



BRAZILIAN THEROPODS FROM THE EQUATORIAL ATLANTIC MARGIN: BEHAVIOR AND ENVIRONMENTAL SETTING

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ABSTRACT: The São Luís Basin, located on the equatorial coastal region of Brazil, shows a diversified Upper Cretaceous biota. The commonest vertebrate fossils and ichnofossils belong to a theropod dinosaurian fauna that is widespread over that geographic area. The theropod footprints and associated bone fragments are found in fine-grained quartzose sandstones, deposited in nearshore environments submitted to tidal currents. They are found in six localities of São Luís and Alcântara counties: Ponta da Guia, Ponta do Farol, Praia do Boqueirão, Ilha do Medo, Praia da Baronesa and Ilha do Cajual. There are trails and isolated footprints attributed to large and small theropods and ornithischians. The best preserved footprints are found at Ponta da Guia and Praia da Baronesa. The ichnocoenoses of Ponta da Guia and Praia da Baronesa, are discussed from the view point of dinosaurian social behavior. A gregarious behavior was observed among the Ponta da Guia theropods - a rare herding structure in this dinosaur group. The randomly oriented trackways and isolated footprints at Praia da Baronesa were interpreted as the record of a "foraging area" for theropods. There they would search for fishes, turtles and other organisms, found in small lagoons and channels of a tidal flat environment. The footprint-bearing strata of São Luís Basin are considered to compose a megatracksite alongside the early equatorial Atlantic ocean. Its geological context - a low-gradient coastal plain - allowed the establishment of specific dinosaur groups. There was a probable ecologic "segregation" of large-sized and small-sized theropods, in this way giving rise to a regional paleobiogeographic and palaeoecologic distribution pattern of the theropod communities.

RESUMO: A bacia de São Luís, localizada na região equatorial do Brasil, apresenta uma biota do Cretácico superior bastante diversificada. Trata-se de uma bacia tipo rifte cuja origem se relaciona com a abertura da margem atlântica no intervalo geocronológico compreendido entre o Aptiano e o Cenomaniano. Os fósseis e icnofósseis de vertebrados mais comuns nesta bacia pertencem a uma fauna de dinossáurios teropodomorfos, a qual está distribuída numa ampla área geográfica. As pegadas e fragmentos ósseos de terópodes são encontrados em arenitos quartzosos finos, depositados em ambientes litorais sujeitos a correntes de maré. Ocorrem em seis localidades dos municípios de São Luís e Alcântara (estado do Maranhão): Ponta da Guia, Ponta do Farol, Praia do Boqueirão, Ilha do Medo, Praia da Baronesa e Ilha do Cajual. As pistas e pegadas isoladas foram atribuídas a pequenos e grandes terópodes, além de ornitíscios, sendo que as pegadas melhor preservadas são oriundas da Ponta da Guia e Praia da Baronesa. Com base nas icnocoenoses da Ponta da Guia e Praia da Baronesa, é discutido o comportamento social destes dinossáurios. Foi observado o hábito gregário entre os terópodes da Ponta da Guia - uma estrutura organizacional rara neste grupo de dinossáurios. A orientação aleatória e as várias pegadas isoladas da Praia da Baronesa foram interpretadas como o registo de uma área de alimentação. Os di-

nossáurios desta região poderiam procurar peixes, tartarugas e outros organismos em pequenas lagoas e em canais da planície de maré durante períodos de maré baixa, representando assim uma “área de alimentação” para terópodes de tamanho médio e pequeno. As camadas com pegadas fósseis na bacia de São Luís são consideradas como parte de um “megatracksite”, localizado ao longo da linha de costa durante a fase inicial do oceano Atlântico equatorial. O contexto geológico deste “megatracksite” - uma planície costeira de baixo gradiente - possibilitou o estabelecimento de grupos específicos de dinossauros. Existiu uma provável segregação ecológica dos terópodes de grande e de pequeno tamanho, havendo assim uma distribuição paleobiogeográfica e paleoecológica das comunidades de terópodes.

INTRODUCTION

During the opening of the Atlantic margin in the equatorial region of Brazil (Aptian-Cenomanian time), tectonic action gave rise to numerous rift basins. At the same time, structural reactivation of the Precambrian basement in the interior of the continent, allowed the subdivision of formerly wide sedimentary areas into smaller new basins. The São Luís basin (Fig. 1), located on the northern region of Maranhão State (Brazil), had its origin in this context. This is the only basin in the equatorial Brazilian margin whose Cretaceous outcrops display sediments of this geological phase. In other equatorial basins, coeval deposits have submerged in the continental platform.

