UNIVERSIDADE DO VALE DO RIO DOS SINOS – UNISINOS
UNIDADE ACADÊMICA DE PESQUISA E PÓS-GRADUAÇÃO
PROGRAMA DE PÓS-GRADUAÇÃO EM GEOLOGIA

ANÁLISE ICNOLÓGICA DO PERMIANO INFERIOR DA BACIA DO PARANÁ E SUA APLICABILIDADE EM ESTUDOS DE DINÂMICA DA LINHA DE COSTA

Jorge Villegas Martín

Orientadora:
Dra. Renata Guimarães Netto

Co-orientador

Dr. Ernesto Luiz Correa Lavina

São Leopoldo, fevereiro de 2019

ANÁLISE ICNOLÓGICA DO PERMIANO INFERIOR DA BACIA DO PARANÁ E SUA APLICABILIDADE EM ESTUDOS DE DINÂMICA DA LINHA DE COSTA

Jorge Villegas Martín

Tese de Doutorado apresentado como parte
das exigências para a obtenção do título de Doutor, pelo
programa de Pós-Graduação em Geologia
da Universidade do Vale do Rio dos Sinos
(UNISINOS).
Área de Concentração: Geologia Sedimentar
Linha de Pesquisa: Paleontologia Aplicada

Banca
Profa. Dra. Renata Guimarães Netto
Prof. Dr. Francisco Manoel Wohnrath Tognoli
Prof. Dr. Luis Alberto Buatois
Profa. Dra. Noelia Beatriz Carmona

São Leopoldo, fevereiro de 2019

M379a Martín, Jorge Villegas.
Análise icnológica do permiano inferior da Bacia do Paraná e sua aplicabilidade em estudos de dinâmica da linha de costa / Jorge Villegas Martín. – 2019.
41 f. : il. ; 30 cm.

Tese (doutorado) – Universidade do Vale do Rio dos Sinos, Programa de Pós-Graduação em Geologia, 2019.
"Orientadora: Profa. Dra. Renata Guimarães Netto Coorientador: Prof. Dr. Ernesto Luiz Correa Lavina."

1. Icnologia. 2. Permiano inferior. 3. Paleobatimetria relativa. 4. Bacia do Paraná. I. Título.
CDU 55

Dados Internacionais de Catalogação na Publicação (CIP)
(Bibliotecária: Amanda Schuster – CRB 10/2517)

Dedicatória

A minha esposa Jennifer Ruiz Mesa, que se não fosse por sua dedicação, força, paciência e seus conselhos eu com certeza não estaria hoje aqui

AGRADECIMENTOS

À minha orientadora, Renata Guimarães Netto, por ter oportunizado uma formação científica pautada em uma abordagem qualitativa e por toda a paciência e dedicação durante o andamento da tese

A toda minha familia, principalmente a meu pai, mãe, tia, sogra, sogro e irmãs, que mesmo desde longe sempre me apoiaram e deram forca

Ao pesquisador e amigo Rodrigo Scalise Horodyski pelas inúmeras discussões e valiosas sugestões para o desenvolvimento da tese

Aos amigos Gerson e Simone por todo o apoio nos momentos difíceis no desenvolvimento da tese.

Ao meu coorientador, Ernesto Luis Correa Lavina por seu apoio e discussões

Aos demais professores do Programa de Pós-Graduação em Geologia (PPGeo) pelos ensinamentos e discussões em todas as etapas do doutorado; especialmente a Paim, Francisco, e Joice.

Aos colegas e amigos da Unisinos, Daniel Sedorko, Tiago Girelli, Samuel H. Noll, Mateus de Vargas, Mauro Daniel Bruno, e João Dobler Lima pelo apoio nas diversas atividades do desenvolvimento da tese.

A todos os colegas do itt fóssil que de uma forma ou outra me apoiaram nesta caminhada.

Esta pesquisa não teria sido concluída sem o auxílio de diversas instituições: (1) à Coordenação de Aperfeiçoamento de Pessoal de Nível Superior pelas diferentes modalidades de bolsa concedidas durante o período de doutorado (CAPES-Prosup), (2) ao Conselho Nacional de Desenvolvimento Científico e Tecnológico pelo projeto que financiou parte desta pesquisa, referidos nos artigos; (3) À Universidade do Vale do Rio dos Sinos, em especial ao Programa de Pós-Graduação em Geologia da Unisinos pelo apoio institucional e de infraestrutura durante todo o processo de doutoramento; (4) ao ITT Fóssil da Unisinos pelo apoio nas fotografias de exemplares; e (5) ao Museu de História Geológica do Rio Grande do Sul (MHGEO) e ao Laboratório de História da Vida e da Terra (Lavigæa) da Unisinos pelo apoio no processamento e tombamento de amostras contendo icnofósseis.

A CPRM por fornecer acesso aos testemunhos em Caçapava usados neste estudo.

Ao amigo Alexandre, por tudo seu apoio durante meu trabalho com os testemunhos na CPRM em Caçapava.

A Sofie por ficar sempre de meu lado e acalmar meu coração nos momentos difíceis de desenvolvimento da tese.

Às secretarias do Programa de Pós-Graduação em Geologia (Unisinos), Raquel Coelho, Jéssica Rosler e Bruna Severo pelo apoio em todos os trâmites institucionais durante o período do doutourado.

Aos colegas que auxiliaram nas atividades de campo, Camile Graziele, Gabriela Correa.

A Lucas, do departamento de Geomensura da faculdade de Geologia da UNISINOS, por toda sua ajuda na elaboração das figuras.

RESUMO

Esta tese tem como abordagem principal o uso de dados icnológicos como indicadores de assinaturas estratigráficas, parâmetros paleoambientais e paleoecológicos. Neste sentido, o diagnóstico de alterações nas suítes icnológicas e icnofácies ao longo da sucessão do Permiano inferior da Bacia do Paraná, permitiu inferências da dinâmica relativa da linha de costa em uma maior escala (3ª ou 2ª ordem). Neste estudo prospectou-se a sucessão do Permiano inferior (formações Rio Bonito, Palermo e Irati) em diferentes testemunhos para identificar sua composição faciológica e icnológica. Esta análise integrada possibilitou o diagnóstico de assinaturas paleoambientais de estresse como densa ocorrência de *Palaeophycus* nos depósitos de Rio Bonito (escassez de oxigênio) e assinaturas estratigráficas-chave como Glossifungites demarcando superfícies autogênicas e alogênicas (limites de sequência). A variação na distribuição vertical das associações icnológicas (Icnofácies Skolithos e Cruziana empobrecida-Cruziana arquetípica-Cruziana distal) e associações de litofácies (estuarino-“shoreface” inferior-“offshore”) de base ao topo reforçam o caráter transgressivo da sucessão estudada. Em síntese, esta tese demonstra a utilidade dos dados icnológicos para resolver questões paleoambientais, estratigráficas e paleobiológicas.

Palavras-chave: Icnologia, Permiano inferior, Paleobatimetria relativa, Bacia do Paraná.

ABSTRACT

This thesis approaches the application of ichnological data as stratigraphic signatures to infer paleocological and paleoenviromental parameters. In this way, the suite and ichnofacies changes through the early Permian succession of the Paraná Basin permitted to infer the coastline relative dynamics in higher scale (3^{ra} and 2 order). The study of this succession included the lithological and ichnological composition of the Rio Bonito, Palermo, and Irati formations recovered in different cores. This analysis permitted to identify signatures of paleoenviromental stress (depleted oxygen and salinity) evidenced by the high density of *Palaeophycus* in the Rio Bonito deposits and stratigraphic signatures such as autogenic and allogenic surfaces demarked by *Glossifungites* suites in the Rio Bonito and Palermo formations, respectively. The vertical distribution of ichnofacies from base to top (impoverishes Skolithos– archetypal Cruziana– distal Cruziana (lower ichnodiversity) ichnofacies), and distinctive sedimentologic signatures (estuarine – lower shoreface – offshore subenvironments) reinforcing the transgressive character of the early Permian succession. Thus, this thesis demonstrates the utility of the ichnological data for resolving stratigraphic, paleoenvironmental and paleoecological questions.

Keywords: Icnology, early Permian, Relative paleobatymetry, Paraná Basin.

INTRODUÇÃO

A Icnologia é a ciência onde se estuda as interações dos organismos com o substrato (Ekdale et al. 1984, Buatois e Mángano 2011). O estudo dos icnofósseis nos últimos anos tem alcançado uma maior importância, já que a Icnologia é amplamente reconhecida como ciência interdisciplinar, pois fornece dados relevantes para as reconstruções paleoecológicas e paleoambientais, para a sedimentologia e a estratigrafia (Meléndez 1989, Buatois et al. 2002, Buatois & Mángano 2011). Além disso, os icnofósseis proporcionam uma rica informação sobre a presença de numerosas espécies, muitas das quais não deixaram restos corpóreos no registro fóssil (Martínez & Santoja 1994, Fernandes et al. 2007).

O uso da paleoicnologia para interpretações paleoecológicas e paleoambientais é baseado na capacidade de tais interações em refletir, o comportamento da fauna bentônica em resposta às condições do meio. Neste sentido, a análise icnológica têm sido útil para inferir variações nas taxas de salinidade, oxigenação e sedimentação, energia hidrodinâmica, consistência do substrato, paleobatimetria relativa e disponibilidade de suprimento alimentar (Bromley & Ekdale 1984, Ekdale 1988, Pemberton & Wightman 1992, Buatois et al., 1992, 2001, Bromley 1996, Martin 2004, Buatois & Mángano 2011). O uso da Icnologia para análises destes parâmetros vem sendo aplicado nos depósitos da sucessão sedimentar Rio Bonito-Palermo (Permiano inferior, Bacia do Paraná) há cerca de 30 anos, a partir de estudos em escala de alta resolução (e.g., Netto & Gonzaga 1985, Boeira & Netto 1987, Netto 1987, 1992, 1994, 1998, Nogueira & Netto 2001a,b, Tognoli & Netto 2003, Buatois et al. 2007, Gandini et al. 2010). No entanto, o uso da ferramenta icnológica em escala de baixa resolução (e.g., 3ª ou 2ª ordem) e seu potencial para sinalizar com acurácia variações da linha de costa e que permitam correlações estratigráficas em escala de bacia ainda inexistem.

A aplicabilidade da Icnologia no diagnóstico de parâmetros paleoecológicos e paleoambientais deriva sua utilidade para determinação e construção de curvas de oscilação da paleobatimetria relativa. É conhecido que mudanças relativas no nível do mar podem acarretar alterações nas condições físico-químicas do meio, as quais podem influenciar no padrão comportamental preservado pela fauna bentônica originando variações na composição das suítes icnológicas e icnofácies. Neste sentido, alguns poucos trabalhos têm demonstrado a importância dos icnofósseis para contribuir na determinação da dinâmica do nível relativo do mar (4ª ordem em diante) (e.g., Bromley and Asgaard 1993, Savrda 1995, Savrda et al. 2001, Fielding et al. 2006, Rodriguez-Tovar et al. 2010, Paranjape et al. 2014).

Assim, usar a Icnologia como ferramenta para estas interpretações é crucial, pois não há registro biogênico mais adequado para a análise dos fatores previamente mencionados do que os icnofósseis. Presume-se que a análise icnológica em uma amostragem contínua possa contribuir de forma significativa para definir curvas da dinâmica de variação do nível relativo do mar em uma escala de menor resolução estratigráfica (3ª ou 2ª ordem). Assim nesta tese são abordadas as estratégias de colonização do ecoespaço na sucessão do Permiano inferior da Bacia do Paraná (formações Rio Bonito, Palermo e Irati) representadas pelas suítes icnológicas e icnofácies, e sua aplicabilidade em estudos para determinar a dinâmica relativa na linha de costa.

DEFINIÇÃO DA HIPÓTESE

O paradigma das Icnofácies, como postulado por Seilacher (1967) e refinado posteriormente por diversos estudos, reconhece agrupamentos preferenciais de estruturas biogênicas a um zoneamento paleoambiental relativamente específico. Assim, mudanças no empilhamento das suítes icnológicas sinalizariam alterações na paleobatimetria relativa, já que tais estruturas refletem o comportamento da fauna bentônica ante a determinados parâmetros que podem variar com a batimetria. Contudo, tais sinalizações aparentemente são mais evidentes em escalas de 4ª a 6ª ordem, as quais possuem caráter local ou regional restrito. No intuito de validar a eficácia da análise icnológica como ferramenta relevante para a determinação e curvas da dinâmica da linha de costa e dos principais parâmetros que controlaram a distribuição dos organismos bioturbadores, propôs-se, nessa tese, testar a hipótese de que os dados icnológicos são úteis para definir a dinâmica do nível do mar em uma escala temporal estratigráfica maior de 3ª ordem.

