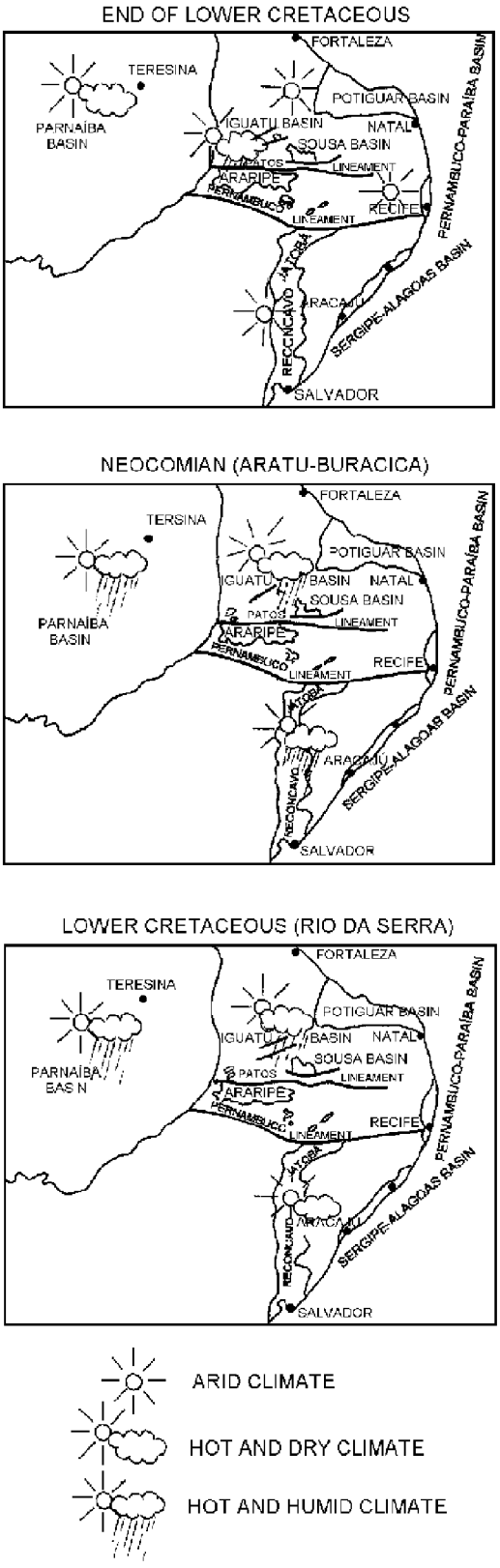

Figure 2. Aspects of palaeoclimatic evolution during the Early Cretaceous in northeast Brazil.

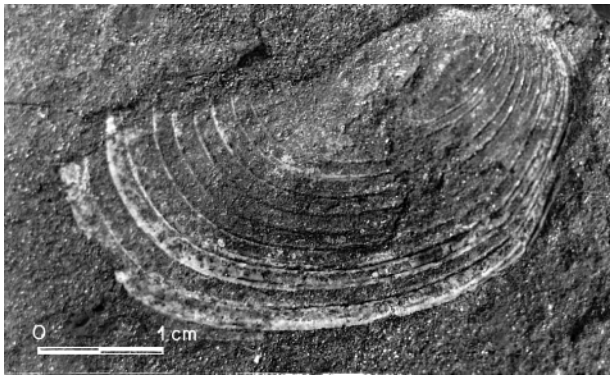

Figure 3. Some perennial and temporary lakes of the Aratu Stage (Lower Barremian) contained a giant conchostracan palaeolimnadiopsidean. Sousa Formation, Sousa Basin, locality of Pedregulho.

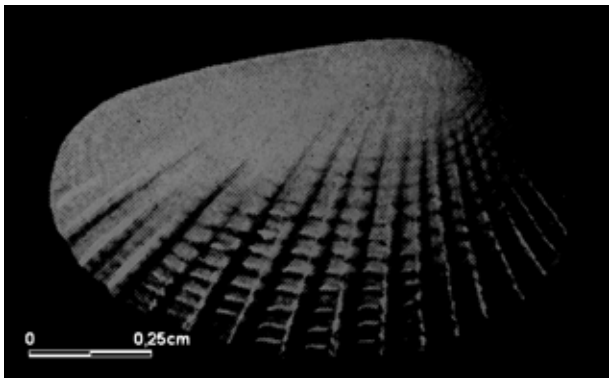

Figure 4. An endemic conchostracan esthereliidean from lacustrine deposits of the Sousa Formation, Sousa Basin, locality of Passagem das Pedras (reproduced from Maury, 1934).

during the Early Cretaceous. The Brazilian northeast interior basins (included in the mid-latitude tropical domain), were limited by the fracture zones of Pernambuco-Birao-Khartoum (north of the Congo Craton), Portalegre and Paraíba.

During the early Mesozoic, a hot and arid climate was typical in the southern hemisphere. This is well recognized throughout the widespread aeolian deposits along the Brazilian and African intracratonic basins. The connection between South America and Africa as a single, large continental block, did not permit a higher humidity in what was (at that time) the continental interior.

With the break up of this continent and the establishment of a lacustrine and fluvial system among the new rift basins, the climate gradually became more humid. These environmental changes may have been linked to the same tectonic events that drove the

separation of South America and Africa and led to the origin of the equatorial Atlantic Ocean.

During the Early Cretaceous, hot climatic conditions were widespread, although there was probably a wide range of humidity (Figure 2). According to Petri (1983) and Lima (1983), in the earliest Cretaceous the climate was more humid in regions located to the south of the tropical domain (Recôncavo-Tucano-Jatobá basins). Despite a hotter and drier climate to the north, interpretations of depositional environments and fossils suggest the existence of some lakes which, during the Neocomian, locally provided more humid conditions.

