ICHNOLOGY OF LATIN AMERICA

SELECTED PAPERS

RENATA GUIMARÃES NETTO
NOELIA BEATRIZ CARMONA
FRANCISCO MANOEL WOHNRATH TOGNOLI
(EDITORS)

MONOGRAFIAS DA SOCIEDADE BRASILEIRA DE PALEONTOLOGIA, 2

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Renata Guimarães Netto
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CONTENTS

PART I. SYNTHETIC STUDIES

PART II. CASE STUDIES

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PREFACE

Ichnology, the study of traces, is a fast growing field that feeds from different and diverse disciplines such as sedimentology, stratigraphy, biology and paleontology. The special publication "Ichnology of Latin America - Selected Papers" arose after the Latin American Symposium on Ichnology 2010 (SLIC 2010) that was held from October 30th to November 7th, 2010, in Sao Leopoldo, south of Brazil. About eighty participants attended the conference, representing 21 institutions from South America, 1 from Central America, 3 from North America, 3 from Europe, and 1 from Asia. The ichnologic community of Latin America is not only one of the largest, but also one of the most active. In that sense, it was worthy to produce this special volume as a synthesis of the current knowledge of ichnology in Latin America.

Two papers address the importance of the trace fossils in the terminal Proterozoic-early Phanerozoic successions of South America. Netto (p. 15-26) synthesizes the knowledge of biogenic structures, body fossils and microbially induced sedimentary structures of the terminal Proterozoic basins of southern Brazil, and discusses the possible relationship between these beds and those from the Avalonian terrane. Buatois & Mángano (p. 27-36) review the ichnology of the Ediacaran-Cambrian Puncoviscana Formation of the North of Argentina from a paleoecologic and macroevolutionary perspective, emphasizing the importance of the feeding strategies related to microbial matgrounds recorded in this succession, as well as the appearance of new body plans and sophisticated feeding strategies.

The other contributions explore part of the Phanerozoic ichnologic record in Latin America. Netto *et al.* (p. 37-68) make a synthetic review of the ichnology of the Paraná Basin in southern Brazil, with emphasis in the invertebrate record. Alonzo-Muruaga *et al.* (p. 69-81) present the state-of-art of the ichnology of the Upper Paleozoic deposits of Paganzo and Calingasta-Uspallata basins, in the northwestern Argentina. Carmona *et al.* (p. 83-97) characterize the most representative trace fossils from the Neogene marine deposits of Patagonia (southeastern Argentina), providing an analysis of this ichnofauna considering local paleoceanographic conditions and exploring its relation with the establishment of the Modern Evolutionary Fauna. VillegasMartín & Rojas-Consuegra (p. 99-106) synthesize the knowledge of the Cuban ichnology through the analysis of the existing literature and the material available in collections. These authors also discuss the future perspectives of this discipline in Cuba. Finally, Souto (p. 107-115) overviews the records of vertebrate's coprolites found in different units of Latin America, providing a general evaluation of morphologic aspects necessary to describe these structures, and introducing the new methods to study them.

Some case studies are also presented herein, reflecting the emergent ichnological research in Latin America. Invertebrate and vertebrate bioturbaton as well as bioerosion are the main addressed themes. Souza *et al.* (p. 119-128) present an initial approach to the ichnology of the Lower Devonian

Maecuru Formation (Amazonas Basin, northern Brazil). Dentzien-Dias *et al.* (p. 129-139) describe vertebrate trace fossils from the Upper Jurassic Guará Formation (south of Brazil) and the Batoví Member of the Tacuarembó Formation (north of Uruguay), which contain numerous dinosaur tracks, dominated by theropod and sauropod tracks and different vertebrate burrows. Frank *et al.* (p. 141-157) synthesize the present knowledge of large tunnels assigned to Cenozoic vertebrates in the southern states of Brazil, and try to identify the possible tracemakers among the South American Megafauna representatives.

In the field of bioerosion, Richiano *et al.* (p. 159-177) focus on the bioerosion structures in Quaternary marine mollusks from the Atlantic Argentine coast (from Rio de la Plata to the south of Santa Cruz province) while Lopes (p. 179-194) describes the bioerosion and bioincrustation in Quaternary body fossils from the Coastal Plain of Rio Grande do Sul State (CPRS), in southern Brazil.

There is much more of the ichnology of Latin America than what is presented in this book. Several high quality papers have been published in indexed journals in the last 30 years, and innumerous papers were published in local journals since the 1950s. An important part of this knowledge is missing in this book, but future editions of the Latin American Symposium on Ichnology will help to fill this gap. To all contributors that helped to construct this compendium, our sincere gratitude. Our special thanks to Jordi M. de Gibert, who was a great enthusiast of the ichnologic research developed in Latin America and who contributed to make this book a reality until his passing, last September.

Renata G. Netto
Noelia B. Carmona
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IN MEMORY OF JORDI MARIA DE GIBERT

Science is a patently *human* endeavor. While we scientists sometimes try to tell ourselves that cold objectivity and pure logic are our goals, in truth it is simple human curiosity and a passion for understanding that drives us in our work. Science is not ever divorced from the humanity of the scientist.

Early in the morning hours of September 23, 2012, the world lost a truly brilliant – and genuinely human – young scientist, Jordi Maria de Gibert-Atienza. Although just four and a half decades in age, Jordi was a visionary leader in the ichnologic community. His sudden and unexpected death was a tragic loss to all of us. The worldwide community of ichnologists is small and collegial, so his loss is felt dearly. Mutual interests and personal friendships bring together ichnologists from all continents, who have created an enviable legacy of working together with uncommon synergy. In recent years Jordi has been at the very center of our international community and has served as a major catalyst for that synergy. John Donne (1572-1631) wrote, "No man is an island, entire of itself. Each is a piece of the continent, a part of the main." Jordi clearly was an important piece of the ichnologic craton! John Donne continued, "Each man's death diminishes me, for I am involved in mankind." Jordi's death may diminish us in the present, but his life expanded us for the future!

Jordi was born, raised and thrived in the rich intellectual and cultural center of Barcelona, Spain. His city's colorful history, vibrant lifestyle and independent spirit inspired and motivated him. But Jordi also was a man of the world – an explorer who traveled on almost every continent of our planet for both scientific inquiry and personal enrichment. Throughout his professional career, Jordi's ichnologic contributions were diverse, expansive and always thoughtful. His trace fossil papers did not just answer the basic questions, "what does it look like?" and "where is it located?" – they also addressed the much more interesting questions, "what does it mean?" and "why is it important?"

As a student at the University of Barcelona, Jordi excelled under the exceptional mentoring and support of Jordi Martinell and the close friendship and collaboration with Rosa Domènech, both of whom have remained among his dearest lifelong friends. Following his doctoral studies in Barcelona, Jordi began a productive association with Roland Goldring at the University of Reading in England, and the two worked on a number of projects and published several insightful papers together. In the late 1990's Jordi came to the University of Utah, where he joined me as a post-doctoral research associate in several collaborative projects, and during his two and a half years in Utah he even taught a few paleontology classes at the University. Jordi and I continued to work together on trace fossil projects in Spain, and just this past summer we initiated two new studies in eastern Spain that are currently in progress. Eventually Jordi was accepted into the faculty ranks of his own academic birthplace and home at the University of Barcelona, where he was very active in teaching and research right up until the moment of his untimely death.

Jordi's published contributions to ichnology are well known and widely respected for many things, including especially his critical examination and application of marine ichnnocoenoses and ichnofacies in both their paleobiologic and sedimentologic contexts. With many different colleagues, he wrote descriptively about fish trace fossils, lacustrine ichnocoenoses, echinoid ichnofabrics, crustacean burrows and worm borings in fossil whale bones. He wrote interpretively about salinity control of ichnofacies in the Mesozoic of Utah and substrate control of ichnofacies in the Cenozoic of Spain. He wrote philosophically about recognizing "homologous" and "homoplastic" behaviors in the trace fossil record. He named several new ichnotaxa (e.g., *Sinusichnus sinuosus*), erected a new ethologic category ("Fixichnia") for surficial etching scars on hard substrates, and established a new ichnofacies (*Entobia* Ichnofacies) for the recurrent trace fossil associations in rocky shore paleoenvironments. He wrote several papers that incorporated ichnologic data with sequence stratigraphic interpretations and paleoclimatic reconstructions. In our most recent paper together (along with Guillem Mas), which appeared in print just a few weeks before his death, Jordi deciphered the complexly spiraling morphology and unusual ethologic implications of an enigmatic trace fossil in the Miocene of Mallorca.

Within the worldwide ichnologic community, Jordi was not just a crucial player but in fact was a key leader. He singlehandedly established and managed the "SKOLITHOS" listserver to facilitate informal communication among ichnologists, and he was a prime mover and the first secretary of the International Ichnological Association. He was among the hard-working organizers of several seminal research conferences in Spain, including the Bioerosion Workshop in Barcelona in 2000, the Crustacean Ichnology Workshop in Lepe in 2010, and the International Ichnofabric Workshop in Colunga in 2011. Just shortly before his recent death, he proudly and enthusiastically volunteered to organize and host the next Ichnia Congress in Barcelona in 2016.

Isaac Newton (1642-1727) famously wrote, "If I have seen farther than others, it is because I stood on the shoulders of giants." Ichnology has benefited from the far-sighted vision of many giants, on whose shoulders we all have stood. I frequently stood on Jordi's shoulders. (And maybe he stood on mine at times.) But standing in one place and gazing afar does not advance our science; we must move ahead. Jordi gazed afar and pointed us in several directions towards bright new horizons. Thanks for your inspiration, Jordi, my friend. Now on we go!

Tony Ekdale

Jordi Maria de Gibert (May 29, 2010, Lepe, Spain)

PART I

SYNTHETIC STUDIES

EVIDENCES OF LIFE IN TERMINAL PROTEROZOIC DEPOSITS OF SOUTHERN BRAZIL: A SYNTHESIS

Renata Guimarães Netto

ABSTRACT

This paper aims to synthesize the knowledge of the biogenic structures preserved in some beds of the Terminal Proterozoic basins of southern Brazil. Simple horizontal (*Cochlichnus, Planolites, Palaeophycus*), meandering (*Gordia, Helminthoidichnites*), and probing (treptichnid morphologies) feeding burrows, horizontal (*Arthraria*) dwelling burrows and plug-shaped (*Bergaueria, Beltanelliformis*) resting burrows, medusa-like and 'Vendobionta' basal disk imprints (*Aspidella, Cyclomedusa, Charnia, Intrites, Panvarcorina, Sekwia*), and microbially induced sedimentary structures (*Arumberia*-type structure, *Kinneyia*-type structure, elephant-skin structures, wrinkle structures, *Chancelloria*-like structures, among others) occur in Camarinha (Paraná State), Itajaí (Santa Catarina State), and in some stratigraphic units of the Camaquã (Rio Grande do Sul State) basins, conferring an Ediacaran age for these deposits. Most of these records are preserved chiefly in fine-grained turbiditic beds originally assumed as non-marine, and at the soles of braidplain delta sandstones (in the Camaquã Basin). The biota composition is similar to the Ediacaran biotas from Avalonian terrains, suggesting a pathway between these terrains and the Rio de la Plata craton during the Ediacaran.

Key words: biogenic structures, Ediacara, 'Vendobionta', Camarinha Basin, Itajaí Basin, Camaquã Basin.

INTRODUCTION

The oldest biogenic structures registered in Southern Brazil occur in the Ediacaran volcano-sedimentary deposits of the Itajaí (Santa Catarina State, SC), Camaquã (Rio Grande do Sul State, RS) and Camarinha (Paraná State, PR) basins (Figure 1). These basins record the depositional events that took place during the late phases of the Brasiliano orogeny at southern Brazil and the Pan-African cycle at southern Africa (*ca* 600-470 Ma) (e.g., Macedo *et al.*, 1984; Gresse *et al.*, 1996; Paim *et al.*, 2000). Several geological evidences led to the correlation of the three basins and also the Itajaí and Camaquã basins with the Vanrhynsdorp and Nama basins (southern Africa) (e.g., Gresse *et al.*, 1996; Brito Neves *et al.,* 1999). However, the paleontological and paleoichnological record known until now in these basins are more similar to the fossil record found in Avalonian terrains (Newfoundland, Canada, see Brasier, 1992; Gehling & Narbonne, 2007; Liu *et al.*, 2010) than those found in the Kalahari craton (S of Namibia and N of Cape Province, South Africa), which was juxtaposed with the Rio de Plata craton at the end of the Neoproterozoic (e.g., Brito Neves *et al.,* 1999; Mallmann *et al.*, 2004). This paper summarizes the available knowledge on the ichnology of the Proterozoic deposits in southern Brazil, aiming to open new perspectives for future studies.

THE ITAJAÍ BASIN

The Itajaí Basin is a narrow, ENE-WSW disposed elongate depositional basin in the East of Santa Catarina State, near the Itajaí River valley (Figure 1) and its geological history starts in the Cryogenian (*ca* 640 Ma, Silva *et al.*, 2002), during the Marinoan Glaciation. Its sedimentary infill dates from the early Ediacaran, as well as its closure, due the so-called Brasiliano/Pan-African collage (Brito Neves *et al.*, 1999) in Western Gondwana (Zucatti-da-Rosa, 2006). The basin was filled by volcano-sedimentary rocks that represent a basal continental system (Gaspar Formation) and an upper bacinal system (Campo Alegre Formation) (Appi & Souza Cruz, 1990). The coarse-grained deposits exposed in the northern portion of the basin correspond to alluvial and delta fans while the southern deposits are chiefly represented by turbidites (Appi, 1991). Four stratigraphic sequences were recognized by Teixeira *et al.* (2004). Fine-grained rhythmic turbiditic deposits representing prodelta settings occur in all of them, being common from sequence 2 through 4 and they might represent different glacio-eustatic pulses in a periglacial context. Paleontological evidences recorded in prodeltaic rhythmites along the four sequences constrain the fossiliferous turbiditic deposits to marine settings (Paim *et al.*, 1997).

Evidences of life

Netto & Zucatti-da-Rosa (1997) preliminarily reported the occurrence of the ichnogenera *Diplocraterion* (in a supposed bedding preservation), *Gordia* and *?Oldhamia* while Leipinitz *et al.* (1997) and Paim *et al.* (1997) reported the occurrence of the sponge-like structures *?Choia* sp. and *Chancelloria* sp. The authors attributed an Early Cambrian age to these rhythmites based on the presence of *Chancelloria* sp. which, according to Conway Morris (1992), is restricted to this interval. However, SHRIMP U-Pb zircon geochronology data from acid tuffs intercalated with the prodeltaic rhythmites provide an age of 606±8 Ma for these deposits (Silva *et al.*, 2002), indicating that deposition of sequence 2 may have started during the Ediacaran (Zucatti-da-Rosa, 2006; Gradstein *et al.*, 2012).

Detailed studies carried on by Zucatti-da-Rosa (2006) also reported the occurrence of components of the 'Vendobionta' (*sensu* Seilacher, 1992) in these beddings, such as faint disk impressions resembling *Cyclomedusa* and *Charniodiscus*, *Aspidella* sp. and *Parvancorina* sp. (Figures 2A-D). Wrinkle structures produced by microbial mats are abundant in these beds (Figure 2E). The structures originally described as *Chancelloria* sp. were reinterpreted as network-pattern microbial mats (named informally as "chancellorid mats" by Zucatti-da-Rosa, 2006; Figure 2F), due to absence of spicules. Besides, the observed network pattern is similar to the structure of modern mats formed by filamentous bacteria *Pseudanabaena* spp. Microfossils are represented by simple spheromorphic achritarchs.

The trace fossil assemblage was also revised, being composed mainly of thin, elongated meandering

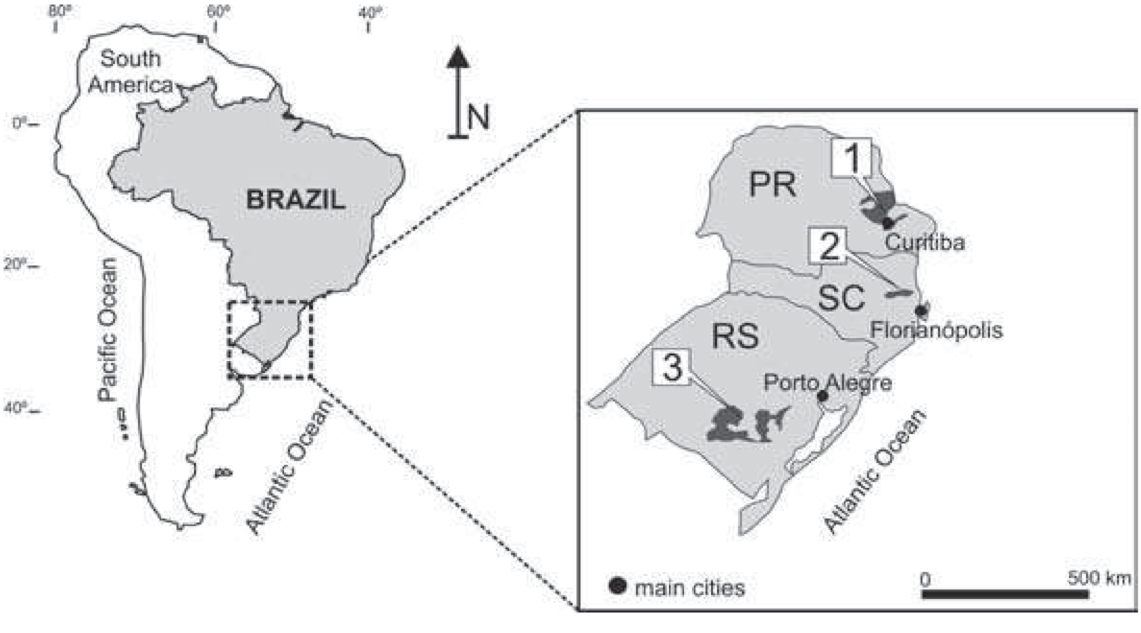

Figure 1. Location map of volcano-sedimentary basins with Terminal Proterozoic deposits at southern Brazil: 1, Camarinha Basin (Paraná State, PR); 2, Itajaí Basin (Santa Catarina State, SC); 3, Camaquã Basin (Rio Grande do Sul State, SC).

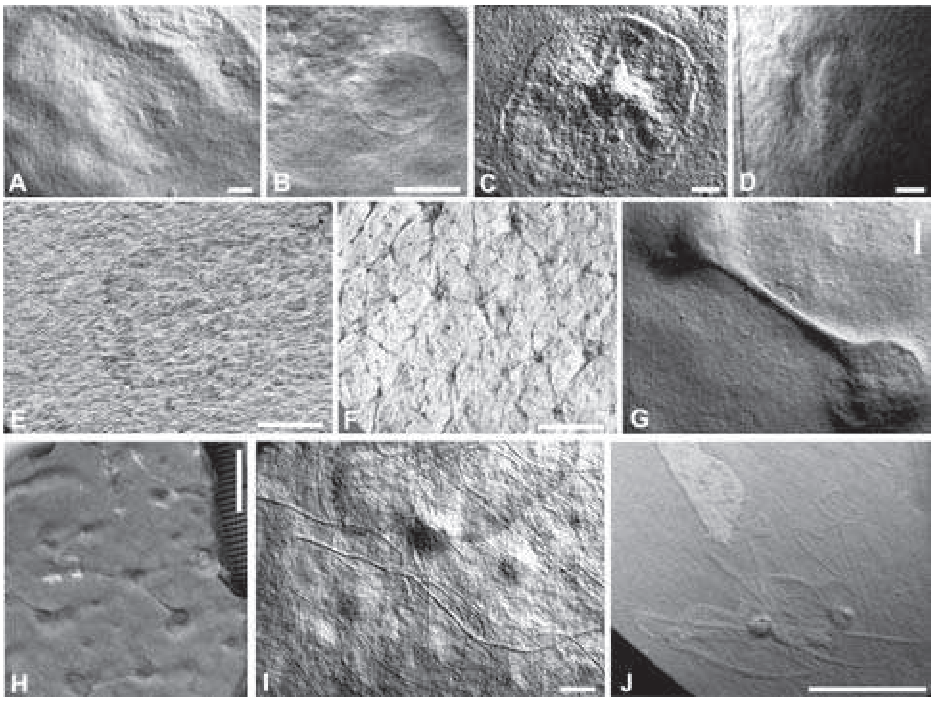

Figure 2. Biogenic structures recorded by Zucatti-da-Rosa (2006) in Itajaí Basin. A, *Cyclomedusa* sp.; B, *Charniodiscus* sp.; C, *Aspidella* sp.; D, *Parvancorina* sp.; E, wrinkle structures; F, *Chancelloria*-like structures; G-H, Morphotype I; I, *Helminthoidichnites* isp.; J, Morphotype II. Scale bars: 1 mm (A, C, D, G) and 10 mm (B, E, F, H-J).

horizontal burrows attributed to *Helminthoidichnites* isp. (preliminarily described as *Gordia* by Netto & Zucatti-da-Rosa, 1997) (Figure 2I). The dumb-bell shaped structures assigned to *Diplocraterion* by Netto & Zucatti-da-Rosa (1997) were re-described as impressions ("morphotype I", Figures 2G-H) and occur in the same beds bearing *Helminthoidichnites* isp. and the "chancellorid mats" in some particular outcrops. The radiate structures assigned to ?*Oldhamia* by Netto & Zucatti-da-Rosa (1997) were reinterpreted by Zucatti-da-Rosa (2006) as *Choia?* based in a comparative analysis of the morphological features of the structures preserved in the prodelta rhythmites and those diagnostic of both taxa. However, the lacking of spicules, as observed in the *Chancelloria*-like structures constrained a more precise identification. "Morphotype II" structure (Figure 2J) was assumed as a tectograph (*sensu* Seilacher *et al.*, 2000) but its possible relationship with microbial mats was not discarded.

Discussion

Both "morphology I" and *Choia?* structures were recorded mainly in sequence 2, at the same levels from where the dated acid tuffs come from. The dumb-bell shaped structures illustrated by Zucatti-da-Rosa (2006) (Figures 2G-H) suggest vertical entrance of burrows passively filled connected to each other by a narrow straight line. It resemble the entrance burrows of *Diplocraterion* in bedding view, but no vertical shafts were observed associated with them, which suggests shallow, plug-shaped structures. Also, the morphology of the structures tentatively attributed to *Choia*, characterized by horizontal grooves in radial disposition converging to a central point, is coherent with structures produced by grazing activity. As the samples illustrated by Zucatti-da-Rosa (2006:fig. 20) are clearly preserved in substrates rich in wrinkle structures, it is plausible to suppose that these structures represent grazing furrows or burrows made by mat grazers or undermat miners, respectively. In this way, if they do not represent true primitive *Oldhamia*, they mimic the ecologic niche occupied by *Oldhamia* tracemakers.

Diplocraterion and *Oldhamia* have been reported since the very base of the Cambrian (e.g., Crimes & Anderson, 1985; Crimes, 1987, 1992; Buatois & Mángano, 2003, 2004; Seilacher, 2007), but there is no report of their occurrence in Ediacaran rocks. Otherwise, the indisputable biogenic character of the "morphotype I" and *Choia?* structures from the Itajaí Basin requires further studies to support a better understanding of their paleoecological and paleobiological significance.

THE CAMAQUÃ BASIN

The Camaquã Basin (Figure 1) records the depositional events that took place during the late phases of the Brasiliano orogeny at southernmost Brazil (*ca* 620-470 Ma). According to Paim *et al.* (2000), five different sub-basins were superimposed in this depositional locus during that time whose stratigraphic record was preserved as five unconformity-bounded units (allogroups). The oldest depocenter was situated at west and the youngest at east (Paim *et al.*, 2000:figs. 3, 5). Microbially induced sedimentary structures (MISS, see Noffke, 2010) are common to abundant in the siliciclastic rocks of almost all allogroups, and trace fossils and "Vendobionta' impressions have been found in the Bom Jardim and Santa Bárbara allogroups.

The Maricá Allogroup (*ca* 620-592 Ma) represents the main deposition of the initial foreland basin and is characterized by alluvial and turbidity current facies on the eastern part, assumed as being the deep portion of the basin (Paim *et al.*, 2000). The western part represents the shallower portion of the basin, where the basal alluvial facies are overlain by storm-dominated, shallow marine deposits (Paim *et al.*, 2000).

The Bom Jardim Allogroup (*ca* 592-573 Ma) represents the main deposition of the following phase (retroarc strike-slip basin) and includes geological evidences of the segmentation of the initial foreland basin into partially interconnected sub-basins generated under transpressional stresses (Paim *et al.*, 2000). The development of fan deltas and braidplain deltas, and an intense, basic to intermediate volcanism of shoshonitic affinity suggestive of plate subduction (tardi-collisional) characterized the geological history of these sub-basins.

The sedimentary succession of the Bom Jardim Allogroup is composed mainly by alluvial conglomerates which give place, to the east, to sandstones and mudstones forming turbidites in subaqueous portion of deltaic systems (Paim *et al.*, 2000). The presence of abundant and diverse MISS and simple trace fossils suggest shallow deposits and marine influence or influx.

The Santa Bárbara Allogroup (559-540 Ma) represents the infill of the central-eastern strike-slip basins, which, except for the absence of volcanic activity, developed in the same overall setting of the previous basin. The siliciclastic sedimentary rocks related to this allogroup represent the progradation of braidplain deltas (lower alloformation) and fan deltas (upper alloformation) into shallow, most lacustrine environments (Paim *et al.*, 2000). However, the presence of trace fossils and basal disk impressions of 'Vendobionta', as well as relatively abundant MISS preserved in sandstone beds of braidplain delta facies association (Netto *et al.*, 1992; Netto, 1994, 1998, 2000; Martini-da-Rosa, 1999; Netto & Martini-da-Rosa, 2001a,b; Netto *et al.*, 2007), reinforces the shallow condition interpretation and suggest marine incursions in these settings or a depostional setting sporadically or partially connected to the sea (Paim *et al.*, 1992, 2000; Martini-da-Rosa, 1999; Netto & Martini-da-Rosa, 2001a,b; Netto *et al.*, 2007).

Evidences of life

Inferred biogenic structures forming a sort of network pattern associated with star-like punctuations are commonly observed in the fine-grained rhythmites that characterize the turbidity current facies of the Maricá Allogroup. These structures resemble the *Chancelloria*-like structures described by Zucatti-da-Rosa (2006) in rhythmites of equivalent facies in the Itajaí Basin (which represents the contemporaneous deposits of the Camaquã Basin in Santa Catarina State) and are assumed here as resultant of microbial mat development.

Microbially induced sedimentary structures composed the main biological record in the Bom Jardim Allogroup deposits (Figure 3). Wrinkle structures, elephant skin structures, *Kynneia* and *Arumberia*-type structures, ripple leveling structures, erosional remnants/pocket structures, and other less remarkable structures are abundant in some outcrops, preferentially preserved at the top of the sandy beds of the turbidity current facies from braidplain delta facies association (Figures 3, 4A-D). Trace fossils are less common, represented by simple, unbranched, unlined horizontal burrows (*Planolites* isp.) and hemispheric "blob"-like structures (*Beltanelliformis* isp.) (Figure 4E), donut-like basal disk imprints (*Intrites* sp.) and some incipient, short bilobated furrows (Figure 4F), all of them preserved in positive hyporelief.

The most diverse biological record in the whole Camaquã Basin occurs in the sedimentary rocks of the Santa Bárbara Allogroup. It is represented mainly by horizontal, simple burrows (*Cochlichnus* isp., *Planolites* isp., *Palaeophycus* isp.), probing burrows (treptichnid morphologies), plug-shaped burrows (*Bergaueria hemispherica*, *Beltanelliformis* isp.), horizontal dumb-bell shaped burrows (*Arthraria antiquata*), basal disk imprints (*Aspidella* sp., *Intrites* sp., *Sekwia* sp.) and MISS (e.g., wrinkle, elephant-skin, *Arumberia*-type and *Kinneyia*-type structures) (Figure 5) (Netto *et al.*, 2007).

Netto *et al.* (1992) and Paim *et al.* (1992) reported the first discoveries of trace fossils in deposits of the Camaquã Basin while Netto (1994, 1998, 2000), Martini-da-Rosa (1999) and Netto & Martini-da-Rosa (2001a,b) improved the knowledge and promoted some reviews. Martini-da-Rosa (1999) focused her study on the ichnofauna of the Santa Bárbara Allogroup, highlighting its occurrence in particular beds, preferentially at the soles of the sandstones and associated fine-grained heterolithic deposits of the braid delta plain facies association (*sensu* Paim *et al.*, 1992, 2000).

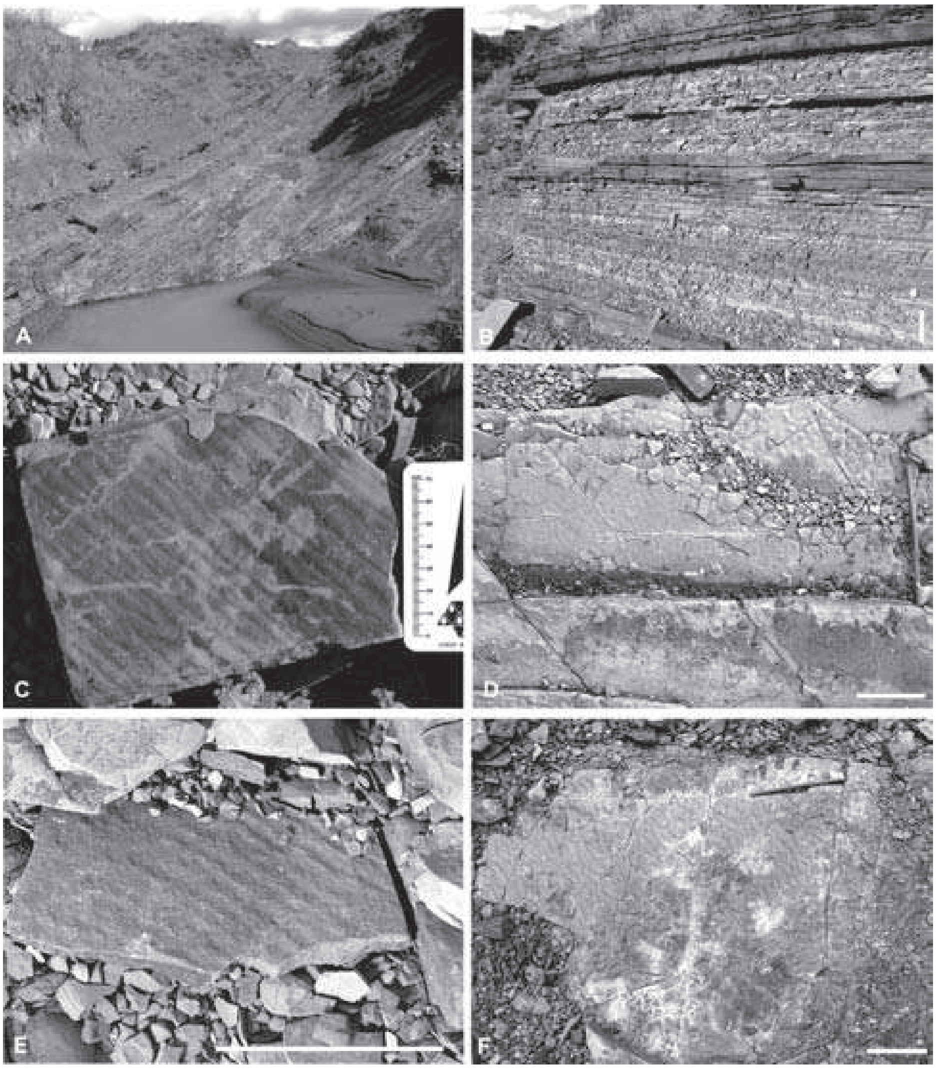

Figure 3. Biogenic structures from Bom Jardim Allogroup. A-B, General (A) and detailed (B) view of the turbidite succession at Pilau Farm (Cachoeira do Sul, RS). C-F, ripple marks stabilized by microbially activity. Scale bars: 10 cm.

Cochlichnus, Didymaulichnus, Diplocraterion?, Gyrolithes, Intrites, Planolites, Rusophycus, Skolithos? and possibly *Cruziana*, as well as non indentified structures, were reported as a preliminary study by Netto *et al.* (1992). This assemblage was organized in two suites, according to their stratigraphic occurrence: the older composed of *Didymaulichnus, Intrites* and *Planolites,* and the younger formed by all the previously cited ichnogenera except *Intrites*. Based on this record, Netto *et al.* (1992) placed the ichnofossiliferous deposits in the Ediacaran–Cambrian boundary.

The revision of the Santa Bárbara's trace fossil assemblage started with Netto (1994), who questioned the validity of *Diplocraterion?*. The original identification took into account paired circular depressions which were assumed as the openings of narrow-spaced shafts of vertical U-shaped burrows. However, detailed observations showed that they represent, in fact, circular medusa-like imprints closely disposed. The great amount of medusa-like imprints and the tectonic character of the basin led to a more extensive review, in order to better characterize the true biogenic record and to differentiate the trace fossils from the body imprints and tectographs. *Cruziana* and *Gyrolithes* were discarded by Netto (1998) who suggested that *Torrowangea* and *Phycodes*, as well as *Arumberia* and other related microbially induced sedimentary structures that might occur.

The detailed study made by Martini-da-Rosa (1999) invalidated most of the ichnogenera previously described in the sedimentary rocks of the Santa Bárbara Allogroup. The trace fossil assemblage became restricted to the occurrence of *Bergaueria hemispherica, Cochlichnus* isp., *Intrites* isp., *Palaeophycus* isp., *Phycodes* cf.

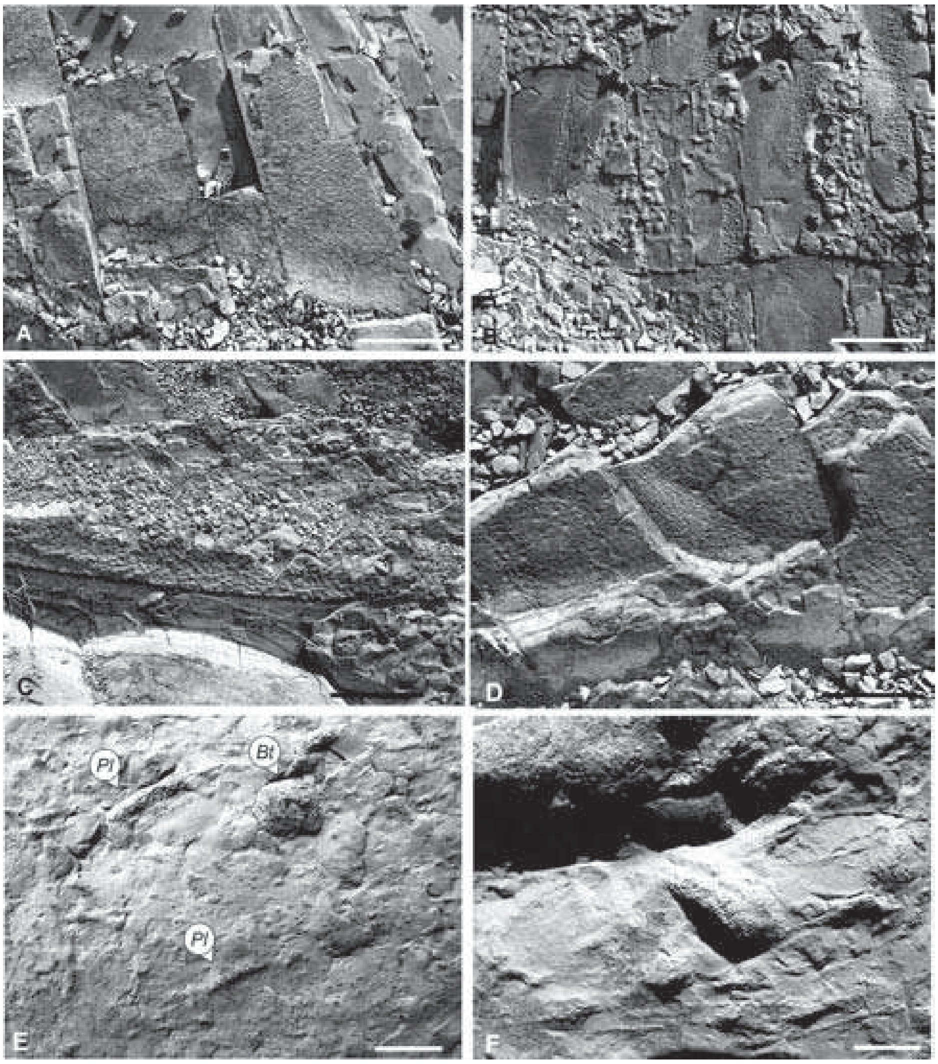

Figure 4. Biogenic structures from the Bom Jardim Allogroup. A-C, Wrinkle structures; D, erosional remnants/pocket structures; E, simple, discrete *Planolites* isp. (*Pl*) and *Beltanelliformis* isp. (*Bt*); F, bilobated furrow. MISS preserved at top surfaces, trace fossils preserved in hyporelief. Scale bars: 10 cm (A-D) and 10 mm (E-F).

pedum [*Phycodes pedum* was re-described by Narbonne *et al.* (1987) as *Treptichnus pedum* and further detailed discussion was provided by Jensen (1997)] and *Planolites* isp., while *Beltanelliformis* sp. (medusa-like imprints) represented the body fossil assemblage. This fossil assemblage structure was reinforced by Netto & Martini-da-Rosa (2001a,b), who included *Sekwia* sp. in the body fossil assemblage, as well as other circular, medusa-like imprints with tripartite or radial internal ornamentation (Figures 5B, I, J).

The last review was made by Netto *et al.* (2007), who discussed the status of the structures attributed to *Phycodes* (= *Treptichnus*) cf. *pedum* by Martini-da-Rosa (1999). Following the studies carried by Jensen *et al.* (2000) in ichnofossiliferous deposits of the Huns Member of Schwarzrand Subgroup (Nama Group, Namibia), the specimens from the Santa Bárbara Allogroup were named *Treptichnus* isp. due to its more rectilinear trajectory, if compared with that from *Treptichnus pedum*. In spite the clear treptichnid morphology of these burrows (Figure 5D), their poor preservation did not allow to access the complete diagnostic ichnotaxobases to infer a particular ichnotaxa. Netto *et al.* (2007) also reviewed the status of the medusa-like imprints, suggesting that the tripartite and radial circular imprints should be included in *Aspidella* sp. (Figures 5G, J), in accordance to the extensive review made by Gehling *et al.* (2000). *Intrites* sp. was also moved from the trace fossil to the body fossil assemblage and *Beltanelliformis* isp. (Figures 5B, E, G, I-J) was assumed as a trace fossil rather than a body disk imprint.

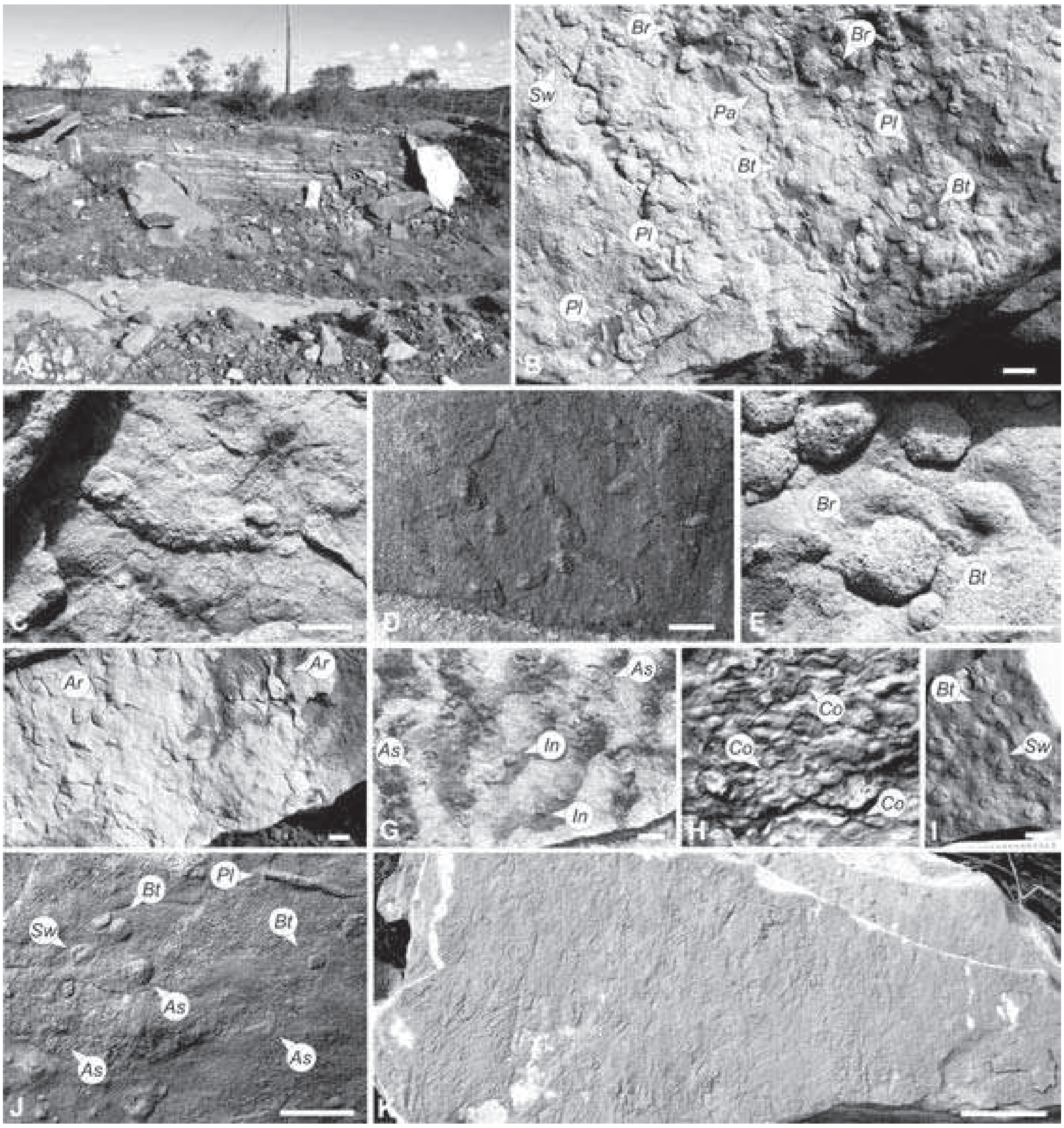

Figure 5. Biogenic structures from the Santa Bárbara Allogroup. A, General view of the heterolithic and sandstone facies at Minas do Camaquã (RS) region (out of scale); B, fine-grained sandstone bed with *Bergaueria hemispherica*, *Beltanelliformis* isp., *Palaeophycus* isp., *Planolites* isp., and *Sekwia* sp.; C, detail of *Palaeophycus* isp.; D, detail of a treptichnid burrow; E, detail of *B. hempsherica* and *Beltanelliformis* isp.; F, *Arthraria antiquata*; G, *Aspidella* sp. and *Intrites* sp. over palimpsest ripples; H, *Cochlichnus* isp. in a crowded *Beltanelliformis* isp. bed; I, *Beltanelliformis* isp. and *Sekwia* sp. in thin-bedded heterolithic deposits; J, *Aspidella* sp., *Sekwia* sp., *Beltanelliformis* isp., and *Planolites* isp. in a mica-rich, fine-grained, reddish sandstone bed; K, wrinkle structures preserved in the same beds illustrated in J. Biogenic structures in G and K preserved in epirelief, all other specimens preserved in hyporelief. Scale bars: 10 mm. Abbreviations: *As, Aspidella* sp.; *Br, Bergaueria hemispherica*; *Bt, Beltanelliformis* isp.; *Co, Cochlichnus* isp.; *Dp, Diplocraterion* isp; *In, Intrites* sp.; *Pa, Palaeophycus* isp.; *Pl, Planolites* isp.; *Tr, Treptichnus* isp.; *Sw, Sekwia* sp.

Arthraria antiquata is reported herein to the Santa Bárbara Allogroup, preserved in the soles of thin-bedded, tabular, massive sandstones with synaeresis cracks (Figure 5F). It represents horizontal dumb-bell shaped burrows formed by two rounded deeper terminations connected by a shallower rectilinear stem. In spite of it resembles *Diplocraterion* openings in bedding view, or even *Bifungites*, true vertical shafts are lacking. According to the review made by Fillion & Pickerill (1984), the absence of vertical shafts differentiates *Arthraria* from the abovementioned ichnogenera. *Arthraria* have been reported in Lower Paleozoic rocks and the oldest record seems to be from Upper Cambrian (Mángano *et al.*, 2005). Its occurrence in the Santa Bárbara Allogroup extends its range to the terminal Proterozoic. A synthesis of the evolution on the studies of the biogenic structures from the Santa Bárbara Allogroup can be found in Table 1.

In spite of the common presence of MISS in the sedimentary rocks of the Santa Bárbara Allogroup, they are less abundant and less diverse than in the sedimentary rocks of the Bom Jardim Allogroup. Also, the *Chancelloria*-like structures seem to be restricted to the sedimentary rocks of the Maricá Allogroup.

Discussion

The trace and body fossil assemblages preserved in the deposits of the Camaquã Basin suggest the occurrence of simple, bilaterian, mobile epifaunal and infaunal organisms able to excavate shallow burrows. Most of these burrows occur in MISS-rich substrates, suggesting that microbial mats were the main source of food for grazing animals, probably undermat miners. The presence of *Aspidella* sp., *Intrites* sp. and *Sekwia* sp. reveals that a sessile Ediacaran epifauna was well-established in some settings, which suggests the existence of a more complex community, in order to guarantee an adequate food supply to sessile organisms. The occurrence of cnidarian resting traces (*Bergaueria hemispherica* and *Beltanelliformis* isp.) reinforces the relative diversity of these epifauna.

Otherwise, the presence of the *Chancelloria*-like structures in the rhytmites of the Maricá Allogroup and the abundance and diversity of MISS at the top of the thin-bedded sandstones of the Bom Jardim Allogroup suggests extensive development of microbial mats in the earlier deposits of the Camaquã Basin. The considerably diminishing of MISS in the Santa Bárbara Allogroup sandstones coincides with the increasing of the bioturbation activity and the diversification of the burrowers, if compared with the discrete bioturbation recorded in the Bom Jardim Allogroup. This scenario is coherent with the Agronomic Revolution hypothesis (Seilacher & Pluffger, 1994; Seilacher, 1999) to explain the faunistic changes through the Ediacaran–Cambrian boundary (e.g., Narbonne *et al.,* 1987; Crimes, 1994; Landing, 1994; Jensen *et al.,* 1998, 2000; Narbonne, 1998; Droser *et al.,* 1999; Buatois & Mángano, 2004, 2012). Taking into account the ichnozones proposed by Crimes (1994), Netto *et al.* (2007) placed the deposits of the Santa Bárbara Allogroup in the Ichnozone IA (Ediacaran). However, the occurrence of burrows representing strategic behaviors well-established in Early Paleozoic, like the treptichnid burrows and *Arthraria antiquata*, suggest a late Ediacaran age, close to the Ediacaran–Cambrian boundary.

According to Paim *et al.* (2000), only the Maricá Allogroup represents full deposition under marine conditions in the Camaquã Basin. The sedimentary rocks that filled the basin after its segmentation in small sub-basins mainly represent alluvial, fluvial and deltaic deposits (Bom Jardim, Acampamento Velho, Santa Bárbara allogroups), and subordinate aeolian deposits (Guaritas Allogroup), developed through the different stages of the basin. The presence of metazoan biogenic structures in some beds (and especially in the Santa Bárbara Allogroup) forced Paim *et al.* (1992, 2000) to assume the existence of marine incursions into the braidplain deltas, as all well-known record of the Ediacaran biota are related to shallow marine ecosystems. The occurrence of glauconite in some of these fossiliferous beds (Martini-da-Rosa, 1999) also reinforced this interpretation.

The low ichnodiversity observed in the sedimentary rocks of the Bom Jardim and Santa Bárbara allogroups, allied to (i) the continental character of the deposits; (ii) the preferential preservation of the trace fossils in the soles of the sandstones and rhythmites of braidplain deltas; (iii) their virtual absence in the turbiditic rhythmites; and (iv) the non-recurrent character of the trace fossil assemblages (preserved in some particular beds, but not in all beds of the same sedimentary succession) led Netto *et al.* (2007) to infer that this particular record might represent a tentative of the marine faunas to survive in brackish-water environments, after being carried in by marine surges. The occurrence of synaeresis cracks in beds containing *Arthraria* reinforces this hypothesis, as salinity fluctuations caused by salinity input in freshwater or oligohaline settings has been invoked as a cause for synaeresis cracks generation (Plummer & Gostin, 1981).

Recent geochemical analyses in fossil-rich Ediacaran beds suggest that they might be deposited in non-marine environments. Miller *et al.* (2008) analyzed some isotopic data from microbialites and stromatolitic beds of the Dhaiqa Formation (NW Arabian Shield) containing cylindrical, horizontal bifurcated and looping structures that resemble burrows and were assumed as possible metazoan trace fossils. These deposits underlying diamictites developed during Glaskiers glaciations and have an estimated age between ≤600 and 530 Ma. Even considering that the geochemistry of these deposits could support correlation with marine environments, Miller *et al.* (2008) concluded that the unradiogenic $^{87}Sr/^{86}Sr$ and $\delta^{13}C_{carb}$ variation data were consistent with a non-marine/lacustrine setting, developed in a protected area, close to the open sea. Similar interpretation was made by Bristow *et al.* (2009) to sections of the Doushantuo Formation containing pre-Ediacaran fossil embryos (mostly compared with cnidarian embryos) in the Yangtze Gorges area (S China). Based on the chemical composition of the clay minerals, Bristow *et al.* (2009) concluded that the fossil-bearing rocks were deposited under alkaline conditions. The (i) spatial and temporal restriction

Table 1. Synthetic review of the biogenic structures and fossil biota described in deposits of the Santa Bárbara Allogroup (Camaquã Basin, RS).

	Netto *et al.* (1992)	Netto (1994)	Netto (1998)	Martini-da-Rosa (1999)	Netto & Martini-da-Rosa (2001a,b)	Netto *et al.* (2007)	This review
Trace fossils							*Arthraria antiquata*
						Beltanelliformis isp.	*Beltanelliformis* isp.
				Bergaueria hemispherica	*Bergaueria hemispherica*	*Bergaueria hemispherica*	*Bergaueria hemispherica*
	Cochlichnus	*Cochlichnus*	*Cochlichnus*	*Cochlichnus* isp.	*Cochlichnus* isp.	*Cochlichnus* isp.	*Cochlichnus* isp.
	?*Cruziana*	?*Cruziana*					
	Didymaulichnus	*Didymaulichnus*	*Didymaulichnus*				
	Diplocraterion?						
	Gyrolithes	*Gyrolithes*	*Gyrolithes*				
	Intrites	*Intrites*	*Intrites*	*Intrites* isp.	*Intrites* isp.		
				Palaeophycus isp.	*Palaeophycus* isp.	*Palaeophycus* isp.	*Palaeophycus* isp.
			?*Phycodes*	*Phycodes* cf. *pedum*	*Phycodes* cf. *pedum*	*Treptichnus* isp.	Treptichnid burrows
	Planolites	*Planolites*	*Planolites*	*Planolites* isp.	*Planolites* isp.	*Planolites* isp.	*Planolites* isp.
	Rusophycus	*Rusophycus*					
	Skolithos?	*Skolithos*?	*Skolithos*?				
			?*Torrowangea*				
Fossil biota			*Arumberia*	*Arumberia* sp.	*Arumberia* sp.		
						Aspidella sp.	*Aspidella* sp.
				Beltanelliformis sp.	*Beltanelliformis* sp.		
						Intrites sp.	*Intrites* sp.
					Sekwia sp.	*Sekwia* sp.	*Sekwia* sp.
MISS						*Arumberia*	*Arumberia*
						Wrinkle structures	Wrinkle structures
							Leveling structures
							Elephant-skin
							Kynneia-type structures
							Palimpsest ripples

of saponite in the studied beds, (ii) lack of redox-sensitive trace element enrichment in demonstrably anoxic sediments and (iii) distinctive C/N ratios of organic matter in saponitic mudstones support the hypothesis that parts of the Doushantuo Formation represent an isolated non-marine basin "which implies that non-marine environments may have been hospitable for early animals" (Bristow *et al.*, 2009:13194). Knauth (2005) also considered the hypothesis that life might be developed first in non-marine settings when discussed the temperature and salinity history of Precambrian ocean based in oxygen isotopic data. Thus, the hypothesis that the fossil biota of the Camaquã Basin could inhabit non-marine settings cannot be completely discarded.

THE CAMARINHA BASIN

The Camarinha Basin is a small basin located at the central-east of the Paraná State that contains the Neoproterozoic-Early Cambrian volcano-sedimentary succession known as the Camarinha Formation (Figure 1). It consists of conglomerates, breccias, sandstones, siltstones and mudstones deposited by gravity flows and turbiditic currents in deltaic settings, composing a 4,000 m-thick turbiditic succession (Moro & Brito Neves, 2005). Trace fossils were reported in some samples coming from outcrops of the Camarinha Formation near Curitiba (PR) by Ciguel *et al.* (1992). *Gordia arcuata, Planolites montanus,* and *Skolithos* isp. compose the burrow assemblage, but around 200 specimens of resting traces attributed to medusa-like organisms also occur. Unfortunately, the sudden death of Henrique Ciguel in 1991 interrupted his studies of the ichnofauna from the Camarinha Formation, which was not resumed since.

Originally assumed as continental, the ichnofossiliferous deposits of the Camarinha Formation were reinterpreted by Ciguel *et al.* (1992) as marine. The authors also constrained the deposits between the Ediacaran (still called 'Vendian' in Ciguel *et al.*, 1992) and the Tommotian, based on the trace fossil assemblage.

Discussion

The medusa-like resting traces were described as having an oval morphology with a ratio proportion of 2:1, showing internal wrinkle features and a central pit. Based on this description, Netto *et al.* (2007) raised the possibility that these resting traces represent the body fossil *Aspidella* (Gehling *et al.,* 2000). Further studies of the collected samples should be done to confirm this suspect, but Ciguel *et al.* (1992) did not mention in which repository these samples were housed.

FINAL REMARKS

The studies about the ichnofauna and the biota fossil of the Ediacaran deposits of southern Brazil are still in their beginnings. Even in their infancy, these studies showed that *Aspidella* is widespread in all basins and that simple bilaterian and plug-shaped trace fossils are common, being represented mainly by the ichnogenera *Planolites* and *Bergaueria*. Microbially induced sedimentary structures are abundant and diverse, revealing relatively quiet waters and enough time for the extensive mat growth. Typical Ediacaran body fossils are absent, but treptichnid burrows, present in almost all classic Ediacaran fossil strata, occur in the Santa Bárbara Allogroup.

The presence of *Aspidella* sp. in the Itajaí, Camaquã, and Camarinha basins imposes an Ediacaran age to the fossiliferous successions of these basins and suggests a close relationship between these beds with those from the Avalonian terrains. The occurrence of faint imprints of *Cyclomedusa* sp*., Charnia* sp*.,* and *Parvancorina* sp. in the Itajaí Basin reinforces this hypothesis. Further studies concerning detailed description of the biogenic structures and petrographic and isotopic analyses of the host rocks will allow the better understanding of the biology and the physical attributes of this biota and the inhabited settings.

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ICHNOLOGY OF THE EDIACARAN-CAMBRIAN PUNCOVISCANA FORMATION OF NORTHWESTERN ARGENTINA: RECENT PROGRESS IN UNDERSTANDING ITS POTENTIAL IN PALEOECOLOGY AND MACROEVOLUTION

Luis Alberto Buatois
María Gabriela Mángano

ABSTRACT

The Ediacaran-Cambrian Puncoviscana Formation of northwestern Argentina is a classic unit that provides valuable information on a critical time in the history of the marine biosphere. Research during the last decade has significantly changed our view of this ichnofauna. The Puncoviscana ichnofauna displays a wide variety of ethological categories, including feeding structures (*Circulichnis montanus*, *Multina* isp., *Pilichnus* cf. *dichotomus*, *Oldhamia alata, O. antiqua, O. curvata, O. flabellata, O. geniculata, O. radiata, Treptichnus pollardi, Saerichnites* isp., *Volkichnium* isp.), grazing traces (*Archaeonassa fossulata*, *Cochlichnus anguineus*, *Helminthoidichnites tenuis*, *Helminthopsis abeli, H. tenuis*, *Psammichnites saltensis*), locomotion traces (*Asaphoidichnus trifidus*, *Didymaulichnus lyelli*, *Dimorphichnus* isp., *Diplichnites* isp., *Tasmanadia cachii*) and dwelling traces (*Palaeophycus tubularis*). This ichnofauna displays strong similarities with other trace-fossil assemblages worldwide in rocks now considered of Fortunian age, a view more consistent with recent geochronologic and chronostratigraphic data from northwest Argentina. While the relatively diverse *Psammichnites* association (illustrating the *Cruziana* Ichnofacies) characterizes the wave-influenced shallow-marine deposits of the eastern belt, the less diverse *Oldhamia* association typifies the deep-marine turbidite systems represented by the western belt. In contrast to previous views, the *Nereites* Ichnofacies is not present in the Puncoviscana Formation. The Puncoviscana ichnofauna illustrates the importance of feeding strategies related to the development of microbial matgrounds and the appearance of new body plans (as revealed by arthropod-produced trace fossils) and sophisticated feeding strategies (*Psamichnites saltensis*, *Oldhamia* ispp.).

Key words: ichnology, Ediacaran, Cambrian, Puncoviscana Formation, Argentina.

INTRODUCTION

The Ediacaran-Lower Cambrian Puncoviscana Formation of northwestern Argentina (Figure 1) is a thick, folded and metamorphosed succession containing a wide variety of trace fossils, which were documented for the first time in the seventies (Mirré & Aceñolaza, 1972; Aceñolaza & Durand, 1973; Aceñolaza, 1978). Subsequently, additional ichnotaxa were described and several reviews were published during the eighties and nineties (e.g., Aceñolaza & Durand, 1982; Durand & Aceñolaza, 1990; Aceñolaza *et al*., 1999). During the last decade, the significance of the Puncoviscana ichnofauna has been re-evaluated in the light of new ideas on the paleobiology of this critical time in the history of life. Recent developments of the Puncoviscana ichnofauna include analysis of its biostratigraphic significance, the recognition of a more complex paleoenvironmental framework, re-evaluation of the present ichnofacies, identification of associated microbially induced sedimentary structures, and assessment of its importance in evolutionary

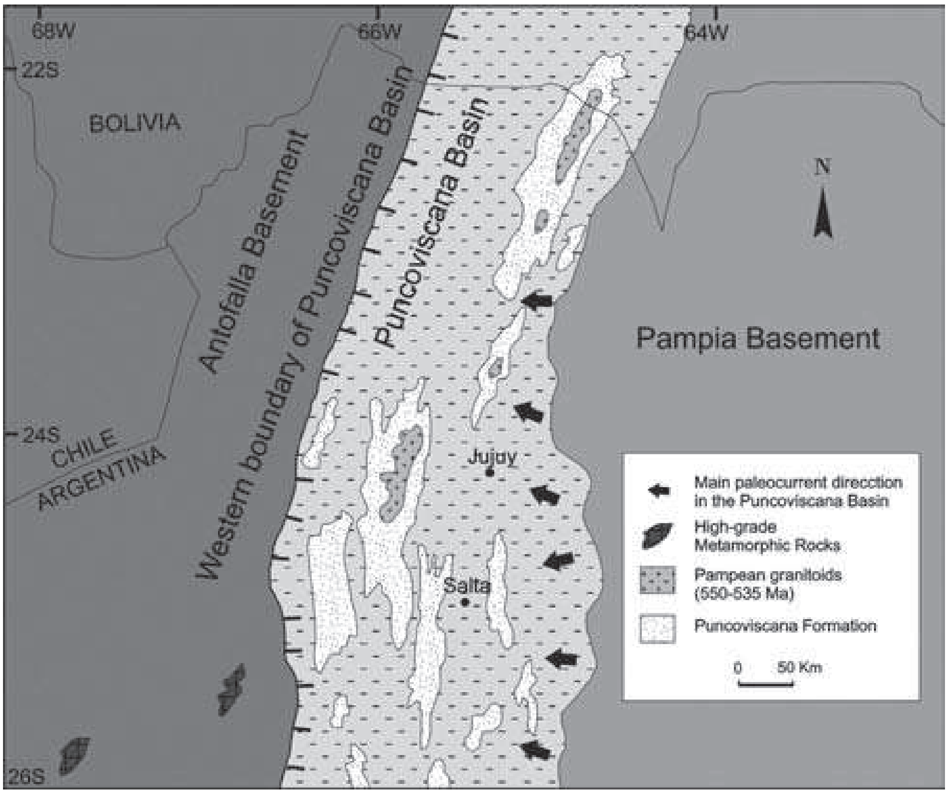

Figure 1. General map showing distribution of outcrops of the Puncoviscana Formation and overall extension of the Puncoviscana Basin (after Ramos, 2008).

paleoecology (e.g., Buatois & Mángano, 2003a,b, 2004, 2012; Seilacher *et al.*, 2005). In this paper, we briefly review these recent developments and further outline the significance of the Puncoviscana ichnofauna.

CHARACTERISTICS OF THE PUNCOVISCANA ICHNOFAUNA

A systematic revision of the Puncoviscana ichnofauna is beyond the scope of this paper, but critical ichnotaxonomic assessments have been published elsewhere (e.g., Buatois & Mángano, 2003a, 2004; Seilacher *et al.*, 2005). A related ichnofauna present in the Guachos Formation is not included in this study (see Seilacher *et al.*, 2005). The Puncoviscana ichnofauna displays a wide variety of ethological categories, including feeding structures (*Circulichnis montanus*, *Multina* isp., *Pilichnus* cf. *dichotomus*, *Oldhamia alata, O. antiqua*, *O. curvata*, *O. flabellata*, *O. geniculata*, *O. radiata, Treptichnus pollardi, Saerichnites* isp., *Volkichnium* isp.), grazing traces (*Archaeonassa fossulata*, *Cochlichnus anguineus*, *Helminthoidichnites tenuis*, *Helminthopsis abeli*, *H. tenuis*, *Psammichnites saltensis*), locomotion traces (*Asaphoidichnus trifidus*, *Didymaulichnus lyelli*, *Dimorphichnus* isp., *Diplichnites* isp., *Tasmanadia cachii*) and dwelling traces (*Palaeophycus tubularis*). Notably absent are farming traces/traps, also known as graphoglyptids (see reinterpretations by Buatois & Mángano, 2003a, 2004). All the trace fossils are oriented parallel to bedding, and therefore they did not produce significant vertical mixing of the sedimentary particles, allowing preservation of the primary sedimentary fabric.

BIOSTRATIGRAPHIC SIGNIFICANCE

Establishing a chronostratigraphic framework for the Puncoviscana Formation is a challenging task because of the geologic complexities of this unit. The Puncoviscana Formation represents the metasedimentary basement of northwest Argentina and it consists of a thick, folded succession of wackes and mudstone, with subordinate presence of conglomerate, limestone and volcanic rocks (Figures 2A-F). The unit has been affected by very low grade regional metamorphism, ranging from slates to schists (Do Campo & Nieto, 2003; Do Campo & Guevara, 2005). Rocks of different types, degrees of metamorphism and tectonic deformation are, in fact, included under the name "Puncoviscana Formation", and the possibility of further subdivision has long been recognized (e.g., Mon & Hongn, 1988, 1991; Hongn, 1996; Moya, 1998; Becchio *et al*., 1999; Mángano & Buatois, 2004). However, the intense deformation of the Puncoviscana Formation makes the establishment of a sound stratigraphic subdivision extremely difficult to say the least.

Originally, the Puncoviscana Formation was considered of Precambrian age (Turner 1960, 1972), but the discovery of the ichnogenus *Oldhamia* (Figures 3A-F) provided uncontroversial evidence of a Cambrian age at least for the hosting strata (Mirré & Aceñolaza, 1972;

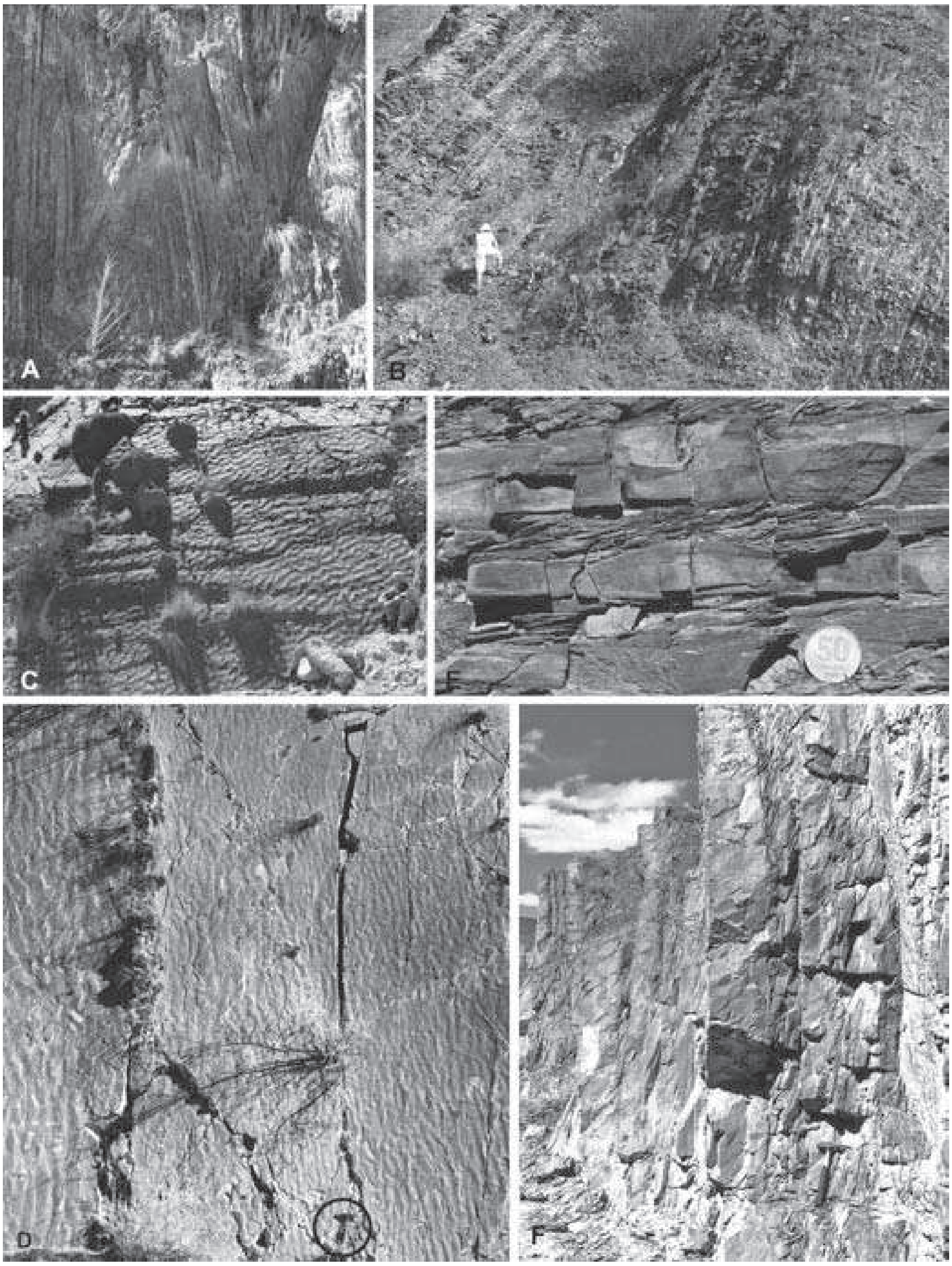

Figure 2. Outcrop photographs of the Puncoviscana Formation. A, Chevron folds. El Alisal (Quebrada del Toro); B, general view of interbedded shallow-marine sandstone and mudstone forming a parasequence set. Top is on the upper left. Purmamarca (Quebrada de Humahuaca); C, bedding plane showing sinuous-crested ripples with a tendency to develop interference ripples. Upstream of Garganta del Diablo, Sierras de Tilcara; D, bedding plane showing sinuous-crested and flattened quasi-symmetric ripples. Rio Corralito (Quebrada del Toro). Hammer is circled; E, interbedded mudstone and sandstone with symmetric rippled tops. Angosto de Cachi; F, general view of interbedded deep-marine turbidite sandstone and background mudstone. San Antonio de Los Cobres. Scale in D: 33.5 cm in length.

Aceñolaza & Durand, 1973). A number of geochronologic studies have recently provided key information on the age of this unit. These studies have indicated that sedimentation in the Puncoviscana basin encompassed the terminal Proterozoic to early Cambrian (Ramos, 2000, 2008; Hongn *et al.*, 2010). Escayola *et al.* (2011) provided high-quality TIMS and SHRIMP U-Pb zircon geochronology data indicating that deposition may have started during the latest Ediacaran, but it took place mainly during the Fortunian, coeval with 540-535 Ma calc-alkaline arc volcanism.

Another line of evidence is provided by the trace fossils themselves, as demonstrated by the seminal paper of Aceñolaza & Durand (1973). Since the discovery of trace fossils in the metamorphic basement, the ichnofauna has been considered as indicative of a Tommotian age, essentially Cambrian Stage 2 of the present scheme (Durand, 1993). However, subsequent work noted the similarities of the Puncoviscana ichnofauna with other ichnofaunas worldwide in rocks now considered of Fortunian age (Buatois & Mángano, 2003a, 2004; Mángano & Buatois, 2004). These authors noted that the restriction of trace fossils to bedding planes, the absence of vertical bioturbation and the dominance of lifestyles associated with microbial mats favor a Fortunian age, rather than a Cambrian Stage 2. Notably, although the Puncoviscana Formation may range into the Ediacaran, no Precambrian trace fossils have been documented yet. Aceñolaza (2003) regarded strata with *Psammichnites saltensis* (formerly *Nereites saltensis*) and *Tasmanadia* as Ediacaran, but the rationale of this decision is unclear and the proposal has been rejected based on the fact that arthropod trackways and phobotactic behaviors are unknown in Ediacaran ichnofaunas (see Jensen, 2003; Mángano & Buatois, 2004; Seilacher *et al.*, 2005; Jensen *et al.*, 2006).

In short, integration of geochronologic and ichnologic information suggests that the Puncoviscana Formation is mostly of Fortunian age, but most likely

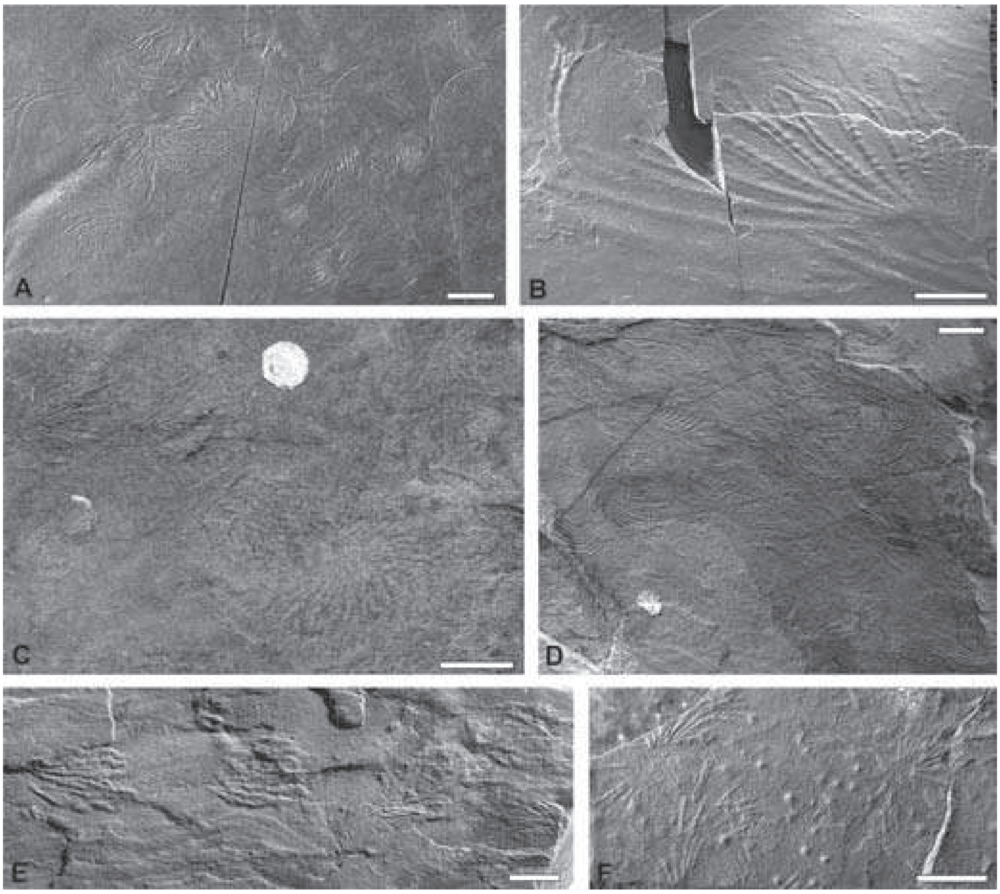

Figure 3. Ichnospecies of *Oldhamia* in the Puncoviscana Formation. A, *Oldhamia alata*. El Mollar (Quebrada del Toro); B, *Oldhamia geniculata*. Los Chorrilos (Quebrada del Toro); C, *Oldhamia antiqua*. San Antonio de Los Cobres; D, *Oldhamia curvata*. Quebrada del Suncho (Sierra de la Ovejería); E, *Oldhamia flabellata*. San Antonio de Los Cobres; F, *Oldhamia radiata*. San Antonio de Los Cobres. Scale bars: 10 mm long.

ranging into the terminal Ediacaran. In addition, this reinterpretation of the available data is more consistent with recent ideas regarding the age of the overlying Mesón Group, originally considered middle to late Cambrian, but now thought to be late early to middle Cambrian (see discussion in Mángano & Buatois, 2004).

PALEOENVIRONMENTAL CONTEXT AND ICHNOFACIES RECOGNITION

The Puncoviscana Formation has historically been considered as recording sedimentation in deep-marine environments (Omarini & Baldis, 1984; Ježek, 1990; Aceñolaza *et al.*, 1999), but this view has changed in recent years with the increasing realization that some deposits accumulated in shallow-marine areas (Buatois & Mángano, 2003a,b, 2004, 2012). As a result of these studies, a more complex paleoenvironmental framework consisting of deep-marine turbidite systems along a western belt and shallow-marine environments influenced by wave action along an eastern belt has been proposed (Buatois & Mángano, 2003a,b, 2004) (Figure 4).

Shallow-marine deposits encompass lower-offshore to middle/lower-shoreface facies, commonly forming coarsening-upward parasequences and displaying structures indicative of oscillatory flows (Buatois & Mángano, 2003a,b, 2004) (Figures 2B-E). This paleoenvironmental scheme has been embraced by subsequent authors (e.g., López de Azarevich *et al.*, 2010). The presence of abundant glauconite layers interbedded with conglomerate in some outcrops of the eastern belt also supports sedimentation in shallow-marine settings (van Staden & Zimmermann, 2003). Recent studies suggested the presence of tidal rhtythmites in some of the Puncoviscana deposits (López de Azarevich *et al.*, 2010). However, tidal rhtythmites are typically present in low-energy protected areas (e.g. middle estuary), and their preservation potential in open-marine wave-affected settings is hard to explain.

Shallow-marine deposits of the Puncoviscana Formation contain an abundant and relatively diverse ichnofauna, including *Archaeonassa fossulata*, *Asaphoidichnus trifidus*, *Cochlichnus anguineus*, *Didymaulichnus lyelli* (Figure 5A), *Diplichnites* isp., *Helminthopsis tenuis*, *Helminthoidichnites tenuis*, *Multina* isp. (Figure 5B), *Pilichnus* cf. *dichotomus* (Figure 5C), *Psammichnites saltensis* (Figures 5D-E), *Oldhamia alata* (Figure 3A), *O. geniculata* (Figure 3B), *Palaeophycus tubularis*, *Tasmanadia cachii, Treptichnus pollardi* (Figure 5F) and *Volkichnium volki* (Buatois & Mángano, 2004, 2012). *Psammichnites saltensis* is the dominant ichnotaxon in these deposits. Trace-fossil assemblages range from the shelf to the offshore trasition, being absent in the higher-energy shoreface facies. The existence of this trace-fossil association (referred herein to as the *Psammichnites* association, but in early papers as the *Nereites* association) has

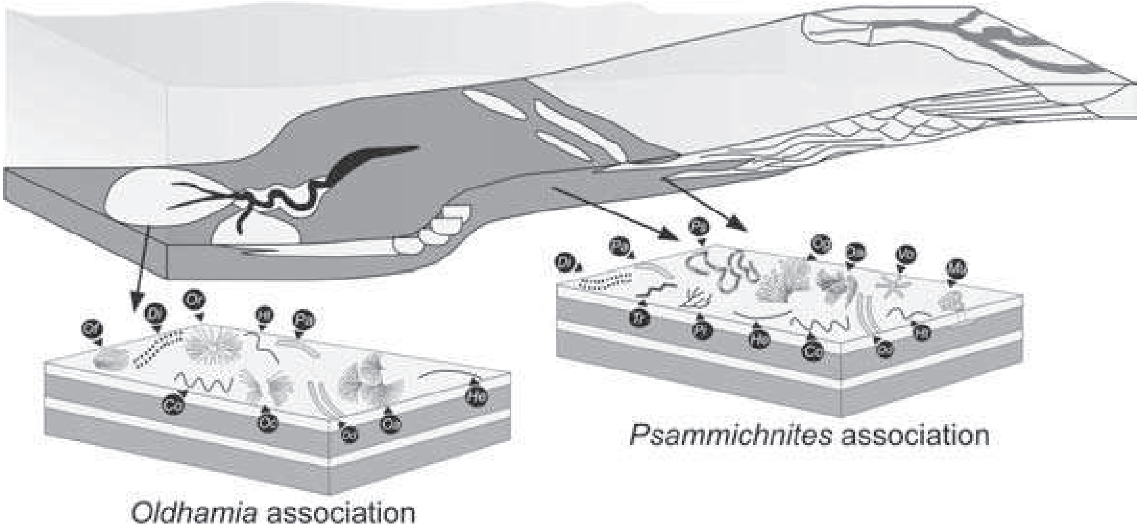

Figure 4. Schematic paleoenvironmental reconstruction of the Puncoviscana Formation showing its two trace-fossil associations. Elements of the shallow-marine *Psammichnites* association include *Cochlichnus anguineus (Co)*, *Didymaulichnus lyelli (Dd)*, *Diplichnites* isp. *(Di)*, *Helminthoidichnites tenuis (He)*, *Helminthopsis tenuis (Hp)*, *Multina* isp. *(Mu)*, *Pilichnus* cf. *dichotomus (Pi)*, *Psammichnites saltensis (Ps)*, *Oldhamia alata (Oal)*, *O. geniculata (Og)*, *Palaeophycus tubularis (Pa)*, *Treptichnus pollardi (Tr)* and *Volkichnium volki (Vo)*. The *Oldhamia* association is represented by *Cochlichnus anguineus (Co)*, *Didymaulichnus lyelli (Dd)*, *Diplichnites* isp. *(Di)*, *Helmithoidichnites tenuis (He)*, *Helmithopsis tenuis (Hp)*, *Oldhamia antiqua (Oa)*, *O. curvata (Oc)*, *O. flabellata (Of)*, *O. radiata (Or)*, and *Palaeophycus tubularis (Pa)*.