Tectonic settings at the end of the Early Cretaceous, originated by the South America - African drifting gave rise to this basin. Intense faulting through the present-day northern coast of Maranhão State originated thick sedimentary deposits.

The outcrop area of the São Luís Basin comprises Upper Cretaceous (Cenomanian) reddish siliciclastics (sandstones, siltstones, shales and mudstones) and some carbonates. These lithologies are grouped into the Itapecuru Formation, which attains 2,000 m in thickness. Of total only 100 m of this unit are seen in outcrops.

Remains of a diversified paleobiota are found in this area, which include plants (angiosperms), mollusks, fishes (bone fragments, scales, teeth) and reptiles (bones, teeth and ichnofossils). The commonest vertebrate fossils and ichnofossils belong to a theropod dinosaurian fauna that occurs over a wide geographic area. Environmental interpretation of the fossil-bearing lithofacies allows reconstruction of a sandy tidal plain area, cut by freshwater and tidal channels, thus composing the scenery of a littoral area submitted to a hot and dry climate.

Of all ichnofossil localities in the São Luís Basin, two display the most abundant theropod tracks. The best one is located at Ponta da Guia (São Luís County) where it is possible to observe the parallel orientation of four large theropod trails, pointing out to a possible gregarious behavior. This aspect of

theropod paleobiology, although uncommon, was already recorded by LEONARDI (1984, 1989) and THULBORN & WADE (1979, 1984) from tracks of the Toro-Toro ichnofauna (El Molino Formation, Maastichtian - Bolivia) and the Queensland ichnofauna (Winton Formation, Albian-Cenomanian - Australia).

This study presents a global view of theropod ichnofossil and fossil data from the equatorial São Luís Basin. In addition, it discusses the results of palynological analyses that further contribute to a better understanding of the environment where this dinosaurian fauna lived and respective age.

GEOLOGY OF THE SÃO LUÍS BASIN

The São Luís Basin is a Cretaceous rift basin of 18,000 km², whose evolution is related to the origin of the Brazilian equatorial margin. According to ROSSETTI (1996a), the sedimentary framework of this basin was strongly influenced by plate tectonics. During the Aptian, the simple shear stress associated with lithospheric thinning led to the initial rifting. The basin has an asymmetrical profile and is bounded from the neighboring Parnaíba and Barreirinha basins by the Ferrer-Urbano Santos (south), Tocantins (west) and Rosário (east) structural highs. Their pre-Cretaceous depositional history is linked with that of Parnaíba Basin, which altogether comprised a single, broad sedimentary area during the Paleozoic.

In Figure 2 there is a summary of the lithostratigraphy of São Luís Basin, whose total sedimentary thickness attains 4,500 m (ARANHA *et al.*, 1990). The outcrops of Cretaceous rocks are named as the Itapecuru Formation. These rocks consist of reddish sandstones, siltstones, shales and mudstones, with some interbedded carbonates composed of marls and limestones. The main sedimentary structures are channel and planar cross-stratification, ripple-marks, fluidization structures, mud-cracks, herringbone cross-stratification and hummocky cross-stratification. The fossils found in these rocks are palynomorphs, plants (angiosperms), mollusks (Mytilidae, Inoceramidae, Pectinidae, Plicatulidae, Limidae, Ostreidae, Trigonidae and Matricidae),