At that time, South America was still connected to Africa, and the Atlantic Ocean was in its initial developing phase. In the present northeastern Brazil, in an area of hundreds of square kilometres, ephemeral rivers and shallow lakes constituted important environments for an abundant endemic biota (Figures 3, 4) in many basins limited by faults.

3. The Sousa Basin

3.1. Geology

The Sousa Basin comprises an area of 1250 km^2, located in the west of Paraíba state, in the counties of Sousa and Uiraúna. The basement is composed of highly metamorphosed Precambrian rocks (aligned structurally in a northwest–southeast or east–west direction). The predominant rocks are migmatites, granites, gabbros and amphibolites. The main lithologies in the Sousa Basin are clastic rocks, including breccias and conglomerates, sandstones, siltstones, mudstones and shales. In some cases the carbonate content is high in the form of marls and thin (cm-thick) limestones.

A formal lithostratigraphic subdivision of the Cretaceous in the Sousa Basin, and the neighbouring Uiraúna/Brejo das Freiras and Pombal basins, was erected by Mabesoone (1972) and Mabesoone & Campanha (1973/1974). These authors identified the Rio do Peixe Group, with a total thickness of 2870 m, and subdivided it into the Antenor Navarro, Sousa and Piranhas formations. The Antenor Navarro and Piranhas formations are composed of immature sediments, including breccias and conglomerates, with pebbles of metamorphic and magmatic rocks in a coarse arkose matrix. These lithologic types are located near the faulted margins of the basin. Towards the basin-depocenter, there are conglomeratic and fine sandstones, sometimes interbedded with siltstones and shales. Cross-channel and tabular stratification, climbing-ripples and ripple marks are the main

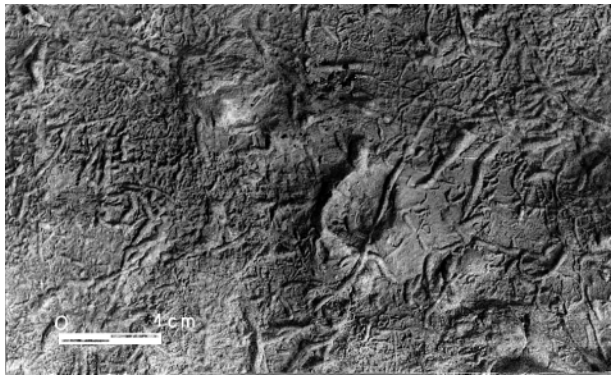

Figure 5. Dense invertebrate bioturbation in rocks of the Sousa Formation (Aratu Stage), Sousa Basin.

sedimentary structures. The Sousa Formation is composed of reddish sandstones, siltstones, mudstones and carbonate nodules; marls also occur. Common sedimentary structures include mud cracks, convolute structures, ripple marks, climbing ripples, rain prints and evidence of bioturbation (Figure 5).

Sedimentation in the basin was controlled by regional tectonic processes (Lima Filho, 1991). During Dom João time (latest Jurassic 'Purbeckian' stage), because of crustal extension, a sigmoidal basin developed at the inflection of the northwest–southwest and east–west faults. During Rio da Serra time (Berriasian–Hauterivian), under the same tectonic stress pattern, the basinal area increased, and its shape became rhomboidal. Eventually, probably at the end of Aratu time (Lower Barremian Stage), there was a change in the tectonic pattern and the sediment accumulation rate began to decline.

The deposits reflect direct control of the sedimentation by tectonic activity. Along the faulted borders of the basin, deposition consisted of alluvial fans. These pass distally into an anastomosing fluvial system. In the central region of the basin, a meandering fluvial system with a wide floodplain was established where perennial and temporary lakes were developed.

3.2. Palaeontology and age of deposits

The existence of an abundant ichnofauna of vertebrates, consisting of footprints and tracks of carnosaurs, coelurosaurs and ornithopods, is one of the leading characteristics of the basin. Invertebrate ichnofossils such as tracks and burrows produced by arthropods and annelids are also common. Despite the strong reddish colour, typical of sediments that accumulated in subaerial environments, there

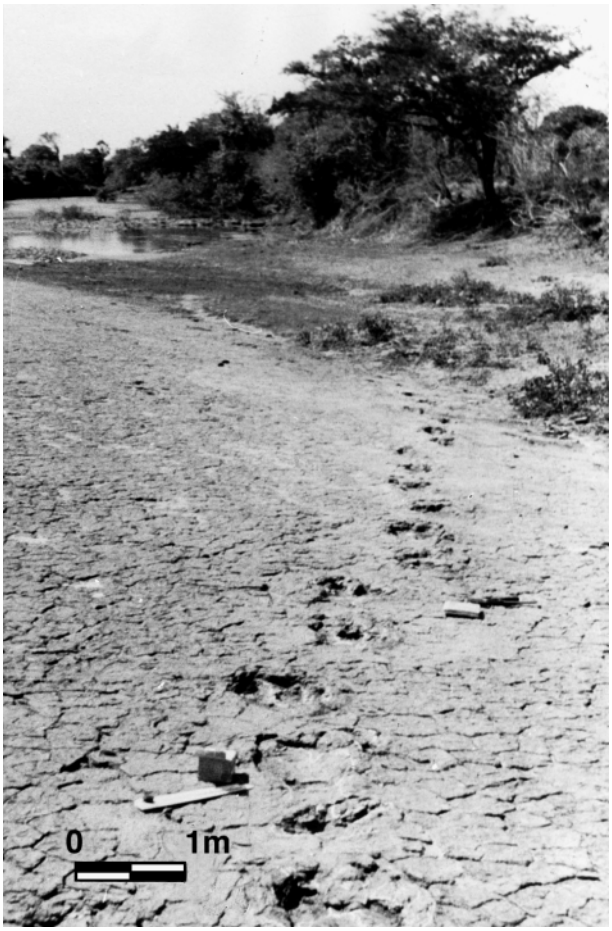

Figure 6. Ornithischian trackway at Passagem das Pedras in the Sousa Formation, Sousa Basin.