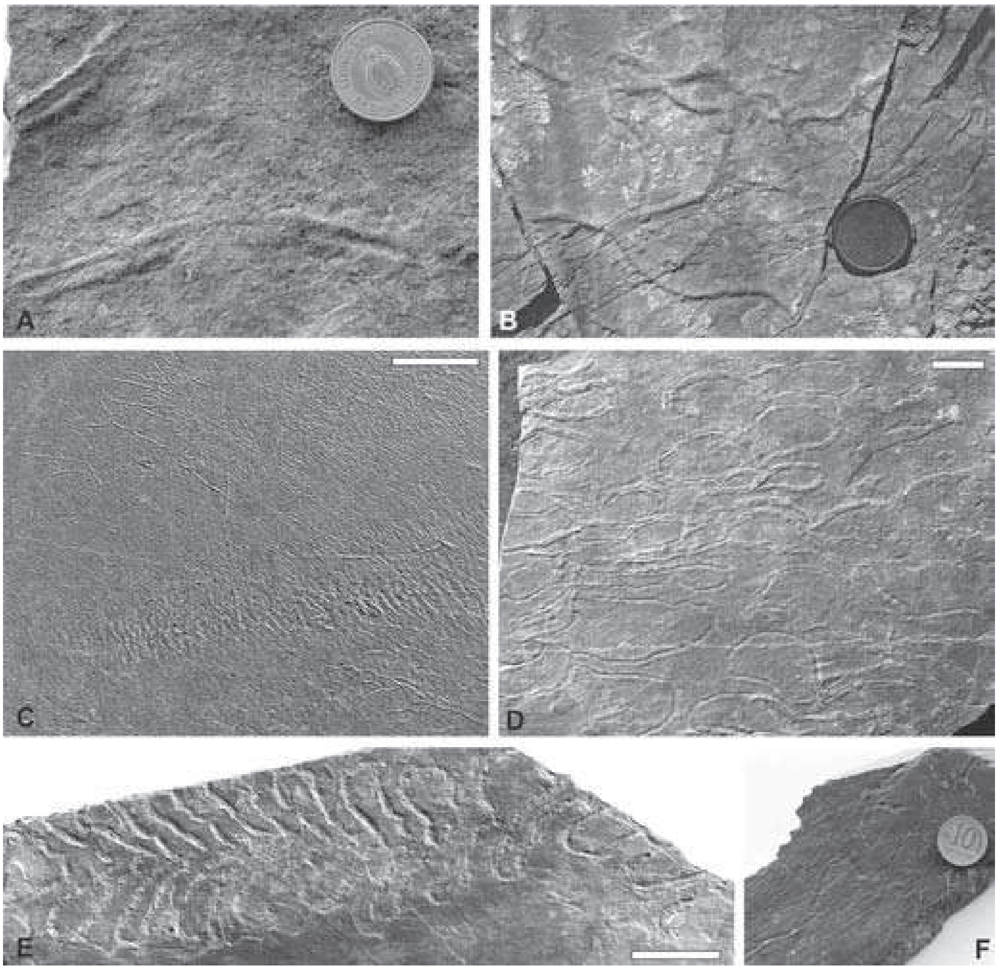

Figure 5. Elements of the shallow-marine association. A, *Didymaulichnus lyelli*. SE of Salta city. B, *Multina isp*. El Mollar (Quebrada del Toro); C, *Pilichnus cf. dichotomus*. Note associated microbially induced wrinkle marks. El Mollar (Quebrada del Toro); D-E, *Psammichnites saltensis*. Campo Quijano (Quebrada del Toro) (D) and Cachi (E). F, *Treptichnus pollardi*. Quebrada del Toro. Scale bars: 18 mm (A, F) and 55 mm (B) in diameter; 10 m (C), 50 mm (D), and 20 mm (E) wide.

been recognized since the early studies on Puncoviscana ichnology (e.g., Aceñolaza *et al.*, 1976). However, this association was regarded as an example of the archetypal *Nereites* Ichnofacies (Durand & Aceñolaza 1990). Buatois & Mángano (2004) noted that the shallow-marine association of the Puncoviscana Formation is best regarded as an early Phanerozoic example of the *Cruziana* Ichnofacies.

Deep-marine deposits were essentially formed in turbidite systems, encompassing channel, sandstone-lobe and lobe-fringe deposits (Ježek, 1990; Buatois & Mángano, 2003b). The latter are represented by beds stacked, forming coarsening- and thickening-upward cycles of thin-bedded turbidites that pass upwards into thick-bedded massive turbidites (Figure 2F). Structures indicative of oscillatory flows have not been found in these deposits, supporting a deep-marine context (Buatois & Mángano, 2003b, 2004). The deep-marine ichnofauna is present in the lobe-fringe deposits, and includes *Circulichnis montanus* (Figure 6A), *Cochlichnus anguineus* (Figure 6B), *Didymaulichnus lyelli*, *Diplichnites* isp. (Figure 6C), *Helmithoidichnites tenuis* (Figure 6D), *Helminthopsis abeli*, *Helmithopsis tenuis* (Figure 6E), *Oldhamia antiqua* (Figure 3C), *O. curvata* (Figure 3D), *O. flabellata* (Figure 3E), *O. radiata* (Figure 3F), and *Palaeophycus tubularis* (Buatois & Mángano, 2003b). This association is dominated by grazing trails, such as *Helminthoidichnites tenuis, Helminthopsis tenuis*, and some *Oldhamia* ichnospecies (particularly *O. flabellata* and *O. radiata*). As with the other association, this ichnofauna has been known for a long time as the *Oldhamia* association (e.g., Aceñolaza *et al.*, 1976). Similar to Cambrian deep-marine associations elsewhere (e.g., Hofmann & Cecile 1981; Lindholm & Casey 1990; Hofmann *et al.* 1994), the turbiditic Puncoviscana association is distinctively different from

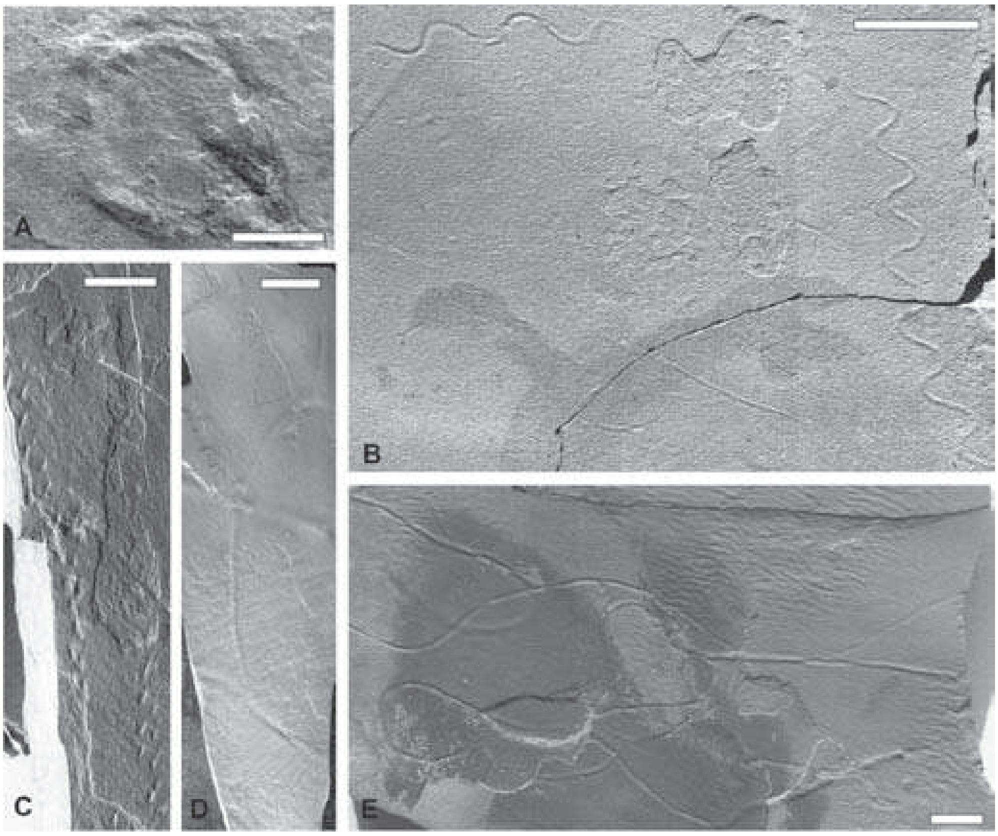

Figure 6. Elements of the deep-marine association. A, *Circulichnis montanus*; B, *Cochlichnus anguineus*; C, *Diplichnites isp*; D, *Helminthoidichnites tenuis*; E, *Helminthopsis tenuis*. Note associated microbially induced wrinkle marks. All photographs are from San Antonio de los Cobres. Scale bars: 10 cm long.

the archetypal *Nereites* Ichnofacies. Cambrian deep-marine trace-fossil associations are typically dominated by nonspecialized grazing trails and *Oldhamia*, and lack the diagnostic graphoglyptid and highly patterned structures that characterized the *Nereites* Ichnofacies in younger rocks (Orr, 2001; Uchman, 2004; Buatois *et al.*, 2009; Buatois & Mángano, 2011a).

EVOLUTIONARY SIGNIFICANCE AND THE ROLE OF MICROBIAL MATS

The Puncoviscana ichnofauna provides solid information on animal-substrate interactions and the appearance of novel body plans during a critical time in the history of life. In particular, this ichnofauna highlights the significance of microbial mats during the Ediacaran-Cambrian transition. Interactions between organisms and matgrounds were widespread during Ediacaran times, but persisted into the early Cambrian, becoming more complex with the appearance of novel body plans and more sophisticated behavioral programs (Buatois & Mángano, 2011b, 2012). Undermat mining and mat grazing were widespread strategies as revealed by the Puncoviscana ichnofauna. In particular, the complex morphology exhibited by several ichnospecies of *Oldhamia* (e.g., *O. alata*) evidences an increase in the complexity of animal-matground interactions: a relatively advanced behavioral program that allowed a more efficient exploitation of mat resources. The branching pattern of minute *Pilichnus* cf. *P. dichotomus* also reflects the sealing of the substrate by microbial mats and the use of a geochemical gradient to obtain food (Mángano *et al.*, 2012).

The appearance of new players resulting from the Cambrian explosion is also evident from the abundance of arthropod-generated structures, such as trackways and scratch marks. The presence of these trace fossils in Fortunian strata further reinforces the pattern of arthropod ichnofossils occurring stratigraphically below their body-fossil counterparts (Narbonne *et al.*, 1987). In addition, sophisticated grazing strategies are also evidenced by *Psammichnites saltensis* in shallow-marine settings (Seilacher *et al.*, 2005).

Finally, the study of the Puncoviscana ichnofauna from the perspective of ichnoguild and tiering analysis has provided information on the strategies employed by early Phanerozoic animals to exploit the infaunal ecospace (Buatois & Mángano, 2003b, 2004, 2012). Overall, the tiering structure of these early Cambrian benthic communities was relatively simple in both shallow and deep water. Although most of biogenic structures were emplaced very close to the sediment-water interface, some organisms may have penetrated several centimeters into the sediment (up to 8 cm and 3 cm in shallow-marine tempestites and deep-marine turbidites, respectively), as indicated by trace fossils cross-cutting inorganic sole marks.

CONCLUSIONS

The Puncoviscana Formation represents a key unit to explore animal-substrate interactions at the beginning of the Phanerozoic. Renewed interest on the ichnology of this unit has resulted in exciting developments during the last decade, allowing a clearer understanding of its environmental framework and macroevolutionary significance. The Fortunian age of the Puncoviscana ichnofauna is consistent with precise geochronologic data and with recent changes in the chronostratigraphic framework of the early Paleozoic of northwest Argentina. The combination of shallow- and deep-marine deposits makes this unit ideal to address proximal-distal trends in trace-fossil distribution along a depositional profile. A critical analysis of the Puncoviscana ichnofauna suggests that the *Nereites* Ichnofacies is not present in this unit. Instead, the *Cruziana* Ichnofacies occurs in the shallow-marine deposits, and a classic association worldwide dominated by grazing trails and *Oldhamia* is present in the deep-marine deposits. From an evolutionary standpoint, the Puncoviscana ichnofauna illustrates the importance of feeding strategies linked to the development of microbial mats and the appearance of novel body plans and sophisticated feeding strategies during an early phase of the Cambrian explosion.

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ICHNOLOGY OF THE PHANEROZOIC DEPOSITS OF SOUTHERN BRAZIL: SYNTHETIC REVIEW

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ABSTRACT

The ichnology of the Phanerozoic rocks in southern Brazil is presented and discussed herein considering its expression in the Paleozoic–Mesozoic Gondwanan units of the Paraná Basin and the Pleistocene–Holocene deposits of the southern Brazilian coastal plain. The Gondwanan units of the Paraná Basin record a complete transgressive-regressive second order depositional sequence, represented by marine deposits of the Paraná Group, glacially-influenced deposits of the Itararé Group, marginal-marine to marine deposits of the Guatá and Passa Dois groups and non-marine deposits of the Passa Dois, Rosário do Sul and São Bento groups. Trace fossils are present in all of these units, represented by many different ichnogenera and ichnospecies and arranged in a lot of ichnological assemblages that reflect specific paleoecological conditions in each moment of the basin filling. The southern Brazilian coastal plain deposits are better exposed in the Rio Grande do Sul littoral and are composed of four barrier-island systems that represent the transgressive-regressive cycles of the Patos Group. Its ichnological content characterizes a diverse ichnofauna, which includes marine trace fossils, with conspicuous occurrences of *Ophiomorpha nodosa* and *Ophiomorpha puerilis*, as well as its continental counterparts (mainly insect nests). This paper intends to present a review of the main ichnologic studies that have been developed in southern Brazil since the beginning of the 1980s, and to discuss some specific topics about paleobiology, paleoecology and paleogeography as far as ichnological analysis integrated with sedimentology and stratigraphy are concerned.

Key words: ichnology of southern Brazil, ichnology of Paraná Basin, ichnology of Rio Grande do Sul Coastal Plain, Phanerozoic trace fossils.

INTRODUCTION

Trace fossils are abundant in Phanerozoic sedimentary rocks of southern Brazil, especially in the Paraná Basin, a large cratonic basin (*ca* 1.5x10^6 km^2) located in the central-south area of South America (Figure 1) which comprises a thick succession of about 7,000 m of sedimentary and magmatic rocks deposited between the Ordovician and the Upper Cretaceous (Milani, 1997; Milani *et al.*, 1998, 2007). It is one of the most studied basins in Brazil due to its fossiliferous content (e.g., Ponta Grossa, Rio do Sul, Irati, Rio do Rasto, Santa Maria and Bauru formations), potential source rocks (e.g., Ponta Grossa and Irati formations), reservoir-quality rocks (e.g., Furnas, Rio Bonito, Piramboia and Botucatu formations, Itararé Group), wide range of depositional systems and thick magmatic rocks in the depocenter. The (chrono)stratigraphic framework has been widely discussed since the beginning of the 1970s but only in the last decade absolute dating and detailed micropaleontological studies have contributed to a better understanding of the chronostratigraphy of the Carboniferous–Permian interval (Mizusaki *et al.*,

Figure 1. Location map of the Paraná Basin and its extension in southern Brazil. For a detailed chronostratigraphic chart, see Milani *et al.* (2007). Abbreviations: PR, Paraná State; SC, Santa Catarina State; RS, Rio Grande do Sul State.

2002; Mauller *et al.*, 2004; Grahn, 2006; Santos *et al.*, 2006; Uriz *et al.*, 2008). Under a basin scale approach, six second order sequences can be recognized in the Paraná Basin: Rio Ivaí Supersequence (Ordovician-Silurian), Paraná Supersequence (Silurian-Devonian), Gondwana I Supersequence (Carboniferous-Permian), Gondwana II Supersequence (Triassic), Gondwana III Supersequence (Jurassic-Cretaceous) and Bauru Supersequence (Cretaceous) (see Milani *et al.*, 1997, 2007).

In southern Brazil, trace fossils are common in almost all deposits in the Paraná Basin successions and compose particular assemblages that represent colonization in marine, marginal-marine and non-marine settings from the Devonian to the Cretaceous (e.g., Aceñolaza & Ciguel, 1986, 1989; Balistieri, 2003; Balistieri & Netto, 2002; Balistieri *et al.*, 2002, 2003; Boeira & Netto, 1987; Borghi & Fernandes, 2001; Buatois *et al.*, 2001a,b, 2007; Campanha, 1985; Ciguel & Netto, 1989; Dias-Fabrício & Guerra-Sommer, 1989; Dentzien-Dias *et al.*, 2007, 2008, 2009, 2012a,b; Faccini *et al.*, 1989; Fernandes, 1998; Fernandes & Melo, 1985; Fernandes *et al.*, 1987, 1990, 2002; Gandini & Netto, 2012; Gandini *et al.*, 2004, 2007, 2010; Guerra-Sommer *et al.,* 1985; Lermen, 2006; Lima, 2010; Lima & Netto, 2012; Marques-Toigo *et al.,* 1989; Martini-da-Rosa *et al.*, 1994; Netto, 1987, 1988, 1989, 1992, 1994, 1998, 2000, 2007; Netto & Gonzaga, 1984; Netto *et al.*, 1991, 1994, 2007, 2009, 2010, 2011, 2012a; Nogueira & Netto, 2001a,b; Rodrigues *et al.*, 1988; 1989; Silva *et al.*, 2005a,b, 2007, 2008a-c; Stevaux *et al.*, 1983; Tognoli & Netto, 2000, 2003, 2004a,b, 2010; Tognoli *et al.*, 2002, 2003, 2007, 2008). The major record corresponds to invertebrate trace fossils, but vertebrate tracks, trackways, burrows and coprolites are also recorded (see for example the contributions of Dentzien-Dias *et al.,* 2012b and Souto, 2012 in this book).

The youngest trace fossil record of southern Brazil occurs in the Pleistocene deposits of the coastal plain of the Rio Grande do Sul and Santa Catarina states (Tognoli *et al.*, 1998; Grangeiro *et al.*, 2003; Gibert *et al.*, 2006, 2012; Netto *et al.*, 2012b). The deposits of the Rio Grande do Sul Coastal Plain (PCRS) are better exposed and are composed of four lagoon-barrier systems developed since the early Pleistocene (e.g., Tomazelli *et al.*, 2000). The well-known ichnological content is associated with the lagoon-barrier systems III (Pleistocene) and IV (Holocene), but it is necessary to consider that system IV is modern, *i.e.*, formal ichnogenera and ichnospecies must not be applied. Despite of this, studies on neoichnology in the Rio Grande do Sul Coastal Plain (PCRS) have been developed since the last decade (Grangeiro *et al.*, 2003; Netto & Grangeiro, 2009; Netto *et al.*, 2012b). They have been useful as an analogue for a better understanding of the trace fossil distribution in deposits of the lagoon-barrier system III and the potential tracemakers, as well as the evolution of the PCRS under the point of view of sedimentary processes and paleoecology as indicated by the ichnological data. Bioerosion is also common in shells and in mammalian fossil bones accumulated in the "concheiros" of the PCRS, which are discussed by Lopes (2012) in this book.

The aim of this paper is to summarize the ichnofossiliferous record of the Phanerozoic of southern Brazil based on previous studies developed mainly after the 1980s. These studies have been developed by different authors and research groups in surface and subsurface deposits, both in outcrops and cores, and they intend to show how ichnology can be an additional source of data useful for depositional interpretations.

THE DEVONIAN RECORD

Geological overview

The Silurian-Devonian Paraná Supersequence (Furnas and Ponta Grossa Formations; for a chronostratigraphic chart, see Milani *et al.*, 2007) is made up of three depositional sequences: (i) a lowermost sequence, disposed from west to east that corresponds to the deposits formed during the coastal onlap over the basement and comprising the transgressive and highstand systems tract of the Furnas Formation (lower and middle sections); (ii) the middle sequence, composed of conglomerates of lowstand system tract and transgressive facies toward the contact zone with Ponta Grossa Formation; and (iii) the uppermost sequence, which corresponds to transgressive deposits (São Domingos Member) associated with warm currents causing the decline of the Malvinokaffric Fauna. The Silurian–Devonian sequence is separated from the upper Itararé Group (Upper Carboniferous–Lower Permian) by a slightly angular unconformity (Assine, 1996). The maximum flooding surface was in the Late Emsian during the deposition of the Jaguariaíva Member.

The origin of the psamitic Late Silurian to Early Devonian Furnas Formation is a matter of controversy. Although body fossils have not been found yet, trace fossils are present throughout the unit. Based on different facies associations, Assine (1996, 1999) subdivided the Furnas Formation into three units. The lower unit is made up of sandstones and conglomerates deposited in large alluvial-coastal plains. A westward paleoslope with source-area at east and an approximate north-south paleoshoreline were deduced from paleocurrent data. The fine to coarse-grained, cross-bedded sandstones of the middle unit are arranged in cosets separated by shale beds. *Rusophycus* and *Cruziana* trace fossils support a marine origin for the middle unit (Assine & Góis, 1996; Assine, 1999). Paleoflow toward southwest is oriented obliquely with respect to the shoreline and probably had been produced by tidal currents. The cross-bedded coarse-grained sandstones of the upper unit, bearing bimodal to polimodal paleocurrents patterns, are interpreted as subaqueous sandwave and dune deposits formed by tidal currents. Winnowed pebble lags are common at the top of cosets being considered product of tidal currents enhanced by storm waves.

'Transitional Beds' ('Camadas de Transição' in Portuguese) was the name used by Petri (1948) to represent an approximately 20-m thick interval of interbedded sandstone and siltstones bearing marine fossils present at the top of the Furnas Formation. It occurs near Jaguariaíva (PR) and constitutes fining-upward cycles grading from coarse-grained sandstones to shales. Very fine to fine-grained sandstones commonly show cross-laminations and cross-stratifications. However, they are frequently obliterated by trace fossils (Tognoli *et al.*, 2002, 2003; Netto *et al.*, 2011).

The Ponta Grossa Formation is a predominantly fine-grained unit deposited under marine conditions as attested by its macro and microfossil content. This unit was subdivided in three members. The Jaguariaíva Member is the lower unit, Emsian in age, formed by homogeneous gray to dark gray fossiliferous and ichnofossiliferous silty shales, with a great amount of organic carbon preserved locally, constituting a potential source rock of hydrocarbon in the Paraná Basin. The Tibagi Member is the middle unit of the Ponta Grossa Formation, Eifelian in age. It is characterized by the presence of fossiliferous fine to very-fine lenticular sandstones, presenting local occurrences of hummocky cross-stratification interbedded with silty shales. The uppermost unit is the Givetian–Frasnian São Domingos Member, made up of gray shales, locally bituminous, interbedded with thin fine-grained sandstones. Its fossil content is similar to the Jaguariaíva Member but the number of species is smaller and typical Malvinokaffric elements are missing.

Trace fossil record

Furnas Formation and 'Transitional Beds'

Trace fossils have been reported in the Furnas Formation in Paraná State since the beginning of the 20th century as bioturbation (Clarke, 1913), *Arenicolites* (Carvalho, 1941) and worm-like remains ("*Fraena*", Lange, 1942, 1954). But specific ichnological studies were carried out only after 1980, recording the ichnotaxa *Conostichus* isp., *Cruziana* isp., *Didymaulichnus lyelli, Furnaisichnus langei, Lockeia* isp., *Palaeophycus tubularis, P. alternates, Rusophycus dydimus, Planolites vulgari, Skolithos* isp. in Paraná State (e.g., Aceñolaza & Ciguel, 1986, 1989; Rodrigues *et al.*, 1988; 1989; Borghi & Fernandes, 2001; Fernandes *et al.*, 2002).

Detailed studies developed in the last ten years involving the integrated analysis of the ichnology and sedimentology of the Furnas Formation in Paraná State have revealed the occurrence of a more diverse marine trace fossil assemblage. Assine (1999), Tognoli *et al.* (2002, 2003), Tognoli & Netto (2010) and Seilacher (2007) recognized the presence of *Cruziana acacensis, Rusophycus* cf. *acacensis,* and *?Psammichnites* isp. (Figure 2A) in the exposed beds of the Furnas Formation in the surroundings of São Luiz do Purunã (PR). Y-shaped horizontal bifurcated burrows occur in the same beds containing *?Psammichnites* isp., having been interpreted by Tognoli *et al.* (2002, 2003) as *Thalassinoides* isp. *Furnaisichnus langei* (Borghi & Fernandes, 2001) also occurs in similar beds composing a monospecific suite (Figures 2B-C). This ichnoassemblage occur preferentially in the middle unit bedding planes, which show a moderate to high degree of bioturbation. Crawling is the

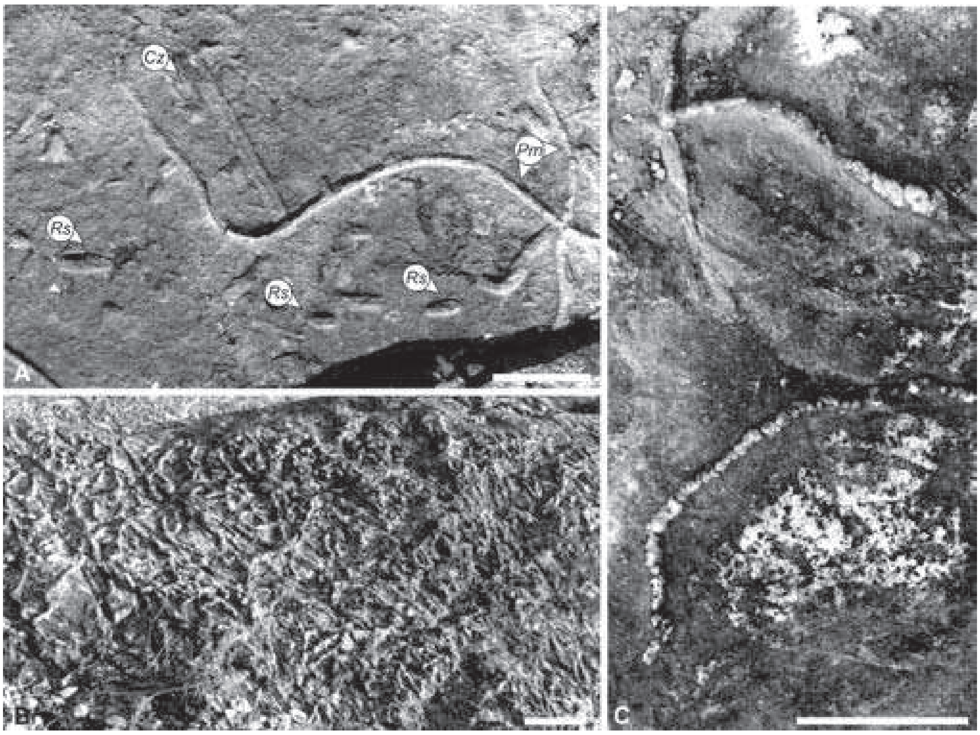

Figure 2. Trace fossils of the Furnas Formation in São Luiz do Purunã (PR) area. A, *Cruziana acacensis* (*Cz*), *Rusophycus* cf. *acacensis* (*Rs*) and *?Psammichnites* isp. (*Pm*); B, crowded occurrence of *Furnaisichnus langei* at the top of a medium-grained sandstone bed; C, detail of *F. langei* packing fill arrangement. Scale bars: 10 cm.

dominant behavior, represented by well-developed shallow burrows (*?Psammichnites* isp. and *Furnaisichnus langei*), commonly showing loops and intersections. Shallow furrows (*Cruziana acacensis*) and resting traces (*Rusophycus* cf. *acacensis*) are also common, and dwelling/feeding galleries (*Thalassinoides* isp.) are locally observed. Trilobites, crustaceans and mollusks seem to be the main tracemakers. The trace fossil association suggests a proximal *Cruziana* Ichnofacies suite, and the observed primary sedimentary features indicate colonization of a marine subtidal setting.

The deposits of the 'Transitional Beds' (Figure 3) exposed in Tibagi and Jaguariaíva (PR) are frequently obliterated by trace fossils, composing two distinct suites. The most pervasive suite forms a composite ichnofabric of *Rosselia, Cylindrichnus,* and *Lockeia* (Figure 3A)*,* with occasional *Skolithos,Arenicolites, Thalassinoides, Palaeophycus, Planolites* and *Teichichnus,* showing moderate to high degree of bioturbation. This suite occurs preferentially in the interbedded fine- to very fine-grained, cross-laminated sandstones and mudstones. The other suite is composed of a crowded ichnofabric formed almost exclusively by *Rosselia socialis* (Figures 3B-C) preserved in amalgamated fine-grained sandstones thin beds with hummocky cross-stratification. The *Rosselia* suite shows a high degree of bioturbation, obliterating the primary sedimentary structures in some beds. The trace fossil association and the degree of bioturbation in both suites suggest a *Cruziana* Ichnofacies assemblage developed in lower shoreface settings.

Ponta Grossa Formation

The ichnofossil content of the Ponta Grossa Formation is best known by the trace fossil assemblage from the Jaguariaíva Member, exposed mostly in Jaguariaíva (PR). *Zoophycos* and *Bifungites* are the most conspicuous ichnogenera in the Ponta Grossa Formation (e.g., Campanha, 1985; Fernandes & Melo, 1985; Ciguel & Netto, 1989; Fernandes, 1998; Fernandes *et al.*, 2002). Leonardi (1982, 1983) described a supposed amphibian track in the Devonian deposits of the Ponta Grossa Formation, erecting a new ichnogenus and ichnospecies, *Notopus petri.* A review made by Roĉek & Rage (1994) discarded the amphibian origin and re-allocated this trace in *Asteriacites*, as it represents an incomplete resting trace of asteroid or ophiuroid echinoderms.

Zoophycos is the main component of a composite ichnofabric containing also *Phycosiphon* and *Chondrites* (Figures 4A-C). The composite *Zoophycos*-dominated ichnofabric (Figure 4A) superimposes another

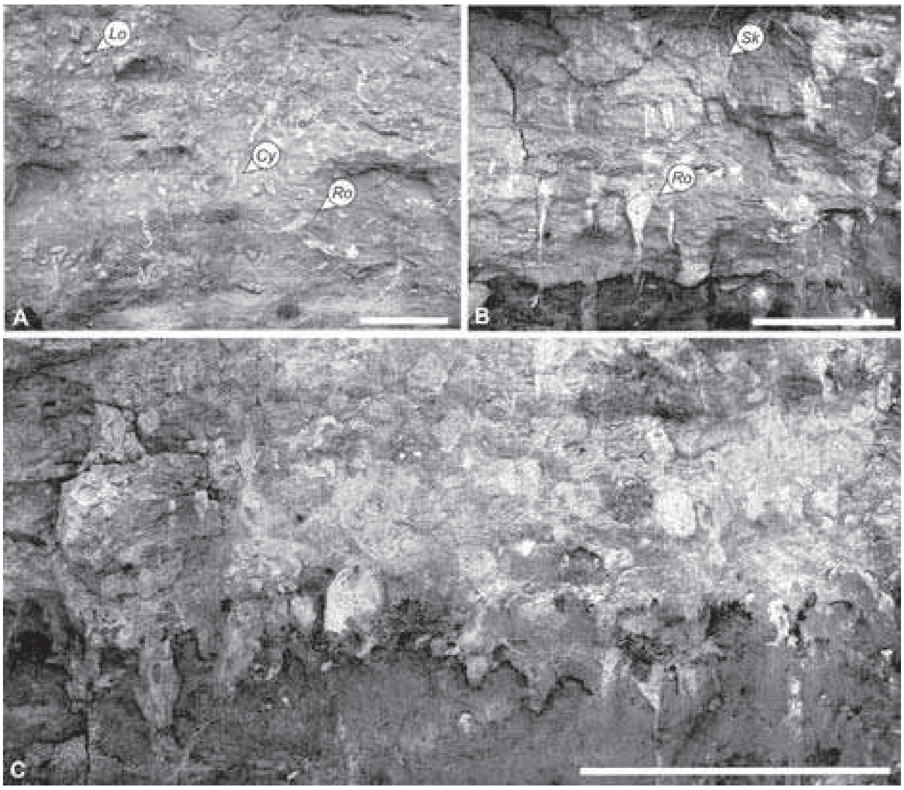

Figure 3. Trace fossils from 'Transition Beds' exposed in Jaguariaíva (PR). A, *Rosselia socialis* (*Ro*), *Cylindrichnus* isp. (*Cy*) and *Lockeia* isp. (*Lo*), the main components of the ichnofauna preserved in this unit; B, *Rosselia socialis* suite, with occasional *Skolithos linearis* (*Sk*); C, general aspect of the crowded *Rosselia* ichnofabric. Scale bars: 10 cm.

composite ichnofabric formed by *Rhizocorallium, Palaeophycus, Planolites, Helminthopsis* and *Teichichnus* (Tognoli *et al.*, 2002, 2003; Tognoli & Netto, 2010) (Figure 4C). Each composite ichnofabric characterizes a particular trace fossil suite: the *Rhizocorallium*-dominated suite represents colonization of shallower, possibly disaerobic shelf substrates while the *Zoophycos*-dominated suite suggests deeper substrates with anaerobic conditions. Rodrigues *et al.* (2003) diagnosed obrution events in these shales, based in the occurrence of conularid fossil preserved in life position. The trace fossil association and the degree of bioturbation in both suites suggest a distal *Cruziana* Ichnofacies assemblage. The *Rhizocorallium*-dominated suite characterizes deposition in lower shoreface-offshore transition settings, while the *Zoophyos*-dominated suite indicates colonization in offshore settings. The superimposition of the *Rhizocorallium*-dominated suite by the *Zoophycos*-dominated suite represents a signature of transgressive events in shelf marine environments.

An archetypical *Cruziana* Ichnofacies suite occurs in the silty shale deposits associated with thin beds of very fine-grained sandstones with hummocky cross-stratification of the Tibagi Member near Arapoti (PR). It is represented by a highly diverse ichnofauna which is composed of ichnofabrics of *Asterosoma, Chondrites, Cylindrichnus, Helminthopsis, ?Lennea, Lingulichnus, Palaeophycus, Phycosiphon, Planolites, Rhizocorallium, Rosselia, Skolithos, Taenidium,* small *Thalassinoides* and bottoms of U-shaped burrows (Figure 4D). The amount of bioturbation is high, covering around 80% of the exposed beds, locally 100%. This suite represents the record of the infaunal invertebrate community that colonized the shelf substrates below the fairweather wave-zone. The presence of marine ichnogenera, the high ichnodiversity and the high amount of bioturbation suggest the establishment of moderate-to-low hydrodynamic conditions between storm surges in lower shoreface settings.

Trace fossils also occur in the shales of São Domingos Member, preserved through the whole exposed succession near Tibagi (PR) but being more abundant at the very top of the sedimentary sequence. *Asterosoma, Chondrites, Cylindrichnus, Diplocraterion, Gordia, Halopoa, Helminthopsis, Hemidallia, ?Lennea, Lingulichnus, Lockeia, Macaronichnus, Palaeophycus, P. striatus, Planolites, Rhizocorallium, Rosselia, Skolithos, Taenidium satanassi* and *Zoophycos* compose the ichnofauna of the São Domingos Member (Figure 4E). The degree of bioturbation is moderate in the sandy sedimentary

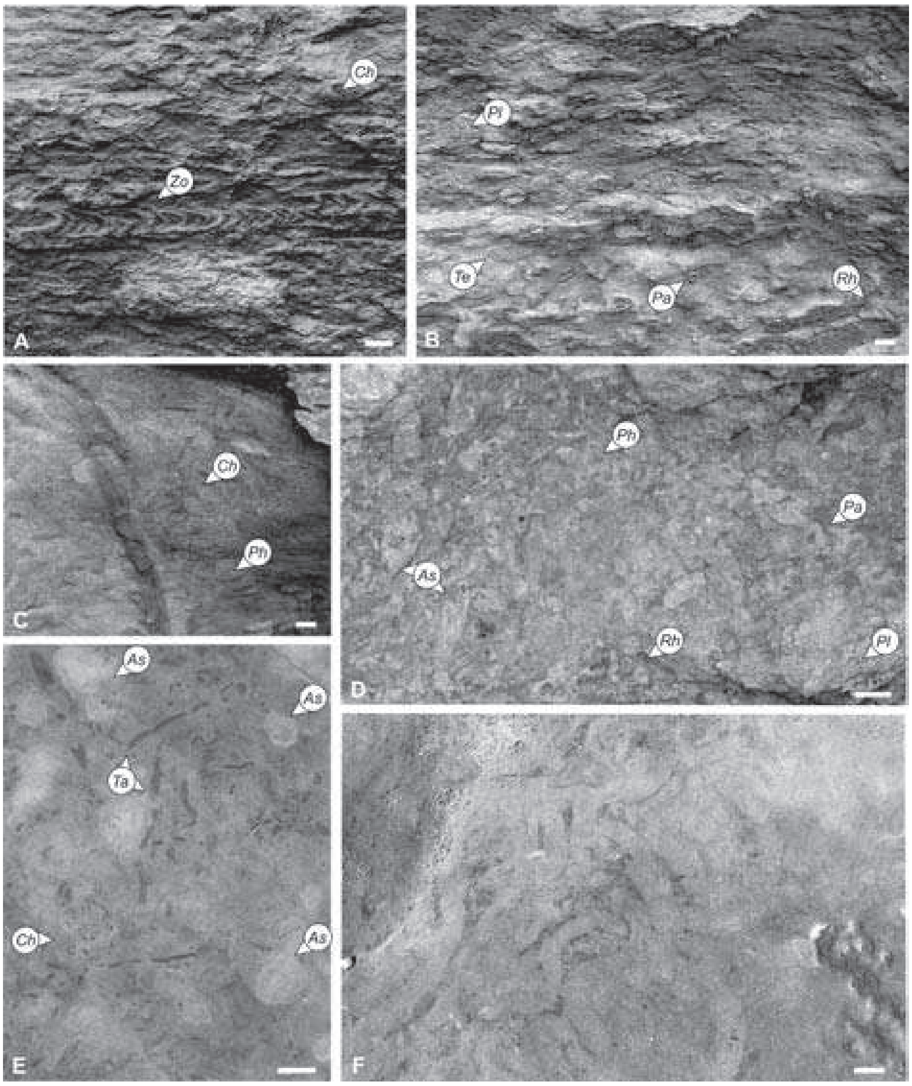

Figure 4. Ichnofabrics preserved in mudstones of the Ponta Grossa Formation in Jaguariaíva, Arapoti and Tibagi regions (PR). A, *Zoophycos*-dominated ichnofabric; B, *Rhizocorallium*-dominated ichnofabric; C, *Chondrites*-dominated ichnofabric; D, highly bioturbated composite ichnofabric in very fine-grained heterolitic beds associated with fine-grained sandstones with hummocky-cross stratification; E, *Asterosoma-Taenidium-Chondrites*-dominated ichnofabric representative of the distal *Cruziana* Ichnofacies at the top of Ponta Gorssa Formation succession; F, mollusk trails reworking the mudstone beds illustrated in E. Abbreviations: *As*, *Asterosoma*; *Ch*, *Chondrites*; *Le*, *Lennea*; *Pa*, *Palaeophycus*; *Ph*, *Phycosiphon*; *Pl*, *Planolites*; *Rh*, *Rhizocorallium*; *Ta*, *Taenidium*; *Te*, *Teichichnus*; *Zo*, *Zoophycos*. A-C from Jaguariaíva Member, D from Tibagi Member, E-F from São Domingos Member. Scale bars: 10 mm.

facies and high in the muddy ones. Trace fossil distribution reveals the existence of six different suites that represent colonization in distinct shelfal settings, from offshore to shoreface/foreshore settings. Undetermined mollusk trails resembling psammichnitid undertraces (*sensu* Seilacher, 2007) (Figure 4F) are abundant in some beds, superimposing the more distal suites. The trails show sharp borders marked by phytodetritus accumulation, suggesting colonization in shallower substrates. The trace fossil composition and the high degree of bioturbation characterize an assemblage representative of the *Cruziana* Ichnofacies.

THE UPPER CARBONIFEROUS-LOWER PERMIAN RECORD

The Itararé Group

Geological overview

The Itararé Group sedimentary succession is distributed in surface and subsurface along the central, southeast and south regions of Brazil, thinning out southwards along the eastern outcrop belt (Santos *et al.*, 1996). It is related to the third Ice House Age, recording glacio-lacustrine and glacio-marine environments with marine influence increasing upwards (Zálan *et al.*, 1990; França & Potter, 1988, 1991). All of them are composed, in different arrangements, of massive shales, diamictites, rhythmites and fine- to medium-grained sandstones with trough cross-stratification. Most of the sedimentary rocks resulted from deglaciation and are well exposed in the eastern border of the Paraná Basin, mostly in the south of São Paulo State, north and center of Santa Catarina State and center and south of Rio Grande do Sul State (Figure 1).

Correlations between subsurface and surface deposits of the Itararé Group are difficult, mostly due to the diachronic character of the glacially-influenced deposits and the lenticular geometry of the sand bodies and diamcitites, which are dominant in the whole succession. Three lithostratigraphic units are recognized in subsurface: Lagoa Azul, Campo Mourão and Taciba formations (França & Potter, 1988, 1991), as well as in surface deposits, named Campo do Tenente, Mafra and Rio do Sul formations, respectively from the base to the top (Schneider *et al.*, 1974). The Lagoa Azul Formation has no equivalent surface deposits. The Campo Mourão Formation is assumed as equivalent to Campo do Tentente and Mafra formations, and is also equivalent to the basal portion of Rio do Sul Formation, called Lontras Shale. The Taciba Formation includes the sedimentary rocks which belong to the medium and upper parts of Rio do Sul Formation (see Milani *et al.*, 2007).

Glacial striated pavements are frequent in surface deposits, as well as faceted pebbles and cobbles dispersed into diamictites and fine-grained sandstones and shales. Reddish mudstones with dropstones, and subordinated rhythmites and diamictites with sandy matrix are the main lithologies of the Campo do Tenente Formation. The Mafra Formation corresponds to the sandy portion of the Itararé Group, consisting of complex tidal bars deposits, mostly formed by sandstones with trough cross-bedding and ripple-drift cross-lamination, and lower shoreface sandstones with wave ripples and hummocky cross-stratification. Grayish silty and argilaceous rhythmites and massive diamictites, both with faceted clasts and grains, are subordinated. Each depositional unit records a basin subsidence phase, characterized by a depositional cycle which starts with sandy deposits passing upward to mudstones and intercalated diamictites.

The top of Mafra Formation and the Rio do Sul Formation concentrate mostly deposits originated by diachronic deglaciation cycles. The rhythmites preserved at the top of the Mafra Formation and the rhythmites that characterize the top of the Rio do Sul Formation represent two distinct deglaciation events, followed by interglacial periods (e.g., Canuto, 1993). The Rio do Sul Formation is composed by the alternation of dark shales mixing fully marine and non-marine fossils, fine laminated rhythmites and diamictites, as well as lower shoreface sandstones with horizontal lamination, ripple-drift cross-lamination and hummocky cross-stratification. Paleontological and sedimentological data of the marine deposits interbedded with glacial-influenced deposits suggest periodical flooding of the basin margins. These flooding deposits occur in response to syntectonic movements resulting from the ice cap migration, promoting rapid subsidence in some areas, and to the glacio-eustatic control of the deglaciation water influx (Gravenor & Rocha-Campos, 1983). Thus, the shallow marine deposits represent short-term trangressive events and paleovalley infill controlled by climatic fluctuations, the landscape physiography, tectonics and isostatic equilibrium (Saad, 1977; Gravenor & Rocha-Campos, 1983).

The dominantly glacio-marine deposits of the Rio do Sul Formation represent the last glacial episodes in the Paraná Basin and the maximum flooding event related to Gondwana deglaciation. According to Buatois *et al.* (2006), immense meltwater discharges influenced sedimentation in addition to exerting erosional forces and drastic oscillations in climate. These factors had impacted the distribution, abundance and evolution of biotas through time. The main studies stressing this approach took into account the ichnofauna (e.g., Buatois *et al.*, 2006, 2010; Netto *et al.*, 2009, 2012a). Major trace fossil assemblages are found within deglaciation facies and have been recorded in several Gondwana basins. The best studied assemblages come from southern Brazilian, southern African and northwest Argentinian sedimentary rocks which represent deposition in fjords that opened toward a shallow sea (Buatois *et al.*, 2006, 2010; Netto *et al.*, 2012a).

Trace fossil record

Despite trace fossils had been described in the Itararé Group deposits early in the 20th century by Maury (1927), studies focused on ichnology have had a major development only in the 1980s (Guerra-Sommer *et al.*, 1985; Fernandes et. al., 1987; Netto, 1987; Dias-Fabrício & Guerra-Sommer, 1989; Marques-Toigo *et al.*, 1989). Integrated studies on the sedimentology and ichnology of the deglaciation deposits started to be developed in the last decade (Nogueira & Netto, 2001a, b, Balistieri & Netto, 2002; Balistieri, 2003; Balistieri *et al.*, 2002, 2003; Buatois *et al.*, 2006, 2010; Netto *et al.*, 2009), bringing new light to a better interpretation of the depositional settings.

Four distinctive trace fossil assemblages were recognized in the Itararé Group deposits of southern Brazil: two intimately related to thin siltstone-claystone rhythmites, one to heterolithic deposits and another one with massive siltstones. The most common trace fossil assemblage in the glacial rhythmites consists of arthropod trackways and "resting" traces, attributed to merostomes, isopod crustaceans and apterygote insects. In the Itararé Group, trackways include ichnospecies of *Maculichna*, *Umfolozia, Kouphichnium, Protichnites* and *Glaciichnium* (Lermen, 2006; Gandini *et al.*, 2007; Netto & Lermen, 2006; Balistieri *et al.*, 2002, 2003; Netto *et al.*, 2012a) (Figures 5A-C, F-G, 6B). Crustacean resting traces are rarer, being represented by *Gluckstadtella cooperi* (Figure 5D) in the Paraná and Karoo (Southern Africa) basins. A particular suite composed exclusively of *Diplichnites gouldi* and *Diplopodichnus biformis* (Figure 5E) also occurs, being the most conspicuous trace fossil assemblage in thin-bedded rhythimites of the Paraná Basin (Nogueira & Netto, 2001b; Balistieri *et al.*, 2002, 2003; Gandini *et al.*, 2007; Buatois *et al.*, 2006, 2010; Netto *et al.*, 2009). *D. gouldi* and *D. biformis* have been interpreted as 'myriapod' trackways (e.g., Johnson *et al.*, 1994; Keighley & Pickerill, 1996, 2003; Balistieri *et al.*, 2003; Netto *et al.*, 2009).

The other trace fossil assemblage recorded in the deglaciation rhythmites is dominated by nonspecialized surficial trails and very shallow horizontal burrows (*Cochlichnus*, *Gordia*, *Helminthoidichnites,* and *Mermia* ichnospecies; Figures 5D, 6A-D) and deeper burrows representing deposit-feeding behaviors (*Hormosiroidea meandrica*, *Treptichnus* isp., *T. pollardi, Nereites isp., Palaeophycus* isp., *Planolites* isp.; Figures 6A, C). Accessory components include arthropod locomotion (*Cruziana problematica*; Figures 5A, H) and "resting" traces (*Rusophycus* isp., *R. carbonarius, Tonganoxichnus* isp.; Figures 5I-J), molluskan-type trails and burrows (*Dydimaulichnus,*

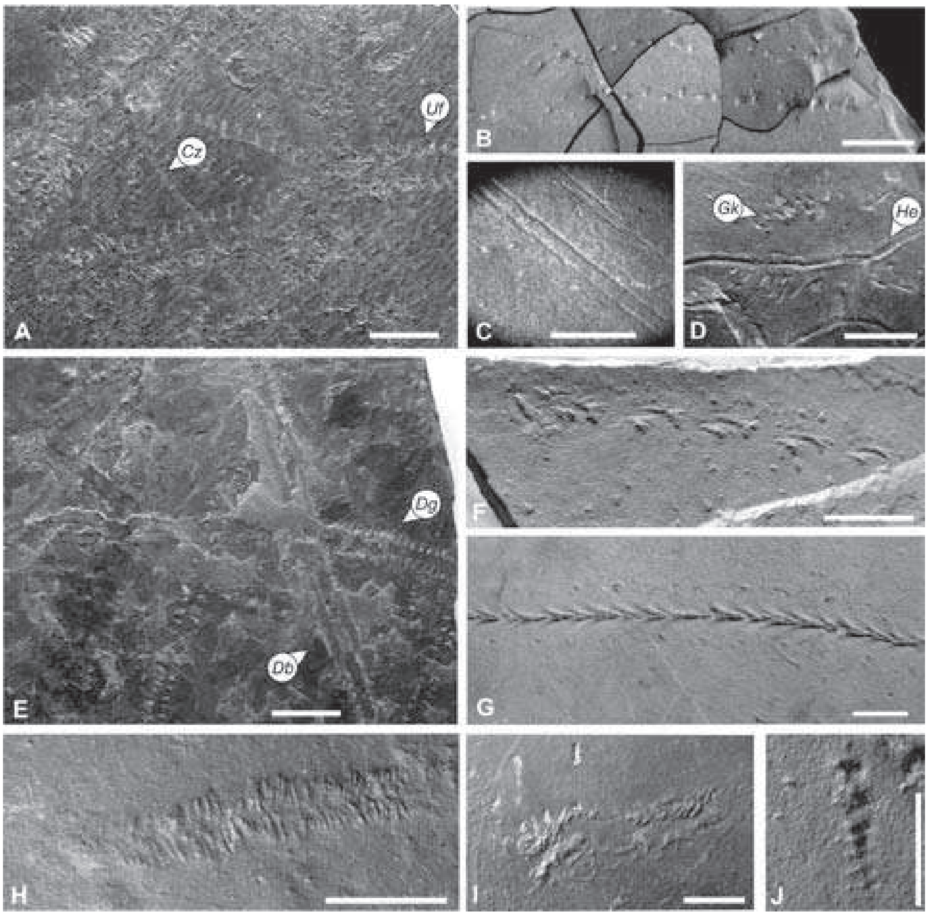

Figure 5. Arthropod trackways, furrows and resting traces preserved in glacial rhythmites of the Itararé Group. A, *Umfolozia sinuosa* (*Uf*) cross-cutting shallow furrows of *Cruziana problematica* (*Cz*); B, *Maculichna varia*; C, *Protichnites* isp.; D, *Gluckstadtella cooperi* (*Gk*) overlying shallow burrows [*Helminthoidichnites tenuis* (*He*)]; E, *Diplichnites gouldi* (*Dg*) and *Diplopodichnus biformis* (*Db*); F, *Kouphichnium* isp.; G, *Glaciichnium* isp.; H, *Cruziana problematica*; I, *Rusophycus* cf. *carbonarius*; J, *Tonganoxichnus* isp. A-C, E-I preserved in positive hyporelief; D, J preserved in negative epirelief. Scale bars: 10 mm.

Lockeia, and *Protovirgularia* ichnospecies; Figures 6E-F), nonspecialized vertical burrows (*Arenicolites* isp., *Diplocraterion* isp., *Skolithos* isp.), and fish trails (*Undichna consulca*; Figure 6G). The structure of the trace fossil assemblage and the ichnotaxa recorded are consistent with the *Mermia* Ichnofacies.

In the southern Brazilian deposits of the Itararé Group, these two main trace fossil assemblages occur together in some thin-bedded varve-like rhythmites in which the *Scoyenia* ichnocoenosis always superimposes the *Mermia* ichnocoenosis, in palimpsest preservation (Balistieri, 2003; Buatois *et al.*, 2006, 2010; Netto *et al.*, 2009). The dominance of *D. gouldi* and *D. biformis* in Gondwanan glacial rhythmite beds might be a taphonomic effect resulting from the preservation of the last population emplaced in an environment shifting from freshwater to terrestrial, which reinforces the hypothesis of time-averaging in invertebrate freshwater-influenced trace fossil assemblages in glacial settings, as discussed by Netto *et al.* (2009). *Diplocraterion* and *Protovirgularia* are particular exceptions in the Itararé Group ichnofauna, and may suggest deposition nearby the mudflats flanking fjord valleys, where marine influence is stronger and the benthic fauna tolerate sharp salinity fluctuations (Balistieri, 2003; Buatois *et al.*, 2006, 2010; Netto *et al.*, 2009).

Netto *et al.* (2009) suggested that the Itararé Group rhythmites represent periodic turbiditic deposition in shallow lakes that were formed during deglaciation rather than annual depositional cycles normally invoked to interpret Pleistocene rhythmites that characterize Quaternary glaciomarine and glaciolacustrine deposits. The shallow condition of the lakes is supported by (i) the frequent superimposition of the *Mermia* ichnocoenosis by the atypical *Scoyenia* ichnocoenosis, which is dominated exclusively by 'myriapod' trackways, and (ii) the abundance of sedimentary structures induced by the presence of microbial mats. This model was compared with modern postglacial landscapes in Alaska and Antarctica, and reinforced by the common occurrence of freshwater ponds and lakes that develop in shallow depressions excavated by ice mass movements in marginal-marine plains in high-latitude settings (Horne & Goldman, 1994).

Glaciomarine deposits overlie the ichnofossiliferous thin-bedded rhythmites in the Paraná Basin, and

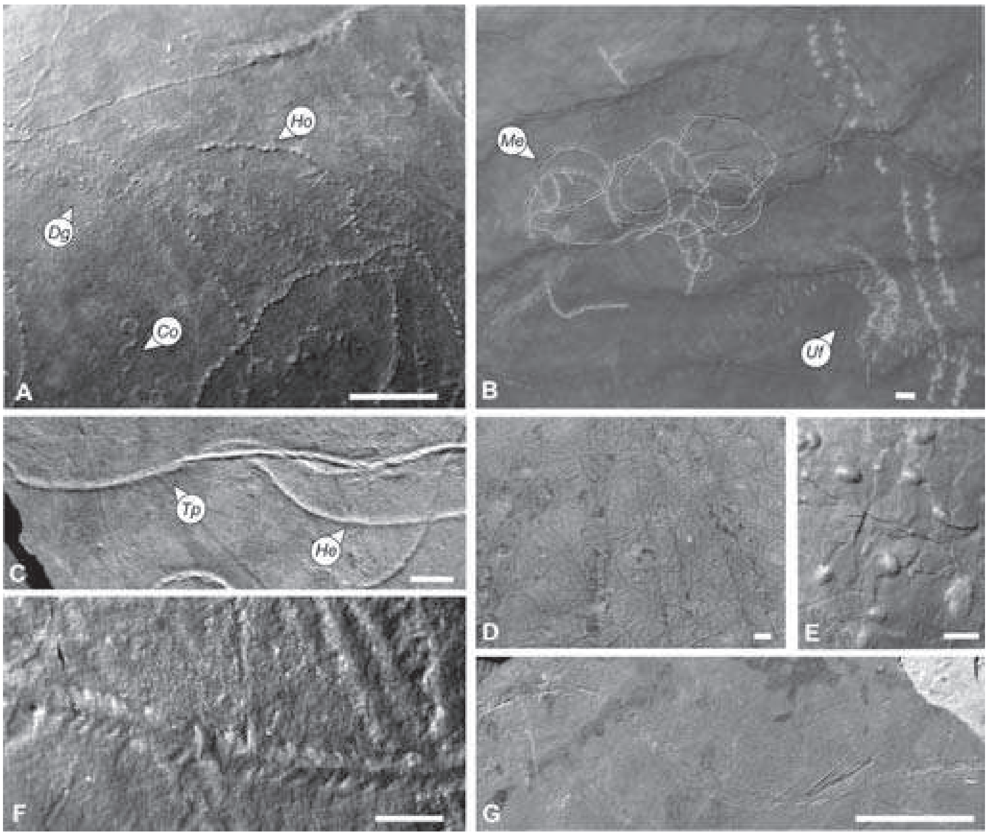

Figure 6. Shallow burrows and trails preserved in glacial rhytmites of the Itararé Group. A, *Hormosiroidea meandrica* (*Ho*), *Cochlichnus* isp. (*Co*) and *Diplichnites gouldi*; B, *Mermia* isp. (*Me*) and *Umfolozia sinuosa* (*Uf*, undertrack preservation); C, *Treptichnus pollardi* (*Tp*) and *Helminthoidichnites tenuis* (*He*); D, *H. tenuis* composing a monospecific suite; E, *Lockeia siliquaria*; F, *Protovirgularia* isp.; G, *Undichna consulca*; H, Scale bars: 10 mm.

are present in other Gondwanan basins (Buatois *et al.*, 2010; Netto *et al.*, 2012). They are composed of trough-stratified, wavy-bedded, fine-grained sandstones, fine- to very fine-grained sandstones and siltstones with flaser and wavy bedding, and massive siltstones and shales. Massive siltstones locally contain sharply-bounded burrows (*Thalassinoides* isp., *Diplocraterion* isp., *Palaeophycus* isp., *P. striatus, ?Rhizocorallium* isp., and *Gyrolithes*-like burrows; representative of *Glossifungites* Ichnofacies (Balistieri & Netto, 2002; Netto *et al.*, 2007) (Figures 7A-D, H). The presence of the *Glossifungites* suite indicates local transgressive erosional exhumation and firmground colonization in fjord valley flanks.

The ichnofauna of shallow glaciomarine Gondwanan areas are preserved in the fine-grained heterolithic strata and are mainly composed of ?*Arenicolites, Chondrites, Diplocraterion*, *Palaeophycus*, *Phycosiphon, Planolites*, *Rhizocorallium* and *Thalassinoides* (Figures 7E-G) and are well represented in the Rio do Sul Formation in Santa Catarina and Rio Grande do Sul states (Balistieri, 2003; Buatois *et al.,* 2006, 2010). Glaciomarine trace fossils are small when compared with equivalent ichnofaunas from normal marine settings, and comprise non-specialized feeding burrows produced by trophic generalists. The overall structure and composition of the assemblage are consistent with impoverished *Cruziana* Ichnofacies suites that are normally found in brackish-water settings (e.g., Buatois *et al.,* 2005). Dropstones and diamictites with faceted clasts occur throughout most of the succession and thick deposits of fossiliferous marine shales record periods of maximum flooding in the Gondwanan glacial environment. Framboidal pyrite crystals and *Tasmanites* are present in almost all levels of the Rio do Sul Formation, attesting the marine character of the depositional settings. However, there is an interval in which pyrite and *Tasmanite*s are absent but *Botryococcus* is present, suggesting a major freshwater input. Additionally, the presence of wavy ripple laminations and ripple drift cross laminations indicate the presence of wave and current processes.

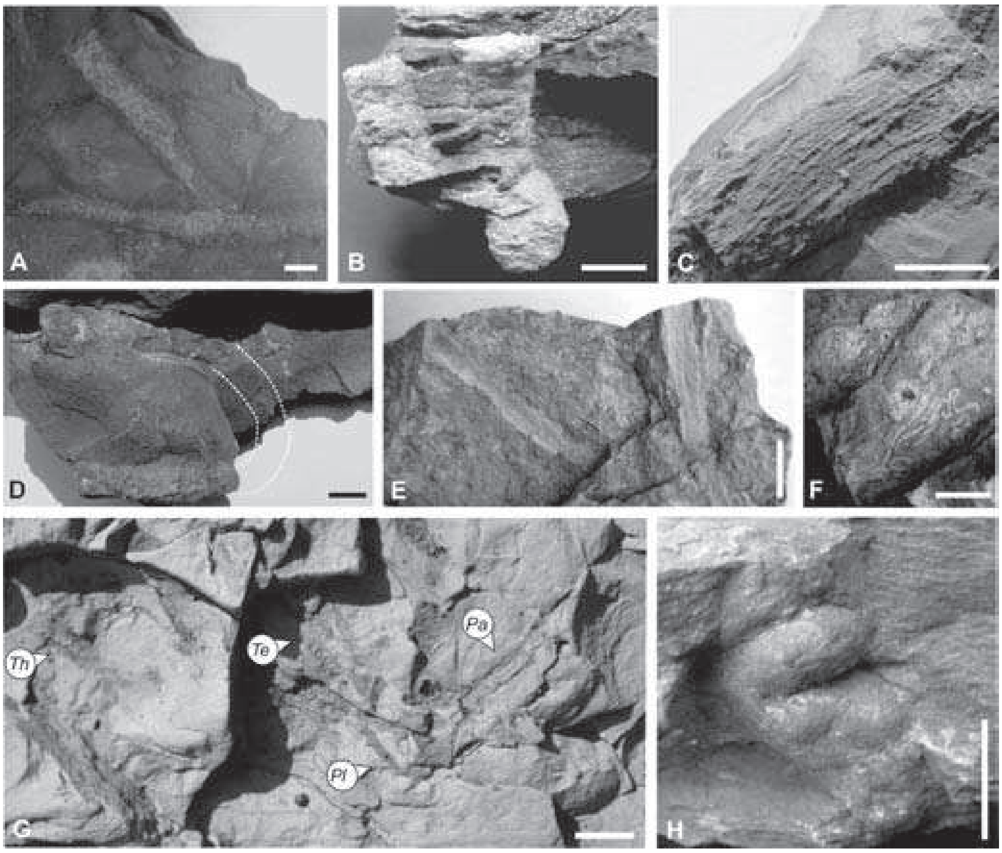

Figure 7. Deep burrows preserved in massive siltstones (A-D, G) and fine-grained heterolithic deposits (E-G) of the Itararé Group. A, *Thalassinoides* isp.; B, *Diplocraterion* isp.; C, *Palaeophycus striatus*; D, *Rhizocorallium* isp.; E, *Palaeophycus* isp.; F, *Phycosiphon* isp.; G, *Palaeophycus* isp. (*Pa*), *Planolites* isp. (*Pl*), *Teichichnus* isp. (*Te*), *Thalassinoides* isp. (*Th*); H, *Gyrolithes*-like burrows. Scale bars: 10 mm.

THE PERMIAN RECORD

The Guatá Group

Geological overview

The deposits of the Guatá Group (Sakmarian–Artinskian) represent a remarkable transgressive event in the Paraná Basin that succeeds the final Gondwana deglaciation. The Rio Bonito Formation concentrates deltaic, estuarine and coastal deposits resultant from the sea-level rising and inundation of the outwash plains at fjord-valley margins, and the Palermo Formation characterizes the shallow marine deposition. Huge coalfields developed in the coastal plain deposits in all eastern border of the Paraná Basin, in which the Candiota coalfield is the most expressive one, containing at least 6 staked coal seams, the deepest one having *ca* 9 m in thickness (e.g., Schneider *et al.*, 1974; Lavina & Lopes, 1987; Milani *et al.*, 2007).

The basal portion of the Rio Bonito Formation (Triunfo Member) is composed of conglomerates, sandstones, mudstones and coal deposits formed in fluvio-deltaic settings. The middle portion (Paraguaçu Member) is composed mainly of very fine- to fine-grained sandstones and fine-grained, bioturbated heterolithic deposits that characterize a marine transgression. Corase- to fine-grained sandstones, fine-grained heterolithic deposits, mudstones and coal compose the upper portion of the Rio Bonito Formation (Siderópolis Member) which was deposited in coastal settings, mostly representing tide-dominated estuaries that give place, toward the top, to wave-dominated estuaries and backbarrier lagoon deposits. The Palermo Formation represents the shelf deposits of the Guatá Group, composed mostly of very fine- to fine-grained sandstones with parallel lamination and trough, hummocky (HCS) and swalley (SCS) cross-stratification interbedded with fine-grained, densely bioturbated heterolithic deposits forming wavy and lenticular bedding. These sand-rich deposits characterize sedimentation in foreshore to lower shoreface settings. Toward the top, the sandstone beds become sparse and mudstones dominate the upper portion of the succession, remarking deposition throughout the offshore transition zone to lower offshore settings (e.g., Medeiros & Thomaz Filho, 1973; Schneider *et al.*, 1974; Aboarrage & Lopes, 1986; Lavina *et al.* 1985; Lavina & Lopes, 1987; Netto, 1994; Buatois *et al.*, 2001a,b, 2007; Tognoli, 2002, 2006; Tognoli & Netto, 2003; Gandini *et al.*, 2010).

The Rio Bonito Formation bears the major record of the "*Glossopteris* Flora" in southern Brazil. Sphenophytes, lycophytes, pteridophytes, pteridophylls (*incertae sedis*), cordaitophytes, coniferophytes and glossopteridophytes compose the main plant megafossil record, which is preserved as impressions of stems, leaves, reproductive structures and seeds in the muddy deposits of the Triunfo and Siderópolis members (e.g., Guerra-Sommer & Cazzulo-Klepzig, 2000; Vieira & Iannuzzi, 2000; Adami-Rodrigues & Iannuzzi, 2001; Jasper *et al.*, 2003; Iannuzzi & Souza, 2005; Iannuzzi, 2010). Mollusk-shell accumulations also occur in Paraguaçu Member deposits, being well represented in Taió (SC) and Vila Nova do Sul (RS), as well as isolated brachiopod and echinoderm remains (e.g., Rocha-Campos, 1964; Simões & Rocha-Campos, 1991; Simões *et al.*, 1998; Schmidt-Neto, 2010). Mollusk shells have also been recorded in Palermo Formation beds in São Sepé (RS) (Simões, 1992; Netto, 1994).

The Rio Bonito and Palermo formations have been studied since the beginning of 20th century, due to the economic interest in coal exploitation. In spite of the abundant bioturbation, most of the stratigraphic studies developed up to middle 1980s were focused only in lithology and primary sedimentology structures and the deposits of the Rio Bonito Formation were interpreted as fluvio-deltaic. The advance of ichnologic studies during the 1990s (Netto, 1994, 1998) and the development of studies integrating the ichnologic, sedimentologic and sequence-stratigraphic evidence allowed to review this interpretation and assume that the Rio Bonito Formation was deposited preferentially under tide-dominated estuarine conditions (Netto, 1994; Buatois *et al.*, 2001a,b, 2007; Gandini *et al.*, 2010). These studies also provided detailed insights into depositional evolution of the Paraná Basin. The evaluation of the ichnologic content allowed distinguishing between restricted, brackish-water environments in the Rio Bonito Formation and regionally extensive, fully marine settings of the Palermo Formation (Netto, 1994).

Trace fossil record

Trace fossils have been reported in the Guatá Group since 1960s, when Salamuni (1962), Salamuni & Alessi (1966) and Habekost (1978, 1993) reported the occurrence of 'tubes of worms' and 'bioturbation' in deposits of Palermo Formation in Paraná and Santa Catarina states. Rocha-Campos (1964) described an unidentified feature associated with the fossiliferous sandstones that, only few years ago, was associated with *Rosselia socialis* (Tognoli *et al.*, 2007). The first formal ichnological study in the Guatá Group was developed by Stevaux *et al.* (1983) who identified the presence of *Monocraterion, "Nereis", Planolites, Rhizocorallium, Scoyenia, Teichichnus* and *Terebellina*, as well as *spreiten* burrows in subsurface deposits distributed into six distinct trace fossil associations representative of proximal offshore to lagunar settings.

Netto & Gonzaga (1985) developed a detailed study on the ichnofauna of the Guatá Group in subsurface and surface deposits from Cachoeira do Sul (RS). *Arenicolites, Diplocraterion, Planolites, Rosselia?, Teichichnus, Thalassinoides* and *Skolithos* were recognized, as well as mollusk resting traces, trails and unindentified arthropod burrows. This assemblage was organized in two different suites, representative of shallow marine environments (*Skolithos* and *Cruziana* ichnofacies). Since then, several ichnological studies were carried on in the sedimentary units of the Guatá Group, focusing mainly on the integrated sedimentologic and ichnologic analyses.

The ichnofauna of the Rio Bonito Formation is concentrated mainly in the sedimentary successions that characterize the Paraguaçu and Siderópolis members. The Paraguaçu Member is well exposed in Taió (SC) and is represented by a predominantly muddy succession intercalated with sandy fossiliferous bedding bearing marine mollusk and echinoderm body fossils and abundant trace fossils (e.g., Tognoli, 2002, 2006; Tognoli *et al.*, 2007). The ichnological content varies from low to high degree of bioturbation and low to high ichnodiversity. It includes *Arenicolites, Bergaueria, Chondrites, Cylindrichnus, Diplocraterion, Helminthopsis, Ophiomorpha, Palaeophycus, Phycosiphon, Planolites, Rhizocorallium, Rosselia, Teichichnus, Skolithos, Zoophycos* and escape structures. This ichnofauna is observed preferentially in cores and is arranged in distinctive trace fossil suites that show a notable relationship with the different facies associations (e.g., Tognoli, 2002, 2006). A particular suite composed exclusively by *Rosselia* ichnofabric is observed in amalgamated beds of fine-grained sandstones with hummocky (HCS) and swaley (SCS) cross-stratification and shell accumulations preserved at the top of the beds (e.g., Tognoli, 2002, 2006) (Figures 8A-D).

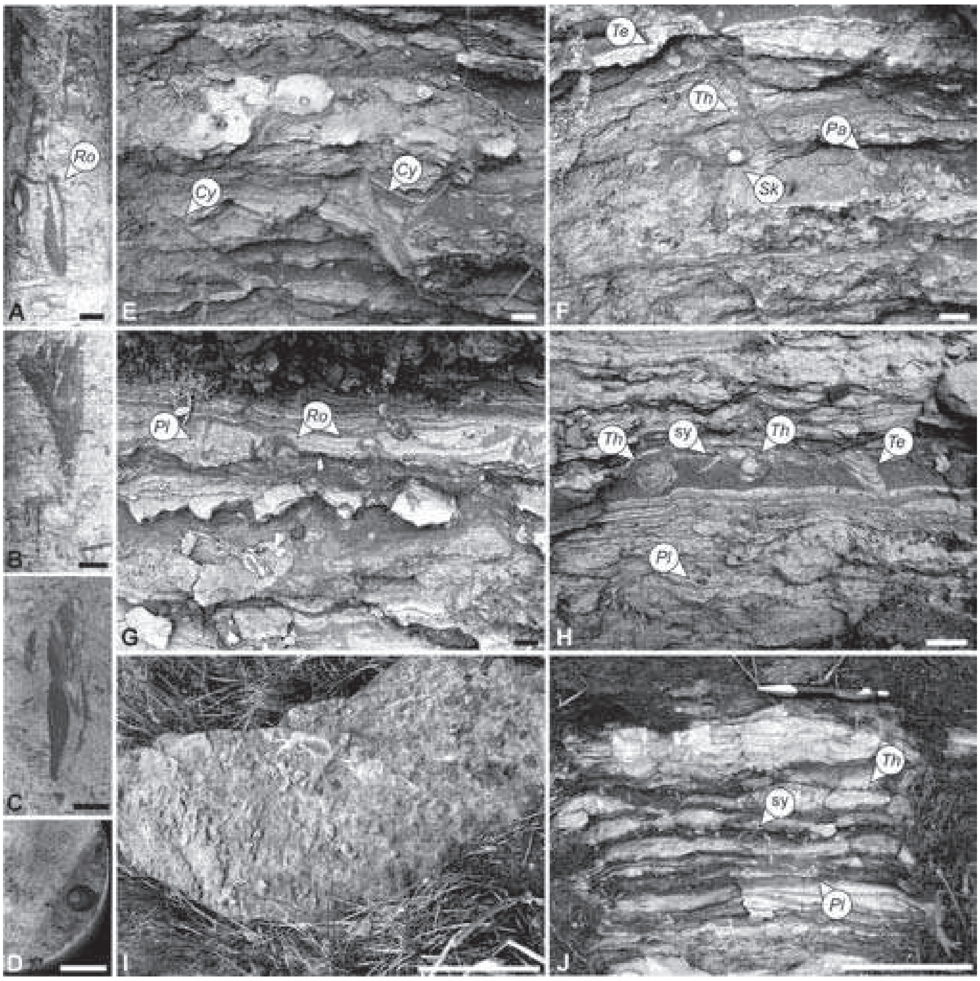

Figure 8. Ichnofabrics from the Rio Bonito/Palermo sedimentary succession. A-D, *Rosselia* ichnofabric from the Paraguaçu Member showing the thick mud, concentric lining and both typical preservational forms: funnel-shape (B) and spindle-shape, stacked (C) burrows; E-J, some components of the composite ichnofabric commonly observed in the Siderópolis Member. Abbreviations: *Cy*, *Cylindrichnus*; *Pa*, *Palaeophycus*; *Pl*, *Planolites*; *Ro*, *Rosselia*; *Sk*, *Skolithos*; *Te*, *Teichichnus*; *Th*, *Thalassinoides*; sy, synaerenis cracks. Scale bars: A-H, 10 mm; I-J, 10 cm.

The ichnofauna of the Siderópolis Member is characterized by the presence of sparse bioturbation preserved in heterolithic deposits in estuarine bay settings (e.g., Netto & Gonzaga, 1985; Boeira & Netto, 1987; Netto *et al.*, 1991; Netto, 1994, 1998, 2000; Buatois *et al.* 2001a,b, 2007; Tognoli, 2002, 2006; Tognoli & Netto, 2000, 2003, 2004a,b, 2007; Tognoli *et al.*, 2007, 2008; Gandini *et al.*, 2010). *Cylindrichnus, Palaeophycus*, *Planolites, Teichichnus, Thalassinoides* and mollusk trails are the main observable ichnogenera, both as trace fossils or ichnofabric (Figures 8E-J). *Ophiomorpha* and *Skolithos* may occur associated with reactivation surfaces (e.g., Netto, 1994; Netto *et al.*, 1996; Buatois *et al.* 2001a,b, 2007; Gandini *et al.*, 2010; Gandini & Netto, 2012). The bioturbation degree is low at the base, being moderate toward the top. The low ichnodiversity (compared with those expressed in the whole sedimentary succession), the low degree of bioturbation and the small size of the burrows reflect stressed environmental conditions and suggest colonization of brackish water settings. These deposits are punctuated by ravinement surfaces demarcated by *Glossifungites* suites represented by firmground *Thalassinoides* and rare *Gyrolithes*-like burrows (better observed in cores) (Netto *et al.*, 2007) (Figure 9A-B). *Craticulichnus iruiensis* (Martini-da-Rosa *et al.*, 1994) (Figure 9C), a resting trace attributed to a merostomate was defined in marine sedimentary facies of the Rio Bonito Formation.

Specimens and ichnofabrics of *Arenicolites, Asterosoma, Bergaueria, Chondrites, Cylindrichnus, Diplocraterion*, *Helminthopsis, Lockeia, Macaronichnus, Monocraterion, Ophiomorpha, Palaeophycus, Phycosiphon, Planolites, Rhizocorallium, Rosselia, Skolithos, Teichichnus* and *Thalassinoides* have been reported in the Palermo Formation (Figures 9D-O) both in cores and outcrops (e.g., Netto & Gonzaga, 1985; Boeira & Netto, 1987; Netto *et al.*,

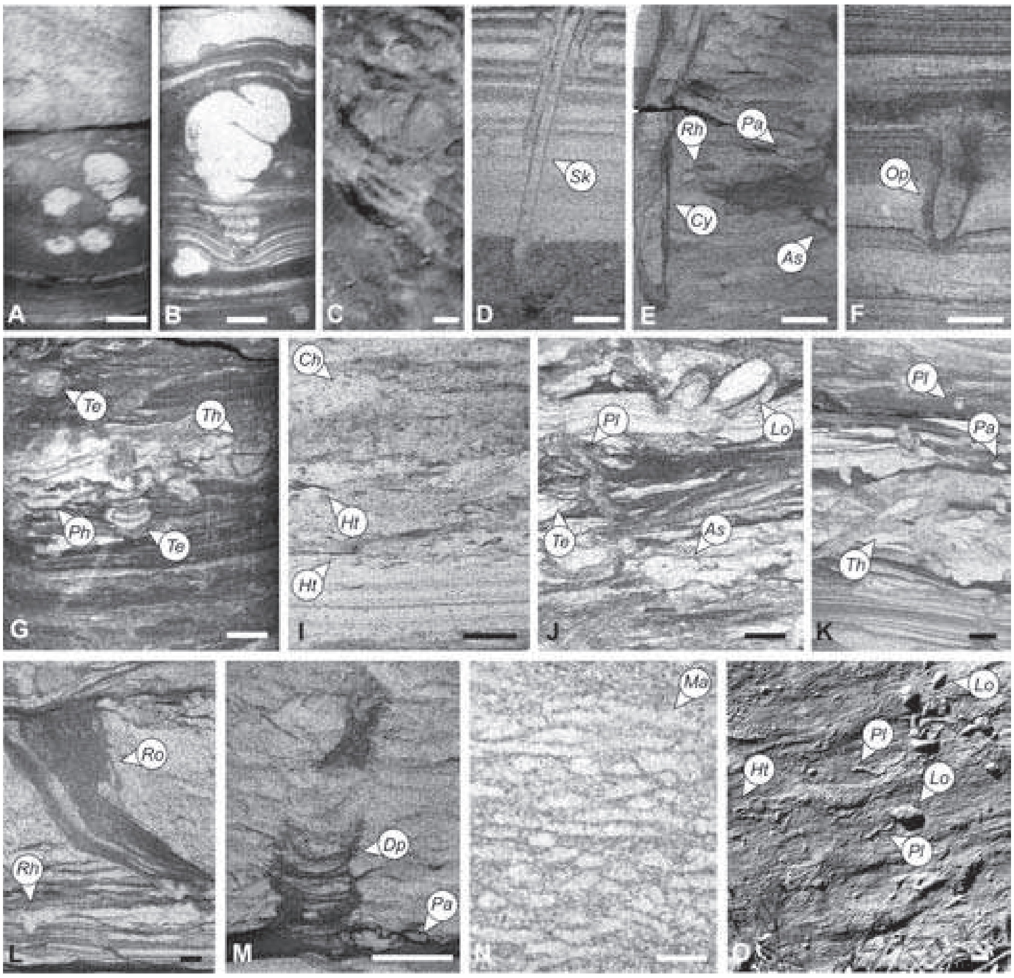

Figure 9. A-C, Trace fossils from marginal-marine deposits of the top of Siderópolis Member: *Gyrolithes*-like burrows in *Glossifungites* suite (A-B) and *Craticulichnus iruiensis* (C); D-O, marine ichnofaauna from Palermo Formation. Abbreviations: *As, Asterosoma; Ch, Chondrites; Cy, Cylindrichnus*; *Dp, Diplocraterion*; *Ht, Helminthopsis*; *Lo, Lockeia*; *Ma, Macaronichnus*; *Op, Ophiomorpha*; *Pa, Palaeophycus*; *Ph, Phycosiphon*; *Pl, Planolites*; *Rh, Rhizocorallium*; *Ro, Rosselia*; *Sk, Skolithos*; *Te, Teichichnus*; *Th, Thalassinoides*. Scale bars: 10 mm.

1991; Netto, 1994, 1998, 2000; Martini-da-Rosa *et al.*, 1994; Buatois *et al.* 2001a,b, 2007; Tognoli, 2002, 2006; Tognoli & Netto, 2000, 2003, 2004a,b, 2007; Tognoli *et al.*, 2007, 2008; Gandini *et al.*, 2010; Gandini & Netto, 2012). The degree of bioturbation is typically high and the tiering structure is relatively complex, being observable only in cores. They characterize a diverse lower shoreface-offshore transition to upper-offshore ichnofauna, typical of the *Cruziana* Ichnofacies. The lower offshore is composed of totally bioturbated mudstones with small and compressed *Thalassinoides* as the only discrete traces (also only observable in cores). These deposits are punctuated by transgressive surfaces of erosion demarcated by the presence of *Glossifungites* suites, in which *Thalassinoides* is the main (and sometimes, the unique) component.

The Passa Dois Group

Geological overview

The Passa Dois Group corresponds to a 3rd order sequence that begins with offshore marine sedimentation (Taquaral Member, Irati Formation) overlying the shelfal marine deposits of the Guatá Group. Through the top, the sequence is composed of the black, pirobetuminous shales and carbonates of the Irati Formation, representing shoaling up deposits. The Serra Alta and Teresina formations compose the transgressive system tract that characterizes the upper half of the sequence and culminates with the deltaic and lacustrine deposits of the Rio do Rasto Formation (Milani *et al.*, 2007).

In southern Brazilian deposits of the Passa Dois Group, trace fossils have been reported mainly in the Teresina and Rio do Rasto successions (Netto, 1992; Lima & Netto, 2012). *Chondrites* had been observed locally in shales of the Irati Formation cropping out in Santa Catarina and Rio Grande do Sul states, without formal record. Bioturbation also occurs in the heterolithic deposits of the Serra Alta Formation, but no further relevant information is provided in the literature.

The Teresina Formation is characterized by a thick succession of purple shales intercalated with thin, discrete, very fine-grained sandstones forming lenticular and wavy bedding. Fine-grained tabular sandstones with low-angle trough, hummocky and swalley cross-stratification can be observed at the top of the succession interbedded with heterolithic siltstone and mudstone deposits. Thin carbonate beds with cone-in-cone structures and shrinkage cracks are locally observed. These deposits characterize sedimentation in offshore to shoreface settings in a wave-dominated shelfal marine environment (e.g., Schneider *et al.*, 1974; Lavina, 1988; Netto, 1992; Klein *et al.*, 1999; Warren, 2008; Lima & Netto, 2012) and represent shoaling upward cycles. The deposits exposed at Dom Pedrito (RS) also show evidence of unidirectional currents action, possibly related to a nearby prograding delta. They form stacked coarsening- and thickening-upward cycles that are overlaid by retrogradational/agradational cycles (Lima, 2010).