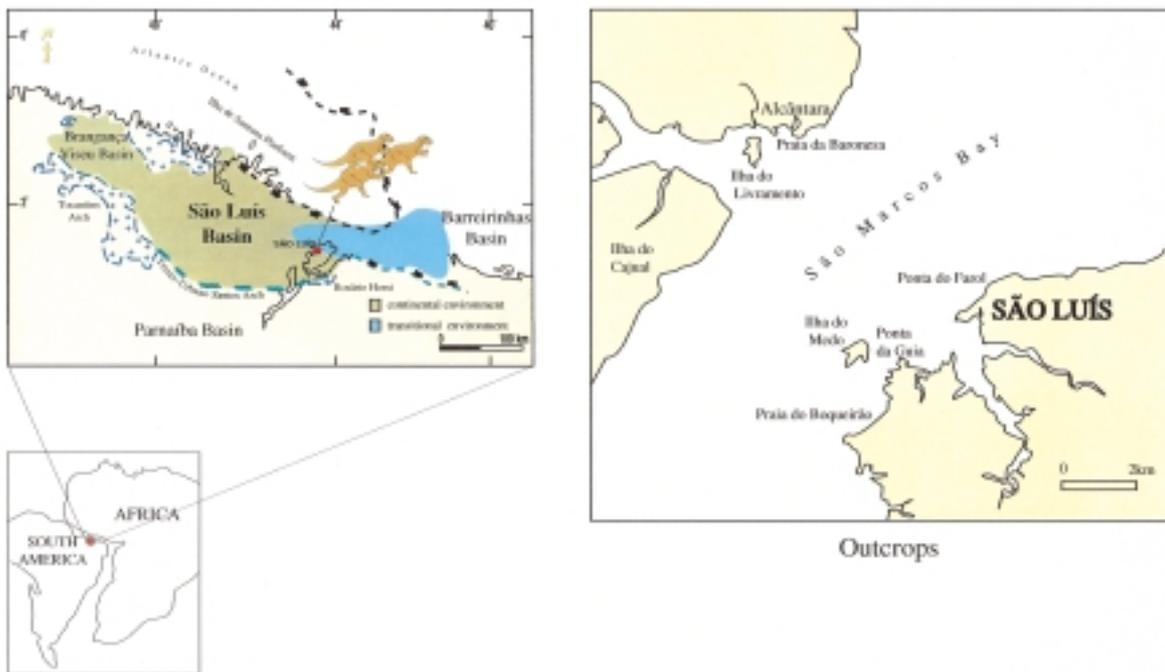


Fig. 1 - Location map of São Luís Basin, Brazil, and its paleogeographical position during Cenomanian.

fishes (Dipnoi, Elasmobranchia and Actinopterygii), reptiles (Dinosauria, Crocodylia and Chelonina). There are also vertebrate (dinosaurian footprints) and invertebrate ichnofossils.

The environmental interpretation of outcrop lithofacies points out to estuarine, nearshore and shallow marine environments affected by both tidal and storm processes (KLEIN & FERREIRA, 1979; ROSSETTI, 1994, 1996a). According to ROSSETTI (1996a), the architectural distribution of some deposits of the Itapecuru Formation revealed a prograding, barred coast, probably in the distal (seaward) portion of a wave-dominated estuarine system.

THEROPOD FOOTPRINTS: EVIDENCE OF GREGARIOUS BEHAVIOR

The theropod footprints and the associate bone fragments in the São Luís Basin are found in fine-grained quartzose sandstones, with large scale cross-stratification. RODRIGUES, LOVATO & CAYE (1990) considered such lithofacies as the result of deposition in nearshore environments submitted to tidal currents. These authors considered the possibility of subaerial exposure of subaqueous dunes with aeolian reworking. Alongside the coastline of a shallow marine environment lived an abundant dinosaurian fauna.

The dinosaurian footprints on São Luís Basin are found in six localities of São Luís and Alcântara

counties: Ponta da Guia, Ponta do Farol, Praia do Boqueirão, Ilha do Medo, Praia da Baronesa and Ilha do Cajal (CARVALHO & ARAÚJO, 1995). There are trails and isolated footprints attributed to large and small theropods, and ornithischians. The best preserved footprints localities are at Ponta da Guia and Praia da Baronesa.

The footprints found at Ponta da Guia are considered to have been produced by two different groups: theropods and ornithopods. The ones attributed to theropods are large-sized and show relationships with carnosaurs. Four trails present parallel orientation, a possible evidence of a gregarious behavior. The ornithopod footprints were assigned to hadrosaurians.