OBJETIVO GERAL DA TESE

Construir a curva de oscilação do nível relativo do mar para o Permiano inferior da Bacia do Paraná a partir da análise integrada da icnofauna com as associações de fácies e estratigrafia.

Objetivos específicos da tese

- Compreender o significado paleobiológico, paleoecológico e paleoambiental de níveis com alta concentração de *Palaeophycus* na Formação Rio Bonito.

•. Analisar as assinaturas icnológicas de colonização em substratos *firmground* e sua relação com as superfícies estratigráficas na sucessão Rio Bonito – Irati da Bacia do Paraná.

• Realizar inferências paleoecológicas, paleoambientais e paleobatimétricas a partir da análise integrada das associações de fácies e a icnofauna

Para cumprir a hipótese foi necessário primeiramente entender ocorrências ou situações particulares de associações de traços fósseis ocorrendo nos depósitos permianos. Assim, foi importante compreender melhor a colonização de *Palaeophycus* em alta densidade nos depósitos marinhos da Formação Rio Bonito, onde se esperaria maior icnodiversidade. Isto permitiu identificar uma situação de estresse paleoambiental de escassez de oxigênio em contexto de baixa energia hidrodinâmica para estes horizontes estratigráficos (Artigo 1- *Permian macroburrows as microhabitats for meiofauna organisms: an ancient behaviour common in extant organisms*). Também foi importante compreender as ocorrências de suítes de Glossifungites por sua importância para demarcar superfícies estratigráficas importantes (artigo 2- *Glossifungites suites demarking autogenic and allogenic sedimentary surfaces: a case study in estuarine and shoreface deposits)*. Finalmente estes resultados conjuntamente com as demais ocorrências dos traços fósseis permitiu construir as curvas de paleobatimetria relativa para o Permiano inferior da Bacia do Paraná (artigo 3- *Evaluating the resolution of the ichnological record for determine the coastline relative dynamic: a case study in transgressive post-glacial deposits*). Neste terceiro manuscrito se cumpre a hipótese elencada na tese ao se demonstrar a aplicabilidade da análise icnológica para a definição de curvas de paleobatimetria relativa em segunda ou terceira ordem. Intenciona-se submeter este manuscrito ao periódico “Journal of Sedimentary Research” ou “Palaeogeography, Palaeoclimatology, Palaeoecology”.

Capitulo 1. Permian macroburrows as microhabitats for meiofauna organisms: an ancient behaviour common in extant organisms

Lethaia
AN INTERNATIONAL JOURNAL OF PALAEONTOLOGY AND STRATIGRAPHY

Permian macroburrows as microhabitats for meiofauna organisms: an ancient behaviour common in extant organisms

JORGE VILLEGAS-MARTÍN AND RENATA GUIMARÃES NETTO

LETHAIA

Villegas-Martín, J. & Netto, R. G. 2019: Permian macroburrows as microhabitats for meiofauna organisms: an ancient behaviour common in extant organisms. *Lethaia*, Vol. 52, pp. 31–43.

Meiofaunal organisms are indirectly influenced by the activity of benthic macroinvertebrates within the sediment, which plays a role in modifying physical and chemical characteristics of the habitat. The association of meiofaunal organisms and macroburrows is well known in modern environments, but the record of this relationship in the geological record is still incipient. This study documents diminutive burrows (*Helminthoidichnites tenuis*) associated with the surface of macroburrows (*Palaeophycus tubularis*) in Early Permian deposits. The cylindrical shape and meandering to loop trajectory of the diminutive burrows indicate that they were produced by small free-living meiofaunal nematodes. Apparently, *P. tubularis* (open burrow) constituted a favourable microhabitat for nematodes, providing the following: (1) protection against erosive processes and meiofauna predators; (2) oxygen access to more in-depth layers within the sediment; (3) temperature stabilization; and (4) food supply due to mucus impregnation in the macroburrow walls by the *Palaeophycus* tracemaker. The association between *H. tenuis* and *P. tubularis* constitutes the first fossil record of a symbiotic relationship between meiofaunal nematodes and macrobenthic organisms (polychaetes). It also suggests that ecological strategies such as mutualism or commensalism, which are common between extant nematodes and macrobenthic invertebrates, were available in the behavioural programme of these organisms since the Early Permian. ☐ *Bioturbation, commensalism, mutualism, nematode traces, palaeoecology, Permian.*

Jorge Villegas-Martín ✉ *[jvillegasmartin@gmail.com], and Renata Guimarães Netto [nettorg@unisinos.br], Geology Graduate Program, Unisinos University, Av. Unisinos, 950 93022-000 São Leopoldo Rio Grande do Sul, Brazil;* *manuscript received on 27/02/2018; manuscript accepted on 13/05/2018.*

Modern benthic habitats have meiofauna organisms as components of diminutive size and rapid turnover rates. Meiofauna exhibit a high abundance of individuals and diversity of taxa, contributing to organic productivity in many sedimentary habitats and playing a relevant role in benthic food webs. Additionally, meiofaunal communities are indirectly influenced in different ways by the activity of benthic macroinvertebrates through burrowing, gallery and tube building within the sediment (e.g. Reise & Ax 1979; Pinto & Bemvenuti 2003; Rosa & Bemvenuti 2005). These burrowing activities change the physical and chemical characteristics of the habitat such as oxygenation, water circulation, nutrient concentration in the sediment and temperature (e.g. Reise & Ax 1979; Creed & Coull 1984; Reise 1985; Warwick *et al.* 1986; Meyers *et al.* 1987; Ólafsson *et al.* 1990; Jones & Jago 1993; Mortimer *et al.* 1999; Ólafsson 2003; Pinto & Bemvenuti 2003; Rosa & Bemvenuti 2005).

Laboratory and field studies demonstrated that a variety of meiofauna organisms commonly occur in association with burrows of benthic macrofauna (e.g. DePatra & Levin 1989; Pinto & Bemvenuti 2003; Rosa & Bemvenuti 2005; Volkenborn *et al.* 2007; Shimanaga *et al.* 2012). An approach to identify this relationship between meiofauna organisms and macroburrows in the fossil record is the presence of structures resulting from animal behaviour (trace fossils). Diminutive traces attributed to some meiofauna organisms have higher chances of preservation than the tracemaker remains, as the preservation potential of soft-bodied animals is very low.

Here, we report evidence of diminutive trace fossils associated with *Palaeophycus tubularis* Hall, 1847 in Early Permian post-glacial deposits from southern Brazil (Rio Bonito Formation, Paraná Basin). These diminutive traces are attributed to the ichnospecie *Helmintoidichnnites tenuis* Fitch, 1850 and were produced by meiofauna organisms such as nematodes. The palaeobiological and palaeoecological significance of the *H. tenuis*–*P. tubularis* association is also interpreted and discussed.

DOI 10.1111/let.12288

Geographical and geological context

The trace fossils studied here come from a small deposit of the Rio Bonito Formation sedimentary succession cropping out in the Cambaí Grande area, near Vila Nova do Sul town (state of Rio Grande do Sul, southern Brazil, coordinates 53°59′23″W/ 30°17′31″S; Fig. 1). These occur in heterolithic deposits composed of massive or laminated siltstone and fine-grained sandstone with wavy lamination and combined-flow ripples (Fig. 2). The Rio Bonito Formation characterizes the base of the transgressive deposits that followed the demise of Gondwana glaciation in Paraná Basin during the Early Permian (Cagliari *et al.* 2014, 2016). The Paraná Basin is a vast intracratonic basin (circa 1.5 × 10^6 km^2) located in the central-southern portion of Brazil (Zálan *et al.* 1990; Milani *et al.* 2007). The basin fill reaches a maximum thickness of 8000 m in the depocenter (Zálan *et al.* 1990) and consists mainly of Late Ordovician to Late Cretaceous sedimentary and subordinate volcanic rocks (Milani *et al.* 2007).

The tectonic and depositional evolution of the Paraná Basin and subsidence cycles coincided with the major orogenic phases in the history of southwestern Gondwana. Six second-order depositional supersequences are delimited comprising Rio Ivaí (Ordovician–Silurian), Paraná (Silurian–Devonian), Gondwana I (Carboniferous to Early Triassic), Gondwana II (Triassic), Gondwana III (Jurassic–Cretaceous) and uppermost Bauru (Cretaceous;

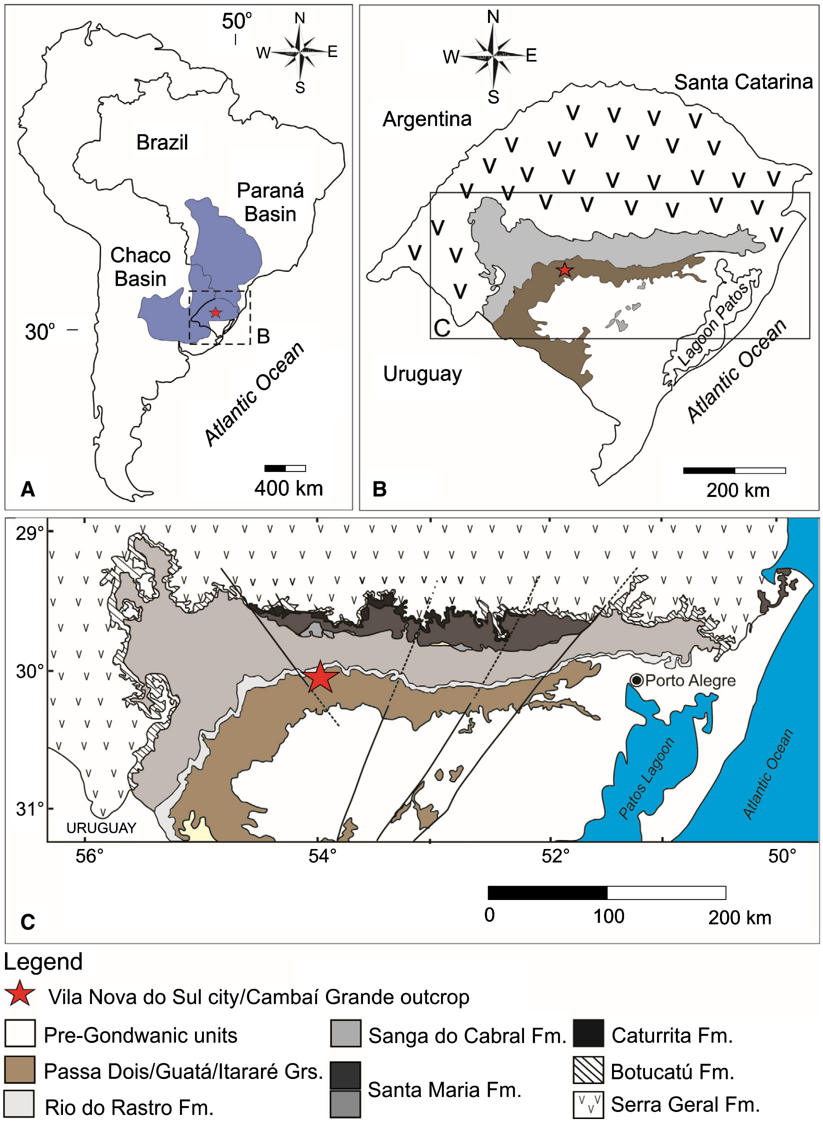


Fig. 1. Geographical location and geological map of the Cambaí Grande area (red star), Vila Nova do Sul municipality (the Rio Grande do Sul State, south of Brazil). Adapted from Faccini *et al.* (2003). [Colour figure can be viewed at wileyonlinelibrary.com]