The coarsening and thickening upward cycles developed at the top of the Teresina Formation emphasizes the progradational trend of the sedimentation that characterizes the upper Permian deposits of the Paraná Basin and are assumed by some authors as the basal Serrinha Member of the Rio do Rasto Formation (e.g., Schneider *et al.*, 1974; Lavina, 1988; Netto, 1992; Warren, 2008). The Rio do Rasto Formation is composed mainly of tabular, sigmoidal and lenticular sandstone beddings intercalated with laminated siltstones and massive mudstones. Sigmoidal cross-bedding sandstones with trough cross-stratification and climbing ripples intercalated with massive muddy deposits are the main observed lithologies. Plant and reptile remains and mud cracks are common (e.g., Langer *et al.*, 2009; Dias-da-Silva, 2012). These deposits have been interpreted as deltaic and are overlaid by lenticular sandstones with high-angle trough cross-stratification that represent distributary channels (e.g., Lavina 1988; Netto, 1992; Warren, 2008).

Sandstones representative of eolian dunes, damp interdunes and sand sheets that compose the upper Piramboia Formation occur interbedded with the sandstones of the top of Morro Pelado Member, recording the transition to eolian systems that characterizes the uppermost Permian deposits of the Paraná Basin (e.g., Lavina *et al.*, 1993; Dias, 2008).

Trace fossil record

The ichnofauna of the Passa Dois Group in southern Brazil was recorded firstly by Netto (1988, 1992) in fine-grained heterolithic deposits and sandstones with hummocky and swaley cross-stratification that was assumed as belonging to the base of the Rio do Rasto Formation (= Serrinha Member). Recently, Lima (2010) and Lima & Netto (2012) reviewed this ichnofauna, based on the assemblage exposed at Cerro Chato outcrop (Dom Pedrito, RS), assuming the deposits as representative of the upper part of theTeresina Formation succession. Trace fossils were also recognized at the soles and tops of sandstone beds with trough cross-stratification and climbing ripple lamination (Lima, 2010). According to Lima & Netto (2012), the trace fossil assemblage is composed of *Bergaueria* isp., *Cochlichnus anguineus*, *Cruziana problematica*, *Diplocraterion* isp., *Diplopodichnus biformis*, *Helminthopsis* isp., *Lockeia siliquaria*, *Multina minima*, *Palaeophycus striatus*, *Palaeophycus tubularis*, *Planolites beverleyensis*, *Planolites montanus*, *Teichichnus* isp., *Thalassinoides* isp. and undetermined mollusk and soft-bodied animal traces (Figure 10).

Shallow and simple horizontal to oblique burrows produced at the interface between the sandy and mud layers are the main components of the ichnofauna. Feeding is the dominant behavior, followed by resting, dwelling and displacement, as well as discrete grazing activity. Burrows that suggest a more complex behavioral pattern are rare. The amount and diversity of the bioturbation are low, and *Planolites montanus* is the dominant ichnotaxon in the succession. Lima & Netto (2012) interpreted this assemblage as representative of colonization in a subaquatic environment with moderate to low hydrodynamic energy. The general characteristics of the ichnofossiliferous assemblage refer to the *Cruziana* Ichnofacies (Netto, 1992). However, the significantly low ichnodiversity, the low index of bioturbation and the dominance of simple feeding structures led Lima & Netto (2012) to infer a benthic fauna stressed by salinity fluctuations. Two main

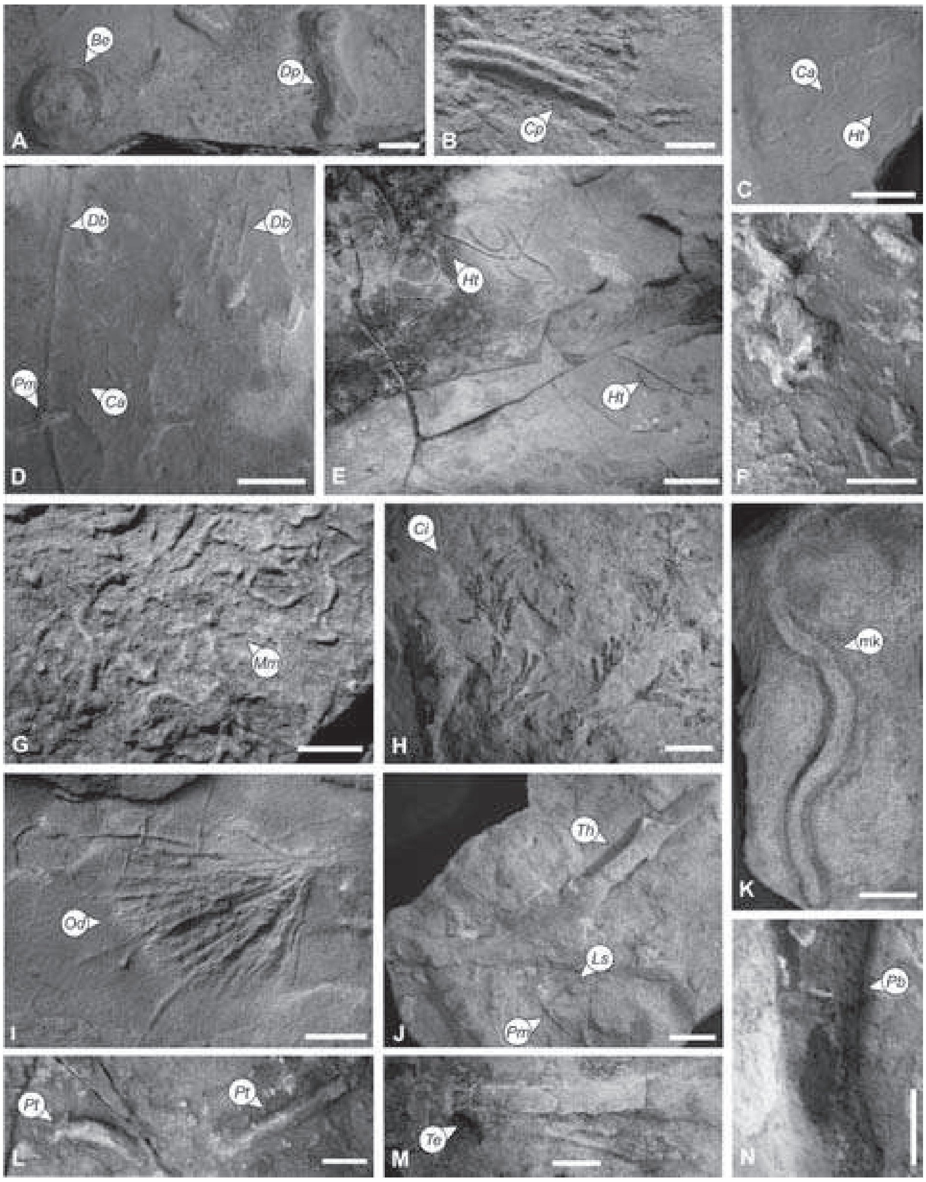

Figure 10. Trace fossil assemblage from Teresina Formation. Abbreviations: *Be, Bergaueria*; *Ca,Cochlichnus anguineus*; *Ci, Chondrites* cf. *intrincatus*; *Cp, Cruziana problematica*; *Dp, Diplocraterion*; *Db, Diplopodichnus biformis*; *Ht, Helminthopsis*; *Ls, Lockeia siliquaria*; *Mm, Multina minima*; *Od, Oldhamia*; *Pt, Palaeophycus tubularis*; *Pb, Planolites beverleyensis*; *Pm, Planolites montanus*; *Te, Teichichnus*; *Th, Thalassinoides*; mk, undetermined mollusk trails. Scale bars: 10 mm.

trace fossil suites were recognized by Lima (2010): a brackish-water suite and a freshwater suite. The freshwater suite is represented by monospecific and multiespecific occurrences of *Cochlichnus anguineus*, *Cruziana problematica, Diplopodichnus biformis* and *Planolites montanus* in distinct current-generated sandstone beds and it was interpreted by Lima (2010) as suggestive of deltaic influence at the lower shoreface, in a restricted shallow sea context.

Netto (1988, 1992) also reported the occurrence of *Planolites beverleyensis*, *Planolites montanus*, *Teichichnus rectus* and *Thalassinoides suevicus* in sandstone sigmoidal cross-bedding exposed in Tiarajú outcrop (São Gabriel, RS). This material was not reviewed by Lima (2010) and Lima & Netto (2012) and further revision based on the ichnotaxobases approach (Bromley, 1990) must be done to confirm the ichnotaxonomic status of this assemblage.

Dentzien-Dias *et al.* (2012a,b) described a wide variety of vertebrate coprolites in lacustrine facies of the Rio do Rasto Formation in São Gabriel (RS). Vertebrate burrows also occur in sandstone facies of the Piramboia Formation, showing distinct morphologies (Dentzien-Dias *et al.*, 2009). They are preserved in full relief and apparently had a dwelling or resting purpose. Some burrows are elongated and concave at the base, with morphology resembling *Piscichnus*, others are irregular in shape and may represent small tetrapod aestivation burrows (Netto *et al.*, 2010) (Figure 11). However, further studies are necessary to evaluate their significance and the possible tracemakers.

THE MESOZOIC RECORD

Geological overview

The most complete Mesozoic record of the Paraná Basin characterizes the Gondwana II Supersequence (Milani *et al.*, 2007) and it is mainly exposed in Rio Grande do Sul State (Figure 1). Fluvial, deltaic, lacustrine and eolian facies developed under arid climatic conditions characterize the Triassic deposits, which give place to huge eolian systems through the Jurassic and maybe Early Cretaceous (e.g., Scherer *et al.*, 2000). The Triassic deposits are represented by the Rosário do Sul Group (see Scherer *et al.*, 2000; Milani *et al.*, 2007), which is divided into the Sanga do Cabral, Santa Maria and Caturrita formations (e.g., Lavina *et al.*, 1993; Zerfass *et al.*, 2003). The Jurassic–?Cretaceous deposits are represented by the Guará and Botucatu formations (e.g., Scherer *et al.*, 2000; Dentzien-Dias *et al.*, 2007, 2008). In southern Brazil, trace fossils have been reported in Sanga do Cabral, Caturrita and Guará formations, as well as the top of Alemoa Member (Santa Maria Formation) (Netto, 1989; Faccini *et al.*, 1989; Gandini *et al.*, 2004; Netto *et al.*, 2004; Netto, 2007; Dentzien-Dias *et al.*, 2007, 2008; Silva *et al.*, 2005a,b, 2007, 2008a-c).

The Sanga do Cabral Formation (Lower Triassic) is composed of fluvial-eolian deposits that overlie the Passa Dois Group (e.g., Faccini *et al.*, 1989). The succession is composed of fine-grained sandstones with sigmoidal cross-bedding,

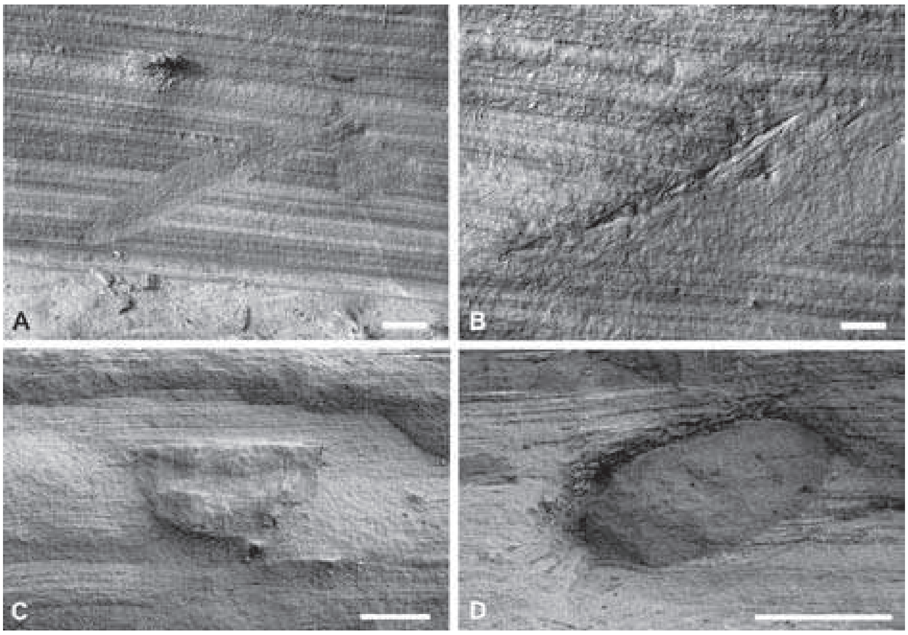

Figure 11. Vertebrate burrows from Piramboia Formation. Scale bars: 10 cm.

tangential cross-stratification and climbing ripples, interbedded with laminated siltstones interpreted as homopycnal delta front deposits. Lenticular fine-grained sandstones with medium-size trough cross-stratification represent braided fluvial channels, and fine-grainded sandstones showing big-size planar cross-stratification associated with sandstone beds having parallel lamination, climbing ripples, and bioturbation, were assumed as representative of eolian dunes and humid interdune sandy sheets (Faccini *et al.*, 1989).

The Santa Maria Formation (Middle to Late Triassic) includes the most extensive fluvial-lacustrine system of the Paraná Basin. The basal Passo das Tropas Member consists of conglomerates and coarse sandstone lenticular beds deposited in a braided fluvial system while the upper Alemoa Member is characterized by massive or fine-laminated, reddish, calciferous nodule-rich mudstones, intercalated with siltstones and fine-grained sandstones, and levels of calcrete (e.g., Scherer *et al.*, 2000; Zerfass *et al.*, 2003; Silva *et al.*, 2008c). The Alemoa Member records deposition in meandering fluvial channels with point bars and in alluvial plains, including floodplain deposits and paleosols. Crevasse channels, crevasse splays and lacustrine deltas are represented in the lower part of the overlying Caturrita Formation, whereas braided-fluvial-channel deposits occur at the top (e.g., Scherer *et al.*, 2000). Thickening-, slightly coarsening- and shallowing-upward recurrent cycles, each cycle starting with massive mudstone, grading into heterolithic beds and capped by lenticular trough cross-bedded and climbing- ripple-laminated, fine- to medium-grained sandstone show locally dense bioturbation and characterize the crevasse deposits of the Caturrita Formation. Both units contain abundant remains of cynodonts, dicynodonts, thecodonts, dinosaurs and early mammals, as well as a *Dicroidium* flora, conifers and conchostracans (e.g., Scherer *et al.*, 2000; Zerfass *et al.*, 2003; Silva *et al.*, 2008c).

The Guará Formation deposits cropping out in the southwestern portion of the Rio Grande do Sul State are composed of fine to coarse-grained sandstone and rare mudstones, deposited by fluvial and eolian sedimentary processes (Scherer *et al.*, 2000). The eolian deposits show large cross-beddings with grainflow, grain-fall and wind-ripple lamination, interpreted as large eolian dune deposits, and/or horizontal wind-ripples strata, composed of fine to coarse-grained sandstones interpreted as eolian sand sheet deposits (Scherer & Lavina, 2005). The Guará Formation accumulation was controlled by oscillations between arid and semi-arid conditions (Scherer & Lavina, 2006).

Trace fossil record

The first trace fossil record in the Mesozoic deposits of southern Brazil was made by Netto (1989) who described the occurrence of a *Scoyenia* ichnocoenosis in eolian sandstones of Sanga do Cabral Formation cropping out in Novo Hamburgo and surroundings (RS). This ichnocoenosis was composed of *Beaconites* (=*Anchorichnus*) *coronus, Skolithos* isp. and *Arenicolites* isp. and was interpreted as representative of arthropod burrowing activity in humid interduna deposits (Netto, 1989; Faccini *et al.*, 1989). *Beaconites coronus* is also abundant in eolian deposits cropping out in Santana do Livramento (RS) (Netto *et al.*, 2010) (Figure 14E). Originally assumed as belonging to the Sanga do Cabral Formation (e.g., Netto, 1989; Faccini *et al.*, 1989), these deposits were later assigned to the Guará Formation (e.g., Scherer & Lavina, 2005, 2006).

In Santa Maria Formation, abundant and laterally spreading rhizoliths descend from the thin carbonate sandstone layers at the top of Alemoa Member in Predebom Farm (São João do Polêsine, RS) (Figures 12A-B). Few and small *Planolites* isp. and *Skolithos linearis* occur associated with the rizolith-rich beds forming a freshwater to terrestrial, low-diversity suite assignable to the *Scoyenia* Ichnofacies (Netto, 2007). Discrete ichnofabrics containing *Skolithos linearis, Taenidium barretti,* and arthropod trackways occur in the heterolithic beds of the lower succession of the Caturrita Formation at the same locality. Trace fossils are not present in sandstone beds of the basal cycle. However, a crowded assemblage dominated by *Skolithos* (*S. linearis, S.* cf. *serratus*), with subordinate horizontal *T. barretti* and rare *Arenicolites* isp., disrupts the primary sedimentary structures of the sandstone beds in the second and third cycles (Figures 12C-K). Small rootlets are also present on the top of the second and third sandstone packages.

Tetrapod tracks and trackways are common and well preserved at the top of the outcrop (Silva *et al.*, 2007, 2008a-c) together with *Scoyenia gracilis, Beaconites coronus*, *Planolites montanus, Diplichnites gouldi, Permichnium* isp., vertical shafts, small rootlets and mud cracks (Gandini *et al.*, 2004), composing a *Scoyenia* Ichnofacies suite (Figure 13). Most of tracks and trackways preserved in Predebon outcrop were produced by small size animals. In fact, this outcrop bears the major ichnodiversity of tetrapod footprints in the Paraná Basin deposits. According to Silva *et al.* (2007, 2008a-c), nine morphotypes can be found in the Caturrita Formation beds: *Rhynchosauroides* isp., *Rhynchosauroides retroversipes*, *Rhynchosauroides?* isp., autopodia scratch marks, *Dicynodontipus* isp., *Dicynodontipus protherioides*, *Incertae sedis* theromorphoid tracks, undetermined dinosaur tracks, and *Grallator*? isp. (for illustrations, see Silva *et al.*, 2007, 2008a-c).

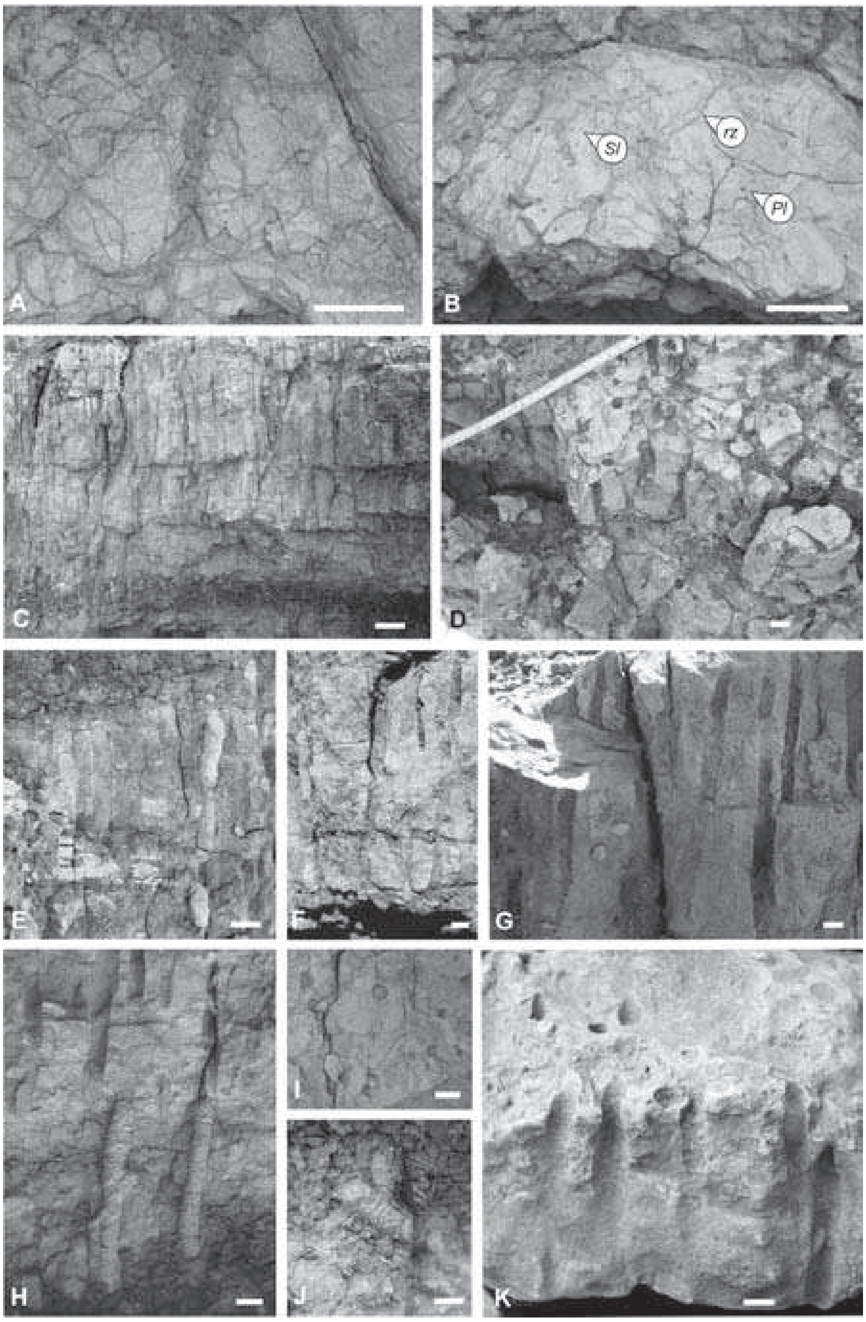

Figure 12. Triassic biogenic structures preserved in the central portion of Rio Grande do Sul State. A-B, Rhizoliths, small *Planolites* isp. (*Pl*) and *Skolithos linearis* (*Sl*) from the top of the Alemoa Member (Santa Maria Formation); C, general view of the non-marine *Skolithos*-dominated piperock preserved in sandstone beds of the Caturrita Formation; D-E, *Skolithos linearis*; F, *Arenicolites* isp.; G-H, *Taenidium barretti*; I, openings of *S. linearis*; J, meniscate burrow fill of *T. barretti*; K, *Skolithos* cf. *serratus*. Scale bars: 10 mm.

The ichnospecies *Rhynchosauroides retroversipes* and *Dicynodontipus protherioides* were described from specimens collected in Predebon outcrop and, until now, their occurrence is restricted to this locality.

According to Silva *et al.* (2007, 2008a-c), the footprints preserved in the Santa Marina and Caturrita formations might be attributed tho the tretrapod fauna whose skeletons are commonly found in their beds: *Rhynchosauroides retroversipes*, *Rhynchosauroides* isp., half-swimming footprints and *Rhynchosauroides*? isp. might be attributed to lizard-like animals, possibly sphenodontids; *R. retroversipes* suggest locomotion of a lacertoid reptile with autopodia resembling the primitive condition of the amniotes, and, together with *Dicynodontipus protherioides* and *Dicynodontipus* isp., might be attributed to small-size advanced cynodonts, possibly

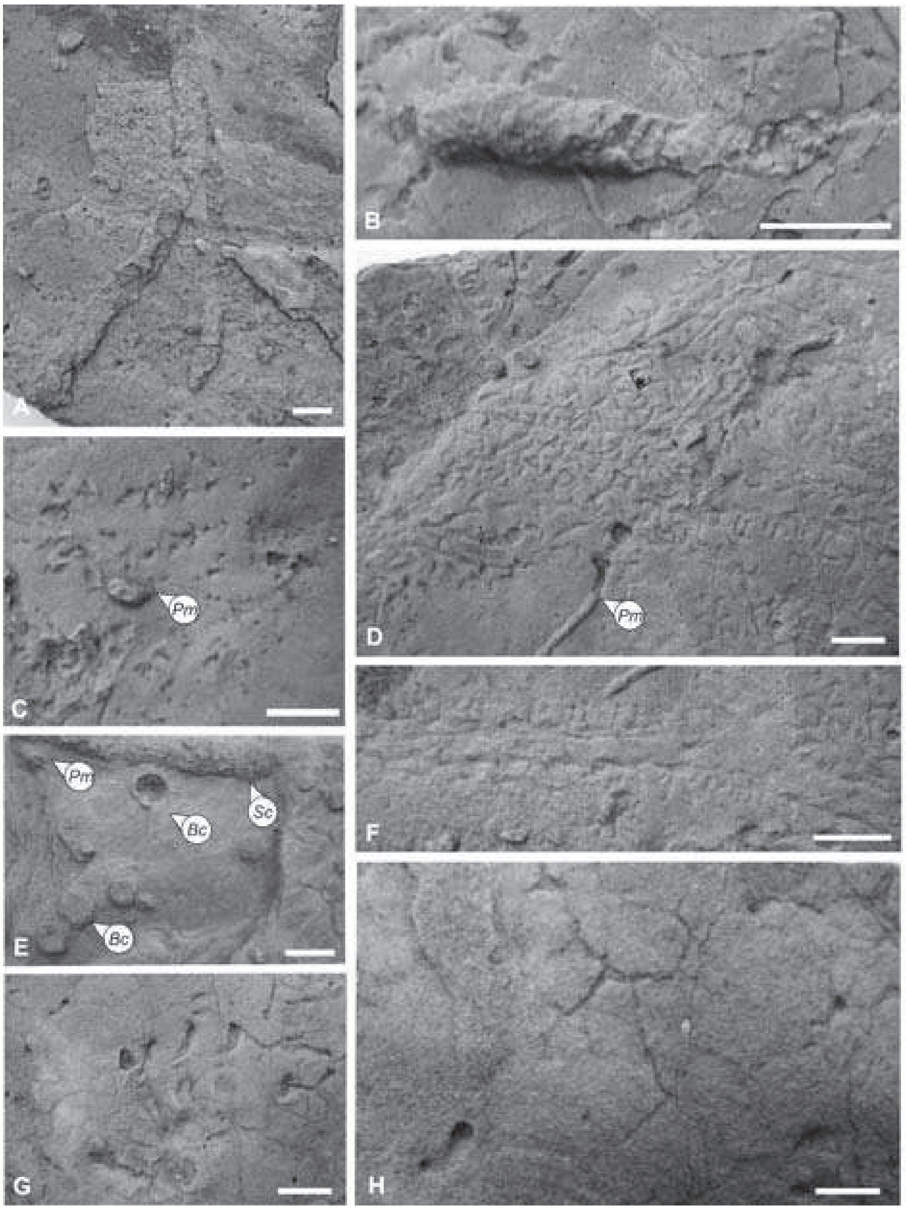

Figure 13. The *Scoyenia* Ichnofacies assemblage from Caturrita Formation. A, *Scoyenia gracilis*; B, *Beaconites coronus*; C, *Planolites montanus* (*Pm*) and undetermined arthropod tracks; D, arthropod trackways; E, openings of deep inclined *B. coronus* (*Bc*), associated with *S. gracilis* (*Sc*) and *P. montanus* (*Pm*); F, *Diplichnites gouldi*; G, tetrapod track; H, small rootlets. Scale bars: 10 mm.

tritelodontids. The undetermined dinosaur tracks and *Grallator?* isp. were attributed to primitive dinosaurs, mainly *Staurikosaurus*, *Saturnalia* and *Sacisaurus*, which are morphologically related to the recorded footprints and that commonly occur at the top of the Santa Maria Formation and at the Caturrita Formation.

Netto (2007) attributed the record of rizoliths at the top of Alemoa Member to extensive paleosol development during periodic subaereal exposure of the substrates. These paleosols may represent cyclic (?seasonal) exposure of the lake margins, possibly due to shoaling upward events.

Netto (2007) also analyzed the paleobiologial, paleoecological and stratigraphic significance of the *Skolithos* piperock of Predebon outocrop and concluded that non-marine environments may represent successive opportunistic colonization in subaerial environments rather than equilibrium succession due to high-frequency deposition in subaquatic environments. Insects are assumed to be the tracemakers of *Skolithos linearis* (midge larvae) and *Sholithos* cf. *serratus* (tiger beetle), and oligochaetes are inferred as the *Taenidium barretti* burrower. Substrate dewatering and subaerial exposure played an important role in piperock generation after deposition of the sandy beds of the Caturrita Formation. The local occurrence of the non-marine *Skolithos*-dominated composite piperock in the Caturrita Formation, intercalated within rhythmic deposits hosting the *Scoyenia* Ichnofacies, suggests an opportunistic colonization after overbank flows in floodplains. The observed palimpsest preservation reflects three different, successive colonization events, characterizing a depositional hiatus by non-deposition and reflecting low rates of erosion of firmgrounds. The *S.* cf. *serratus* ichnofabric is substrate-controlled and demarcates relevant surfaces in high-resolution analysis. According to Silva *et al.* (2007, 2008a-c), the tracks and trackways from the Predebon outcrop also reveal oscilation of the water content of the substrate, having been produced underwater and under semi-aquatic and semi-terrestrial conditions, in wet and dump substrates. Underwater tracks could have been produced in the central parts of channels with greater water depths, whilst the other forms of track preservation may have been formed closer to the margins and were subject to greater degrees of subaerial exposure.

The fossil record of the Guará Formation is composed by a rich vertebrate ichnofauna of theropod, sauropod and ornithopod footprints as well as burrows excavated, probably, by mammals. Tracks and trackways can be seen both in vertical section and in plane-bedding view near Palomas Hill (Santana do Livramento, RS) (Dentzien-Dias *et al.*, 2007, 2008; 2012b; Netto *et al.*, 2010). The footprints observed in section are about 50 cm wide and the undertracks reach around 45 cm in depth and the spatial orientation of the tracks indicates that the animal was moving from East to West. On the top of the outcrop, a series of trackways and isolated footprints can be seen on surface (Figures 14A-B). The footprints are all rounded (Figure 14B), without digit traces, and medium diameter of 50 cm. Two almost parallel trackways can be observed, as well as some isolated footprints. One of the isolated footprints shows deformational features

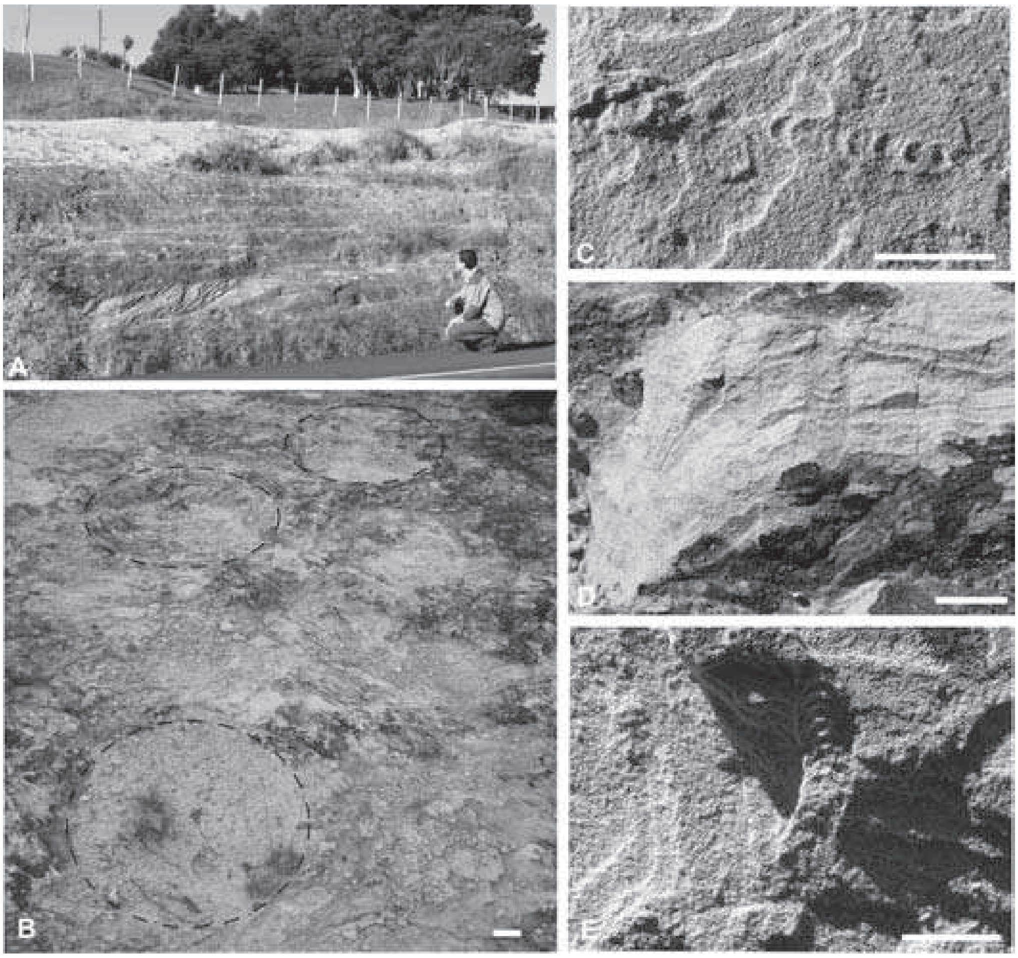

Figure 14. Trace fossils from Guará Formation. A, General view of the ichnofossiliferous eolian sandstones at Palomas Hill (Santana do Livramento, RS); B, sauropod trackway exhibiting only pes footprints; C-D, *Taenidium barretti* in horizontal (C) and vertical (D) preservation; E, *Beaconichnus coronus* (observe the wall). Scale bars: A, C-E, 10 mm; B, 10 cm.

that suggest that the animal was moving from NW to SE (Dentzien-Dias *et al*., 2007). The trackways were made by a quadruped despite the fact that there is no manus track (Figure 14B). Based on the evidence of pace angulation patterns and footprint shape, Dentzien-Dias *et al.* (2007, 2008) attributed the trackways to the pes of a sauropod with a body size similar to an extant elephant.

Inside most of the footprints, as well as in sandstones with climbing-ripple lamination, several inclined, vertical and horizontal meniscate burrows assigned to *Taenidium barretti* and *Beaconites coronus* (Figures 14C-E) can be observed. In section, these small burrows begin as vertical tubes which become horizontally enlarged at their bases, forming little chambers. These burrows were attributed by Netto (1989) to arthropods and the environmental setting suggests insect larvae as the main tracemaker.

All sauropods footprints previously cited occur in the eolian sand sheets facies. They occur at different levels inside the same package, suggesting preservation as undertracks (Dentzien-Dias *et al*., 2008, 2012b). The preservation of these undertracks only occurred because of a certain degree of wetness in the substrate, also evidenced by the adhesion strata (Dentzien-Dias *et al*., 2008).

THE PLEISTOCENE RECORD

Geological overview

The well-known Cenozoic ichnological record in southern Brazil is mainly concentrated in Pleistocene deposits exposed in the south littoral of Santa Catarina State and the littoral of Rio Grande do Sul State. Trace fossils are particularly well recorded in the Chuí Formation from the Rio Grande do Sul coastal plain ("Planicie Costeira do Rio Grande do Sul", PCRS). This plain extends for about 33,000 km^2 along the eastern part of Rio Grande do Sul State, parallel to the present shoreline (Figure 15). The PCRS has been formed during the Quaternary by the progradation of sediments deriving from the western highlands. The proximal part of the plain consists of alluvial fans fed by the Precambrian Sul-riograndense Shield and by Paleozoic and Mesozoic sedimentary rocks and the volcanic plateau of Serra Geral. The distal region is composed of four lagoon-barrier depositional

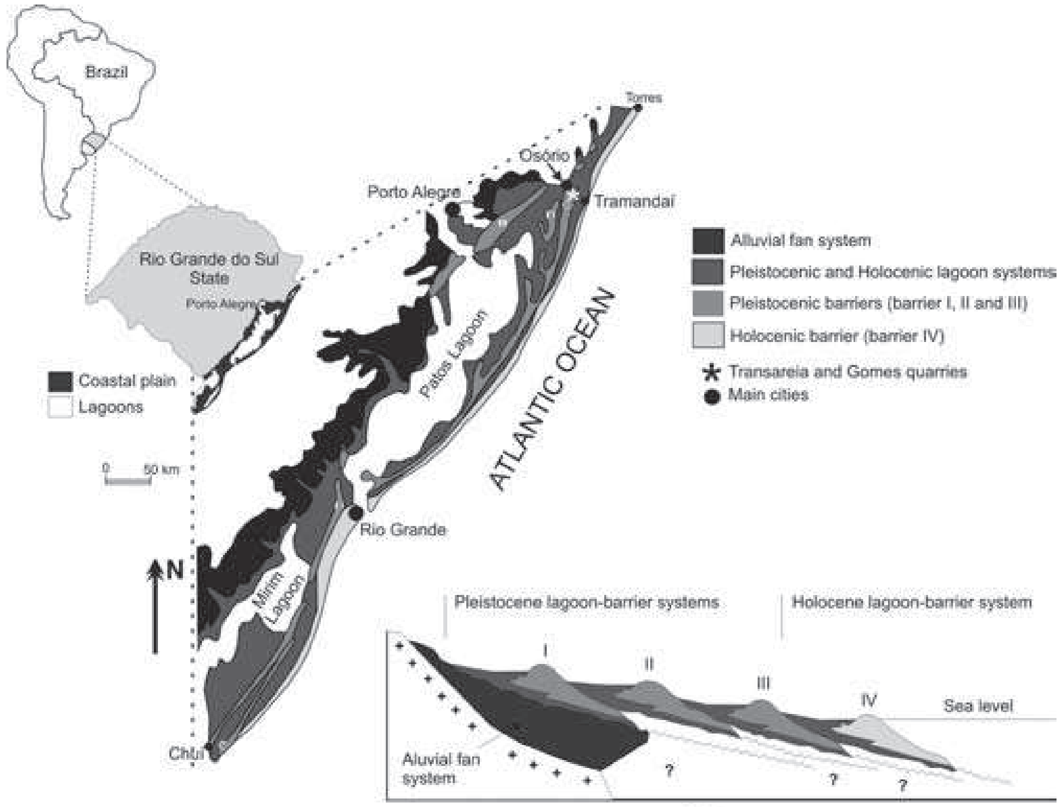

Figure 15. Location map of the Rio Grande do Sul Coastal Plain (PCRS) and schematic distribution of the lagoon-barrier systems that characterize the PCRS sedimentary succession (modified from Tomazelli & Villwock, 2000).

systems (e.g., Tomazelli & Villwock, 2000). They are known as lagoon-barrier systems I to IV, and they were formed during high-stand sea levels related to glacio-eustatic cycles during the Quaternary. The oldest systems are located to the west, while the youngest are situated to the east as a result of the progradation of the plain. Systems I to III are Pleistocene, and System IV is Holocene (Tomazelli & Villwock, 2000).

The Chuí Formation deposits extend all along the coast of Rio Grande do Sul State and belong to Lagoon-Barrier System III (Figure 15). Detailed sedimentologic study of this system was accomplished by Tomazelli *et al.* (1982), Tomazelli (1985) and Tomazelli & Dillemburg (2009). From base to top, the barrier consists of shallow marine, beach and eolian deposits composed of quartzose, fine-grained, well-sorted sand. The lagoonal facies consist of silty and muddy fine sands with carbonate and ferruginous concretions. Radiometric dating of fossils in the marine sands (Martin *et al.*, 1982) and thermoluminescence dating of eolian sands (Poupeau *et al.*, 1985) coincide in assigning an age of *ca* 120 ky to System

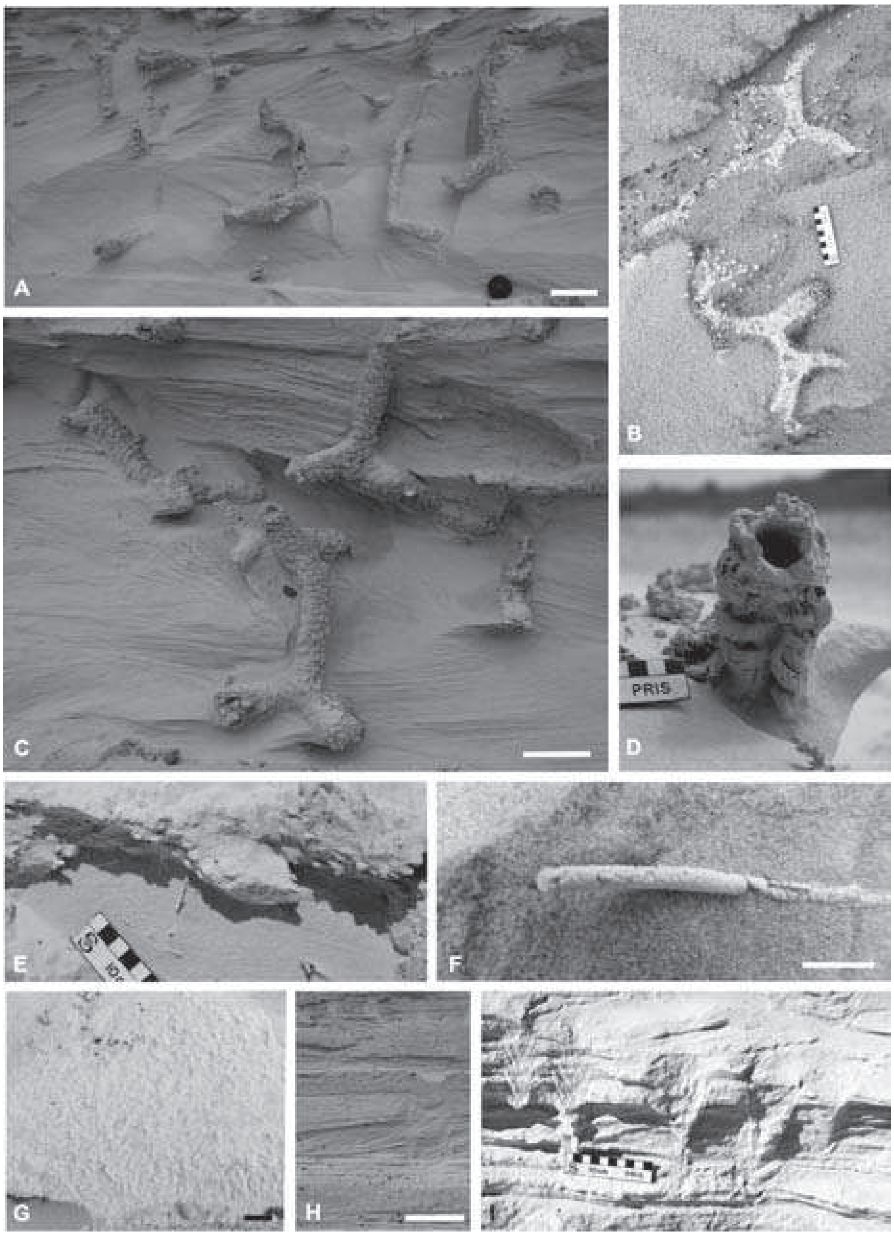

Figure 16. Marine trace fossils from the Pleistocene deposits of the PCRS Lagoon-Barrier System III at Osório region (RS). A-C, *Ophiomorpha nodosa* burrow system; D, *Cylindrichnus helix* reworking the *O. nodosa* outer wall; E-F, *Ophiomorpha puerilis*; G, *Macaronichnus* isp.; H, *Diplocraterion parallelum*; I, *Rosselia socialis*. Scale bars: G, 10 mm; A, C, H, 10 cm.

III. Hence, it corresponds to the last transgressive peak of the Pleistocene in South Atlantic Brazilian littoral, known as the Cananéia Transgression (Suguio & Martin, 1978).

A representative section of Chuí Formation can be seen in Gomes and Transareia quarries, in Osório (RS) (Figure 15). Two main units are differentiated: a lower sandy marine unit and an upper sandy eolian unit. They correspond to facies B and A, respectively, of Tomazelli *et al.* (1982). These authors described an additional underlying unit consisting of silty-muddy sands that was only temporarily exposed. The marine unit consists of well-sorted fine-grained mainly quartzose sands with an observed maximum thickness of 5.5 m. They exhibit horizontal lamination, and low-angle, herringbone, and planar cross-stratification, besides symmetrical ripples at the uppermost part.

Trace fossil record

Trace fossils are ubiquitous in the Chuí Formation, the most obvious are the extensive *Ophiomorpha nodosa* burrow systems (Figures 16A-D) occurring mainly in the lower half of the unit (Tognoli & Netto, 1998; Tognoli *et al.*, 1998; Gibert *et al.*, 2006; Netto *et al.*, 2012b). *Ophiomorpha puerillis* (Figures 16E-F) and *Cylindrichnus helix* (Figure 16D) occur in close association with *O. nodosa*, being recorded particularly in Osório and Transareia quarries, the locality of both ichnospecies (Gibert *et al.*, 2006, 2012). Very abundant, small *Macaronichnus* isp. (Figure 16G) and rare *Diplocraterion parallelum* (Figure 16H) also occur in the lower half of the unit. The upper half hosts abundant *Rosselia socialis* (Figure 16I). Ichnologic and sedimentologic data indicate that this unit was deposited in a very shallow subtidal setting.

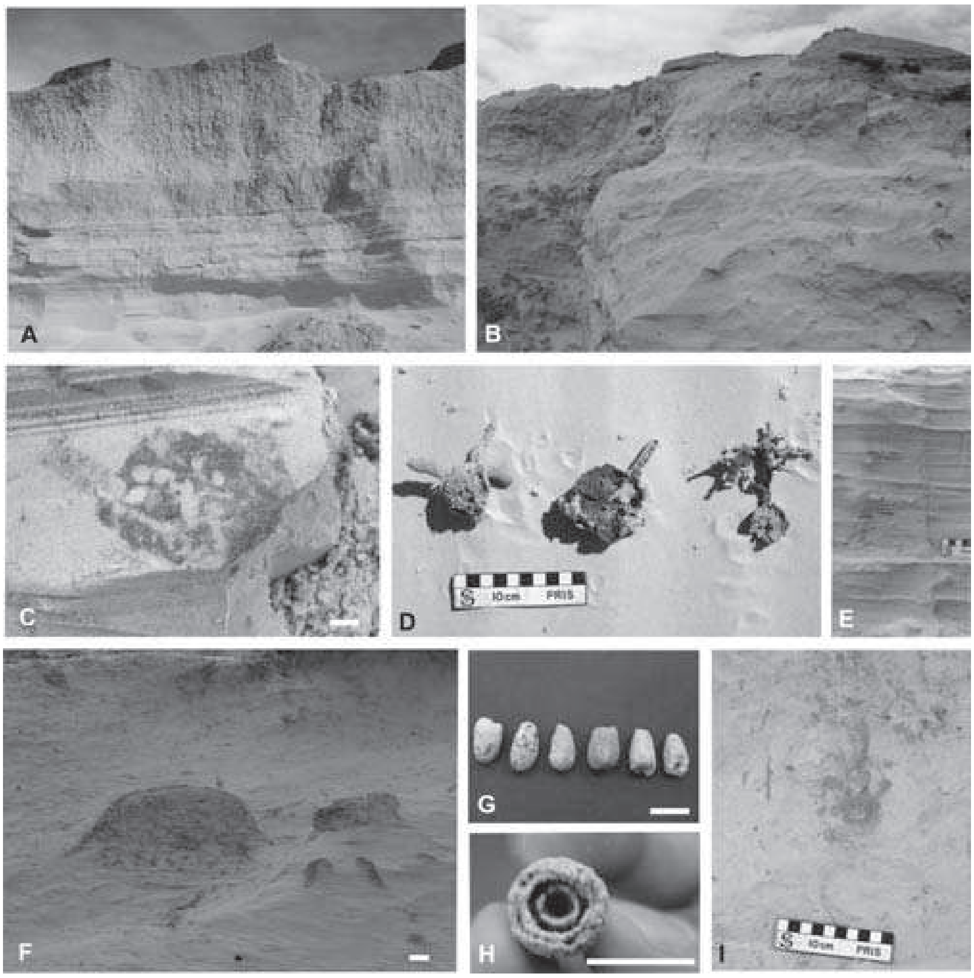

Figure 17. Terrestrial trace fossils from the Pleistocene deposits of the PCRS Lagoon-Barrier System III at Osório region (RS). A-B, Rhizolits descending from a pedogenic surface; C-D, ant or termite nest chambers (*?Vondrichnus*); E-F, termite nests *Krausichnus* isp. (E) and *Termitichnus* isp. (F); G-I, individual cells (G-H) and a possible complete bee nest (I) cf. *Celliforma*. Scale bars: G-H, 10 mm; C, F, 10 cm.

The upper eolian unit comprises about 5 m of fine-grained sands showing planar cross-lamination intercalated with several few-centimeter-thick horizons having higher mud content. A strongly pedogenized horizon consisting of reddish fine- to medium-grained sandstones is found at the top of the unit. Insect burrows are very abundant, including *Krausichnus, ?Vondrichnus* and wasp cells (cf. *Celliforma*) (Figure 17) (Grangeiro & Netto, 2002; Grangeiro *et al.*, 2003; Gibert *et al.*, 2006; Netto *et al.*, 2007). Isolated meniscate burrows (cf. *Taenidium*) are probably related to termite nestings. These traces originate in the paleosoil horizon (and some probably in the muddier intercalations as well) and penetrate into the eolian sands. Root traces are abundant in some levels but they are generally poorly preserved, suggesting vegetation dominated by grasses and bushes.

FINAL REMARKS

The ichnology of the above-mentioned deposits reinforces the role of the ichnology as a powerful tool for facies analysis and interpretation of the sedimentary record including its stratigraphic surfaces. However, the huge outcrop belt, the small number of ichnologists working in the different successions and the necessity of a consistent database to support high resolution stratigraphic studies have been limiting the development of the ichnology as part of an integrated approach in facies analysis. All sedimentary basins in Brazil have an excellent potential for new discoveries and approaches in ichnology. The role of the trace fossils as modifiers of the rock properties (e.g., cementation, porosity, permeability, etc) has been subject of studies since the end of the 1990s and much more studies are required in order to better understand their effects on reservoir properties, among others applications.

In spite of this, ichnological studies had contributed with important data to a better understanding of the Phanerozoic sedimentary deposits from southern Brazil. The interpretation of the Furnas Formation as marine deposits was only accepted after an integrated approach made by Assine (1996, 1999) involving sedimentology, stratigraphy and trace fossil analysis. Studies developed in more recent years have revealed a more diverse marine trace fossil assemblage in the southern Brazilian deposits of the Furnas Formation, helping to include them in a shallow marine framework. *Zoophycos* and *Bifungites* have been reported in literature as the most conspicuous ichnogenera in the Jaguariaíva Member of the Ponta Grossa Formation. However, in the last ten years *Zoophycos* has been identified as the main component of a composite ichnofabric containing also *Phycosiphon* and *Chondrites*, that superimposes another composite ichnofabric formed by *Rhizocorallium, Palaeophycus, Planolites, Helminthopsis,* and *Teichichnus*. The trace fossil association and the degree of bioturbation in both suites suggest a distal *Cruziana* Ichnofacies in which oxygenation seems to be the main paleoecological factor controlling the distribution of the fauna and, consequently, of the ichnological suites (Tognoli *et al.*, 2002, 2003; Tognoli & Netto, 2010). The ichnology of the Tibagi and São Domingos Members is still very poorly known and much more research is necessary.

The study of the ichnology of the southern Brazilian deposits of the Itararé Group had a major development in the 1980s but only in the last decade integrated studies on sedimentology and ichnology of the deglaciation deposits started to be developed, bringing new light to refine the interpretations of the associated depositional settings. The superb preservation of the morphological details of trace fossils preserved in muddy siltstones and shales helped to diagnose the structure of the trace fossil assemblages, which represent particular expressions of the *Mermia* and *Scoyenia* ichnofacies (Netto *et al.*, 2009, 2012a). The integration between ichnological data, microfossil content, sedimentary structures and depositional features are consistent with glacially-influenced deposits with alternating conditions of salinity and energy. These conditions are related with the deglaciation processes and consequent release of freshwater in the depositional systems (Buatois *et al.*, 2006, 2010; Netto *et al.*, 2012a). New studies have been developed in order to refine these interpretations and elucidate doubtful aspects.

The Rio Bonito and Palermo formations are the most famous bioturbated units in the Paraná Basin. The mottled aspect of the Palermo Formation is one of the main criteria used for recognizing this unit in mapping activities and core descriptions. Their ichnological content has been reported in the geological literature since the beginning of the 1960s, previously identified as 'tubes of worms'. Fifty years after the first reports, both formations are, maybe, the most studied Brazilian bioturbated deposits. Nowadays, the entire succession can be understood from ichnology. This was made possible after an intense work of integration with sedimentological and stratigraphical data. The main aspects revealed by the ichnological analyses are the unequivocal signatures of the fully marine and brackish water assemblages of trace fossils as well as the significance of stratigraphic surfaces demarcated by firmground suites of the *Glossifungites* Ichnofacies (Buatois *et al.*, 2001a,b, 2007; Gandini *et al.*, 2010; Netto, 1994; Netto *et al.*, 2007; Tognoli, 2002, 2006; Tognoli & Netto, 2003). The refined interpretations of the different facies associations related with the marine and marginal-marine deposits of both units are supported (and in some cases dependent) by the trace fossil suites. The presence of coal deposits in the Rio Bonito-Palermo succession and the consequent availability of a close-spaced grid of cored and logged boreholes permit the development of high-resolution stratigraphic studies in this succession. In this type of approach, ichnology has a great potential and can help to better understand the dynamics of the depositional systems, especially in terms of sedimentary processes and paleoecological data.

The first ichnological study of the Passa Dois Group in southern Brazil was only made in the end of the 1980s (Netto, 1988).It is quite curious the lack of interest in the sedimentology, stratigraphy and ichnology of this unit, especially the Serra Alta, Teresina and Rio do Rasto formations if compared with the same aspects of the underlying Devonian and Carboniferous –Permian units of the Paraná Basin. In the last years, new studies brought a new approach about the ichnology of the Passa Dois Group (Lima, 2010; Lima & Netto, 2012). The trace fossil assemblge was revised and its composition, allied with the low ichnodiversity and the low degree of bioturbation were assumed as a response of salinity variations in a lower shoreface, possibly due to deltaic influence in a restricted shallow sea. Another approach was provided by Dentzien-Dias *et al.* (2009, 2012a,b), who described a wide variety of vertebrate coprolites in lacustrine facies of the Rio do Rasto Formation and vertebrate burrows in sandstones of the Piramboia Formation.

The Mesozoic record of trace fossils in southern Brazil is quite interesting and diverse. Arthropod burrows in humid interdune deposits, rhizoliths, coprolites, tracks and a number of different invertebrate traces are reported in the literature. Rhizolits occur associated with invertebrate and vertebrate traces at the top of the Alemoa Member of the Santa Maria Formation. Tracks and trackways include those related with dinosaurs that have been found in both the Santa Maria and Caturrita formations. The association of rhizoliths, invertebrate and vertebrate trace fossils have permitted to interpret such deposits as paleosoils developed near lake margins with periodic subaerial exposure (Netto, 2007). Some stratigraphic surfaces were also recognized by a substrate-controlled *Skolithos* cf. *serratus* suite and by a palimpsest preservation that evidence a depositional hiatus by nondeposition and low rates of erosion. Additionally, the Guará Formation records a rich vertebrate ichnofauna of theropod, sauropod and ornithopod footprints as well as burrows probably excavated by mammals. Based on the evidence of pace angulation patterns and footprint shape and size, Dentzien-Dias *et al.* (2007, 2008) has attributed the trackways to the pes of a sauropod with a body size similar to an elephant.

Finally, the ubiquitous presence of extensive *Ophiomorpha nodosa* burrow systems in the Rio Grande do Sul Coastal Plain (PCRS) deposits have been used since the 1980s to recognize the position of the paleoshorelines (Tomazelli *et al.*,1982). A number of different works that have been performed since the end of the 1990s (Tognoli & Netto, 1998; Tognoli *et al.*, 1998; Gibert *et al.*, 2006; Netto *et al.*, 2012) has contributed to improve the ichnological knowledgement of this unit, with description of two new ichnotaxa, *Cylindrichnus helix* and *Ophiomorpha puerilis* (Gibert *et al.*, 2006). The abundance of insect burrows at the top of the Chuí Formation and its association with root traces revealed the presence of paleosoil horizons capping the subtidal deposits at the north portion of the PCRS, a sort of evidence that had never been discussed before in these deposits.

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ICHNOLOGY OF THE LATE PALEOZOIC PAGANZO AND CALINGASTA-USPALLATA BASINS OF WESTERN ARGENTINA

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ABSTRACT

Several trace fossil assemblages have been recorded in the upper Paleozoic Paganzo and Calingasta-Uspallata basins of northwestern Argentina. In the Paganzo Basin, ichnofossil assemblages are widespread, being present in both the Lower and Upper sections of the Paganzo Group. The *Mermia*, depauperate *Cruziana* and depauperate *Mermia* Ichnofacies are common in the lower section. They occur in glacial-postglacial settings and in transgressive settings not connected directly with ice masses. In the Upper section, the *Scoyenia* Ichnofacies, as well as eolian-related trace fossil assemblages, occur in connection to more arid continental facies. The ichnological record of the Calingasta-Uspallata Basin is relatively scarce. In this basin, the depauperate *Cruziana* Ichnofacies has been documented in post-glacial deposits of the Hoyada Verde Formation, suggesting stressed conditions related to a wave-dominated prograding deltaic system. Archetypal and more diverse *Cruziana* Ichnofacies have not been recorded yet in these basins, contrary to the situation observed in other Gondwanic settings. The vertebrate trace fossil record of the late Paleozoic in Argentina is still poor.

Key words: Upper Paleozoic, ichnofacies, depauperate *Cruziana*, *Mermia, Scoyenia*, Argentina.

INTRODUCTION

The upper Paleozoic Paganzo and Calingasta-Uspallata basins of northwestern Argentina host thick sedimentary successions that preserve locally abundant and varied trace fossils. Studies have been historically focused on sedimentological, stratigraphical and biostratigraphical aspects, with ichnological and paleoecological aspects receiving less attention. Nevertheless, during the last two decades a renewed interest in the late Paleozoic ice age and its related deposits in Gondwana resulted in several ichnological studies (Aceñolaza & Buatois, 1991, 1993; Buatois & Mángano, 1992, 1993, 1995a, 2003, 2004; Pazos, 2000, 2002a,b; Mángano *et al.*, 2003; Buatois *et al.*, 2006, 2010; Pazos *et al.*, 2007, among others), increasing significantly the knowledge on the ichnofaunas from the Paganzo and Calingasta-Uspallata basins. The aim of this paper is to provide a general review of the ichnology of the upper Paleozoic of this part of Gondwana.

GEOLOGICAL SETTING

The Paganzo and Calingasta-Uspallata basins lie along the southwestern margin of Gondwana (Figure 1) representing the retroarc and arc-related basins described by Limarino & Spalletti (2006). They are part of a series of foreland basins (López-Gamundí *et al.*, 1994; López-Gamundí, 2010) developed along the southwestern active Paleopacific margin after the end of the Protoprecordillera orogeny (Spalletti *et al.*, 2010). The Protoprecordillera (Amos & Rolleri, 1965) was the main topographic high, a north-south-trending discontinuous belt that separated mostly

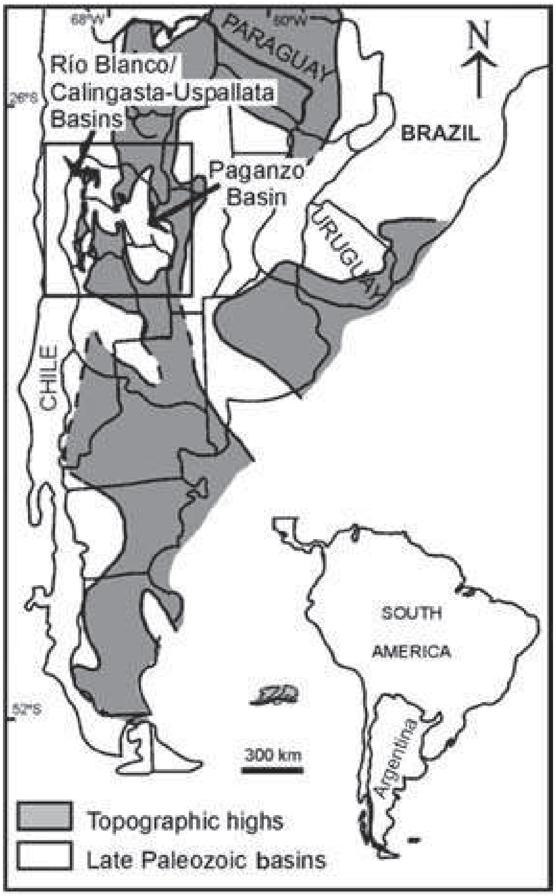

Figure 1. Late Paleozoic basins of southern South America and location of the Paganzo and Calingasta-Uspallata basins.

marine deposits of the Calingasta-Uspallata and Río Blanco basins on the west from the mostly continental deposits of the Paganzo Basin on the east (Figure 2). Sedimentation in the Calingasta-Uspallata and Rio Blanco basins took place from the Early Carboniferous (Sessarego & Cesari, 1989; Limarino *et al*., 2006) to the Permian. On the other hand, the Paganzo Basin began to subside towards the end of the Early Carboniferous and continued until the Early Permian (Cisuralian, Limarino *et al*., 2006; Perez Loinaze *et al*., 2010). The sedimentary successions containing ichnofossils correspond both to Carboniferous and Permian Systems, and represent a wide variety of paleoenvironmental settings.

THE PAGANZO BASIN

The Paganzo Basin (Figure 2) is one of the largest (about 140,000 km^2) upper Paleozoic depositional areas recognized along the western margin of Gondwana (Salfity & Gorustovich, 1983; López-Gamundí *et al*., 1994). It was limited to west by the "Protoprecordillera" and to the east and south by the Pampean and Pie de Palo topographic highs, respectively, whereas the Puna high represented its northern boundary (Figure 2). According to Limarino *et al.* (2006), it can be described as a multihistory basin with: (i) the foreland stage, developed in an embryonic "proto-Paganzo Basin" during the Protoprecordilleran orogeny; (ii) the postorogenic stage, characterized by the widening of the basin, probably as a consequence of the collapse of the Protoprecordillera during the Late Carboniferous–Early Permian; and (iii) the overfilled stage, characterized by continental deposition during the first stage of the Gondwana breakup (latest Early Permian–Late Permian).

Sedimentation in the Paganzo Basin occurred in sub-basins partially separated by internal basement highs. The sedimentary filling of the Paganzo Basin is characterized by continental deposition to the east and increasing participation of marine deposits to the west (Limarino, 1987; López-Gamundí, 1989; Fernández-Seveso & Tankard, 1995; Net, 1999; Limarino *et al*., 2002, 2006).

Upper Paleozoic strata were included within the Paganzo Group (Bodenbender, 1896; Azcuy & Morelli, 1970a,b), which was divided into two stratigraphic intervals, referred to as the Lower (Late Carboniferous) and Upper (Permian) sections. Within this subdivision, different lithostratigraphic nomenclatures have been established in various areas of the basin. The lower section in the Famatina Range corresponds to the Agua Colorada Formation (Turner, 1962) which is mainly composed of glacial diamictite, fluvial conglomerate, sandstone and mudstone related to a fjord system (Limarino *et al*., 2006; Limarino *et al*., 2010). Similar Carboniferous strata in the Sierra de Sañogasta area are known as the Lagares Formation (Azcuy & Morelli, 1970b). The easternmost outcrops of Upper Carboniferous rocks appear in the Sierra de Malanzán. In this area, the lower section of the Paganzo Group is divided into the Malanzán and Loma Larga formations (Andreis *et al*., 1975). The former is composed of massive diamictite, resedimented diamictite, sandstone and mudstone that are deposited in lacustrine, fjord-type and alluvial-fan environments (Andreis *et al*., 1986; Buatois & Mángano, 1995a; Gutierrez & Limarino, 2001). The Loma Larga Formation comprises conglomerate, sandstone and mudstone that were deposited in braided fluvial systems (Net & Limarino, 1999). Along the western margin of the Paganzo Basin, the lower section of the Paganzo Group is divided into the Guandacol and Tupe formations (Andreis *et al*., 1975). The former corresponds to a thick column (up to 200 m thick) of diamictite, shale, mudstone and sandstone that are mainly deposited in drowned glacial valleys at the end

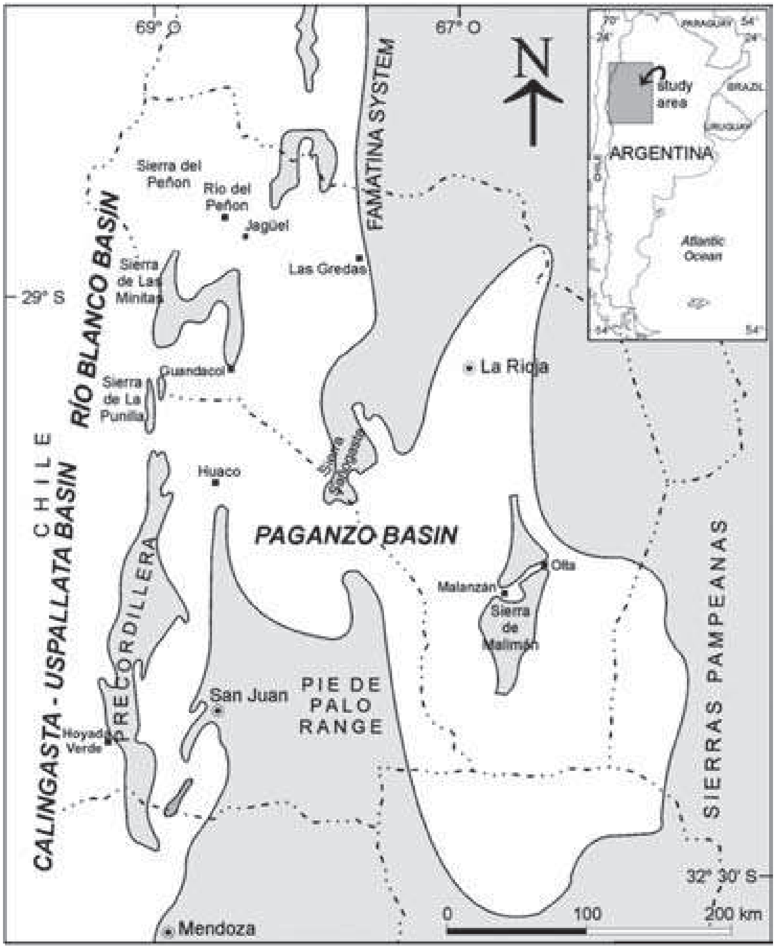

Figure 2. Late Carboniferous paleogeography of the Paganzo and Calingasta-Uspallata basins (modified from Salfity & Gorustovich, 1983).

of the Gondwanan glaciation (Limarino & Césari, 1988; Buatois & Mángano, 1995a). The bulk of the Guandacol Formation is Bashkirian in age (Upper Carboniferous) and the lowermost part is close to the Bashkirian–Serpukovian boundary (Gulbranson *et al.,* 2010). The Tupe Formation comprises sandstone, conglomerate, mudstone and thin coal levels, which accumulated in different types of fluvial systems (Desjatdins *et al*., 2009; Tedesco *et al*., 2010).

The Permian record is characterized by continental sedimentation. Thick red-beds occur throughout the Paganzo Basin, corresponding to the Patquía Formation (Andreis *et al*., 1975) and its equivalents, the De la Cuesta (Turner, 1962) and La Colina (Azcuy & Morelli, 1970b) formations. The Patquía Formation is composed of fluvial sandstone, mudstone and conglomerate that pass upward into eolian, lacustrine and ephemeral fluvial deposits (Spalletti, 1979; Caselli & Limarino, 2002; Spalleti *et al*., 2010).

Ichnological studies in this basin can be traced back to the 1950s, with the erection of *Orchesteropus atavus* (Frenguelli, 1950; Casamiquela, 1965) based on material from the Guandacol Formation. Since this pioneering work, other authors mentioned the presence of this ichnotaxon in different areas of the basin (Aceñolaza, 1970; Aceñolaza & Cravero 1978; Bossi & Andreis, 1985; Caballé & Furque, 1987).

Ichnology of the Lower section: depauperate *Cruziana* and *Mermia* ichnofacies

The Guandacol Formation is one of the most significative units bearing trace fossils. This unit has been analyzed in a number of studies mostly in Cuesta de Huaco (Pazos, 2000; Buatois *et al*., 2010; Schatz *et al*., 2011), and Huerta de Huachi (Buatois & Mángano, 2003) in San Juan Province, and, into a lesser extent, in Sierra de Máz in La Rioja Province (Aceñolaza & Buatois, 1991, 1993). In Cuesta de Huaco, two main ichnofacies are represented: depauperate *Cruziana* and *Mermia*. In Huerta de Huachi, only the latter has been recorded. A non-bioturbated black shale that represents maximum flooding separates both trace fossil assemblages in Cuesta de Huaco. The depauperate *Cruziana* Ichnofacies occurs in the lowermost strata of the unit, below the the black shale representing a transgressive interval (Buatois *et al.*, 2010; Schatz *et al.*, 2011). Elements of this assemblage occur in a wide variety of lithologies, including mudstone, very fine- to fine-grained sandstone with current and combined-flow ripples, debris-flow granule conglomerate and very coarse-grained sandstone (Buatois *et al.*, 2006, 2010; Schatz *et al.*, 2011). It is composed of monospecific suites of bilobate trails (Figure 3) that historically have been assigned to *Didymaulichnus lyelli* and some other bilobate structures. The taxonomic affinities of these bilobate trace fossils were recently analyzed by Schatz *et al.* (2011), who recognized four ichnospecies: *Diplopodichnus biformis, Cruziana diplopoda, Cruziana* cf. *problematica* and *Rusophycus carbonarius*. The first two ichnospecies mainly occur in thinly bedded stratified diamictite (granule conglomerate and very coarse-grained sandstone), whereas the other two are generally present in very-fine to fine-grained sandstone layers interbedded with dropstone-bearing mudstone. Some morphological features (e.g., ridges and furrows ornamented with scratch marks) suggest that the structures were produced by arthropods. Schatz *et al.*, (2011) proposed notostracans and trilobites as the potential tracemakers of *Cruziana* cf. *problematica*–*Rusophycus carbonarius* and *Cruziana diplopoda*–*Diplopodichnus biformis* in these deposits. The small size of the trace fossils and the low ichnodiversity indicate a depauperate *Cruziana* Ichnofacies, most likely representing brackish-water conditions in a stressfull environment (Buatois *et al.*, 2010; Schatz *et al.*, 2011). Density of trace fossils is low in the debris-flow deposits and relatively high in muddy-dominated intervals, reflecting different colonization windows as a result of contrasting sedimentation rates. This assemblage has been only found in the western margin of the basin (Buatois *et al.*, 2010).

Elements of the *Mermia* Ichnofacies (Figure 4) have been recorded in different areas of the basin. In the Guandacol Formation (western region), this assemblage is located above the maximum flooding shale, and it occurs in parallel-laminated siltstone and current ripple cross-laminated and parallel-laminated very fine-grained sandstone that are mostly deposited by delta-fed underflow currents and suspension fallout. This assemblage occurs through the middle interval of the postglacial succession, representing early highstand systems tract deposition. It is relatively diverse, and it is dominated by nonspecialized grazing trails, such as *Mermia carickensis, Gordia marina, Helminthopsis tenuis*, *Helminthoidichnites tenuis*; simple feeding traces represented by *Treptichnus pollardi*, *Circulichnis montanus*; arthropod trackways, such as *Diplichnites gouldi*, *Umfolozia* isp., *Maculichna carboniferus*, and *Orchesteropus atavus*; and the fish trails *Undichna insolentia* and *Undichna britannica* (Buatois *et al.*, 2006, 2010). These structures are preserved on bedding planes, recording emplacement in very shallow tiers, with a degree of bioturbation (as seen in cross section) that is invariably zero. The assemblage is typical of freshwater environments and it represents an example of the *Mermia* Ichnofacies (Buatois *et al.*, 2010). There is a general agreement that melting of the ice caps released a significant amount of freshwater to fjord and related coastal areas (Buatois *et al.*, 2001, 2006, 2010; Pazos, 2002b; Buatois & Mángano, 2003). Therefore, freshwater conditions may have prevailed for some time in these fjords, allowing the establishment of this ichnofauna in post-glacial settings. Some elements of the *Mermia* Ichnofacies (*Gordia marina* and *Orchesteropus atavus*) have been also documented

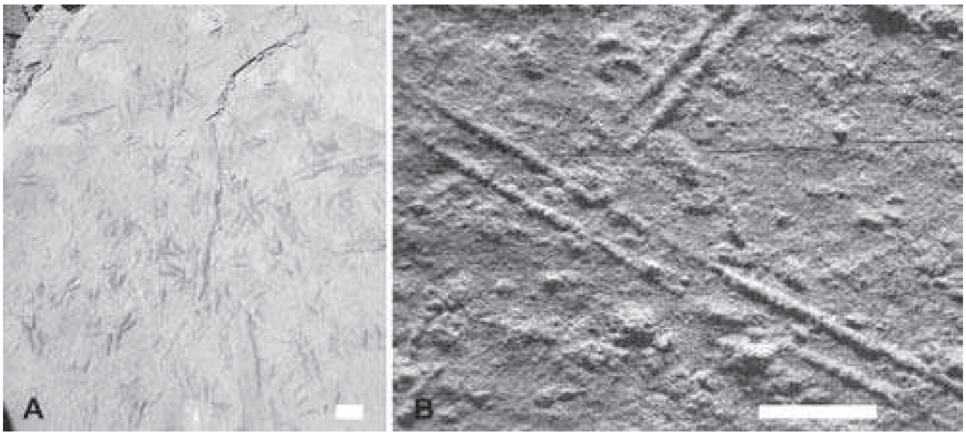

Figure 3. Bilobate structures from the Gunadacol Formation at the Cuesta Huaco area (Paganzo Basin). A, *Rusophycus carbonarius* assemblage on the bedding plane; B, *Diploplodichnus biformis*. Scale bars: 10 mm.

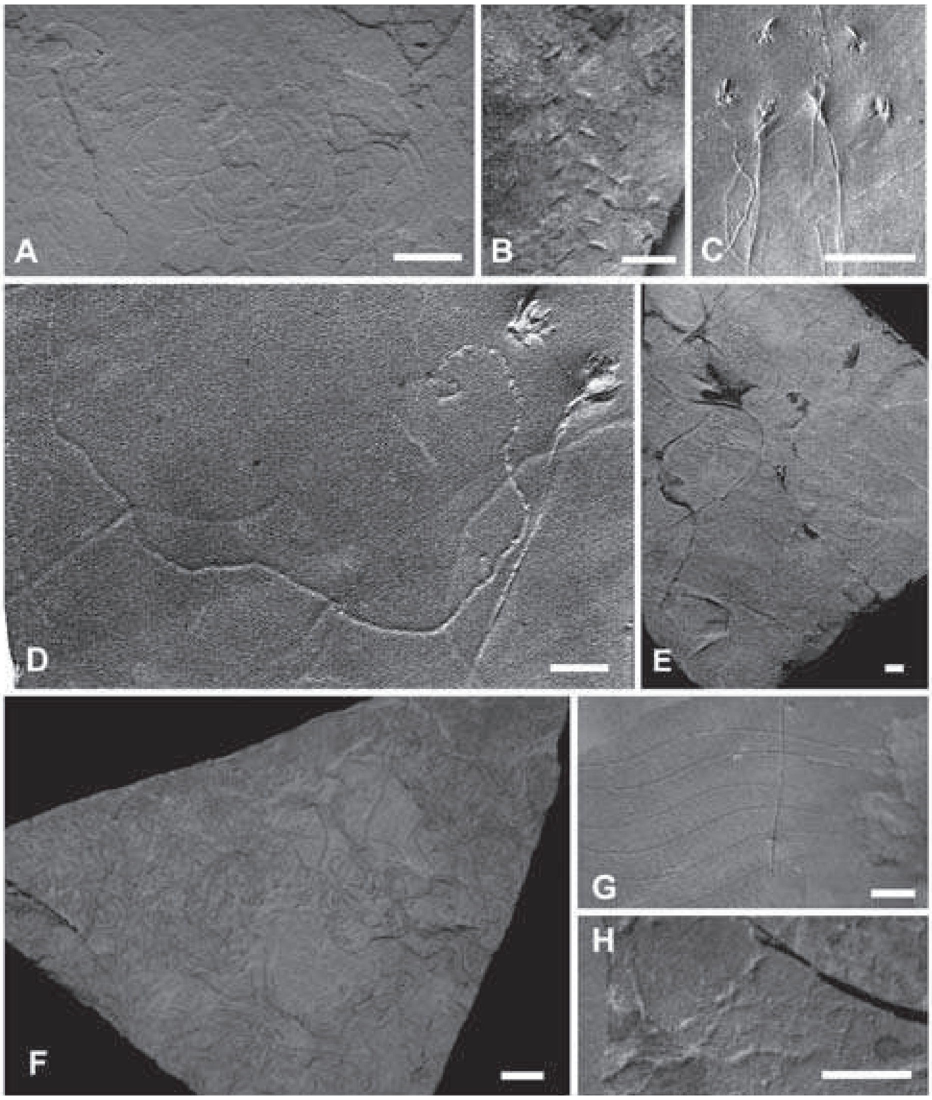

Figure 4. Elements of the *Mermia* Ichnofacies. A, *Mermia carickensis*; B, *Maculichna carboniferus*; C, *Orchesteropus atavus*; D, *Helminthopsis tenuis*; E, *Undichna britannica* with *Mermia carickensis*; F, *Mermia carickensis*; G, *Undichna insolentia*; H, *Cochlichnus anguineus*. A-E from the Guandacol Formation (Huerta de Huachi, Paganzo Basin), F-H from the Agua Colorada Formation (Sierra de Narvaéz, Paganzo Basin). Scale bars: 10 mm.

by Aceñolaza & Buatois (1991, 1993) in outcrops of the Guandacol Formation exposed in the Sierra de Máz area.

In the eastern region, the *Mermia* Ichnofacies has been recorded in the coeval Agua Colorada Formation at Sierra de Narváez, Catamarca Province (Buatois & Mángano, 1993). It consists of high-diversity suites occurring in parallel-laminated mudstone formed by suspension fallout and low-density turbidity currents, and in delta-fed, very fine-grained sandstone and siltstone deposited from underflow currents (Buatois & Mángano, 1994). It includes *Circulichnis montanus*, *Cochlichnus anguineus*, *Gordia marina*, *Gordia indianaensis*, *Helminthoidichnites tenuis*, *Helminthopsis tenuis*, *Mermia carickensis*, *Orchesteropus atavus*, *Rusophycus* isp., *Treptichnus pollardi*, *Undichna britannica*, and *U. insolentia*, among other forms. A low-diversity suite, consisting of *Gordia marina* and *Mermia carickensis*, occurs at the event colonization after major breaks in environmental conditions (Buatois & Mángano, 1995b).

Subsequently, a similar assemblage, although poorly preserved and less diverse, has been found in the Agua Colorada Formation at Bajo El Manzano (La Rioja Province). Trace fossils in this locality occur in parallel-laminated siltstone immediately above a dropstone-bearing siltstone interval (Buatois *et al.*, 2010). These fine-grained deposits are sandwiched between pebble conglomerate and very coarse- to medium-grained sandstone, which accumulated in low-sinuosity fluvial systems, and sandstone, siltstone and conglomerate of fluvio-deltaic origin. Farther to the east, the coeval Malanzán Formation contains a low-diversity suite of grazing trails, recording colonization of turbidite sandstone (Buatois & Mángano, 1995a; Buatois *et al*., 2010).

Near the locality of Huaco (western region), in the upper levels of the Tupe Formation, elements of the *Mermia* and *Cruziana* ichnofacies were recorded by Desjardins *et al.* (2010). The former is present in fine-grained heterolithic facies. It consists of *Helminthopsis abeli* and *Treptichnus pollardi*. This represents an impoverished example of the *Mermia* Ichnofacies. It indicates the activity of arthropods, nematodes and/or worms found in subaqueous freshwater substrates in small water bodies formed in temporary inundated floodplains in a transgressive coastal plain. The depauperate *Cruziana* Ichnofacies includes two assemblages. The first assemblage, composed of *Halopoa* isp., *Palaeophycus crenulatus* (Figure 5A) and *Planolites montanus*, occurs in thin-bedded, tabular sandstone. This assemblage may record the activity of arthropods and worms in a low-energy distal-bay environment dominated by background sedimentation with sporadic storm episodes. The second assemblage is monospecific, comprising only *Rhizocorallium commune* (Figure 5B) and it is preserved at the interface between a sandstone bed and the overlying mudstone. This assemblage suggests the activity of crustaceans that inhabited the muddy substrate of a low-energy environment. These last two assemblages indicate brackish-water conditions (Desjardins *et al*., 2010).