Dinosaurian social behavior was analysed by CURRIE (1983), LEONARDI (1980; 1989), LOCKLEY (1986, 1991), LOCKLEY, HOUCK & PRINCE (1986), LOCKLEY *et al.* (1992) and THULBORN (1990). The inferences about herding among dinosaurs can be supported upon ichnological analyses. The trackways in a preferred direction can be a proof of gregariousness, although a physical feature on the environment could have controlled a series of individuals that have passed on a same area at different time intervals. A way to distinguish herd trackways from physically controlled pathways is the presence of trackways with different moving direction from the ones that were considered as indicative of a gregarious behavior. The intertrackway spacing is another criterion in favor of herding. The regular space be-

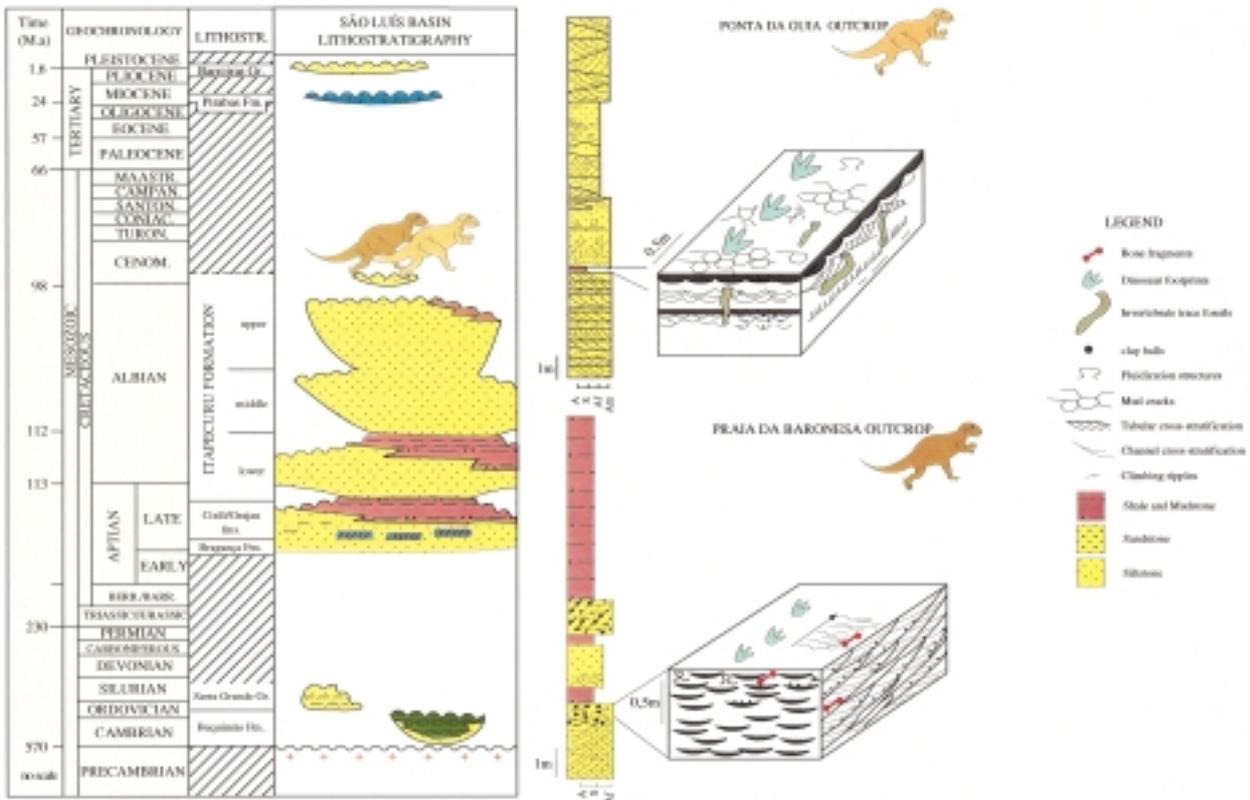


Fig. 2 - Stratigraphy summary of São Luís Basin.

tween adjacent trackways suggests animals walking in some kind of regular formation (LOCKLEY, 1991). The gregariousness on dinosaur faunas was already inferred from some Brazilian ichnofaunas. GODOY & LEONARDI (1985), LEONARDI (1980, 1989), CARVALHO & LEONARDI (1993) recognized this ethological aspect in Lower Cretaceous ichnofaunas from Sousa Basin (Sousa Formation) and Parnaíba Basin (Corda Formation) at Northeastern Brazil.

The mapped trackways at Ponta da Guia show a group of four large theropods trackways that present clear morphological similarity (Fig. 3-4). The angular range of movement directions is only 20°, and the maximum intertrackway spacing is 4 m. These facts constitute good evidence to postulate the gregariousness among the producers. Because there are tracks in different directions, it is possible to consider the absence of a physical barrier of the landscape configuration that could have controlled the movement direction of individuals (Fig. 5).