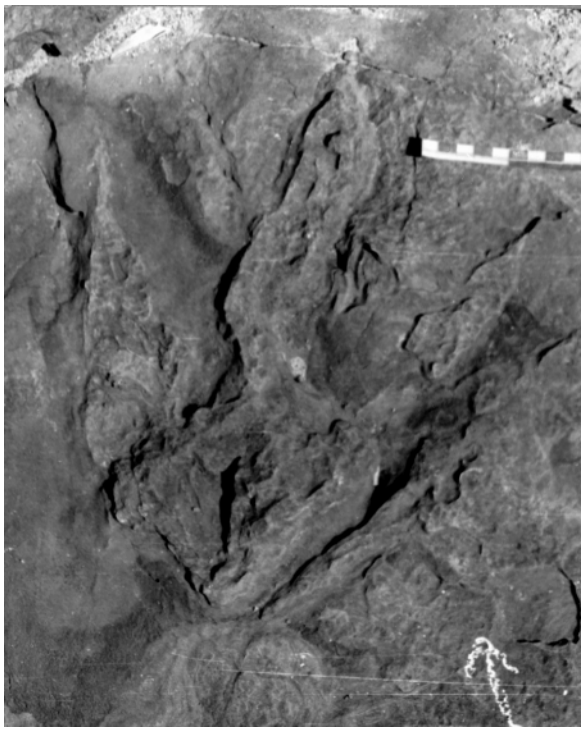

Figure 7. Theropod footprint at Fazenda Caiçara-Piau, Sousa Formation, Sousa Basin. Scale bar represents 10 cm.

are some levels of greenish shales, mudstones and siltstones where fossils are common. These consist of ostracods, conchostracans, plant fragments, palynomorphs and fish scales.

The sediments were first dated by Moraes (1924), who proposed a Comanchean age (Lower Cretaceous) for dinosaur tracks at Passagem das Pedras. From an analysis of ostracods Braun (1966, 1969, 1970) and Mabesoone & Campanha (1973/1974), suggested an age between the Berriasian and Hauterivian. The palynological assemblages are characteristic of the Rio da Serra (Berriasian–Hauterivian) and Aratu (Lower Barremian) local stages (Lima & Coelho, 1987; Regali, 1990).

3.3. The dinosaurian ichnofauna and its stratigraphic context

The dinosaurian footprints and tracks in the Sousa Basin occur in at least 22 localities in clastic deposits within all these formations of the Rio do Peixe Group. They consist of 78 dinosaurian trackways divided into 50 Carnosauria, ten Theropoda individuals, seven Iguanodontidae, three Coelurosauria, three Sauropoda and two *incertae sedis*, as well as three tracks of dubious classification between Carnosauria or Iguanodontidae. Approximately 350 isolated footprints have also been found. These are dominated by carnivorous dinosaur tracks (Leonardi *et al.*, 1987a–c; Carvalho & Leonardi, 1992).

Footprints are rare in the Antenor Navarro and Piranhas formations. The lithofacies, sedimentary structures and geometry of the beds point to sedimentation in fan-delta, alluvial fan and anastomosing fluvial environments. Footprints are preserved only in fine sediments that accumulated as subaerial sandy bars in alluvial fans and anastomosing rivers close to the basin margins.

In the Sousa Formation the generally finer grain size of the sediments rendered them more suitable for footprint preservation (Figures 6, 7). The essentially microclastic sequence points to lacustrine, swampy and meandering-braided fluvial palaeoenvironments (Figure 8). Through the study of conchostracans, Carvalho & Carvalho (1990) and Carvalho (1993)