In a different context, in floodplain deposits of the Tupe Formation in the locality of Huerta de Huachi, San Juan province, Buatois & Mángano (2002) documented an ichnofauna corresponding to a depauperate *Mermia* Ichnofacies mainly composed of invertebrate and plant trace fossils. The assemblage consists of *Archaeonassa fossulata*, *Didymaulichnus lyelli*, *Helminthoidichnites tenuis*, *Palaeophycus tabularis*, *Planolites* isp., and root traces. This ichnofauna is characterized by low diversity, dominance of very simple forms, superficial or very shallow trace fossils, that shows a combination of locomotion, grazing and dwelling structures, and production by arthropods and vermiform organisms. These basic features reflect subaqueous production in unstable conditions and temporary floodplain water bodies.

Ichnology of the Upper section: *Scoyenia* Ichnofacies

Continental deposits of the Upper section of the Paganzo Group contain a relatively abundant association of trace fossils. Aceñolaza & Buatois (1993) reported the presence of the *Scoyenia* Ichnofacies, comprising *Beaconites barretti* (Figure 5C), *Didymaulichnus lyelli*, *Palaeophycus striatus* and *Palaeophycus tabularis*, in massive to parallel stratified medium- to fine-grained sandstone in the La Colina Formation at Sierra de Los Colorados (La Rioja Province). Subsequently, Buatois *et al.* (1996) recorded meniscate striated trace fossils (Figure 5D) crosscutting some elements of the previously described suite. This ichnofauna suggests colonization of firm substrates formed along the desiccated margins of a floodplain water body.

An ichnofauna largely dominated by arthropods trackways (Figures 5E-F) has been reported by Zhang *et al.* (1998) in Permian ephemeral lacustrine deposits cropping out at Bordo Atravesado, Cuesta de Miranda (La Rioja Province). The trace fossil assemblage is composed of *Cruziana problematica*, *Diplocraterion* isp., cf. *Diplopodichnus biformis*, *Kouphichnium*? isp., *Merostomichnites aicuñai*, *Mirandaichnium famatinense*, M*onomorphichnus lineatus*, *Palaeophycus tubularis*, *Umfolozia sinuosa* and *Umfolozia* cf. *U. longula*, representing an example of the *Scoyenia* Ichnofacies.

In addition, Krapovickas *et al.* (2010) reported two ichnofossil assemblages in the Patquía Formation in the Paganzo area (La Rioja Province) illustrating the *Scoyenia* Ichnofacies and aeolian-related ichnofacies showing affinities with the *Octopodictnus–Entradichnus* Ichnofacies (Hunt & Lucas, 2007; Ekdale *et al*., 2007; Buatois & Mángano, 2011). The former is present in the lower interval of the unit, in red mudstone, and fine- to coarse-grained sandstone of fluvial origin. It consists of an ichnofauna characterized by *Rusophycus carbonarius*, *Cruziana problematica* and *Palaeophycus tubularis*. These trace fossils suggest sub-superficial to superficial activity of branchiopod crustaceans (notostracans) and insects. The aeolian-related ichnofacies occurs in the red, cross-bedded, medium- to fine-grained sandstone deposited in eolian systems of the upper interval. This last trace fossil assemblage shows a low diversity and low abundance of trace fossils. It is characterized by horizontal to vertical burrows (assigned to *Palaeophycus tubularis* and *Skolithos* isp., respectively), arthropod trackways and tetrapod footprints (e.g., *Chelichnus duncani*, oval digit imprints, short parallel grooves and sinusoidal grooves). This assemblage indicates the superficial activity of artropods (insects and arachnids) and vertebrates (probably mammal-like reptiles).

THE CALINGASTA-USPALLATA BASIN

The Calingasta-Uspallata Basin (Amos & Rolleri, 1965; Amos, 1972) (Figure 2) is an arc-related basin that constitutes the southern prolongation of the Río Blanco Basin (Limarino & Spalleti, 2006). The so-called Proto-precordillera was a paleotopographic high that separated the western Rio Blanco and Calingasta-Uspallata basins

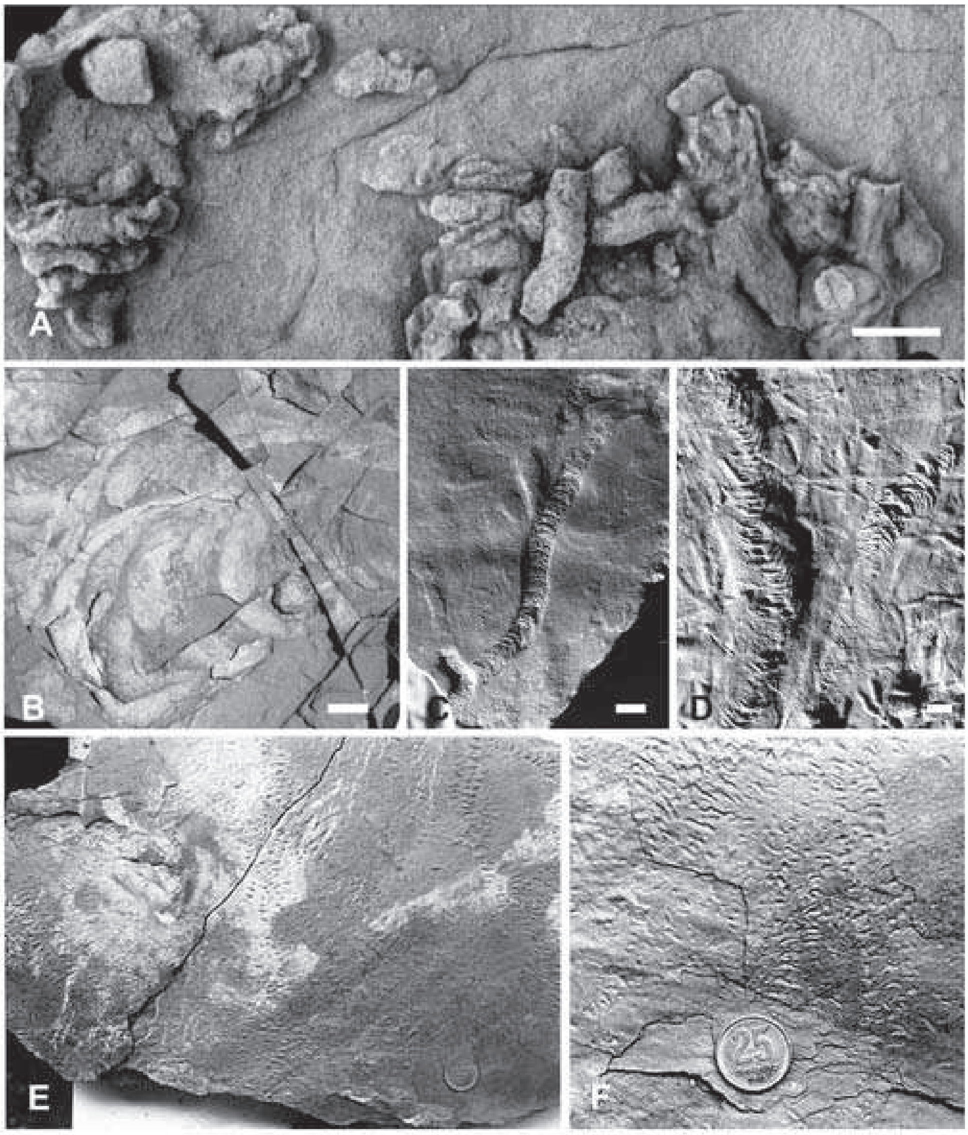

Figure 5. A, *Palaeophycus crenulatus*; B, *Rhizocorallium commune*; C, *Beaconites barretti*; D, meniscate striated trace fossils on bedding plane; E-F, arthropod trackways. A-B from the Tupe Formation (Huaco area), C-D from the La Colina Formation (Sierra de Los Colorados, Paganzo Basin), and E-F from Bordo Atravesado (Cuesta de Miranda, Paganzo Basin). Scale bars: 10 mm. Coin in E and F: 2.5 cm in diameter.

from the eastern Paganzo area (Salfity & Gorustovich, 1983; González-Bonorino, 1991; López-Gamundí *et al*., 1994; Isbell *et al*., 2011) (Figure 2).

Outcrops are located in the western flank of the Precordillera of San Juan and Mendoza and to the west, in the geological province of Cordillera Frontal. Several lithostratigraphic units ranging from Upper Carboniferous to Permian have been defined in this basin. Successions reflect different depositional environments, ranging from glacial to postglacial settings, marine shelves and transitional enviroments.

Due to the fact that few ichnologic studies have been carried out in this basin, this paper deals only with the units containing trace fossils (for a review of the stratigraphy of Calingasta-Uspallata Basin, see Azcuy *et al*., 1999).

Ichnology: depauperate *Cruziana* Ichnofacies

The ichnologic knowledge of the Calingasta-Uspallata Basin is patchy in comparison with that of the Paganzo Basin. The Upper Carboniferous Hoyada Verde Formation (Mésigos, 1953) in the Sierra de Barreal (San Juan Province) is ichnologically the best known unit. This formation is mainly composed from base to top of laminated mudstone and diamictite, laminated mudstone with dropstones, fossiliferous black shale with the "*Levipustula* fauna", mudstone interbedded with fine- to very fine-grained sandstone, and fine-grained sandstone. Peralta *et al.* (1997) indicated the presence of *Conostichus* in the fossiliferous black shale, whereas burrows assigned to *Arenicolites* isp., and arthropod trackways assigned to *Merostomichnites* isp. and *Umfolozia* isp. have been reported from the fine-grained deposits by these authors. However, the absence of photos precludes confirmation of the ichnotaxonomic assignments. In the upper levels of the unit, particularly in the postglacial fine-grained sandstone, Mángano *et al.* (2003) analyzed trace fossils atribuited to the ichnospecies *Psammichnites implexus* and *P. plumieri* (Figure 6 A-B) (formerly assumed as *Helmintoida* by Peralta *et al.*, 1997). *Psammichnites* represents the feeding activity of a marine mobile organism conected to the surface by a siphon (Mángano *et al.*, 2003). The *Psammichnites implexus* and *P. plumieri* assemblage characterizes the upper levels of the postglacial interval in the Hoyada Verde Formation, and its very low ichnodiversity reflects stressed conditions in marginal-marine settings, most likely deltaic influence (Mángano *et al.*, 2003). Recently, Alonso-Muruaga *et*

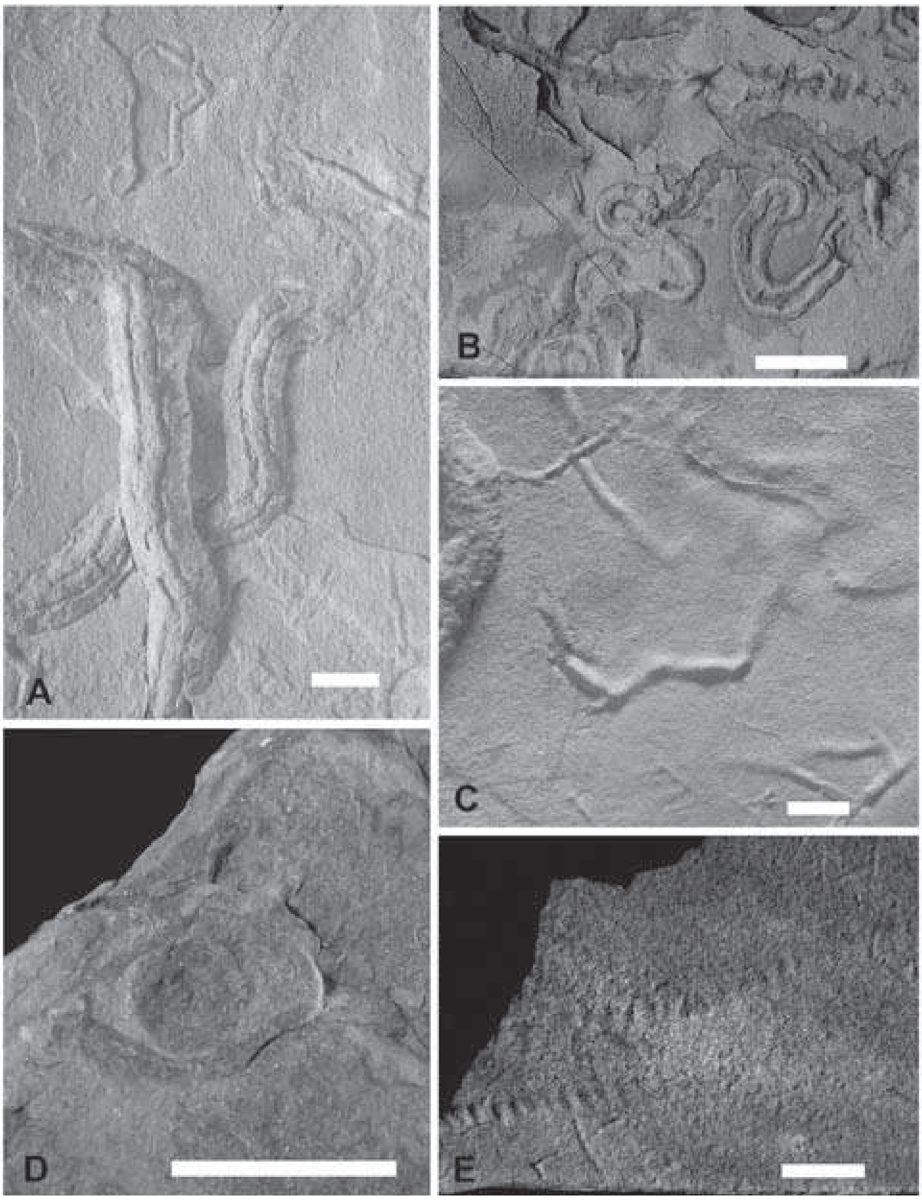

Figure 6. Trace fossils from the Hoyada Verde Formation (Sierra de Barreal, Calingasta-Uspallata Basin). A, *Psammichnites plummeri*; B, *Psammichnites implexus*; C, *Treptichnus bifurcus*; D, *Lingulichnus verticalis*; E, arthropod trackway. All the trace fossils are on bedding plane. Scale bars: 10 mm.

al. (2012) characterized the trace-fossil content of the Hoyada Verde Formation and analyzed its environmental implications. In addition to *Psammichnites plummeri* and *P. implexus*, these authors also recognized the ichnotaxa *Lingulichnus verticalis, Lockeia* isp., *Palaeophycus* isp., *Ptychoplasma vagans*, *Protovirgularia* isp., *Treptichnus bifurcus* (formerly poligonal traces of bryozoans? in Peralta *et al.*, 1997), and arthropod trackways (Figure 6). This ichnoassemblage is characterized by a dominance of horizontal trace fossils and subordinate presence of vertical and inclined structures, reflecting the dominant activity of mobile deposit feeders. Besides, the trace fossils are restricted to bedding planes, whereas shallow vertical structures are only locally present, resulting in very low or virtual absence of vertical bioturbation. This ichnofauna illustrates a stressed expression of the *Cruziana* Ichnofacies, suggesting a context that departs from that expected in normal shallow-marine settings. Based on the integration of sedimentologic and ichnologic data, a wave-influenced prograding deltaic system was inferred for the postglacial upper levels of the Hoyada Verde Formation.

Only isolated recordings are available for other units of the basin. Taboada (1986) mentioned the presence of *Tisoa* isp. in the Lower Permian Agua del Jagüel Formation (Mendoza Province). In the same unit, Lech & Buatois (1990) recorded the ichnospecies *Bergaueria hemisphaerica* and *Conostichnus ornatus*. The same authors also indicated the presence of *Rosselia socialis* in the Upper Carboniferous–Lower Permian Santa Elena Formation (Mendoza Province). In fine-grained deposits of the Upper Carboniferous Leoncito Formation (San Juan Province), Lech (1986) recognized structures produced by burrowing anemones. Ongoing research allowed detecting the presence of the ichnogenus *Macaronichnus* in sandstone of the Agua del Jagüel Formation and of *Phycosiphon incertum* in mudstone intervals interbedded with diamictite in the Leoncito Formation.

DISCUSSION

This review shows that trace fossils are locally abundant and relatively diverse in the Paganzo and Calingasta-Uspallata basins (Table 1). The depauperate *Cruziana* and *Mermia* Ichnofacies are common and relatively widespread, involving spatial and temporal recurrence in these basins. The *Mermia* Ichnofacies, typical of freshwater conditions, is widespread in Carboniferous units of the Paganzo Basin, being also present in its depauperate expression. The replacement of the depauperate *Cruziana* Ichnofacies by the *Mermia* Ichnofacies in the glacial-postglacial deposits of Guandacol Formation is interpreted as the response of benthic faunas subject to extreme freshwater influx during deglaciation events (Buatois *et al.*, 2006, 2010). On the other hand, the replacement of the depauperate *Mermia* Ichnofacies by the depauperate *Cruziana* Ichnofacies in the Tupe Formation reflects the shift from nonmarine freshwater settings to marine brackish-water conditions as a result of transgression during times of climatic amelioration (Desjardins *et al.*, 2010). The impovershed *Cruziana* Ichnofacies recognized in the upper interval of the Hoyada Verde Formation suggests a deltaic environment rather than a prograding strandplain. In addition, Permian continental deposits contain invertebrate ichnofaunas that typify the *Scoyenia* Ichnofacies which, in turn, also reflect an important lowering of the water table with respect to Late Carboniferous

Table 1. Ichnofacies distribution in the late Paleozoic Paganzo and Calingasta-Uspallata basins.

BASIN	AGE	ICHNOFACIES			
		Mermia	***Cruziana*** **(depauperate)**	***Scoyenia***	***Octopodichnus-Entradichnus***
Paganzo	Permian (Upper Section)			Patquía Fm. La Colina Fm. Bordo Atravesado (Patquía Fm.)	Patquía Fm.
	Upper Carboniferous (Lower Section)	Tupe Fm. Guandacol Fm. Agua Colorada Fm. Malanzán Fm.	Tupe Fm. Guandacol Fm.		
Calingasta-Uspallata	Upper Carboniferous		Hoyada Verde Fm.		

times, in connection with a progressive aridization in the region (see López-Gamundí *et al*., 1992)

FINAL REMARKS

This review demonstrates how ichnologic evidence constitutes a useful tool to unlock ecological signatures and to assist in reconstructing peri-Gondwanan environments. Interestingly, examples of the more diverse archetypal *Cruziana* Ichnofacies have not been recorded yet in these basins. This contrasts with the situation documented in other Gondwanan basins (e.g., Australia, see Bann *et al*., 2004; Bann & Fielding, 2004) where this ichnofacies is well represented.

Moreover, the state of ichnologic knowledge of both basins is disparate. The bulk of ichnologic information comes from the Paganzo Basin, where trace fossils have been recognized in differents areas and stratigraphic intervals (see Table 1). In contrast, a handful of studies have dealt with the ichnology of the Calingasta-Uspallata Basin. Nevertheless, this relative lack of ichnologic data is probable not because of the absence of trace fossils in these rocks, but rather to the lack of studies on the subject, as it has already been observed by Aceñolaza & Buatois (1991). The vertebrate trace-fossil record of the late Paleozoic of Argentina remains poorly explored.

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ICHNOLOGY OF CENOZOIC MARINE DEPOSITS FROM PATAGONIA (SOUTHERN ARGENTINA): THE ROLE OF THE MODERN EVOLUTIONARY FAUNA IN NEOGENE INFAUNAL ECOSYSTEMS

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ABSTRACT

Neogene deposits from Patagonia are characterized by extremely diverse ichnofaunas, including a great variety of feeding (e.g., *Asterosoma, Helicodromites, Phycosiphon, Rosselia, Teichichnus*), grazing (e.g., *Nereites, Scolicia, Taenidium*) and dwelling (e.g., *Balanoglossites, Gastrochaenolites, Gyrolithes, Ophiomorpha, Siphonichnus, Spongeliomorpha, Schaubcylindrichnus, Thalassinoides*) structures. Subordinately, locomotion (e.g., *Protovirgularia*) and equilibrium/escape structures (e.g., *Scalichnus*) occur. Trace fossils in open-marine deposits are abundant and diverse, with extremely complex tiering structures, and most commonly characterized by the presence of the archetypal *Cruziana* Ichnofacies. On the contrary, restricted, commonly tide-influenced, brackish-water environments show low to moderate ichnodiversity, monospecific associations, trace fossils generally of small sizes, and the presence of an impoverished *Cruziana*-*Skolithos* Ichnofacies. Irregular echinoid structures are abundant mainly in open-marine environments while those produced by bivalves and crustaceans dominate the open-marine and brackish-water ichnofaunas, reflecting the peak of the Modern Evolutionary Fauna. Ichnofaunas of modern aspect seem to have been well established in shallow-marine, open environments since the Mesozoic, and this is particularly well exemplified in the Neogene ecosystems from Patagonia, where finely tuned climax communities display vertical niche partitioning and a remarkable use of the infaunal ecospace. These observations agree with the trends exhibited by the body-fossil record, which show that for the Late Cenozoic middle-latitude successions, marine paleocommunities include a greater representation of infaunal organisms, especially of deep-burrowers. In addition, local influence of nutrient-rich waters brought to the surface during upwelling events along the Patagonian coast may have also contributed to the increasing complexity seen in these Neogene infaunal ecosystems.

Key words: Neogene ichnofauna, shallow marine, Patagonia, Miocene, Modern Evolutionary Fauna, paleoceanic circulation.

INTRODUCTION

The concept of Evolutionary Faunas (Sepkoski, 1981) allows to evaluate the most important changes in the composition of marine biotas through time. Three main Evolutionary Faunas have been recognized: (i) the Cambrian (composed mostly of trilobites, inarticulate brachiopods, hyolithids, and eocrinoids); (ii) the Paleozoic (consisting principally of articulate brachiopods, crinoids, corals, and stenolaemate bryozoans); and (iii) the Modern (composed mostly of gastropods, bivalves, bony fishes, malacostraceans and echinoids) Evolutionary Faunas (Sepkoski & Miller, 1985). Although all these faunas originated in the early Phanerozoic, each one shows different diversification rates, displays higher maximum diversity and more ecologic complexity than the previous one (Sepkoski & Miller, 1985). In particular, the Modern Evolutionary Fauna reveals a maximum familial diversity nearly twice that of the Paleozoic Fauna, reaching a peak in diversity in the late Cenozoic.

All these analyses have been based on the study of body fossils. However, ichnologic information also provides important clues to understand how the origination and establishment of evolutionary faunas impacted in the infaunal ecosystems. Neogene marine deposits of Patagonia, outcropping extensively along the Atlantic coast of the Río Negro, Chubut and Santa Cruz provinces, Argentina, contain extremely abundant and diverse trace fossils. Although the body fossils and sedimentary facies of these successions have received considerable attention (Frenguelli, 1929; Feruglio, 1949; Expósito, 1977; Cione, 1978; Bellosi, 1987, 1995; Bellosi & Barreda, 1993; Paredes, 2002; del Río, 2002), ichnologic aspects have been addressed only recently (Lech *et al.*, 2000; Carmona *et al.*, 2002; Buatois *et al.*, 2003a; Carmona & Buatois, 2003; Scasso & Bellosi, 2004; Carmona, 2005; Olivero & López-Cabrera, 2005; Carmona *et al.*, 2006; 2008; Parras & Griffin, 2009; Cuitiño & Scasso, 2010).

Therefore, the main purposes of this paper are to: (i) characterize and illustrate the most representative trace fossils from the Neogene marine deposits of Patagonia; (ii) describe the typical ichnoassemblages found in both open-marine and brackish-water deposits, as well as the trace-fossil suites that occur in firmgrounds, evaluating their paleoecology and ethology; (iii) analyze this ichnofauna considering local paleoceanographic conditions; and (iv) understand these ichnoassemblages with respect to secular changes in bioturbation linked to the development of the Modern Evolutionary Fauna.

GEOLOGIC SETTING AND PALEOGEOGRAPHY OF PATAGONIA DURING THE NEOGENE

Since the latest Mesozoic, the extra-Andean Patagonian areas were flooded by successive transgressive events of different magnitude (Malumián, 1999). These transgressive sediments were principally deposited in shallow-marine environments, most of them with significant tidal influence and low wave action (Malumián, 1999). This author recognized five Cenozoic sedimentary cycles that were controlled by tectonic, eustatic and climatic fluctuations. The first to third cycles occurred from the Maastrichtian to the Early Oligocene. The fourth cycle comprises two extensive transgressive events, the first one that occurred in the late Oligocene (Juliense transgression) – early Miocene (Leonense–Superpatagoniense transgressions), whereas the second one occurred during the Middle to early Late Miocene (Entrerriense transgression). Finally, the fifth cycle (late Miocene–Pliocene) includes restricted marine deposits produced by marine transgressions in the proximities of the modern coast line (Malumián, 1999).

The Paleogene–Early Neogene paleosol record (Bellosi & Gonzalez, 2010), along with terrestrial paleobotanical and palynological assemblages (Barreda & Palazzesi, 2007; Palazzesi & Barreda, 2007) from Patagonia, suggest that regional climatic fluctuations mirrored global changes (Zachos *et al.*, 2001). In the marine setting, Malumián (1999) considered that Patagonia was affected by the water masses that reached its coasts from the Austral Ocean. In particular, from the late Oligocene to the early Miocene, there is evidence of greater development of superficial Antarctic waters (Malumián, 1999). This is supported by the Neogene foraminifer content, which suggests that the water temperature values were cooler than tropical waters (Malumián, 1999). Also, during the mid Miocene there is evidence of an increment in the temperature, recording the Neogene climatic optimum.

In this contribution we will focus on Neogene deposits from the Valdés, San Jorge and Austral Basins. Field work was especially concentrated on deposits outcropping on the Atlantic coast of Rio Negro (Late Miocene–Early Pliocene Rio Negro Formation), Chubut (Lower Miocene Chenque Formation) and Santa Cruz provinces (Lower Miocene Monte Leon Formation), due to the great preservation of trace fossils and the highest ichnodiversities in these deposits. Trace fossils were analyzed at several localities (Figure 1), the majority of which consist of vertical cliff sections and extensive horizontal surfaces that represent the abrasion platforms exposed during low tide. Superb preservation allows three-dimensional reconstructions of the trace fossils. The studied strata were mostly deposited in shallow-marine environments, both under normal salinity conditions (e.g., shoreface environments) and in restricted, marginal-marine, tide-influenced environments.

CHARACTERIZATION OF THE NEOGENE ICHNOFAUNA

Ichnoassemblages in fully marine, brackish-water and firmground deposits

The analyzed Neogene successions from Patagonia comprise mostly shallow-marine deposits, encompassing both open-marine and marginal-marine environments (Bellosi, 1987, 1995; Buatois *et al.*, 2003a; Carmona *et al.*, 2008, 2009). In turn, tide-dominated

Figure 1. Map showing the location of the studied formations.

marginal-marine successions include both estuarine and deltaic deposits (Carmona *et al.*, 2008). Additionally, in some of these deposits, surfaces associated with erosional exhumation of the substrate are produced, generating firmgrounds.

Open-marine settings consist of upper-, middle- and lower-shoreface, and offshore-transition successions, which have been recognized in the Río Negro Formation (Middle Marine Member) (Zavala & Freije, 2000), lower sequences of the Chenque Formation (Punta Borja, Playa Las Cuevas, Punta Delgada, Playa Alsina, Rada Tilly localities) (Carmona *et al.*, 2008), and in the Monte León Formation (Monte León National Park) (Parras & Griffin, 2009). In general, upper- and middle-shoreface deposits consist of glauconitic sandstone with trough cross-stratification and planar lamination. The trace-fossil suite represents the *Skolithos* Ichnofacies, and is typically characterized by heavily lined, deeply penetrating vertical structures such as *Ophiomorpha* and less commonly *Skolithos* (Figures 2A-B). Additionally, mobile intrastratal, large, deposit-feeding trace fossils, such as *Macaronichnus*, also occur in the more energetic facies. In more distal deposits (such as those of the lower shoreface to offshore transition), there is an evident decrease in grain size and the dominance of elements of the *Cruziana* Ichnofacies (Figures 2C-F). Most commonly, these deposits consist of thoroughly bioturbated very fine-grained silty sandstone, and only locally are parallel lamination and discrete shell layers observed. Trace fossils are abundant and ichnodiversity is high, being characterized by the presence of the archetypal *Cruziana* Ichnofacies. Deposit- and detritus-feeding structures, such as *Asterosoma, Chondrites, Helicodromites, Nereites, Phycosiphon*, *Planolites, Thalassinoides*, *Teichichnus*, *Rosselia*, *Scolicia, Schaubcylindrichnus* and *Taenidium* are common elements (Figure 2).

Successions deposited in restricted settings (e.g., estuaries and deltas) have been also recognized in the Neogene deposits of Patagonia, mostly in the upper sequences of the Chenque Formation (e.g., in Cerro Viteau, Cerro Hermite, Caleta Olivia, and the roadcut on National Route 3 localities) (Bellosi, 1995; Carmona, 2005; Carmona *et al.*, 2006, 2008, 2009), in the Río Negro Formation (La Lobería, Playa Bonita and Espigón localities) (Carmona *et al.*, 2012), and in the Monte León Formation. Deposits in tide-influenced estuarine settings comprise tidal flats, subtidal sandbars and channels. The tidal-flat deposits mainly consist of heterolithic beds with well-preserved sedimentary structures and low to moderate degrees of bioturbation. The trace-fossil suites of these deposits comprise principally deposit-feeder structures, such as *Thalassinoides* (mostly with tidal fill, Figure 3A), *Asterosoma* and *Planolites*. Under more energetic conditions (e.g., sandbar and channel deposits), the ichnodiversity is low to moderate, being trace-fossil suites commonly monospecific. In these settings, traces of organisms adapted to cope with high energy are dominant (e.g., large *Macaronichnus* and heavily lined *Ophiomorpha* and *Rosselia,* Figures 3B-D). Overall, these characteristics (e.g., low to moderate ichnodiversity, monospecific associations, presence of an impoverished *Cruziana*-*Skolithos* Ichnofacies) suggest a stressful environment, affected by salinity and turbidity fluctuations. Interestingly, it is not common to observe reduction in the size of the trace fossils, a characteristic commonly associated with stressful conditions (e.g., Pemberton & Wightman, 1992; MacEachern & Pemberton, 1994; Buatois *et al.*, 2005). In addition, in the localities from the Río Negro Formation, microbially induced sedimentary structures (MISS) have been recognized in the tidal-flat deposits (Figure 3E, Carmona *et al.*, 2012).

Tide-influenced delta deposits (Figure 4) have also been studied in the analyzed successions (Carmona *et al.*, 2009). Two main subenvironments are recognized: prodelta and delta-front, stacked forming a progradational coarsening-upward succession. The prodelta deposits display low to moderate bioturbation intensities, although a high degree of bioturbation occurs locally. The trace-fossil assemblage is dominated by

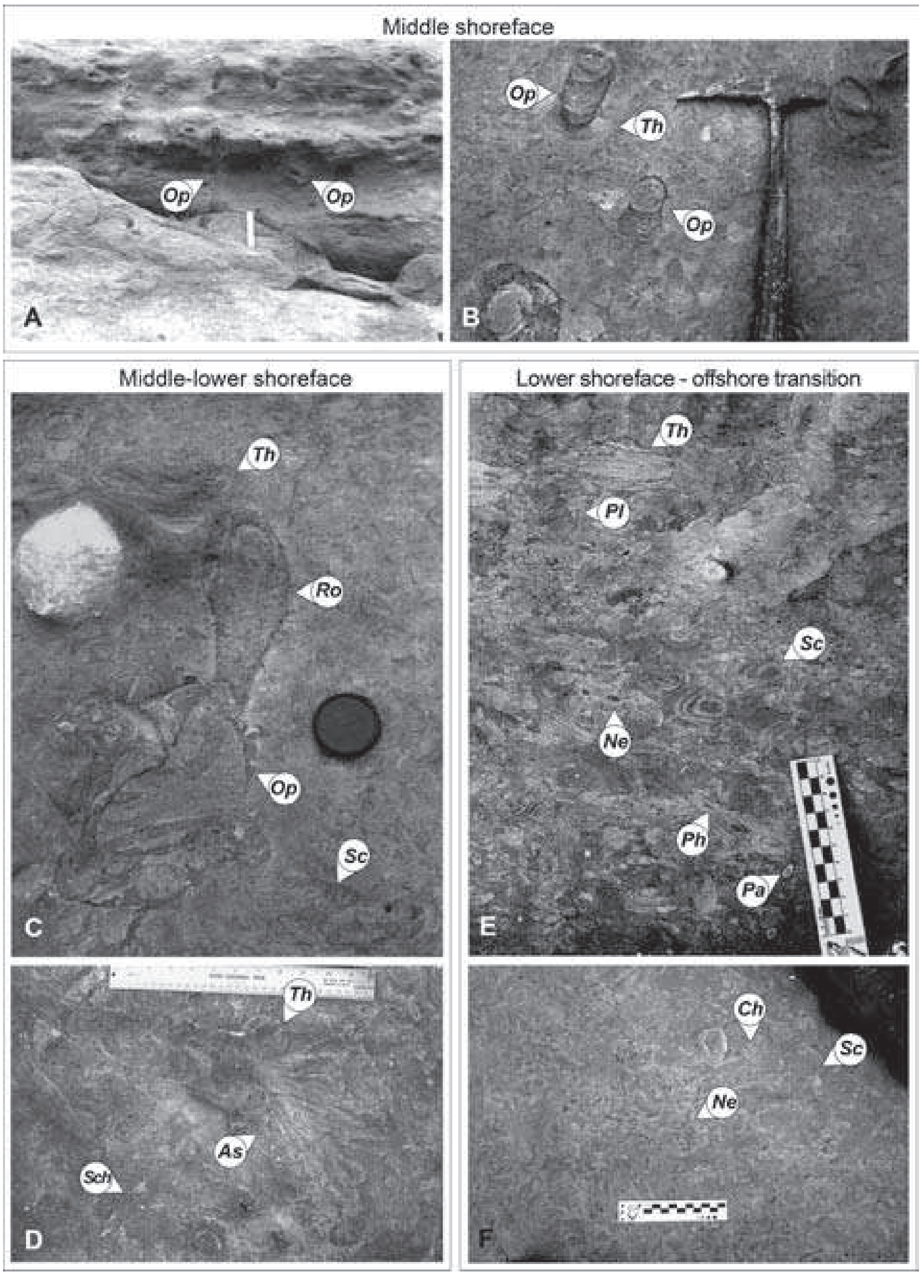

Figure 2. Ichnology of fully marine deposits. A, Shafts of *Ophiomorpha* (*Op*), Chenque Formation; B, cross section view of *Ophiomorpha* (*Op*) and *Thalassinoides* (*Th*), Chenque Formation; C, *Rosselia* (*Ro*), *Ophiomorpha* (*Op*), *Thalassinoides* (*Th*) and *Scolicia* (*Sc*), Chenque Formation; D, bedding plane view, *Asterosoma* (*As*), *Schaubcylindrichnus* (*Sch*) and *Thalassinoides* (*Th*), Chenque Formation; E, cross section view, *Thalassinoides* (*Th*), *Scolicia* (*Sc*), *Planolites* (*Pl*), *Palaeophycus* (*Pa*), *Phycosiphon* (*Ph*), *Nereites* (*Ne*), Chenque Formation; F, bedding plane view, *Chondrites* (*Ch*), *Scolicia* (*Sc*), *Nereites* (*Ne*), Chenque Formation. Scales: A, 15 cm long; C, 5.5 cm in diameter.

deposit-feeder structures, such as *Planolites*, *Teichichnus* and *Phycosiphon*; subordinate and rare elements include *Asterosoma*, *Nereites*, *Protovirgularia*, *Rosselia*, *Schaubcylindrichnus*, and *Thalassinoides* (Figures 4A-C). This assemblage is considered a stressed expression of the archetypal *Cruziana* Ichnofacies. The delta-front succession shows two main facies representing distal to proximal deposits. The distal delta-front facies is almost completely obliterated by equilibrium trace fossils of bivalves. Subordinately, deposit-feeding structures, such as *Teichichnus*, *Thalassinoides*, and *Schaubcylindrichnus*, also occur. The trace-fossil suite in proximal delta-front facies is dominated by large *Rosselia* and *Macaronichnus* in the sandier beds, whereas *Nereites* and *Protovirgularia* are commonly present in mudstone drapes blanketing the sandstone foresets (Figures 4D-F). The intensity of bioturbation is commonly low, although some intervals may show relatively

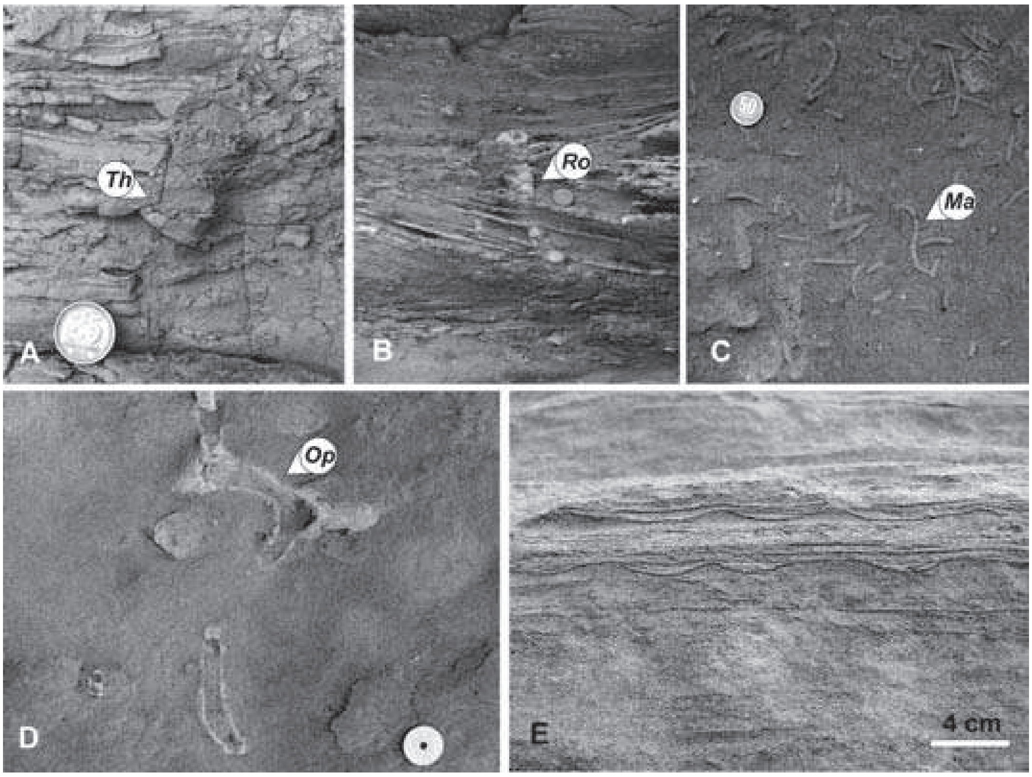

Figure 3. Ichnology of estuarine deposits. A, Cross section view, *Thalassinoides* (*Th*) with tidal fill, Chenque Formation; B, cross section view, *Rosselia* (*Ro*), Chenque Formation, C, bedding plane view, *Macaronichnus* (*Ma*), Chenque Formation; D, bedding plane view, *Ophiomorpha* (*Op*), Chenque Formation; E, cross section view of tidal-flat deposits with teepee structures, Río Negro Formation (see also Carmona *et al*., 2012). Scales (in diameter): A-B, 24.3 mm; C, 25.4 mm; D, 28.4 mm.

higher values. The trace-fossil suite in the delta-front facies corresponds to an impoverished expression of the proximal *Cruziana* ichnofacies. The described ichnofaunas show features typical of deltaic environments (MacEachern *et al*., 2005). These include alternation of unburrowed and bioturbated intervals, juxtaposition of stressed and relatively diverse suites, opportunistic colonization of substrates and suppression of the *Skolithos* Ichnofacies.

River-influenced deltaic deposits have been also recorded in the Monte León Formation (Figure 5). As it occurs in the tide-influenced delta deposits, the intensity of bioturbation is in general low. In the heterolithic prodelta beds, there is a dominance of locomotion structures of bivalves (*Protovirgularia*, Figure 5A). In addition, *Nereites, Asterosoma* (Figures 5B-C) and small *Rosselia* specimens also occur. The delta-front deposits present very few trace fossils, most of them representing equilibrium-escape structures. Additionally, thin, unburrowed hyperpycnal levels also occur in this succession (Figure 5D).

Firmground surfaces with development of the *Glossifungites* Ichnofacies have been recognized and characterized in the Neogene strata (Figure 6). This ichnofacies can be observed delineating surfaces with sequence-stratigraphic significance, such as the one recognized between the Sarmiento and Chenque formations (e.g., in Astra, Infiernillo and Bahía Solano localities), which contains specimens of *Gastrochaenolites* and *Thalassinoides* (Figures 6A-C, see also Carmona *et al*., 2006). This suite occurs in a co-planar surface that results from amalgamated lowstand and transgressive marine erosion. Firmground suites also occur in other studied sections (in Playa Las Cuevas, Punta Delgada, Bahía Solano localities in the Chenque Formation; in La Lobería and El Espigón localities in the Río Negro Formation; and in the Parque Nacional Monte León, in the Monte León Formation), demarcating other discontinuities, such as transgressive surfaces of erosion or regressive surfaces of marine erosion (Buatois *et al*., 2003a; Carmona, 2005). These suites consist of specimens of *Thalassinoides*, *Siphonichnus*, and *Spongeliomorpha*; subordinately *Balanoglossites* and *Rhizocorallium* may also occur (Figures 6D-E). In other cases, autocyclic development of the *Glossifungites* Ichnofacies has also been recorded, especially in areas where there is a sharp contrast between the underlying muddy substrates and the overlying sandy strata (e.g., in margins of tidal-channel deposits and their associated tidal-flats in the Cerro Hermitte,

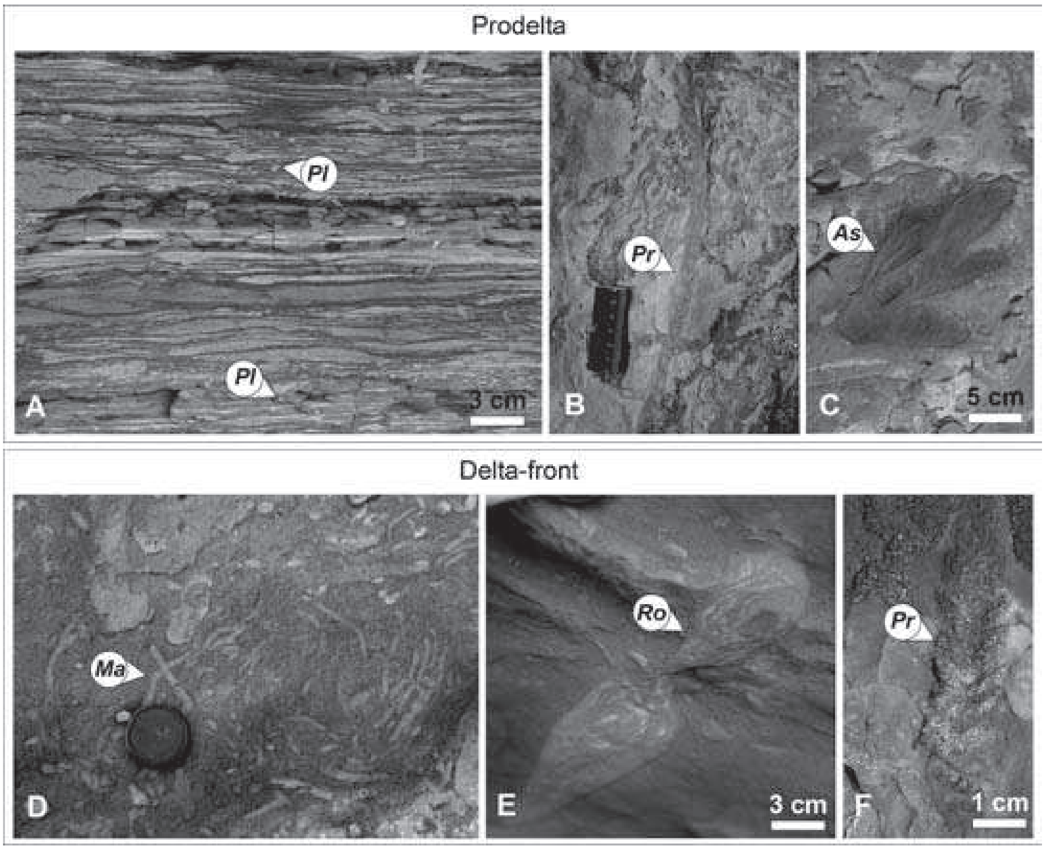

Figure 4. Ichnology of tide-influenced deltaic deposits in the Chenque Formation. A, Cross section view, *Planolites* (*Pl*); B, bedding plane view, *Protovirgularia* (*Pr*); C, bedding plane view, *Asterosoma* (*As*); D, bedding plane view, *Macaronichnus* (*Ma*); E, cross section view, *Rosselia* (*Ro*); F, bedding plane view, *Protovirgularia* (*Pr*). Scale in D: 55 mm in diameter.

Cerro Viteau and Cerro Antena localities of the Chenque Formation, Figure 3A).

Most common bioturbators and tiering structure

The most common ichnotaxa observed correspond to the activity of crustaceans and bivalves as the dominant groups, occurring both in fully-marine and in brackish-water settings. The crustacean burrows recorded in these Neogene deposits include: *Thalassinoides* (dwelling-feeding), *Ophiomorpha* (dwelling), *Spongeliomorpha* (dwelling) as the dominant crustacean ichnogenera, and subordinately ?*Gyrolithes* (feeding, dwelling and possibly gardening) and *Maiakarichnus* (brooding) (Figure 7). Bivalve structures are also diverse and comprise various ethologies, such as *Protovirgularia* (locomotion), *Gastrochaenolites* (dwelling), *Siphonichnus* (equilibrium), *Scalichnus* (equilibrium/escape), and other equilibrium structures of byssate bivalves (Figure 8). In fully marine deposits, such as those accumulated in lower-shoreface settings, grazing structures produced by stenohaline irregular echinoids (e.g., *Scolicia*) are extremely common, together with other vagile, deposit-feeder structures (Figure 9).

Tiering consists of the vertical partitioning of the infaunal and epifaunal space (Ausich & Bottjer, 1982; Bromley & Ekdale, 1986). The vertical distribution of the infaunal organisms responds to different physical, chemical and biological parameters (Bromley, 1996). Unraveling the tiering structure in intensely bioturbated successions may be difficult and it is necessary to determine properly the complex cross-cutting relationship. In the studied successions, particularly in those deposited under fully marine conditions, very complex tiering structures have been recognized, reflecting the development of finely tuned climax communities that display vertical niche partitioning and a remarkable use of the infaunal ecospace (Buatois *et al*., 2003b; Carmona *et al*., 2003; 2008; Carmona, 2010). For example, in lower-shoreface to offshore-transition deposits, nine tiers and six ichnoguilds have been recognized (Figure 10A) (Buatois *et al*., 2003b). This tiered ichnocoenosis includes vagile, deposit-feeder structures that produce a mottled texture close to the sediment surface,

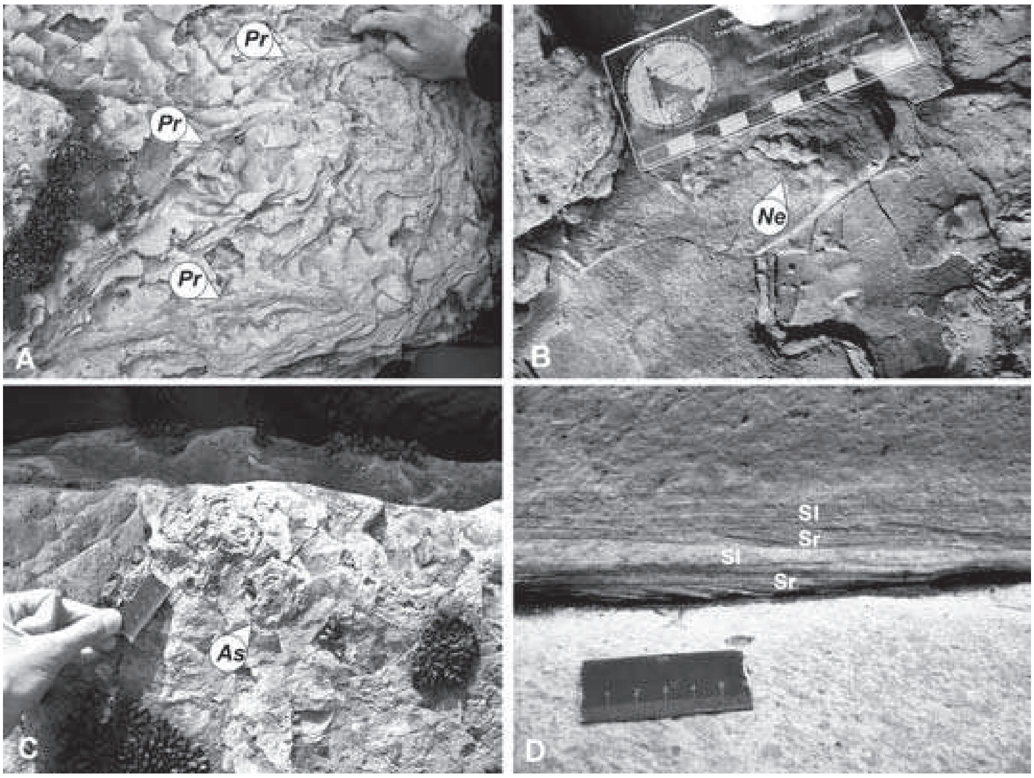

Figure 5. Ichnology of river-influenced deltaic deposits in the Monte León Formation. A, Bedding plane view, *Protovirgularia* (*Pr*); B, bedding plane view, *Nereites* (*Ne*); C, bedding plane view, *Asterosoma* (*As*); D, cross section view of unburrowed, hyperpycnal levels. Note recurrent transitions between sandstone with parallel lamination (Sl) and current ripples (Sr).

a *Thalassinoides-Asterosoma-Rosselia* ichnoguild that includes semi-vagile, deposit-feeder traces in the shallow tiers, a *Schaubcylindrichnus-Palaeophycus* ichnoguild consisting of vagile, suspension- and deposit-feeder structures in the middle tiers, a *Scolicia-Phycosiphon-Helicodromites-Teichichnus-Taenidium* ichnoguild comprising vagile, deposit-feeder structures in the middle tiers, a *Thalassinoides* ichnoguild that consists of stationary, deposit-feeder structures in the deep-tiers, and a *Chondrites* ichnoguild that includes non-vagile, deposit-feeder or chemosymbiont structures in the deepest tiers. The complexity of the tiers in the lower-shoreface deposits of Patagonia is equivalent to those described for the uppermost Cretaceous Chalk of Denmark (Ekdale & Bromley, 1991), with nine recognized tiers and four major ichnoguilds. In more proximal positions within the shoreface (e.g., lower shoreface), six ichnoguilds and seven tiers are represented (Figure 10B, Carmona *et al.*, 2003), including a *Planolites montanus* ichnoguild comprising vagile, very shallow-tier, deposit-feeder structures; an *Asterosoma-Rosselia* ichnoguild that includes semi-vagile, shallow-tier, detritus- and deposit-feeder structures; an *Ophiomorpha* ichnoguild consisting of stationary, middle-tier, suspension-feeder structures; a *Thalassinoides-Schaubcylindrichnus* ichnoguild that includes semi-vagile to vagile, middle-tier, deposit-feeder structures; a *Phycosiphon* ichnoguild consisting of vagile, deep-tier, deposit-feeder structures; and a deep *Chondrites* ichnoguild, comprising non-vagile, deposit-feeder or chemosymbiont structures. In both examples, the high degree of bioturbation and the high ichnodiversity indicate slow or discontinuous sedimentation in well-oxygenated open-marine settings under normal marine salinity conditions. Also, in both cases there is a clear dominance of deposit-feeder organisms, which reflects that the amount of organic matter was not a limiting factor within these substrates. An alternative explanation is that these organisms were highly specialized in the use of different resources within the substrate (e.g., microorganisms, amorphous matter), optimizing thus the exploitation of the food supply. Additionally, in the ichnocoenosis recorded in more proximal positions (middle to lower shoreface) suspension-feeder structures tend to be more abundant, revealing probably more heterogeneous conditions than in more distal positions. On the contrary, in more restricted deposits (e.g., deltaic and estuarine deposits), the tiering structure is much more simple than in the fully marine successions, with only few tiers and ichnoguilds.

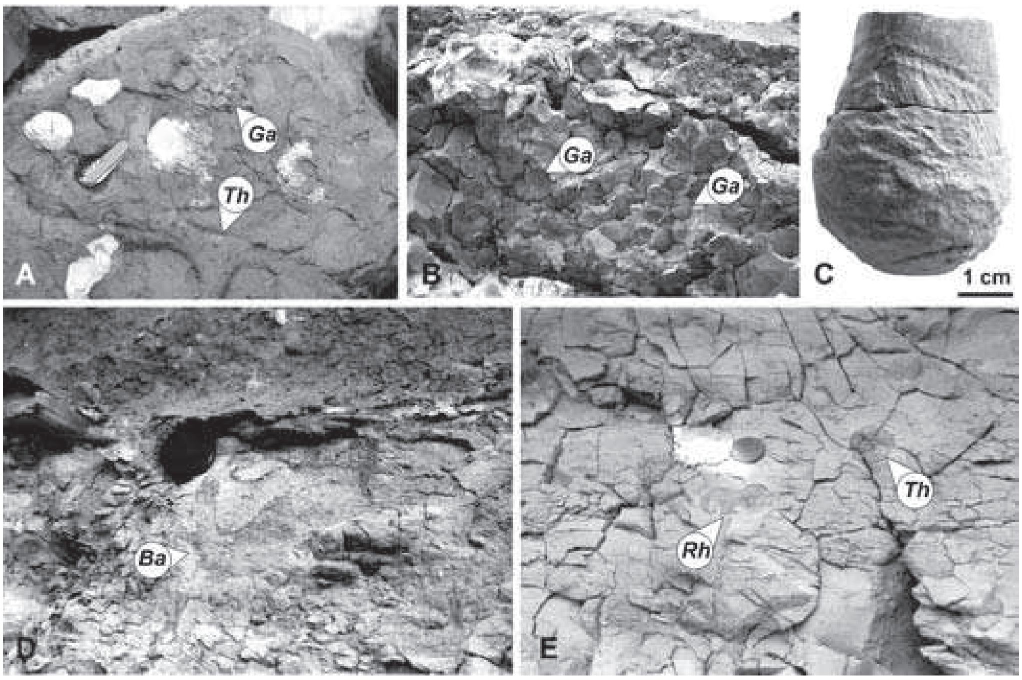

Figure 6. Ichnology of firmground deposits. A, Bedding plane view, *Thalassinoides* (*Th*) and *Gastrochaenolites* (*Ga*), Chenque Formation; B, basal view of several specimens of *Gastrochaenolites* (*Ga*), Chenque Formation; C, lateral view of one specimen of *Gastrochaenolites* (*Ga*), showing in the upper portion the bivalve cast well preserved, Chenque Formation; D, cross section view, *Balanoglossites* (*Ba*), Chenque Formation; E, cross section view, *Rhizocorallium* (*Rh*) and *Thalassinoides* (*Th*), Chenque Formation. Scales: A, 10 cm long; D, 55 mm in diameter; E, 18.2 mm in diameter.

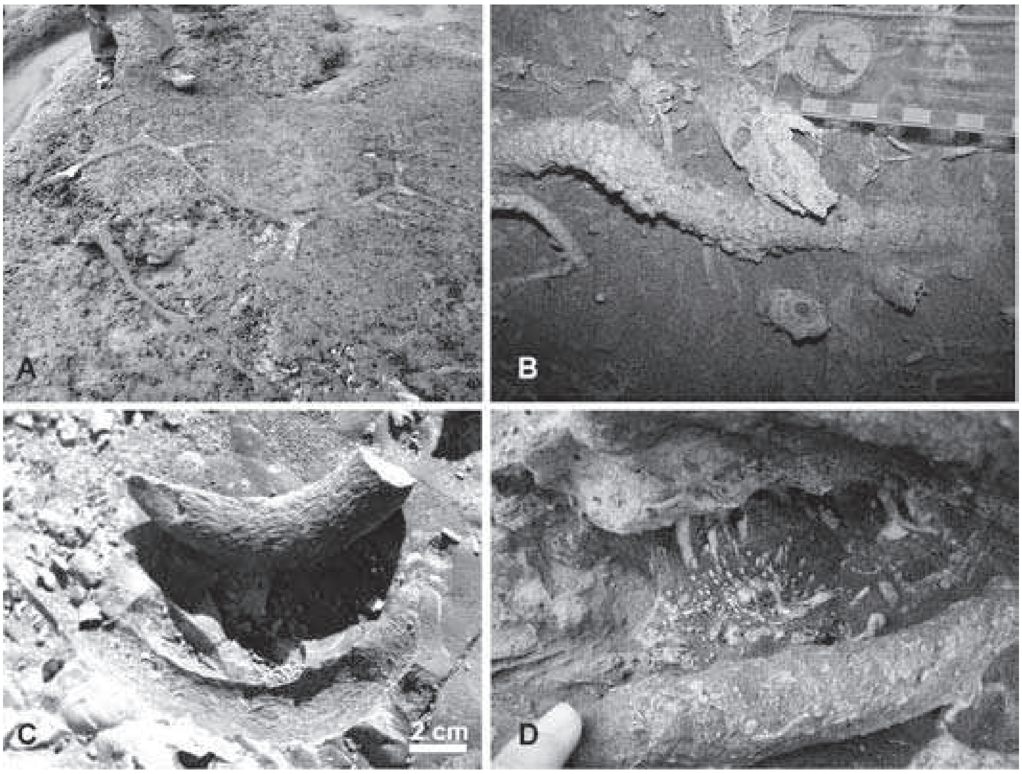

Figure 7. Crustacean structures. A, Bedding plane view of *Thalassinoides*, Monte León Formation; B, lateral view of *Ophiomorpha*, Monte León Formation; C, *Spongeliomorpha*, Chenque Formation; D, lateral view of *Maikarichnus*, associated with *Thalassinoides*, Río Negro Formation.

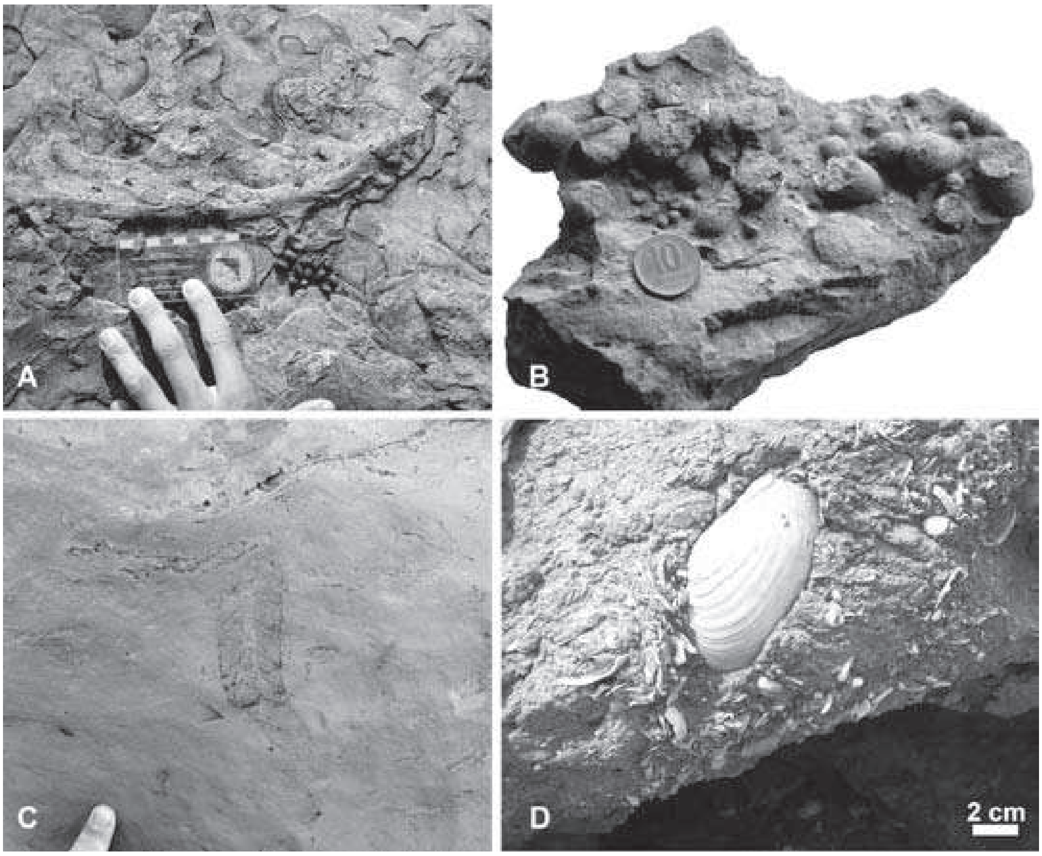

Figure 8. Bivalve structures. A, Bedding plane view of *Protovirgularia*, Monte León Formation; B, basal view of several specimens of *Gastrochaenolites*, Chenque Formation; C, cross section view of *Siphonichnus*, Río Negro Formation; D, cross section view of *Scalichnus*, Monte León Formation. Scale in B: 18.2 mm in diameter.

PALEOCEANOGRAPHIC AND EVOLUTIONARY SIGNIFICANCE

Two different perspectives are employed in order to understand the complexity of Neogene ichnofaunas from Patagonia: (i) the local, paleoceanographic context, and (ii) the global perspective within the context of the Modern Evolutionary Fauna.

Paleoceanographic context

It is believed that the position of Patagonia during the Cenozoic was equivalent to its modern position, being located in middle austral latitude that did not exceed the modern one by more than 5° (Somoza *et al.*, 1995; Beck, 1999, Malumián, 1999). Therefore, it is possible to consider that the prevalent paleoceanographic situation during the deposition of the studied successions was relatively similar to the modern one. Although data from the paleoflora (Barreda & Palazzesi, 2007; Palazzesi & Barreda, 2007), the paleosols (Bellosi & Gonzalez, 2010), and the terrestrial mammals (Kramarz & Bellosi, 2005; Madden *et al.*, 2010) indicate that the Miocene climate was relatively warm, several lines of evidence indicate the presence of cool waters for the early and late Miocene along the Patagonian coast, namely forams (Malumián, 1999), dinoflagellates (Guler, 2003), penguins (Acosta Hospitaleche, 2007), cetaceans (Caviglia, 1979), and phosphatic concretions (Scasso & Castro, 1999). The occurrence of the ichnogenus *Macaronichnus* in the studied deposits (Carmona, 2005; Carmona *et al.*, 2008) is also interpreted as related to the presence of cold-waters. This ichnogenus occurs mostly in intermediate to high-latitude shallow-marine deposits from the Mesozoic onwards (Pemberton *et al.*, 2001; Gibert *et al.*, 2006; Carmona *et al.*, 2008; Bromley *et al.*, 2009; Quiroz *et al.*, 2010), and it is attributed to the activity of opheliid worms, which are known from temperate and subarctic waters (McConnaughey & Fox, 1949; Bellan & Dauvin, 1991). Therefore, this ichnogenus has been suggested as an indicator of nearshore settings from intermediate- to high-latitude areas (Pemberton *et al.*, 2006, Carmona *et al.*, 2008), and also from low-latitude coastal environments influenced by upwelling conditions (Quiroz *et al.*, 2010).

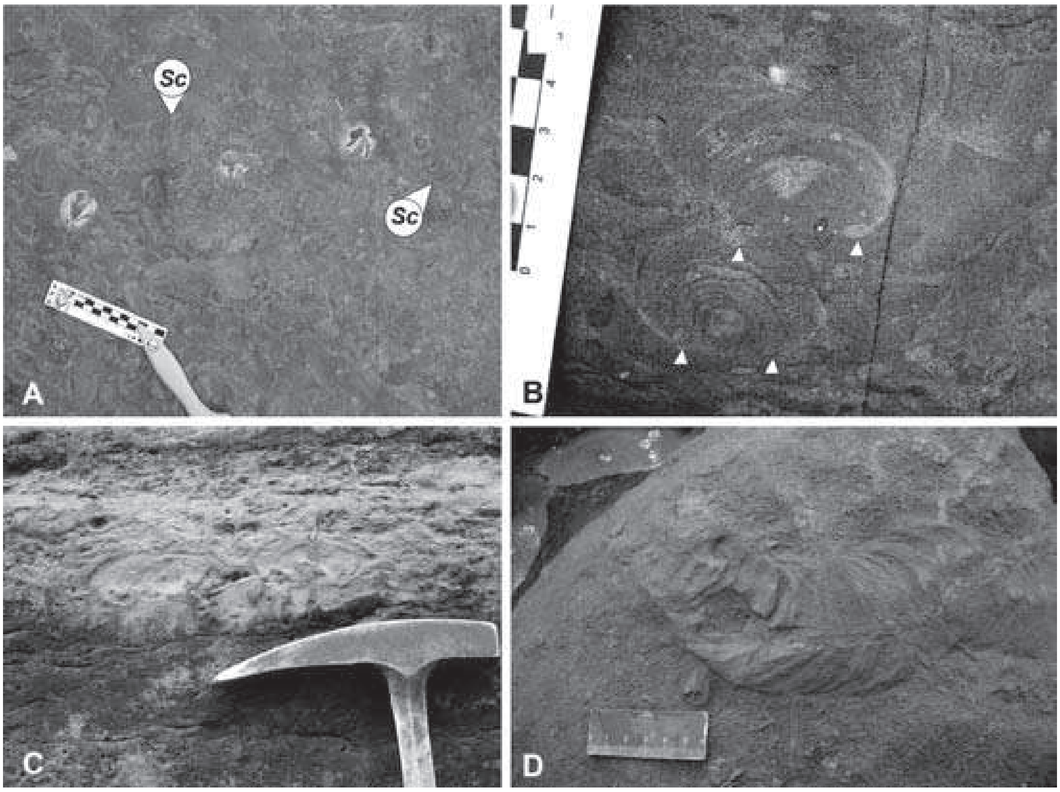

Figure 9. Echinoid structures. A, Bedding plane view of *Scolicia* specimens associated with the body fossils of their tracemakers, Chenque Formation; B, cross section view of two specimens of *Scolicia*, showing the drain channels at the base of these structures (white arrows), Chenque Formation; C, cross section view of *Scolicia* specimens, Monte León Formation; D, bedding plane view of *Scolicia*, Monte León Formation. Scale in C: 15 cm long (hammer head).

In addition, information of dinoflagellate associations in the studied deposits (e.g., the Rio Negro Formation, Guler, 2003; Guerstein *et al.*, 2010, and the Monte León Formation, Guerstein, pers. comm.) reveals the existence of abundant protoperidinacean dinoflagellate cysts. Protoperidinaceans are common in areas with high productivity, being considered thus as good indicators of upwelling processes (Guler, 2003 and references therein). Recent theoretical models indicate that unlike other wind-driven systems, the Patagonian Shelf upwelling is driven by the interaction of the Malvinas Current with the bottom topography (Matano & Palma, 2008). This interaction forces cold nutrient-rich waters to the surface, fertilizes photosynthetic phytoplankton, and sustains a steady high level of biological productivity near the Patagonian Shelf Break Front (Garcia *et al.*, 2008; Lutz *et al.*, 2010). Although the shelf-break is relatively far from the coast, numerical simulations (e.g., Palma *et al.*, 2008) and analysis of in-situ and remote observations (Piola *et al.*, 2010) show that Malvinas waters spread inshore. There is additional evidence that supports the suggestion of important upwelling during the Miocene. For example, the presence of phosphatic deposits in Miocene deposits of Patagonia (Gaiman Formation, Scasso & Castro, 1999), and the occurrence of thick and widespread *Turritella* beds (Windhausen, 1924; Bellosi, 1987) in the lower sequences of the Chenque Formation. In modern seas, turriteline gastropods occur primarily in areas of cool, nutrient-rich waters commonly associated with upwelling (Allmon, 1988; Jones & Allmon, 1995).

The primary productivity of coastal upwelling areas represents 90% of the primary production worldwide (Nelson *et al.*, 1995). In the Patagonian Shelf, the nutrient-rich Malvinas waters sustain a marine ecosystem with a productivity rate larger than 300 gC/m^2/yr (Acha *et al.*, 2004; Heileman, 2009). In a recent paper, Suto *et al.* (2012) explored the idea that eutrophication not only increased the abundance of primary producers, but it also promotes the increment of zooplankton and large predators, and thus, can stimulate evolutionary diversification events among marine organisms. These authors stated that after the Eocene–Oligocene boundary, with the opening of the Drake Passage, several oceanic environmental fluctuations, such as the overall cooling of the planet, may have acted as evolutionary triggers for the marine biota (Suto *et al.*, 2012). The high complexity recorded for the Miocene infaunal communities of Patagonia could be clearly reflecting the changes on marine organisms promoted by changes in paleoceanographic circulation after the Oligocene.

Evolutionary context

During the Mesozoic, the development of the Modern Evolutionary Fauna led to important ecological changes in marine communities (Sepkoski, 1990). Some of these changes involved the acquisition of additional ecologic guilds that were not present in the Cambrian and Paleozoic Evolutionary Faunas, particularly with respect to the exploitation of the deep infaunal ecospace (Thayer, 1983; Bambach, 1983; Sepkoski, 1990). The Modern Evolutionary Fauna is dominated by mollusks, crustaceans, and echinoids, as the main benthic organisms (Sepkoski, 1981). Interestingly, these are the same groups that were identified as the dominant trace-makers in the studied Neogene deposits from Patagonia (see section above; Most common bioturbators and tiering structure). Thus, the establishment of the Modern Evolutionary Fauna is clearly reflected by this ichnologic record.

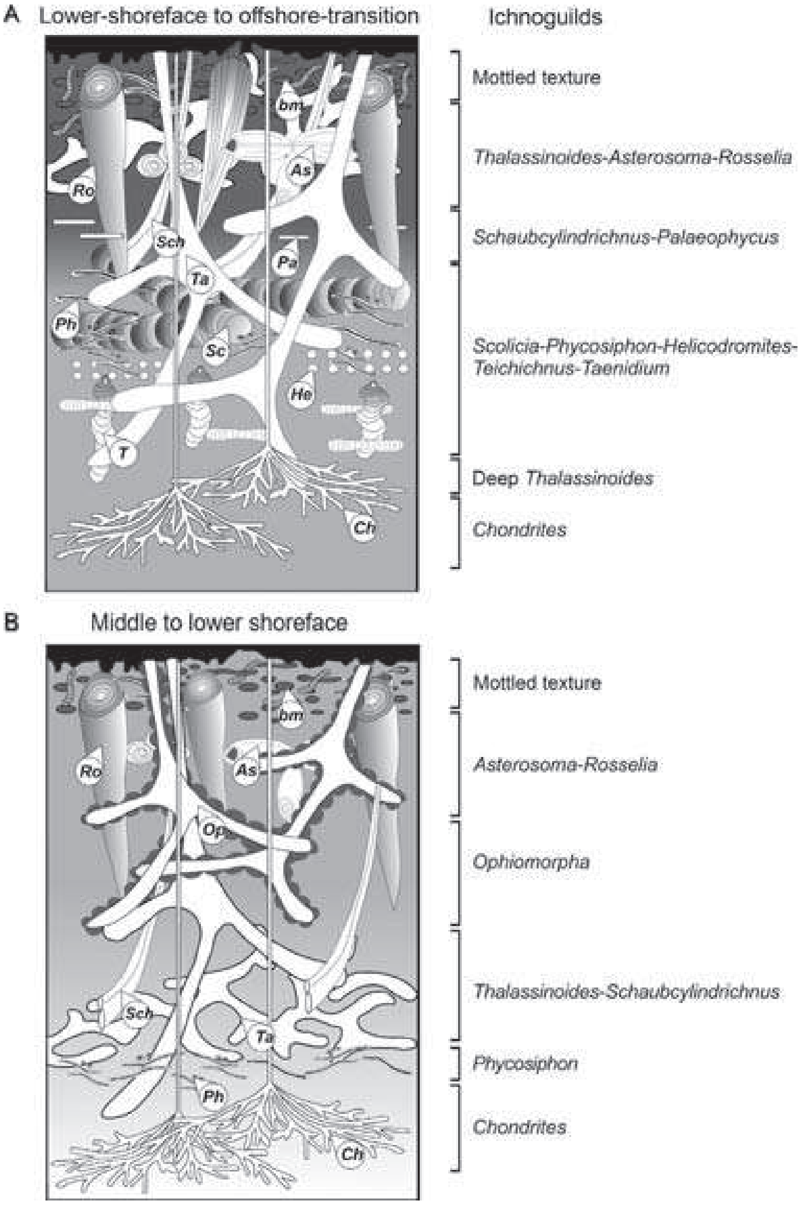

Figure 10. Tiering structures and ichnoguilds of lower-shoreface to offshore-transition deposits (A) and lower-shoreface deposits (B) from the Chenque Formation.

The complex tiering structure deciphered from this analysis seems also to reflect the major reorganization of the shallow-marine benthic communities that occurred due to the Mesozoic marine revolution, during which predation rates increased substantially (Vermeij, 1977, 1987; Thayer, 1983; Aberhan *et al.*, 2006), particularly with the evolution of homarid and palinurid lobsters, malacostracan crustaceans, opistobranch gastropods, and asteroid starfishes, among others (Bambach, 2002; Aberhan *et al.*, 2006). Coupled with this increment in predation rates, there is a marked increase in the intensity and depth of bioturbation from the Mesozoic onwards (see for example Kidwell & Brenchley, 1996). Sediment feeders produce the resuspension of the bottom sediment, clogging the filter apparatus of suspension-feeder organisms, excluding them from the benthic community (Aberhan *et al.*, 2006). Analysis of changes in the nature of bedding and storm stratification also reveals that sediment homogenization is much more common during the Mesozoic and Cenozoic than in the Paleozoic (Sepkoski *et al.*, 1991; Aberhan *et al.*, 2006). These two characteristics (exclusion of the suspension-feeders and complete homogenization of the substrate) are clearly seen in the Neogene shallow-marine deposits of Patagonia. In addition, the complex tiering structure recorded reflects a higher partitioning of the infaunal niche and represents a departure with respect to Mesozoic and Paleogene ichnofaunas in siliciclastic settings, being only equivalent to the tiering structure documented for Cretaceous chalk of northern Europe (Ekdale & Bromley, 1984) and southern United States (Frey & Bromley, 1985).

Finally, this study suggests that from a global perspective, the Miocene may represent a pivotal moment in the evolution of shallow-marine infaunal communities, coupled with the local influence of the paleoceanographic circulation established after the Oligocene that may have promoted innovations in the benthic marine communities of Patagonia.

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ICHNOLOGY OF CUBA:
PRESENT STATE OF KNOWLEDGE

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ABSTRACT

Works on Cuban ichnology are rare and ichnofossils are only incidentally mentioned in the literature, usually under general terms. The aims of the present paper are: (i) to review the existing literature on Cuban ichnology up to date, (ii) to present the trace fossil material available in collections, and (iii) to make an evaluation of the perspectives for future studies in the Island. Only few historic studies have been conducted on Cuba mostly focused on Jurassic, Cretaceous and Paleogene marine invertebrate traces. More recently, studies have focused on bioerosion structures and deep sea trace fossils, which are also ichnofossils that are more frequently found in collections stored in research institutions in the island. Thus, these two lines of research offer the main opportunities for the development of ichnological work in Cuba in the near future.

Key words: ichnology, Cuba, collections, bioerosion, deep sea.

INTRODUCTION

Ichnology is a relatively young science, compared to other paleontological and geological disciplines, which has experienced a great development in the last decades. It is considered an interdisciplinary science (Gámez-Vintaned & Liñán, 1996), because (apart from systematic paleontology) it offers important contributions to other fields such as paleoethology, sedimentology or stratigraphy (Meléndez, 1989; Buatois *et al.*, 2002). It provides the only available record for the presence of many organisms in ancient paleoenvironments, particularly soft-bodied taxa, which are of great importance in interpretations of depositional and paleoecological conditions (Fernandes *et al.*, 2007).

In the Caribbean region, there are ichnological studies in several countries, such as Colombia (Domenech *et al.*, 2008), Carriacou (Pickerill *et al.*, 2002), Barbados (Donovan & Harper, 2007), Grand Cayman (Pleydell & Jones,1988) or Puerto Rico (Edinger & Risk, 1994), but they are only extensive in Jamaica where several geologic formations have been studied (e.g., Pickerill *et al.*, 1992, 1993, 1998; Donovan, 2002; Donovan & Pickerill, 2003; Donovan & Harper, 2007; Donovan *et al.*, 2001; Blissett & Pickerill, 2004).

There are few studies on ichnofossils in Cuba and contributions to this science are rare. Although trace fossil from Cuba are mentioned in the literature, those reports are usually very superficial and general and even ambiguous terms are used, such as “bioglifos”, “jeroglifos”, “huellas”, “channels”, “bioturbación” or “bioerosión” structures without an in-depth ichnotaxonomic treatment (e.g., Jakus, 1983; Albear & Iturralde-Vinent, 1985; Pszczółkowski, 1987, Rojas-Consuegra, 1999).

In the last years, a limited number of preliminary papers have been published, more focused on ichnologic topics and using a more modern approach to ichnology (Rojas-Consuegra & Villegas-Martín, 2009; Villegas-Martín & Rojas-Consuegra, 2008, 2010, 2011; Villegas-Martín, 2009; Villegas-Martín *et al.*, 2011). Current and future progress in studies in Cuba will supply further evidence for the reconstruction of ancient environments in the archipelago and its geological history.

The objectives of this work are: (i) to provide a compendium of the state of the knowledge of Cuban ichnology, (ii) to introduce the Cuban trace fossil material available in collections, and (iii) to discuss perspectives for future studies in the Island.

Biodeposition structures are not included in this paper, although some work on vertebrate coprolites have been published, in most cases, limited at the superficial description (form and dimensions) of the sample (Arredondo & Villavicencio, 2004; Jiménez Vásquez *et al.*, 2005).

AN OVERVIEW OF THE EXISTING LITERATURE ON THE CUBAN ICHNOLOGY

Invertebrate ichnology

Concerning invertebrate ichnofossils, a pioneering paper on ichnotaxonomy was published by Bröniman and Rigassi (1963). These authors, in a study conducted on the geology and paleontology of the city of Havana and surrounding towns, identified traces related to *Chondrites* Sternberg, 1833 in limestones and sandy lutite intercalations of the Capdevila Formation (Eocene) from Artemisa Province in western Cuba (Table 1). More recently, Segura-Soto (1990) dealt with the ethological classification of invertebrate ichnofossils.

Among those initial papers that mention ichnofossils, the most important one is probably that by Rojas-Consuegra (2004), who recorded structures on shells of some rudist species from the Cretaceous Jimaguayú Formation. Later, López-Martínez (2006) also reported bioerosion structures on gastropods from the Miocene Lagunitas Formation. He interpreted them as a consequence of the boring activity of balanid crustaceans.

At this stage of knowledge, the Polish geologist Pszczółkowski (2002) published a paper that may be considered the "real pioneering work" of the Cuban ichnology. Pszczółkowski studied the Cretaceous Vaquería Formation (Upper Maastrichtian) from central Cuba and described predominantly horizontal fossil galleries in marls, 30-50 cm long, displaying T-shaped branching, with circular or elipsoidals cross section, which he identified as belonging to the ichnogenus *Thalassinoides* Ehrenberg, 1944. Lately, Pszczółkowski and Myczyński (2009), in a study of the Guasasa Formation (Tumbitas Member) from the Jurassic of western Cuba, reported

Table 1. Synthesis of the ichnofossils identified in Cuban deposits.