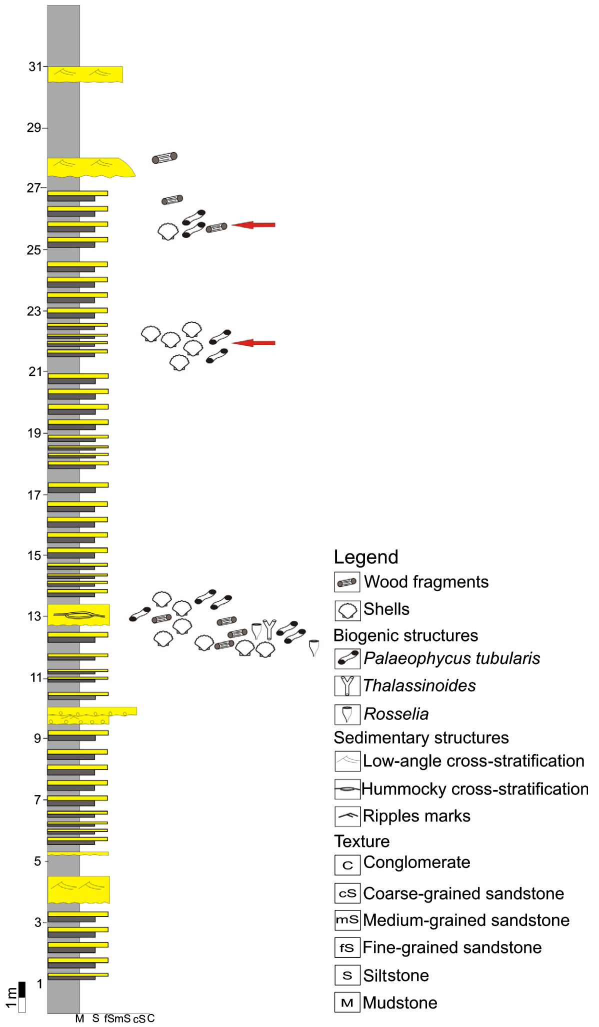


Fig. 2. Schematic profile of the Rio Bonito Formation sedimentary succession (Cambai Grande outcrop) exposed in the Vila Nova region (the Paraná Basin), signalling the distribution of the *Palaeophycus* ichnofabric and shells per bed and the levels where occur the high concentrations of *Palaeophycus* with diminutive trace fossils (red arrows) in this study. [Colour figure can be viewed at wileyonlinelibrary.com]

Milani *et al.* 2007). The Rio Bonito Formation is the basal unit of the Gondwana I Supersequence (Milani *et al.* 2007) and records part of the transgressive phase of the transgressive–regressive cycle that characterizes the Gondwana I Supersequence (Lopes & Lavina 2001; Holz 2003). It is composed mostly of very fine- to very coarse-grained sandstone with trough and hummocky cross-stratification, conglomerate, fine-grained heterolithic deposits, mudstone (parallel-laminated and massive) and coal seams (e.g. Schneider *et al.* 1974; Lavina *et al.* 1985; Lavina & Lopes 1986; Buatois *et al.* 2001a, 2007; Tognoli 2002; Gandini *et al.* 2010; Holz *et al.* 2010).

The sedimentary facies of the Cambaí Grande area consist of conglomerate, siltstone, claystone, heterolithic beds and coarse- to fine-grained sandstone. The fine-grained sandstone shows low-angle and hummocky cross-stratification, while the coarser sandstone shows trough cross-stratification and parallel lamination (Table 1). Bivalve molluscs (genus *Heteropecten, Schizodus, Myonia, Praeundulomya, Volselina, Oriocrassatella*), inarticulate brachiopods (*Orbiculoidea*), unidentified echinoids and plant fragments (Glossopteris Flora) are the primary body fossils in Cambaí Grande area (e.g. Dolianiti 1945; Martins & Sena Sobrinho 1950, 1952).

Trace fossils of mesohaline and fully marine invertebrate organisms are common in the median and upper portions of the Rio Bonito Formation (Paraguaçu and Siderópolis members, respectively; e.g. Netto 1994, 1998; Buatois *et al.* 2001a,b, 2007; Gandini *et al.* 2010). They are represented in the study area mostly by ichnofabrics of *Asterosoma, Bergaueria, Conichnus, Gyrolithes, Lockeia, Macaronichnus, Palaeophycus, Phycosiphon, Planolites, Rosselia, Siphonichnus*, flattened *Teichichnus* and *Thalassinoides* (Table 1).

The basal deposits of the Rio Bonito Formation (Triunfo Member) had been assumed as accumulated in fluvial-deltaic settings (e.g. Lavina *et al.* 1985; Lavina & Lopes 1986; Holz *et al.* 2010). The median and upper portions, otherwise, were interpreted as tide- and wave-dominated shallow marine and estuarine deposits (e.g. Netto 1994, 1998; Buatois *et al.* 2001a,b; Tognoli 2002; Lopes *et al.* 2003). Based on sedimentological and palaeontological data, the deposits of the Rio Bonito Formation in the Cambaí Grande area were assumed as representative of a lagoon-barrier system formed in deltaic and estuarine settings (Elias *et al.* 1999, 2000).

Materials and methods

The material studied is housed in the palaeontological collection of MHGeo Museum at Unisinos University (samples ULVG-12286 to 122892). The description of trace fossils was made by direct observations in the field and laboratory, using collected samples. The description considered the main general ichnotaxobases (general morphology, burrow walls, burrow infill, branching), as expressed in Bromley (1990) and followed the guidelines for ichnotaxonomy and the stratinomic classification as stated by Bertling *et al.* (2006) and Seilacher (1964), respectively. Additional detailed information was also considered, such as the maximum outer diameter, cross-cutting relationships, burrow trajectory and external surface features. Optical microscopy

Table 1. Sedimentary facies of the Cambai Grande area

Facies	Texture	Sedimentary structures	Fossil/trace fossil content	Depositional process	Facies association	Sedimentary environment
Conglomerate	Paraconglomerate composed of intraformational and extraformational clasts; some clasts are angular; sandy matrix	Chaotic	Absent	Debris flows	Glacially influenced deposits	Outwash plains
Fine- to medium-grained sandstone with dropstones	Fine- to medium-grained sandstones with striated and faceted gravels and pebbles; dropstones (basement rocks)	Low-angle cross-stratification	Absent	Uni-directional flows	Glacially influenced deposits	Outwash plains
Fine- to medium-grained sandstone with intraclasts	Fine- to medium-grained sandstones with intraclasts at the base of sandstone beds; erosive base, cutting granite intraclasts	Low-angle cross-stratification	Absent	Uni-directional flows	Fluvial–deltaic deposits	Inner estuary delta
Silty sandstone	Silty sandstone, locally with intraclasts up to granules	Low-angle cross-stratification, undulated tops, coal mud drapes	Plant remains	Low-energy uni-directional flows	Fluvial–deltaic deposits	Inner estuary delta
Coarse- to medium-grained sandstone	Coarse- to medium-grained sandstone forming fining-upward cycles; erosive bases; bioturbation scale 1, locally 2	Medium- to low-angle cross-stratification, bidirectional ripples, combined-flow ripples, double mud drapes, flaser structures, hizobioturbation	Ichnofabric of *Thalassinoides*, tiny horizontal burrows *Rosselia*, *Palaeophycus tubularis,* plant remains	Uni-directional and bidirectional flows	Tide-influenced deposits	Estuarine channels
Coarse-grained sandstone	Coarse- to very coarse-grained, poor selected, arkose sandstone forming amalgamated beds	Trough cross-stratification varying from high to low angle	Absent	Uni-directional/ bidirectional flows	Tide-influenced deposits	Estuarine channels
Fine-grained sandstone	Fine-grained, quartz sandstone	High-angle cross-stratification	Absent	High-energy uni-directional flows	Tide-influenced deposits	Estuarine channels
Heterolithic bedding	Organic-rich siltstone interbedded with micaceous and carbonaceous claystone, locally also interbedded with very fine-grained sandstone forming lenticular thin bedding and wave bedding; bioturbation scale 2–4, locally 5	Low-angle cross-lamination, double mud lamination, wave and combined-flow ripples, flaser structures in siltstone and sandstone; massive claystone; starved ripples, syneresis cracks, stiffgrounds, biostabilized beds, carbonaceous mud intraclasts and rhizobioturbation occur locally	Shells Ichnofabrics of *Rosselia*, *Gyrolithes*, *Lockeia*, *Palaeophycus*, *Palaeophycus tubularis*, *Planolites*, *Thalassinoides*, *Teichichnus*, *Bergaueria*, *Phycosiphon*, *Asterosoma*, *Conichnus* *Chondrites*, plant remains	Uni-directional, bidirectional and oscillatory combined flows	Tide- and wave-influenced deposits	Estuary mouth/ Estuarine bay

(continued)

Table 1. (continued)

Facies	Texture	Sedimentary structures	Fossil/trace fossil content	Depositional process	Facies association	Sedimentary environment
Very fine-grained sandstone	Very fine-grained, quartz sandstone; bioturbation scale 3–4, locally 2–3	Low-angle cross-lamination on top, combined-flow ripples; locally syneresis cracks, oxidized pyrite, ball and pillow structures, biostabilized surfaces; starved ripples and double mud drapes locally	Shells Ichnofabrics of *Asterosoma*, *Bergaueria, Conichnus, Lockeia*, *Palaeophycus, Planolites, Psammichnites, Rosselia, Siphonichnus, Thalassinoides,* vertical shafts mollusc escape burrows	Uni-directional, bidirectional and oscillatory combined flows	Wave-influenced deposits	Estuary mouth/ Estuarine bay
Fine-grained sandstone with HCS	Fine-grained, quartz sandstone forming amalgamated beds; bioturbation scale 4–5 (only at the base of the deposits)	Hummocky cross-stratification, low-angle cross-stratification, wave ripples; biostabilized surfaces on bed tops forming elephant skin	Shells Ichnofabrics of *Rosselia*, *Thalassinoides* *Palaeophycus* escape burrows, plant remains	Oscillatory flows	Storm-influenced deposits	Estuary mouth/ Estuarine bay
Coal/carbonaceous mudstone	Carbonaceous mudstone and coal forming lenses or beds	Massive beds with wrinkle structures and shrinkage cracks on bed tops; rhizobioturbation occurs locally	Plant remains gastropods	Suspension sediments with high organic content	Lagoon deposits	Mud flats
Claystone	Claystone	Massive	Absent	Suspension sediments	Lagoon deposits	Mud flats
Medium-to fine-grained sandstone	Medium- to fine-grained well-sorted, quartz sandstone	Low-angle to very low-angle cross-lamination; fuzzy lamination	Ichnofabric of *Macaronichnus*	High-energy oscillatory combined flows	Beach deposits	Estuarine mouth

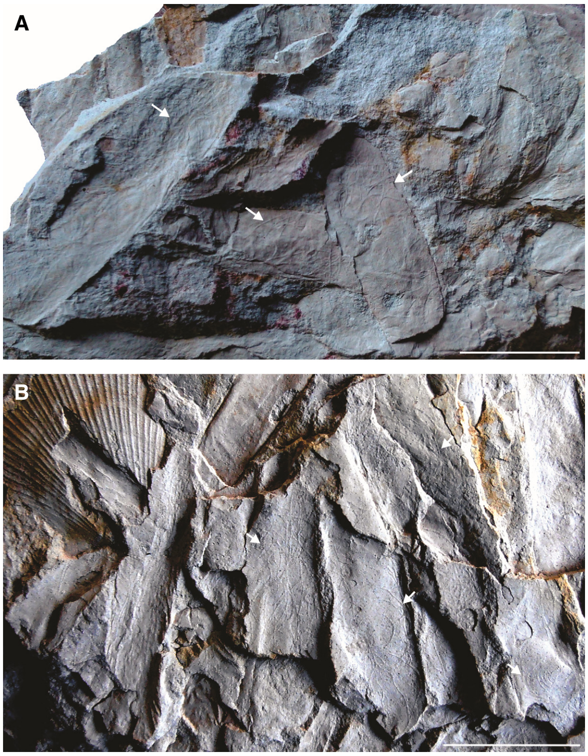


Fig. 3. High density of *Palaeophycus* in the Cambaí Grande outcrop. Some *Palaeophycus tubularis* containing *Helminthoidichnites tenuis* (white arrow). A, ULVG-12286. B, ULVG-12288. Note that *H. tenuis* occurs exclusively associated with *P. tubularis* walls. Scale = 10 mm. [Colour figure can be viewed at wileyonlinelibrary.com]

was used for the description of the tiny burrows and digital calliper for macroburrow and diminutive burrow measurements.

Results

Morphology and ichnotaxonomy of the macroburrows

The macroburrows with diminutive burrow are preserved as positive semi-relief and, less commonly, as full relief (Figs 3, 4). Burrows vary from subcylindrical to horizontally flattened in cross-section and show a preferential straight to slightly curved trajectory. Burrow margins show a discrete muddy lining. True branching was not observed, but burrow intersections are frequent (Fig. 3). The external surface of the burrow walls is predominantly smooth, except in the regions where the diminutive burrows are present. Burrow infill is compact and similar to the host rock, but with a more reddish colour (Fig. 3). Burrow diameter (or width in collapsed burrows) ranges from 3.0 to 7.6 mm.