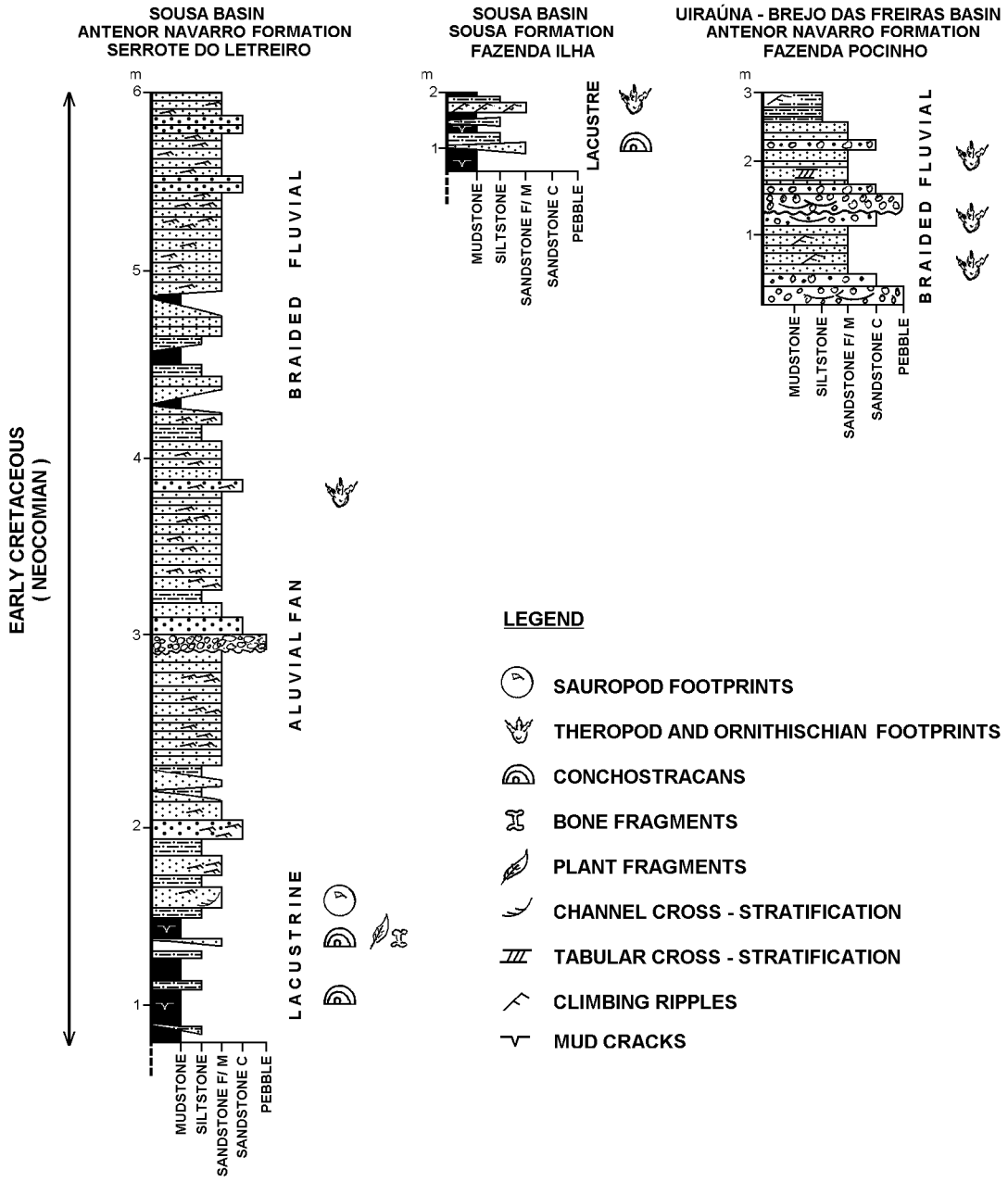

Figure 8. Stratigraphical profiles from the dinosaurian footprints areas, Sousa and Uiraúna-Brejo da Freiras basins.

inferred the physical and chemical characters of the lakes along whose margins dinosaur disturbance was significant. They were small temporary lakes, hot and shallow, in which the water chemical conditions had an alkaline character (pH between 7 and 9). The dimensions of some of the conchostracans (up to 3.5 cm in length), suggest that an ecological optimum must have existed in which large amounts of nutrients and chemical ions such as calcium and phosphorus were present (Figure 9).

4. Uiraúna-Brejo das Freiras (Triunfo) Basin

4.1. Geology

Located in the west of the state of Paraíba in the counties of Uiraúna, Poço, Brejo das Freiras, Triunfo and Santa Helena, this basin of 480 km^2 is an assymmetric graben which was controlled by a northwest transcurrent fault system. The Precambrian basement is composed of magmatic (granites, gabbros and diorites) and metamorphic (migmatites, gneisses,

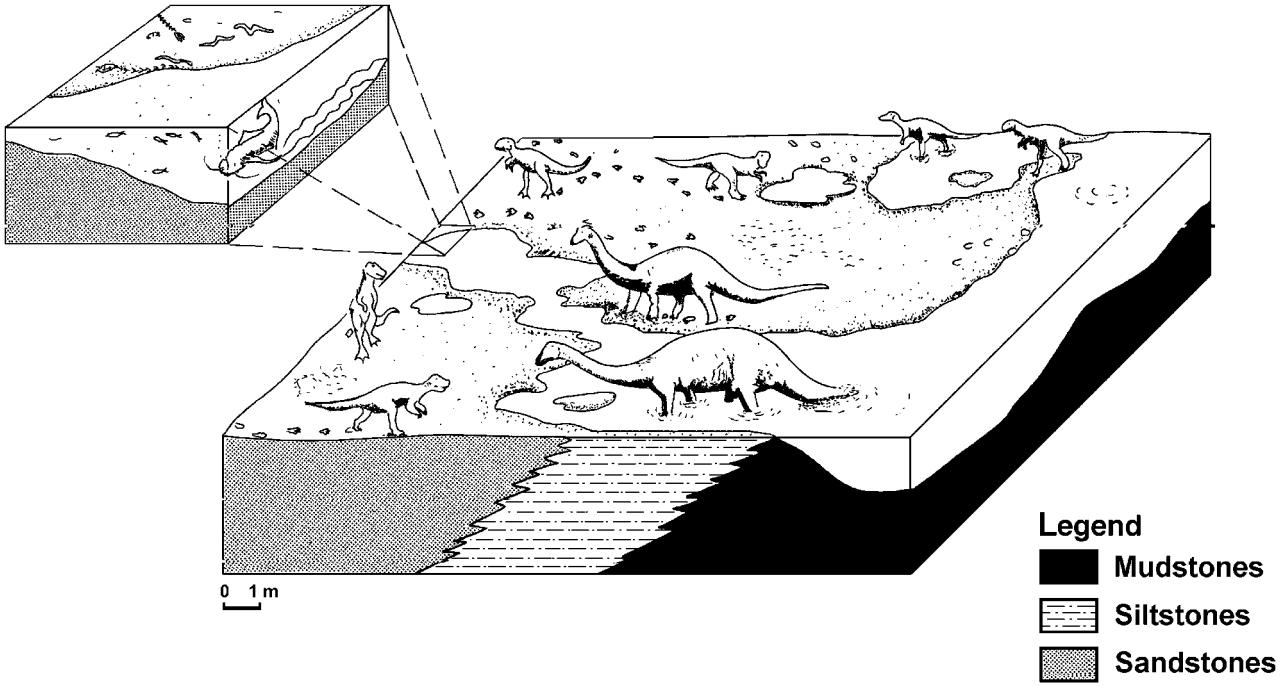

Figure 9. Hypothetical reconstruction of the depositional environment at Fazenda Caiçara-Piau (Sousa Basin), a swampy environment during the Aratu stage (Sousa Formation).

quartzites and marbles) rocks. In the basin, the main lithologies are clastic rocks: breccias, conglomerates, sandstones, siltstones, shales and mudstones. Limestones are rare, occurring as nodules or as cm-thick levels in marls.