Ichnogenus	Formation	Age	Reference
Chondrites *Planolites*	Guasasa	Jurassic	Pszczółkowski & Myczyński, 2009
Thalassinoides *Chondrites*	Vaquería Provincial	Cretaceous	Pszczołkowski, 2002 Villegas-Martín *et al.*, 2011
Teredolites	Peñalver	K-Pg boundary	Villegas-Martín & Rojas-Consuegra, 2011
Chondrites *Scolicia* *Planolites* *?Psammichnites* *Taenidium* *Helminthorhaphe* *Cosmorhaphe*	Capdevila	Eocene	Bröniman & Rigassi, 1963 Villegas-Martín & Rojas-Consuegra, 2010
?Ophiomorpha *Cosmorhaphe* *Entobia* *?Planolites*	Vertientes	Eocene	Villegas-Martín & Rojas-Consuegra, 2010 Menéndez-Peñate *et al.*, 2011
Entobia *Oichnus* *Centrichnus*	Lateritic sediments	Miocene	Villegas-Martín, 2009

different types of horizontal galleries in limestones, which were identified as *Chondrites* Sternberg, 1833 and *Planolites* Nicholson, 1873.

Thus, until very recently, most significant contributions on Cuban ichnofossils were done by foreign researches working in the Island. Nevertheless, in the past few years, the interest for trace fossils has raised and a series of preliminary studies have been carried out by the author of this contribution and collaborators, which are revealing the potential for ichnological work in Cuba. Thus, Villegas-Martín (2009) identified bioerosion structures in Miocene gastropod and bivalve shells redeposited in lateritic sediments of Moa, eastern Cuba, including the ichnogenera *Entobia* Bronn, 1837,?*Oichnus* Bromley, 1981, and *Centrichnus* Bromley & Martinell, 1991 (Figure 1), in Miocene gastropod and bivalve shells redeposited in lateritic sediments of Moa, eastern Cuba. A later revision revealed that the trace assigned to *Centrichnus* (Figure 1A) actually corresponds to *Caulostrepsis* Bromley and D' Alessandro, 1983 (Gibert, pers. comm., 2011). Also, a relatively diverse assemblage of bioturbation structures was recognized in the sandy turbidites of the Eocene Capdevila and Vertientes formations (Villegas-Martín & Rojas-Consuegra, 2010). Trace fossils were assigned to *Scolicia* Quatrefagues, 1849, *Planolites* Nicholson, 1873, ?*Ophiomorpha* Lundgren, 1891, *Cosmorhaphe* Fuchs, 1895, *Helmintorhaphe* Seilacher, 1977, ?*Psammichnites* Torell, 1870, and *Taenidium* Heer, 1877 (Figure 2). Later revision revealed that the trace assigned to ?*Psammichnites* actually could correspond to a preservation variant of *Scolicia*.

Work in other turbiditic formations allowed to report *Chondrites* Sternberg, 1833 (Figure 3) in the Cretaceous (Provincial Formation) and the Paleogene (Nazareno Formation) (Villegas-Martín *et al*., 2011). Menéndez-Peñate *et al.* (2011) in a paleontological study of the basal turbidite in the Vertientes Formation from the Paleogene of Ciego de Avila (central Cuba), identified bioerosion structures on a lithoclast, related to *Entobia* isp. and one horizontal gallery in sandstones related to ?*Planolites* isp.

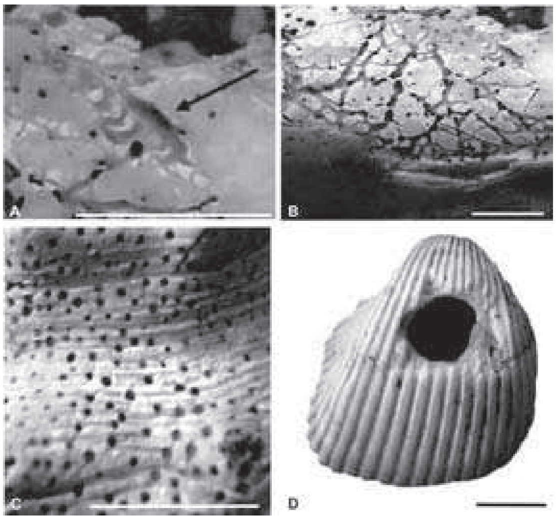

Figure 1. Bioerosion structures recorded in the lateritic sediments (from Villegas-Martín, 2009). A, *Centrichnus* isp.; B-C, *Entobia* isp.; D, *Oichnus* isp. Scale bars: 10 mm.

Finally, Villegas-Martín and Rojas-Consuegra (2011) analyzed the significance of the presence of two ichnospecies of bivalve borings (*Teredolites clavatus* Leymerie, 1842 and *T. longissimus* Kelly & Bromley, 1984) on wood fragments found in a megablock made up by sandstones and lutites included in the Cretaceous–Paleogene boundary (K/Pg) deposits of the Peñalver Formation in western Cuba (Figure 4).

Vertebrate ichnology

Vertebrate ichnology in Cuba has received even less attention than invertebrate trace fossils. Only two general mentions in the literature are known. The first, and also the oldest report of trace fossils in the Island, was provided by Fernándes de Castro (1864) who interpreted them as casts of the claws of the Cuban sloth *Megalocnus rodens* (Quaternary) in limestones in a cave in San Antonio de Los Baños, Artemisa Province, western Cuba. This material was also reported by de la Torre (1910), who figured some specimens (Figure 5). A more recent report was made by Rojas-Consuegra (1999), who found footprints produced by vertebrates in volcanomictic sandstones of the Contramaestre Formation (Cretaceous) in Sierra de Najasa (western Cuba). In both cases, additional material and studies are needed to evaluate the validity of the findings.

CUBAN TRACE FOSSILS IN COLLECTIONS

Only a few collections in Cuba include ichnofossils today. The existing material is the result of collateral collection carried out as part of geologic and paleontologic expeditions. These ichnological specimens are stored in the collections of the *Museo Nacional de Historia Natural de Cuba* (MNHNC) and the *Instituto de Geología y Paleontología* (IGP) at La Habana, the *Museo de Arqueología*, Sagua la Grande (*Arqueocentro*) in Villa Clara Province, central Cuba, and the *Museo de Geología de la Universidad de Moa*, Holguin Province, in eastern Cuba. The material catalogued as trace fossils in those institutions is limited, but further exploration of the collections will probably increase the number of the ichnological specimens.

At the MNHNC collections, trace fossils are derived from Jurassic, Cretaceous, and Paleogene units. Jurassic and Cretaceous specimens are mostly bioerosion structures found on xylic (wood) and skeletal

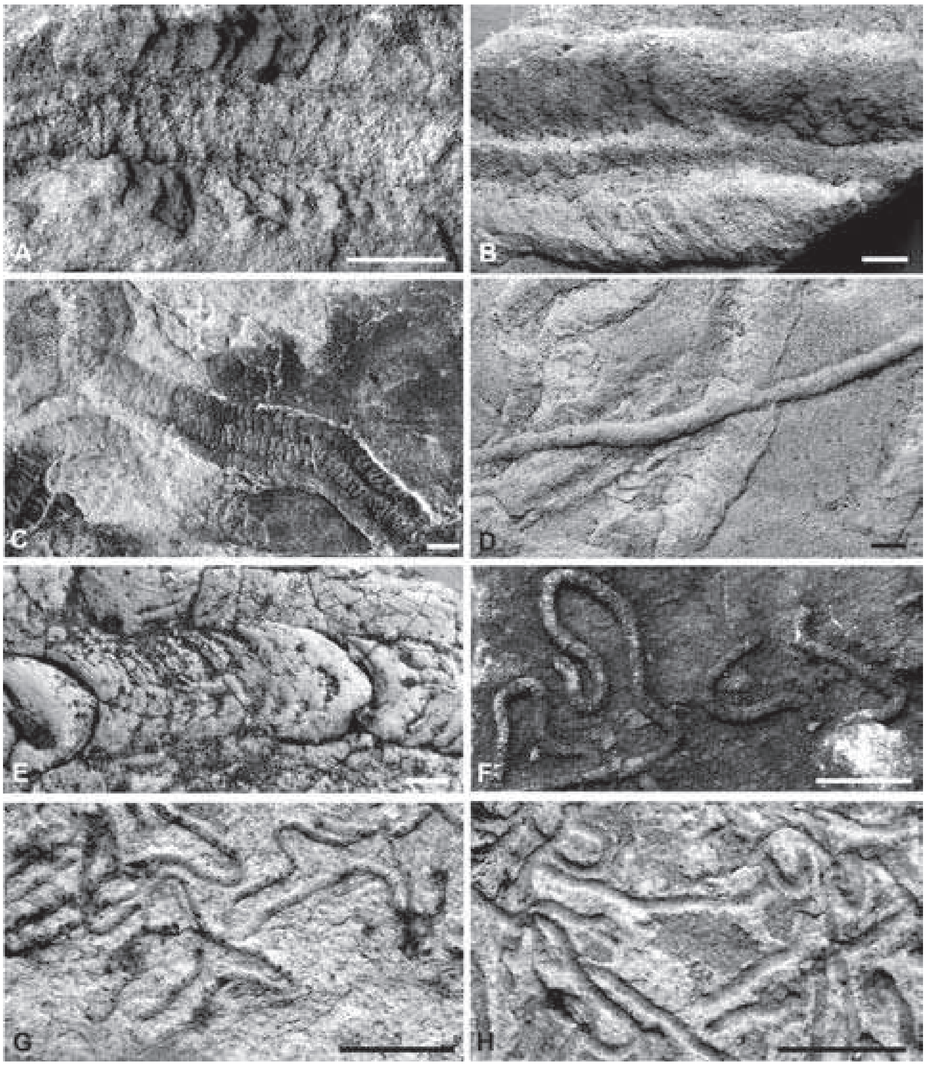

Figure 2. Trace fossils from sandy turbidites of the Eocene Capdevila and Vertientes formations (from Villegas-Martín & Rojas-Consuegra, 2010). A-B, *Scolicia* isp.; C, *Scolicia prisca*; D, *Planolites* isp. and ?*Psammichnites* isp. (probably *Scolicia* isp.); E, *Taenidium* isp.; F-G, *Cosmorhaphe* isp.; H, ?*Ophiomorpha* isp. Scale bars: 10 mm.

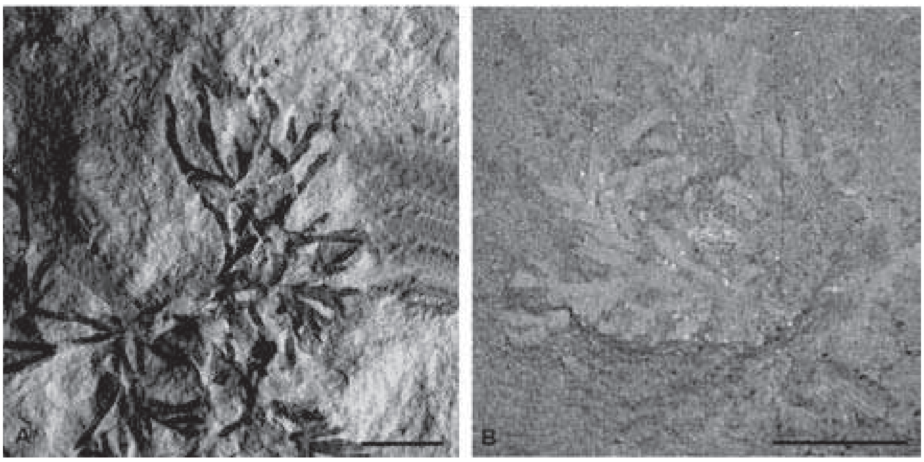

Figure 3. Galleries assigned to *Chondrites* isp. in the Nazareno Formation from the Paleogene (A) and the Cretaceous Provincial Formation (B) (after Villegas-Martín & Rojas-Consuegra, 2011). Scale bars: 10 mm.

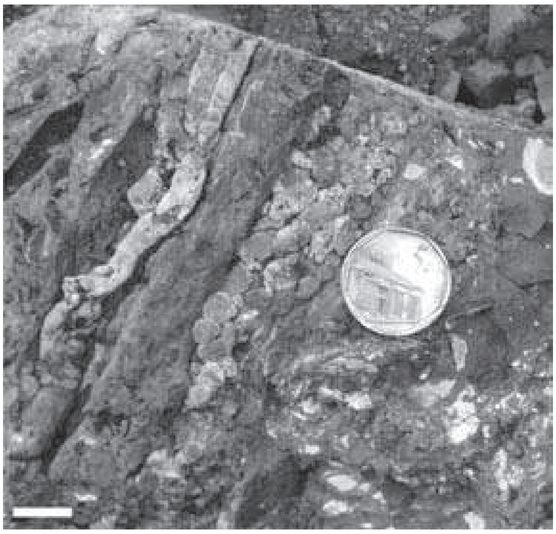

Figure 4. Wood borings assigned to the ichnogenus *Teredolites* in deposits of the Peñalver Formation (modified from Villegas-Martín & Rojas-Consuegra, 2011). Scale bar: 10 mm.

Figure 5. Record made by de la Torre (1910) of the structures preserved in limestones and assigned to the claw impression of the Cuban sloth *Megalocnus rodens* in a cave in San Antonio de Los Baños, western Cuba (modified from Carlos de la Torre, 1910).

(shells) substrates coming from coastal marine settings, predominantly borings in rudist of the Jimaguayú Formation (Cretaceous). Meanwhile, Paleogene ichnofossils are bioturbation traces, including horizontal locomotion and feeding structures and graphoglyptids, preserved on sandstones and mudstones, of the Capdevila and Vertientes formations. These trace fossils are typical elements of the *Nereites* ichnofacies (Seilacher, 1967) and come from sedimentary units interpreted as deposited in deep sea fans with turbiditic sedimentation. Nowadays, the collection at the MNHN is the one that contains more ichnological specimens in Cuba, and part of these materials has been studied in recent works (Villegas-Martín & Rojas-Consuegra, 2008, 2010, 2011; Rojas-Consuegra & Villegas-Martín, 2009, Villegas-Martín *et al.*, 2011). There is also additional material not yet studied in the collection.

The material from IGP and *Arqueocentro* is yet poorly known. The collection at *Arqueocentro* is constituted by a small number of samples of rocks from the Paleogene Ranchuelo Formation with horizontal bioturbation structures, most of them produced by the locomotion of invertebrates in a muddy substrate.

Collections at the Museo de Geología of the Universidad de Moa are also limited, with only a few ichnological specimens known. These are bioerosion traces occurring on Neogene bivalve and gastropod shells (Villegas-Martín, 2009).

FUTURE PERSPECTIVES

The almost complete lack of studies devoted to the trace fossils of Cuba, together with the extensive Mesozoic and Cenozoic stratigraphic record, offer an excellent opportunity for the future development of ichnology, which should help in contributing to decipher the complex geologic and paleobiologic history of this area of the Caribbean. The review of existing literature and ichnological material currently stored in collections allows foreseeing which will be the most promising lines of ichnological research to be developed in the forthcoming years.

Ichnology of deep marine settings

In Cuba, Cretaceous and Paleogene sedimentary units formed on deep marine settings abound (e.g., Vertientes, Capdevila, Provincial, Nazareno, Santa Clara, Ancón formations). Material from collections demonstrates that trace fossils are a common feature in, at least, some of these formations (Provincial, Nazareno, Vertientes and Capdevila). Preliminary results provide a hint about the potential information that can be obtained in the island from the study of the ichnofauna of these deposits. The existence of trace fossils in both Cretaceous and Tertiary units suggests that it could be possible to analyze how ichnoassemblages change through the K/T boundary in a region located close to the alleged meteor impact area. In Cuba, the K/T boundary deposits have already been studied (e.g., Alegret *et al.*, 2005; Goto *et al.*, 2008; Yamamoto *et al.*, 2010) and possible bioturbation structures have been reported from the top layers of these deposits at localities such as Loma Capiro, Villa Clara Province, Central Cuba, and Cantera Victoria I, western Cuba (Rojas-Consuegra, pers. comm., 2011).

Bioerosion

Bioerosion (either chemical or mechanical) is an important mechanism for a variety of marine invertebrates inhabiting or exploiting hard substrates, and its study in the fossil record provides interesting paleocological and paleoenvironmental information. In Cuba, there are important collections of invertebrate shells (mollusks and other groups) and wood, but they have never been studied from the point of view of substrates for boring organisms. Nevertheless, preliminary revision of such material has revealed common bioerosion trace fossils. As mentioned previously, borings are known from Cretaceous rudists and Neogene bivalves and gastropods. Meanwhile, borings in wood fragments from the Jurassic and Cretaceous have also been identified. These general observations and data are the basis for future studies on bioerosion.

FINAL REMARKS

Most records of Cuban ichnofossils in the literature are referred by either ambiguous (or general) terms such as "bioglifos", "jeroglifos", "huellas", "channels", "bioturbación" or "bioerosión" structures . Among published references to ichnofossils, invertebrate traces are much more frequent than those of vertebrates. In the former group, there are some important but restricted studies in which traces have been referred to the ichnogenera *Chondrites* (Capdevila Formation, Eocene), *Thalassinoides* (Vaquería Formation, Eocene), and *Chondrites* and *Planolites* (Guasasa Formation, Jurassic).

In recent years, studies have identified the ichnogenera *Scolicia*, *Planolites*, *Taenidium*, *Cosmorhaphe*, *Helmintorhaphe*, ?*Ophiomorpha*, ?*Psammichnites* (Capdevila and Vertientes formations, Eocene), and *Chondrites* (Nazareno Formantion, Eocene and Provincial Formation, Cretaceous). Also, different bioerosion structures were recognized, in mollusks (*Entobia*, *Oichnus* and *Centrichnus* in Miocene laterites), lithoclast (*Entobia* in the Vertientes Formation), and wood (*Teredolites* in the Peñalver Formation, K-T boundary). Vertebrate traces are poorly known. The most significant record is that of an alleged cast of the claws assigned to the Quaternary sloth *Megalocnus rodens* from a cave in San Antonio de Los Baños, Artemisa Province.

Ichnofossil material is scarce in Cuban collections, being only found at collections of the *Museo Nacional de Historia Natural de Cuba* (MNHN), *Instituto de Geología y Paleontología* (IGP), *Arqueocentro* and *Universidad de Moa*. The collection at the MNHN stores the most important ichnological collection.

The limited interest in trace fossils until now allows to foretell an important development of this discipline in Cuba for the near future. Revision of literature and collections provide the basis to evaluate the most promising lines of investigation: ichnology of deep marine sediments and bioerosion in coastal mineral and xylic substrates.

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COPROLITE OCCURRENCES IN LATIN AMERICA

Paulo Roberto Figueiredo Souto

ABSTRACT

Coprolites have been found and described in the scientific literature since the last century. The traditional paleontological approach focused on description of the material and identification of the producer has changed to a more applied approach in recent years. The analysis of morphology and microstructure of the coprolites has allowed the understanding of a number of questions related to the behavior, physiology and environment of various species of extinct animals, such as predation, parasitism and nesting. The main goal of this study is to provide a brief historical overview, to elucidate some important descriptive aspects, to comment on new methods for studying coprolites, and to provide a general evaluation of the morphological characteristics of vertebrate's coprolites found in different localities, ages and lithologic units in Latin America.

Key words: Andean America, Brazil, ichnology, vertebrate coprolite, human coprolite.

INTRODUCTION

The first description of coprolites in the seventeenth century occurred in 1678 by naturalist Martin Lister (El-Baz, 1968). However, the first official study of the coprolites nature was established only in the nineteenth century by Buckland (1829a) for coprolites from the Lower Jurassic of the south coast of England. Häntzschel *et al.* (1968) conducted a literature review containing about 200 works on many different aspects of coprolites of vertebrates and invertebrates of different ages and origins.

The diverse fossilized food wastes are classified in general as bromalites (from the Greek *brom*: food preserved within or expelled by oral or anal opening). These residues are differentiated with regard to their origin as coprolites, cololites, regurgitolites and urolites (Hunt, 1992). However, the paleoichnological research has focused on integrating trace fossils within a sedimentological and stratigraphical approach since the 1980s, mostly based on the classification of invertebrate trace fossils. Most of paleoichnological studies of continental systems were restricted to dinosaur tracks until the beginning of the 1990s (Lockley, 1991).

The increasing importance on the study of coprolites has also reinforced its significance in paleoparasitologic studies of different vertebrate species situated between 3,700 and 2,500 years B.P. These studies have systematiccaly allowed the investigation of parasites occurrence in coprolites, contributing to the knowledge of the evolution of the host-parasite relationships (Vanzolini & Ab'Saber, 1968; Scott, 1987; Ferreira *et al.*, 1980). This type of information has permitted to understand how the life has adapted over the environmental changes and clarify the reasons that resulted in the extinction of many species due to ecological changes.

NOMENCLATURE

The term coprolite comes from the Greek *kopra*: copro and *litho*: stone, and it has been used specifically to designate any excrement that is petrified or mummified and was eliminated by the anal opening (Buckland, 1829b), being restricted to dung fossils produced by vertebrates and macroinvertebrates. According to Thulborn (1991), fossil feces produced by microinvertebrates and having less than a millimeter length are identified as microcoprolites. This term avoids the term fecal pellet that frequently is associated with morphology rather than with the producer organism. In the case of liquefied coprolites produced by sea birds and bats, it is used a word of the Quechua Indians, the term guano (*huanu*) that is used to classify excrement deposits produced by these animals (Hutchinson, 1950).

Proposed by Agassiz (1833), the term cololite (enterolite) is used in the identification of fossilized excrements preserved inside the digestive tract of vertebrates and invertebrates (Pollard, 1990). The material ejected by the mouth cavity, originated in the gastrointestinal tract and subsequently fossilized, is called regurgitolite (McAllister, 1988). Very difficult to identify in the fossil record and more frequent in Quaternary sediments, regurgitolites are usually associated with fish, sharks, snakes and rapitorial birds (Korth, 1979).

The term urolith means petrified urine and it was first applied by Duvernoy (1844) in France to describe liquid excretions produced by lizards. Residues preserved in sediments of the Triassic in Germany, associated with ichthyosaurs, and of the Late Cretaceous, attributed to reptiles, were also classified as uroliths (Leydig, 1896; Voigt, 1960). However, in the New World, only at the beginning of this century the first large impressions produced by the extrusion of liquid material preserved in the Mesozoic sediment was found and associated to the dinosaurs in the Morrison Formation in the United States (McCarville & Bishop, 2002) and in the Botucatu Formation in the Brazil (Fernandes *et al.*, 2004).

The coprolites are a consequence of the presence of heterotrophic activity in the environment and are recorded since the early Paleozoic. The coprolites from the Silurian have been collected in the United States (Branner & Newson, 1902), Iceland (Gilmore, 1992), Australia (Öpik, 1953) and Canada (Logan & Hunt, 1954). Spiral coprolites are mostly known from the Carboniferous-Permian interval (Buckland, 1829a,b; Johnson, 1934; Neuymayer, 1904; Waterston *et al.*, 1985; Ragonha, 1987; Hunt *et al.* 1998). These remains are fossilized feces associated with earlier stages of vertebrate evolution and produced by the first large marine invertebrates and primitive fishes.

The first large coprolites deposited in terrestrial environments were produced by mammal-like reptiles. They were found in sediments of the Permian and Triassic from different areas, including the Beaufort Group in South Africa (Smith, 1996) and Chinle Group in the United States (Hunt *et al.*, 1998). From the Jurassic to the Cretaceous , most coprolites are attributed to dinosaurs and they are present in continental ecosystems in different locations (Bertrand, 1903; Matley, 1939; Chin, 1990).

After the extinction of some faunas at the end of the Cretaceous, large coprolites are associated with the presence of Cenozoic mammals. For the occurrence of coprolites of Tertiary age there are numerous specimen descriptions, such as those found in the Oligocene White River Group (Vogeltantz, 1967) and the Eocene Golden Valley Formation (Jepsen, 1963), both in the United States. The coprolites recorded from Quaternary sediments are relatively frequent in environments associated with caves and glaciers due to more favorable conditions of preservation (e.g., Scott, 1987).

Although the ichnotaxonomy used for some authors (Hunt *et al.*, 1998; Hunt & Lucas, 2007; Buchs *et al.,* 2009), the binomial system of nomenclature for coprolites is considered inappropriate by others, because the variability of shapes and patterns of fecal similarities make it difficult to associate them with their producers. The criteria frequently used for the classification of coprolites consist of applying a parataxonomy based on the description of the morphology, morphometric analysis, the organic inclusions associated with the material and, if possible, the relationship with the fossil assemblage. These factors determine the way in which coprolites are differentiated and then grouped, according to their formation processes, into distinct morphotypes: cylindrical, ovoid, conical, spiral and liquefied shapes (Figure 1).

CLASSIFICATION AND ANALYSIS

Morphology

The characterization of the coprolite morphology is based on measurements of thickness, length, weight and density, according to the criteria proposed by Amstutz (1958), Thulborn (1991) and Hunt *et al.* (1994). The diagnosis and identification of surface ornamentation and impressions resulting from the evacuation process are also essential elements in biological and taphonomic interpretation.

The description of the coprolites involves the observation of the morphology (e.g., shape and ornamentation) and morphometry (length, thickness, weight and density), which form the basis for the description of a sample. In the case of thickness, a measure of

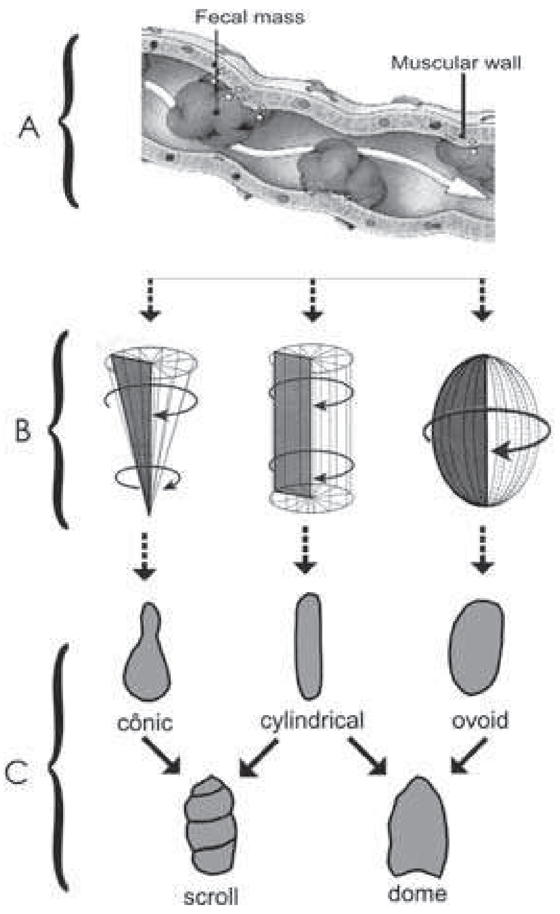

Figure 1. Coprogenesis. A, longitudinal section of intestinal tract with fecal mass flux; B, kinds of food transit and compaction flux; C, patterns of fecal shapes.

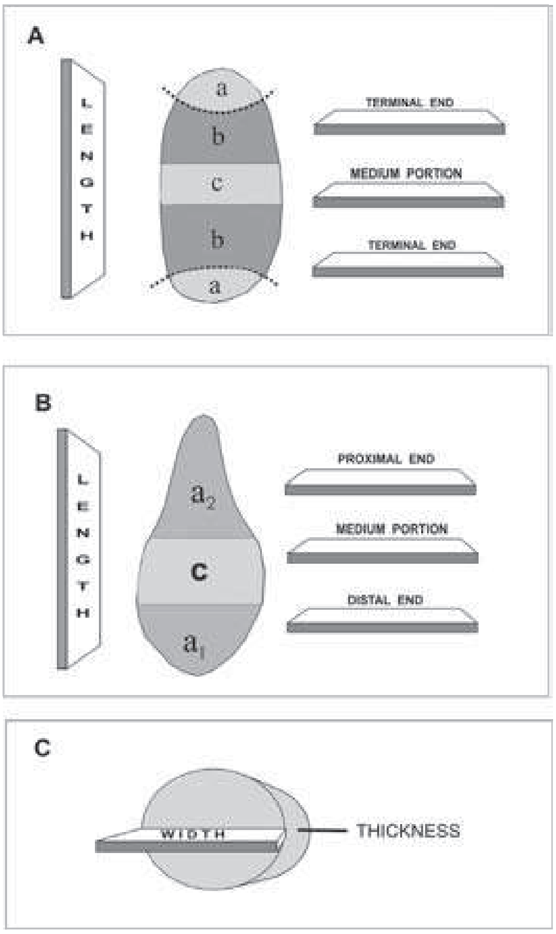

Figure 2. Fecal structure. A, isopolar form; B, anisopolar form; C, transversal section.

the circumference should be estimated by the ratio between the diameter and radius of a line segment. In some cases, the average between the major and minor radius from the center also provides information about the elasticity of the intestinal tube of the producer. The comparative study with recent feces also provides elements that help identify the characteristics found in fossil specimens (Chame, 2003).

In the morphological description, the analysis provides important diagnostic features of the extremities, mainly because the structures can be classified according to the type of polarity as isopolar (same ends) or anisopolar (different ends). This last term was proposed by Thulborn (1991) to replace the term heteropolar (Figure 2). These allow the differentiation of the excrement. According to the sequence of evacuation, they are known as distal portion (the initial portion expelled) and proximal portion (the last portion expelled) and therefore they provide information about physical aspects relating to consistency and dung deposition.

The deformations in the terminal portions resulting from the fecal mass extrusion mechanism can be preserved on the surface as types of deformations that help in external characterization. These marks can be folded, resulting in ornaments with a pin shape and concave deformations. The grooves caused by the action of muscles are found along the surface in a longitudinal or transverse direction, and may be dispersed throughout the coprolite or concentrated in the extremities. However, grooves in coprolites from newborn individuals hardly occur due to the liquefied consistency, because the anal muscle is not completely formed so urine and defecation occur simultaneously and automatically.

Externally, on the surface of the coprolites may be preserved patterns of marks caused by the volatilization of fluid (carbon dioxide and methane) that exists within the fecal mass as a result of environmental conditions where they were deposited. These marks can be classified into desiccation cracks, characterized by deep cracks due to exposure and dry surface under conditions of arid climate; and syneresis cracks, characterized by many branches around the structure, indicating deposition under aqueous conditions, in wet climate. Also, changes may occur in the mechanical structure of the coprolite after the defecation act, such as compression (impact) and load flow (curving) of the structure (Hunt *et al.*, 1994; Antunes *et al.*, 2006). The excrements in nature are a rich source of nutrients, being rapidly degraded by bacterial activity, fungal and insectivorous (Putman, 1984). In terms of diagenesis, they can be absorbed by the atmosphere and compressed or permineralized (Häntzschel *et al.*, 1968). However, the chemical composition is an important factor in preserving the structure of the coprolite and it depends of the producer's diet. Edwards (1973) suggests that the calcium phosphate is present in feces of carnivore and it acts as an agent which potentiates the permineralization of the structure. In addition, the silicification is a favorable factor in the preservation of the structure due to the ingestion of hard parts of plants and it contributes to the solidification of herbivores coprolites (Rodriguez de la Rosa *et al.*, 1998; Chin, 1990).

Chemical analysis

The state of lithified coprolites requires the use of an appropriate methodology to study them and to reduce the irreversible loss of material. Priority is given to non-invasive techniques that allow the obtainment of more information. The analysis involves the chemical composition of the internal structure and it is performed by radiologic procedures of x-ray diffraction (Sawyer, 1981; Castro *et al.,* 1988), x-ray fluorescence (Edwards, 1973; Fikentscher, 1933) and infrared spectroscopy (Hallgren, 1987). These radiometric methods of quantitative and qualitative analysis are highly precise and they process a large number of samples in a short time using the same calibration parameters. The chromatographic procedures can also be used for analysis of organic molecules (amino acids and proteins) preserved inside of the coprolite (Weber & Lawler, 1978).

COPROLITES IN LATIN AMERICA

Although the study of coprolites in Latin America has increased during the last century, the tendency in the study of the coprolites here has acquired two distinct lines: (i) research of coprolites in the mummified condition of hominid and mammalian megafauna from the end of the Cenozoic that covers most of the occurrences of the Central and Andes regions and (ii) vertebrate coprolites of different ages in Brazil. This trend is the result of research from longstanding of archaeological remains related to developing the paleoparasitology approach to mummified materials and the difficulty of investigating the very lithified materials. However, recent research in Latin America has showed a significant increase in different areas and ages (Figure 3).

Central and Andean areas

Most records of coprolites in the areas of Central America and Andean America are associated primarily with human excrement in mummified remains related to the presence of pre-Columbian populations (Callen, 1967; Patrucco *et al.,* 1983; Ferreira *et al.,* 1988; Aufdereheide *et al.,* 2005). Human coprolites currently provide an expanding array of information about the diet, health, and ecology of prehistoric people in the Americas where there is excellent preservation and intensive archaeological research in Mexico, Chile and Peru. Central and Andean America have potential for more expansive work (Reinhard & Bryant, 1992).

Studies related to non-human coprolites in a petrified condition are scarce in the Central and Andean regions of Latin America. The oldest work published on coprolites in the region was written by Spillmann (1929), which describes mummified excrement of mastodons. Even in the middle of the last century, the work of Rusconi (1947, 1949) describes labyrinthodont coprolites from Triassic sediments preserved in the region of Mendoza, Argentina. After the 1940s no relevant work about coprolites in Latin America was

Figure 3. Main occurrences of coprolites in Latin America.

published with the exception of Royo & Gomez (1960), who described reptiles and mammal coprolites of the Miocene Uranco Formation, in Venezuela. The expansion of the paleontological fieldwork during the end of the twentieth century has motivated the researchers to explore the vast potential of the coprolites, including the behavior inferences and analysis of microbiologic information. The coprolites of the Permo-Triassic period are described in Argentina by Contreras (1995), who said that these specimens were associated with rhynchosaurs preserved in the Ischigualasto Formation, and Mancuso *et al.* (2004), who associated coprolites with fishes, amphibians and reptiles found in the Cuyana Basin. The occurrence of Cretaceous coprolites is best known by the work of Rodriguez de La Rosa *et al.* (1998) who described plant structures preserved inside of the coprolites found in the Cerro del Pueblo Formation in Mexico. Recent works report on coprolites associated with carnivorous mammals in Uruguay from the upper Pleistocene Sopas Formation (Verde & Ubilla, 2002) and in Argentina in the Rio Chico Group (Paleocene-Eocene) southeast of Chubut (Krause *et al.*, 2007) and marsupial predators in the Santa Cruz Formation (Miocene) (Tauber *et al.*, 2007).

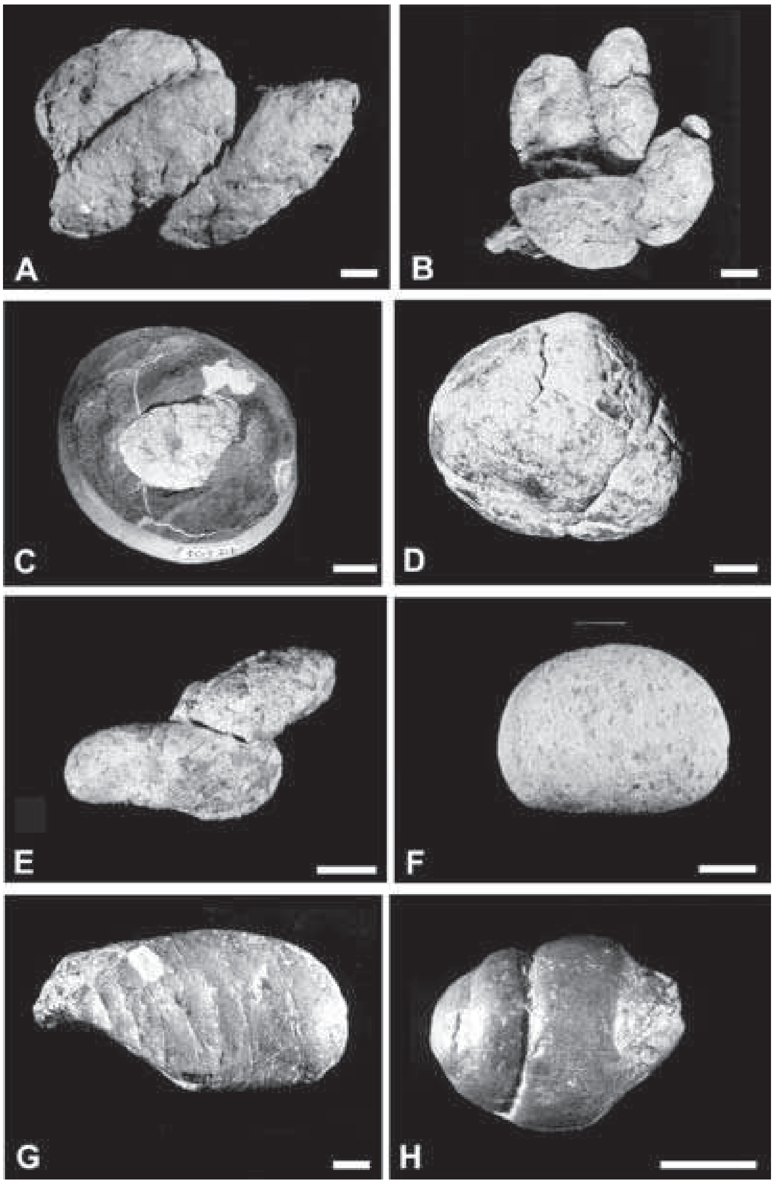

Figure 4. Coprolites associated with Mesozoic sediments in Brazil. A-B, dicinodontosaur coprolites of the Paraná Basin (Middle Triassic); C, fish coprolite from the Araripe Basin (Lower Cretaceous); D, sauropod coprolite of the Paraná Basin (Upper Cretaceous); E, coprolite of crocodilyform of the Bauru Basin (Upper Cretaceous); F, sauropod coprolite from Bauru Basin (Upper Cretaceous); G-H, dinosaur coprolite (G) and cartilaginous fish (H) coprolites from the São Luis Basin (Upper Cretaceous). Scale bars: 10 mm.

Brazilian area

In the Latin America the coprolite occurrences of the Paleozoic are only known in Brazilian rocks, the most representative from the Paraná Basin are coprolites recorded in the Pimenteiras Formation (Middle Devonian) in Goiás State (Ferreira & Fernandes, 1983), two important records of Permian age in the Corumbataí Formation in São Paulo State (Ragonha, 1987) and in the Pedra de Fogo Formation of Piauí State (Souto & Schwanke, 2009), both associated with *Chondrichtyan* fishes of the genus *Xenacanthus*.

Other two occurrences of coprolites are recorded in the Triassic Santa Maria Formation in Rio Grande do Sul State, where they are represented by fecal masses associated with a mammal-like reptile fauna (Souto, 2000); there are also significant occurrences of coprolites from the Cretaceous Santana Formation of the Araripe Basin, Ceará State (Souto, 2002; Viana & Richter, 1998) and from the Alcântara Formation, Maranhão State, at the São Luis Basin (Souto & Medeiros, 2002). The coprolites from the Alcântara Formation are associated with cartilaginous fishes and reptiles, while in the Santana Formation (Araripe Basin) the coprolites are associated almost exclusively with fishes. In the Marilia and Adamantina formations of the Paraná Basin, the coprolites are mainly associated with the crocodyliforms (Nobre *et al.*, 2005; Souto *et al.*, 2005; Brandt Neto *et al.*, 1992; Souto & Magalhães Ribeiro, 1999). The coprolite occurrences are verified in other basins of the Cretaceous as the Alagoas Basin (Maceió Formation) and the Tucano Basin (São Sebastião Formation). Both are well preserved and associated with carnivorous fishes (Figure 4).

During the Cenozoic, the record of vertebrate coprolites is mainly related with the presence of large mammals, birds and fishes. In the Paleogene, there are important occurrences associated with the Paleocene mammals from the São José de Itaboraí Basin (Souto, 2007) and, from the Oligocene of the Taubaté Basin (Castro *et al.*, 1988), the occurrences are associated with fishes and carnivorous birds from the Solimões Formation (Costa & Costa, 1988). During the Neogene, coprolites are present in Rio Grande do Sul State (Kerber & Oliver, 2008) associated with megateriid sloths, cats, horses and glyptodonts from the Touro Passo Formation. From the Holocene, mummified human and animal coprolites are described from the caves of Minas Gerais and Parnaíba regions. In Pernambuco State (Araujo *et al.*, 1984) samples were used in the study of paleoparasitology (Figure 5).

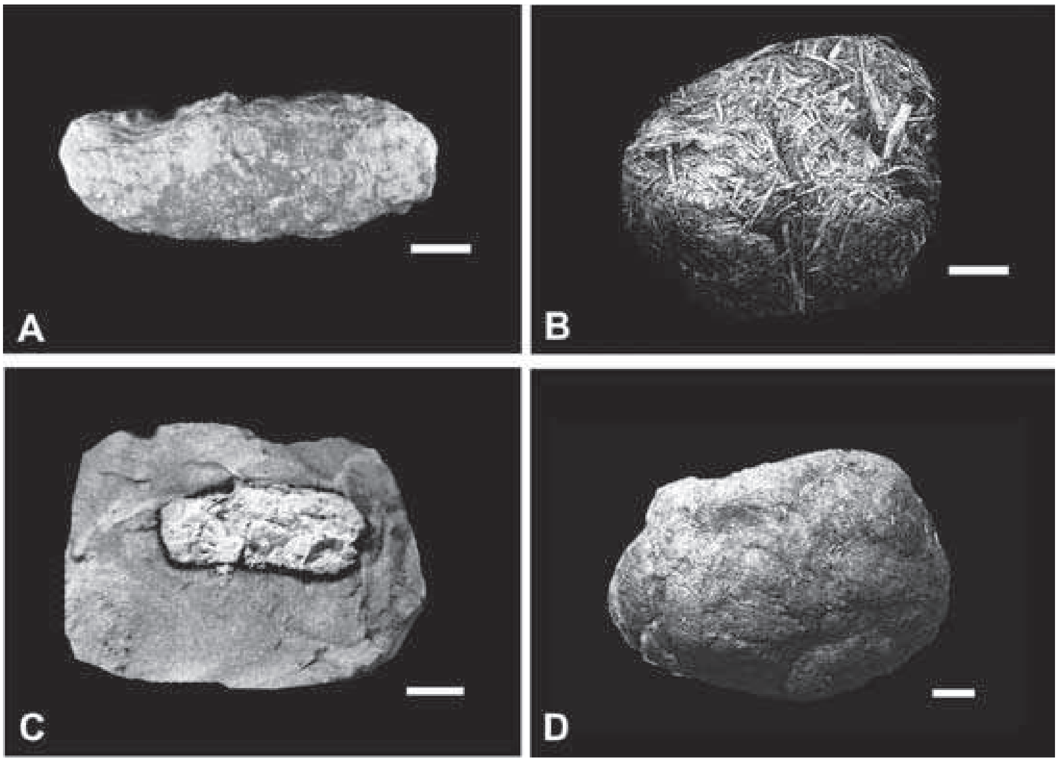

Figure 5. Coprolites associated with Cenozoic sediments. A, ungulate coprolite from the São José de Itaboraí Basin (Brazil); B, mastodont coprolite from the Pampean region (Argentina); C, bird coprolite from the Taubaté Basin (Brazil); D, big sloth coprolite in Patagonia (Argentina). Scale bars: 10 mm.

FINAL REMARKS

Nowadays, after more than two centuries since the first report on coprolites, the limited condition of the information on them is due to the fact that coprolites were not properly considered by researchers until the middle of last century and, therefore, they were long considered only as objects of curiosity.

This study aims at providing an overview of coprolites to researchers interested in the study of trace fossils, as well as in paleontology in general. Although the application of a taxonomy or parataxonomy to coprolites is questionable, the aspects showed in this work aim to establish diagnostic methods and supply descriptive parameters and information about the coprolite research.

In the last years, the increase of technological resources and the grown of scientific knowledge, specifically in the areas of ecology and ethology, make it possible to obtain detailed information by investigating coprolites structure. The importance of studying coprolite and their application to paleoecological and paleoenvironmental reconstructions has become evident. The evidence of this fact is the number of scientific manuscripts now produced around the world using coprolites, which almost doubled in the last 10 years if compared to the number of scientific works published in the middle of last century.

Currently, international meetings are organized around the world dedicated to the study of trace fossils of vertebrates. Latin America's great legacy recorded over these years of investigation on coprolites is the research centers' recognition that include in their collections large number of coprolites from this area. In Brazil, collections are stored by the Geosciences Institute of *Universidade Federal do Rio de Janeiro*, Mineral Production National Department and Paleoparasitology Laboratory of the Public Health School of the Oswaldo Cruz Institute, all located in Rio de Janeiro State.

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PART II

CASE STUDIES

TRACE FOSSILS FROM THE MAECURU FORMATION (LOWER DEVONIAN) OF THE AMAZON BASIN, AND PALEOENVIRONMENTAL INFERENCES

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ABSTRACT

This paper discusses the trace fossil assemblage of the deposits of Maecuru Formation (Lower Devonian, Urupadi Group, Amazonas Basin, North of Brazil) exposed along the Trombetas River (Pará State, North of Brazil). The Maecuru Formation is composed of fine-grained sandstones and mudstones deposited in delta settings developed in shallow marine (neritic) environment subject to glacial incursions. *Arthrophycus, Cruziana, Cymataulus, Lockeia, Palaeophycus, Rusophycus* and two unidentified morphologies compose the trace fossil assemblage found in three outcrops. The ichnofauna occurs in sequences of massive body of fine-grained to medium-grained sandstones, in some cases showing lenticular geometry, with bed-parallel stratification, hummocky cross-stratification and climbing ripples. The trace fossil assemblage characterizes the *Cruziana* Ichnofacies and, together with the sedimentological features, suggests deposition in shallow, moderate to low-energy marine environment with wave influence, in a proximal shoreface.

Key words: trace fossils, *Cruziana* Ichnofacies, Maecuru Formation, Amazonas Basin, Devonian.

INTRODUCTION

The Amazon Basin is an intracratonic basin of the South American platform, with an area of 5.10^5 km^2. The basin is located in parts of Amazonas and Pará states (N Brazil) and its deposition ranged from Proterozoic to Recent. The Lower-Middle Devonian sequence was formed on a transgressive-regressive cycle, resulting on the deposition of the Maecuru Formation (base of Urupadi Group). The Maecuru Formation is composed of fine-grained sandstones and neritic-delta mudstones deposited in a marine environment with glacial incursions (Cunha *et al.*, 2007).

A diverse marine invertebrate fauna has been described from the Maecuru Formation, including brachiopods, bivalves, gastropods and tentaculitoids (Cunha, 2001) as well as trilobites (Silva & Fonseca, 2005), coral elements, bryozoans, chitinozoans, acritarchs and sporomorphs. Scolecodonts and ostracods have also been reported (Caputo, 1984) in addition to Conulata (Fonseca & Costa, 1999), crinoids (Scheffler *et al.*, 2006) and vertebrates, represented by conodont elements (Caputo, 1984). The endobenthic and epibenthic biodiversity of the deposits of the Maecuru Formation is complemented by the presence of trace fossils. This paper aims to report the occurrence of trace fossils in the Maecuru Formation and describe the main ichnogenera recorded in the studied outcrops.

GEOLOGICAL SETTING

The studied area is located along the Trombetas River in Pará State (Figure 1A). The area is limited by geographical coordinates 55°52’/57°16’ W, 0°42’/1°35’ S, in an area of approximately 15,150 km^2. The studied material came from three outcrops along this river (TMB-02, TMB-05 and TMB-06).

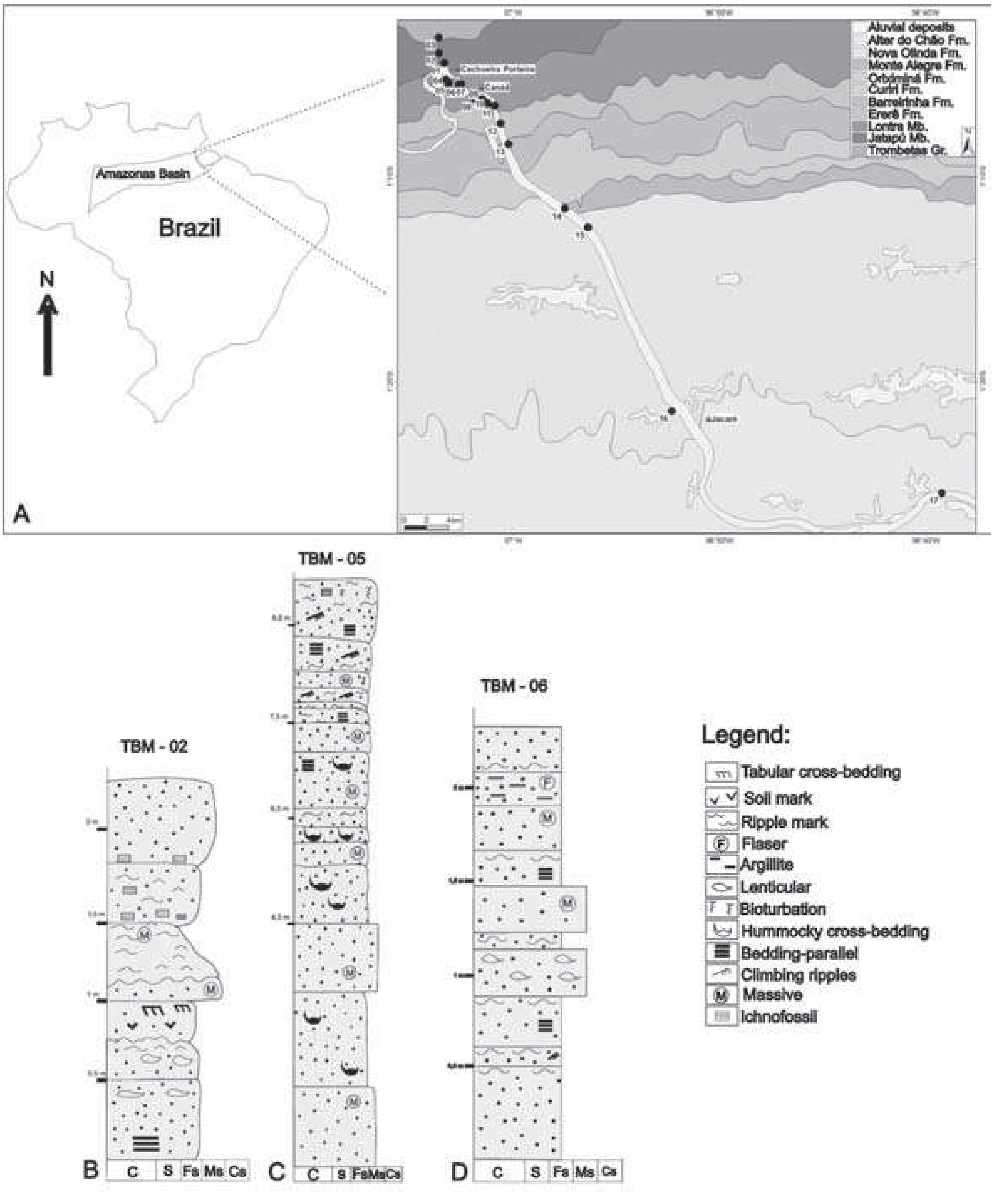

Figure 1. A, Location map of the Amazonas Basin and outcrops studied. The numbers 2, 5 and 6 represent the outcrops related to Maecuru Formation; B-D, lithologic log of the TMB-02, TMB-05 and TMB-06 outcrops, respectively.

The lithology of the studied outcrops (Figures 1B-D) consists of sequences of massive bodies of fine-grained to medium-grained sandstones, sometimes being lenticular. The observed sedimentary structures include low to medium-scale, low angle cross-stratification, with paleocurrent directions to N76 and N106. Two kinds of ripple marks were observed: large and symmetric ripple marks of approximately 70 cm wavelength and 2 cm of extent, and linguoid ripple marks, indicating bimodality (paleocurrent directions to N32 and N308), with wave interference. Bed-parallel stratification was also observed. Other sedimentary structures, including hummocky cross-stratification, climbing ripples, load casts and small channels are regionally present.

MATERIALS AND METHODS

The field work took place from November 24 to 28 of 2008, in the vicinity of Porto Trombetas municipality and Cachoeira Porteira town, Pará State, Brazil. Sixteen outcrops along Trombetas River were studied. Lithologic logs of all outcrops visited were made. On this basis, some outcrops were identified as belonging to the Maecuru Formation and ichnofossils were recorded at three sites (TMB-02, TMB-05 and TMB-06). The collected samples were catalogued and deposited in the *Laboratório de Preparação de Fósseis* of *Universidade Federal do Paraná* (UFPR), identified as UFPR 0033 IC to 0039 IC (Ichnofossil Collection). Some samples described here could not be collected due to difficulty of access.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Arthrophycus* Hall 1852

(Figures 2A-B, 3A-B)

Description. Two incomplete specimens, measuring up to 32 cm in length and consisting of a principal axis with many branches (UFPR 0033 IC) or not branched (UFPR 0034 IC). In transverse section, each burrow has a subquadrangular cross section from 1 to 1.2 cm in width. Transverse corrugations regularly spaced are visible along the entire length, with 4 ribs per centimeter. The overlapping branches are bundled on the same layer. A medial groove can be observed in specimen UFPR 0034 IC, suggesting a bilobate structure, but this is not evident in the full length of the specimen. The specimens are preserved in positive hyporelief.

Analyzed material. Samples UFPR 0033 IC and UFPR 0034 IC.

Discussion. *Arthrophycus* is characterized by regular transverse ridges, subquadrangular cross-section and a ventral median furrow, being preserved mainly in horizontal plan and in positive hyporelief (Häntzschel, 1975; Seilacher, 2000). Both specimens studied herein display the diagnostic features of the ichnogenus *Arthrophycus*, including regular transverse ridges, a squarish cross-section, 5-15 mm in diameter, a median furrow, predominantly horizontal components and preserved in positive hyporelief (e.g., Seilacher, 2000). The extensive palmately branched burrows and the straight to gently curved and self-penetrating galleries allow to attribute tentatively the specimen UFPR 0033 IC to *Arthrophycus alleghaniensis* Harlan, 1831 (according to Rindsberg & Martin, 2003). Moreover, the palmate burrows system is J-shaped as in *A. alleghaniensis*

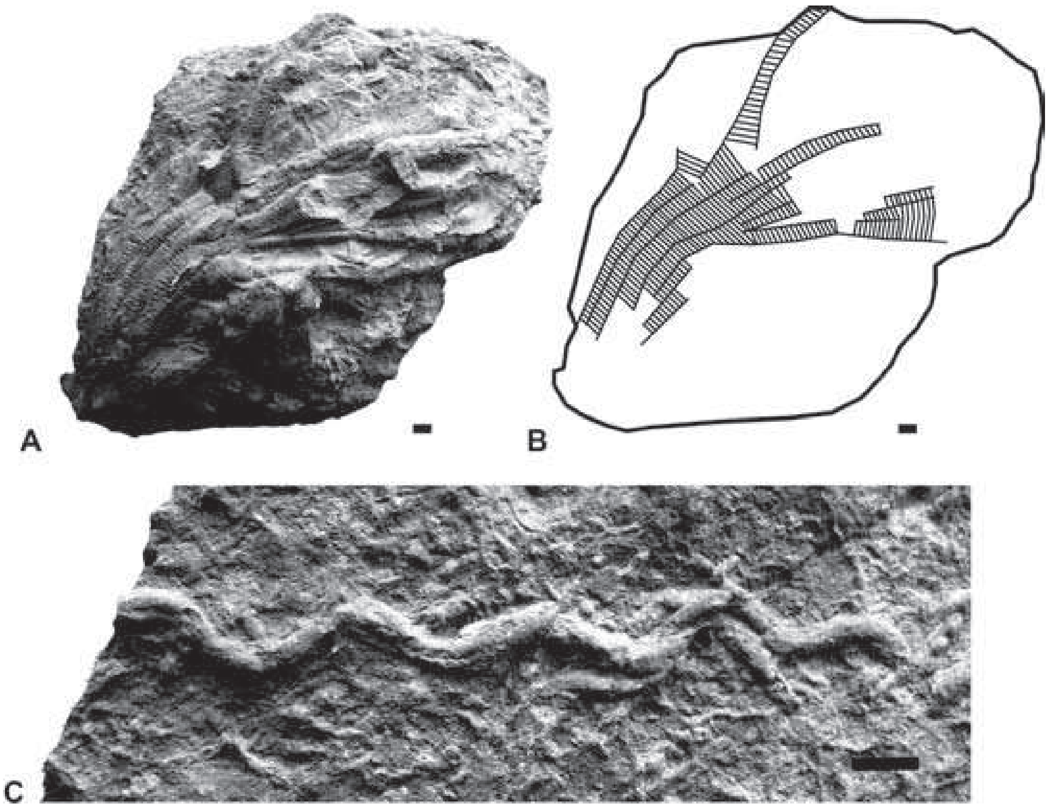

Figure 2. A-B, *Arthrophycus* (UFPR 0033 IC, sample sketch in B); C, *Cymataulus* (UFPR 0039 IC). Scale bars: 10 mm.

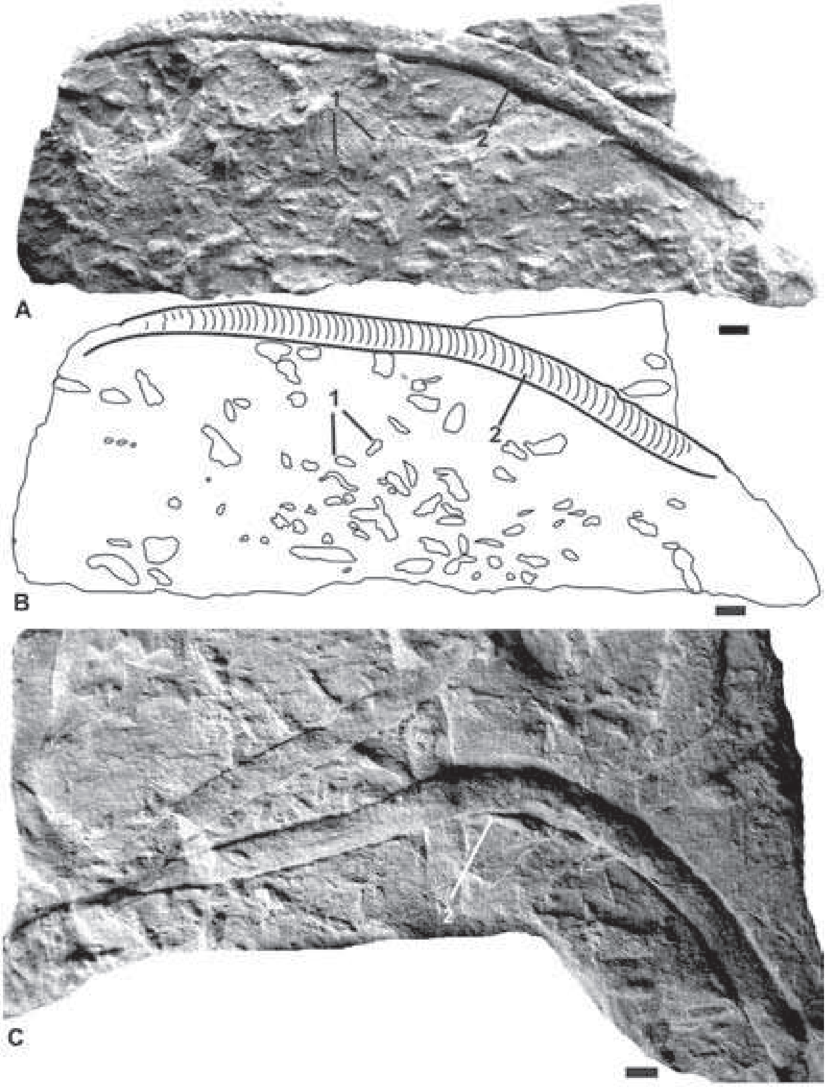

Figure 3. A, *Lockeia* (1) and *Arthrophycus* (2) (UFPR 0034 IC, sample sketch in B); C, *Palaeophycus* (2) observed *in situ*. Scale bars: 10 mm.

diagnosis (after Seilacher, 2007). The specimen UFPR 0034 IC displays a simple burrow, apparently without ramifications (although the burrow is incomplete), and reveals some resemblance with *Arthrophycus brongniartii* Harlan, 1832. However, the specimen is not so well preserved and some diagnostic features are lacking. This specimen occurs in close association with *Lockeia*.

The ichnogenus *Arthrophycus* has been interpreted as a feeding trace (*Fodinichnia*) (Häntzschel, 1975; Pickerill *et al.*, 1991; Mángano *et al.*, 2005; Seilacher, 2007), probably made by a long wormlike animal like an arthropod or annelid (Häntzschel, 1975; Pickerill *et al.*, 1991; Seilacher, 2000; Mángano *et al.*, 2005), although Rindsberg & Martin (2003) had proposed a trilobite or limulid-shaped animal as the *Arthrophycus* tracemaker. On the other hand, Brandt *et al.* (2010) suggested that another groups of lesser-known arthropod and non-arthropod could be investigated to be the tracemaker, such as lobopods. The parallel and co-planar burrows or bundled and multiplanar burrows that characterize *Arthrophycus* and their different orientations may reflect differences in the tracemaker's behavior for a more efficient sediment feeding, depending on the resource availabilities (Seilacher, 2000; Brandt *et al.*, 2010). According to Rindsberg & Martin (2003), randomly oriented trace fossils characterize resource-rich, low-energy environments, while aligned traces are typical of resource-poor, higher energy environments.

Arthrophycus is best known from Ordovician and Silurian sandstones and its presence on these rocks indicates a shallow marine condition (shoreface) (Seilacher, 2000; Rindsberg & Martin, 2003). In addition, according to Mángano *et al.* (2005), no reliable examples of this ichnogenus are known from deep-marine environments. *Arthrophycus* can be found worldwide from Cambrian to Carboniferous (Nogueira *et al.*, 1999), although the occurrence of this ichnogenus in Devonian and Carboniferous strata has been questioned (Mángano *et al.*, 2005). Nevertheless, a new ichnospecies, *Arthrophycus minimus*, was described from Upper Cambrian-Lower Tremadocian of northwest Argentina (Mángano *et al.*, 2005) and another new specimen, *Arthrophycus parallelus*, was described from the Late Carboniferous of Michigan (USA) (Brandt *et al.*, 2010).

In Brazil, *Arthrophycus* is reported only in Silurian and Devonian rocks (Fernandes *et al.*, 2000), as in the Vila Maria Formation (Llandovery; Burjack & Popp, 1981; Fernandes *et al.*, 1995; Fernandes, 1999) and Furnas Formation (Lower Devonian; Moreira *et al.*, 1998; Fernandes *et al.*, 2000), from the Paraná Basin; and in the Nhamundá Formation (Llandovery; Derby, 1879; Clarke, 1899; Boucot, 1975; Nogueira *et al.*, 1999), Pitinga Formation (Llandovery/Wenlock; Caputo, 1984), and Manacapuru Formation and Trombetas Group (Lower Devonian; Wanderley Filho *et al.*, 2005; Cunha & Tarapanoff, 1985), in the Amazonas Basin. According to Fernandes (1996), the branching pattern of the specimen UFPR 033 IC is proper of the specimens of *Arthrophycus* found in the Trombetas "Formation" (considered as Trombetas Group since Caputo, 1984), but it differs from those recorded in Vila Maria Formation in which dichotomous branching predominates.

Ichnogenus *Cruziana* D'Orbigny, 1842
(Figures 4A-B)

Description. Straight bilobate structure with obliquely transverse striation and a medial furrow. The structure is parallel to stratification, preserved in negative epirelief. Specimen UFPR 0035 IC (Figures 4A-B) measures 11 cm in length and 4 mm in diameter. The specimen observed *in situ* shows a sinuous trajectory and a well marked medial furrow with transverse striae along each lobe. It occurs in positive hyporelief, associated with many unidentified traces. Specimen UFPR 0035 IC has a reduced size compared to the specimen observed *in situ*.

Analyzed material. UFPR 0035 IC and one specimen observed *in situ* at TMB-05 outcrop.

Discussion. *Cruziana* is a trace fossil characterized by bilobed trails, with cross ribs obliquely placed, set

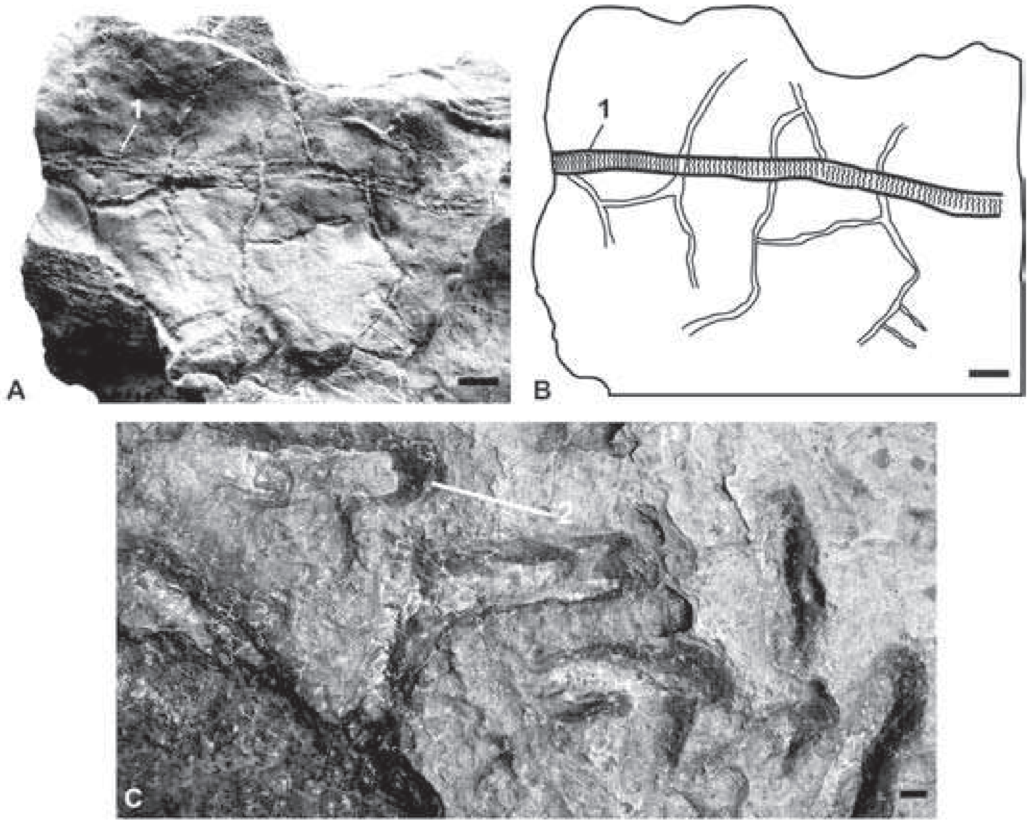

Figure 4. A-B, *Cruziana* (UFPR 0035 IC, sample sketch in B); C, *Rusophycus* (2) observed *in situ*. Scale bars: 10 mm.

at acute angle and regularly distributed (Häntzschel, 1975). This ichnogenus is used to name all bilobed burrow that records the displacement of trilobites or trilobitomorph arthropods (Fernandes, 2001; Seilacher, 2007) ranging from Cambrian to Recent. In spite of that, other arthropod (*e.g.*, notostraceans, isopods, anomurans) can produce *Cruziana*, specimens from Lower Paleozoic shallow marine environments that are generally assigned to trilobites (Seilacher, 2007).

At the Paraná Basin, *Cruziana* is recorded in the Ponta Grossa Formation (Fernandes, 1996) and Furnas Formation (Fernandes, 1999), both Devonian in age and it is also recorded in the Rio do Sul Formation (Nogueira & Netto, 2001a,b) and Teresina Formation (Lima & Netto, 2012), both Permian in age. At the Parnaíba Basin, *Cruziana* is recorded in the Pimenteira, Cabeças and Longá formations (Muniz, 1982; Borghi *et al.*, 1999; Fernandes, 2001).

Ichnogenus *Cymataulus* Rindsberg, 1994
(Figure 2C)

Description. Elongate meandering structure, parallel to stratification and preserved in positive hyporelief. The burrow has a constant and regular sinuosity, of 2.6 cm wavelength and 12 cm extent. The ichnofossil is preserved with numerous smaller burrows that were not identified. The excavation is well defined, semicircular in cross section and is about 4 mm in width.

Analyzed material. Sample UFPR 0039 IC.

Discussion. This specimen is attributed to ichnogenus *Cymataulus*, characterized by horizontal, branched or simple, wavy burrows, of relatively short length (Rindsberg, 1994). According to Rindsberg (1994), wave-like burrows have been described as *Cochlichnus*, which corresponds to a trail (not a burrow) preserved both in epirelief and hyporelief. In this context, many trace fossils similar to the burrow described herein were named *Cochlichnus*. Some shrinkage cracks preserved in wave ripple depressions were described by Muniz (1985) as *Cochlichnus*. However, the full relief morphology observed in the analyzed specimen and the regular meandering pattern exclude the possibility of this structure being a special case of desiccation feature.

This occurrence characterizes the first record of *Cymataulus* in Brazil. According to Rindsberg (1994), this ichnogenus possibly represents a dwelling burrow of wormlike invertebrates, especially due to its relatively short length and the fact that some wave-like burrows (*e.g.*, *"Cochlichnus"* from the Cretaceous of Colorado, U.S.A., described by Chamberlain, 1976) consist of stacked horizontal laminae.

Ichnogenus *Lockeia* James, 1879
(Figures 3A-B)

Description. Oblong and oval burrows with smooth surface, curved sides and rounded extremities. Some burrows present a D-shaped morphology, and both extremities are rounded. Sharp contour may occur. Burrows in sample UFPR 0034 IC are preserved in positive hyporelief, and occur in the same strata as *Arthrophycus*, while burrows observed *in situ* are preserved in positive hyporelief. The specimens of *Lockeia* described herein have sizes ranging from 3 to 10 mm in length and 1.2 to 5 mm in width.

Analyzed material. Sample UFPR 0034 IC and another one examined *in situ*.

Discussion. *Lockeia* is a bilaterally symmetrical trace fossil, shaped like the lower part of a bivalve with an outline of hypichnion almond- or a heart-shaped outline –, and lower end with sharp median ridge (Rindsberg, 1994). This ichnogenus is assigned to the activity of burrowing bivalve mollusks and is considered as a resting trace (*Cubichnia*) (Rindsberg, 1994; Fernandes, 1996). The stratigraphic distribution of the group is quite long, from Upper Cambrian to Pleistocene (Fillion & Pickerill, 1990).

Lockeia was described in the Amazonas Basin, from the Nhamundá (Lower Silurian) (Fernandes *et al.*, 2002) and Manacapuru formations (Early Devonian, Lockovian age) (Wanderley Filho *et al.*, 2005). In the Jatobá Basin, it was observed in the Inajá Formation (Devonian) (Fernandes *et al.*, 2002). In the Paraná Basin, it occurs in the Vila Maria (Silurian), Furnas and Ponta Grossa formations (Devonian) (Fernandes, 1996), and in the Rio do Sul (Balistieri *et al.*, 2002), Rio Bonito (Upper Carboniferous-Lower Permian) (Fernandes *et al.*, 2002) and Teresina formations (Permian) (Lima & Netto, 2012). This ichnogenus is also described from the Araripe Basin, in the Santana Formation (Cretaceous) (Fernandes *et al.*, 2002).

Ichnogenus *Palaeophycus* Hall, 1847
(Figure 3C)

Description. Straight to slightly curved, elongate burrows that intersect each other at some points. The structures are incomplete and parallel to stratification, the longest specimen measuring approximately 27 cm. These smooth structures are tubular and cylindrical, well demarcated, with well-defined walls and no branches, preserved on positive hyporelief, and measuring 1.5 cm in diameter in the entire length. The burrow fill consists of the same lithology as the rock.

Analyzed material. Specimens examined *in situ*.

Discussion. *Palaeophycus* corresponds to cylindrical or subcylindrical galleries, horizontal to bedding, branched and irregularly winding (Häntzschel, 1975). This ichnogenus ranges from upper the Precambrian to Holocene strata (Fernandes, 1996). According to this author, *Palaeophycus* is produced by the displacement of wormlike organisms within the sediment. According to Pemberton & Frey (1982), this ichnogenus is considered as a dwelling burrow constructed probably by polychaetes.

Palaeophycus has been already described from many Brazilian formations. In the Parnaíba Basin, it occurs in the Pimenteira (Borghi *et al.*, 1999) and Longá (Muniz, 1982) formations (Devonian). This ichnogenus is also described from the Paleozoic of the Paraná Basin, in the Vila Maria (Silurian) (Fernandes, 1996), Furnas (Ciguel *et al.*, 1996; Fernandes, 1996; Fernandes & Borghi, 1997) and Ponta Grossa formations (Devonian) (Fernandes, 1996), and in the Rio do Sul, Rio Bonito/Palermo, Estrada Nova, Teresina and Corumbataí formations (from Upper Carboniferous to Permian, Fernandes *et al.*, 2002; Lima & Netto, 2012). In the Bauru Basin, it is represented in the Cretaceous Adamantina Formation (Fernandes & Carvalho, 2006). It was also reported in the Paleozoic?/Cretaceous Cariri Formation (Araripe Basin), the Itapecuru Group (Cretaceous, Grajaú Basin), the Campos and Carapebus formations (Campos Basin) (Fernandes *et al.*, 2002), besides Ediacaran Santa Bárbara Allogroup (Martini-da-Rosa, 1999; Netto *et al.*, 2007).

Ichnogenus *Rusophycus* Hall, 1852
(Figure 4C)

Description. Horizontal, short shallow bilobated burrows with smooth (weathered) borders. A well-marked median groove divides the structure in two lobes. Burrows can occasionally be deep (Figure 4C) and are preserved in negative epirelief or in positive hyporelief. Average width is 2 cm and length up to 6.5 cm. Specimens found at TMB-05 outcrop occur associated with many unidentified traces.
Analyzed material. Three specimens examined *in situ* in TMB-05 and TMB-06 outcrops.
Discussion. *Rusophycus* is a resting trace (*Cubichnia*) (Häntzschel, 1975; Muniz, 1981; Rindsberg, 1994; Seilacher, 2007) assigned to trilobites and similar arthropods, characterized by a short bilobed trace with a deep median groove, obliquely to transversely wrinkled and oval to coffeebean-shaped (Rindsberg, 1994).

In Brazil, *Rusophycus* occurs in the Devonian of the Parnaíba Basin, in the Longá (Muniz, 1981, 1982), Pimenteira (Borghi *et al.*, 1999), Cabeças (Kegel, 1965) and Itaim formations (Fernandes *et al.*, 2002). This ichnogenus had already been recorded in the Inajá Formation of the Jatobá Basin (Muniz, 1984), and in the Paraná Basin, in the Furnas (Fernandes, 1996), Ponta Grossa (Devonian) (Fernandes *et al.*, 1993; Fernandes, 1996), Rio do Sul (Upper Carboniferous-Lower Permian) (Nogueira & Netto, 2001b; Balistieri *et al.*, 2002) and Rio Bonito/Palermo formations (Lower Permian) (Fernandes *et al.*, 2002).

Arrow-shaped structure
(Figures 5A-B)

Description. Arrow-shaped structure 12.5 cm long and up to 1.4 cm wide, with a small constriction (1.1 cm in width) in the medial portion. Although the structure is preferentially straight, some small irregular path is observed. Preserved in positive hyporelief associated with desiccation features.
Analyzed material. Sample UFPR 0036 IC.
Discussion. It was not possible to associate the morphology of this structure with any previously described trace fossil.

V-shaped structure and associated forms
(Figures 5C-D)

Description. V-shaped structure with one of the branches more prominent than the other. This structure measures 6.5 cm in length and the distance between the branches is about 0.5 cm at the base of the V angle and 1 cm on the opposite end. It is preserved in positive hyporelief and occurs in association with unidentified biogenic structures.
Analyzed material. Sample UFPR 0038 IC.
Discussion. This structure does not correspond to any other trace fossil morphology previously described in the ichnologic literature.

PALEOENVIRONMENTAL INFERENCES

The low ichnodiversity and the few amount of trace fossils found in the studied deposits of the Maecuru Formation did not allow extrapolation of paleoenvironmental interpretations for large areas of the Amazonas Basin. However, some paleoenvironmental inferences could be made for the studied area. According to the paleoecological model suggested by Seilacher (1967), the assemblage described herein can be included in the *Cruziana* Ichnofacies. This ichnofacies is composed of dominantly horizontal burrows excavated in shallow marine settings and representative of *Fodinichnia*, *Domichnia*, *Repichnia*, *Cubichnia* and *Pascichnia* ethological groups.

This marine ichnofacies, associated with fine-grained to medium-grained sandstones, bedding-parallel stratification, hummocky cross-stratification and climbing ripples, indicates a shallow, wave influenced coastal environment (shoreface), on the continental shelf. The environmental conditions that allowed the

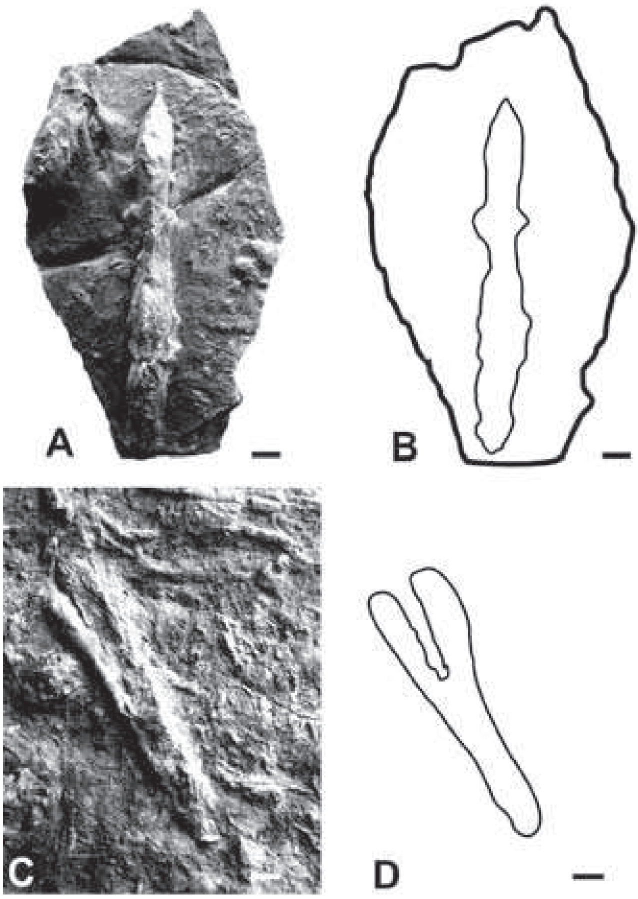

Figure 5. A-B, Arrow-shaped structure (UFPR 0036 IC, specimen sketch in B); C-D, V-shaped structure (UFPR 0038 IC, specimen sketch in D). Scale bars: 10 mm.

development of the endobenthic occupation in the studied deposits were probably those of a moderate to low-energy depositional system. According to Seilacher (1967), there is a rich food supply on the substrate at these settings and low amount of organic matter suspended in the water column that tends to settle at the sea bottom in quiet waters.

FINAL REMARKS

The ichnocoenosis described here is composed of *Arthrophycus, Cymataulus, Cruziana, Lockeia, Palaeophycus* and *Rusophycus*, all identified for the first time in the Maecuru Formation. This ichnofossil assemblage is represented by horizontal burrows, with a predominance of feeding behavior (*Fodinichnia*). This assemblage belongs to Seilacher's *Cruziana* Ichnofacies which includes feeding, dwelling, crawling and resting traces.

The presence of fine-grained to medium-grained sandstones, associated to sedimentary structures and the presence of a *Cruziana* ichnofacies allows to infer a shallow, moderate to low-energy marine paleoenvironment, with a rich food supply in the sediment. This marine environment belongs to a wave-influenced shoreface depositional system.