The herding evidence among theropods, although rare, is also found in other ichnofaunas. LEONARDI (1984, 1989) described a group of 60, and another of 32, unidirectional carnosaurian track-

ways from El Molino Formation (Maastrichtian Toro-Toro Basin, Bolivia). A mixed herding of ornithopods and coelurosaurs was recorded by THULBORN & WADE (1979, 1984) from the Winton Formation (Albian-Cenomanian - Queensland, Australia). The uncommonness of well documented evidence of a gregarious behavior among theropods can be explained by the paleoecological analysis of FARLOW (1976, *apud* THULBORN, 1990). He considered that carnosaur might have hunted singly or in small packs, what could explain the high frequency of individual carnosaur tracks.

The other main theropod footprint assemblage is located at Praia da Baronesa. It is composed by randomly oriented trackways and isolated footprints (Fig. 6). They are always associated with fluidization structures and present superficial colour stains (blue-gray, green or red). CARVALHO (1994) explained the fluidization around the footprints as the result of a "dinostatic pressure" in water-saturated and low coesive sediments. Such substrate aspect is corroborated by the metatarsal impressions in many footprints. KUBAN (1991b) considered that this preservational character could be indicative of a behavior response to a soft substrate. The elongate plantigrade footprints would be explained by a low



Fig. 3 - A theropod trackway from Ponta da Guia outcrop, São Luís Basin.

posture assumed whenever a dinosaur foraged in mud flats or shallow water for small food items, stalking larger prey or while approaching other dinosaurs.

A common feature in the Praia da Baronesa footprints is the contrasting colours from the surrounding substrate. There is a range from reddish to blue-gray colours, contrasting with the light greenish hue of the substrate. KUBAN (1991a) also observed this feature in dinosaur tracks of the Glen Rose Formation (Lower Cretaceous, Texas - USA). He explained this taphonomic aspect as the result of secondary sediment infilling on the original track depressions and oxidation of iron on the surface of infilling material.

The substrate where the theropod tracks of Praia da Baronesa are found also contain many skeletal remains of a diversified fauna. There are fishes from the families Myliobatidae, Semionontidae, Enchondontidae and Sparidae. Reptile remains include Pelomedusidae (Testudines), Mosasauridae and Theropoda (EUGÊNIO, 1994). VILAS-BÔAS & MEDEI-

ROS (1997) considered the theropod remains (isolated teeth) as indicative of a group with dromosaurid affinities. These fossils are found in fine-grained sandstones deposited in a tidal-channel environment (Fig. 7).

The erratic distribution of footprints at Praia da Baronesa could indicate a “foraging area” to the theropods. The theropods would search for fishes, turtles and other organisms, foraging food in the small lagoons of a tidal flat. During low-tide periods, subaerial exposure of the sediments allowed the di-noturbation. This could be a good foraging area for the theropod dinosaurs, due to the presence of aquatic animals caught in small water ponds along the exposed channels of the tidal plain.

ENVIRONMENTAL SETTING OF THEROPOD COMMUNITIES

The environmental scenery during the Cenomanian, in the São Luís Basin comprises many subenvironments associated with an estuary that occupied a low-gradient coastal plain. Distinct dinosaur communities are found in this geological context.



Fig. 4 - An isolated theropod footprint from Ponta da Guia outcrop, São Luís Basin.