The lithostratigraphic terms used in the Uiraúna-Brejo das Freiras Basin are the same as for the Sousa Basin. However, only the Antenor Navarro and Sousa formations are present. The total thickness of these deposits is unknown. Besides the breccias and conglomerates near the faulted margins, there are coarse arkosic sandstones and medium-fine quartzose sandstones with an argillaceous matrix or siliceous cement in the Antenor Navarro Formation. The main sedimentary structures are cross-channel and planar stratification. As the basin is an asymmetric graben, the finer-grained lithologies are distributed in the south-southeast region of the basin where tilting was greater than elsewhere. Such deposits are referred to the Sousa Formation, which comprises shales and mudstones interbedded with sandstones and siltstones. The main sedimentary structures are ripple marks, climbing ripples, mud cracks, convolute lamination and those indicating fluidization.

The origin of this basin, in common with the Sousa Basin and others, was a result of reactivation of basement transcurrent faults. Deposition of coarse grained sediments on the margins occurred under the strong influence of tectonic activity. The tilted blocks created a pronounced rupture in terrain topography, and in the southern part of the basin, the decrease in gradient favoured the establishment of meandering fluvial and lacustrine environments.

4.2. Palaeontology and age of the deposits

Conchostracans, bone fragments, and both invertebrate and vertebrate ichnofossils occur in the Uiraúna-Brejo das Freiras Basin. Except for the dinosaur footprints, which are located close to the northern margin, the fossiliferous localities are in the central-south region of the basin. There are no micropalaeontological or palynological records for the sediments, which inhibits precise determination of their age. However, as noted by Carvalho *et al.* (1993a, b), the geological setting for the ichnofossils on the basin margins is the same as that of the Sousa Basin. The palaeoenvironmental interpretation indicates coalescing alluvial fans and an anastomosing fluvial system. By analogy with the sediments dated by palynology in the Sousa Basin, and considering the similarities among the ichnofaunas, the main depositional phase in the Uiraúna Basin probably dates from between the Rio da Serra and Aratu stages (Berriasian–Lower Barremian).

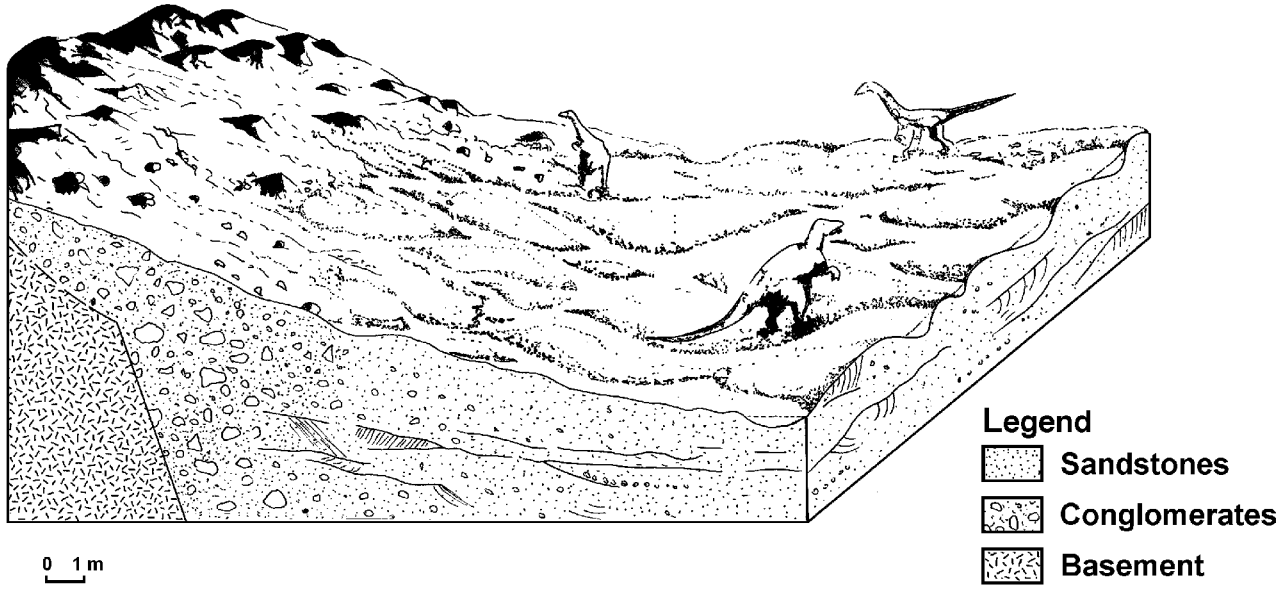

Figure 10. Idealized reconstruction of the depositional environment at Fazenda Pocinho (Uiraúna-Brejo das Freiras Basin), Antenor Navarro Formation.

4.3. The dinosaurian ichnofauna and its stratigraphic context

There are few footprints in the Uiraúna Basin. Hitherto, just four isolated footprints and two incomplete tracks have been identified (Carvalho, 1996). Among the isolated footprints, there are three that probably belong to theropods. The poor preservation of the others does not allow the identification of the producers. One incomplete trackway consists of just two footprints; these are digitigrade, tridactyl and mesaxonic. There is a protuberance at the proximal border of the footprints that would correspond to finger I or to a more distal pad of finger IV. The rounded extremities of the fingers, without clear claws, suggest that they were made by a small ornithopod. These footprints are preserved in a fine sandstone and do not show morphological details.