The morphological characteristics allow us to ascribe the macroburrows to *Palaeophycus tubularis* (e.g. Pemberton & Frey 1982; Fillion & Pickerill 1990; Uchman 1995, 1998). *Palaeophycus* has been registered in a variety of environments, from non-marine to deep marine settings, and is known in the fossil record since the Precambrian (e.g. Pemberton & Frey 1982; Buatois & Mángano 1993, 2002; Buatois *et al.* 1997).

Morphology and ichnotaxonomy of the diminutive burrows

The tiny burrows are cylindrical to subcylindrical in cross-section and are preserved preferentially in positive semi-relief (ridge) although a few burrows preserved in negative semi-relief (groove) may occur (Fig. 4). Burrow fill is compact and similar to the host rock. The diminutive burrows occur exclusively in the *P. tubularis* wall and explore the visible portions of the inner surface thoroughly. The burrow diameter is relatively constant along the same structure, ranging from 0.16 to 0.20 mm, with the predominance of 0.16 mm. The main burrow trajectories are irregularly meandering and locally looped (Fig. 4), except for one specimen that exhibits a circular trajectory (Fig. 4G). Loops are variable in length, some being very wide (Fig. 4A, C). Intersections and overprinting are frequent (Fig. 4A, B, D). The tiny burrows are preserved preferentially in larger macroburrows.

The morphological characteristics described herein allow ascribing the diminutive burrows to *Helminthoidichnites tenuis*. The ichnogenus *Helminthoidichnites* has been registered in marine and non-marine settings and is known in the fossil record from Precambrian to Quaternary (e.g. Hofmann & Patel 1989; Narbonne & Aitken 1990; Buatois *et al.* 1997, 1998; Uchman *et al.* 2004, 2009; Lima *et al.* 2015).

Discussion

The Palaeophycus tubularis *tracemaker*

The millimetric-scale diameter of the *Palaeophycus tubularis* specimens preserved in the Cambaí Grande area suggests macroinvertebrates as tracemakers. *Palaeophycus* represents a combined feeding-temporary dwelling burrow made by organisms with filtering, suspensivorous and carnivore feeding behaviours (e.g. Pemberton & Frey 1982; Fillion & Pickerill 1990; Buatois & Mángano 1993, 2002; Uchman 1995, 1998). The smooth character of the

Fig. 4. Close-up view of the *Helminthoidichnites tenuis* preserved within of *Palaeophycus tubularis*. A–F, *H. tenuis* with meandering and looping trajectory. High concentration of *H. tenuis* showing the common intersections between burrows and the prevalent meandering trajectory (B, D). G, ULVG-12288; rare *H. tenuis* specimen showing circular trajectory (A, C, F) ULVG-12288, (B, D) ULVG-12287, (E) ULVG-12286. Scale = 100 μm. [Colour figure can be viewed at wileyonlinelibrary.com]

burrow walls and the existence of a clayish lining in *P. tubularis* specimens from the Rio Bonito Formation suggest a wormlike organism as tracemaker, potentially a polychaete. *Glycera* and Nereid polychaetes were proposed as modern *Palaeophycus* tracemakers (Osgood 1970; Pemberton & Frey 1982).

Some *Palaeophycus* ichnospecies show delicate ornamentation in burrow walls that is used as a morphological attribute for ichnospecies differentiation (e.g. Pemberton & Frey 1982; Buckman 1995; Uchman 1995, 1998). This ornamentation resulted from excavation activity in more cohesive substrates and includes the following: (1) wrinkled ridges, mainly longitudinal, usually traceable for short distance; (2) fine, continuous, parallel, longitudinal striae; (3) sharp, anastomosing, threadlike striations; (4) longitudinal or oblique, irregular, coarse ridges and wrinkles; (5) alternately striated and annulated scratch marks with periodically varying diameter; and (6) axially continuous annulation (e.g. Pemberton & Frey 1982; Buckman 1995; Uchman 1995, 1998; Jensen 1997; Zhang & Zhao 2015). At first sight, the diminutive burrows (*Helminthoidichnites tenuis*) that occur in close association with the *P. tubularis* from Cambaí Grande area look like ornamentation. In microscopic view, however, they show morphological features such as tubes traceable for long distances and a diameter relatively constant across the same structure. Furthermore, the ornamentation, in general, is more uniform in arrangement, whereas the distribution of *H. tenuis* associated with the macroburrows exhibits a more random and irregular (meanders and loops) distribution. Thus, they do not constitute ornamentation. The presence of diminutive burrows in the *Palaeophycus* wall has never been reported before.

The clayish lining might be generated by mucus impregnation in the burrow wall as a product of the animal metabolism. Mucus creates a microenvironment that provides nutrients for other organisms, mostly those from micro- and meiofauna. This bioirrigation process is observed in burrows of extant organisms that are temporarily or permanently open, such as crustaceans and polychaete burrows (Botto & Iribarne 2000; Volkenborn *et al.* 2007) and can be preserved in the fossil record (de Gibert *et al.* 2006).

The diminutive Helminthoidichnites tenuis *tracemaker*

Helminthoidichnites tenuis is regarded as a grazing trace (pascichnia) and has been suggested as the result of arthropod, wormlike animals, including annelids, nematomorphs and insect larvae displacement in search for food (e.g. Buatois *et al.* 1997, 1998; Schlirf *et al.* 2001; Uchman *et al.* 2009). Some of these organisms, however, can be discarded as tracemakers of the diminutive burrows studied here. Annelids can be excluded because the smallest annelid egg has 50–70 μm in diameter, exceeding the diameter of *H. tenuis* found in association with *Palaeophycus tubularis*. Specimens of *Helminthoidichnites* that were attributed to arthropods, insect larvae and nematomorphs are larger (diameter 0.5–2.7 mm, see Buatois *et al.* 1997, 1998; Uchman *et al.* 2009) than the tiny *H. tenuis* described in this study. Additionally, some well-preserved specimens of *Helminthoidichnites* that were attributed to arthropods exhibit two sets of very fine, densely packed slightly oblique striae (0.1 mm or less) that were interpreted as imprints of two rows of short legs (Uchman *et al.* 2009). These features are absent in the *H. tenuis.*

The circular cross-section and the micrometric-scale diameter (0.16–0.20 mm) of the *H. tenuis* specimens associated with *P. tubularis* point to a slim body of a wormlike animal from meiofauna. Meiofauna organisms such as nematodes, copepods, foraminifera, nauplii, ostracodes and turbellarians have been commonly found in association with extant macroinvertebrate burrows in shallow marine environments (e.g. Meyers *et al.* 1987; DePatra & Levin 1989; Jensen *et al.* 1992; Pinto & Bemvenuti 2003; Rosa & Bemvenuti 2005; Shimanaga *et al.* 2012; Taylor & Cunliffe 2015). The cylindrical morphology and the trajectory of Permian *H. tenuis* suggest the displacement of a nematodelike organism within the substrate. Furthermore, previous to this register, cryptobioturbation found in deposits from the Rio Bonito Formation was attributed to meiofaunal nematodes by Netto *et al.* (2008).

Burrow diameter depends on tracemaker body size. Some extant meiofauna free-living nematodes also show body size diameters that are equivalent to those of the *H. tenuis* specimens preserved in the studied samples (see Heip *et al.* 1985). Experiments in modern environments and laboratory with extant free-living meiofaunal nematodes produced similar diminutive burrows (Jensen 1996) as a result of the undulatory movement of the body (Wallace 1968; Lee & Biggs 1990; Robinson & Perry 2006). The changes in trajectory, from irregularly meandering to sinusoidal and looping patterns found in these Permian specimens, might be a response to the food availability in the area explored by nematodes (Anderson *et al.* 1997).

Furthermore, nematode morphotype also influences the traces produced. Thus, the burrows produced by nematodes can be shorter and sinusoidal or elongated and thin, according to the tracemaker morphology (Platt & Warwick 1980). The ichnogenus *Cochlichnus* is an example of short sinusoidal burrows that are produced in modern settings by short-bodied nematodes (R.G. Netto personal observation). *H. tenuis*, as registered in the studied samples, represents the record of a tracemaker with body plans longer and thinner than those that produce *Cochlichnus*. They exhibit a morphological pattern that is equivalent to the burrows made by extant juvenile nematodes, as illustrated by Riemann & Helmke (2002; Fig. 4A). The occurrence of nematodes in the Palaeozoic fossil record can be expected, as palaeoscolecids (nematode ancestors) are commonly recorded in the early Palaeozoic strata (Whittard 1953; Conway Morris 1997; Botting *et al.* 2012).

Thus, nematodes are plausible candidates as tracemaker of the diminutive *H. tenuis* specimens found in association with *P. tubularis* in the heterolithic deposits of the Rio Bonito Formation; however, other tracemakers cannot be totally ruled out.

Palaeobiological insights about nematodes

The pre-Mesozoic record of free-living nematodes is scarce, due to the low potential of preservation of the tiny soft bodies (Poinar *et al.* 2008; Poinar 2011). Nevertheless, burrows that could be attributed to these organisms (e.g. *Helminthoidichnites, Helminthopsis, Cochlichnus*, *Gordia*) and many undifferentiated thin horizontal burrows are indirect evidence of nematodes in Late Proterozoic and Palaeozoic metazoan communities (e.g. Buatois & Mángano 1993, 2002; Buatois *et al.* 1997, 2014; Baliński *et al.* 2013; Parry *et al.* 2017; Tarhan 2017). Although the petite size of some Palaeozoic burrows has been attributed to meiofauna nematodes (Parry *et al.* 2017; Tarhan 2017), the record of burrowing activity attributed directly to meiofaunal nematodes in pre-Mesozoic rocks is scarce until now. Thus, the scarcity of anatomical evidence of fossil nematodes bodies makes trace fossils a primary source of information on their evolution. The presence of free-living meiofaunal nematode burrows in Early Permian deposits improves the understanding of the nematode fossil record, as the assured record of fossil nematodes is known usually in amber from Cretaceous age and younger strata (Poinar 2011). The Palaeozoic record of fossil nematodes is restricted to the Early Palaeozoic. These few records include *Palaeonema phyticum*, preserved in plant remains (Early Devonian, Scotland; Poinar *et al.* 2008), *Nemavermes mackeei* (Early to Late Carboniferous, USA; Schräm 1973, 1979), and *Scorpiophagus baculiformis* and *S. latus* (Early Carboniferous, Scotland; Størmer 1963). However, the nature of the latter two fossils as nematodes has been questioned (see Boucot & Poinar 2010).

The diameter of *H. tenuis* specimens preserved in the *P. tubularis* wall in the studied material is considerably smaller than those observed in free-living fossil nematodes, which usually vary from 2.0 to >6.0 mm (Schräm 1973, 1979; Arduini *et al.* 1983). This observation was also expressed by Baliński *et al.* (2013) who mentioned the differences in diameter among trace fossils and nematode bodies may constitute a taphonomic bias, as large specimens are more easily preserved as fossils.

Palaeoecology of the Palaeophycus–Helminthoidichnites *association*

Trace fossils are found principally in the heterolithic deposits from Cambaí Grande area. The ichnoassemblage is composed of simple and complex burrows made by facies crossing invertebrates that inhabited shallow marine and marginal marine settings (e.g. Buatois *et al.* 2005; Gandini *et al.* 2010; MacEachern *et al.* 2012). *Palaeophycus* is one of the most ubiquitous trace fossils in this assemblage and occurs in almost all trace fossil suites preserved in the heterolithic beds. In some specific levels, however, *Palaeophycus tubularis* is the unique macroburrow in the trace fossil suite, forming dense concentrations that can be named crowded *Palaeophycus* ichnofabric (CPI; Fig. 3). The CPI is recurrent in the middle portion to the top of the sedimentary succession in the study area which represents the transgressive cycle of the Rio Bonito Formation (Netto 1994, 1998; Elias *et al.* 1999, 2000; Buatois *et al.* 2001a, 2007; Gandini *et al.* 2010). It occurs beneath and between thin mollusc-dominated shell concentrations. The close relationship between the CPI and the fossil shell concentrations allows inferring substrate colonization by *P. tubularis* tracemakers either concomitant with or immediately after the events that formed the shell accumulations. The siltstone and very fine- to fine-grained sandstone compositions of the heterolithic beds suggest deposition in quiet or more protected environments.