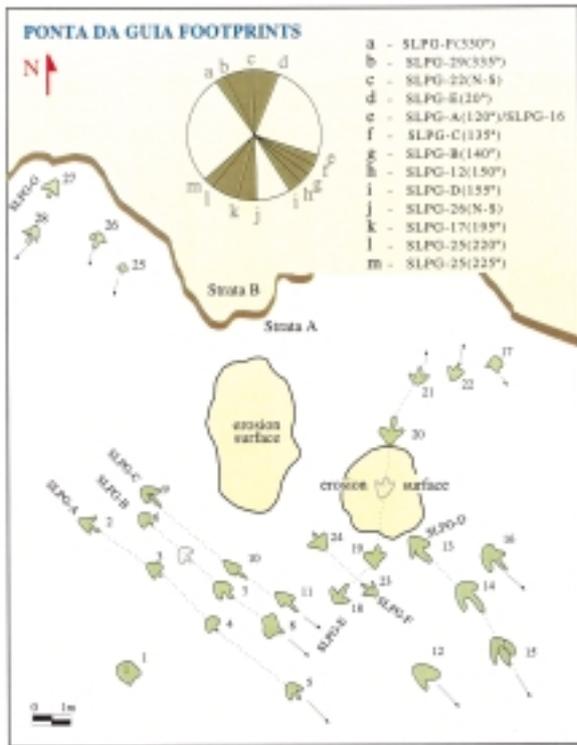


Fig. 5 - Footprints map distribution at Ponta da Guia. The diagram on the upper right corner shows the main movement directions of the dinosaurian fauna (Modified from CARVALHO, 1995 and CARVALHO & GONÇALVES, 1994).

ROSSETTI (1996b) recognized two depositional intervals (lower and upper successions) in outcrops of the São Luís Basin. The lower succession, observed at Ilha do Livramento, consists of a regressive interval - an upward transition from seaward to landward settings. ROSSETTI (1996a) grouped these strata into four facies associations, and attributed them to the following depositional settings: upper shoreface, foreshore, tidal channel, and lagoon-washover. It is in the well sorted and fine-grained sandstones assigned to the upper shoreface facies that skeletal theropod remains are found, such as teeth and bone fragments (Fig. 8). Sandstones of this facies contain large-scale, low-angle cross-beddings that are interpreted by ROSSETTI (1996a) to result from the drift of large-scale bedforms in a depositional setting characterized by the combined flows of storm-generated and tidal-generated currents. This author considered that such deposits revealed a prograding, barred coast probably formed on the seaward portion of a wave-dominated estuarine system.

The footprint bearing-strata are found in the upper succession of ROSSETTI (1996b). The upper succession consists of tidal-dominated deposits at-

tributed to channel, sand flat, delta, and bay fill depositional settings of an estuary. EBERTH & BRINKMAN (1997) considered that portions of ancient estuarine paleochannels have high theoretical potential for burial and preservation of vertebrate skeletal remains. They described a mud-filled incised-valley system in the Dinosaur Park Formation (Canada, Late Campanian) that shows this preservational potential. Much like in the deposits of Itapecuru Formation (São Luís Basin), there are sedimentological and paleontological features indicating mixed marine and non-marine influences.

The fossil tracks and skeletal remains found in the fine-grained sandstones and siltstones of Praia da Baronessa are related to a tidal channel setting. During low-tide periods, subaerial exposure of the bedforms allowed them to suffer dinoturbation. The strata at Ponta da Guia were grouped by CARVALHO (1995) and CARVALHO & GONÇALVES (1994) into two facies associations. They were considered as the result of tidal flat and aeolian sedimentation. The track-bearing strata are fine-grained sandstones,



Fig. 6 - Theropod footprints from Praia da Baronessa outcrop (Itapecuru Formation, São Luís Basin). There are an abundant association of theropod footprints and teeth on the same stratigraphic level.

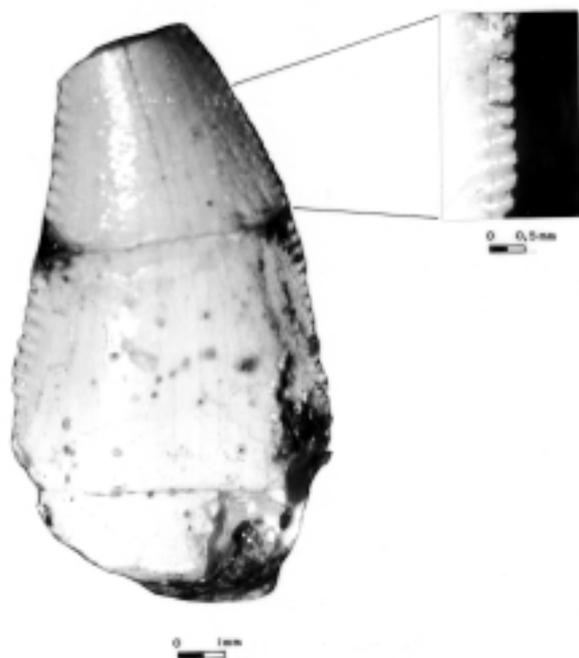


Fig. 7 - Theropod tooth with probable dromeosaurid affinities from Praia da Baronesa outcrop (Itapecuru Formation, São Luís Basin).

interbedded with argillaceous siltstones, that show small-sized channel and tabular cross-stratification, ripple-marks, mud-cracks and clay-balls, laid down in a sand flat depositional environment. The theropod footprints were probably produced in the supratidal region of a low-gradient tidal flat, where the preservational potential is greater.