The stratigraphic succession where they occur, in the Antenor Navarro Formation, begins with conglomeratic sandstones which are overlain by coarse and immature sandstones. They were encountered in a sequence of interbedded medium to fine grained sandstones and siltstones. The main sedimentary structures are cross-channel and planar stratification. The beds show a tabular geometry (Figure 8). The succession has been interpreted as an alluvial fan deposit (Figure 10). The footprints would have been made during periodic breaks of sedimentation when channel sand bars became subaerial owing to discharge fluctuations.

5. Araripe Basin

5.1. Geology

The Araripe Basin contains one of the larger outcrop areas of Cretaceous rocks (12,200 km^2) among the northeast intracratonic basins. It is located in the southern part of Ceará state, in the west of Pernambuco state and in eastern Piauí. The basement is composed of magmatic and metamorphic rocks Granites occur on the western and southern margins; gneisses and migmatites are the main high grade metamorphic lithologies. Metasediments, such as quartzites and other low grade metamorphic rocks, including chlorite-schists, phyllites and marbles, are also present.

The basin is filled with conglomerates, sandstones, siltstones, shales, mudstones, marls, limestones, gypsum and anhydrite. The lithostratigraphic subdivision of these rocks has been discussed and reviewed by many authors. The most widely accepted terms for the lithostratigraphic units (Beurlen, 1963, 1971; Cavalcanti & Viana, 1992) are the Cariri, Brejo Santo, Missão Velha, Santana and Exu formations.

Some authors have interpreted the evolutionary history of the Araripe Basin in a multi-historic context, starting in the Palaeozoic (Assine, 1992; Brito Neves, 1990; Ponte, 1992). However, as shown by Carvalho *et al.* (1993b, 1994), the rocks originally considered to be part of a Palaeozoic cycle (Cariri Formation) contain a dinosaurian ichnofauna similar

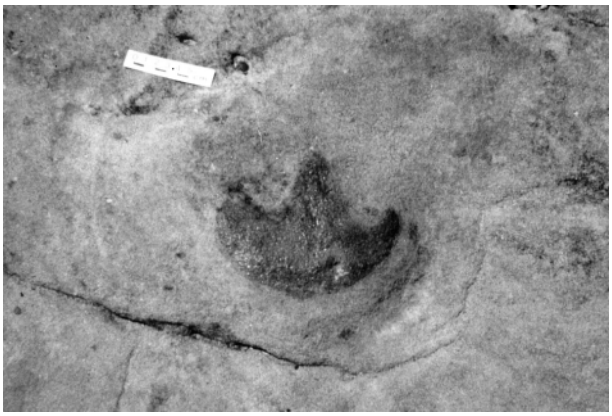

Figure 11. Probable ornithischian footprint from Milagres (Araripe Basin), Cariri Formation (Lower Cretaceous). Scale bar represents 5 cm.

to that found in Cretaceous rocks in neighbouring basins. In common with other intracratonic basins of the northeast, the Araripe Basin had its origin during a Neocomian tectonic event.

5.2. *Palaeontology and age of the deposits*

There are many fossiliferous deposits in the Araripe basin. Microfossils, ichnofossils, plants, invertebrates and vertebrates of Cretaceous age are abundant. A review of these palaeofaunas and palaeofloras can be found in Lima (1978) and Maisey (1991). The chronological distribution of the rocks of the basin is between local stage D. João ('Purbeckian' ?) and the end of the Albian.

5.3. *The dinosaurian ichnofauna and its stratigraphic context*

Dinosaur footprints in the Araripe Basin have been identified at one locality. They include a single trackway, isolated prints of theropods, and one print of a probable ornithopod (Figure 11). They are all tridactyles, mesaxonic and preserved in concave epirelief, with a convex displacement rim. They occur in a fine-grained sandstone interbedded with coarse sandstones within the Cariri Formation. The coarsening-upwards cycles show cross-channel, tabular cross-stratification and climbing ripples (Figure 12). The palaeoenvironmental interpretation of such deposits is one of coalescent alluvial fans and an anastomosing fluvial system (Carvalho *et al.*, 1994).