The *Palaeophycus–Helminthoidichnites* association occurs exclusively in the CPI, lacking in isolated occurrences of *P. tubularis*. The density of *P. tubularis* and the absence of other macroburrows in CPI suggest ecologically stressing conditions during substrate colonization (e.g. Buatois *et al.* 2005). The presence of *Palaeophycus* in almost all trace fossil suites in the heterolithic beds and the absence of other ichnotaxa in CPI led to infer that, among the benthic macroburrowers, only the *Palaeophycus* tracemakers tolerated the stress conditions established in the quiet settings where the shell beds were accumulated. Salinity fluctuations, oxygen depletion, turbidity, high-frequency sedimentation rate and chemical toxicity are the chief stressing conditions that affect shallow benthic communities (e.g. Bromley 1996; Buatois & Mángano 2011; MacEachern *et al.* 2012). Polychaetes and meiofaunal nematodes that inhabit marginal marine and shallow marine settings can be relatively tolerant to most of these conditions. The sedimentary deposits from Cambaí Grande area have been assumed by Elias *et al.* (1999, 2000) as estuarine deposits. Like polychaetes, free-living nematodes are common in estuaries (Estcourt 1967; Heip *et al.* 1985; Kalejta & Hockey 1991; Pinto & Bemvenuti 2003; Volkenborn *et al.* 2007). Bouwman (1983) estimated 200 species of estuarine nematodes, some forming high-density populations (Van Damme *et al.* 1980). Nematode-dominated meiofauna communities are commonly found exploring open crab and macroinfaunal polychaete burrows excavated in intertidal estuarine settings (e.g. Pinto & Bemvenuti 2003; Rosa & Bemvenuti 2005). Ecological stress is common in estuarine settings, being triggered chiefly by salinity fluctuations and oxygen depletion (e.g. Wignall 1993). Additionally, in the Cambaí Grande area the fossil concentrations are characterized by dense shell pavements which may restrict the oxygen circulation into the substrate deeper layers. Also, the stability of the substrate in photic zones might favour the development of microbial mats that seal the substrate surface and create oxygen-depleting zones few centimetres down into the substrate. In fact, biostabilized beds are frequently observed in the heterolithic deposits with shell concentrations in the studied sedimentary succession. *Palaeophycus* is a horizontally oriented shallow burrow that remains open while the tracemaker lives inside (e.g. Pemberton & Frey 1982). Mucus impregnation in the burrow limits provides also relative stability for these burrows and isolates the interior of the burrow from non-severe oxygen-depleting conditions into the substrate (e.g. Bromley 1996).

The preservation of diminutive *H. tenuis* in the *P. tubularis* wall indicates that small-sized organisms, specifically tiny nematodes, explored the microenvironment formed in the limits of the macroburrows during the Early Permian. Similar microhabitat associated with marine invertebrate burrows is known to be inhabited by populations of meiofauna, including nematodes (Meyers *et al.* 1987; Jensen *et al.* 1992). As *H. tenuis* characterizes a grazing trace of a non-chemosymbiont organism, the search for food and maybe better-oxygenated zones might be the primary factors conditioning the behaviour by the nematodes.

Thus, the non-branched, simple, chiefly straight open *P. tubularis* burrows can provide free water circulation into the burrow, increasing oxygenation rates into the substrate and the nutrient enrichment by mucus input (Warwick *et al.* 1986; Jensen *et al.* 1992). Additionally, mucus impregnation favours the establishment of microbial communities, creating a thin organic-rich mantle around the macroburrows. In fact, the exceptional tridimensional preservation of the tiny *H. tenuis* (Fig. 4) suggests that microbial communities were probably present in the *P. tubularis* wall. Microbial biofilms play an essential role in exceptional fossil preservation (Goldring & Seilacher 1971; Seilacher *et al.* 1985; Seilacher 2008). Meiofauna organisms including nematodes have been registered to inhabit the burrow walls' lining made by echiuran polychaetes (Jensen *et al.* 1992). Finally, macroburrows also accumulate organic detritus (Hogue & Miller 1981) and create temperature and spatial refuge against meiofaunal predators (Powers & Cole 1976; DePatra & Levin 1989). Thus, the enhancement in oxygenation rates caused by bioirrigation and availability of food made the walls of *P. tubularis* a suitable microenvironment for meiofaunal nematodes during intervals of sustained environmental stress that limited the substrate colonization by the benthic macrofauna.

Although meiofauna is ubiquitous in both modern marine and freshwater environments, their palaeoecological aspects are still little explored. The preservation of *H. tenuis* in *P. tubularis* walls records ancient ecological interactions that might represent mutualism or commensalism behaviour. Ecological interactions of this type (commensalism) involving macroinvertebrates were registered previously in the fossil record (de Gibert *et al.* 2006). Examples involving meiofauna and macrofauna ecological relationship are virtually absent in the fossil record. However, laboratory essays and observations in modern environments show that meiofaunal nematodes are among the dominant groups associated with benthic macrofauna activities inside or surrounding macroburrows (DePatra & Levin 1989; Rosa & Bemvenuti 2005).

The *H. tenuis*–*P. tubularis* association suggests that the utilization of microhabitats originated by macrobenthic activity (macroburrows) by meiofaunal bilaterians is an ecological strategy available among invertebrates since the Early Permian.

Conclusions

The morphology of the macroburrows (*Palaeophycus tubularis*) preserved in the Early Permian deposits of the Rio Bonito Formation suggests that they were produced by polychaetes. The size, morphology and trajectory of the diminutive burrows (*Helminthoidichnites tenuis*) suggest a tiny, elongated, slender nematode as tracemaker.

The occurrence of *H. tenuis* exclusively in the *P. tubularis* wall suggests that nematodes potentially exploited the suitable microhabitat originated by polychaetes in their burrow limits, constituting the first fossil record of meiofaunal nematode activity associated with macroinvertebrate burrows. The *P. tubularis–H. tenuis* association also demonstrates that symbiotic ecological relationships like mutualism and commensalism were available in the biotic realm at least since the Early Permian.

Acknowledgements. – We thank the Micropaleontological Technology Institute (ittFossil, UNISINOS University) for the use of laboratory facilities. G. Krahl is thanked by his assistance with microphotography; D. Sedorko, H. Smicht-Neto and R.S. Horodyski for helpful discussions; L.A. Hartman and F. Rodriguez-Proto for English revision and manuscript improvement. The authors express their gratitude also to F. Tognoli, K. Kochhann and R. Gandini for helpful reviews. The authors benefited from insightful comments of A. Uchman and an anonymous reviewer. JVM thanks to CAPES by the Ph.D. grant. RGN thanks the Brazilian National Council for Scientific and Technological Development (CNPq) by the research grants 401826/2010-4 and 303863/2016-1. This paper is a contribution to the project CAPES/PVE/88881.062157-2014-01.

References

Anderson, A.R.A., Younc, I.M., Sleeman, B.D., Griffiths, B.S. & Robertson, V.M. 1997: Nematode movement along a chemical gradient in a structurally heterogeneous environment. 1. Experiment. *Fundamental and Applied Nematology 20*, 157–163.

Arduini, P., Pinna, G. & Teruzzi, G. 1983: *Eophasma jurassicum*n. g. n. sp., a new fossil nematode of the Sinemurian of Osteno in Lombardy. *Atti della Società Italiana di Scienze Naturali a del-Museo Civico di Storia Naturale, Milano 24*, 61–64.

Baliński, A., Sun, Y. & Dzik, J. 2013: Traces of marine nematodes from 470 million years old Early Ordovician rocks in China. *Nematology 15*, 567–574.

Bertling, M., Braddy, S.J. & Bromley, R.G. 2006: Names for trace fossils: a uniform approach. *Lethaia 39*, 265–286.

Botting, J.P., Muir, L.A., VanRoy, P., Bates, D. & Upton, C. 2012: Diverse middle Ordovician palaeoscolecidan worms from the Builth-Llandrindod inlier of central Wales. *Palaeontology 55*, 501–528.

Botto, F. & Iribarne, O. 2000: Contrasting effects of two burrowing crabs (*Chasmagnathus granulate* and *Uca uruguayensis*) on sediment composition and transport in estuarine environments. *Estuarine, Coastal and Shelf Science 51*, 141–151.

Boucot, A.J. & Poinar, G.O. Jr 2010: Predation and feeding behaviors. *In* Boucot, A.J. & Poinar, G.O. Jr (eds): *Fossil Behavior Compendium*, 79–118. CRC Press, Boca Raton, FL.

Bouwman, L.A. 1983: A survey of nematodes from the Ems estuary part II: species assemblages and associations. *Zoologische Jahrbücher Abteilung für Systematik, Ökologie und Geographie der Tiere 110*, 345–376.

Bromley, R.G. (ed.) 1990: *Trace Fossils. Biology and Taphonomy*, 280 pp. Unwin Hyman, London.

Bromley, R.G. (ed.) 1996:*Trace Fossils. Biology, Taphonomy and Applications*, 2nd ed, 361 pp. Chapman and Hall, London.

Buatois, L.A. & Mángano, M.G. 1993: Trace fossils from a Carboniferous turbiditic lake: implications for the recognition of additional non marine ichnofacies. *Ichnos 2*, 237–258.

Buatois, L.A. & Mángano, M.G. 2002: Trace fossils from Carboniferous floodplain deposits in western Argentina: implications for ichnofacies models of continental environments. *Palaeogeography, Palaeoclimatology, Palaeoecology 183*, 71–86.

Buatois, L.A. & Mángano, M.G. 2011: *Ichnology: Organism-Substrate Interactions in Space and Time*, 370 pp. Cambridge University Press, Cambridge.

Buatois, L.A., Jalfin, G. & Aceñolaza, F.G. 1997: Permian nonmarine invertebrate trace fossils from southern Patagonia, Argentina, ichnologic signatures of substrate consolidation and colonization sequences. *Journal of Paleontology 71*, 324–336.

Buatois, L.A., Mángano, M.G., Maples, C.G. & Lanier, W.P. 1998: Ichnology of an upper carboniferous fluvio-estuarine paleovalley: the tonganoxies and stone, buildex quarry, eastern Kansas, USA. *Journal of Paleontology 72*, 152–180.

Buatois, L.A., Netto, R.G. & Mángano, M.G. 2001a: Reinterpretación paleoambiental de la Formación Rio Bonito (Pérmico de la Cuenca de Paraná) en el yacimiento de carbón de Iruí, Rio Grande do Sul, Brasil: integración de análisis de fácies, icnología y estratigrafia secuencial de alta resolución. *Geogaceta 29*, 27–30.

Buatois, L.A., Netto, R.G. & Mángano, M.G. 2001b: Paleoenvironmental and sequence stratigraphic analyses of Lower Permian marginal- to shallow marine coal-bearing successions of the Paraná Basin in Rio Grande do Sul, Brazil, based on ichnological data. *Ciência, Técnica, Petróleo, Seção Exploração de Petróleo 20*, 171–176.

Buatois, L.A., Gingras, M.K., MacEachern, J.A., Mángano, M.G., Zonneveld, J.P., Pemberton, S.G., Netto, R.G. & Martin, A. 2005: Colonization of brackish-water systems through time: evidence from the trace-fossil record. *Palaios 20*, 321–347.

Buatois, L.A., Netto, R.G. & Mángano, M.G. 2007: Ichnology of Permian marginal- to shallow marine coal-bearing successions: Rio Bonito and Palermo Formations, Paraná Basin, Brazil. *In* MacEachern, J.A., Bann, K.L., Gingras, M.K. & Pemberton, S.G. (eds): *Applied Ichnology*, 167–178. SEPM Short Course Notes 52. SEPM, Tulsa.

Buatois, L.A., Narbonne, G.M., Mángano, M.G., Carmona, N.B. & Myrow, P. 2014: Ediacaran matground ecology persisted into the earliest Cambrian. *Nature Communications 5*, 3544.

Buckman, J.O. 1995: A comment on annulate forms of *Palaeophycus* Hall 1847: with particular reference to *P. 'annulatus'* sensu Pemberton and Frey 1982, and the erection of *P. crenulatus* ichnosp. nov. *Ichnos 4*, 131–140.

Cagliari, J., Lavina, E.L.C., Philipp, R.P., Tognoli, F.M.W., Basei, M.A.S. & Faccini, U.F. 2014: New Sakmarian ages for the Rio Bonito formation (Paraná Basin, southern Brazil) based on LA-ICP-MS UePb radiometric dating of zircons crystals. *Journal of South American Earth Sciences 56*, 265–277.