ROSSETTI (1996b) considered that the lower and upper successions are part of two incised valley fills. The lower succession was deposited at a time of slow rise in relative sea-level, during the highstand tract of an older incised valley. Meanwhile, the upper succession record the transition from the transgressive to the highstand systems tract of a younger incised valley.

PALYNOLOGY

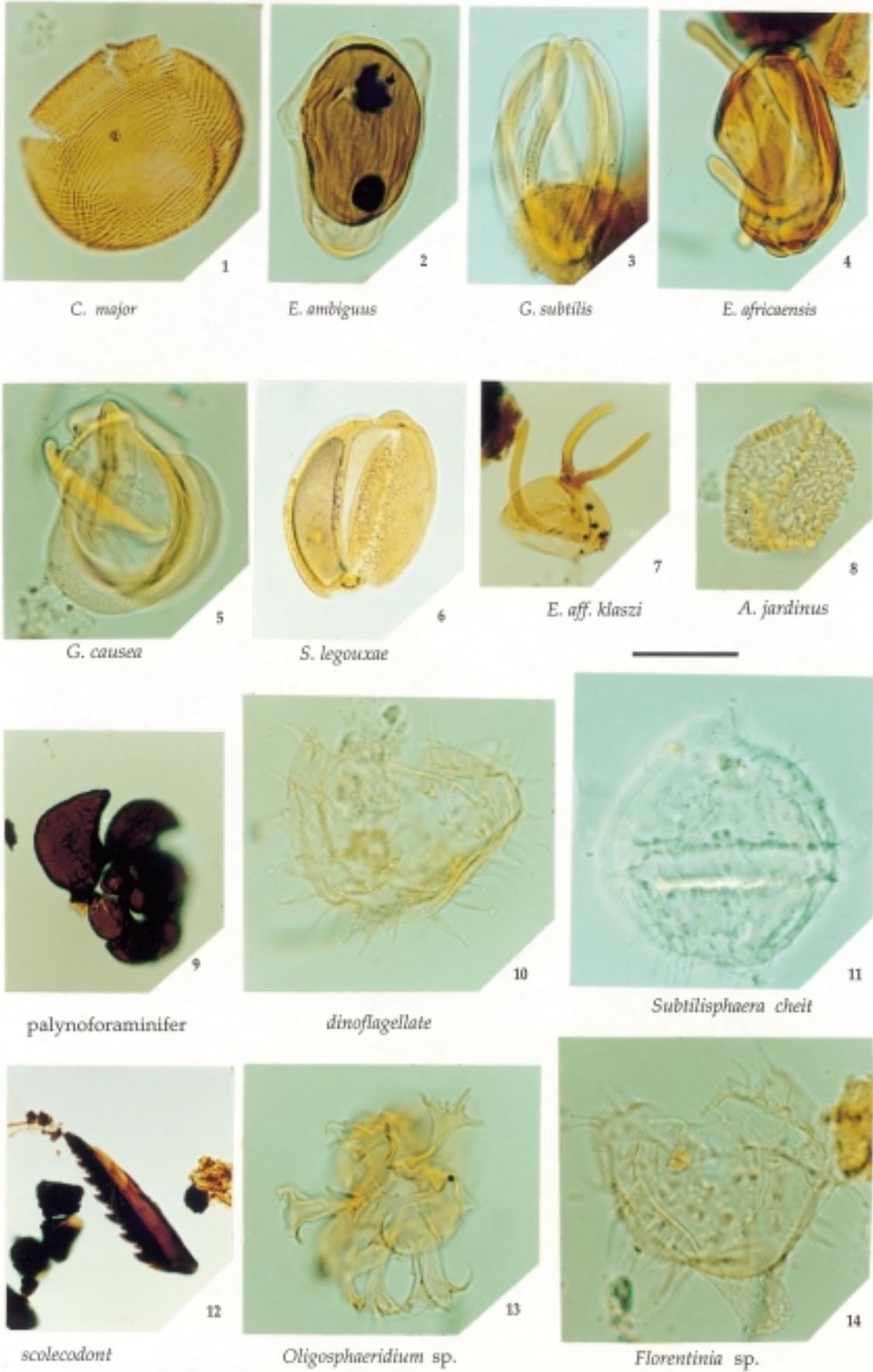
Through palynological analyses (Fig. 9) it is possible to obtain a better understanding of some environmental aspects under which the theropod fauna lived (PEDRÃO, 1995).