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VERTEBRATE FOOTPRINTS AND BURROWS FROM THE UPPER JURASSIC OF BRAZIL AND URUGUAY

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Valeria Mesa
Daniel Perea
Cesar Leandro Schultz

ABSTRACT

The Upper Jurassic Guará Formation (Brazil) or Batoví Member of the Tacuarembó Formation (Uruguay) crops out to the south of the Paraná Basin. This unit is composed of fine to coarse-grained sandstones and rare mudstones which represent fluvial and eolian depositional systems. The eolian facies of the Guará Formation (Late Jurassic) reveal footprints and trackways of vertebrates (dinosaurs), as well as burrows made by small vertebrates. Dinoturbated levels occur in eolian sand sheets of both Guará Formation and Batoví Member. All footprints and trackways are preserved in eolian dunes, sand sheets and interdune deposits. The Upper Jurassic Guará/Tacuarembó Formation contains numerous dinosaur tracks, dominated by theropod and sauropod tracks together with different vertebrate burrows. The occurrence of sauropod trackways with different gauge patterns in the same outcrop is unusual and suggests that this group formed herds that inhabited wet eolian sand sheets in the south of the Paraná Basin during the Late Jurassic. The size and shape of the burrows are compatible with excavations of therapsids, based on similar therapsid burrows found in South Africa and Antarctica. These burrows are likely to represent a permanent shelter used for dwelling and breeding. Only one burrow is smaller and subvertical, with a high "J" angle, probably produced by a very small mammal, similar to a rodent.

Key words: Paraná Basin, Jurassic, Guará Formation, Tacuarembó Formation, vertebrate ichnofossils.

INTRODUCTION

Vertebrate tracks and trackways are a well-known source of paleontological information, being the oldest sample devonian in age (Niedźwiedzki *et al.*, 2010). Vertebrate ichnofossils have been studied since 1828, when the first footprints were discovered (Pemberton *et al.*, 2007). Dinosaur footprints are known throughout the all Mesozoic, including descriptions of sauropods, theropods, ornithopods, stegosaurs, ankilosaurs, and others (Gillette & Lockley, 1986; Lockley, 1991, 1997; Lockley & Hunt, 1995; Radley *et al.*, 1998; Fornós *et al.*, 2002; Carvalho, 2004; Milán *et al.*, 2004; Moreno & Benton, 2005; Milán & Loope, 2007; Santos *et al.*, 2009). However, if compared with tracks, burrows continue to be understudied. Fortunately, a continuous series of papers approaching burrows have been published in the last decade (Miller *et al.*, 2001; Groenewald *et al.*, 2001; Damiani *et al.*, 2003; Hasiotis, *et al.*, 2004; Loope, 2006a, 2008; Sidor *et al.*, 2008; Riese *et al.*, 2011).

The Jurassic vertebrate ichnological data is mainly based on dinosaurian footprints on a global scale (Lockley, 1991, 1997; Lockley & Hunt, 1995; Day, *et al.*, 2002; Loope, 2006b, Santos *et al.*, 2009). The late Jurassic is characterized by the abundance of sauropod and theropod tracks but other groups are also known, such as ornithopods, crocodiles and mammal-like reptiles (Lockley & Hunt, 1995). In Brazil and Uruguay, only in the last decade dinosaurs tracks have been found in Jurassic strata, all located in the Guará and Tacuarembó formations (Dentzien-Dias *et al.*, 2007, 2008a; Mesa & Perea, 2010; Mesa *et al.*, 2010).

The fossil record of the Guará Formation (Scherer *et al.*, 2000; Scherer & Lavina, 2005, 2006) is composed by a rich vertebrate ichnofauna of theropod, sauropod and ornithopod footprints (Dentzien-Dias *et al.*, 2007, 2008a) as well as burrows probably excavated by mammals. The first outcrop with vertebrate ichnofossils in the Tacuarembó Formation was described by Mesa & Perea (2010) and yields a trackway with 16 rounded sauropod footprints with 40 cm in diameter. It also contains a rich and diversified fossil record, including crocodyliform, semionotiform fishes, gastropods, conchostracans, and dinosaurs (Mones & Figueiras, 1980; Ferrando *et al.*, 1987; Perea *et al.*, 2001, 2003, 2009).

In this work we present a review of all vertebrate trace fossils found in the Upper Jurassic of the Paraná Basin, both in Uruguay and Brazil. New data on sauropod footprints and vertebrate burrows are also presented.

GEOLOGICAL AND CHRONOSTRATIGRAPHICAL SETTING

Upper Jurassic strata from the Paraná Basin are made up of fluvio-eolian rocks that crop out in its south margin. These strata are named Guará Formation in Brazil (Scherer *et al.*, 2000; Scherer & Lavina, 2005, 2006) and Batoví Member from the Tacuarembó Formation in Uruguay (Perea *et al.*, 2009). These rocks have a wide geographical distribution (Figure 1), cropping out in the southwestern portion of Rio Grande do Sul State and reaching northwest Uruguay, where their limit is controlled by a NW-trending fault system. Lithologically, they are composed of fine to coarse-grained sandstones and rare mudstones of fluvial and eolian depositional systems (Lavina *et al.*, 1985; Scherer *et al.*, 2000).

The sandstones, especially the eolian ones, are highly friable due to weathering. Although highly variable, the Guará Formation has an average thickness of 200 m and unconformably overlies the fluvial deposits of the Early Triassic Sanga do Cabral Formation. The Guará Formation is unconformably overlaid by the eolian deposits of the Early Cretaceous Botucatu Formation (Table 1; Scherer *et al.*, 2000; Scherer & Lavina 2005).

Figure 1. Location map of the Guará Formation (Brazil) and Batoví Member (Uruguay) outcrop belt in Brazil and Uruguay.

Table 1. Schematic correlation between Mesozoic formations of Brazil and Uruguay.

Period	Litostratigraphic Units		
	Brazil	**Uruguay**	
Lower Cretaceous	Botucatu Fm.	Tacuarembó Fm.	Rivera Member
Upper Jurassic	Guará Fm.		Batoví Member
Lower Triassic	Sanga do Cabral Fm.	Buena Vista Formation	

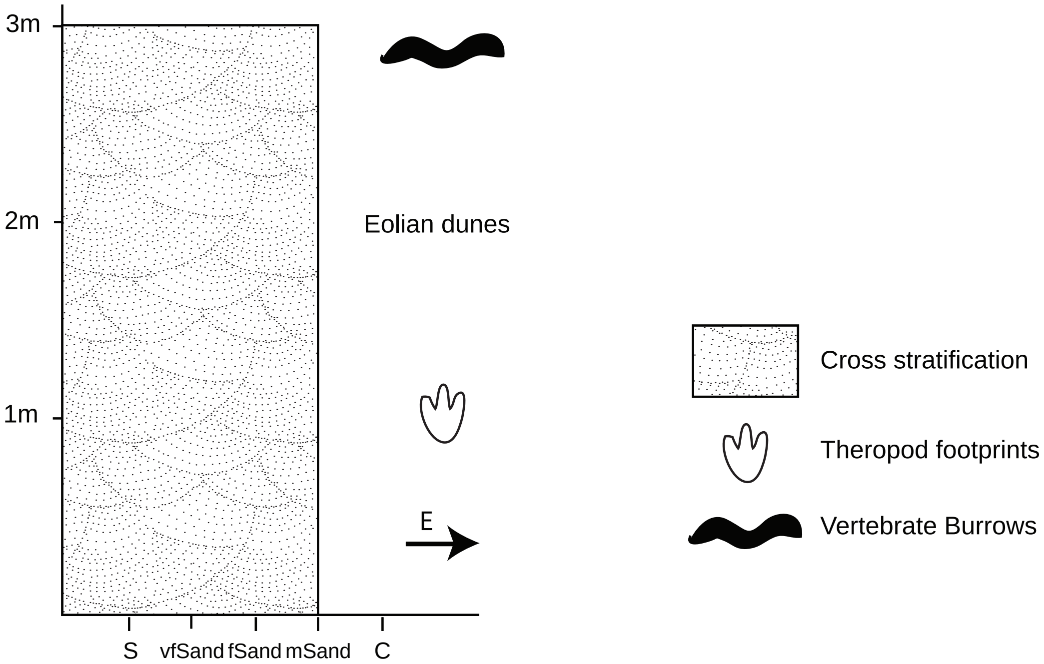

Figure 2. Stratigraphic section of the outcrop, near the city of Rosário do Sul (Brazil), where theropod footprints and burrows occur.

The Guará Formation displays a well-defined facies shift along its outcrop belt. On its northern portion it is characterized by coarse-grained to conglomeratic sandstones with trough and planar cross-bedding, as well as low-angle laminations, interpreted as braided river deposits (Scherer *et al.*, 2000; Scherer & Lavina, 2005, 2006). Hitherto, no fossils have been found in these facies.

Southwards, the fluvial facies thin out and are interdigitated with fine-to-medium grained sandstones with large-scale cross-stratification and horizontal lamination, interpreted as eolian dune and sand sheets deposits, respectively (Scherer & Lavina, 2005). In these eolian facies, trackways and footprints of sauropod, theropod and ornithopod dinosaurs, as well as burrows were found (Dentzien-Dias *et al.*, 2007, 2008a) (Figure 2). In the eolian sand sheet deposits, a vertical transition between wind ripples and adhesion strata (crinkled lamination) reflects changes in the substrate wetness. These changes could be associated with either modifications of the rate of water table fluctuation or dry sand availability. The accumulation of eolian facies in the Guará Formation was controlled by oscillations between arid and semi-arid conditions (Scherer & Lavina, 2005, 2006).

The fossil record of the Batoví Member of the Tacuarembó Formation includes crustaceans, mollusks, fishes, and reptiles (theropod dinosaurs, crocodyliforms and turtles), all of them found in the fluvial and fluvio-lacustrine facies (Perea *et al.*, 2009). These fossil remains consist mainly of isolated scales, teeth, spines and molds of bones concentrated in thin and patchy bonebeds (Perea *et al.*, 2001, 2003, 2009). The first record of an interdune bioturbated by footprints and trackways was recently published by Dentzien-Dias *et al.* (2008b).

According to Perea *et al.* (2009), the shark *Priohybodus arambourgi* D'Erasmo, 1960, recorded in the Batoví Member and Saharian and Arabic Peninsula formations, has a Late Jurassic-Early Cretaceous biochron. The dipnoi *Asiatoceratodus tiguidiensis* Vorobyeva, 1967 also delimits an age from the Late Jurassic to the Middle Cretaceous for the Batoví Member. More precisely, those authors propose a Kimmeridgian–Tithonian age for the lower portion of the Tacuarembó Formation (Batoví Member). By lithological correlation, the same age should also be attributed to the Guará Formation, with an ichnofauna composed by an association of theropod, sauropod and ornithopod dinosaur tracks and trackways.

MATERIALS AND METHODS

In the Guará Formation 60 footprints were found: 15 theropod tracks, 6 ornithopod tracks, 22 sauropod tracks, and 17 unidentified. Six vertebrate burrows were recognized in two outcrops. All these traces were found in eight outcrops. In the Tacuarembó Formation one trackway was found in one outcrop.

Four footprints were collected and registered in the Laboratory of Paleovertebrates of the *Universidade Federal do Rio Grande do Sul* (UFRGS PV 0003 J/K , UFRGS PV 0004 J/K and UFRGS PV 0005 J/K). All the footprints and trackways were photographed and measured, using the parameters of Leonardi (1987). The burrows were measured in line according with the methodology used by Miller *et al.* (2001). After that, one of the burrows and one of the sauropod foorprints were cut through in order to observe possible internal structures.

DESCRIPTION OF THE VERTEBRATE ICHNOFOSSILS

Sauropod tracks

Sauropod footprints occur only in the eolian sand sheet layers (Dentzien-Dias *et al.*, 2007). Some of these tracks can be seen in section and in plan view and produce well-defined deformations in the stratification. The footprints are all rounded, with no impression of digits, and they have a mean diameter of 50 cm. Undertracks reach around 45 cm in depth (see Dentzien-Dias *et al.*, 2008a). In section, the deformation of the stratification inside footprints is clearly asymmetric, with a deeper portion at the right side of each footprint, which resulted from the pressure created by the anterior portion of the foot during the step.

In the surface, two trackways are clearly visible (Figure 3). Both of the trackways are sub-parallel. One of the trackways has a pace stride average of 1.30 m, a pace angulation of 56º, the width is 1.10 m. This trackway is clearly wide-gauge (footprints are widely spaced from the track midline). The other trackway has a pace angulation of 107º, a stride of 1.50 m, the width of pace is 0.60 m and is a narrow-gauge trackway (footprints lie close to, or intersect, the midline of the trackway). These footprints were produced by middle-sized sauropods (Dentzien-Dias *et al.*, 2008a), with a body size similar to that of an extant male African elephant, with 2 m of leg length. According to Dentzien-Dias *et al.* (2007, 2008a,b), no manus prints were found, probably due to the overlap of the pes overstepping the manus prints, a common phenomenon in sauropod trackways (Moreno & Benton, 2005). However, one partial print of a manus was found in the last field trip. This manus print has the common semi-circular shape associated with sauropods, and is positioned slightly in front of the pes (Figure 4; Table 2). It is 22 cm in width and 15 cm in length. This new evidence supports the interpretation of these footprints as being produced by sauropods (Dentzien-Dias *et al.*, 2007).

In the case of the ichnofossils of the Tacuarembó Formation, the manus prints are not preserved, only the footprints. The Uruguayan sauropod footprints are all part of the same trackway, which extends for almost 12 m. Pes footprints intersect the midline and they are also rounded to subrounded, in some cases subtriangular, with a mean diameter of 40 cm. They present crenulations at the borders. In contrast to

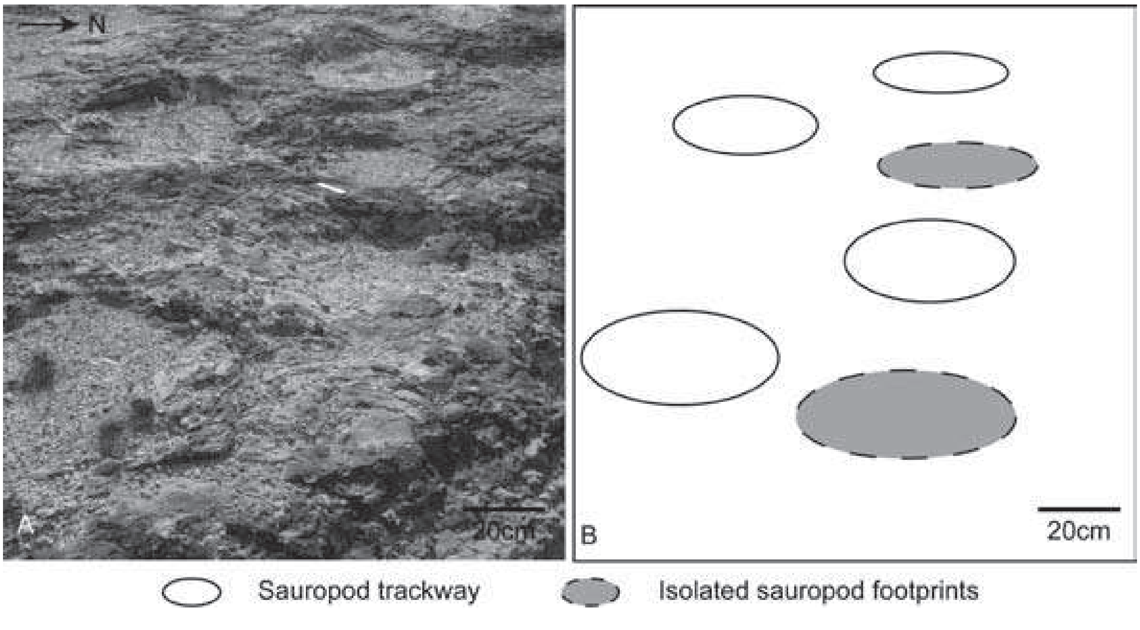

Figure 3. Sauropod trackway from the Guará Formation. A, Photograph showing all the footprints; B, schematic drawing of the partial sauropod trackway with two isolated footprints. Scale bars: 10 cm (white), 20 cm (black).

Figure 4. Sauropod tracks from the Guará Formation with manus and pes prints. Scale bar: 5 cm.

the Brazilian tracks, they have a friable sedimentary filling. When the filling is removed, they have variable depths but morphological/anatomical details are absent (Mesa & Perea, 2010; Mesa *et al.*, 2010).

Theropod tracks

Theropod tracks occur in the eolian sand dunes and in the sand sheets. The theropod footprints are tridactyl, with marks of sharp claws at their ends, narrow in width and with a "V" shaped heel (Figure 5). The size of the tracks differs, measuring from 17 to 35 cm in length and 15 to 26 cm in width (Table 2). A series of isolated theropod tracks were found and three trackways could be differenciated in a dinoturbated level. The orientation of all trackways is either from southwest to northeast or from northeast to southwest.

Ornithopod tracks

The ornithopod tracks are also tridactyl, with a "U" shaped heel, widely splayed toes and rounded claw traces in the tip of the toes. Only one trackway could be attributed to an ornithopod, with a pace angulation of 155° and the stride length of 1.20 m. Two isolated footprints are also attributed to an ornithopod on the basis of their morphology, the larger one with 25 cm long and 23 cm wide, showing well

Table 2. Characteristics of different vertebrate traces found in the Upper Jurassic strata of the Paraná Basin.

Biogenic structure	Diagnosis	Sizes	Localities
Sauropod tracks	Quadrupedal trackways with superimposed footprints Pes are rounded and manus are half-moon shape	Pes: ~50 cm in diameter Manus: 22 cm wide, 15 cm long	Brazil: Santana do Livramento Uruguay: Cuchilla del Ombú (Tacuarembó)
Theropod tracks	Bipedal trackways Tridactyl footprints with sharp claws	17 to 35 cm long, 15 to 26 cm wide	Brazil: Rosário do Sul
Ornithopod tracks	Bipedal trackways Tridactyl footprints with "U" shaped heel and rounded toes ends	15 to 25 cm long, 13 to 23 cm wide	Brazil: Rosário do Sul
Vertebrate burrows	Lens-shaped, straight to slightly curved in plan view; some describe curves and/or bifurcate Rounded subvertical with a high "J" angle	20 cm wide, 10 cm thick, 0.40 m to 2.80 m long; 5 cm in diameter, 25 cm long	Brazil: Rosário do Sul, Cacequi
Dinoturbated levels	Superimposed tracks	Occur in sequences of 30 cm to 1 m in section	Brazil: Rosário do Sul Uruguay: Cuchilla del Ombú (Tacuarembó)

Figure 5. Theropod footprint from the Guará Formation. Arrows show the sharp claw prints.

defined outlines, and the smaller one with 15 cm long and 13 cm wide (Figure 6; Table 2). The size of the biggest ornithopod track led us to attribute it to a bipedal ornithopod about 2 m in height.

Dinoturbated levels

Sequences of eolian sand sheets that are completely bioturbated by superimposed trackways deforming the strata occur in Brazil (Dentzien-Dias *et al.*, 2007) and Uruguay (Dentzien-Dias *et al.*, 2008b). In cross-section, laminae are smoothly folded and are rarely broken. The central axis of the track is called shaft by different researchers (Allen, 1989; Loope, 2006b). This shaft is clearly seen in section (Figure 7). In some cross-sectioned tracks, a marginal upfold can be seen (Figure 7).

These bioturbated levels occur in sequences of 30 cm to 1 m of eolian sand sheets and they are preserved in cross-section (Table 2), showing that layers are completely bioturbated by overprinted footprints (Figure 7). This would suggest a frequent transit of animals in that region at the time of the layers deposition. Another tracksite reveals a layer of eolian sand sheets, about 30 cm thick, totally disturbed by dinosaur footprints that can be seen in section and on the surface (see Dentzien-Dias *et al.*, 2007, 2008a).

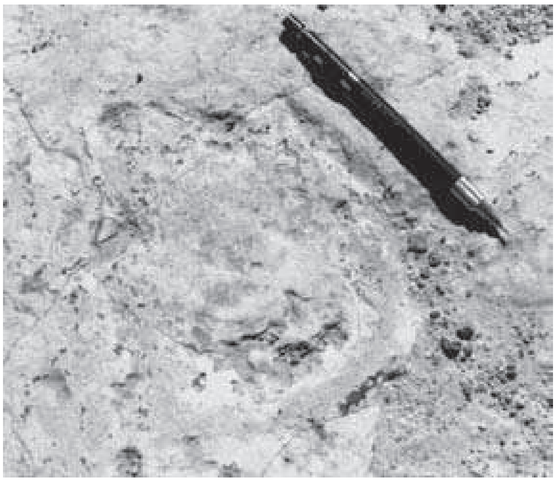

Figure 6. Ornithopod footprint with well defined "U" shape heel. Scale: 16 cm in length.

Vertebrate burrows

All the burrows were excavated in stratified eolian dunes and subsequently filled with massive sand (Dentzien-Dias *et al.*, 2007). One of the burrows is filled, in the top, with collapsed stratified sand (Figures 8-9). Typically, the burrows are straight to slightly curved in plan view and, in lateral view, they are horizontal to gently inclined downwards. However, some of them describe curves and/or bifurcations (Table 2).

The external surfaces of the burrows have been weathered, therefore no well-defined linings or scratch marks can be observed. These burrows are lens-shaped in transverse section and have a regular width of about 20 cm (Figure 8). They are around 10 cm thick and 0.40 m to 2.80 m long. In some portions, these burrows are covered by little blocks of stratified sandstones. The massive sandstones that fill the burrows are interpreted as the floor, while the stratified blocks evidently represent the collapse of roof parts inside the burrows (Dentzien-Dias *et al.*, 2007, 2008a). Only one burrow is smaller than the others, round-shaped, with 5 cm in diameter, and is subvertical with a high "J" angle.

DISCUSSION

Body fossils of vertebrates like theropods, a mesoeucrocodylian, indeterminated crocodyliforms and chelonians have been recorded for the Tacuarembó Formation (Soto & Perea, 2008; Mesa *et al.*, 2008; Soto *et al.*, 2010; Fortier *et al.*, 2011). Chelonian remains are not commonly found in the Tacuarembó Formation and tracks of this group have not been found to date. The same could be said about

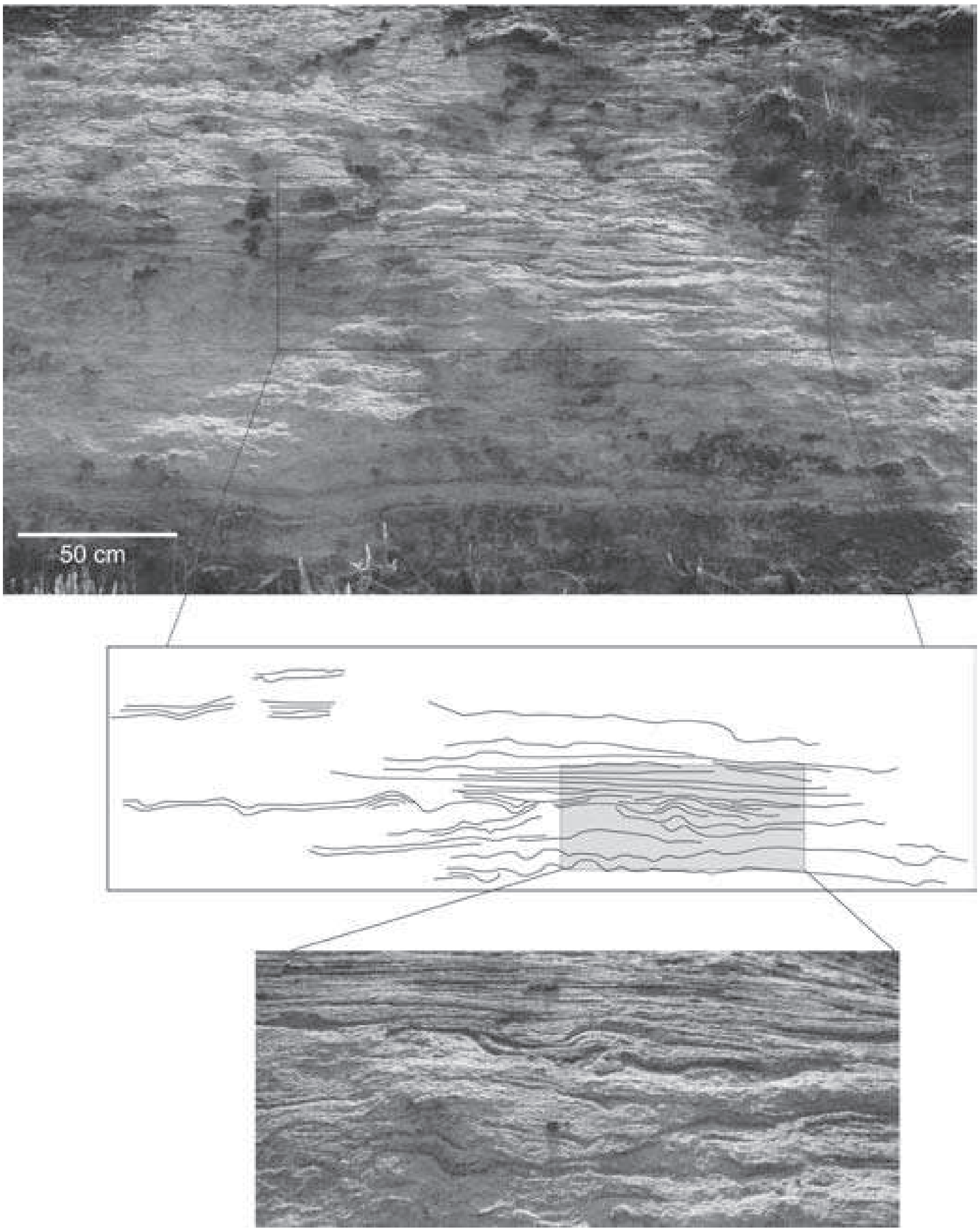

Figure 7. Dinoturbated level from Batoví Member in Uruguay. Note the concave-up deformation in the eolian sand sheet and the marginal upfold (arrow) seen in cross-sectioned tracks.

crocodyliforms. Dinosaurs are the only group represented in both formations. Sauropod tracks are found in both. Theropods are represented by teeth found in the Tacuarembó Formation, and by footprints in the Guará Formation. However, so far, no body fossils were found in the Guará Formation, even though there are fluvial facies in Brazil. According to Scherer & Lavina (2005), the fluvial facies thin out to the south and are interdigitated with fine-to-medium grained sandstones with large-scale cross-stratification and horizontal lamination, interpreted as eolian dunes and sand sheets deposits, respectively. The same interdigitation of eolian and fluvial facies could be seen in Uruguay. This bias in the fossiliferous record might be because the Guará Formation was only prospected for fossils in the last decade, with a non-continuous field work. We do believe that field work carried on by paleontologists and stratigraphers from both countries should be made to elucidate this question.

The occurrence of sauropod trackways with narrow- and wide-gauge in the same outcrop is unusual, especially because many of the tracksites that suggest gregarious behavior reveal only one type of trackway gauge. This suggests that the gauge is an indicator of particular types (families?) of trackmaker (Lockley & Hunt, 1995; Day *et al.*, 2002). The Guará Formation sauropod trackways are narrow- and wide-gauge, trend in a west direction and are subparallel to each other. This signal suggests that the sauropods formed a single herd of two different gauges. According to Day *et al.* (2002), sauropods may have formed multispecies herds as part of a defense against predation and/or as a byproduct of shared migration routes, as extant mammals. Alternatively, Castanera *et al.* (2012) have shown examples where the gauge changes along the length of a single trackway. The gauge variations, in the sauropod trackways described by these authors, seem to be associated with an individual behavior represented by a change in the direction of travel and with an abnormal gait that could be associated with the substrate consistency or other ethological /preservational factors. The Guará Formation trackways were formed in the same substrate and preserved in the same conditions, and no indications are noted in the change of travel direction. For this reason, we believe that the Guará Formation sauropod trackways indicate that sauropod herds may have contained more than one species.

The dinoturbated levels are quite widespread in late Mesozoic deposits, where large gregarious dinosaurs were abundant or inclined to repeatedly frequent wet substrates (Lockley & Hunt, 1995). This phenomenon is recurrent in the wet eolian sand sheet layers from Late Jurassic of Uruguay and Brazil and might indicate that in wet periods a large amount of dinosaurs lived in the south of the Paraná Basin. These bioturbations are very similar to other eolian strata as the Lower-Jurassic Navajo Sandstones and Middle Jurassic Entrada Sandstones in Arizona-Utah (Loope, 2006b; Milàn & Loope, 2007) and the Cenozoic of Nebraska Sand Hills (Loope, 1986). The marginal upfold, seen in cross-sectioned tracks, is analogous to those described by Loope (2007) and Allen (1989) that is generated as material is pushed up and out of the shaft.

One of the burrows shows a partial collapse of the upper part of the tunnel. This collapse left the stratification deformed and filled the top of the burrow. This happened when the burrow was already abandoned and partially filled by massive sand (Figure 9).

The size and shape of the burrows are compatible with excavations of therapsids, based on similar therapsid burrows found in South Africa and Antarctica (Smith, 1987; Groenewald, 1991; Miller *et al.*, 2001; Groenewald *et al.*, 2001; Damiani *et al.*, 2003; Hasiotis, *et al.*, 2004; Loope, 2006a; 2008; Sidor *et al.*, 2008, Riese *et al.*, 2011). According to Riese *et al.* (2011), these burrows are likely to represent a permanent shelter used for dwelling and breeding. There is not enough data to determine if the constructor lived there individually or in social groups. Only one burrow is smaller

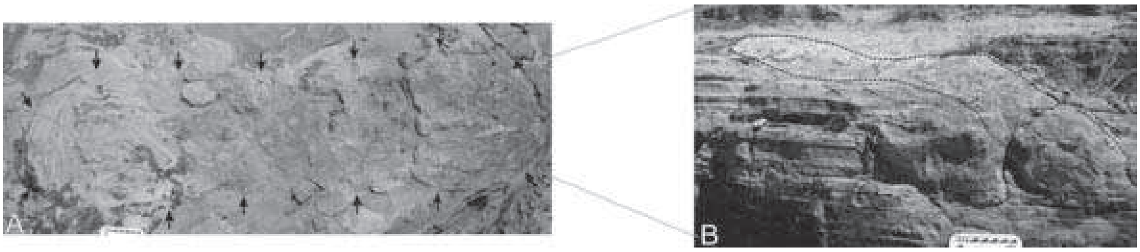

Figure 8. Burrows in plan and section views. A, Plan view of a 22-cm-wide and 105-cm-long fossil burrow; B, section of the burrow. Note the stratified sand collapse that filled the burrow during the diagenesis (see Figure 9). Arrows and dashed line delimitate burrow's margins. Scale: 6 cm.

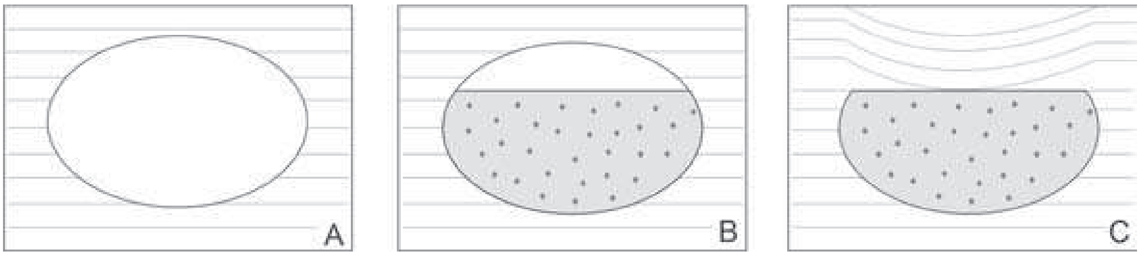

Figure 9. Reconstruction of the infilling of burrow. A, Open burrow; B, abandoned burrow, 2/3 filled with massive sand; C, collapse of the burrow's roof, filling with deformed stratification.

and sub-vertical with a high "J" angle, which was certainly excavated by a different animal than the one that excavated the larger burrows, probably a very small mammal, similar to a rodent.

FINAL REMARKS

The Upper Jurassic Guará/Tacuarembó Formation contains numerous dinosaur tracks, dominated by theropod and sauropod tracks and different vertebrate burrows. The tracks appear in eolian sand sheets and, occasionally, in eolian cross-strata. The burrows are found in eolian cross-strata. The tracks from the Guará Formation, as shown herein, prove that even when it is difficult to recognize the footprints, because of the absence of relief, some anatomic detail can be preserved to identify the trackmaker. Factors as non-cohesive sediment and erosion have influenced the poor preservation of some footprints. However, in cross-section, the deformation of the stratification facilitates the recognition of the tracks (Dentzien-Dias *et al.*, 2008b), even though it does not enable the recognition of the trackmaker.

Alternatively, marks of sharp claws, number of digits, heel morphology and width of the footprints were preserved, allowing the differentiation of theropod tracks from those of ornithopods. The print of a sauropod manus, described for the first time for the Guará Formation, associated with the pes prints (Dentzien-Dias *et al.*, 2007) confirms that those tracks were truly made by middle-sized sauropods.

Nevertheless, at least six fossil footprint sites and two fossil burrow sites have been described for the Guará Formation. Most serve as evidence of dinosaur activity, mainly theropods and sauropods, but only one shows the activity of ornithopods. Evidence of smaller animals, such as lizards and/or mammals, is known through burrows only. The presence of a reduced number of ornithopod tracks is consistent with the poor Jurassic record of this group during this age (Lockley & Hunt, 1995). The large number of sauropods tracks and trackways also confirm how abundant they were in the late Jurassic (Lockley & Hunt, 1995; Lockley, 1997).

The difference between the track and the bone records proves that, even without the preservation of relief, tracks provide additional ecological information that is not available from the bone record. Tracks of theropods, ornithopods and middle-sized sauropods are present in the Brazilian part of the Guará/Tacuarembó Formation. Hitherto, the bioturbated levels and the sauropod tracks are the only common fossils found in Uruguay and in Brazil. The sauropod trackway of the Tacuarembó Formation is the first and only dinosaur track described for Uruguay to this date. However, a very similar level of sauropod tracks was found in Brazil. But while the first vertebrate trace fossils were found in Brazil, body fossils have only been found in Uruguay. This difference may be due to the fact that, in Brazil, the fossiliferous prospection in the region where the Guará Formation crops out is recent, dating back 10 years only, whereas in Uruguay it has been going on for over 40 years. It is to be hoped that future field prospection will provide new findings of body fossils in Brazil and more ichnofossils in Uruguay.

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CENOZOIC VERTEBRATE TUNNELS IN SOUTHERN BRAZIL

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ABSTRACT

This work updates the present knowledge about the tunnels excavated by Cenozoic vertebrates in the four southernmost states of Brazil and discusses whether the producers of the different kinds of tunnels can be identified and how. At a regional scale, tunnels are common in the states of Rio Grande do Sul and Santa Catarina, but rare in the states of Paraná and São Paulo. A few isolated occurrences are known from some other states, but data is still too scarce to allow any conclusion. Only ~30% of these tunnels are not entirely clogged with sediments and can be entered for investigation. The diameters of the tunnels range in three intervals of ~0.8, ~1.3 and > 2.0 m and lengths of individual tunnels may reach up to 100 m. Often, several clogged and/or open tunnels show up on the same location, suggesting that the tunnels form systems. The interconnected tunnels and chambers of such systems sum tunnel lengths of several hundred meters. On the walls of ~20% of the tunnels, three different groups of structures can be found: (i) inorganic marks such as grooves produced by running water and anthropogenic traces such as Indian rock art, post-colonial tool marks and vandalism (scratches); (ii) scratches from the paleovertebrates that dug the tunnel; and (iii) traces from re-occupying animals, extinct or not. Some tunnels host several thousand traces, especially digging scratches. Biogenic action produced by plant roots and inorganic processes, represented by running water inside the tunnels, produces a characteristic set of clogging and destruction features. The roof of the tunnel often collapses and the broken material is washed inside the tunnels. On the surface, this process results in a series of aligned craters and holes while the tunnel is clogged with sediments. The producers, considering the South American Megafauna during the Cenozoic, possibly were giant armadillos and ground sloths. The present wetness of the tunnels suggests that they were excavated during a drier climate than today, mainly for shelter. Ongoing investigations aim to clarify the questions that remain such as ventilation of the tunnel systems and the origin and interpretation of the surface structures on the walls.

Key words: ichnofossils, paleovertebrates, burrows, tunnels, South America, megafauna.

INTRODUCTION

Large-diameter ichnofossils in the form of tunnels excavated by Cenozoic fossorial vertebrates are, so far and to our knowledge, restricted to South America. Only a few places in other continents host structures of the same kind, but those are much older and much smaller, with maximum lengths and diameters of 6.0 and 0.5 m, respectively (e.g., Groenewald, 1991; Miller *et al.*, 2001; Popa & Kedzior, 2006; Varrichio *et al.*, 2007; Martin, 2009; Sidor *et al.*, 2009; Modesto & Botha-Brink, 2010; Riese *et al.*, 2011; Talanda *et al.*, 2011). The South American tunnels ("paleocuevas" in Spanish and "paleotocas" in Portuguese) are sometimes called "paleoburrows", but this term is best known as applied to *Domichnia*-type ichnofossils of invertebrates (worms, mollusks and crustaceans) (e.g., Bromley, 1990, Buatois & Mángano, 2011). The preferred term for the much larger South American paleovertebrate structures is "tunnels".

Despite the probable occurrence of paleovertebrate tunnels (from now on referred as "tunnels" in this text) in the entire South American continent, descriptions of such structures are available only from Argentina and Brazil. In Argentina, many dozens of big-sized (Ø of up to 2.0 m) tunnels, 97% of them completely filled with sediments ("crotovines" or "krotovinas"), can be found in the region between the cities of Mar del Plata and Miramar. Most of them have appeared at the cliffs along the Atlantic coast and some have been found during underground construction works (Imbellone & Teruggi, 1988; Imbellone *et al.*, 1990). The origin of these tunnels has been attributed to giant armadillos (Quintana, 1992) and ground sloths (e.g., Zárate *et al.*, 1998; Vizcaíno *et al.*, 2001).

In Brazil, the first written record of tunnels was presented by Padberg-Drenkpol (1933), who speculated about the origin of tunnels. Later, teams of archaeologists found and described several dozens of tunnels during archaeological prospectings (e.g., Chmyz & Sauner, 1971; Rohr, 1971, 1984). Recent paleontological research of these structures started with Berqvist & Maciel (1994) and later with the team of the Paleotocas Project (Buchmann *et al.*, 2003, 2005, 2008a,b, 2009a-c; Buchmann, 2008; Frank *et al.*, 2008a, b, 2009; Lopes *et al.*, 2009; Frank *et al.*, 2010a-h; Frank & Buchmann, 2009; Ogando *et al.*, 2010; Stevaux *et al.*, 2010; Landell *et al.*, 2010; Lima *et al.*, 2010). These papers have added a huge volume of new information on the subject, raising several questions and many research possibilities. This contribution presents an overview of the tunnel research done until now in Brazil, detailing the characteristics of the tunnels and outlining the challenges of this research in the future, especially concerning more precision about the producers of these structures.

MATERIAL AND METHODS

The discovery of tunnels relies on systematic regional fieldwork, inspecting every huge anthropogenic cut in the terrain, which allows recognizing the open and sediment-filled tunnels that sometimes show up when the cuts surpass the thick weathering profile and expose the less altered rocks (and tunnel remnants) in the inner portions of the hills. Nevertheless, many tunnels are hidden in such a way that they can only be found after putting considerable effort in getting a hint from somebody familiar with the area, then finding and contacting a person who knows the place and, finally, using a huge logistical support structure to inspect the tunnels. People are contacted through a media program that raises public awareness related to these tunnels (Frank *et al.*, 2010a). Methods of the media program include regular releases to newspapers, reports in TV programs and pamphlets that are distributed in public places. Additionally, a homepage (www.ufrgs.br/paleotocas), several videos (on www.youtube.com) and an e-mail (paleotocas@gmail.com) were made available to the public. The latest news is reported in a bimonthly bulletin, which is accessible as a PDF file on the homepage and printed for people without internet access. More than half of the tunnels in our database, including some of the most interesting, were found through the media program.

After finding the tunnels, their location is registered (geographic coordinates) and the tunnels are measured (width, height, orientation, and inclination). The local geological and geomorphological aspects are annotated and pictures are taken to register the structure as a whole as well as special details. Digging scratches are measured, their numbers are estimated, and silicone casts are made of specific sections. Sediment-filled tunnels are only measured (width and height) and photographed.

The preservation of the traces of the tunnel walls and roofs is one of the biggest challenges of tunnel research. For a detailed study, casts have to be made. These casts must be made not on horizontal surfaces, like in the case of footprint casts, but on vertical and usually negative surfaces. Several materials have been tried out until now such as plaster and several kinds of silicone. The casting material must have an adequate fluidity, be chemically harmless and has to work on humid surfaces. The ongoing, geologic or anthropogrenic, destruction of the tunnels turns this into a pressing issue.

Dating the tunnels is almost impossible because common geochronological methods are useless in such a situation. In crotovines and in some tunnels without erosional features, it may be possible to recover, using special techniques (e.g., Freeman, 2010), microfossils from sediments inside the tunnels to apply palinological methods for some time constraints. As a whole, however, attempts with such methods have never been made and they still must be tested as a valid geochronological method for tunnels.

GEOLOGY OF THE STUDY AREA

The research on the vertebrate tunnels found in the south of Brazil started in Rio Grande do Sul State (RS) and was extended to Santa Catarina (SC), Paraná (PR), São Paulo (SP) and Minas Gerais (MG) states (Figure 1). Tunnels have been found excavated in unconsolidated substrates, sedimentary rocks and weathered igneous and metamorphic rocks of any geological age. Loose sediments of floodplains, coastal plains and alluvial fans host tunnels less often.

Most of the tunnels were found in two geological domains: the Paraná Basin and the Basement. The Paraná Basin is an intracratonic basin with an area of more than 1.10^6 km^2 that extends from Uruguay to the center of Brazil (Zalán *et al.*, 1990). In this basin, many tunnels were excavated in the Upper Jurassic – Lower Cretaceous coarse, reddish, continental aeolian sandstones of the Botucatu Formation and in the weathering mantle of the volcanic basaltic and rhyolitic rocks of the Lower Cretaceous Serra Geral Formation (Paraná-Etendeka Continental Flood Basalt Province) (Peate, 1997). The Basement covers the center of RS and a narrow strip along coast of the Atlantic Ocean, to the north. There, *in-situ* weathered, coarse-grained, Precambrian plutonic rocks such as granites, and similar metamorphic rocks like gneiss, provided to the paleovertebrates substrates suitable for digging.

CHARACTERISTICS OF THE TUNNELS

A large dataset of tunnels discovered until June 2011 with around 200 open tunnels and 300 sediment-filled tunnels, in almost 150 different spots in the five southern Brazilian states, supports the characteristics described herein. Tunnels with a high degree of preservation always repeat a well-defined morphology that is characteristic and diagnostic for all of them, even if sometimes a set of destruction features (described next) masks this shape. This work updates the present knowledge about the tunnels, and discusses whether the producers of the different kinds of tunnels can be identified and how it can be done. The tunnels cited and illustrated are listed in Table 1.

Figure 1. Location map of South America and Brazil showing the study area. It includes five states in the south and southeast of Brazil: Rio Grande do Sul (RS), Santa Catarina (SC), Paraná (PR), São Paulo (SP) and Minas Gerais (MG).

General shape

The final shape of the tunnels is composed of a sequence of queued ellipsoidal sections whose longer axes are horizontally aligned (like a row of lying eggs). The length of these sections start at around 0.5 m, they are, most often, a little bit longer than 1 m, but they can reach 2.5 m. Each section has a slightly concave roof and equally slight concave lateral walls. Vertical "arches" separate neighboring sections. This shape is very evident and most commonly found in the roof of smaller-sized tunnels and may be called the "successive-excavation-steps shape" (Figure 2). In larger tunnels (width > 2.0 m), this shape is less developed but easily recognized.

Tunnel size

Diameter

The diameter measurements consider only original diameters, evidenced by roofs and lateral walls with claw scratches (digging traces). Extremely well preserved empty tunnels are the exception. Tunnels are very often much higher than they were originally, because running underground waters erode its floors and rock slabs fall from the roof, subsequently disintegrating and washing away. These processes may double the width of the tunnels and the height may reach up to 4.0 m. On the other hand, tunnels filled with sediments constitute more than 60% of the occurrences. Only partly filled tunnels show a flat bottom and a lower height than width. Measurements of the diameters of completely filled tunnels are used with caution because it is not usually possible to see if the man-made cut that exposes the filled tunnel is exactly perpendicular to the tunnel axis. On the cuts, the filled tunnels often show nearly perfect circular sections (Figure 3D).

Original diameters of the tunnels are grouped in three size categories (Figure 3). The smallest tunnels have widths that range from 60 to 90 cm (Figure 3A). Usually, their height is somewhat smaller around 50 or 70 cm. Diameters of the most common tunnels range from 1.2 to 1.5 m (Figure 3B). The largest tunnels present widths of more than 2.0 m, and up to 4.1 m (Figure 3C). Their sections are not circular, but elliptical. The height of these tunnels may reach 2.0 m. Height and width usually decreases toward the end of the tunnel by at least 30%.

Length

It seems that the proximal sections of most of the tunnels are usually filled with sediments and remain hidden. These tunnels are only found after large man-made excavations remove the front part of the tunnel-bearing hills. For this reason, many lengths refer to tunnel remnants. Tunnel remnants with lengths between 3 and 20 m are very common. Longer tunnels may reach lengths of 30 to 40 m, especially if they were excavated in lithified rocks like sandstones. These tunnels are usually very well preserved, with a low degree of infilling and/or collapsing.

In Porto Alegre and Viamão cities (RS), 18 tunnels have been found measuring more than 50 m and up to 100 m (Stevaux *et al.,* 2010). The tunnels are excavated in *in situ* weathered plutonic rocks such as granites and gneiss and have been heavily impacted by the forest that grew up above them, with a lot of clogging and collapsing features. Their size always falls within the range of smaller tunnels. Similar features occur in the weathered material (eluvium and colluvium) that covers volcanic rocks (Serra Geral Formation) in the North of the same state. The measuring of these tunnels is more difficult due to their small sizes, associated destruction features and the water that usually flows inside them.

Tunnel orientation

The orientation of the tunnels is related to their size: tunnels with diameters of more than 2.0 m are

Table 1. Location of the paleovertebrate tunnels cited and portrayed in this text. Abbreviations: RS, Rio Grande do Sul State; SC, Santa Catarina State; MG, Minas Gerais State.

Code	Municipality and State	Property	Latitude S	Longitude W
Site-01	Novo Hamburgo (RS)	João	29º 40' 45.79"	51º 08' 34.16"
Site-02	Urubici (SC)	João Lima	28º 03' 23.68"	49º 28' 40.60"
Site-03	Boqueirão do Leão (RS)	Laudir Ogliari	29º 19' 23.81"	52º 26' 17.53"
Site-04	Sapiranga (RS)	CETRISA	29º 40' 11.59"	51º 00' 32.58"
Site-05	Campo Bom (RS)	Loteamento Fauth	29º 40' 03.45"	51º 03' 08.13"
Site-06	Estância Velha (RS)	Manoel	29º 40' 05.50"	51º 09' 26.90"
Site-06	Urubici (SC)	Raimundo Wiggers	28º 00' 46.70"	49º 32'08.40"
Site-07	Urubici (SC)	Donizetti Willemann	28º 03' 21.00"	49º 28' 30.60"
Site-08	Rio Acima (MG)	Caverna P-38	20º 01' 52.00"	43º 40' 48.00"
Site-09	Nova Hartz (RS)	Loidemar	29º 34' 57.62"	50º 56' 54.75"
Site-10	São José do Hortêncio (RS)	Paulo Führ	29º 29' 39.35"	51º 12' 28.91"
Site-11	Lindolfo Collor (RS)	Josoé Amorim	29º 34' 43.72"	51º 13' 29.69"
Site-12	Urubici (SC)	Fazenda	27º 57' 55.60"	49º 30' 33.40"
Site-13	Urubici (SC)	Bar do Hélio	28º 01' 12.50"	49º 35' 08.50"
Site-14	Ivoti (RS)	Loteamento Zang	29º 36' 44.46"	51º 10' 32.88"
Site-15	Porto Alegre (RS)	Beco do David	30º 05' 10.10"	51º 08' 51.74"
Site-16	Sapiranga (RS)	Est. Amaral Ribeiro	29º 37' 43.10"	50º 58' 08.10"
Site-17	Viamão (RS)	Fazenda Refúgio	30º 07' 28.12"	51º 03'38.14"

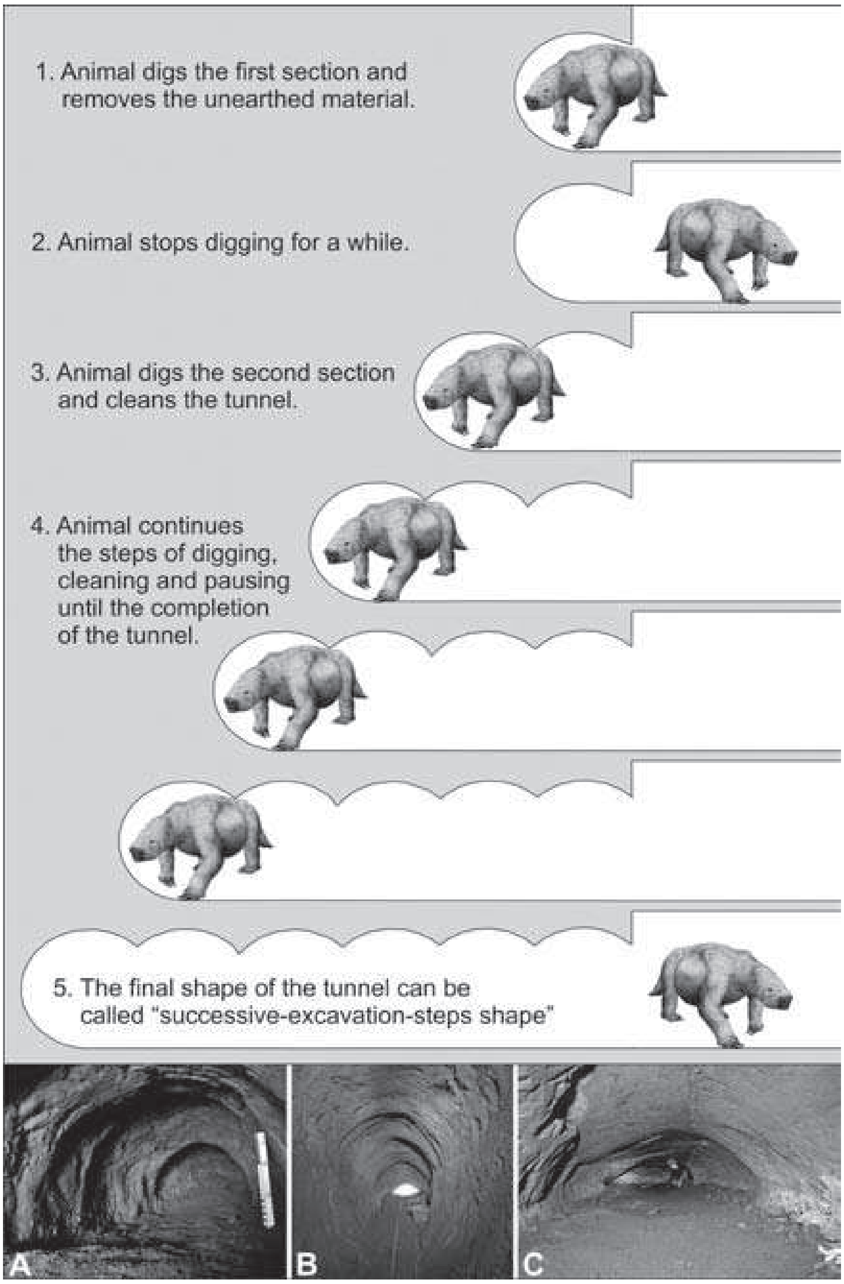

Figure 2. Schematic diagram (not to scale) of the stepwise construction (1 to 4) and the final shape (5) of a tunnel, in vertical sections parallel to the tunnel axis. A, Tunnel representing stages 1 to 3 (width ~80 cm, Site-01); B, tunnel representing the stage 4 (width ~1.3 m, Site-02); C, tunnel representing the stage 5 (width ~2.5 m, Site-03). A ground sloth like *Glossotherium robustum* may have produced the tunnels (illustration by Renato Pereira Lopes, 2007).

mostly horizontal, whereas tunnels with smaller diameters may rise or descend several meters along a tunnel section of a few dozens of meters. Such vertical changes may reach values of 3 m along a tunnel section of 30 m, for example. Measuring of these changes in elevation is usually impossible in filled tunnels, in short tunnels remnants and in tunnels of smaller sizes with erosional and clogging features, most often with running water inside.

However, some filled tunnels have been monitored during the anthropogenic excavations that exposed them and it was possible to verify, but not to measure, that the filled tunnels are usually orientated upwards inside the hills. The same conclusion was reached for the tunnels excavated in regoliths of plutonic and metamorphic rocks, despite the normal clogging and erosional features of these tunnels. Usually, they start at a lower point on the hillside, always

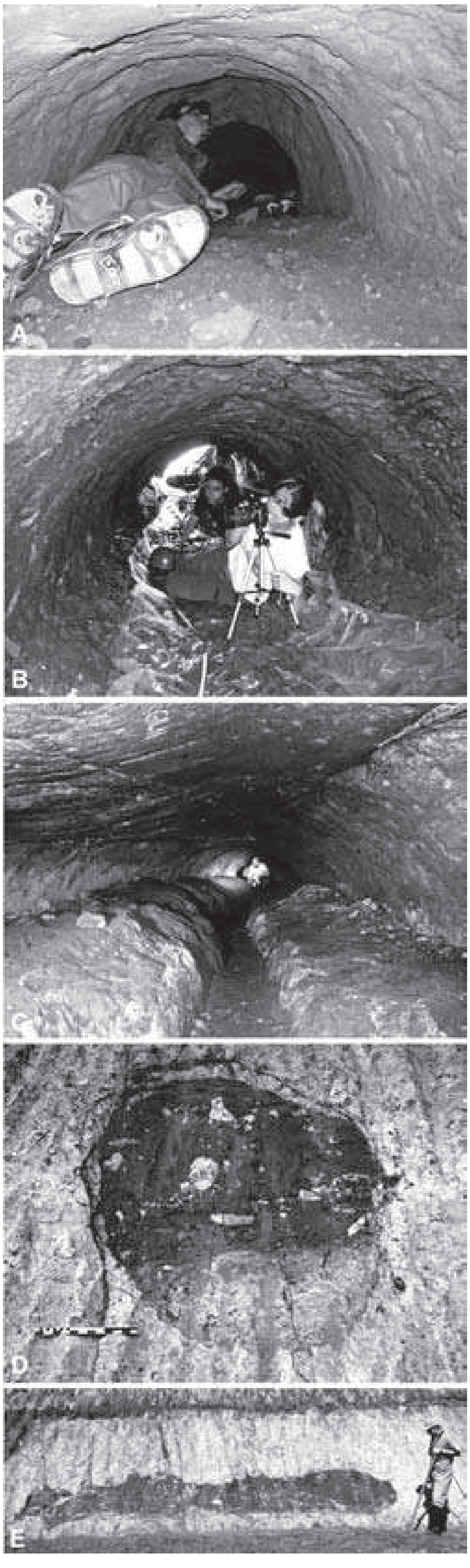

Figure 3. Paleovertebrate tunnel sizes. A, Smaller tunnels (width ~80 cm; Site-01); B, middle-sized tunnels (width ~1.4 m; Site-04); C, bigger tunnels (width ~3.0 m; Site-03); D-E, filled tunnel and its longitudinal section (E) (Site-05). Scale bars: 30 cm. Person in E is 1.7 m tall.

near a water source like a creek or river. Following the erosional features that align on the surface alongside the tunnels (craters, dolines, vertical cylindrical shafts, etc), a line up the hill can be traced, up to a final crater near the top of the hill that allows the entrance to the end of the tunnel.

In some cases, sets of interconnected tunnels form systems (see clustering and tunnel networks next) that are mostly open and well preserved.

Clustering and tunnel networks

In contrast with many isolated tunnels that are spotted in undisturbed terrains, anthropogenic cuts that remove huge volumes of sediments or altered rocks may expose hillsides with clusters of tunnels, either open or filled with sediments. At Site-05, for example, a 110 m long and 10 m high cut exposed 30 filled tunnels. At Site-06, a 30-m long cut exposed two open tunnels and two crotovines. At Site-04, a 40 m-long cut exposed three open tunnels and 10 filled tunnels (Figure 4, on the top) (all site details in Table 1). At this last site, three 1-m wide tunnels converged to a circular chamber with an arched roof and a flat floor. At floor level, its diameter was of 1.7 m and its height reached 0.6 m in the middle of the chamber (Frank & Buchmann, 2009). Such occurrences show that the tunnels studied herein form complex three-dimensional networks, also including chambers, with several openings to the surface and with total lengths that may reach more than 100 m.

Remains of such tunnel systems are better preserved in sites of SC than in those of RS. Site-07 (Table 1) was studied by Rohr (1971) as SC-Urubici-10. The tunnel is located at the top of a small hill besides a creek. The open section of the tunnel is 18 m long, 1.4 to 2.1 m wide and ~0.8 m high. The extremes of this section of the tunnel are clogged with sediments; both clogged tunnels descend the hillsides. From the accessible section of the tunnel, two other clogged tunnels branch out to the east and two other clogged tunnels branch out to the west, suggesting that the entire hill, whose diameter is of ~50 m, is crossed by tunnels in all directions. Site-08 (SC-Urubici-12 of Rohr, 1971) shows a highly complex outline (Figure 4, at the bottom) and again several clogged tunnels branch out from the accessible section of the tunnel system in several directions. In MG, a tunnel system (Site-09, whose investigation is not finished yet) has shown a total tunnel length of 340 m.

Regional density

At first, tunnels were known only from a few scattered points in the southern states of Brazil. Systematic fieldwork in the metropolitan region

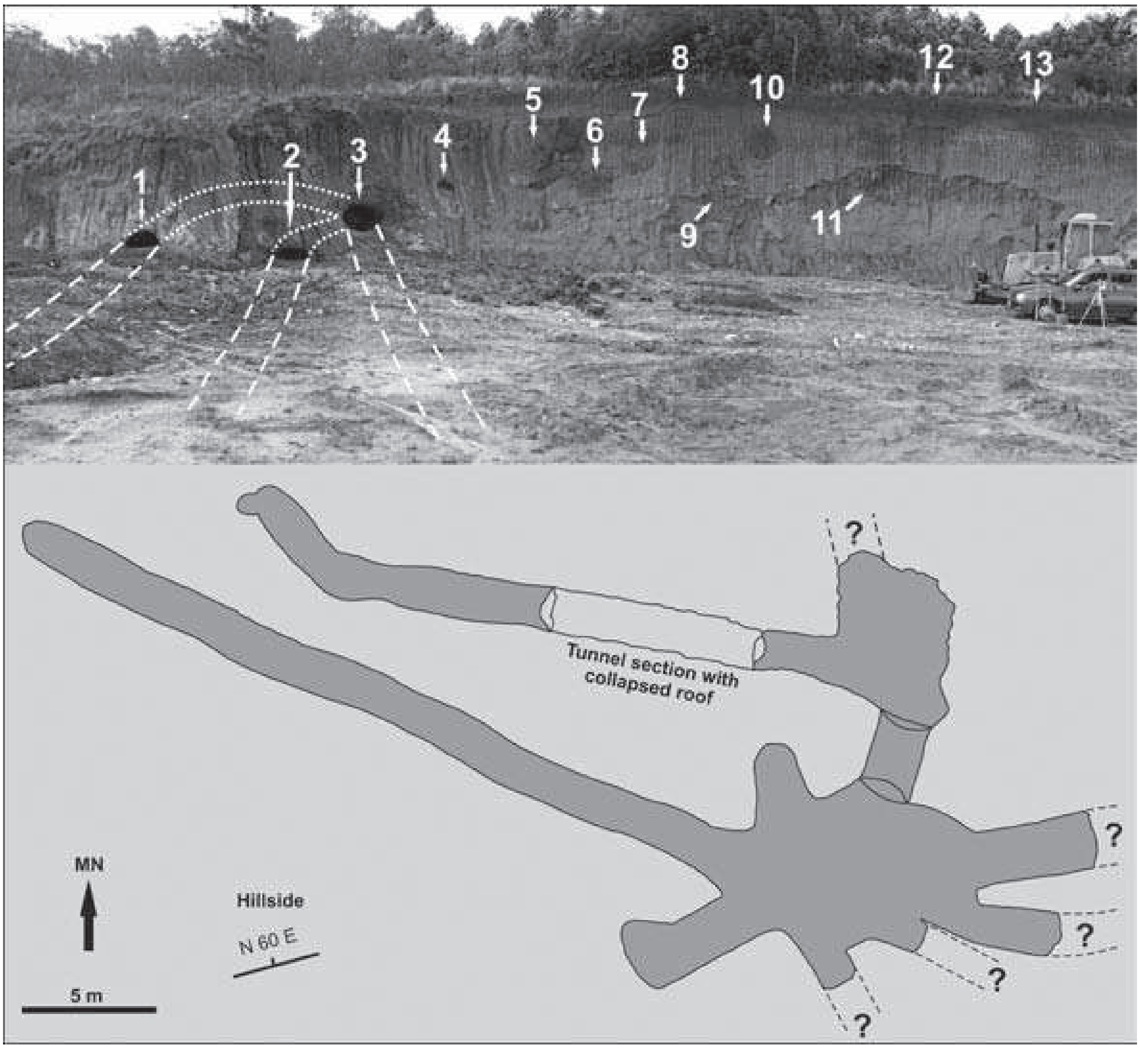

Figure 4. Top: Site-04. Remains of a tunnel system exposed in 2010, with three open tunnels (1-3) and at least ten clogged tunnels (4-13). Dotted lines indicate the position of hidden tunnels, dashed lines the former position of the destroyed tunnels, as told by the engineering firm employees. A chamber (see text) is located right behind the entrance 3. Bottom: Site-08. Floor plan of another tunnel system (Site-12).

of Porto Alegre (RS) has shown that these tunnels may have a high regional density. In this region, locations with one or more tunnels sometimes are at distances of only 500 m from each other (Frank *et al.*, 2009). Despite the many factors that destroy and hide the tunnels in these mostly urban areas, a regional tunnel system density of at least one system each 15.5 km^2 was calculated. The actual density is much higher, at least one system each 5 km^2. In some cases, it seems that each hill hosts one or more locations with tunnels.

Considering the south and southeast of Brazil, it seems that the density is high in RS and SC (Figure 1). In contrast, PR and SP, in spite of thousands of kilometers of road survey, intensive digital prospecting in the internet and the media program, have turned up less than a dozen spots with tunnels. Research in MG is only at the beginning and not conclusive so far.

As a rule, relief and the outcropping rocks are the main factors that dictate the regional density of tunnels. Plain regions and the ones with outcropping unweathered crystalline rocks are devoid of tunnels. Hills and mountains with very steep hillsides, on the other hand, have suffered several landslide events through geological time and the tunnels, if present, have probably been destroyed.

If the local geomorphology is composed of smooth hills, the usually very thick (>10 m) weathering mantle hides the tunnels, which are usually clogged with sediments. These hidden tunnels only appear if large anthropogenic excavations remove a portion of the hill. In different towns and cities, such excavations are common around the old urban core, in the ring-like area where present urban expansion encroaches on former rural areas.

The highest tunnel densities, considering the database constructed until now, occur at two altitude intervals: 0-100 m and 700-1,000 m. These regions show relatively high hills formed of sediments and rocks that allow excavations (alluvial fans, sedimentary rocks, weathered plutonic and volcanic rocks, etc). An outstanding example is Urubici (SC), with more than, so far, 35 locations with tunnels of different sizes identified and, with some of them, placed close together (e.g., 4 locations in 1,300 m). This situation is due to a rare local combination of factors, such as a favorable geological constitution for digging (sedimentary rocks) and an appropriated relief (high hills).

Internal surface morphology

From the whole set of paleovertebrate tunnels found so far, four groups can be distinguished based on their internal surface morphologies on the walls – i.e., features that may be classified according to their origin and that may provide hints about the identity of the tunnel producer. From the whole set of tunnels, 60-70% are completely filled with sediments (Frank *et al.,* 2008) (Figures 3D-E). Only a few show some distinct features on small exposed parts of their walls. From 10 to 15% show variable degrees of filling but show no distinct features such as the tunnels with collapsed roofs and/or walls. The same applies to those excavated in *in situ* weathered plutonic (e.g., granites) and volcanic (e.g., basalts, rhyolites) rocks and in the regolith (eluvium, colluvium and alluvium) derived of such lithotypes. 10 to 15% of the tunnels exhibit only grosser features such as large digging traces along its walls. Faint traces, like dragging imprints, are usually not found. This group includes tunnels hosted in laterites (in MG) and in sandstones – usually the coarse sands of the Botucatu Formation. Only a small percentage of tunnels, around 5-10% of the whole set, show a high diversity of imprints. Such tunnels are usually the ones excavated in fine-grained sediments like weathered clayey material or clayey sand – and siltstones. Even faint marks like drag marks are preserved; sometimes of exceptional quality.

Inside the tunnels of these last two groups, the lateral walls and the roofs are usually covered with hundreds to several thousands of marks and traces. In contrast, the floors of the tunnels only very rarely show some kind of trace since the bottom of the tunnels is easily eroded or covered with sediments. Some of the tunnels in sandstones show completely smooth lateral walls and roofs, with digging traces only near the base of the walls and at the end of the tunnel. A short overview will be given about the traces and the marks, tentatively classifying them accordingly to their origin in four groups.

Inorganic and anthropogenic features

Underground waters entering the tunnels are the rule in the present, wet climate of Southern Brazil. Very distinctive features in several tunnels excavated in sandstones are vertical grooves on the tilted out tunnel sides (Figures 5A-B). These grooves are 2-3 mm wide and up to 1 m long, developing one next to the other, sometimes even covering the entire side of the tunnel. Like small channels, they were carved by water that slowly oozes out from the walls through the porous and permeable sandstone and flows down the tunnel sides, carrying sand grains down to the floor of the tunnel.

If the tunnel entrance is clogged, the entire tunnel may flood with water. The standing water, often very muddy, covers the walls of the tunnels with a layer of clay until it seeps out. The layer covers and masks all kinds of features on the walls. If the tunnel dries out, mud cracks develop on this layer (Figure 5C). Sometimes, horizontal clayey overhangs develop on the tunnel walls, with a width up to 10 cm perpendicular to the wall and a length that may reach 50 cm (Figure 5D). The genesis of this feature has not been understood, but it must be related to the flooding of the tunnel.

Some tunnels host, on lateral walls, 2-3 cm deep sinuous grooves, sometimes with a thicker end or beginning (Figure 5E). These grooves are mostly vertical or subvertical on the tunnel walls and do not occur on the roof. Holes in the walls are associated with these grooves. The width of the holes ranges from 2 to 5 cm and their depth is of a few centimeters. In some cases, only a few scattered holes are present, but the tunnel side may show regions with densely spaced holes (Figure 5F).

Anthropogenic features are common in open tunnels with sizes that allow human presence inside. Brazilian history divides such features in pre-colonial and colonial. Pre-colonial traces are the petroglyphs (rock art) produced by several different Indian Traditions that lived in Southern Brazil (e.g., Rohr, 1971, 1984; Prous, 1991) and who sometimes used the tunnels. Post-1500 traces are represented by tool (pickax) marks, which have been produced by people who dug inside the tunnels to look for treasures (Rohr, 1971, 1984), and vandalism, such as name-scratching on the walls of the tunnels, that has often been inflicted by visitors.

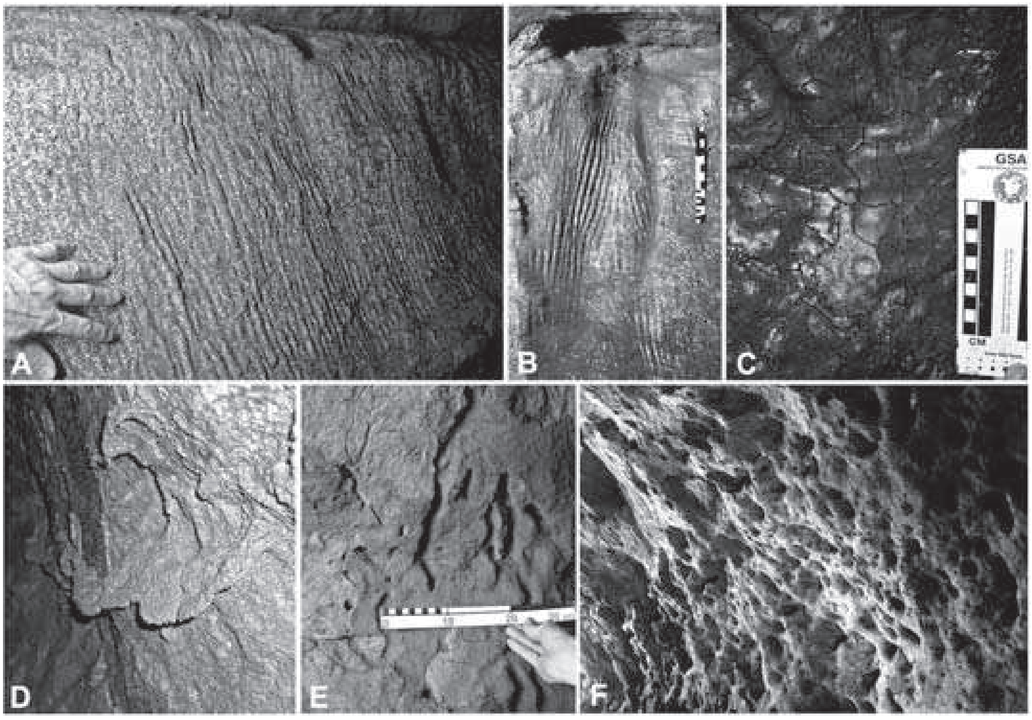

Figure 5. A, Lateral wall of a tunnel covered with parallel vertical grooves (Site-10); B, grooves originate and radiate from a water entrance inside the tunnel wall (Site-10); C, mud cracks in the clay layer of a vertical wall of a former water-filled tunnel (Site-04); D, clayey overhang formed at the wall (width of the overhang ~6-8 cm; Site-04); E, deep sinuous grooves and holes on the vertical wall of a tunnel (Site-01); F, the wall of a tunnel is covered with 2-4 cm wide holes (Site-01). Scale bar in B: 30 cm.

Features produced by burrowing paleovertebrates

In some cases, complex surface features are found on the walls. Common morphologies are composed of large grooves whose width and length may reach 4.0 and 60 cm, respectively (Figures 6A-B). Their orientation is mostly horizontal to subvertical. It is often possible to confirm two or three parallel marks (Figure 6C). Density is highly variable: in some tunnels, even the larger ones, only a few dozen of these structures can be found, whereas other tunnels may show 2,000 to 4,000 (e.g., Frank *et al.,* 2010c). In MG, a tunnel excavated in laterites has shown well-defined grooves at a height of 3.1 m. While many grooves develop a similar pattern, a single tunnel shows a very different one (Site-11). In this tunnel, the grooves are short (4 to 15 cm long), narrow (0.8 cm), mostly vertical and with a density up to 700 grooves per square meter. This density is around 2-3 times higher than the one of the common grooves (Lima *et al.,* 2010) (Figure 6D).

Several other types of features are much rarer than the grooves. In some tunnels excavated in finer-grained (clayey) material, we found flat surfaces, up to 50 cm long and 20 cm wide (Figure 6E). At Site-01, two of the six tunnel remains show very distinctive small and discrete features with an alignment up to four crests (Figure 6F). Cone-shaped marks around 10 cm wide and up to 5 cm deep are very rare (Figure. 6G). In several tunnels, the roofs and the upper part of the lateral walls are formed by completely smooth surfaces (Figure 6H).

Features produced by animals that re-occupied the tunnels

Smaller holes near the roof of open tunnels may be occupied by small groups of bats. At the entrances of these holes, there are often radiating grooves, a few mm wide and with lengths between 10 to 20 cm. The number of these grooves varies from a handful to around 20.

PRESERVATION OF THE TUNNELS

After the burrower and later occupants abandon the tunnel, biogenic and abiogenic processes destroy the tunnels. Anthropogenic destruction may be direct and complete when removing a hill partially or completely. In a few tunnels, which were thought to bear hidden treasures, minor anthropogenic destruction occurred through pickaxes, shovels, and other tools. Indirect anthropogenic destruction occurs when exotic trees (*Eucalyptus* sp.) are planted on the surface above the tunnels. Their roots are much deeper than those of native plants and hit the

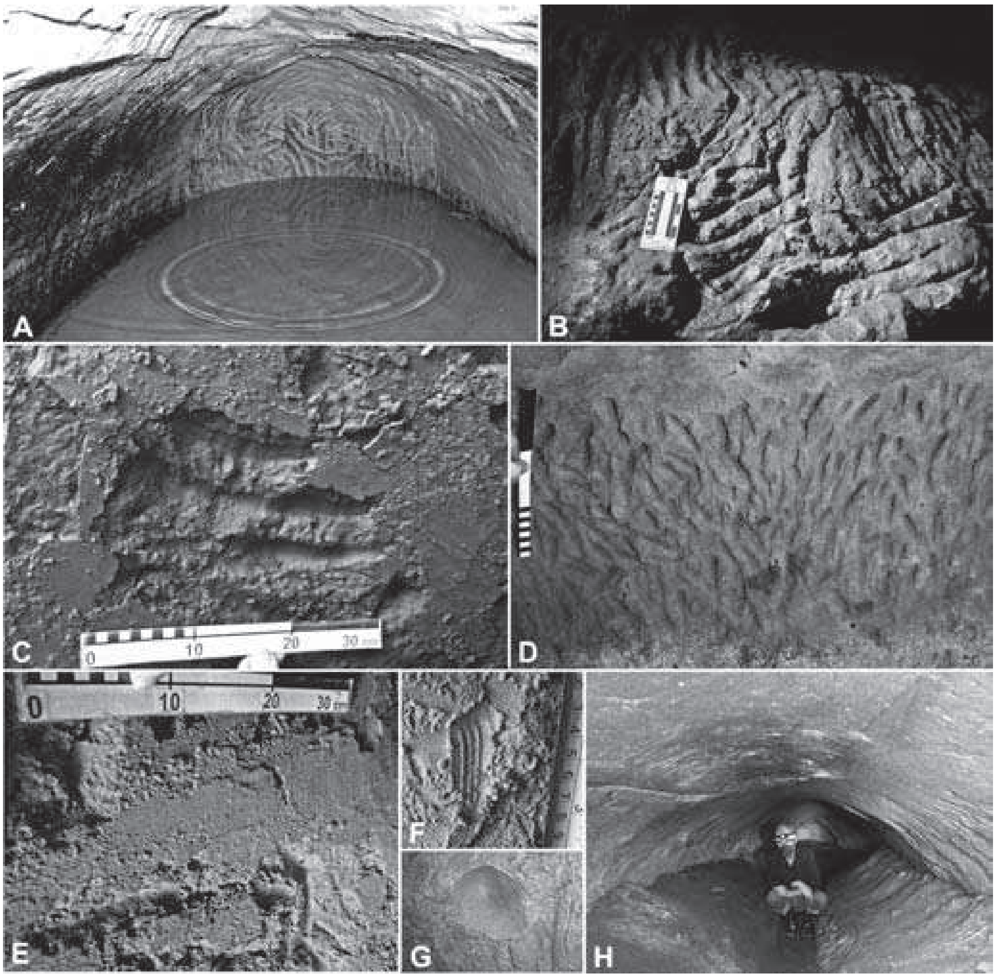

Figure 6. Features related to paleovertebrates. A, Dead end of a 1.3-m wide tunnel with standing water on the floor and water dripping from the roof, with dozens of grooves (Site-12); B, huge grooves on a tunnel wall (Site-08); C, three parallel grooves at a tunnel side (Site-01); D, strikingly different groove pattern (Site-11); E, flat surface on a tunnel wall (Site-01); F, small and delicate (= centimetric) feature (Site-01); G, cone with a diameter of ~10 cm (Site-04); H, half-filled 3-m wide tunnel, with anthropogenic trench and original smooth roof (Site-03). Scale bars: 10 cm (B) and 30 cm (C-E). Person for scale in H 1.84 m tall.

tunnels, speeding up the destruction processes (see next). As a rule, however, the lithotypes that host the tunnels are very tough and digging is very tiring. The speed of weathering processes is higher in fine-grained alluvium and sedimentary rocks and in weathered materials (regolith, weathered igneous rocks) and slower in sandstones. Clogging and erosion are the most important processes.

Clogging processes

Materials that fill the tunnels may be divided in three main categories: (i) clay brought in by underground waters, (ii) materials (sediments, rock fragments, etc) from the tunnels themselves (endogenic), and (iii) materials from outside the tunnel (exogenic). Underground waters that fill the tunnels in some cases are muddy and, after the flooding of the tunnel, stand still for a long time until they seep out. This allows the clay to settle down, forming horizontal layers of very pure clay at the bottom of the tunnels. This process repeats seasonally at every rainy period, particularly in tunnels hosted in the sandstones of the Botucatu Formation, depositing dark brown clay that looks like chocolate and with a good luster. In a few cases, almost the entire tunnel is filled with this dark brown clay. Most often, however, clay layers alternate with layers formed by other materials (sand, pebbles, rock slabs, etc), resulting of a slow and stepwise infilling history of the tunnel (Figure 3D).

Endogenic materials are rock slabs that fell from the lateral walls or the roof (Figure 7F) and loose sand and mud derived from the weathering of farther and

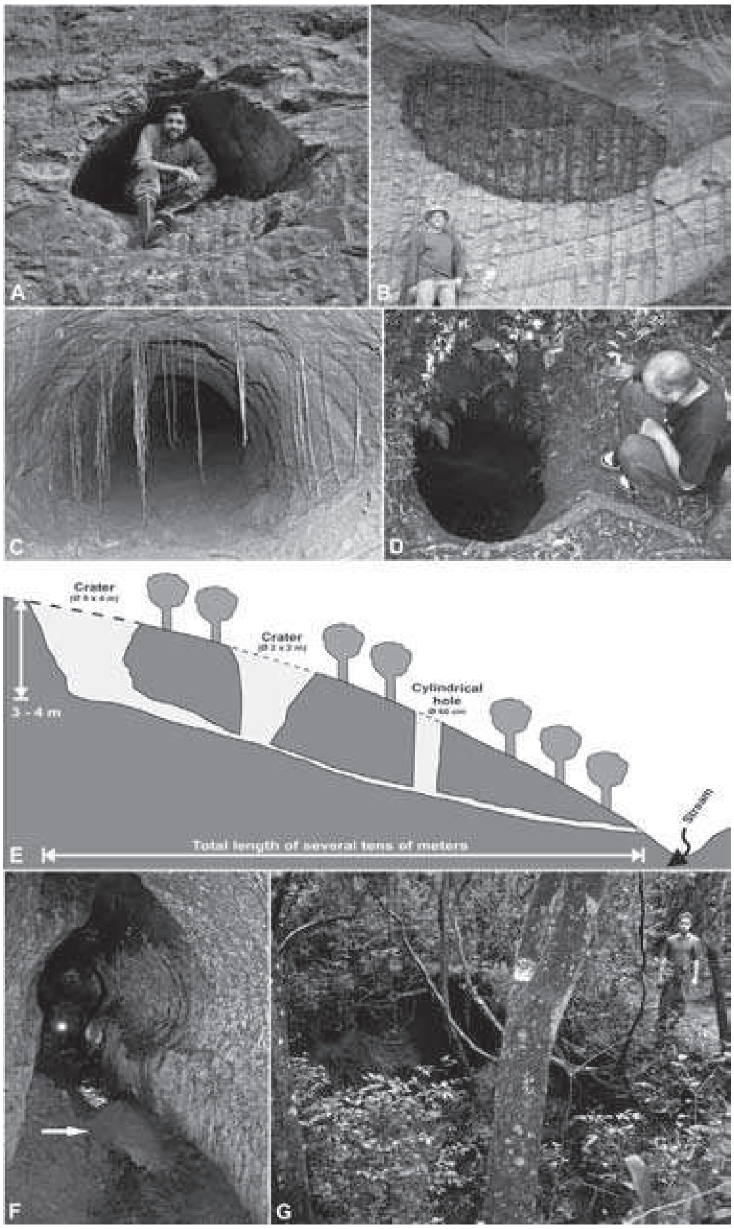

Figure 7. Clogging and erosional processes. A, Tunnel filled by a third. Original lower limit is beneath the right boot of the observer (Site- 13); B, completely filled tunnel in Botucatu Formation sandstones. Its width, of 3.2 m, is such because the tunnel was cut at a curve (Site-14); C, roots hanging from the roof of a 0.9 m wide tunnel (Site-01); D, cylindrical hole, 2 m deep, that connects to a tunnel in depth (Site-15); E, schematic section (not to scale) of a tunnel in weathered plutonic rocks with destruction features like aligned craters and holes; F, keyhole section of a tunnel with eroded floor. The diameter of the upper original circular section is about 1.3 m. Arrow points to a rock slab that has recently fallen from the roof. Background light is from observer (Site-16); G, 10 m wide and 4 m deep crater in the woods that connects to an eroded tunnel in depth. Person (at upper right) is 1.7 m tall (Site-17).

higher lying parts of the tunnels. Tunnels excavated in rocks other than the stable sandstones easily fill with such material (Figure 7A). The same happens with tunnels in weathered plutonic and volcanic rocks. The action of shrub and tree roots is the main biogenic factor of this destructive process. When the root of a plant goes through the roof of a tunnel (Figure 7C), a way down is opened and water drips or even drains permanently into the tunnel, along the roots. As time passes, this link to the surface widens and, after the death of the plant and the rotting of the root, this waterway opens completely, starting a geologically fast destruction phase of the tunnel at this spot. If a big tree grows exactly over the tunnel, its network of long and strong roots destroys the structure of the rock or weathered material on this spot, facilitating the destruction processes. At the end, the broken rock slowly slides down due to creep action or is washed down with time, and the tree remains somehow "hanging" above or at the side of a big (Ø > 5m) crater that appears in the woods, even with a very gentle topography on this spot. This destruction process of the tunnels opens wide (Ø up to 10 m) and deep (up to 4 m) craters (Figure 7G) and cylindrical holes (Ø 0.5-2.0 m) (Figure 7D), and the entire material of the space now occupied by the craters and holes is transported inside and through the tunnels, sometimes filling them completely. It is important to state that gullies, typical erosional features unrelated to paleovertebrate tunnels, are not formed at such sites, but only closed craters that are linked underneath by a more or less clogged tunnel (Figure 7E).