Cagliari, J., Philipp, R.P., Buso, V., Netto, R., Klaus, P., Cunha Lopes, R., Basei, M.A.S. & Faccini, U.F. 2016: Age constraints of the glaciation in the Paraná Basin: evidence from new U-Pb dates. *Journal of the Geological Society 173*, 871–874.

Conway Morris, S. 1997: The cuticular structure of the 495-Myr-old type species of the fossil worm *Palaeoscolex, P. piscatorum* (?Priapulida). *Zoological Journal of the Linnaean Society 119*, 69–82.

Creed, E.L. & Coull, B.C. 1984: Sand dollar, *Mellita quinquiesperforate* (Leske), and sea pansy, *Renilla reniformis* (Cuvier) effects on meiofaunal abundance. *Journal of Experimental Marine Biology and Ecology 84*, 225–234.

DePatra, K.D. & Levin, L.A. 1989: Evidence of the passive deposition of meiofauna into fiddler crab burrows. *Journal of Experimental Marine Biology and Ecology 125*, 173–192.

Dolianiti, E. 1945: Descoberta de fósseis na Formação Maricá, Estado do Rio Grande do Sul. *Mineração e Metalurgia IX*, 1–110.

Elias, A.R.D., Lavina, E.L. & Garcia, A.J.V. 1999: Estratigrafia de seqüências e diagenêse do Permiano Inferior da Bacia do Paraná na Região Centro- Oeste do Rio Grande do Sul, Brasil. *Acta Geologica Leopoldensia 23*, 53–74.

Elias, A.R.D., Garcia, A.J.V. & Lavina, E.L. 2000: Arcabouço Cronoestratigráfico do Eopermiano da Bacia do Paraná na Região Centro-Oeste do Rio Grande do Sul. *Pesquisas em Geociências 27*, 31–44.

Estcourt, I.N. 1967: Ecology of benthic polychaetes in the heathcote estuary, New Zealand. *New Zealand Journal of Marine and Freshwater Research 1*, 371–394.

Faccini, U.F., Giardin, A. & Machado, J.L.F. 2003: Heterogeneidades litofaciológicas e hidroestratigrafia do Sistema Aqüìfero Guarani na Região Central do Rio Grande do Sul. *In* Paim, P.S.G., Faccini, U.F. & Neto, R.G. (eds): *Geometria, Arquitetura e heterogeneidades de corpos sedimentares – um estudo de caso*, 147–173. Editora Unisinos, São Leopoldo.

Fillion, D. & Pickerill, R.K. 1990: Ichnology of the Upper Cambrian? to Lower Ordovician Bell Island and Wabana groups of eastern Newfoundland, Canada. *Palaeontographica Canadians 7*, 1–119.

Fitch, A. 1850: A historical, topographical and agricultural survey of the County of Washington. Part 2-5. *Transactions of the New York Agricultural Society 9*, 753–944.

Gandini, R., Netto, R.G., Kern, H.P. & Lavina, E.L.C. 2010: Assinaturas icnológicas da sucessão sedimentar Rio Bonito no bloco central da jazida carbonífera de Iruí, Cachoeira do Sul (RS). *Gaea – Journal of Geosciences 6*, 21–43.

de Gibert, J.M., Netto, R.G., Tognoli, F.M.W. & Grangeiro, M.E. 2006: Commensal worm traces and possible juvenile thalassinidean burrows associated with *Ophiomorpha nodosa*, Pleistocene, southern Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology 230*, 70–84.

Goldring, R. & Seilacher, A. 1971: Limulid undertracks and their sedimentological implications. *Neues Jahrbuch für Geologie und Paläontologie 137*, 422–442.

Hall, J. 1847: *Natural History of New York, Palaeontology, 1, Containing Descriptions of the Organic Remains of the Lower Division of the New York System (equivalent of the Lower Silurian Rocks of Europe)*, 338 pp. New York State Geological Survey, Van Benthuysen, Albany, NY.

Heip, C., Vincx, M. & Vranken, G. 1985: The ecology of marine nematodes. *Oceanography and Marine Biology Annual Reviews 23*, 399–489.

Hofmann, H.J. & Patel, I.M. 1989: Trace fossils from the type "Etchemian Series" (Lower Cambrian Ratcliffe Brook Formation), Saint John area, New Brunswick, Canada. *Geological Magazine 126*, 139–157.

Hogue, E.W. & Miller, C.B. 1981: Effects of sediment microtopography on small scale spatial distributions of meiobenthic nematodes. *Journal of Experimental Marine Biology and Ecology 53*, 181–191.

Holz, M. 2003: Sequence stratigraphy of a lagoonal estuarine system – an example from the lower Permian Rio Bonito Formation, Paraná Basin, Brazil. *Sedimentary Geology 162*, 301–327.

Holz, M., França, A.B., Souza, P.A., Iannuzzi, R. & Rohn, R. 2010: A stratigraphic chart of the Late Carboniferous/Permian succession of the eastern border of the Paraná Basin, Brazil, South America. *Journal of South American Earth Sciences 29*, 381–399.

Jensen, P. 1996: Burrows of marine nematodes as centres for microbial growth. *Nematologica 42*, 320–329.

Jensen, S. 1997: Trace fossils from the Lower Cambrian Mickwitzia sandstone, South-Central Sweden. *Fossils and Strata 42*, 3–111.

Jensen, P., Emrichs, R. & Weber, K. 1992: Brominated metabolites and reduced numbers of meiofauna organisms in the burrow wall lining of the deep-sea enteropneust *Stereobalanus canadensis*. *Deep-Sea Research 39*, 1247–1253.

Jones, S.E. & Jago, C.F. 1993: In situ assessment of modification of sediment properties by burrowing invertebrates. *Marine Biology 115*, 133–142.

Kalejta, B. & Hockey, P.A.R. 1991: Distribution, abundance and productivity of benthic invertebrates at the Berg River Estuary, South Africa. *Estuarine, Coastal and Shelf Science 33*, 175–191.

Lavina, E.L. & Lopes, R.C. 1986: A transgressão marinha do Permiano Inferior e a evolução paleogeográfica do Super-Grupo Tubarão no Estado do Rio Grande do Sul. *Paula Coutiana 1*, 51–103.

Lavina, E.L., Nowatzki, C.H., Santos, M.A.A. & Leão, H.Z. 1985: Ambientes de sedimentação do Super-Grupo Tubarão na região de Cachoeira do Sul. *Acta Geologica Leopoldensia 9*, 5–75.

Lee, D.L. & Biggs, W.D. 1990: Two- and three-dimensional locomotion of the nematode *Nippostrongylus brasiliensis*. *Parasitology 101*, 301–308.

Lima, J.H.D., Netto, R.G., Graziele, C. & Lavina, E.L.C. 2015: Ichnology of deglaciation deposits from the Upper Carboniferous Rio do Sul Formation (Itararé Group, Paraná Basin) at central-east Santa Catarina State (Southern Brazil). *Journal of South American Earth Sciences 63*, 137–148.

Lopes, R.C. & Lavina, E.L.C. 2001: Estratigrafia de sequencias nas Formações Rio Bonito e Palermo (Bacia do Paraná), na região carbonífera do Jacuí, Rio Grande do Sul. *In* Severiano Ribeiro, H.J.P. (ed): *Estratigrafia de sequencias: fundamentos e aplicações*, 391–419. Ed Unisinos, São Leopoldo.

Lopes, R.da.C., Faccini, U.F., Paim, P.S.G., Garcia, A.J.V. & Lavina, E.L. 2003: Barras de mare na formação Rio Bonito: elementos arquiteturais e geometria dos corpos (Iruí e Canapee RS). *In* Paim, P.S.G., Faccini, U.F. & Netto, R.G. (eds): *Geometria, arquitetura e heterogeneidade de corpos sedimentares: estudo de casos*, 78–92. Ed Unisinos, São Leopoldo.

MacEachern, J.A., Dashtagar, S.E., Kanus, D., Bann, K.L. & Pemberton, S.G. 2012: Sequence stratigraphy. *In* Knaust, D. & Bromley, R.G. (eds): *Trace Fossils as Indicator of Sedimentary Environments*, 157–194. Developments in Sedimentology, vol. *64*. Elsevier, Amsterdam.

Martins, E.A. & Sena Sobrinho, M. 1950: Novos fósseis e a idade da formação Maricá, Rio Grande do Sul. *Boletim do Museu Nacional, Rio de Janeiro 8*, 1–7.

Martins, E.A. & Sena Sobrinho, M. 1952: Perfil Geológico de São Gabriel a Cambaí Grande, Rio Grande do Sul. *Boletim do Museu Nacional, Rio de Janeiro 16*, 1–7.

Meyers, M.B., Fossing, H. & Powell, E.N. 1987: Microdistribution of interstitial meiofauna, oxygen and sulfide gradients, and the tubes of macro-infauna. *Marine Ecology – Progress Series 35*, 223–241.

Milani, E.J., de Melo, J.H.G., de Souza, P.A., Fernandes, L.A. & França, A.B. 2007: Bacia Do Paraná. *Boletim de Geociências da Petrobras, Rio de Janeiro 15*, 265–287.

Mortimer, R.J.G., Davey, J.T., Krom, M.D., Watson, P.G., Frickers, P.E. & Clifton, R.J. 1999: The effect of macrofauna on porewater profiles and nutrient fluxes in the intertidal zone of the Humber Estuary. *Estuarine Coastal Shelf Science 48*, 683–699.

Narbonne, G.M. & Aitken, J.D. 1990: Ediacaran fossils from the Sekwi Brook area, Mackenzie Mountains, northwestern Canada. *Palaeontology 33*, 945–980.

Netto, R.G. 1994: *A paleoicnologia como ferramenta de trabalho na seqüência sedimentar Rio Bonito/Palermo*, 242 pp. Universidade Federal do rio Grande do Sul, Unpublished Doctorate Thesis, Porto Alegre.

Netto, R.G. 1998: Padrão de icnofábricas da sequência sedimentar Rio Bonito/Palermo no RS e seu valor na diagnose paleoambiental. *Acta Geologica Leopoldensia 21*, 209–226.

Netto, R.G., Tognoli, F.M.W., Buatois, L.A. & Mángano, M.G. 2008: Reduction in reservoir potential by cryptobioturbation. A case study in Upper Paleozoic shallow-marine sandstones (Rio Bonito/Palermo sedimentary succession, Paraná Basin, south Brazil). *GSA Joint Annual Meeting, Houston, Abstracts with Program*. v. 1. p. 287.

Ólafsson, E. 2003: Do macrofauna structure meiofauna assemblages in marine soft-bottoms? A review of experimental studies. *Vieet Milieu 53*, 249–265.

Ólafsson, E., Moore, C.G. & Bett, B.J. 1990: The impact of *Melinna palmata* Grube, a tube-building polychaete, on meiofaunal community structure in a soft-bottom subtidal habitat. *Estuarine, Coastal and Shelf Science 31*, 883–893.

Osgood, R.G. 1970: Trace fossils of the Cincinnati area. *Palaeontographica Americana 6*, 281–444.

Parry, L.A., Boggiani, P.C., Condon, D.L., Garwood, R.J., Leme, J.M., McIlroy, D., Brasier, M.D., Trindade, R., Campanha, G.A.C., Pacheco, M.L.A.F., Diniz, C.Q.C. & Liu, A.G. 2017: Ichnological evidence for meiofaunal bilaterians from the terminal Ediacaran and earliest Cambrian of Brazil. *Nature Ecology & Evolution 1*, 1455–1464.

Pemberton, S.G. & Frey, R.W. 1982: Trace fossil nomenclature and the *Planolites-Palaeophycus* dilemma. *Journal of Paleontology 56*, 843–881.

Pinto, T.K. & Bemvenuti, C.E. 2003: Effects of burrowing macrofauna on meiofauna community structure. *Acta Limnologica Brasiliensia 15*, 41–51.

Platt, H.M. & Warwick, R.M. 1980: The store environment. *In* Price, J.H., Irvine, D.E.G. & Farnham, W.F. (eds): *Ecosystems*, vol *2*, 729–759. Academic Press, London.

Poinar, G.O. Jr 2011: The evolutionary history of nematodes: as revealed in stone, amber and mummies. *In* Hunt, D.J. & Perry, R.N. (eds): *Nematology Monographs & Perspectives 9*, 1–429. Brill, Leiden, The Netherlands.

Poinar, G.O. Jr, Kerp, H. & Hass, H. 2008: *Palaeonema phyticum* gen.n., sp.n. (Nematoda: Palaeonematidae fam.n.), a Devonian nematode associated with early land plants. *Nematology 10*, 9–14.