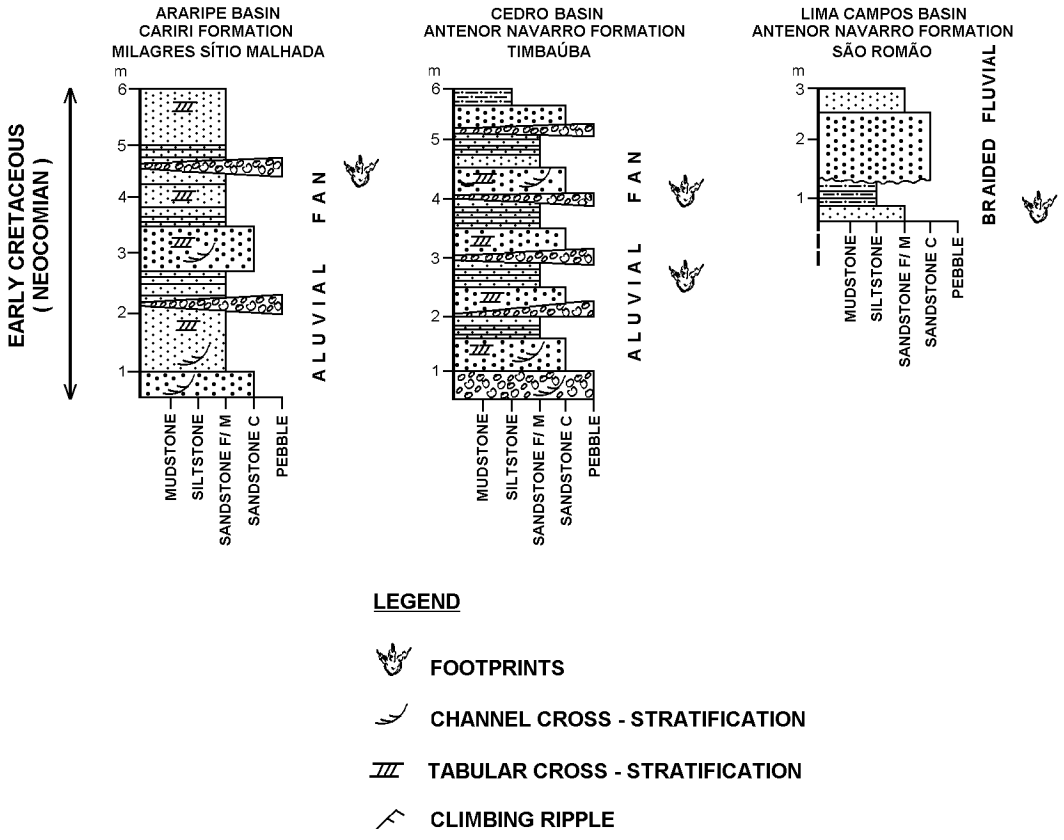

Figure 12. Stratigraphical profiles from the dinosaurian footprint areas, Araripe, Cedro and Lima Campos basins.

6. Cedro Basin

6.1. Geology

The Cedro Basin is located on the border between Pernambuco and Ceará states, and is 690 km^2 in areal extent. It belongs to the rift system developed by transcurrent movements along the Paraíba and Pernambuco lineaments. Its basement is composed of chlorite-schists, phyllites, and metavolcanic and gneissic-migmatitic rocks. Granitic intrusions are also present close to the western, eastern and northern margins. The longest axis of the basin is in an east–west direction, in common with the Precambrian faults of the basement.

The northeast, southeast and southwest regions of the basin are dominated by conglomerates and sandstones, sometimes with interbedded siltstones and shales. In the central-north region, shales and siltstones may interfinger with carbonate or sandstone beds. The northwest margin is dominated by laminated limestones and marls.

The rocks have been attributed to two lithostratigraphic units, the Tacaratu and Aliança formations. These encompass the lithologies close to the margins (conglomerates, sandstones) and in the middle (shales, carbonates) of the basin (Assunção & Miranda, 1983; Sato, 1983). Nevertheless, they are very similar in composition to the Antenor Navarro, Sousa and Santana (Crato Member) formations in the Uiraúna and Araripe basins nearby.

The depositional environments indicated are continental, typical of an interior rift basin, and include alluvial fans and anastomosing rivers close to the basin margins. Shallow, ephemeral lakes developed in areas of low gradient, but laminated limestones up to 20 m thick suggest that some water bodies were perennial lakes.

6.2. Palaeontology and age of the deposits

There is one ichnofossil locality in the Cedro Basin where footprints of carnivorous dinosaurs are present. These are associated with two fossil occurrences that have yielded ostracods, conchostracans and gastropods. The ostracods indicate the local Alagoas stage (Lower Aptian–Lower Albian).

6.3. The dinosaurian ichnofauna and its stratigraphic context

The footprints are not well preserved. They are tridactyl forms, isolated or in possible association but do not represent continuous trackways. They are filled with the same sediment as the surrounding matrix, sometimes having a reddish colour that makes them more visible. The individuals that produced these footprints were probably bipeds, and their general morphology indicates that they were made by theropods.

The stratigraphic levels in which they occur are the top of fining upward cycles. These begin with conglomeratic sandstones, with pebbles of quartz and metamorphic rocks, and are overlain by coarse and fine quartzose sandstones (Figure 12). As in the Uiraúna, Sousa and Araripe basins, the Cedro footprints also occur in deposits interpreted as having accumulated in a fluvial-alluvial fan. The grain size of the sediments that formed the substrate over which the dinosaurs travelled, was probably the main limiting factor on the footprint preservation. Such ichnofossils, in this stratigraphical context, are rare and difficult to recognize (Carvalho *et al.*, 1995).

7. Iguatu, Malhada Vermelha, Lima Campos and Icó basins

7.1. Geology

The areal extent of these four neighbouring sedimentary basins was strongly controlled by the tectonic structures of the Precambrian basement. The Iguatu basin is approximately 780 km^2; Malhada Vermelha is 65 km^2; Lima Campos is 105 km^2 and Icó is 120 km^2. Clastic rocks (conglomerates, breccias and sandstones) are present in all of them, mainly close to the fault zones that delineate their margins. The central areas of the basins that are far from active faults contain successions of fine sandstones, siltstones, shales, mudstones, limestones and marls. Lithostratigraphically these form the Iguatu Group, which comprises Quixoá (coarse sandstones interbedded with conglomerates), Malhada Vermelha (fine sandstones, shales and marls) and Lima Campos (conglomeratic and fine sandstones) formations. Srivastava (1990) suggested, however, that the stratigraphic terminology should follow that of the Sousa Basin (Antenor Navarro, Sousa and Piranhas formations) because they are lithologically similar and belong to the same tectono-sedimentary framework.

7.2. Palaeontology and age of the deposits

The fossils that have been recovered from this sedimentary area include ostracods, conchostracans, molluscs, fishes, bone fragments of reptiles and plants (Carvalho, 1993). This association indicates a temporal range between the Late Jurassic and Early