The palynological content of outcrops in the east portion of São Luís Basin include miospores shed by the local flora, protozoans and polychaets (PEDRÃO *et al.*, 1993; PEDRÃO, 1995; PEDRÃO *et al.*, 1995). Continental palynomorphs are pteridophyte spores (*Crybelosporites* DETTMANN, 1963), gymnosperm pollen grains (*Classopollis major* GROOT & GROOT,

1962, *Equisetosporites ambiguus* HEDLUND, 1966, *Equisetosporites* spp. (DAUGHERTY, 1941) POCOCK, 1964, *Steevesipollenites* spp. STOVER, 1964), angiosperms (*Afropollis jardinus* DOYLE, JARDINÉ & DOERENKAMP, 1982, *Hexaporo-tricolpites emilianovi* BOLTENHAGEN, 1967, *Cretacaeiporites polygonalis* HERNGREEN, 1973, *Cretacaeiporites mulleri* HERNGREEN, 1973) and some taxons of doubtful botanical affinity (*Elateroplicites africaensis* HERNGREEN, 1973, *Galeacornea causea* B JARDINÉ, 1967, *Elaterocolpites castalaini* JARDINÉ, 1967, *Elaterosporites* aff. *klaszi* JARDINÉ, 1967 and *Sofrepites legouxae* JARDINÉ, 1967). The main pollen group in this assemblage (*Classopollis* (PFLUG) REYRE, 1970) derives from gymnosperms of the family Cheirolepideaceae. Secondly, there occur *Equisetosporites* and *Steevesipollenites* pollen grains. All of them are indicative of a hot climate. The angiosperm pollen grains are rare, although the presence of *A. jardinus* indicates an equatorial climate. The occur-



Fig. 8 - Theropod tooth from Ilha do Livramento outcrop (Itapecuru Formation - Upper Cretaceous), São Luís Basin. Scale bar: 1 cm.



rence of perisporate trilete spores in this assemblage also points out to the same climate, and in addition, is indicative of a fluvial influence in the depositional area.

The São Luís assemblages include dinoflagellates such as gonyaulacoids (*Spiniferites* (MANTELL, 1850) SARJEANT, 1970), peridinoids (*Subtilisphaera cheit* BELOW, 1981) and condensates (*Florentinia* spp. DAVEY & VERDIER, 1973, *Oligosphaeridium* aff. *breviconispinum* JAIN, 1977). The dinoflagellates are brown and yellow unicelled algae referred to the Division Pyrrophyta, that are found in the marine plankton. There are also chitinous remains in the palynological assemblage such as palynoforaminifera and scolecodonts.

CONCLUSIONS

The theropod fossils and ichnofossils of the São Luís Basin are a unique record of a dinosaurian fauna which inhabited the Brazilian equatorial margin during Cretaceous times. A gregarious behavior is deduced from the analysis of some ichnocoenoses. The ones including randomly-oriented trackways and isolated footprints were interpreted as the record of a "foraging area" for theropods.

Palynological data is consistent with the inference of fluvial, lagoonal and shallow marine depositional environments under dry and hot climate. The pollen grains and spores are of Cenomanian age. Palynological evidence, the invertebrate fossils and the stratigraphic interpretation all point out to a tidal flat of a low-gradient coastal plain as the most likely environment inhabited by the theropods.

The discussed footprint-bearing strata of São Luís Basin are considered a megatracksite. The dominance of large-sized theropod footprints is detected in the southern area of the basin, which includes the Ponta da Guia region. To the north, ichnocoenoses such as that one of Praia da Baronesa show medium- and small-sized theropod tracks. There was a probable ecologic "segregation" of large and small-sized theropods. Its geological context - a low-gradient coastal plain - probably allowed the establishment of specific dinosaur communities.

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Fig. 9 -The Cretaceous palynomorphs from Ponta do Farol (Itapecuru Formation - Lower Cenomanian), São Luís Basin. (Scale bar: 20 μm).

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