Powers, L.W. & Cole, J.F. 1976: Temperate variation in fiddler crab microhabitats. *Journal of Experimental Marine Biology and Ecology 21*, 141–157.

Reise, K. 1985: *Tidal Flat Ecology: An Experimental Approach to Species Interactions*, 191 pp. Springer-Verlag, Berlin.

Reise, K. & Ax, P. 1979: A meiofaunal 'Thiobios' limited to the anaerobic sulfide system of marine sand does not exist. *Marine Biology 54*, 225–237.

Riemann, F. & Helmke, E. 2002: Symbiotic relations of sediment-agglutinating nematodes and bacteria in detrital habitats: the enzyme-sharing concept. *Marine Ecology 23*, 93–113.

Robinson, A.F. & Perry, R.N. 2006: Behaviour and sensory perception. *In* Perry, R.N. & Moens, M. (eds): *Plant Nematology*, 210–233. CABI Publishing, Wallingford.

Rosa, L.C. & Bemvenuti, C.E. 2005: Effects of the Burrowing Crab *Chasmagnathus granulata* (Dana) on meiofauna of estuarine intertidal habitats of Patos Lagoon, Southern Brazil. *Brazilian Archives of Biology and Technology 48*, 267–274.

Schlirf, M., Uchman, A. & Kummel, M. 2001: Upper Triassic (Keuper) non-marine trace fossils from the Hagberge area (Franconia, south-eastern Germany). *Paläontologische Zeitschrift 75*, 71–96.

Schneider, R.L., Mühlmann, H., Tomamasi, E., Medeiros, R.A., Daemon, R.F. & Nogueira, A.A. 1974: Revisão estratigráfica da Bacia do Paraná. *Anais do Congresso Brasileiro de Geologia, 28. Porto Alegre 1*, 41–65.

Schräm, E.R. 1973: Pseudocoelomates and a nemertine from the Illinois Pennsylvanian. *Journal of Paleontology 47*, 985–989.

Schräm, F.R. 1979: Worms of the Mississippian Bear Gulch Limestone of central Montana, USA. *Transactions of the San Diego Society of Natural History 19*, 107–120.

Seilacher, A. 1964: Biogenic sedimentary structures. *In* Imbrie, J. & Newell, N. (eds): *Approaches to Paleoecology*, 296–316. Wiley and Sons, New York.

Seilacher, A. 2008: Biomats, biofilms, and bioglue as preservational agents for arthropod trackways. *Palaeogeography, Palaeoclimatology, Palaeoecology 270*, 252–257.

Seilacher, A., Reif, W.E. & Westphal, F. 1985: Sedimentological, ecological and temporal patterns of fossil lagerstätten. *Philosophical Transactions of the Royal Society of London B 311*, 5–23.

Shimanaga, M., Masuda, T. & Henmi, Y. 2012: Fine scale meiofaunal distribution around burrows of Ocypodoids (decapoda, Ocypodoidea) in tidal flat sediments. *Crustaceana 85*, 953–974.

Størmer, L. 1963: *Gigantoscorpio willsi,* a new scorpion from the Lower Carboniferous of Scotland and its associated preying microorganisms. *Skrifierutgittav Det Norske Videnskaps-Akademii Oslo 1. Matematisk-naturvidenskapelig Klasse NySerie 8*, 1–171.

Tarhan, L.G. 2017: Meiofauna mute the Cambrian explosion. *Nature Ecology & Evolution 1*, 1423–1424.

Taylor, J.D. & Cunliffe, M. 2015: Polychaete burrows harbour distinct microbial communities in oil-contaminated coastal sediments. *Environmental Microbiology Reports 7*, 606–613.

Tognoli, F.M.W. 2002: *Análise estratigráfica e paleoicnológica do Grupo Guatá no leste paranaense*, 90 pp. IGCE/UNESP, Unpublished Master's Thesis, Rio Claro.

Uchman, A. 1995: Taxonomy and palaeoecology of flysch trace fossils: the Marnoso arenacea Formation and associated facies (Miocene, Northern Apennines, Italy). *Beringeria 15*, 1–115.

Uchman, A. 1998: Taxonomy and ethology of flysch trace fossils: a revision of the Marian Książkiewicz collection and studies of complementary material. *Annales Societatis Geologorum Poloniae 68*, 105–218.

Uchman, A., Milenapika-Biolzi, M. & Hochuli, P.A. 2004: Oligocene trace fossils from temporary fluvial plain ponds: an example from the Freshwater Molasse of Switzerland. *Eclogae Geologicae Helvetiae 97*, 133–148.

Uchman, A., Kazakauskas, V. & Gaigalas, A. 2009: Trace fossils from Late Pleistocene lacustrine varve sediments in eastern Lithuania. *Palaeogeography, Palaeoclimatology, Palaeoecology 272*, 199–211.

Van Damme, D., Herman, R., Sharma, Y., Holvoet, M. & Martens, P. 1980: Benthic studies of the. Southern Bight of the North Sea and its adjacent continental estuaries. Progress Report II: fluctuations of the meiobenthic communities in the Westerschelde estuary. *ICES, CM/L 23*, 131–170.

Volkenborn, N., Hedtkamp, S.I.C., van Beusekom, J.E.E. & Reise, K. 2007: Effects of bioturbation and bioirrigation by lugworms (*Arenicola marina*) on physical and chemical sediment properties and implications for intertidal habitat succession. *Estuarine, Coastal and Shelf Science 74*, 331–343.

Wallace, H.R. 1968: The dynamics of nematode movement. *Annual Review of Phytopathology 6*, 91–114.

Warwick, R.M., Gee, J.M. & Ambrose, J.R.W. 1986: Effects of the feeding activity of the polychaete *Streblosoma bairdi* (Malmgren) on meiofaunal abundance and community structure. *Sarsia 71*, 11–16.

Whittard, W.F. 1953: *Palaeoscolexpis catorum* gen.et sp. nov., a worm from the Tremadocian of Shropshire. *Quarterly Journal of the Geological Society of London 109*, 125–135.

Wignall, P.B. 1993: Distinguishing between oxygen and substrate control in fossil benthic assemblages. *Journal of the Geological Society of London 150*, 193–196.

Zálan, P.V., Wolff, S., de Conceição, J.C., Marques, A., Astolfia, M.A.M., Vieira, I.S., Appi, V.T. & Zanotto, O.A. 1990: Bacia do Paraná. *In* Raja Gabaglia, G.P. & Milani, E.J. (eds): *Origem e evolução de bacias sedimentares*, 135–168. Gavea, Rio de Janeiro.

Zhang, L.J. & Zhao, Z. 2015: Lower Devonian trace fossils and their paleoenvironmental significance from the western Yangtze Plate, South China. *Turkish Journal of Earth Sciences 24*, 325–343.

Capitulo 2. Glossifungites suites demarking autogenic and allogenic sedimentary surfaces: a case study in estuarine and shoreface deposits

Glossifungites suites demarking autogenic and allogenic sedimentary surfaces: a case study in estuarine and shoreface deposits

Jorge Villegas-Martín, Renata Guimarães Netto, Henrique Parisi Kern
Geology Graduate Program, Unisinos University, Av. Unisinos 950, 93022-000 São Leopoldo, RS, Brazil. jvillegasmartin@gmail.com, nettorg@unisinos.br, hpkern@unisinos.br

Corresponding author: Jorge Villegas-Martín

Abstract

The Glossifungites Ichnofacies is a substrate-controlled ichnofacies that occur in omission surfaces and have been used in the identification and interpretation of stratigraphic discontinuities. The early Permian Rio Bonito-Palermo sedimentary succession from the Paraná Basin (southern Brazil) offers an opportunity to discuss the genesis of the omission surfaces demarked by the occurrence of Glossifungites suites. These suites are composed of sharp, unlined burrows with irregular walls and passive infill by generally medium- to coarse-grained sandstones. *Thalassinoides* is the dominant component in the Glossifungites suites in the studied deposits, with local occurrences of *Diplocraterion*, *Gyrolithes,* and *Skolithos*. Based on the ichnological signatures of the distinct Glossifungites suites observed in these deposits and the characteristics of the lithofacies in which they occur, the associated discontinuity surfaces were interpreted as autogenic or allogenic. Glossifungites suites demarking allogenic surfaces occur in association with a sequence boundary and regressive surfaces registered in lower shoreface settings. Glossifungites suites demarking autogenic surfaces are associated with dewatered muddy substrates from the estuarine settings. The trace fossils that characterize the Glossifungites suites in the early Permian of the Paraná Basin are representative of the main ichnogenera that constitute the Glossifungites Ichnofacies throughout the Phanerozoic.

Keywords: Glossifungites suite, sequence stratigraphy, substrate-controlled trace fossil suites, Paleozoic.

1. Introduction

The Glossifungites Ichnofacies is a substrate-controlled ichnofacies that occurs exclusively in compacted, but unlithified substrates (Seilacher, 1967) consisting of dewatered mud and, more rarely, sand (e.g., Pemberton and Frey, 1985; MacEachern et al., 1992a,b, 1997; Pemberton et al., 1992, 2004; MacEachern et al., 2007; Buatois et al., 2008; Dasgupta and Buatois, 2012). It is characterized by the occurrence of vertical and subvertical dwelling burrows and pseudoborings made by arthropods, mollusks, and few soft-body organisms capable to excavate stiffgrounds and firmgrounds (e.g., Gingras et al., 1999; 2001a,b; Savrda et al., 2001a,b; Netto et al., 2007; Buatois and Mángano, 2011). Several ichnotaxa were registered in trace fossil suites that represent the Glossifungites Ichnofacies. The majority of this record characterizes the feeding behavior of suspension-feeders (*Conichnus, Skolithos, Diplocraterion, Arenicolites, Gastrochaenolites, Palaeophycus* and *Bergaueria*) (Pemberton and Frey, 1985; Balistieri and Netto, 2002; Buatois and Encinas, 2006; Fielding et al., 2006; Netto et al., 2007; Pearson et al., 2012; Abdel-Fattah et al., 2016; Belaústegui et al., 2016; Sedorko et al., 2018). However, burrows of deposit-feeders such as *Planolites, Taenidium, Rhizocorallium*, *Zoophycos*, and ?*Chondrites* were also attributed to trace fossil suites of the Glossifungites Ichnofacies (MacEachern and Burton, 2000; Uchman et al., 2000; Cónsole-Gonella, 2009), a matter that still needs review. Dwelling structures of deposit-feeders and organisms that feed outside the burrows, such as *Thalassinoides*, *Spongeliomorpha, Glossifungites*, and *Psilonichnus*, are also commonly present in this assemblage (Seilacher, 1967; Pemberton and Frey, 1985; Savrda, 1991; Bromley and Allouc, 1992; Buatois et al., 2002; Balistieri and Netto, 2002; Netto et al., 2007; Carmona et al., 2006; Gandini et al., 2010; Dasgupta and Buatois, 2012; Belaústegui et al., 2016).

The occurrence of Glossifungites suites has been largely used to demark key stratigraphic surfaces, especially sequence boundaries, represented by allogenic surfaces formed in shelf and slope deposits (Hayward, 1976; MacEachern et al., 1992a,b, 1999; Raychaudhuri et al., 1992; Pemberton and MacEachern, 1995; MacEachern and Burton, 2000; Savrda et al., 2001a,b; Buatois et al., 2002; De Gibert and Robles, 2005; Hubbard et al., 2012). However, Glossifungites suites are common in marginal marine and shallow marine settings, colonizing compacted substrates exhumed by a wave and current ravinement and channel erosion that create autogenic surfaces (Gingras et al., 2002a; Yang et al., 2009; Pearson et al., 2012; Abdel-Fattah et al., 2016). Thus, the recognition of an autogenic or allogenic genesis of the substrate that hosts a Glossifungites suite is crucial for sequence stratigraphy.

Glossifungites suites occur in the Late Carboniferous-early Permian deposits of the Gondwanan Paraná Basin (southern Brazil), in association with distinct stratigraphic surfaces formed during transgressive cycles related to deglaciation events (Rio do Sul

Formation; Balistieri and Netto, 2002; Netto et al., 2012a,b) and during transgressive-regressive cycles that characterize the post-glacial transgressive succession (Rio Bonito and Palermo formations; Netto, 1994, 1998, 2000; Buatois et al., 2001, 2007; Tognoli, 2006; Gandini et al., 2010; Netto et al., 2012b). These surfaces were assumed as sequence boundaries of 3rd and 4th stratigraphic orders. However, most of the Glossifungites suites recorded in the Rio Bonito Formation occur in estuarine deposits, in which an autogenic origin for erosive substrates might be expected. In this paper, we analyze the Glossifungites suites preserved in the marginal-marine and shallow marine deposits of the Rio Bonito-Palermo sedimentary succession, aiming to discuss the genesis of these suites and its stratigraphic significance. We also evaluate the ichnofaunal composition of these suites in the evolutionary context of the *Glossifungites* assemblages through time.