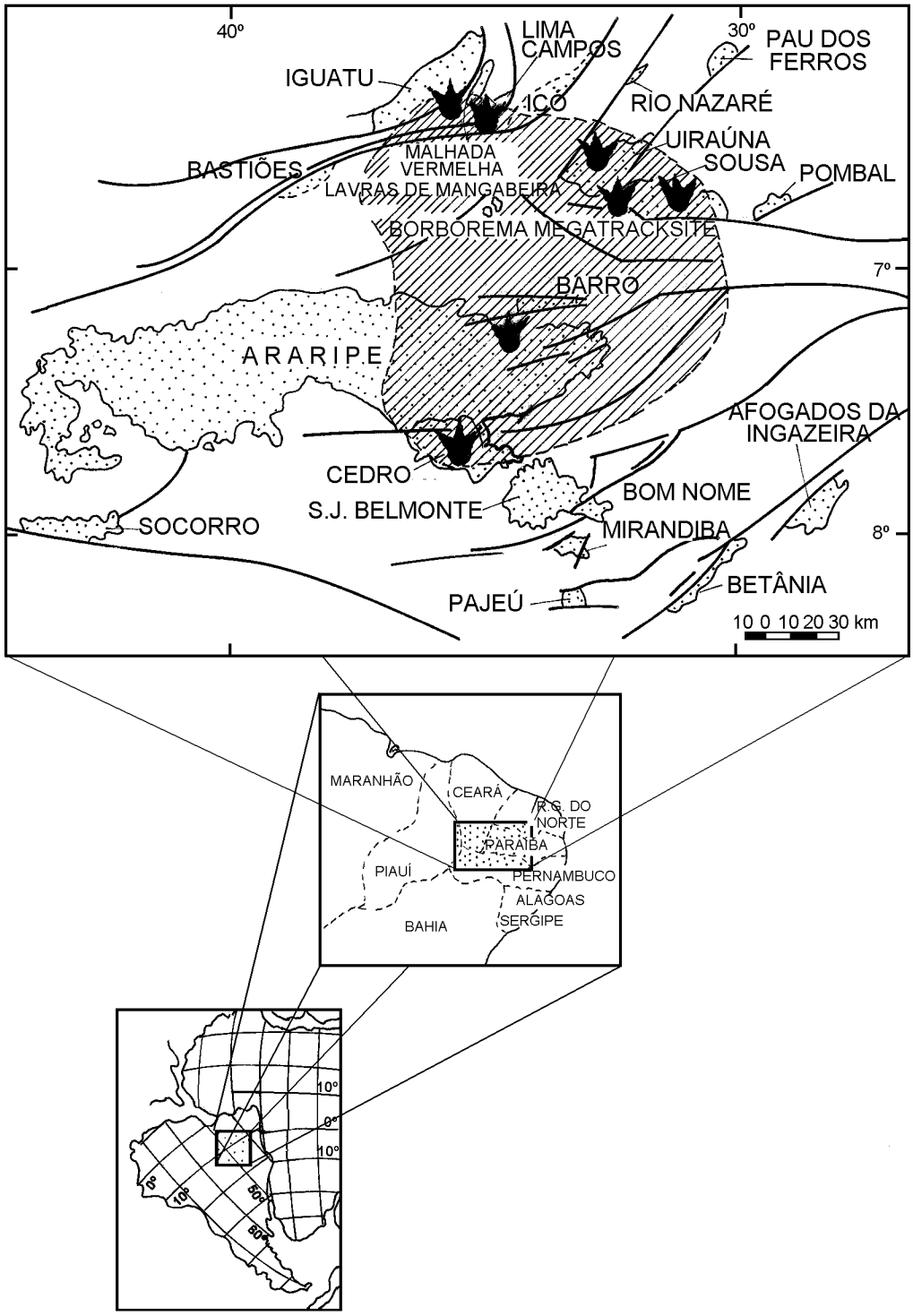

Figure 13. Borborema Megatracksite area during the Early Cretaceous (Rio da Serra and Aratu local stages).

Cretaceous. Analysis of the conchostracans has indicated the presence of forms that are typical of the Rio da Serra (Berriasian–Hauterivian) and Aratu (Hauterivian–Lower Barremian) local stages.

7.3. The dinosaurian ichnofauna and its stratigraphic context

Leonardi & Muniz (1985) and Leonardi & Spezzamonte (1994) recognized tracks of theropod

and ornithopod dinosaurs in the basins of Lima Campos (Quixoá Formation) and Malhada Vermelha (Malhada Vermelha Formation). The palaeoenvironments in these areas were alluvial fans close to the basin margins. Breccias, conglomerates and coarse sandstones indicate the influence of fault reactivations (Figure 12). According to Mabesoone *et al.* (1979), far from the alluvial fans there were anastomosing-meandering fluvial channels and ephemeral lakes.

8. The Borborema megatracksite

In the intracratonic basins of northeast Brazil it is clear that the geographic distribution of dinosaurian footprints is not uniform. The major concentration of footprints is found in siltstones and mudstones in the central part of the Sousa Basin. They also occur in fine sandstones of the Antenor Navarro (Sousa and Uiraúna basins) and Cariri (Araripe and Cedro basins) formations, with the areas near the margins of these basins showing a lower level of 'dinoturbation'. Such factors mirror the time of sediment accumulation and the substrate characteristics, since it is possible that the high accumulation rate of coarse sediments did not allow an extensive biogenic reworking. Besides the grain size, the low water content and the lack of sediment plasticity prevented the preservation of a large number of footprints.

The dinosaur ichnofaunas of these basins fall within the same stratigraphic-time-palaeogeographic context. Viana *et al.* (1993) proposed that the occurrences may comprise a wide megatracksite. The name Borborema for this megatracksite (concept according to Lockley, 1991) has its origin in the structural Province of Borborema, a region where the intracratonic basins are located. It comprises parts of the Iguatu-Malhada Vermelha-Lima, Campos-Icó, Uiraúna, Sousa, Araripe and Cedro basins (Figure 13) and probably embraced a specific ecological zone at the beginning of the Cretaceous. The occurrence of theropods, sauropods, and ornithopods was controlled by the environmental changes resulting from the regional tectonic activity which led to the development of new ecological niches. Although the dinosaurs may have inhabited all of northeast Brazil, their record was restricted to these sedimentary basins. It is possible, as suggested by Jacobs *et al.* (1989), that the dinosaur faunas of West Africa (Koum Basin, Cameroon) were related to those of northeast Brazil. Nevertheless, the varied relationships between the regional tectonic activity, climate and hydrography probably contributed to the diversification of a single fauna, with no parallels outside the gondwanan context.

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