Exogenic materials are the sediments and vegetal remains washed in from outside the tunnel, usually through the entrance or through the open holes and craters. A common process on the surface is the creep movement of the material of the weathering mantle (regolith), slowly sliding down the hillsides through geological times. During rainy periods, the soaking of the weathered material eases and accelerates this process. This way, clay and sand unrelated to the host rock of the tunnels are washed in, filling the tunnels partly or completely. In the light red sandstones of the Botucatu Formation, tunnels filled with exogenic materials are easily spotted at the cuts due to the dark brown or almost black color of the infilling (Figure 7B). Organic material derived from the vegetation on this spot, such as leaves and branches, are also deposited inside the tunnel.

Erosional processes

Paleovertebrate tunnels constitute natural giant macropores of the hosting lithotypes. Rainwater that infiltrates through the porous and permeable rocks leaves the hills and mountains through the tunnels down to main drainage courses. After rain, it is almost impossible to spot a dry tunnel. In some tunnels, we have seen cracks at the walls discharging waters for two weeks after a daylong of heavy rain. Additionally, water constantly drips from the roof of the tunnels. The action of these underground waters is the main factor for eroding the tunnels. The flowing waters erode the floors, creating deep trenches well beneath the former circular section of the tunnels. The final shape of the tunnel is that of a keyhole (Figure 7F) with an upper circular section and a lower rectangular section.

A combined action of clogging and erosional processes is usually seen at the tunnels. Higher portions of the tunnels are eroded and lower portions are clogged. Collapsing of the roof may open, on specific parts of the tunnels, wide spaces that look like former chambers. When mapping and interpreting the tunnels, original surfaces must be carefully separated from walls and features produced by the destruction processes. While the former provide important information about the tunnel, the latter are casual and only give hints about the nature and the intensity of the destruction processes.

DISCUSSION

Despite the few tunnel descriptions found in literature until now, our effort could demonstrate that vertebrate tunnels are a common ichnofossil, at least in Southern Brazil, found in a great number of locations. Ignored by paleontologists, dozens of tunnels have been spotted in the last four decades by archaeologists, who considered them to be "underground Indian galleries" (e.g., Chmyz & Sauner, 1971; Rohr, 1971, 1984; Prous, 1991; Monticelli & Landa, 1999; Farias & Kneip, 2010). Indeed, the few tunnels with rock art on their walls, and that contain ceramic and lithic material inside that attest to occasional human presence, are true archaeological sites. However, the tunnels are usually devoid of any pre-colonial human traces and are only ichnofossils.

The original shape of the tunnels ("successive-excavation-steps shape") probably relates to the stepwise construction of the tunnel, whose excavation is a very energy-consuming process, even if several burrowers work together. Not only is the excavation difficult, but the removal of the unearthed material - the cleaning of the tunnel – also requires a huge amount of work. It must be remembered that the unearthed material weighs more than 2.10^3 $kg.m^{-3}$ of excavated rock. This material has to be removed, sometimes for several dozens of meters, to the entrance of the tunnel and then disposed outside. We hypothesize that the burrowers used to deepen the tunnels episodically, excavating them in sections. Therefore, each arch that separates two sections can be seen as indicative of a pausing by the producers. The same tunnel morphology was recorded in different types of substrates, such as sediments, sedimentary rocks and weathered igneous and metamorphic rocks.

The interpretation of the morphologies of the walls reveals several clues about the tunnel producers. The grooves, the most abundant and conspicuous features related to the diggers, were produced during the excavation of the tunnel and are digging marks, also called claw marks (Buchmann *et al.,* 2009b). If 2 or 3 of them are parallel, they relate to a single paw stroke. Flat surfaces, usually parallel to the tunnel axis, were interpreted as being made by the dragging of the carapace of a *Dasypodidae* digger alongside the tunnel walls. The conical feature found at Site 04 (Figure 6G) was seen as produced when the elbow of the digger rammed the wall accidentally. The completely smooth roofs and walls of some of the larger tunnels in sandstones may be related to the intensive usage of the tunnels for a long time by several generations of huge paleovertebrates, with the back of the animals touching and rubbing the tunnel roof and walls until the surface was evened out and all traces destroyed.

Since all kinds of sediment and rock, other than unweathered crystalline rocks, were found to host tunnels, the age of the host rocks must be seen as rather independent of the age of the tunnels, with a younger age limit placed at the late Pleistocene-Early Holocene, corresponding to the extinction of the megafauna (Fariña & Vizcaíno, 1995). The positions of the tunnels usually fit nicely within the present landscape considering nearby water sources, which seemed to be a control for the paleovertebrates. Therefore, there is a close association of the tunnel entrances with the present base level. Since landscapes underwent a defined cycle with geological time (Pazzaglia, 2003), this also indicates that the age of the tunnels most probably does not extend farther than the Cenozoic.

Therefore, the diggers have to be looked for within the South American Megafauna, a concept applied to mammals whose body masses exceeds a few hundreds of kilos (Fariña & Vizcaíno, 1995). The megafauna includes taxa such as litopterns (*Macrauchenia*), toxodonts (*Toxodon*), llamas (*Lama*, *Hemiauchenia*), horses (*Equus*, *Hippidion*), glyptodonts (*Glyptodon*, *Panochthus*, *Doedicurus*, *Neuryurus, Sclerocalyptus*), bears (cf. *Arctotherium*), saber-toothed cats (*Smilodon*), mastodons (*Stegomastodon*), giant armadillos (*Pampatherium*, *Holmesina*, *Propraopus*) and ground sloths (*Megatherium*, *Eremotherium*, *Glossotherium*, *Lestodon*, *Mylodon, Scelidotherium, Catonyx*) (Fariña & Vizcaíno, 1995). Morphological adaptations for digging are found only among the armadillos and the ground sloths (Bargo *et al.*, 2000), restricting the digger identity, at first, to these two groups.

A fundamental assumption is that a digging animal, vertebrate or invertebrate, does not excavate a tunnel much wider than its body (e.g., Hickman, 1990). If the tunnel is larger than strictly necessary, it will only allow the entry of larger predators. An example of this general rule is found in *Priodontes maximus*, the largest living South American armadillo, whose body mass is around 55 kg. In spite of this size, its tunnels measure only 43 cm in average width and 36 cm in height (Eduardo Fernandez-Duque, pers. comm., 2010). The diameters of the open paleovertebrate tunnels found until now classify them in at least three size ranges (~0.8 m, ~1,3 m, > 2.0 m), with the possibility of a better refinement in future. From the three size classes, the narrowest one can be attributed to giant armadillos of the genera *Propraopus* Ameghino 1881, *Pampatherium* Ameghino 1875 and *Holmesina* Simpson 1930. A similar conclusion was reached by Dondas *et al.* (2009), who attributed 1.0 m wide burrows (Type III) to *Pampatherium typum* (Figure 8).

The medium sized tunnels (width of ~1.3 m) were attributed by Zárate *et al.* (1998), Vizcaíno *et al.*, (2001) and Dondas *et al.* (2009) to digging ground sloths, and the largest tunnels definitively have to be attributed to larger species of ground sloths. Therefore, different species of sloths excavated tunnels with diameters

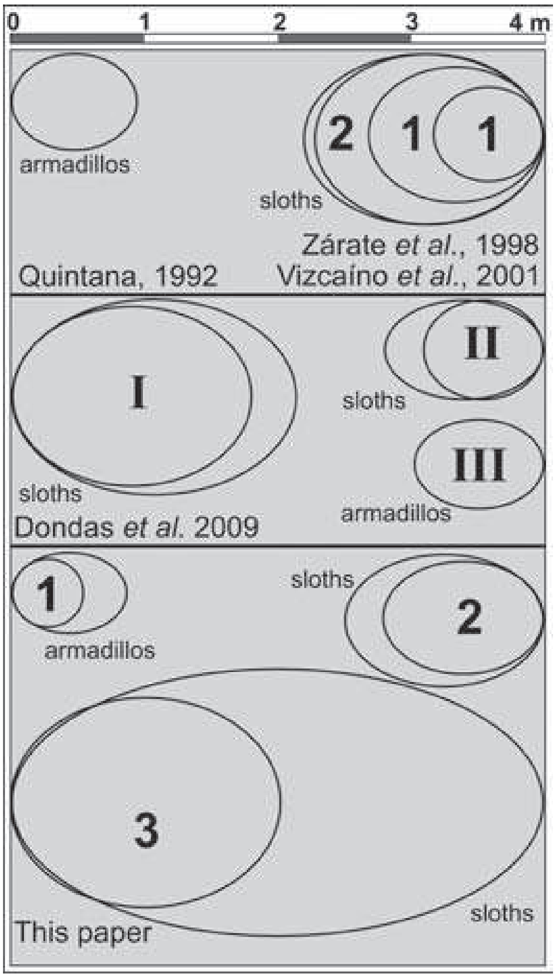

Figure 8. Paleovertebrate tunnel sizes and their probable producers. Each section of the bar at the top equals 1 m. Top left: size of the tunnel described by Quintana (1992), attributed to a dasypodid. Top right: the 2 size classes found by Zárate *et al.* (1998). The interpretation of these tunnels as sloth tunnels was emphasized by Vizcaíno *et al.* (2009). Middle: size classes as proposed by Dondas *et al.* (2009). These authors attributed Type I to a mylodontid, Type II to *Scelidotherium leptocephalum* and Type III to *Pampatherium typum*. Bottom: the 3 size classes of tunnels referred to in this contribution with the suggested producers.

ranging between little more than 1 m to more than 3 m. In the end, the analysis of the digging traces may further advance the definition of the sloth species in the future. However, only double or triple claw marks among the scratches can help by measuring the distance between the grooves and comparing them with the claws of the sloths. Nevertheless, it is not correct to simply compare the bones of the paws of the several different armadillo and sloth species with the grooves inside the tunnels, searching for a fit. One has to consider that the claws of the paws do not fossilize, only the bones, and that the bones are usually much smaller than the claws, as can be seen in present-day armadillos and anteaters. Moreover, in a single species, there may have been larger male and smaller female diggers due to sexual dimorphism, besides smaller digging offspring. The analysis of digging traces has to work with these uncertainty factors.

The length of the tunnels is an intriguing factor in this discussion. As previously described, lengths of several dozens of meters are common and tunnel networks with summed tunnel lengths of several hundred meters have been spotted. Large living burrowers, like the above-cited *Priodontes maximus* and the African aardvark (*Orycteropus afer*), usually excavate tunnels with lengths of less than 10 m, despite the many different predators for both animals. Only the permanent chambered dens, produced and used by the aardvark females, may sum tunnel lengths of some dozens of meters (Knöthig, 2005). Extremely long tunnel systems have to be related to an important factor for the paleovertebrates. Larger predators have to be excluded from this list of factors, since the only big-sized carnivores in the megafauna were the sabertooth cats (*Smilodon*) and the bears (*Arctotherium*), both smaller than the sloths (Fariña & Vizcaíno, 1995). The sloths, due to their much bigger size and the defense provided by their powerful claws, would probably have been immune to predators, much like rhinos and elephants are in Africa today.

The main reason for the long tunnels may be of paleoclimatic nature. In the rainy, present-day climate of Southern Brazil, the tunnels are uninhabitable because of their wetness. Water dripping from the roofs, running on the floors and spouting from cracks in the walls after rainy days is commonplace in the tunnels, even during the drier summer seasons. Some tunnels even fill completely with water and have been used as horizontal water wells by landowners (e.g., Site-12). These facts let us conclude that the tunnels relate to much drier paleoclimates. Whether these paleoclimates were hot or cold remains an open question; both require long tunnels for thermal isolation from the surface climate. Colder paleoclimates could have been a decisive factor for the building of isothermal tunnel systems with year-round warmer temperatures that allow some kind of hibernating of the burrowers during the winter, like present-day bears in the Northern Hemisphere. This factor may explain the high tunnel system density in the high and still cold region of Urubici (SC), mentioned earlier.

Future research of paleovertebrate tunnels will have to answer another set of questions, in addition to the discussion on the burrower identity previously outlined . The oxygen supply of long tunnels is one of those questions. In our team, we have often had trouble in long and/or narrow tunnels with the ongoing consumption of the oxygen of the tunnel atmosphere during inspections that sometimes were as short as 30 min. The big-sized paleovertebrates must have worked out a well-engineered ventilation system for the tunnel systems. It is possible that a main system of habitation tunnels and chambers were connected to several secondary tunnels whose apertures allowed the entry of fresh air. This tentative idea needs field evidence for support and refinement.

The number of tunnels found until now in Southern Brazil strongly suggests that the tunnels are common at least throughout South America, in regions where local favorable factors of geology and geomorphology are available. The dispersion of armadillos and ground sloths during the Tertiary covers the region from Patagonia to Alaska (e.g., White & MacPhee, 2001). If the digging behavior of armadillos and sloths produced the tunnels found in Southern Brazil, the same ichnofossils may be present in large tracks of South America and maybe Central and North America. Digital prospecting of "cave" pictures has already provided a few images of probable paleovertebrate tunnels in Northern Brazil, in the states of Pará, Paraíba, Pernambuco and Roraima, but these tunnels have yet to be inspected. Besides Brazil and Argentina, however, no tunnels have been detected in any other country of the Americas. An information exchange was undertaken with some speleological groups (e.g., Ogando *et al.*, 2010) to verify if these cave enthusiasts know of any caves with the characteristics of the paleovertebrate tunnels, but this attempt was not successful.

CONCLUDING REMARKS

The large set of huge paleomammal tunnels found in southern Brazil show that burrowing behavior was common in that region among specific animal groups of the Cenozoic. The highly variable regional distribution of the tunnels relates partially to local geological and geomorphologic conditions, including a sharp contrast between some Brazilian states with a lot of tunnels (RS and SC) and other states with only a few (PR and SP).

Most tunnels were excavated in sedimentary rocks, weathered igneous and metamorphic rocks and sediments of any age older than the Holocene. Tunnels located in sandstones are especially well preserved, showing its original shape and a plethora of traces on their walls: from diggers and re-occupying animals. Using these tunnels as reference, the remnants of smaller tunnels in weathered igneous and metamorphic rocks can be identified with great confidence, even without any traces on their walls.

After searching for several years through shorter tunnel remnants, several better preserved tunnel systems have been found, showing that the paleovertebrates often, or always, excavated highly complex 3-D tunnel systems. Tunnels of these systems are sinuous and raise and descend inside the hills and mountains, bifurcate and meet at larger chambers; a geometry whose general characteristics still have to be understood.

The confident identification of the diggers of the different sized tunnels is a most challenging issue. Since the possible ages of the tunnels cover the entire Cenozoic and relate to dozens of species of armadillos and sloths, it is not clear how precise this identification will be possible in the future. A system to classify the tens of thousands of digging scratches found inside the tunnels will have to be worked out, focusing only on those that may be compared to paleomammal paws. Even then, the possibility of sexual dimorphism within armadillo and sloth species may raise more difficulties in establishing a relation between scratch sizes and individual digger species. First of all, more tunnels have to be found to base future work on a larger data set.

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BIOEROSION STRUCTURES IN QUATERNARY MARINE MOLLUSKS FROM ARGENTINA

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ABSTRACT

Field and laboratory observations of individual shells of 40 dominant taxa (19 gastropods, 21 bivalves) identified from bulk samples collected in 18 localities along the Atlantic Argentine coast (Río de La Plata-southern Santa Cruz, Patagonia), allowed the recognition of 12 ichnotaxa and durophagous scars. All modes of bioerosion were considered: internal and external at all scales (macro and microborings). The bioerosive structures (*Caulostrepsis, Centrichnus, Entobia, Gastrochaenolites, Iramena, Leptichnus,Maeandropolydora, Oichnus, Pennatichnus, Pinaceocladichnus, Renichnus, Umbichnus*) can be attributed to various activities produced by bivalves, gastropods, annelids, sponges, bryozoans and cirripedians. They belong to three ethological categories: *Domichnia* (dwelling), *Fixichnia* (anchoring) and *Praedichnia* (predation). The only bioturbation structure identified is *Ophiomorpha nodosa*. Overall, they document rich benthic littoral original palaeocommunities in the Bonaerensian and Patagonian areas (Southwestern Atlantic, SWA) and indirectly the first fossil record of Ctenostomate bryozoans for the marine Quaternary in Argentina. In gastropod shells, *Domichnia* structures are dominant (e.g., *Entobia, Maeandropolydora*). Bivalves exhibit predominantly *Praedichnia* traces (e.g., *Oichnus*). The Holocene deposits, where all the identified structures occur, show the highest ichnodiversity. The large macroscale approach in space and time of our study allowed the assessment of a latitudinal ichnodiversity pattern in agreement with that observed for benthic molluskan taxa in response to changes in sea surface temperature conditions of the Mar Argentino. In Patagonia, the ecological interactions remained similar and stable within the original invertebrate palaeocommunities across time, at least since *ca* 400 Ka (MIS11). The dominant ichnogenus recognized is *Entobia* (60%), followed by *Oichnus* (50%); *Maeandropolydora* (47.5%) and *Leptichnus* (35%).

Key words: tracemakers, ethological categories, gastropods, bivalves, coastal area, SW Atlantic.

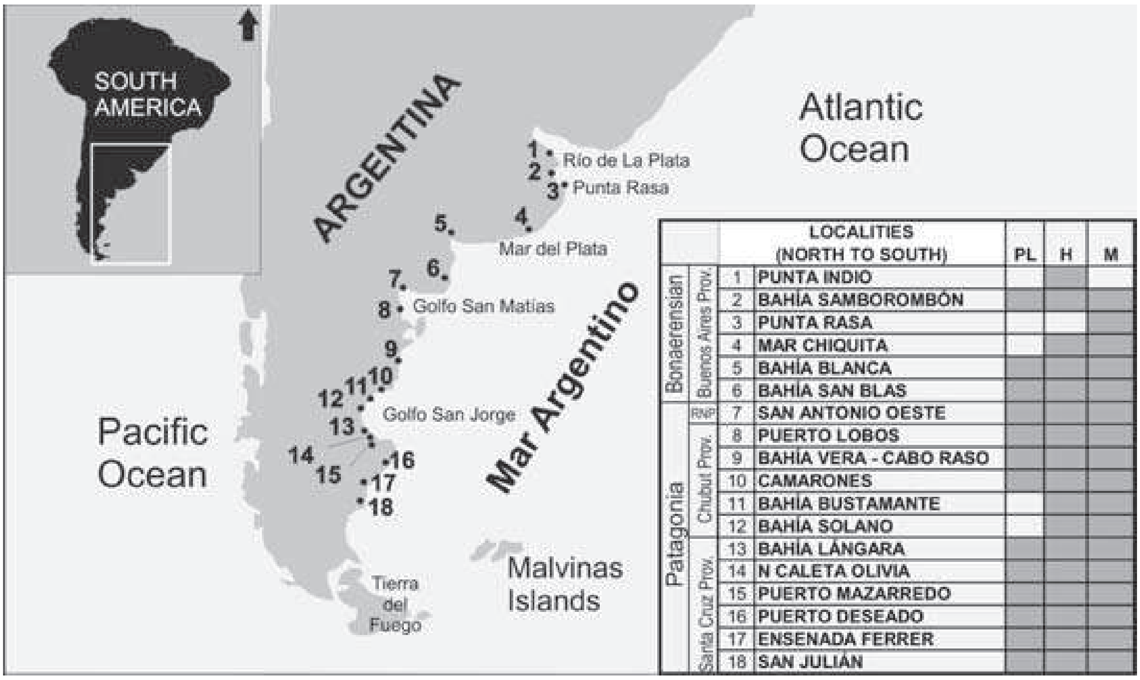
INTRODUCTION

Bioerosion structures are known to represent several kinds of activities by different organisms on hard substrates (Buatois *et al.*, 2002; Taylor & Wilson, 2003; Bromley, 2004; Lorenzo & Verde, 2004; Farinati *et al.*, 2006; Santos & Mayoral, 2008). They can be the result of mechanical and chemical processes or a combination of both in which the most common are boring, drilling, rasping and scraping activities. Substrates can either be inorganic or bioclastic (rocks, woods, bones, shells, among others).

In Neogene marine coastal environments, molluskan shells (mostly of gastropods and bivalves) represent the most common hard substrates to a great variety of tracemakers, such as porifers, polychaetes, bryozoans, and crustaceans. Bioerosion structures offer palaeoecological information concerning the potential producers, their life modes and trophic types, providing a basic framework for an ethological classification of the trace fossils. During the last decades, ichnological studies have been intensively developed and emphasis has been put on their biostratigraphical and evolutive palaeoecological significance (Buatois *et al.*, 2002; Olivero, 2003; Bromley, 2004; MacNaughton, 2007). However, in Latin America, although earlier studies of bioerosion on Quaternary molluskan shells were performed in Argentina by Pastorino & Ivanov (1996) and Farinati *et al.* (2006) and in Uruguay by Lorenzo & Verde (2004), studies from a macroscale perspective in space and time, which are useful to understand changes in ecological interactions between large communities of organisms, have not been carried out yet. This approach is also fundamental to assess whether a latitudinal range of ichnobiodiversity can be recognized in agreement with a latitudinal pattern of biodiversity observed for benthic molluskan taxa in response to local or regional physical conditions of the marine Argentine littoral.

In Quaternary marine deposits from Argentina (SW Atlantic, South America) (Aguirre & Whatley, 1995; Aguirre *et al.*, 2011a), records of dwelling (*Domichnia*), anchoring (*Fixichnia*) and predation (*Praedichnia*) are the most commonly and abundantly preserved. Bivalve and gastropod shells from beach ridges and marine terraces facies of the Bonaerensian and Patagonian coastal areas (Figures 1-3) are dominant in Pleistocene and Holocene parautochthonous skeletal concentrations. These are preserved between the Río de La Plata margin and southern Santa Cruz province, exhibiting a wide range of bioerosive structures. The dominant littoral landforms (beach ridges and marine terraces) are generally composed of coarse sediments: sand shell ridges along the Buenos Aires province and pebbly terraces along Patagonia. Bioturbation signatures are therefore uncommon or seldom distinguished within these levels. An exception to this general rule is observed in distinctive, sedimentary levels (e.g., Bahía Samborombón and Bahía Blanca areas, Buenos Aires province) with dominant fine sandy matrix where *Ophiomorpha nodosa* is a common ichnotaxon.

The material collected and examined in abundant bulk samples along the study area, involving more than 2000 km of coast, provides a wide variety of direct or indirect sources of evidence of the trace-makers which could have altered the original molluskan shells during their feeding and other living activities. The aim of this study is to document and analyze, from an ethological standpoint, bioerosive structures preserved on the dominant molluskan shells from the best exposed Holocene and Pleistocene littoral coastal deposits. The area comprises different sectors along the Bonaerensian (between the Río de la Plata and Bahía San Blas localities) and Patagonian (Río Negro, Chubut and Santa Cruz provinces), including the modern littoral (Mar Argentino, Southwestern



			LOCALITIES (NORTH TO SOUTH)	PL	H	M
Bonaerensian	Buenos Aires Prov.	1	PUNTA INDIO		▨	
		2	BAHÍA SAMBOROMBÓN	▨	▨	▨
		3	PUNTA RASA			▨
		4	MAR CHIQUITA		▨	▨
		5	BAHÍA BLANCA	▨	▨	▨
		6	BAHÍA SAN BLAS	▨	▨	▨
Patagonia	RNP	7	SAN ANTONIO OESTE	▨	▨	▨
	Chubut Prov.	8	PUERTO LOBOS	▨	▨	▨
		9	BAHÍA VERA - CABO RASO	▨	▨	▨
		10	CAMARONES	▨	▨	▨
		11	BAHÍA BUSTAMANTE		▨	▨
		12	BAHÍA SOLANO		▨	▨
	Santa Cruz Prov.	13	BAHÍA LÁNGARA	▨	▨	▨
		14	N CALETA OLIVIA	▨	▨	▨
		15	PUERTO MAZARREDO	▨	▨	▨
		16	PUERTO DESEADO	▨	▨	▨
		17	ENSENADA FERRER	▨	▨	▨
		18	SAN JULIÁN	▨	▨	▨

Figure 1. Area of study in Argentina. Abbreviations: 1-18, sampled localities; PL, Pleistocene; H, Holocene; M, Modern; RNP, Río Negro Province.

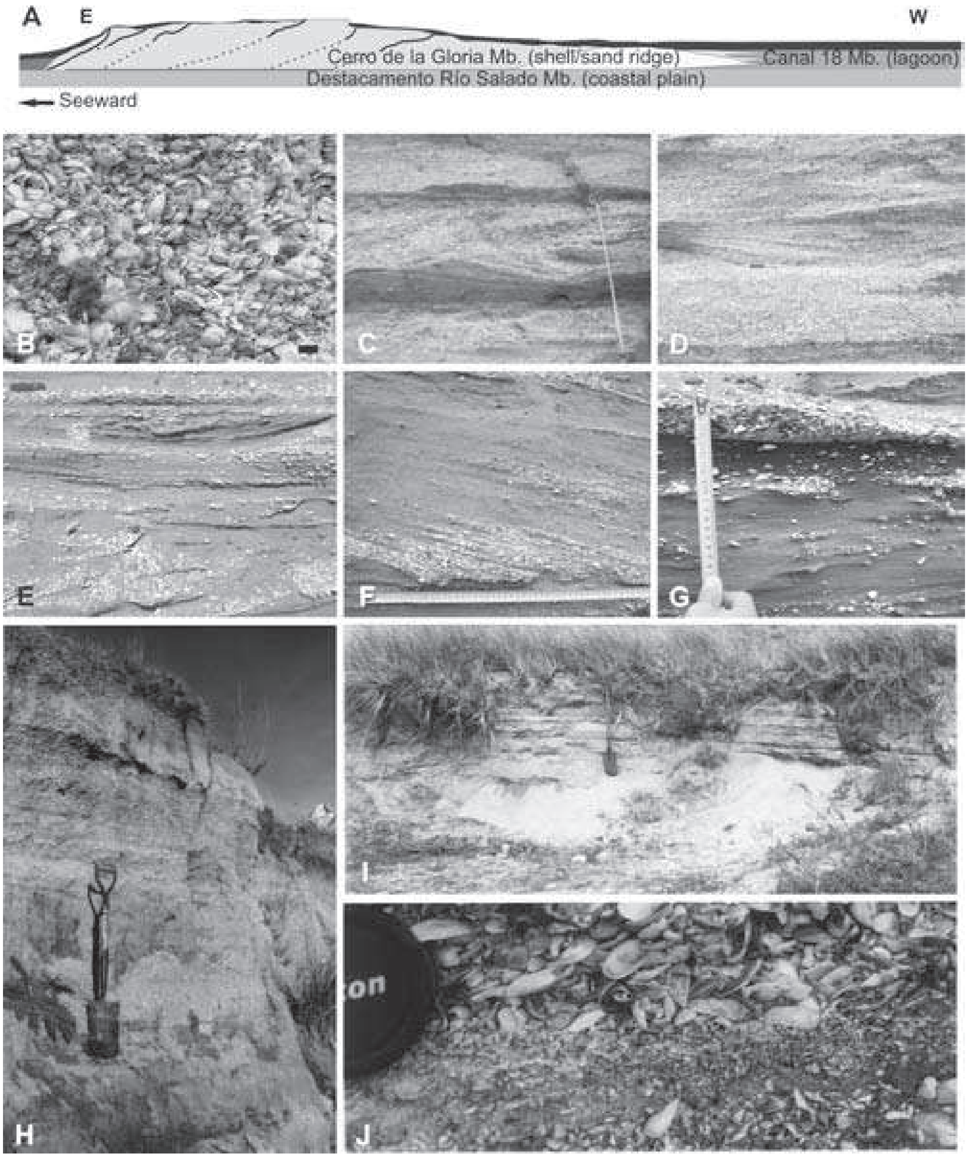


Figure 2. General sedimentological aspects of the marine Holocene deposits from Buenos Aires Province at Bahía Samborombón and Bahía Blanca localities. A, Cartoon sketch of the Holocene deposits of Bahía Samborombón showing the distribution of the units perpendicular to the actual coastline; B, general view of the massive bioclastic rudstone; C-D, different sedimentary structures in the shell ridge (Cerro de la Gloria Member); E-G, pictures of the sand ridge from Cerro de la Gloria Member, showing same shell levels intercalated with the dominant sandy composition. Different sedimentary structures are present; H-I, general views of the Holocene deposits at Bahía Blanca; J, detail picture of the shell levels in the beach ridge. B-G: Bahía Samborombón; H-J: Bahía Blanca (modified from Aguirre *et al*., 2011b). Scale bars in B: 10 mm.

Atlantic margin) (Figure 4; detailed information and complete references in Aguirre *et al*., 2011a).

GEOLOGICAL BACKGROUND

Molluskan assemblages are abundant and exceptionally well preserved in the marine Quaternary of Argentina. The richest and thickest skeletal accumulations (mostly bivalve and gastropod shells) occur in beach ridges and marine terraces which reflect beach palaeoenvironmental parameters during sea-level fluctuations. They comprise a majority of gastropod and bivalve shells, mostly parautochthonous (*sensu* Kidwell, 1986), accumulated during the last transgressive-regressive Mid-Late Pleistocene to Mid-Holocene marine cycles (Marine Isotope Stages, MIS) (Haq *et al*., 1987; Burckle, 1993; Winograd *et al*., 1997; Zachos *et al*., 2001).

These shell concentrations extend almost continuously in the coastal area from the modern supratidal zone to a few kilometers inland, reaching a maximum

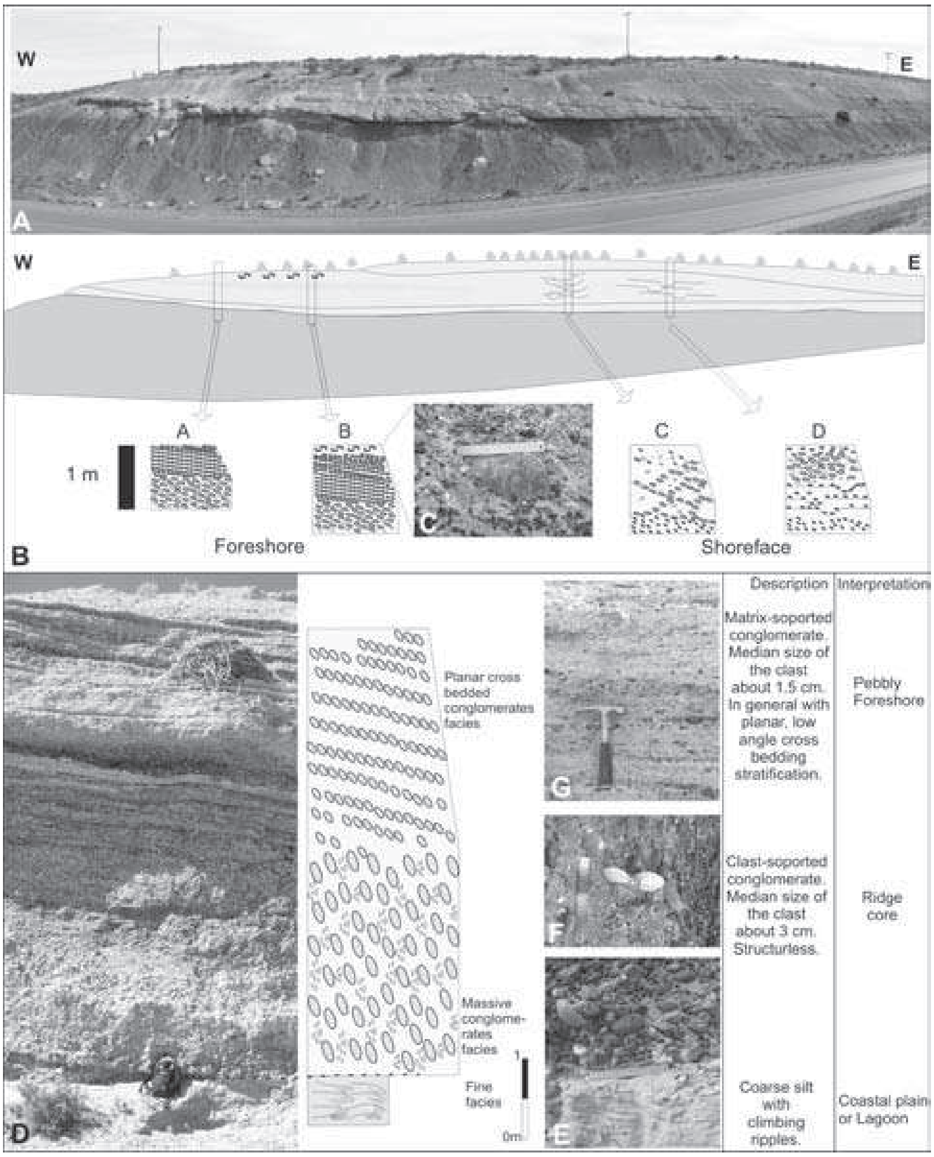
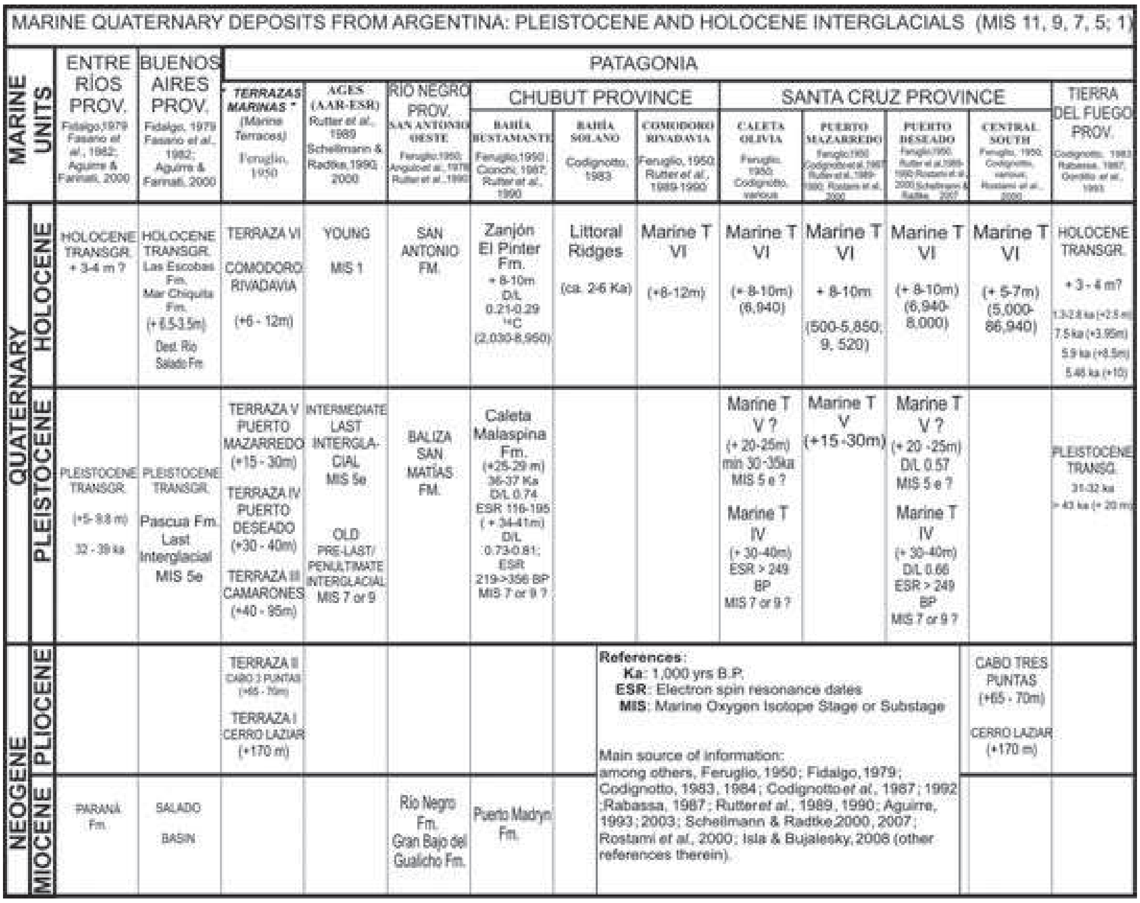


Figure 3. General sedimentological aspects of the marine Pleistocene deposits from Patagonia. A, General view of the Marine Terrace (TM) located at Camarones approximately perpendicular to the modern coastline; B, reconstruction and logging of the TM with general interpretation; C, bioclastic level composed mainly by *Ostrea* sp.; D, a view and a section reconstruction of the TM at Bahía Bustamante; E-G show the main sedimentologic (lithology and structure) aspects of the Marine Terraces at Bahía Bustamante. A-C: Bahía Camarones; D-G: Bahía Bustamante. Abbreviations: M, mud; S, sand; C, conglomerate.

of *ca* 20/30 km in some regions (e.g., south of Bahía Samborombón; Bonaerensian area, Figure 1) but they usually reach *ca* 5-10 km (Camarones, Bahía Bustamante surroundings; Patagonia). Most of the fossiliferous deposits were accumulated during the Holocene (MIS1) and Mid-Late Pleistocene (MIS11 to 5) of which the most continuous and richest ones belong to MIS1, 5 and 7. Previous studies provided complete source of information for morphostratigraphy, sedimentology, geochronological and palaeoecological aspects of these deposits (e.g., Feruglio, 1950; Farinati, 1985; Spalletti *et al.*, 1987; Cionchi, 1988; Codignotto *et al.*, 1988, 1992; Schellmann & Radtke, 2010; Aguirre *et al.*, 2011a, b; Ribolini *et al.*, 2011).

Bonaerensian Quaternary marine deposits

Along the Bahía Samborombón (S 35º58’24”; W 57º27’00’) and Bahía Blanca (S 38º42’41”; W 62º16’02”) coastal sectors occur the best exposed molluskan concentrations, mostly within beach ridge landforms. The fossiliferous deposits are correlated with MIS5 (Late Pleistocene, Pascua Formation and equivalent units) and MIS1 (Mid-Holocene;



MARINE QUATERNARY DEPOSITS FROM ARGENTINA: PLEISTOCENE AND HOLOCENE INTERGLACIALS (MIS 11, 9, 7, 5; 1)														
MARINE UNITS		ENTRE RÍOS PROV.	BUENOS AIRES PROV.	PATAGONIA										
				" TERRAZAS MARINAS "	AGES (AAR-ESR)	RÍO NEGRO PROV.	CHUBUT PROVINCE			SANTA CRUZ PROVINCE				TIERRA DEL FUEGO PROV.
		Fidalgo,1979 Fasano et al., 1982; Aguirre & Farinati, 2000	Fidalgo, 1979 Fasano et al., 1982; Aguirre & Farinati, 2000	(Marine Terraces) Feruglio, 1950	Rutter et al., 1989 Schellmann & Radtke,1990, 2000	SAN ANTONIO OESTE Feruglio,1950; Angulo et al., 1978 Rutter et al.,1990	BAHÍA BUSTAMANTE Feruglio,1950; Cionchi, 1987; Rutter et al., 1990	BAHÍA SOLANO Codignotto, 1983	COMODORO RIVADAVIA Feruglio, 1950; Rutter et al., 1989-1990	CALETA OLIVIA Feruglio, 1950; Codignotto, various	PUERTO MAZARREDO Feruglio,1950; Codignotto et al.,1987; Rutter et al.,1989-1990; Rostami et al., 2000	PUERTO DESEADO Feruglio,1950; Rutter et al.,1989-1990; Rostami et al., 2000 Schellmann & Radtke, 2007	CENTRAL SOUTH Feruglio, 1950; Codignotto, various; Rostami et al., 2000	Codignotto, 1983; Rabassa, 1987; Gordillo et al., 1993
QUATERNARY	HOLOCENE	HOLOCENE TRANSGR. + 3-4 m ?	HOLOCENE TRANSGR. Las Escobas Fm. Mar Chiquita Fm. (+ 6.5-3.5m) Dest. Río Salado Fm	TERRAZA VI COMODORO RIVADAVIA (+6 - 12m)	YOUNG MIS 1	SAN ANTONIO FM.	Zanjón El Pinter Fm. + 8-10m D/L 0.21-0.29 ¹⁴C (2,030-8,950)	Littoral Ridges (ca. 2-6 Ka)	Marine T VI (+6-12m)	Marine T VI (+ 8-10m) (6,940)	Marine T VI + 8-10m (500-5,850; 9, 520)	Marine T VI (+ 8-10m) (6,940-8,000)	Marine T VI (+ 5-7m) (5,000-86,940)	HOLOCENE TRANSGR. + 3 - 4 m? 1.3-2.8 ka (+2.5 m) 7.5 ka (+3.95m) 5.9 ka (+8.5m) 5.46 ka (+10)
	PLEISTOCENE	PLEISTOCENE TRANSGR. (+5- 9.8 m) 32 - 39 ka	PLEISTOCENE TRANSGR. Pascua Fm. Last Interglacial MIS 5e	TERRAZA V PUERTO MAZARREDO (+15 - 30m) TERRAZA IV PUERTO DESEADO (+30 - 40m) TERRAZA III CAMARONES (+40 - 95m)	INTERMEDIATE LAST INTERGLA-CIAL MIS 5e OLD PRE-LAST/ PENULTIMATE INTERGLACIAL MIS 7 or 9	BALIZA SAN MATÍAS FM.	Caleta Malaspina Fm. (+25-29 m) 36-37 Ka D/L 0.74 ESR 116-195 (+ 34-41m) D/L 0.73-0.81; ESR 219->356 BP MIS 7 or 9 ?			Marine T V ? (+ 20-25m) min 30-35ka MIS 5 e ? Marine T IV (+ 30-40m) ESR > 249 BP MIS 7 or 9 ?	Marine T V (+15 -30m)	Marine T V ? (+ 20 -25m) D/L 0.57 MIS 5 e ? Marine T IV (+ 30-40m) D/L 0.66 ESR > 249 BP MIS 7 or 9 ?		PLEISTOCENE TRANSG. 31-32 ka > 43 ka (+ 20 m)
NEOGENE	PLIOCENE			TERRAZA II CABO 3 PUNTAS (+65 - 70m) TERRAZA I CERRO LAZIAR (+170 m)				**References**: **Ka**: 1,000 yrs B.P. **ESR**: Electron spin resonance dates **MIS**: Marine Oxygen Isotope Stage or Substage Main source of information: among others, Feruglio, 1950; Fidalgo, 1979; Codignotto, 1983, 1984; Codignotto et al., 1987; 1992 ;Rabassa, 1987; Rutter et al., 1989, 1990; Aguirre, 1993; 2003; Schellmann & Radtke,2000, 2007; Rostami et al., 2000; Isla & Bujalesky, 2008 (other references therein).					CABO TRES PUNTAS (+65 - 70m) CERRO LAZIAR (+170 m)	
	MIOCENE	PARANÁ Fm.	SALADO BASIN			Río Negro Fm. Gran Bajo del Gualicho Fm.	Puerto Madryn Fm.							

Figure 4. Stratigraphical synthesis of the marine units of Quaternary units sampled in Argentina and correlation with other areas in South America. Neogene deposits where the same molluskan taxa and/or ichnotaxa were observed are mentioned without accurate age correlation due to scarce (Mid-Late Miocene) or none (Pliocene) modern dating available. Complete source of information in Feruglio (1950), Closs & Madeira (1968), Malumián (1970), Fidalgo (1979), Fasano *et al*. (1982), Codignotto *et al*., (1987), Aguirre & Farinati (2000), del Río (2000), Martínez & del Río (2002), Aguirre (2003), Aguirre *et al*. (2008, 2009; complete references therein). Modified from Aguirre *et al*. (2008). The Quaternary is maintained according to the Argentine Committee on Stratigraphy (Riccardi, 2007).

Las Escobas Formation and equivalent units) (Figure 4) and the most interesting examples belong to the Holocene, while the Pleistocene examples are very scarce and present a patchy distribution.

The Pascua Formation (8 m above present m.s.l.) is composed of loessic silts and sandy levels, with abundant concentrations of highly cemented shells, which are linked to estuarine and littoral palaeoenvironments, both intertidal and infralittoral. No sedimentological studies are available for the area. The Holocene sediments (5 m above present m.s.l.) are grouped into Las Escobas Formation (Figure 2A) and are composed of three members: Destacamento Río Salado Member (tidal flat deposits, 5.8-7 ka B.P.), Cerro de la Gloria Member (beach ridge deposits, *ca* 3-8 ka B.P.) and Canal 18 Member (coastal lagoon deposits, 6-7 ka B.P) (Fidalgo, 1979 modified by Fucks *et al*., 2010). The Destacamento Río Salado Mb is about 0.5 m thick and composed of silty to very fine-grained sands with wavy stratification. The Canal 18 Mb is 3 m thick and is composed of fine-grained sands and silts, usually containing both articulated bivalve shells in life position and tabular levels of disarticulated shells with no preferential orientation. In the Cerro de la Gloria Member (bioclastic ridges 200 m wide and 5 m thick, oriented subparallel to the modern coastline, Figure 2A), the main lithologic components are molluskan shells (+ 70 %, Figures 2B-D) (Aguirre *et al*., 2011b) with low proportion of coarse to medium-grained sands. In cross-section perpendicular to the coastline, the ridge shows lenticular, trough and sigmoidal geometry; occasionally there are planar beds (Figures 2C-G). Cross bedding, hummocky cross stratification and parallel stratification are the most common sedimentary structures. All the shells analyzed in this study belong to these beach ridge sections.

Considering the palaeoenvironmental evolution of the studied deposits, the sea-level rise generated a transgressive surface that records the beginning of the Destacamento Río Salado Mb in the Samborombón Bay. During this transgressive stage, sediment flux from the continent was reduced. This event caused several storm episodes in which molluskan shells were accumulated generating the chenier, while the finer-grained sediments were washed by tides. When the chenier was completely formed, a lagoonal environment developed toward the continent (Canal 18 Mb).

On the other hand, at Bahía Blanca area only Holocene deposits were sampled. They are made of ridges exhibiting coarse to medium sandy lithology with high percentages of molluskan shells (Figures 2H-J) (Aliotta *et al*., 2001). A littoral palaeoenvironment of moderate energetic conditions with frequent storm events deposited these ridges forming multi-episodic shell concentrations (tempestites), similar to the Bahía Samborombón Holocene ridges.

Patagonian Quaternary marine terraces

The molluskan shell concentrations along Patagonia (Río Negro, Chubut and Santa Cruz provinces; Figures 1, 3) integrate beach ridges, marine terraces and estuarine deposits locally known as "Marine Terraces" (MT), so-called MTIV, V and VI *sensu* Feruglio (1950). They are derived from at least four Pleistocene high sea-level episodes, MIS 5 (*ca* 125 ka), 7 (*ca* 225 ka), 9 (*ca* 325 ka), 11 (*ca* 400 ka), the last one during the Holocene (MIS1, present day) (Codignotto *et al*., 1988; Rutter *et al*., 1989, 1990; Schellmann & Radtke, 2000, 2003, 2010; Schellmann, 2007). Contrary to the marine Pleistocene deposits displayed along the Bonaerensian sector, the Patagonian Pleistocene deposits (MTIV and V) are very abundant, widely spread and better preserved. They reach between *ca* +10-74 m above m.s.l. and are extensive. However, the best preserved shell concentrations belong to MIS5 (Last Interglacial episode) (Figure 4). The Holocene landforms (MTVI), at ca 5-12 m above present m.s.l., provide the majority of the studied shell materials. This fauna is more diverse, better preserved and has abundant bioerosion structures. In the Río Negro province, Pleistocene littoral ridges and Holocene terraces were surveyed in San Antonio Oeste and the surroundings of Golfo San Matías. The molluskan samples come from Pleistocene deposits assigned to the Baliza San Matías Formation and Holocene deposits of the San Antonio Formation, and ranged between MIS9 and MIS 1. In Chubut province, the best preserved deposits are located at: Puerto Lobos, Bahía Vera-Cabo Raso, Camarones (Figures 3A-C), Bahía Bustamante (Figures 3D-G), Caleta Malaspina, Bahía Solano and Comodoro Rivadavia. The Pleistocene samples belong to MIS11, 9, 7, 5, and most of them are from Caleta Malaspina Formation. (MTV and equivalents). The Holocene deposits are assigned to the Zanjón El Pinter Formation (MTVI and equivalents). In Santa Cruz province, the studied areas are located in Golfo San Jorge (north and south of Caleta Olivia, Puerto Mazarredo, Bahía Sanguinetto), Puerto Deseado-Bahía Laura, Ensenada Ferrer, Rincón del Buque and Puerto Coig surroundings. They belong to MIS9, 7, 5 and 1.

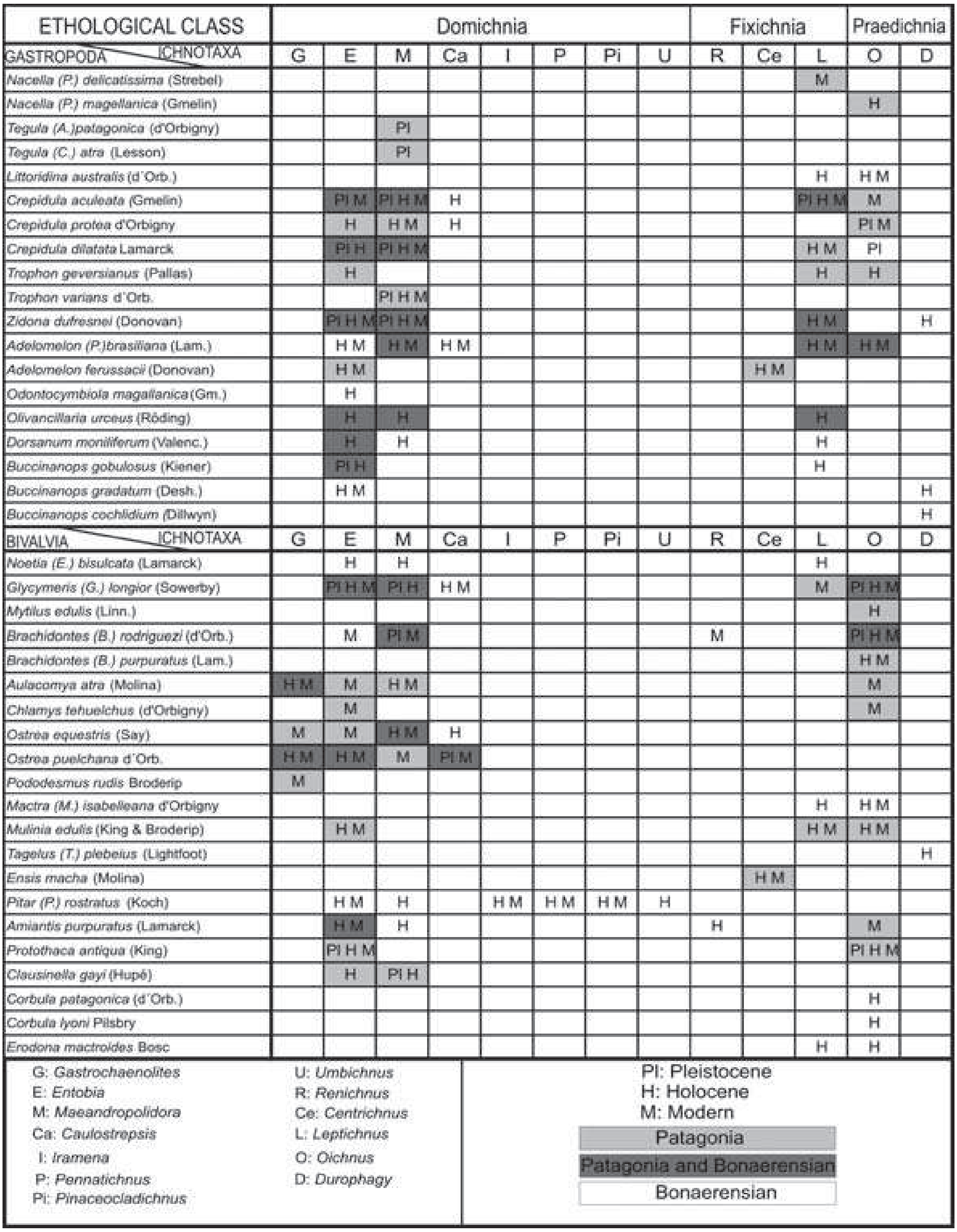
In general, the marine terraces from Patagonia have two different deposits. The central part is mainly composed of massive, clast-supported conglomerate (Figure 3F), with a scarce sandy matrix interpreted as the core terrace. On the other hand, above the massive core, well stratified sediments (fine conglomerates with abundant sandy matrix) are apparent, representing the foreshore and shoreface deposits (Figure 3G). These sediments commonly show low angle planar cross stratification and trough cross stratification. All the shells analyzed in this study come from the upper part of the terraces, where the shells are more abundant and better preserved.

MATERIAL AND METHODS

Different bioerosion structures were considered: internal bioerosion (boring, durophagy) and external bioerosion (scratching, etching) (Bromley, 2004) (Table 1). Following the ichnological methodologies typically applied to marine Neogene successions that were formed in analogous paleoenvironments (Martinell *et al*., 1982; Mayoral, 1987, 1988; Martinell, 1989; Mayoral, 1991; Martinell *et al*., 1999; Farinati & Zavala, 2002; Gibert *et al*., 2004; Lorenzo & Verde, 2004; Farinati *et al*., 2006; Farinati, 2007; Domènech *et al*., 2009), the information provided in this study comes from field observations and sampling from a total of 30 localities. The analyzed shell specimens were collected from Pleistocene and Holocene beach ridge deposits, and along the modern beach in the Bonaerensian and Patagonian coastal sectors along the Atlantic Argentinean coast. Individual shells of dominant taxa collected in bulk samples from 18 selected localities (Figure 1) were washed and sieved in the laboratory and external and internal shell surfaces were characterized.

Emphasis was put on those taxa which can be recognized as the most characteristic, abundant or dominant, and with a wider spatial and temporal distribution (e.g., *Crepidula, Zidona, Buccinanops* among gastropods and *Pitar, Amiantis, Ostrea, Aulacomya* among bivalves). However, there are strong taxonomic differences between the Bonaerensian and Patagonian sectors and no taxon is preserved along the entire area and through the whole time span herein analyzed (Aguirre *et al*., 2011b). This situation makes it difficult to statistically compare the bioerosion patterns of the different taxa from different areas and/or ages (Figure 5).

A total of 500 shells were examined for the identification of the bioerosion ichnotaxa and, later, they were described and illustrated. They were collected from beach ridges and marine terraces facies of Mid to Late Pleistocene and Holocene age (MIS 9-1) and from the modern littoral adjacent to the fossiliferous deposits. Additionally, shell material from museum



ETHOLOGICAL CLASS	Domichnia								Fixichnia			Praedichnia	
GASTROPODA / ICHNOTAXA	G	E	M	Ca	I	P	Pi	U	R	Ce	L	O	D
Nacella (P.) delicatissima (Strebel)											M		
Nacella (P.) magellanica (Gmelin)												H	
Tegula (A.)patagonica (d'Orbigny)			Pl										
Tegula (C.) atra (Lesson)			Pl										
Littoridina australis (d´Orb.)											H	H M	
Crepidula aculeata (Gmelin)		Pl M	Pl H M	H							Pl H M	M	
Crepidula protea d'Orbigny		H	H M	H								Pl M	
Crepidula dilatata Lamarck		Pl H	Pl H M								H M	Pl	
Trophon geversianus (Pallas)		H									H	H	
Trophon varians d´Orb.			Pl H M										
Zidona dufresnei (Donovan)		Pl H M	Pl H M								H M		H
Adelomelon (P.)brasiliana (Lam.)		H M	H M	H M							H M	H M	
Adelomelon ferussacii (Donovan)		H M								H M			
Odontocymbiola magallanica (Gm.)		H											
Olivancillaria urceus (Röding)		H	H								H		
Dorsanum moniliferum (Valenc.)		H	H								H		
Buccinanops gobulosus (Kiener)		Pl H									H		
Buccinanops gradatum (Desh.)		H M											H
Buccinanops cochlidium (Dillwyn)													H
BIVALVIA / ICHNOTAXA	G	E	M	Ca	I	P	Pi	U	R	Ce	L	O	D
Noetia (E.) bisulcata (Lamarck)		H	H								H		
Glycymeris (G.) longior (Sowerby)		Pl H M	Pl H	H M							M	Pl H M	
Mytilus edulis (Linn.)												H	
Brachidontes (B.) rodriguezi (d'Orb.)		M	Pl M						M			Pl H M	
Brachidontes (B.) purpuratus (Lam.)												H M	
Aulacomya atra (Molina)	H M	M	H M									M	
Chlamys tehuelchus (d'Orbigny)		M										M	
Ostrea equestris (Say)	M	M	H M	H									
Ostrea puelchana d´Orb.	H M	H M	M	Pl M									
Pododesmus rudis Broderip	M												
Mactra (M.) isabelleana d'Orbigny											H	H M	
Mulinia edulis (King & Broderip)		H M									H M	H M	
Tagelus (T.) plebeius (Lightfoot)													H
Ensis macha (Molina)										H M			
Pitar (P.) rostratus (Koch)		H M	H		H M	H M	H M	H					
Amiantis purpuratus (Lamarck)		H M	H						H			M	
Protothaca antiqua (King)		Pl H M										Pl H M	
Clausinella gayi (Hupé)		H	Pl H										
Corbula patagonica (d´Orb.)												H	
Corbula lyoni Pilsbry												H	
Erodona mactroides Bosc											H	H	

G: *Gastrochaenolites*
E: *Entobia*
M: *Maeandropolidora*
Ca: *Caulostrepsis*
I: *Iramena*
P: *Pennatichnus*
Pi: *Pinaceocladichnus*

U: *Umbichnus*
R: *Renichnus*
Ce: *Centrichnus*
L: *Leptichnus*
O: *Oichnus*
D: *Durophagy*

Pl: Pleistocene
H: Holocene
M: Modern

Patagonia
Patagonia and Bonaerensian
Bonaerensian

Figure 5. List of ichnotaxa recorded in gastropod and bivalve taxa as observed in shells from the Quaternary deposits sampled. Molluskan taxa listed according to taxonomy. Ichnogenera and durophagous scars are listed according to the ethological classification.

Table 1. Ichnotaxa identified in gastropod and bivalve shells recovered from Pleistocene (Pl), Holocene (H) and modern (M = Recent) deposits in Argentina. Age, area and bibliographic sources are provided. Ethological classification of ichnotaxa and tracemakers are also indicated.

Ichnogenus	Author	Ethology	Tracemakers	References	Age	Areas
Caulostrepsis	Clarke, 1908	Domichnia	annelids	Bromley & D'Alessandro, 1983	Pl -H –M	BON-PAT
Centrichnus	Bromley & Martinell, 1991	Fixichnia	cirripedians	Bromley & Martinell,1991	H- M	PAT
Entobia	Bronn, 1838	Domichnia	sponges	Bromley & D'Alessandro, 1984	Pl -H –M	BON-PAT
Gastrochaenolites	Leymerie, 1842	Domichnia	bivalves	Kelly & Bromley, 1984	H- M	BON-PAT
Iramena	Boekshoten, 1970	Domichnia	bryozoans	Mayoral, 1988	H- M	BON
Leptichnus	Taylor *et al.*, 1999	Fixichnia	bryozoans	Taylor *et al.*, 1999	Pl -H –M	BON-PAT
Maeandropolydora	Voigt, 1965	Domichnia	annelids	Bromley & D'Alessandro, 1983	Pl -H –M	BON-PAT
Oichnus	Bromley, 1981	Praedichnia	gastropods	Bromley, 1981	Pl -H –M	BON-PAT
Pennatichnus	Mayoral, 1988	Domichnia	bryozoans	Mayoral, 1988	H- M	BON
Pinaceocladichnus	Mayoral, 1988	Domichnia	bryozoans	Mayoral, 1988	H- M	BON
Renichnus	Mayoral, 1987	Fixichnia	gastropods	Mayoral, 1987	H- M	BON
Umbichnus	Martinell *et al.*, 1999	Domichnia	unknown	Martinell *et al.*, 1999	H- M	BON
Durophagia		Praedichnia	crustaceans	Martinell *et al.*, 1982	H- M	BON-PAT

collections (fossil and modern) and samples recovered by oceanographic campaigns were compared (Museo de La Plata, Museo Argentino "Bernardino Rivadavia" from Buenos Aires). This analysis allowed the identification of 12 ichnotaxa that can be attributed to various activities of bivalves, gastropods, annelids, sponges, bryozoans and cirripedians (Table 1).

BIOEROSION STRUCTURES

From an ethological perspective (Seilacher, 1953; Bromley, 1996; Gibert *et al.*, 2004) three categories (*Domichnia, Fixichnia, Praedichnia*) have been recognized involving 12 ichnotaxa and durophagous scars (Table 1). They have been documented, at least, since the Mid-Late Pleistocene to the present in successive analyses, although several have been also recorded for Late Oligocene deposits from Patagonia (Parras & Casadío, 2006).

Structures assigned to *Domichnia* (Seilacher, 1953) are created by endoskeletozoan producers (Taylor, 2002), including borings. They are represented by cavities of the shells used as dwellings. *Fixichnia* (Gibert *et al.*, 2004) are represented by attachment scars, caused by episkeletozoans (Taylor, 2002) which anchor or fix themselves to the hard substrate (shell surface). *Praedichnia* (Ekdale, 1985) include drill holes which are perforations through the shell surface produced by carnivores. Durophagous structures are assigned to shell breakage by predator attacks of different taxonomic groups.

Systematic ichnology

Ichnogenus *Caulostrepsis* Clarke, 1908
(Table 1; Figures 6A-C)

Analyzed material. This ichnogenus was found in *Crepidula aculeata, C. protea, Adelomelon brasiliana, Glycymeris longior, Ostrea equestris* and *O. puelchana.*
Stratigraphic range. Devonian to Recent.
Occurrence in Argentina. Oligocene to Recent.

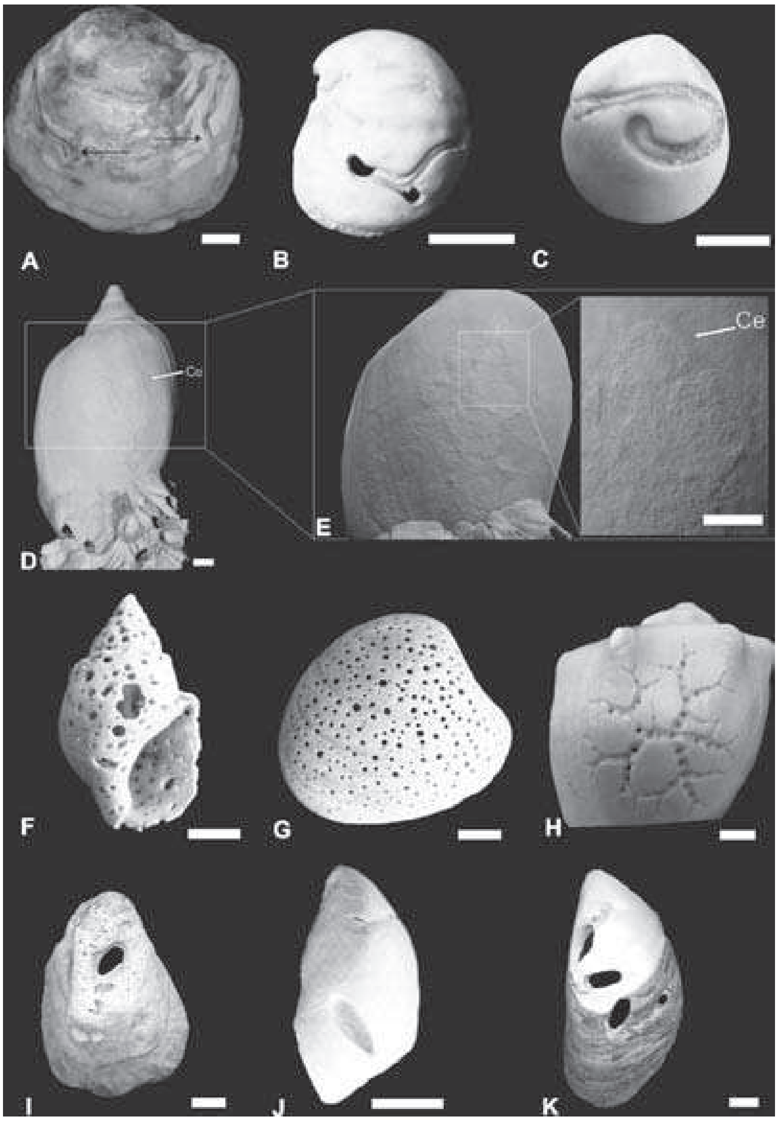


Figure 6. A, *Caulostrepsis* in *Ostrea puelchana* (Pleistocene, San Antonio Oeste, PI-UNS 3170); B, *Caulostrepsis cretacea* in *Crepidula aculeata* (Holocene, Bahía Blanca, PI-UNS 3164); C, *Caulostrepsis taeniola* in *Glycymeris longior* (Modern, Mar Chiquita, PI-UNS 3171); D-E, *Centrichnus* in *Adelomelon ferussacii* (Modern, Ensenada Ferrer, DCG-MLP0007-900); F, *Entobia* in *Buccinanops gradatum* (Holocene, Bahía Blanca, PI-UNS 3165); G, *Entobia* in *Pitar rostratus* (Modern, Bahía Blanca, PI-UNS 3166); H, *Entobia* in *Adelomelon brasiliana* (Modern, Bahía Blanca, PI-UNS 3167); I, *Gastrochaenolites* in *Ostrea* cf *equestris* (Modern, Río Negro, DCG-MLP0007-901); J, *Gastrochaenolites torpedo* in *Ostrea* sp. (Holocene, Bahía Blanca, PI-UNS 3168); K, *Gastrochaenolites* in *Aulacomya atra* (Modern, Río Negro, DCG-MLP0007-902). Scale bars: 10 mm.

Description. U-shaped borings that have a vane connecting the limbs of the U-boring (Bromley, 2004), with more or less complex designs (Bromley & D'Alessandro, 1983).
Ethological classification. *Domichnia*.
Tracemakers. Spionid polychaetes annelids.
Discussion. *Caulostrepsis* has been recognized in Neogene bivalves (Mayoral, 1991; Farinati & Zavala, 2002; Farinati, 2007; Lorenzo & Verde, 2004; Santos & Mayoral, 2008) and bouchardiid brachiopods (Rodrigues *et al*., 2008). Nevertheless, this ichnogenus has not been recorded in *Crepidula* (Gastropoda). Two ichnospecies are recognized: *Caulostrepsis cretacea* Voigt, 1971 (Figure 6B) and *Caulostrepsis taeniola* Clarke, 1908 (Figure 6C).

Ichnogenus *Centrichnus* Bromley & Martinell, 1991
(Table 1; Figures 6D-E)

Analyzed material. This ichnogenus occurs in *Adelomelon ferussacii* and *Ensis macha*.
Stratigraphic range. Cretaceous to Recent.
Occurrence in Argentina. Miocene to Recent.
Description. This ichnogenus comprises centrically arcuate or ring-shaped grooves arranged. The

specimen has 1 cm in diameter. The central part presents a smooth surface (0.5 cm in diameter) while it is surrounded by an external rough ring.
Ethological classification. *Fixichnia.*
Tracemakers: Barnacles.

Ichnogenus *Entobia* Bronn, 1837
(Table 1; Figures 6F-H)

Analyzed material. This ichnogenus was found in *Crepidula aculeata, C. protea, C. dilatata, Trophon geversianus, Zidona dufresnei, Adelomelon brasiliana, A. ferussacii, Odontocymbiola magellanica, Olivancillaria urceus, Dorsanum moniliferum, Buccinanops globulosus, B. gradatum, Noetia bisulcata, Glycymeris longior, Brachidontes rodriguezi, Aulacomya atra, Ostrea equestris, Ostrea puelchana, Mulinia edulis, Pitar rostratus, Amiantis purpuratus, Protothaca antiqua* and *Clausinella gayi.*
Stratigraphic range. Ordovician to Recent.
Occurrence in Argentina. Oligocene to Recent.
Description. Numerous borings with small openings (0.5-1 mm), nearly circular in shape. They are distributed irregularly on the bioclast surface.
Ethological classification. *Domichnia.*
Tracemakers. *Entobia* borings are produced by clionid sponges.
Discussion. Some specimens show a stenomorphic boring system (Figure 6H) (Bromley & D´Alessandro, 1984).

Ichnogenus *Gastrochaenolites* Leymerie, 1842
(Table 1; Figures 6I-K)

Analyzed material. This ichnogenus occurs in *Ostrea puelchana, Ostrea equestris, Aulacomya atra* and *Pododesmus rudis.*
Stratigraphic range. Ordovician to Recent.
Occurrence in Argentina. Oligocene to Recent.
Description. Clavate boring with elongate to ovate aperture and most commonly circular cross section.
Ethological classification. *Domichnia.*
Tracemakers. Borings of this type are constructed by endolithic bivalves such as *Lithophaga.*
Discussion. One ichnospecies is recognized in the studied material: *Gastrochaenolites torpedo* Kelly & Bromley, 1984 (Figure 6J). This ichnospecies is characterized by an elongate smooth boring, widest point closet to mid-line with the base acutely parabolic and an oval aperture.

Ichnogenus *Iramena* Boekschoten, 1970
(Table 1; Figures 7A-B)

Analyzed material. This ichnogenus was found in *Pitar rostratus.*
Stratigraphic range. Jurassic to Recent.
Occurrence in Argentina. Holocene to Recent.
Description. Circular to ovate apertures placed very close to the thin tunnels in a lateral position.
Ethological classification. *Domichnia.*
Tracemakers. Ctenostomata bryozoans.

Ichnogenus *Leptichnus* Taylor,
Wilson & Bromley, 1999
(Table 1; Figures 7C-E)

Analyzed material. This ichnogenus was found in *Nacella delicatissima, Littoridina australis, Crepidula aculeata, C. dilatata, Trophon geversianus, Zidona dufresnei, Adelomelon brasiliana, Olivancilaria urceus, Dorsanum moniliferum, Buccinanops globulosus, Noetia bisulcata, Glycymeris longior, Mactra isabelleana, Mulinia edulis* and *Erodona mactroides.*
Stratigraphic range. Cretaceous to Recent.
Occurrence in Argentina. Oligocene to Recent.
Description. Subcircular, elliptical or pear-shaped pits, uniserially or multiserially arranged.
Ethological classification. *Fixichnia.*
Tracemakers. Cheilostome bryozoans.
Discussion. The mechanism of etching into their calcareous substrates is unknown. The ichnospecies *Leptichnus dromeus* Taylor, Wilson and Bromley (1999) occurs in the studied samples (Figures 7C-D). This ichnospecies is mainly subcircular, elliptical or pear-shaped pits, uniserially arranged, sometimes with a thin groove extending between the pits, but never linking them. The pits have their long axes congruent with the linear direction of the series. Series commonly branch to give new uniserial series. All pits are excavated to approximately the same depth and all of them enter the substrate perpendicularly.

Ichnogenus *Maeandropolydora* Voigt, 1965
(Table 1, Figures 7F-H)

Analyzed material. This ichnogenus was found in *Tegula patagonica, T. atra, Crepidula aculeata, C. protea, C. dilatata, Trophon varians, Zidona dufresnei, Adelomelon brasiliana, Olivancillaria urceus, Dorsanum moniliferum, Noetia bisulcata, Glycymeris longior, Brachidontes rodriguezi, Aulacomya atra, Ostrea equestris, Ostrea puelchana, Pitar rostratus, Amiantis purpuratus* and *Clausinella gayi.*
Stratigraphic range. Triassic to Recent.
Occurrence in Argentina. Oligocene to Recent.
Description. Large, isolated, tubular galleries, irregularly bending and constant in diameter, showing generally a meandering development. Two or more apertures are possible.
Ethological classification. *Domichnia.*
Tracemakers. Spionids polychaetes annelids.
Discussion. *Maeandropolydora* has been recorded in bivalves (especially *Ostrea* by Bromley & D´Alessandro,

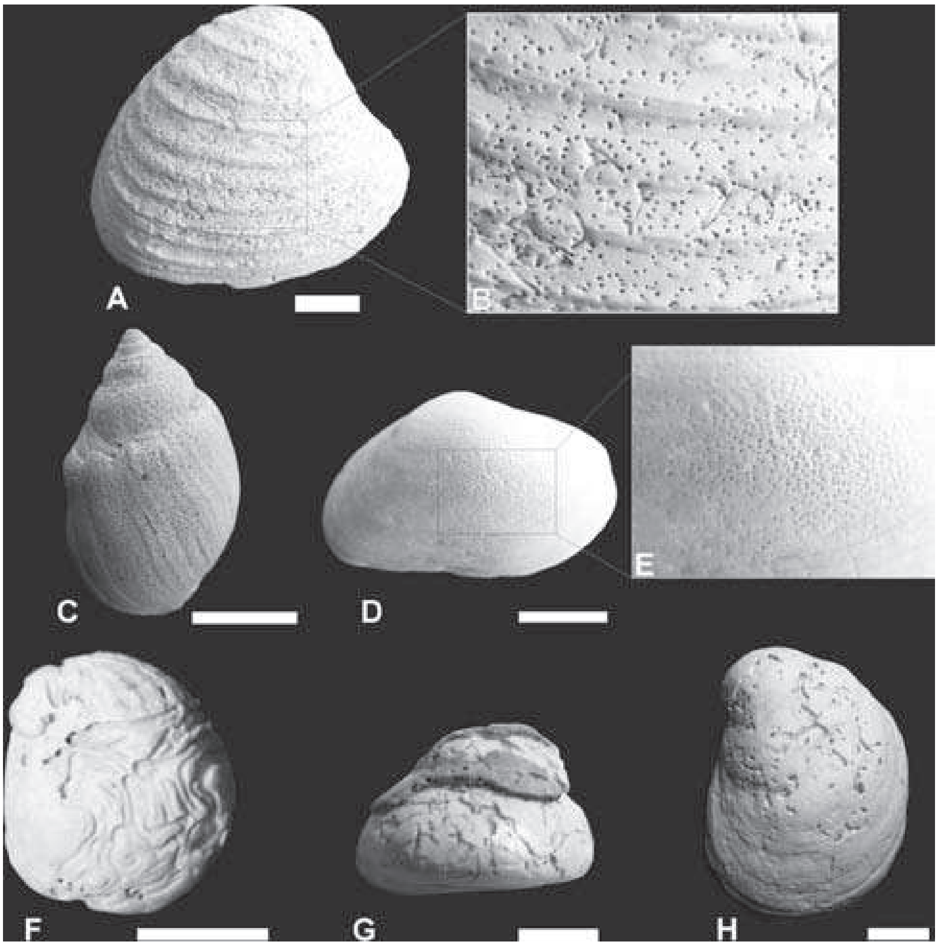


Figure 7. A-B, *Iramena* in *Pitar rostratus* (Holocene, Bahía Samborombón); C, *Leptichnus dromeus* in *Buccinanops globulosus* (Modern. Bahía Blanca, PI-UNS 3169); D-E, *Leptichnus dromeus* in *Mactra isabeleana* (Modern, Bahía San Blas PI-UNS 3173); F, *Maeandropolydora sulcans* in *Crepidula aculeata* (Holocene, Bahía Blanca, PI-UNS 3174); G, *Maeandropolydora* in *Tegula atra* (Pleistocene, Bahía Bustamante, DCG-MLP0007-903); H, *Maeandropolydora* in *Crepidula aculeata* (Modern, Bahía Bustamante, DCG-MLP0007-23). Scale bars: 10 mm.

1983; Farinati & Zavala, 2002; Farinati, 2007), and gastropods (Domènech *et al.*, 2009). Nevertheless, it has not been mentioned previously for the genus *Crepidula* (Gastropoda). One ichnospecies is recognized in the studied material: *Maeandropolydora sulcans* Voigt, 1965 (Figure 7F). This ichnospecies is characterized by cylindrical galleries with long development and constant diameter irregularly twisted into complicated convolutions, commonly looping round and coming into contact with itself.

Ichnogenus *Oichnus* Bromley, 1981
(Table 1; Figures 8A-E)

Analyzed material. *Nacella magellanica, Littoridina australis, Crepidula aculeata, C. protea, C. dilatata, Trophon geversianus, Adelomelon brasiliana, Glycymeris longior, Mytilus edulis, Brachidontes rodriguezi, B. purpuratus, Aulacomya atra, Chlamys tehuelchus, Mactra isabelleana, Mulinia edulis, Amiantis purpuratus, Protothaca antiqua, Corbula patagonica, Corbula lyoni* and *Erodona mactroides.*

Stratigraphic range. Cambrian to Recent.

Occurrence in Argentina. Miocene to Recent.

Description. Circular to subcircular holes oriented essentially perpendicular to their host substrate.

Ethological classification. *Praedichnia.*

Tracemakers. Naticid and muricid gastropods.

Discussion. *O. simplex* Bromley, 1981 (Figures 8A, D) and *O. paraboloides* Bromley, 1981 were recognized in the studied material (Figures 8B-C, E). *O simplex* has a simple cylindrical or subcylindrical form with an axis more or less perpendicular to the substrate surface. On the other hand, *O. paraboloides* is formed by holes "having a spherical paraboloid form, truncated in those cases where the boring penetrates right through the substrate" (Bromley, 1981).

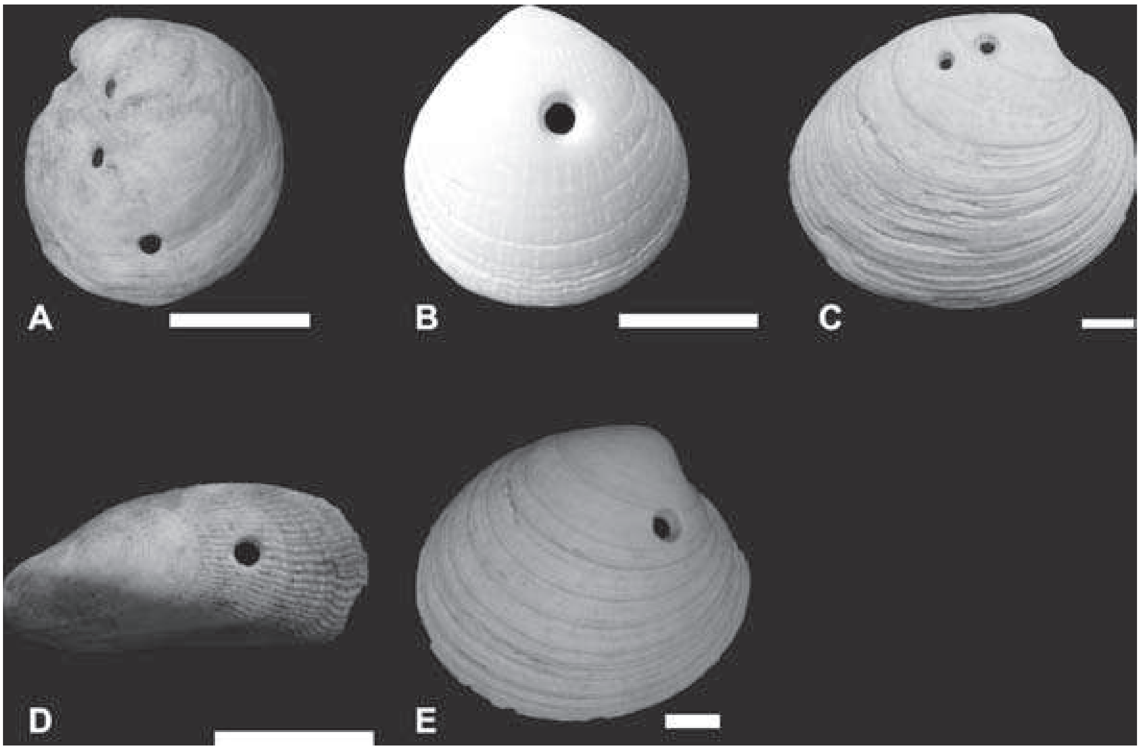


Figure 8. A, *Oichnus simplex* in *Crepidula* sp. (Modern, Bahía Bustamante, DCG-MLP0007-24); B, *Oichnus paraboloides* in *Glycymeris longior* (Modern, Bahía Blanca, PI-UNS 3175); C, *Oichnus paraboloides* in *Protothaca antiqua* (Holocene, Golfo San Jorge, DCG-MLP0007-904); D, *Oichnus simplex* in *Brachidontes rodriguezi* (Modern, Bahía Blanca, PI-UNS 3176); E, *Oichnus paraboloides* in *Protothaca antiqua* (Holocene, Golfo San Jorge, DCG-MLP0007-905); F, *Oichnus paraboloides* in *Protothaca antiqua* (Modern, Punta Pescadero (loc. 9), MLP DCG-0007-148). Scale bars: 10 mm.

Ichnogenus *Pennatichnus* Mayoral, 1988
(Table 1; Figures 9A-B)

Analyzed material. This ichnogenus was found in *Pitar rostratus*.
Stratigraphic range. Jurassic to Recent.
Occurrence in Argentina. Oligocene to Recent.
Description. Elongated thin tunnels; alternately they show primary sub-circular apertures next to the main tunnel. Overall, the arrangement of the tunnel system has a distribution similar to a plume.
Ethological classification. *Domichnia*.
Tracemakers. Ctenostomata bryozoans.

Ichnogenus *Pinaceocladichnus* Mayoral, 1988
(Table 1; Figures 9C-D)

Analyzed material. This ichnogenus was found in *Pitar rostratus*.
Stratigraphic range. Pliocene to Recent.
Occurrence in Argentina. Oligocene to Recent.
Description. Thin tunnels with very regular bifurcations and fusiform apertures parallel to the tunnels.
Ethological classification. *Domichnia*.
Tracemakers. Ctenostomata bryozoans.

Ichnogenus *Renichnus* Mayoral, 1987
(Table 1; Figures 9E-G)

Analyzed material. This ichnogenus occurs in *Brachidontes rodriguezi, Ostrea puelchana* and *Amiantis purpuratus*.
Stratigraphic range. Pliocene to Recent.
Occurrence in Argentina. Holocene to Recent.
Description. Kidney-shaped depressions representing a shallow etching.
Ethological classification. *Fixichnia*.
Tracemakers. Gastropods.

Ichnogenus *Umbichnus* Martinell, Domènech & Bromley, 1999
(Table 1; Figures 9H-I)

Analyzed material. This ichnogenus was found in *Pitar rostratus*.
Stratigraphic range. Pliocene to Recent.
Occurrence in Argentina. Holocene.
Description. Irregular sack-shaped cavity that cuts slightly into the ligament, the boring has a single aperture. In general, it is present in the two valves of the bivalves.
Ethological classification. *Domichnia*.

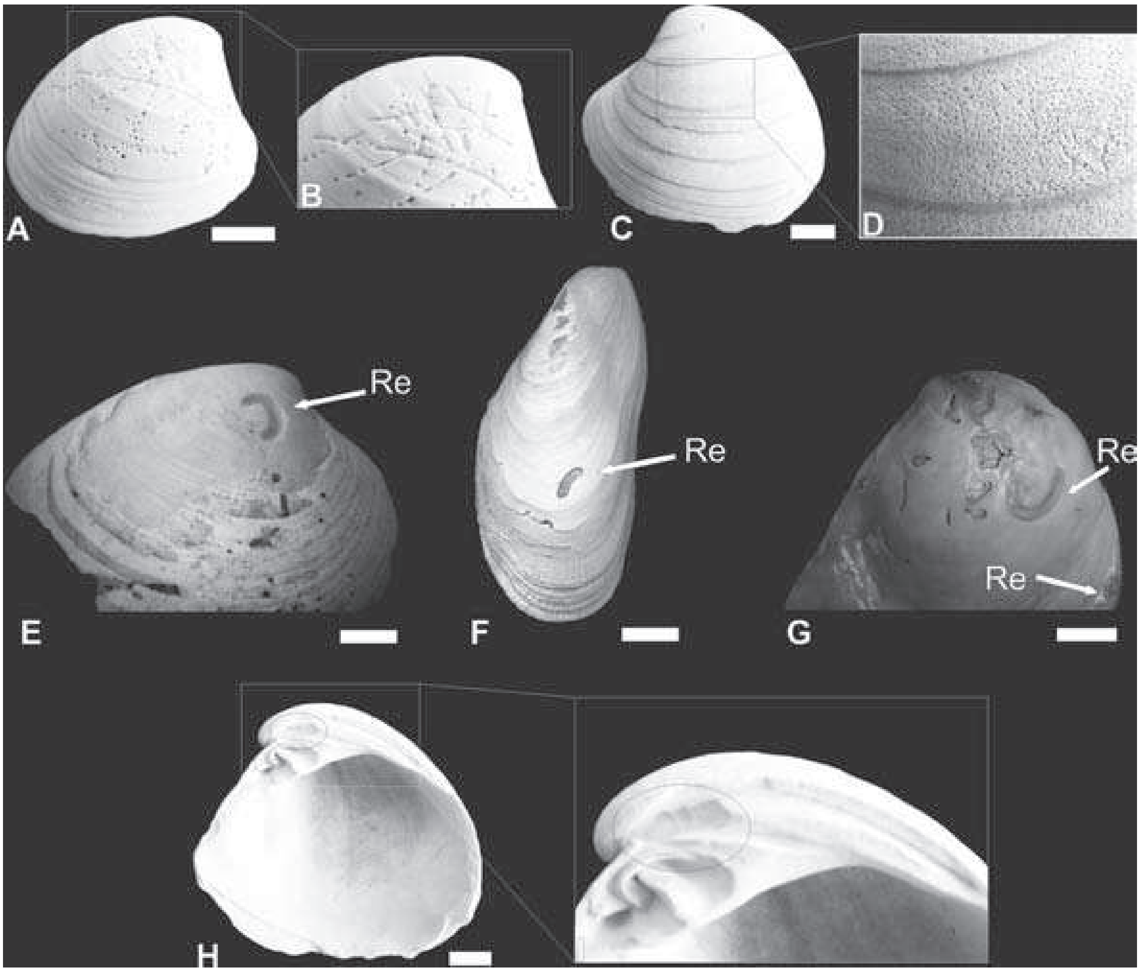


Figure 9. A-B, *Pennatichnus* in *Pitar rostratus* (Holocene, Punta Rasa); C-D, *Pinaceocladichnus* in *Pitar rostratus* (Holocene, Bahía San Blas, PI-UNS 3181); E, *Renichnus* in *Amiantis purpuratus* (Holocene, Bahía Blanca, PI-UNS 3183); F, *Renichnus* in *Brachidontes rodriguezi* (Modern, Mar Chiquita, DCG-MLP0007-906); G, *Renichnus* in *Ostrea puelchana* (Modern, San Antonio Oeste, PI-UNS 3172); H-I, *Umbichnus* in *Pitar rostratus* (Holocene, Bahía Blanca, PI-UNS 3177). Scale bars: 10 mm.

Tracemakers. Unknown.

Discussion. *U. inopinatus* Martinell *et al.*, 1999 is the only recognized ichnospecies within this ichnogenus. It was described in heterodont bivalves and, most likely, the examples here mentioned correspond to the same ichnospecies.

Durophagous scar structures
(Table 1; Figures 10A-D)

Some durophagy structures have been recognized in the marine Quaternary deposits of Argentina. Breakages have been produced on what was, prior to the trauma, the edge of the shell (Ruggiero & Annunziata, 2002). Shell breakage can be assigned to predatory activities of carcinic fauna (Martinell *et al.*, 1982; Martinell, 1989). They are evidenced when the scars are repaired, implying therefore a partial breakage of the shell and its posterior regeneration. They are most common in gastropods (*Buccinanops gradatum, B. cochlidium, Zidona angulata)* than in bivalves.

Associated bioturbation structures

Ichnogenus *Ophiomorpha* Lundgren, 1891
(Figures 10J-L)

Analyzed material. Field observations.

Description. Tridimensional tunnel system that varied between 0.5 and 3 cm in diameter. In the Cerro de la Gloria Member at Bahía Samborombón, these structures penetrate between 0.3 and 0.6 m into the substrate. Occasionally, this ichnogenus penetrates more than 1 meter (Uchman, 2009). The internal surface is smooth, while the external surface contains agglutinated pelletoidal sediment with some shell and wood fragments. This constructional wall is produced to reinforce the structures, avoiding its collapse.

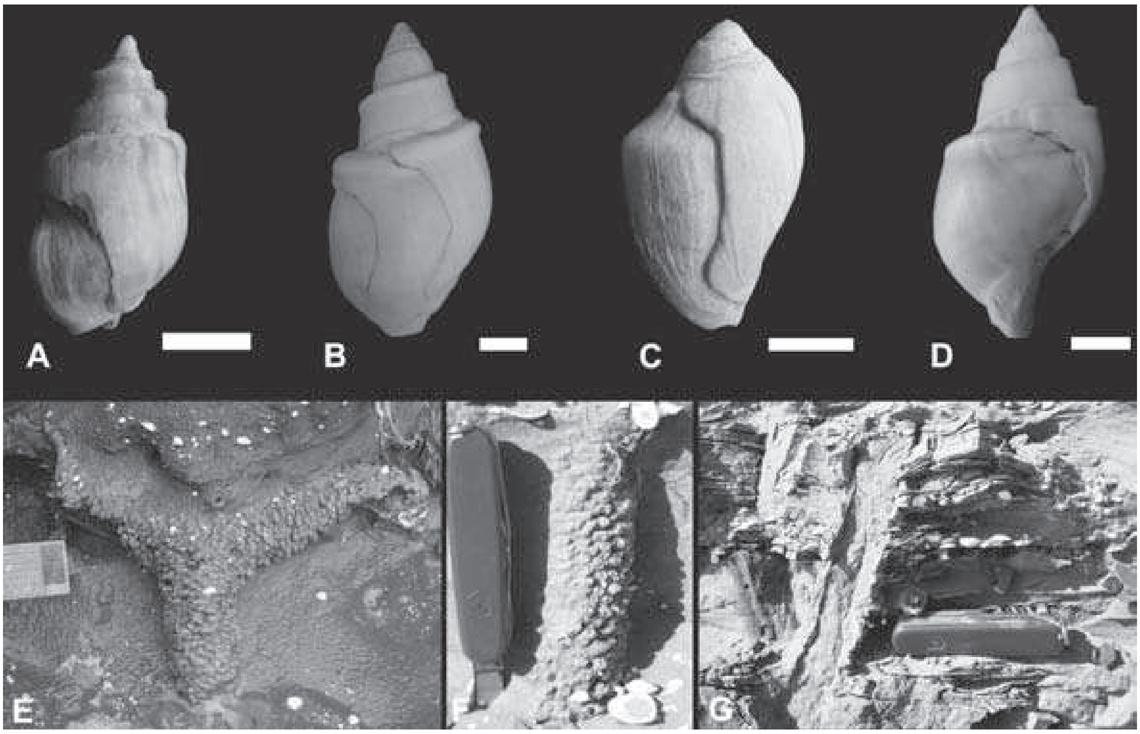


Figure 10. A, Durophagy in *Buccinanops gradatum* (Holocene, Bahía Blanca, PI-UNS 3178); B, durophagy in *Buccinanops gradatum* (Holocene, Bahía Blanca, PI-UNS 3179); C, durophagy in *Zidona angulata* (Holocene, Bahía San Blas, PI-UNS 3182); D, durophagy in *Buccinanops gradatum* (Holocene, Bahía Blanca, PI-UNS 3180); E-G, *Ophiomorpha nodosa* (Holocene, Bahía Samborombón). Picture E is shown in plain view, while pictures F and G are shown in vertical section. Scale bars: 10 mm.

Ethological classification. *Domichnia*.
Tracemakers. Callianassids crustaceans.
Discussion. The studied specimens are assigned to *Ophiomorpha nodosa* Lundgren, 1891. *Ophiomorpha nodosa* is the type species of the ichnogenus.

DISCUSSION

In the marine Quaternary of Argentina, between the Río de La Plata margin and San Julián (Figure 1), the diversity of bioerosive structures observed from a total of 40 molluskan taxa (19 gastropods, 21 bivalves) documents a rich original littoral palaeocommunity along the southern Southwestern Atlantic since, at least, MIS11 (400 ka B.P.). Also, this analysis reveals the occurrence of diverse interspecific relationships between the trace markers (bivalves, gastropods, annelids, sponges, bryozoans and cirripedians) and the molluskan taxa concerned (Figure 5).

The 13 structures identified (*Caulostrepsis, Centrichnus, Entobia, Gastrochaenolites, Iramena, Leptichnus, Maeandropolydora, Oichnus, Pennatichnus, Pinaceocladichnus, Renichnus,Umbichnus,* and durophagous), reveal three kinds of activities: *Domichnia, Fixichnia* and *Praedichnia.*

Firstly, it is interesting to note that the bivalve taxa document all the bioerosion traces while the gastropod taxa only exhibit *Entobia*, *Maeandropolydora*, *Caulostrepsis*, *Centrichnus*, *Leptichnus*, *Oichnus* and durophagous scars.

Secondly, according to our present state of knowledge, Pleistocene samples only show *Caulostrepsis*, *Entobia*, *Maeandropolydora, Leptichnus* and *Oichnus.* By contrast, Holocene shells present all the bioerosive structures identified. In addition, in the modern samples there is no evidence of *Umbichnus* or durophagous scars, although the remaining traces are well documented.

Among gastropods, a high percentage of shells are affected by *Domichnia* (40%) (Figure 11A), while in bivalves *Praedichnia* (41%) are dominant (Figure 11B). The most common and dominant ichnogenera in the study area through the analyzed temporal range are *Entobia* (60% of the whole taxa), *Oichnus* (50%), *Maeandropolydora* (47.5%) and *Leptichnus* (35%) (Figure 5).

Lastly, *Iramena, Pennatichnus, Pinaceocladichnus, Umbichnus, Renichnus* are exclusive for the Bonaerensian area. In Patagonia, only *Centrichnus* is exclusive. The remaining ichnotaxa are present all through the studied area (Figure 5). Interestingly, the occurrence of *Centrichnus*, most abundantly in the modern littoral and Holocene marine terraces from Ensenada Ferrer (48ºS, Santa Cruz province, southern Patagonia), is linked to the occurrence of huge Balanids in cold (Subantarctic) water mass at higher latitudes along the

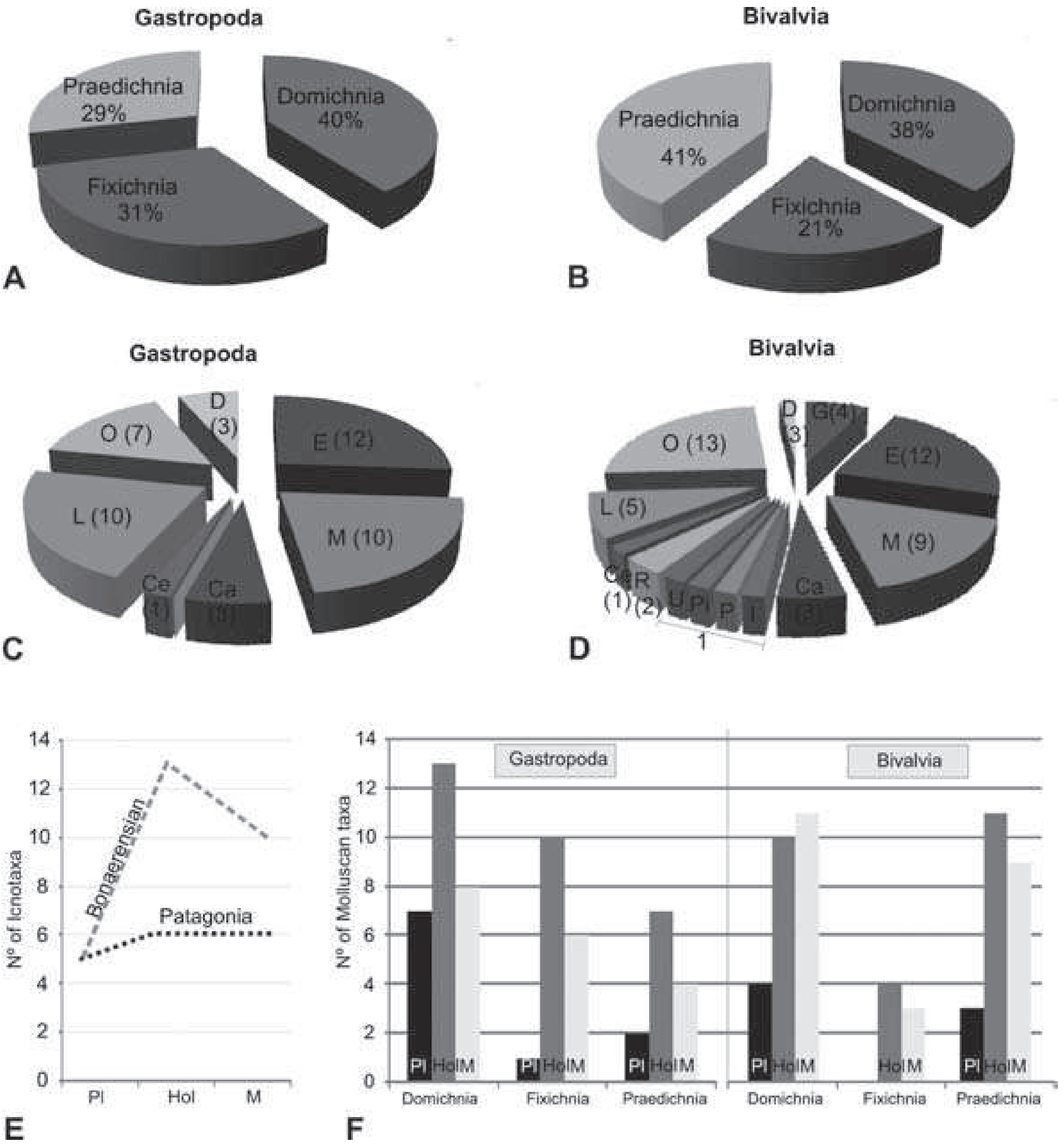


Figure 11. Relative abundance of the ichnogenera and ethological categories recognized in molluskan shells (Gastropoda and Bivalvia) from the marine Quaternary of Argentina (Southwestern Atlantic margin). Abbreviations: Ca, *Caulostrepsis*; Ce, *Centrichnus*; E, *Entobia*; G, *Gastrochaenolites*; I, *Iramena*; L, *Leptichnus*; M, *Maeandropolydora*; O, *Oichnus*; P, *Pennatichnus*; Pi, *Pinaceocladichnus*; R, *Renichnus*; U, *Umbichnus* and D, durophagy. A, Percentage of the ethological categories identified in gastropods; B, percentage of the ethological categories identified in bivalves; C, number of gastropod taxa with different ichnogenera; D, number of bivalve taxa with different ichnogenera; E, ichnodiversity curve across time for bivalves and gastropods taxa; F, number of taxa of gastropods and bivalves according to each of the categories across time. Abbreviations: Pl, Pleistocene; Hol, Holocene; M, Modern.

Southwestern Atlantic (Magellanean Biogeographical province in southernmost Mar Argentino). The cold Malvinas (Falkland) current is probably responsible for the optimal cold sea surface temperature needed for the development of both *Adelomelon ferussacii* and the tracemaker *Megabalanus laevis*.

Overall, the bioerosion trace fossils identified document interspecific relationships between their tracemakers and the host mollusks. Taking into account that most of the bioerosive structures are mainly preserved on the external shell surface (Figures 6-10), it is highly probable that the mollusks were alive the moment the traces were produced, except for a few examples of epifaunal tracemakers (e.g., bryozoans) altering shells of typically burrower infralittoral bivalve taxa (i.e., *Pitar, Amiantis, Mactra*).

The spatial and temporal occurrence of some ichnogenera (e.g., *Maeandropolydora, Leptichnus*) represents a useful indirect evidence for the presence of certain organisms within the original benthonic littoral communities (e.g., porifers, ctenostomate bryozoans, most annelids), most of which are absent or rarely preserved in beach ridges and marine terrace facies. Regarding *Iramena, Pennatichnus* and *Pinaceocladichnus*, our Holocene records along the Bonaerensian coastal sector document for the first time the occurrence of ctenostomate bryozoans in the fossil record for Argentina. It is known that ctenostomates have membranous or gelatinous exoskeletal walls precluding fossilization. This is an example of the high value of ichnological studies leading to more accurate estimations of palaeobiodiversity.

In summary, considering the list of ichnotaxa identified on our molluskan material, the most common bioeroders for gastropod shells are porifers, annelids and bryozoans (*Entobia, Maeandropolydora, Leptichnus*; Figure 11C). On the other hand, for bivalve shells where *Oichnus* is the most frequent structure, carnivorous gastropods are likely the main tracemakers (Figure 11D).

Compared to other studies on individual taxa and/or localities performed previously for deposits of similar age in the Southwestern Atlantic (Pastorino & Ivanov, 1996; Lorenzo & Verde, 2004; Farinati *et al.*, 2006), this study provides a higher ichnodiversity, considering the wider geographical and chronological framework and the higher number (40) of molluskan taxa.

Concerning the ichnodiversity (Figure 11E), comparing the three time spans considered (Table 1, Figure 5), it is interesting to note that the Pleistocene ichnodiversity (5 ichnogenera) is the same all along the Argentine marine deposits. This is outstanding due to the fact that along Patagonia, the marine Pleistocene deposits are abundant and well preserved between Golfo San Matías (localities 7 and 8, Figure 1) and San Julián (locality 18) whereas, along the Bonaerensian coastal area the deposits are not so well preserved, and they exhibit a patchy distribution. On the other hand, in the Holocene deposits, a stronger increase of ichnodiversity is apparent in the Bonaerensian sector in comparison with Patagonia, despite the fact that the fossil beach ridges and marine terraces are similarly well preserved in both areas. In general terms, along the coast of Buenos Aires province, the number of ichnotaxa is nearly twice as the one recorded in Patagonia. This could be explained if we consider that the climatic scenario for the Argentinian marine environment during the Late Pleistocene (MIS9, 7, 5) was unstable but mostly uniformly cold, whereas during the Mid-Holocene the sea surface temperature was slightly warmer, between *ca* 32ºS and *ca* 47ºS (Aguirre *et al.*, 2009), following a latitudinal decrease towards higher latitudes. Besides, our latitudinal pattern of ichnodiversity is in agreement with previous evidence of molluskan latitudinal palaeobiodiversity patterns (Aguirre *et al.*, 2011a). In addition, the lowest slope exhibited by the Patagonian ichnodiversity curve (Figure 11E) suggests that the ecological interactions (which can affect the distribution and abundance of individual taxa) remained similar and stable within the original invertebrate palaeocommunities through time, at least since *ca* 400 Ka (MIS 11).

According to the wide distribution in space and time of the recognized ichnotaxa it could be assumed that the mollusks (live or dead) were available on the sea bottom enabling colonization by the bioeroder organisms during a considerable time interval. This offered the possibility for the trace makers to obtain a hard substrate available within a more general soft-sediment context for the Argentinian coastal zones since the Pleistocene.

Our comparative analysis of bioerosion results, according to the three ethological groups identified across time (Figure 11D), shows that: (i) among gastropods, all the ethological groups are dominant in the Holocene deposits. In addition, *Domichnia* has always been the dominant ethological group, independently of the age considered; and (ii) among bivalves, the pattern of distribution of the ethological groups is less regular. *Domichnia* is dominant in the Pleistocene and modern shells, while *Praedichnia* is dominant in the Holocene samples.

FINAL REMARKS

With these preliminary results we attempt to provide a basic characterization of the bioerosive structures so far observed in the marine Quaternary of Argentina. Due to the huge volume of shell material preserved and collected for this study from the Argentinian Pleistocene and Holocene deposits, as well as along the modern littoral, more detailed studies are still necessary (in course) focusing especially on selected dominant taxa, ichnofacies analysis, organism-tracemaker relationships, quantitative and statistical analyses of bioerosion patterns for a particular species and/or ichnotaxon in different species. These approaches represent the cornerstone for an evolutive palaeoecogical interpretation of the interactions between different taxonomic groups inhabiting the original benthic communities in space and time.

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BIOEROSION AND BIOINCRUSTATION IN BODY FOSSILS FROM THE COASTAL PLAIN OF RIO GRANDE DO SUL STATE, SOUTHERN BRAZIL

Renato Pereira Lopes

ABSTRACT

The Coastal Plain of Rio Grande do Sul State (CPRS), in southern Brazil, is known for the presence of fossil accumulations containing remains of both marine and terrestrial Pleistocene organisms as large biodetrital concentrations on the continental shelf and also in continental outcrops in the Chuí Creek and Mangueira Lake. Many invertebrate remains exhibit bioerosion traces caused by endoskeletozoan organisms, while surface colonization by episkeletozoans is scarce. The trace fossils *Entobia* and *Caulostrepsis* are the most common, followed by *Pennatichnus*, *Gastrochaenolites* and *Maeandropolydora*. *Gastrochaenolites* is found mostly in ostreids and *Oichnus* is mostly absent among fossils from the continental shelf and Mangueira Lake, but it is found in many bivalves from the Chuí Creek. Trace fossils identified as cf. *Clionoides* isp. are recorded for the first time among fossils from the CPRS. Bioincrustation on invertebrates is very scarce, represented by cheilostomate bryozoans, ostreids and cirripeds. Among vertebrate remains found in the continental shelf, bioerosion has been recorded, so far, on three specimens, and remains collected at greater depths are mostly covered by fouling organisms, including serpulid polychaetes and corals. While fossils from shallower areas are affected by bioerosion, bioincrustation affects mostly remains found in deeper areas of the shelf. Ichnological differences among invertebrate fossils found in the continental shelf and those from outcrops in terrestrial environments seem to be related to marine transgressions and regressions that affected the area during the Late Quaternary.

Key words: Quaternary, bioerosion, bioincrustation, *Entobia* ichnofacies, endoskeletozoans, episkeletozoans.

INTRODUCTION

Hard parts of organisms, both vertebrates and invertebrates, can be altered or used by several other organisms for food and/or shelter. Evidences of biogenic activities upon hard organic remains such as shells and bones are widespread in the fossil record, in the form of trace fossils that can be considered as 'fossilized behaviors' and they result from a combination of the substrate type, the organism responsible for the traces and its behavior (Gibert *et al.*, 2004). Biogenic activities on hard skeletal remains can involve the active destruction of the remains (bioerosion) by endoskeletozoan organisms (*sensu* Taylor & Wilson, 2002) or the use of the remains as a substrate for the settlement of episkeletozoans such as algae, bryozoan, corals and ostreids (bioincrustation). Trace fossils produced by endoskeletozoans may be mutually destructive, and those traces emplaced in deeper tiers are more likely to be preserved than those produced more shallowly (Bromley & Asgaard, 1993).

Bioerosion is the alteration of hard substrates by macro and microorganisms, either in the form of chemically and/or mechanically produced structures, such as tunnels and borings, which represent the *Domichnia* or *Praedichnia* ethological classes, or as scraping, rasping and gnawing traces related to the *Paschichnia* ethological class (Warme, 1975; Verde, 2007). Additionally, superficial attachment structures are included within the *Fixichnia* and borings with spreiten are included in the *Equilibrichnia* ethological class (see Gibert *et al*., 2004). Bioerosion is an important process in both modern and ancient marine environments and its study can bring insights on the interspecific ecological interactions and paleoenvironmental conditions (Gibert *et al*., 2007). The boring activity can be performed by several organisms, and the resulting destruction of the substrates such as shells, may return calcium carbonate to the sediment in the form of fine chips (Bromley, 1970; Rützler, 1975). Another important result of bioerosion activities is the weakening of the attacked substrate, making it more prone to mechanical destruction by waves and currents.

While bioerosion is an indirect evidence of the organisms that produced the structures, bioincrustation is usually represented by body fossils of the organisms themselves. Several different organisms can colonize biogenic hard substrates, employing different chemical processes (Taylor & Wilson, 2003). The trace fossils left by both endo- and epibionts are useful tools for paleoecological reconstructions because such traces cannot be transported or mixed together, unless the substrate upon which the traces were produced is subject to transportation (Brett, 1988). The assemblages containing specific trace fossils are characteristic of a given environment because the organisms that produce such traces are adapted to specific environmental conditions (Frey, 1975).

Here is presented a review of the evidence of bioerosion and bioincrustation in invertebrate and vertebrate fossils found in the coastal area of southern Brazil. These fossils consist of remains of Pleistocene marine and terrestrial organisms now preserved in the continental shelf and in continental outcrops, found all along the coast of Rio Grande do Sul State.

GEOLOGICAL SETTING

The fossils were collected along the Coastal Plain of Rio Grande do Sul State (CPRS), in the southernmost portion of the Brazilian coast (Figure 1). The CPRS is 618 km-long, with an average width of 100 km. It is composed of siliciclastic, well-sorted and mature sands, with small fractions of organic matter, biogenic carbonate and diagenetic clays, with some significant concentrations of heavy minerals (Villwock & Tomazelli, 1995). Although fossils can be found all along the coast, they are most abundant in the area to the south of the estuary of Patos Lagoon, where concentrations of Pleistocene marine bioclasts, composed mostly by rounded shell fragments, are found in the continental shelf (Figueiredo Jr., 1975; Lopes & Buchmann, 2008).

The CPRS is the youngest geomorphological unit in Rio Grande do Sul State, and it was formed by sediments transported from continental areas to the coast, after the split between South America and Africa during the Late Cretaceous (Tomazelli *et al*., 2000). Sea-level oscillations correlated to the cyclic glaciations of the Quaternary have affected the environments and geomorphology of the CPRS, as it is shown by abrasion terraces, paleo-fluvial channels and fossils of terrestrial mammals found on the continental shelf today (Kowsmann & Costa, 1974; Corrêa *et al*., 1996; Weschenfelder *et al*., 2008; Lopes & Buchmann., 2010).

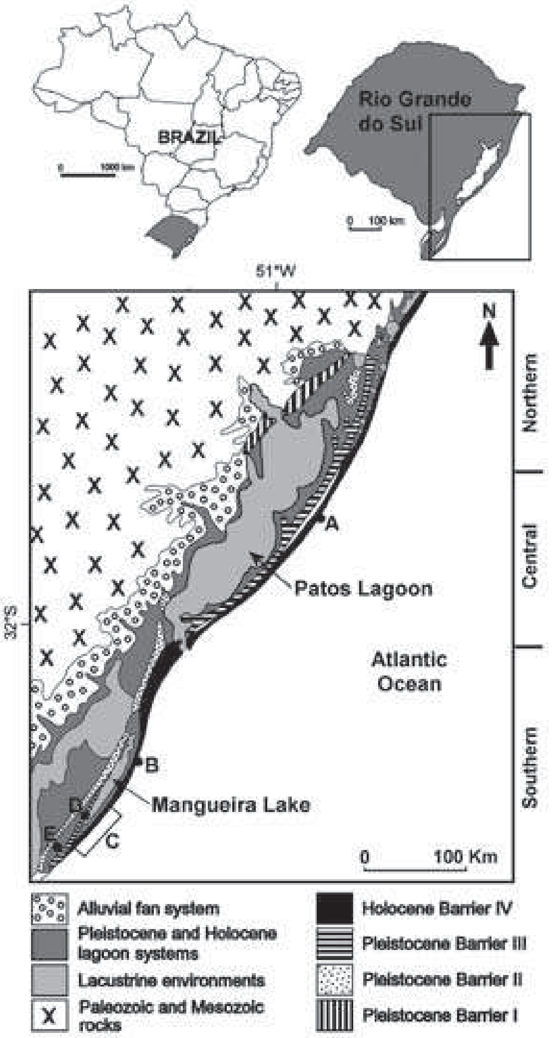

Figure 1. Location of Rio Grande do Sul State, geological structure of CPRS and location of the fossiliferous sites mentioned in the text: A, Mostardas; B, Verga; C, "concheiros"; D, Passo da Lagoa; E, Chuí Creek.

These oscillations reworked the uppermost sediments of the coastal plain and formed two major depositional systems: the Alluvial Fan system and four large Barrier-Lagoon systems. While the Alluvial Fans were formed during a Pliocene sea-level regression, each Barrier-Lagoon System was formed by sea-level highstands during Quaternary interglacial epochs. Although exact ages are not yet available for all these systems, they have been correlated to marine isotope stages (MIS) 11, 9, 5 and 1 (Villwock & Tomazelli, 1995).

THE FOSSILS OF THE CPRS

The presence of concentrations of both marine and terrestrial fossils in the CPRS was first reported in the 19th century by the German Naturalist Hermann von Ihering (Odebrecht, 2003). Throughout the 20th century, most studies have focused on the taxonomic composition of the terrestrial mammalian remains (e.g. Cunha, 1959; Paula Couto & Cunha, 1965; Oliveira, 1992), while few attention has been given to the marine invertebrates (Figueiredo Jr., 1975; Lopes & Buchmann, 2008).

The information presented here was obtained from molluskan and vertebrate fossils found in the central and southern portions of the CPRS, from specimens collected along the beach and in outcrops in terrestrial environments. A few vertebrate remains were collected in the continental shelf by fishing and research vessels, at depths between 20 and 40 m. The concentrations found today on the continental shelf constitute lag deposits formed during the last sea-level transgressions. Those concentrations found on the inner shelf (at depths up to 10-12 m) are being reworked today by erosive processes (Dillenburg *et al.*, 2004). The concentrations found in continental areas are associated with sediments that constitute the barrier-lagoon depositional systems.

Fossils from the continental shelf

The continental shelf of Rio Grande do Sul State, mostly its southern portion, contains several large concentrations of marine and terrestrial organisms, at depths between 0 and 40 m at least (Buchmann *et al.*, 2009). ^{14}C ages obtained in fossil marine shells collected on the shelf showed ages of 17,000 ± 340 yrs BP and more than 30,000 years BP (Figueiredo Jr. 1975), while ESR ages from fossil mammal teeth showed ages between 700,000 and 18,000 years (Lopes *et al.*, 2010). These ages indicate that these concentrations represent several temporally distinct assemblages, reworked and mixed together by the glacioeustatic oscillations that occurred during the Quaternary.

Virtually, all knowledge regarding these remains came from studies on fossil accumulations known as "concheiros", formed on the beach by storm events (Figure 2A). During autumn and winter, storm waves remove fossil shells from the concentrations on the shelf and transport them to the beach, accumulating these remains between the surf zone and the foredunes. The "concheiros" did not exist prior to the 1970s, but today the total thickness exceeds 2 m, reaching some 40 km in length. It is assumed that the fossil concentrations on the shelf represent transgressive lag deposits that are being eroded and reworked by a combination of sea-level fall during the last 6,000 years, marine dynamics and erosive processes related to sediment starvation (Calliari *et al.*, 1998; Dillenburg *et al.*, 2004; Angulo *et al.*, 2006). The most abundant taxa found in this assemblage are bivalves, whereas ostreids are very scarce. However, ostreids are the most common fossil bivalves found in the central portion of the CPRS, near Mostardas, and they are also common near the Verga lighthouse (Lopes, 2011b). Gastropods are also very scarce in the "concheiros".

A remarkable feature of the "concheiros" is the presence of fossil remains of terrestrial mammals, transported from the shelf and concentrated on the beach together with marine invertebrate remains.

Figure 2. A, Detail of the shell concentrations at the "concheiros"; B, shell concentration at the Passo da Lagoa.

The fossils of terrestrial mammals are preserved in deposits that were formed when the continental shelf was exposed during sea-level lowstands correlated to glacial maxima, however, the present-day erosive processes are also eroding and reworking these deposits (Lopes & Buchmann, 2010). Recent shells are also common in the "concheiros", although less abundant than the fossil ones. The latter can be distinguished from the recent shells because of the absence of periostracum, color differences (fossil shells are mostly reddish, but yellow, dark grey and white specimens are also common), and biostratinomic features (Lopes & Buchmann, 2008).

The storm waves are capable of removing and transporting to the beach fossils located only on the inner shelf. Samples collected by fishing and research vessels, however, show that the fossils can be found at depths up to 40 meters below present sea-level (Lopes & Buchmann, 2010). The fossils found in deeper areas are below the depth at which waves can rework the bottom, thus they are never transported to the beach. The physical differences between shallow and deep marine environments are reflected in distinct taphonomic signatures observed on the vertebrate fossils found in these two areas (Lopes *et al.*, 2008; Lopes & Buchmann, 2010).

Fossils from terrestrial outcrops

Fossil assemblages containing remains of marine and terrestrial organisms are found in several outcrops in terrestrial areas in the southern portion of the CPRS. Marine macrofossils, represented mostly by bivalve shells, are found in both surface outcrops and drill holes, and its presence onshore is correlated to sea-level highstands during the Miocene and Pleistocene (Bianchi, 1969; Closs & Forti, 1971; Godolphim *et al.*, 1989).

Closs & Forti (1971) described fossil molluskan assemblages from two areas of the Chuí Creek: one near the town of Santa Vitória do Palmar and the other near its estuary. Those authors, however, did not provide any information regarding the stratigraphic position of the former, and considered both assemblages to represent Holocene molluskans correlating the shells to the Querandinense of Uruguay. Lopes (2010) identified the stratigraphic position of such fossils, at the base of the marine facies exposed on the banks of the Chuí Creek, which indicates a Pleistocene age instead of Holocene. The taxa identified in this assemblage include shallow-living taxa representative of open marine environments but differ from those found in the "concheiros" and Passo da Lagoa (see next) by the presence of some fossil molluskan taxa previously not known from the CPRS (Lopes & Simone, 2012). The other area containing marine fossils is located near the estuary of the Chuí Creek, some 20 km SW of Santa Vitória do Palmar. A Holocene age is supported for this concentration, which represents an estuarine environment some 2 m above the present sea-level, formed during the marine transgression of 6 ky BP (Forti, 1974; Caron, 2007). Fossils from this outcrop have not been studied in detail yet, thus are not included here. Besides remains of marine organisms, fossils of terrestrial Pleistocene mammals are also found in the Chuí Creek, in continental sediments positioned above the marine facies. The mammalian remains include mostly large-bodied faunal elements indicative of Lujanian Stage/Age (Lopes *et al.*, 2009). ESR ages obtained so far indicate ages between 226 and 33,000 years for these fossils (Lopes *et al.*, 2010).

In recent years, a new assemblage, very similar to the "concheiros" one, containing both marine and terrestrial remains, was identified in the southernmost western margin of Mangueira Lake, in the locality known as Passo da Lagoa (see Figure 1) (Lima & Buchmann, 2005; Lopes & Buchmann, 2008). These specimens are all white (Figure 2B), without periostracum, and exhibit the same biostratinomic features seen in fossils from the "concheiros", except for the color. Because these fossils are now under the influence of freshwater, they exhibit signs of corrosion and chemical dissolution. The faunal composition and diversity of this assemblage are essentially the same as those observed in fossils from the "concheiros" (Lopes & Buchmann, 2008).

ICHNOLOGY OF INVERTEBRATE FOSSILS

So far, the only study that included ichnological aspects on invertebrate remains from the southern CPRS is the taphonomic analysis on fossil shells from the "concheiros" and Passo da Lagoa (Lopes & Buchmann, 2008). The results of this study show that both concentrations were formed by similar coastal processes and exhibit essentially the same taxonomic composition, with the bivalves *Amiantis purpuratus*, *Glycymeris longior* and *Pitar rostratus* as the dominant taxa, while gastropods are very scarce. The abundance of *G. longior*, a taxon that inhabits deeper areas, together with shallow-living ones (*A. purpuratus*, *P. rostratus* and *Mactra isabelleana*), indicates that these concentrations are the result of sedimentological processes instead of representing communities preserved *in situ*.

Of the sample analyzed by Lopes & Buchmann (2008), consisting of 450 bioclasts from each concentration, 63% of the specimens from the "concheiros" and 78% from Passo da Lagoa showed no signs of bioerosion or bioincrustation. However, these values represent the total sample, including the most abundant and taxonomically unidentifiable fragments, which exhibit very little bioerosion.

Data presented here are based on the observation of 453 identified fossil shells from the "concheiros", 123 from Passo da Lagoa, 633 from the Chuí Creek (only from the Pleistocene assemblage found near Santa Vitória do Palmar), and 349 ostreids from Mostardas, Verga and the "concheiros". In the "concheiros" and Passo da Lagoa, the most abundant taxa are *A. purpuratus*, *P. rostratus* and *G. longior*; in the Chuí Creek the latter is represented by only one specimen, but *Mactra patagonica* is very common. The only specimens recognized as fossils from Mostardas and Verga are ostreids, represented by *Ostrea puelchana*, *O. equestis* and *Crassostrea virginica*. On all these sites, gastropods are very scarce in comparison to bivalves; *Adelomelon brasiliana* is the most common taxon, followed by *Olivancillaria urceus*, while other species are scarce. Besides mollusks, 584 specimens of fossil echinoids of the species *Encope emarginata* collected from various sites along the shore were also examined (Lopes, 2009, 2011a).

Systematic ichnology

Ichnogenus *Entobia* Bronn, 1838
(Figures 3A-B)

Description. Borings measuring 0.1 to 1.5 mm in diameter, most common on the internal surface of bivalve shells, but sometimes covering most of the external surface of bivalves and gastropods.

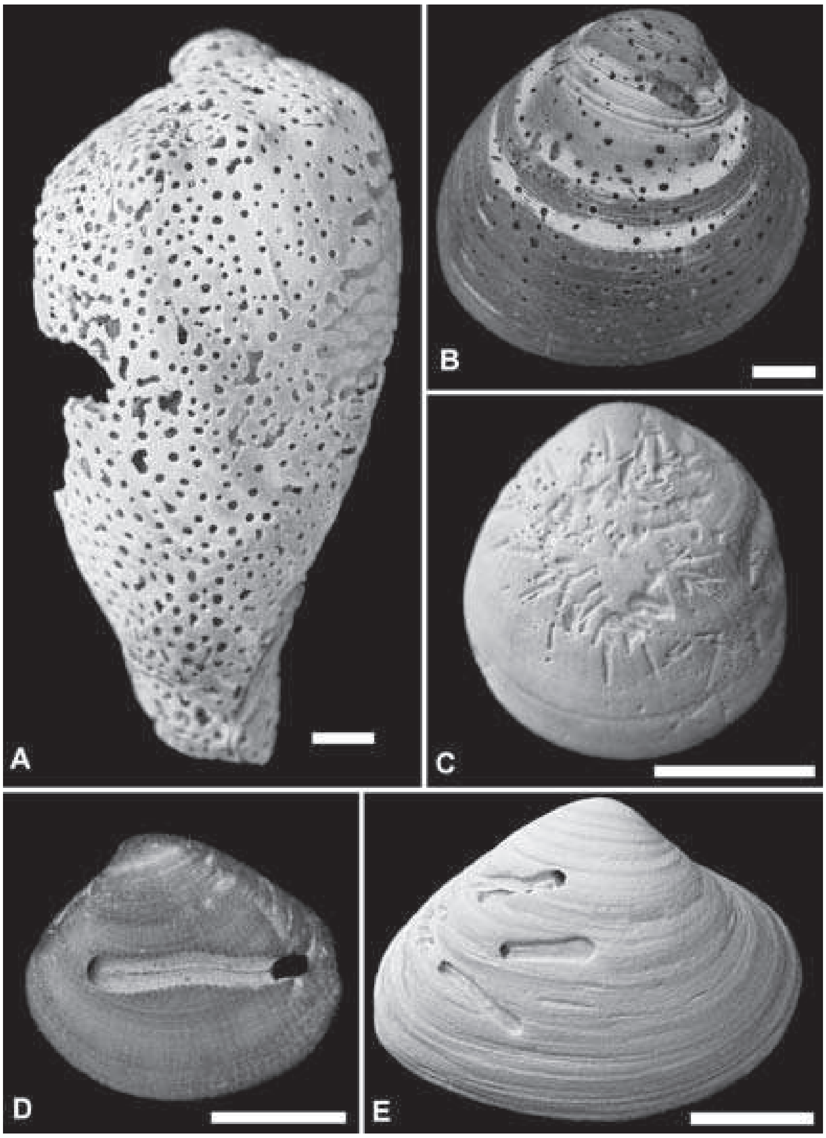

Figure 3. A, Gastropod *Adelomelon brasiliana* with *Entobia*; B, bivalve *Amiantis purpuratus* with *Entobia*; C, *Glycymeris longior* with *Entobia* borings and short grooves identified as cf. *Clionoides* isp.; D, specimen of *Chione cancellata* from the "concheiros", with *Caulostrepsis*; E, *Mactra isabelleana* with *Caulostrepsis* on the anterior end of the valve. Scale bars: 10 mm.

Discussion. *Entobia* is a boring produced by clionid sponges on hard substrates, found in the form of round chambers interconnected by galleries bored below the surface of the substrate. Usually, only the chamber openings are visible (Bromley & D'Alessandro, 1984). This ichnogenus is seen both in bivalves and gastropods from the CPRS. In some fossils, abrasion of the outermost layer of the shells exposed the internal gallery network. Among fossils from the Chuí Creek, only the gastropods *Adelomelon brasiliana* and *Zidona dufresnei* exhibit this trace fossil.

Ichnogenus cf. *Clionoides* Fenton & Fenton, 1932
(Figure 3C)

Description. Straight to slightly curvy shallow grooves, simple or branched, measuring up to 10 mm in length and 1 mm in width.
Discussion. These traces have been observed only on the external surface of bivalves from the "concheiros", and although resemble internal galleries of *Entobia* that are exposed due to abrasion of the shells, the absence of chambers suggest a different origin. These traces are tentatively classified into the ichnogenus *Clionoides* (Häntzschel, 1975). Although Fenton & Fenton (1932) proposed that *Clionoides* was produced by sponges, other authors attribute it to the action of polychaetes (Pickerill *et al*., 1998). The only ichnospecies of this ichnogenus is *C. thomasi*, recorded in marine fossils from the Devonian of the United States (Hoare & Steller, 1967) and the Pleistocene of Jamaica (Pickerill *et al*., 1998).

Ichnogenus *Caulostrepsis* Clarke, 1908
(Figures 3D-E)

Description. In the fossils from the CPRS, this ichnogenus occurs mostly as galleries excavated parallel to the surface (Figure 3D), but in some specimens only the distinct 8-shaped openings, indicative of the genus *C. taeniola* (Bromley & D'Alessandro, 1983) are visible. It occurs in both bivalves and gastropods, mostly on the external surface.
Discussion. *Caulostrepsis* is a boring produced by spionid polychaetes (Domenèch *et al*., 2008) in the form of U-shaped galleries. It is the only trace observed so far in *M. isabelleana*. A remarkable feature regarding the latter is that *Caulostrepsis* is observed mostly on the posterior end of both valves (Figure 3E), correlated to the living position of this bivalve.

Ichnogenus *Maeandropolydora* Voigt, 1965
(Figures 4A-B)

Description. Long, sometimes branched, sinuous grooves produced in molluskan bivalve shells.

Discussion. *Maeandropolydora* is produced by polychaetes, mostly of the family Spionidae (Bromley, 1970; Farinati & Zavala, 2002). Among the molluskan remains from the CPRS, it has been recorded, so far, only in bivalve shells, on the external side of the valves (Figure 4A). In some ostreids this trace can also be found on the internal side of the valves (Figure 4B). Several living spionid polychaetes are known from the CPRS (Seeliger *et al*., 2003), but additional studies are needed in order to correlate the species and the traces they produce.

Ichnogenus *Pennatichnus* Mayoral, 1988
(Figure 4C)

Description. Long round or tear-shaped openings connected to subordinate tunnels which, in turn, are connected to primary tunnels.
Discussion. This ichnofossil is produced by ctenostomate bryozoans (Mayoral, 1988). So far, this trace has been recorded only on the internal surfaces of the bivalves *A. purpuratus*, *P. rostratus* and *G. longior* and also in the gastropod *Adelomelon brasiliana*. This trace is identical to those produced today by bryozoans of the genus *Spathipora* Fischer, 1966. In the Brazilian coast, the species *S. sertum* has been recorded (Marcus, 1938a). An *Olivancillaria urceus* from the Chuí Creek also exhibits this trace on its external surface.

Ichnogenus *Gastrochaenolites* Leymerie, 1842
(Figures 4D-E)

Description. Club-shaped borings produced parallel (Figure 4D) or perpendicular to the surface of the molluskan valves (Figure 4E).
Discussion. This boring is produced by bivalves that mechanically or chemically excavate hard substrates, mostly mytilids (Kelly & Bromley, 1984). In the southern Brazilian coast, the only living mytilid is *Lithophaga patagonica* d'Orbigny, 1847 (Rios, 1994). Among fossils from the CPRS, *Gastrochaenolites* is found only in bivalves, mostly ostreids from Mostardas and Verga beaches, but it is scarce in ostreids from the "concheiros" (Lopes, 2011b), and it was found in one ostreid and one pectinid from the Chuí Creek. The shape of the borings resembles the ichnospecies *G. torpedo* (Kelly & Bromley, 1984). This trace is the only evidence of bioerosion found in fossil echinoids from the continental shelf (Lopes, 2011a).

Ichnogenus *Oichnus* Bromley, 1981
(Figures 4F-G)

Description. Isolated circular to subcircular holes chemically and mechanically excavated perpendicular to the shells, with an external opening larger or equal to the internal one.

Discussion. *Oichnus* is a boring produced by predation activity, mostly by naticid or muricid gastropods (Bromley, 1981). It is very scarce among fossils from the "concheiros" (Figure 4F) and Passo da Lagoa, but it was found in several bivalve specimens from the Chuí Creek. One specimen of *Pitar rostratus* from the latter, exhibits one *Oichnus* boring and another incomplete one that seems a failed attempt of boring the shell (Figure 4G). This trace was not found in gastropods and ostreids from the continental shelf, but some ostreids from the creek exhibit this ichnofossil.

Bioincrustation

Endoskeletozoan organisms are very scarce among the invertebrate remains from the CPRS, represented only by bryozoans, cirripeds and ostreids. Very few shells from the "concheiros" exhibit signs of bioincrustation, and no evidence of this behavior was observed among shells from Passo da Lagoa and the Chuí Creek. Several ostreids from Mostardas, however, exhibit complex patterns of colonization by episkeletozoans, either on the external, internal, or on both sides of the valves (Figure 5A).

The encrusting bryozoans mostly found in fossils belong to the order Cheilostomata. These organisms

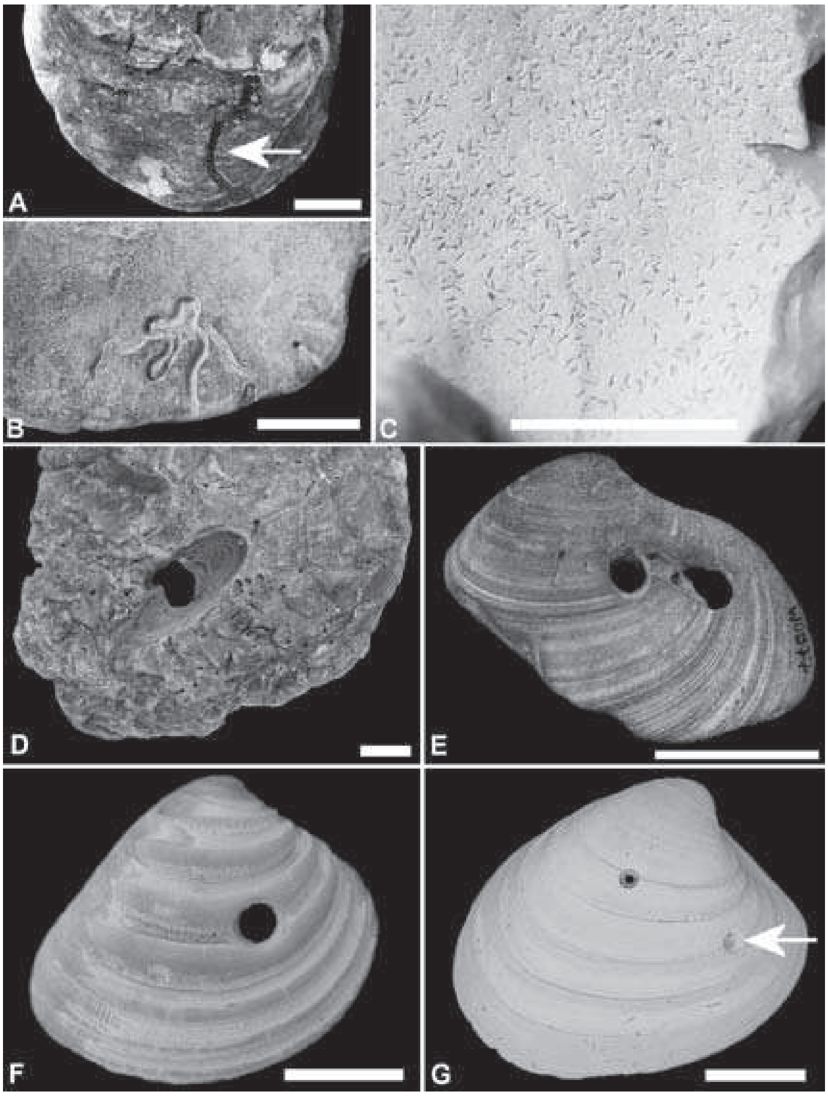

Figure 4. A, *Ostrea puelchana* with *Maeandropolydora* (indicated by arrow) on the external surface of the valve; B, *Maeandropolydora* on the internal surface of *O. puelchana* from Mostardas; C, detail of the internal surface of an *A. purpuratus* with *Pennatichnus*; D, *O. puelchana* with a large *Gastrochaenolites* specimen; E, fragment of *A. purpuratus* with two *Gastrochaenolites*; F, *Chione paphia* from the "concheiros" with *Oichnus*; G, *Pitar rostratus* from the Chuí Creek with *Oichnus* in the central-upper portion and an incomplete boring on the right side, indicated by an arrow. Scale bars: 10 mm.

form thin sheet-like colonies either on the internal or external surface of bivalve shells (Figure 5B). The only gastropods found with bryozoans are two specimens of *O. urceus* from the "concheiros"; these fossils exhibit multilayered bryozoan colonies on top of each other (Figure 5C). Several species of cheilostomate bryozoans, belonging to the genera *Membranipora* and *Conopeum,* are found in the Brazilian coast (Marcus, 1938b).

Cirripeds are seen mostly on ostreids, either as isolated or clustering individuals (Lopes, 2011b). Some cirripeds are recent (Figure 5A), while others are clearly fossils, sometimes filled with sediment lithified by precipitation of calcium carbonate (Figure 5D). One specimen of *G. longior* from the "concheiros" exhibits a colony of cirripeds that grew larger than the bivalve itself (Figure 5E). The only gastropod recorded with cirripeds is one *O. urceus* from the "concheiros" (Figure 5F), and some echinoid specimens exhibit scars left by cirripeds that were removed due to abrasion (Lopes, 2009, 2011a). Encrusting ostreids, both fossils and recents, are found mostly on other ostreids because other bivalves or gastropods are not usually large enough to host this kind of organisms. A remarkable example of bioincrustation occurs in an *Ostrea puelchana* that attached itself to a fossil echinoid of the species *Encope emarginata* (Figure 5G). The large size attained by most encrusting ostreids is a clear indication that the encrusted fossil remained in a stable position for very long time periods.

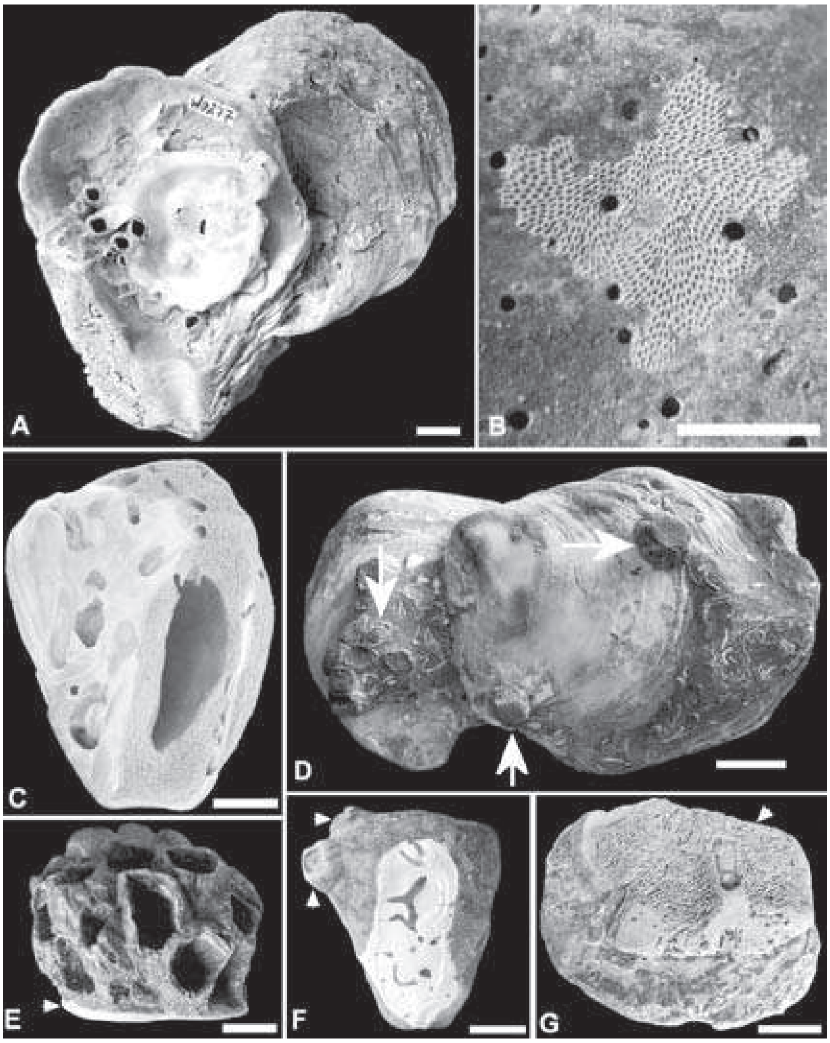

Figure 5. A, A right valve of *O. puelchana* (on the right side of the photo) with an encrusting *O. puelchana* which in turn was colonized by cirripeds, bryozoans and other ostreids; B, detail of the internal surface of an *O. puelchana* showing a colony of cheilostomate bryozoans, the round holes are *Entobia* traces; C, *Olivancillaria urceus* with bryozoan colonies plus *Caulostrepsis*; D, a right valve of *O. puelchana* (on the left side of the picture) colonized by another *O. puelchana*, both exhibiting clustered and isolated cirripeds (indicate by arrows); E, *Glycymeris longior* (indicated by arrow) in lateral view, showing a large colony of cirripeds on its external surface; F, *O. urceus* with two cirripeds (indicated by arrows) and partially covered by lithified sediment (beach rock); G, a fossil echinoid *Encope emarginata* (indicated by arrow) with an encrusting *O. puelchana*. Scale bars: 10 mm.

ICHNOLOGY OF VERTEBRATE REMAINS

Vertebrate remains can be found all along the coastline of Rio Grande do Sul State, removed from fossil concentrations on the inner continental shelf and transported to the beach by storm waves. Although most of such remains consist of broken and abraded unidentifiable parts, well-preserved and even complete bones are found in the "concheiros" (Lopes *et al.*, 2008). The fossils that are transported to the beach by storm waves are associated with biodetrital concentrations found at depths affected by wave action, roughly 10-12 m. Fossils from deeper areas of the continental shelf far from the coastline have been described recently from specimens collected by fishing and research vessels in the 1990s (Lopes & Buchmann, 2010).

Bioerosion

Most of the vertebrate remains found in the continental shelf belong to terrestrial mammals, although fossils of cetaceans and pinnipeds are also found. An analysis of 2391 vertebrate fossils from the paleontological collection of *Universidade Federal do Rio Grande* (FURG) revealed the presence of traces indicative of bioerosion activities in only three fossils of terrestrial mammals. One is an isolated molar of a ground sloth (*Catonyx cuvieri*) that exhibits shallow, sinuous grooves of unidentified origin (Lopes & Pereira, 2010). The other remains include a fragmentary mastodont incisor tooth that exhibits several *Gastrochaenolites* (Figure 6A) and a humerus of a *Toxodon* described by Lopes & Buchmann (2010) that exhibits one *Gastrochaenolites* on the fractured margin of its proximal end (Figure 6B). One partial whale rib also exhibits a sinuous groove on its surface, possibly excavated by a polychaete (Figure 6C).

Bioincrustation

Among the remains of terrestrial mammals, bioincrustation is found mostly on those collected in deeper areas, far from the coast. Some of the episkeletozoans found so far exhibit remains of soft tissues, indicating recent colonization. The terrestrial mammalian remains known from deeper areas of the shelf include the humerus mentioned previously, a partial femur and a partial skull of *Toxodon* and a molar of *Stegomastodon* (Lopes & Buchmann, 2010). The degree of bioincrustation is variable, with fossils almost entirely covered by episkeletozoans, such as the humerus shown in Figure 6B, to fossils with little bioincrustation (Figure 6D). The presence of episkeletozoans is a feature that allowed Lopes *et al.* (2008) to characterize one of the taphofacies (Taphofacies III) identified from vertebrate remains from the continental shelf. The episkeletozoans found on these bones include cirripeds *Balanus* sp., polychaetes of the family Serpulidae, corals *Astrangia rathbuni*, ostreids *Ostrea equestris* and colonies of cheilostomate bryozoans. The serpulids are represented by its carbonate tubes, and four living genera are known from the CPRS (Seeliger *et al.*, 2003). Some ostreids are represented only by the encrusting left valve, which exhibits borings of the ichnogenus *Entobia* on their internal surface (Lopes & Buchmann, 2010).

Bioincrustation is very scarce among terrestrial mammal fossils from shallower areas of the shelf, collected along the beach. The episkeletozoans on these fossils are found mostly on bone cavities, such as foramina or depressions, which could provide shelter against currents and allow the settlement and growth of such organisms (Figure 6D). Besides terrestrial mammals, fossils of whales collected by fishermen at depths up to 40 m exhibit variable degrees of bioincrustation (Figures 6C, F-G).

DISCUSSION

Shells of marine mollusks are subject of alteration by a wide array of organisms, not only after death, but also while the individuals are still alive. In areas where the bottom consists of unconsolidated sediments, shells can provide the only hard substrate available for colonization by epi- and endoskeletozoans. In the southern Brazilian continental shelf, besides molluskan remains, vertebrate fossils are also available for the settlement of such organisms, provided that the fossils remain exposed in the water-sediment interface long enough. The scarcity of borings in most of the vertebrate remains suggests that the structure of the fossilized bones is not suitable for the settlement of endoskeletozoans. The same seems to apply to fossil echinoids, which do not exhibit bioerosion, except for a single record of *Gastrochaenolites* (Lopes, 2011a).

Several ichnogenera were identified from marine fossils (Table 1). Among ichnofossils from the "concheiros", the most common is *Entobia*, while in Passo da Lagoa the most common is *Maeandropolydora*. Although *Caulostrepsis* have not been found among the specimens from the "concheiros" analyzed by Lopes & Buchmann (2008), new samples show the presence of this ichnogenus in both bivalve and gastropod shells. *Oichnus* is very scarce in fossils from the "concheiros" and Passo da Lagoa, and it is absent in ostreids, but it is found in several bivalves from the Chuí Creek (including ostreids). These differences seem to be the result of environmental factors that led to the formation of the concentrations, correlated to sea-level oscillations that affected the CPRS.

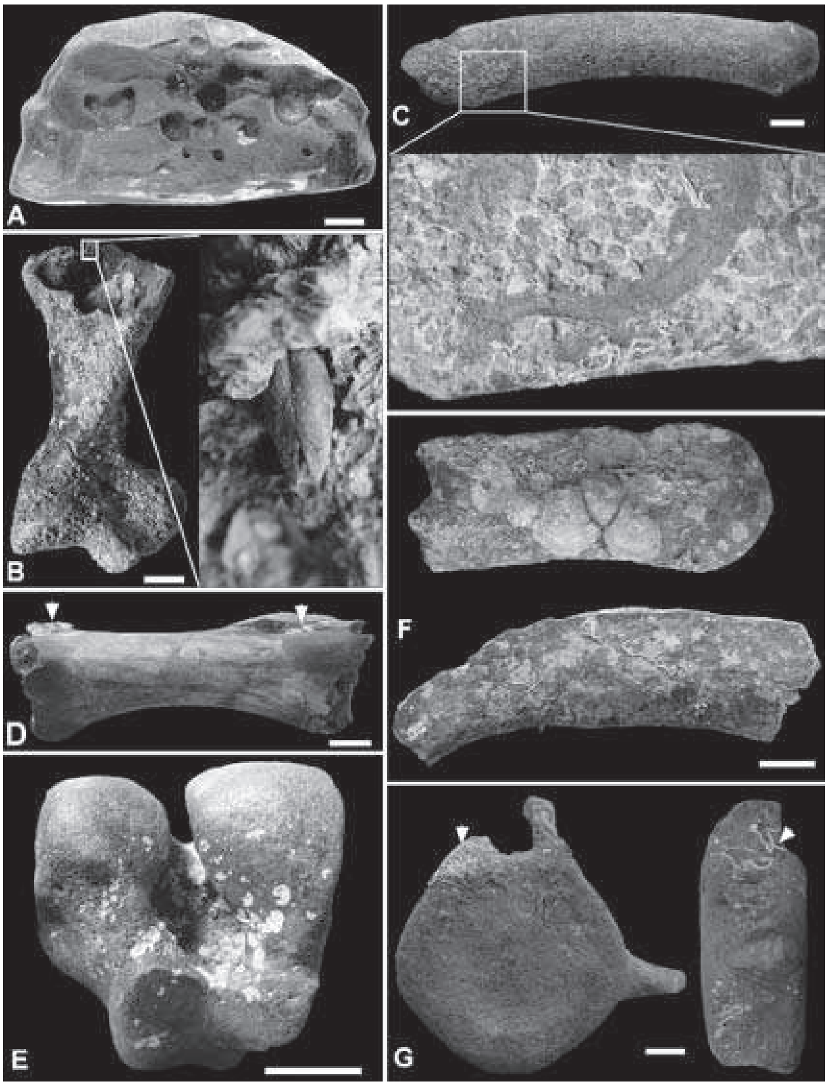

Figure 6. A, Fragment of an incisor of *Stegomastodon* with several *Gastrochaenolites*; B, humerus of *Toxodon* with a *Lithophaga* (on the detail); C, whale rib covered by corals and a possible excavation by a boring polychaete (on the detail); D, unidentified long bone with encrusting corals (on the left) and polychaetes (on the right) indicated by arrows; E, distal end of a femur of *Toxodon*, showing bioincrustation by ostreids and cirripeds; F, whale rib and G, vertebra showing different degrees of bioincrustation. Scale bars: 50 mm.

While the "concheiros" represents the marine transgression of 6 ky BP and Passo da Lagoa seems correlated to the Pleistocene transgression of some 123 ky BP, the taxonomic, taphonomic and ichnologic similarities observed in both concentrations suggest similar environmental processes. The presence of a high proportion of deeper-living taxa, represented by *G. longior* in the "concheiros" and Passo da Lagoa, together with shallow-living ones, such as *A. purpuratus*, *P. rostratus* and mactrids, indicate that these assemblages are parautochtonous (*sensu* Kidwell, 1986) and represent composite, sedimentological concentrations formed by multiple events (Kidwell, 1991) during sea-level transgressions instead of representing paleocommunities. Under transgressive regimes, the sea would erode up to 10 m of the upper sediments of the CPRS, as shown by computer simulations (Dillenburg, 1996), leaving behind coarser sediments (including shells) deposited on the ravinement surface in the form of lag deposits (Assine & Perinotto, 2001). During past marine transgressions, sea-level in the Brazilian coast reached levels several meters above the present one (Angulo *et al*., 2006), thus the deeper-living taxa would have their distribution area expanded landwards, following the migrating environments, which would mix remains of these taxa with remains of the shallow-living ones. This process also seems to be the reason for the abundance of fossils of *E.*

Table 1. List of fossils from the CPRS and associated ichnogenera and episkeletozoans. Abbreviations: *Ent*, *Entobia*; *Cau*, *Caulostrepsis*; *Mae*, *Maeandropolydora*; *Cli*, *Clionoides*; *Pen*, *Pennatichnus*; *Gas*, *Gastrochaenolites*; *Oic*, *Oichnus*; Cir, Cirripedia; Bry, Bryozoa (Cheilostomata); Ost, Ostreidae; Ser, Serpulidae.

LOCALITY / TAXA	ENDOSKELETOZOANS							EPISKELETOZOANS			
Concheiros	*Ent*	*Cau*	*Mae*	*Cli*	*Pen*	*Gas*	*Oic*	Cir	Bry	Ost	Ser
Adelomelon brasiliana	x	x			x						
Adelomelon beckii	x										
Zidona dufresnei	x	x									
Olivancillaria urceus		x							x		
Crassostrea virginica	x	x	x			x					
Crassostrea rhizophorae											
Ostrea equestris											
Ostrea puelchana	x	x	x								
Chlamys tehuelchus											
Trachycardium muricatum		x									
Glycymeris longior	x	x		x	x		x	x			
Pitar rostratus	x	x		x	x						
Amiantis purpuratus	x	x		x	x						
Chione paphia		x					x				
Chione cancellata		x									
Mactra isabelleana		x									
Mactra patagonica		x									
Lunarca ovalis		x									
Encope emarginata						x		x		x	
Vertebrate Fossils						x		x	x	x	x
Mostardas/Verga											
Ostrea puelchana	x	x	x			x		x	x	x	
Ostrea equestris	x	x								x	
Crassostrea virginica	x	x									
Passo da Lagoa											
Olivancillaria urceus											
Crassostrea sp.											
Ostrea equestris											
Ostrea puelchana											
Chlamys tehuelchus											
Glycymeris longior	x		x								
Pitar rostratus		x				x					
Amiantis purpuratus	x										
Mactra isabelleana		x									
Mactra patagonica											

Table 1. Continuation.

LOCALITY / TAXA	ENDOSKELETOZOANS							EPISKELETOZOANS			
Chuí Creek	*Ent*	*Cau*	*Mae*	*Cli*	*Pen*	*Gas*	*Oic*	Cir	Bry	Ost	Ser
Adelomelon brasiliana	x	x									
Zidona dufresnei	x	x									
Bostrycapulus odites	x	x			x				x		
Olivancillaria urceus											
Olivancillaria carcellesi											
Olivancillaria deshayesiana											
Lamniconus l. carcellesi											
Diodora patagonica											
Tegula patagonica											
Mactra patagonica											
Mactra isabelleana											
Mactra cf. janeiroensis											
Pitar rostratus	x						x				
Amiantis purpuratus	x										
Plicatula gibbosa							x				
Chione cancellata							x				
Chione paphia											
Trachycardium muricatum											
Corbula caribaea											
Ostrea equestris		x				x	x				
Crassostrea rhizophorae							x				
Chlamys tehuelchus							x				
Lunarca ovalis											
Glycymeris longior											
Noetia bisulcata											
Anomalocardia brasiliana											
Arcinella brasiliana											

emarginata, a taxon that inhabit greater depths of the continental shelf of Rio Grande do Sul State (Lopes, 2011a). The depth zone affected by wave action would also have migrated landwards of its present position, leaving the lag deposits under stable, low-deposition conditions which would allow settlement of endo- and episkeletozoans on the shells exposed in the water-sediment interface. Most of the bioerosion traces in fossils from the "concheiros" and Passo da Lagoa are observed on the internal surface of the shells, clearly indicating post mortem bioerosion. In Eocene fossils of Antarctica and Miocene fossils of Patagonia, enhanced bioerosion activity correlated to low depositional rates and transgressive regimes was also recorded (Casadío *et al*., 2001; Farinati & Zavala, 2002). After the marine highstand, when sea-level retreated, waves started to erode the once deeper and stable bottoms and rework the sediments and fossils. Studies have shown that some 80% of the coast of Rio Grande do Sul State is currently under erosion, correlated to sediment-starving conditions (Dillenburg *et al*., 2004).

The Pleistocene fossil molluskan assemblage found in the Chuí Creek, on the other hand, seems to represent a shallow-living paleocommunity. The predominant taxa found in this concentration are *A. purpuratus, P. rostratus* and mactrids (*M. janeiroensis, M. guidoi* and *M. isabelleana*), and the assemblage is composed by a combination of unidentified, abraded shell fragments and well-preserved disarticulated valves (although four articulated *Corbula caribaea* were found), representing all ontogenetic stages. Ichnofossils are very scarce on fossils from this assemblage and most bioeroded shells consist of the large gastropods *Z. dufresnei* and *A. brasiliana*. *Oichnus* is found in several bivalves (including ostreids), in higher relative proportion in comparison to bivalves from the "concheiros" and Passo da Lagoa. No ostreid from the continental shelf exhibits this trace. The shell concentration forms a thin horizon, measuring less than 5 cm in thickness, and the mixture of both unidentifiable fragments and complete shells of variable sizes indicates a storm event that concentrated and buried the shells, thus preventing further bioerosion or bioincrustation. The sediment layer containing the shells exhibits crossed and parallel stratification and *Ophiomorpha nodosa* galleries, confirming shallow marine conditions. The gradual transition of this environment to the continental conditions above indicate regressive sea-level regime after the highstand.

Gastrochaenolites is common in ostreids from Mostardas but scarce in ostreids and other bivalves from other areas of the coast. This is probably related to the higher relative abundance of ostreids in Mostardas and the larger size of the ostreid shells, which make them suitable for the settlement of larger mytilids. Another possible explanation is the presence on the southern portion of the continental shelf of submerged paleo-beaches lithified due to precipitation of calcium carbonate (Figueiredo Jr., 1975; Asp, 1999). These structures are the source of beach rock fragments found scattered on the beach today. Many beach rock fragments exhibit several borings made by mytilid bivalves, suggesting that these organisms settle preferentially on these structures rather than on shells. It is noteworthy that *Pennatichnus*, a bioerosion trace made by ctenostomate bryozoans, was not found in ostreids, although it is common in other molluskan fossils from the CPRS (Lopes & Buchmann, 2008) and has been reported in Miocene ostreids from Patagonia (Parras & Casadío, 2006). The absence of ichnogenera an indicative of grazing, such as *Radulichnus,* in all specimens suggests that the shells were not colonized by algae, which could indicate that the remains were either preserved below the photic zone or that the water turbidity blocked sunlight. On the other hand, sponges that produce *Entobia* require clear water, without sediment in suspension (Lorenzo & Verde, 2004). Thus turbidity would not have been a factor that precluded the growth of algae on the shells and other environmental/ecological factors may have been responsible for this absence.

The scarcity of episkeletozoans among invertebrate fossils may be explained by environmental factors, such as water current speed in shallower areas and the relative instability of the shell fragments under such conditions. Experiments using wood samples showed that cirripeds cannot settle under current speed higher than 2 knots (~3.6 km/h) and bryozoans can only settle under current speed below 1.4 knots (~2.6 km/h) (Doochin & Smith, 1951). If shell fragments are moved by bottom currents, which is likely to occur in depths affected by wave action, the episkeletozoans would not have been able to settle. On the other hand, if more complete bivalve shells assume a stable position, with the concave side turned downwards, they become stable, but the water flowing on the convex side could be too strong to allow the settlement of episkeletozoans. Another possible contribution to this pattern could be the condensation of shells due to the removal of finer sediments under a transgressive regime, which would result in less space available for the growing of such organisms. In deeper areas of the shelf, below the influence of waves, the episkeletozoans would have ideal conditions for their settlement. Although invertebrate remains from deeper areas have not been sampled yet, a comparison with the vertebrate remains from the outer continental shelf suggests that invertebrate remains from these areas may exhibit bioincrustation as well.

The maximum current speeds that allow the settlement of boring organisms are between 1.4 and 1.9 knots (3.5 km/h). However, once the organisms have produced the initial boring, they are sheltered from those currents (Doochin & Smith, 1951). Experiments show that the rate of colonization by clionid sponges is higher during the first month and it stabilizes after 6 months (Rützler, 1975), but the colonization can be slowed by occasional covering by sediments (Bromley *et al.*, 1990). With the shells in stable position, boring organisms could also be able to colonize the concave side of the valves, sheltered from strong currents. This could explain why most of the bioeroded bivalves from the "concheiros" and Passo da Lagoa exhibit traces only on the concave side (Lopes & Buchmann, 2008).

Given that vertebrate remains from the outer continental shelf are currently preserved at depths below the influence of waves, bioerosion should also be present. In fact, some encrusting ostreids found on these fossils exhibit *Entobia*, thus the absence of such traces on fossil bones suggest that the microstructure of the fossil bones does not favor the settlement of endoskeletozoans. The same probably applies to fossil echinoids.

The presence of recent bioincrustation on terrestrial mammalian remains from the continental shelf indicates that these remains currently are total or partially exposed on the water-sediment interface, undisturbed by waves. Because wave action cannot erode the depths at which these fossils were collected today, it implies that the remains were reworked and exposed in the past, probably during the last marine transgression around 6 ky BP, thus reinforcing the computer model results of Dillenburg (1996).

The pattern of bioerosion seen on invertebrate remains from the CPRS is characteristic of the *Entobia* ichnofacies defined by Bromley & Asgaard (1993), characterized by the presence of deep tier borings on hard, sediment-free substrates and dominated by *Gastrochaenolites* and *Entobia*. Except for *Oichnus*, all traces belong to the *Domichnia* ethological class.

CONCLUSIONS

The most common bioerosion trace fossils found on fossil bivalve and gastropod remains from the CPRS are *Entobia* and *Caulostrepsis*. *Maeandopolydora* and *Pennatichnus* are also present, although the former has not been found in gastropods and the latter is absent in ostreids. *Oichnus* is found in several fossil shells from the Chuí Creek, including ostreids, but scarce in shells from the "concheiros" and Passo da Lagoa. This trace has not been observed in ostreids from the continental shelf. Although spionid polychaetes leave borings (*Caulostrepsis* and *Maeandropolydora*) on shells, serpulid polychaetes, which build carbonate galleries, have been recorded so far only on vertebrate fossils.

Ichnological differences among invertebrate fossils from the Chuí Creek and the continental shelf (the "concheiros" and Mangueira Lake) seem to be correlated to different environmental conditions (regressive vs. transgressive) in which these fossil concentrations were formed. Bioincrustation is visible mostly on fossil ostreids, which constitute a larger and more stable substrate than smaller bivalves. Fossil echinoids exhibit few signs of bioerosion and bioincrustation. The scarcity of episkeletozoans on invertebrate and vertebrate fossils from shallower areas of the shelf is likely to be related to higher hydrodynamic energy in these areas.

Vertebrate remains from the inner shelf are devoid of bioerosion, and bioincrustation is restricted to sheltered parts of the bones (foramina, depressions, cavities, etc.). Vertebrate remains from the outer shelf are found in deeper areas, not affected by wave action today, and exhibit a higher degree of bioerosion in comparison to fossils from shallower areas. Bioerosion is also very scarce in the former.

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