2. Geological context

The trace fossils studied herein occur in muddy and fine-grained sandy deposits of the Rio Bonito and Palermo formations that represent the early Permian succession of the Paraná Basin (Habekost, 1978, 1983; Lavina et al., 1985; Lavina and Lopes, 1987; Lopes, 1990; Santos et al., 2006). The Paraná Basin is an intracratonic basin covering approximately 1,500,000 km^2 of central-southern Brazil, Paraguay, Uruguay, and northern Argentina (Zálan et al., 1990; Milani et al., 2007) (Fig. 1). The basin infill reaches a maximum thickness of 8000 m approximately in its depocenter (Zalan et al., 1990) and consists mainly of Late Ordovician to Late Cretaceous sedimentary deposits with a minor contribution of volcanic rocks (Milani et al., 2007). The tectonic and depositional evolution of the Paraná Basin originated uplift and subsidence cycles that coincided with the major orogenic phases in the history of southwestern Gondwana, forming regional unconformities that allowed Milani et al. (2007) to delimitate six supersequences. The sedimentary succession of the Rio Bonito and Palermo formations represents the transgressive basal Permian deposits of the Gondwana I Supersequence. These deposits record a 2nd order transgressive-regressive cycle in which the transgressive trend characterizes the post-glacial deposition that marks the final stages of the Late Paleozoic Ice Age in western Gondwana (Eyles et al., 1993; Milani et al., 2007; Bocardi et al., 2009; Limarino et al., 2013; Montañez and Poulsen, 2013; Cagliari et al., 2014, 2016).

The Rio Bonito Formation is composed mostly of very fine- to very coarse-grained sandstone, conglomerate, fine-grained heterolithic deposits, mudstone, and coal seams (e.g., Schneider et al., 1974; Lavina et al., 1985; Lavina and Lopes 1986; Buatois et al., 2001a,b, 2007; Tognoli 2002; Gandini et al., 2010; Holz et al., 2010) deposited during the Asselian-Sakmarian age (Cagliari et al., 2014, 2016; Griffins et al., 2017). A body fossil fauna occurs locally and is composed predominantly of inarticulate brachiopods, asteroid and ophiuroid echinoderms, bivalve and gastropod mollusks, and plant fragments (e.g., Dolianiti, 1945; Martins and Sena Sobrinho, 1950, 1952; Schmidt-Neto, 2010; Schmidt-Neto et al., 2018). The basal deposits of the Rio Bonito Formation (Triunfo Member) had been assumed as accumulated in fluvial-deltaic settings (e.g., Lavina et al., 1985; Lavina and Lopes, 1986; Holz et al., 2010). The median and upper portions, otherwise, were interpreted as tide- and wave-dominated shallow marine and estuarine deposits (e.g., Netto, 1994, 1998; Buatois et al., 2001a,b; Tognoli, 2002, 2006; Lopes et al., 2003).

The Palermo Formation consists mostly of very fine- to fine-grained sandstone, fine-grained heterolithic deposits, and mudstone (e.g., Lavina et al., 1985; Netto, 1994; Buatois et al., 2001a, 2007; Gandini et al., 2010; Holz et al., 2010). An Artinskian age is proposed to the Palermo Formation based on palynology and paleoflora associations (Daemon and Quadros; 1970, Souza and Marques-Toigo, 2005; Iannuzzi and Souza, 2005; Souza 2006). Body fossils are scarce and represented chiefly by gymnosperm wood (*Dadoxylon* sp.), amphibian teeth (*Loxomma* sp.), and bivalves (Schneider et al., 1974; Simões et al., 1998; Schmidt-Neto et al., 2018). This unit records deposition in open marine environments, ranging from lower shoreface to offshore transition zones (e.g., Lavina et al., 1985; Netto, 1994; Buatois et al., 2007).

Trace fossils of mesohaline and fully marine invertebrate organisms are common in the Rio Bonito (median and upper portions) and Palermo formations (e.g., Netto, 1994, 1998; Buatois et al., 2001a,b; 2007; Gandini et al., 2010; Villegas-Martín and Netto, 2018). Bioerosion structures have also been recorded in valves from mollusk-dominated shell beds preserved in the transgressive deposits of the Rio Bonito Formation (Schmidt-Neto et al., 2018).

3. Material and methods

The sedimentological and ichnological data of the studied interval (Rio Bonito and Palermo formations) came from subsurface deposits expressed in cores TG-94-RS, TG-97-RS, TG-228-RS SC-01-RS, HV-39-RS, HV-45-RS, HN-45-RS, CA-74-RS, CA-61-RS, CA-25-RS, and CA-51-RS drilled by the Brazilian Geological Survey (CPRM) and housed in Caçapava do Sul (the Rio Grande do Sul State, south Brazil) (Figs. 1).

The sedimentological and ichnological data from cores TG-97-RS, TG-228-RS, HV-39-RS, HV-45-RS, CA-74-RS, CA-61-RS, CA-25-RS, and CA-51-RS were used herein as originally described and analyzed by Netto (1994). Supplementary ichnological and sedimentological data were obtained on cores IB-01-RS, IB-03-RS, IB-04-RS, IB-06-RS, IB-08-RS, IB-15-RS, IB-17-RS, IB-22-RS, IB-74-RS, IC-20-RS, IC-32-RS, IC-36-RS, IC-56-RS, CA-10-RS, CA-19-RS, CA-20-RS, CA-58-RS, CA-60-RS, CA-62-RS, CA-63-RS, CA-78-RS, IC-03-RS, IC-07-RS, IC-12-RS, and IC-44-RS originally studied by Buatois et al. (2001, 2007) and Gandini et al. (2010).

Trace fossil description was based on the main general ichnotaxobases (*sensu* Bromley, 1990) applicable to ichnofabrics (burrow limit, burrow infill, branching pattern, and presence/absence of spreiten). The criteria for ichnofacies analysis followed the principles stated by Seilacher (1967), Frey and Seilacher (1980), and Pemberton and Frey (1985) for Glossifungites Ichnofacies. Additional detailed information was also considered, such as cross-cutting relationships, burrow trajectory, and external surface features. The bioturbation was quantified using the bioturbation scale (BS) proposed by Reineck (1963) taking into account an average diameter of 4 cm for the cores.

Facies description followed the general description made by Netto (1994) for the Rio Bonito-Palermo sedimentary succession and is summarized in Table 1. For stratigraphic purposes, the base of Palermo Formation was delimited by the establishment of massive storm deposits represented by very fine- to fine-grained sandstone with hummocky cross-stratification interbedded with moderate to high bioturbated heterolithic deposits, following the criteria used by Lavina et al. (1985), Netto (1994), and Buatois et al. (2007).

4. The Glossifungites suite in the Rio Bonito-Palermo sedimentary succession

The main sedimentary facies observed in the Rio Bonito-Palermo sedimentary succession include conglomerate, massive mudstone, laminated and massive siltstone, coal, fine-grained heterolithic deposits with wavy and lenticular structures, fine- to coarse-grained sandstone with trough cross-stratification, hummocky cross-stratification, combined-flow ripples, wave ripples, and parallel lamination, and massive sandstone (e.g., Lavina et al., 1985; Lavina and Lopes, 1986; Netto, 1994; Buatois et al., 2001, 2007; Holz, 2003; Gandini et al., 2010) (Table 1). Bioturbation occurs in almost all these sedimentary facies, with the exception of the conglomerates, and the massive and laminated siltstone occurring in the basal portion of the succession (Netto, 1994, 1998; Buatois et al., 2001, 2007; Netto et al., 2000, 2012; Gandini et al., 2010). Bioerosion structures occur exclusively in mollusk shells preserved in shell beds in the median portion of the Rio Bonito Formation succession (Schmidt-Neto et al., 2018). The distribution of these sedimentary facies throughout the succession allow recognizing four main facies associations: (i) estuarine; (ii) lower shoreface; (iii) transition offshore; and (iv) offshore (Netto, 1994; Buatois et al., 2007; Gandini et al., 2010) (Fig. 2). Glossifungites suites occur in the massive mudstone lithofacies that compose the estuarine deposits that characterize the upper portion of the Rio Bonito succession (Siderópolis Member, *sensu* Schneider et al., 1974), and in the heterolithic deposits lithofacies that compose the lower shoreface facies association, which characterizes the lower portion of the Palermo succession (Table 1; Fig. 3).

Unlined, sharp-walled burrows circular to subcircular in cross-section with up to 10 mm in diameter showing irregular borders passively filled by coarse- to medium-grained sand are the key components of the ichnofabrics observed in these deposits (Fig. 4-5). The absence of wall reinforcement, the prevalence of irregular borders, and the passive infill of the burrows are the main ichnological signatures that indicate the compaction of an unlithified substrate prior to the burrower's colonization (e.g., Pemberton and Frey, 1985; Savrda, 1991; MacEachern et al., 1992a,b; Bromley, 1996; Savrda et al., 2001a,b; Yang et al., 2009; Buatois and Mángano, 2011; Dasgupta and Buatois, 2012). Thus, the presence of these features allows assuming these trace fossil assemblages as Glossifungites suites (*sensu* Bromley, 1990).

The dominant morphology observed in the Glossifungites suites from the Rio Bonito-Palermo sedimentary succession in cores is *Thalassinoides*, but the sparse occurrence of *Diplocraterion*, *Gyrolithes,* and *Skolithos* was also observed (Fig. 4-5). Netto (1994) also mentioned the occurrence of *Ophiomorpha*-like and *Planolites*-like structures in assemblages interpreted as representative of the Glossifungites Ichnofacies, but the revision of these structures allowed including them in *Thalassinoides*. The ichnodiversity is low, and the amount of bioturbation varies from low to moderate (BS 2-4). The observed ichnotaxobases indicate the prevalence of dwelling-feeding burrows of detritus- and suspension-feeder crustaceans and possibly polychaete.

4.1. Glossifungites suites from estuarine mudstones

The Glossifungites suites observed in massive mudstone lithofacies are characterized by sharp burrows with irregular borders filled by medium- to coarse-grained quartz sandstone. They occur in distinct stratigraphic horizons, mostly at the upper portion of the sedimentary succession that characterizes the Rio Bonito Formation (Siderópolis Member) (Fig. 3). Horizontal and inclined burrows predominate in the trace fossil assemblage, with the local occurrence of vertical burrows (Fig. 4). The ichnodiversity is low, almost monotypic, and the abundance of burrows is low to moderate (BS 2-4). *Thalassinoides* is the most common ichnotaxon, with rare *Skolithos* and local occurrence of *Gyrolithes* (Buatois et al., 2007; Netto et al., 2007, 2012b) (Fig. 4). The massive mudstone lithofacies containing Glossifungites suites are usually eroded by or show abrupt contact with the overlying sandstones. Erosive surfaces are usually capped either by medium- to coarse-grained arkose sandstone with bidirectional trough cross-stratification, mudstone drapes, and local occurrence of double mudstone drapes and coal intraclasts or by fine- to medium-grained sandstone with low-angle cross-stratification. Abrupt surfaces usually are capped by quartz fine- to medium-grained sandstone sometimes massive and non-bioturbated, sometimes showing a fuzzy lamination (Fig. 4). Less frequently, the abrupt surfaces are capped by fine-grained sandstone with low-angle cross-stratification and wave ripples showing sparse softground bioturbation represented by *Thalassinoides, Bergaueria, Diplocraterion, Skolithos,* and occasionally *Ophiomorpha* (BS 2) or homogenized by *Macaronichnus* ichnofabric (BS 4-6). This softground assemblage was assumed as an impoverished expression of the Skolithos Ichnofacies in brackish, outer estuarine settings (e.g., Netto, 1994, 2000; Buatois et al., 2005, 2007; Gandini et al., 2010; Netto et al., 2012b). The Glossifungites suite is the unique bioturbation observed in the massive mudstone facies, indicating the original colonization of a barren, firm substrate.

4.2. Glossifungites suites from lower shoreface heterolithic deposits

The occurrence of Glossifungites suites in the fine-grained heterolithic deposits is characterized by the palimpsest preservation of monotypic ichnofabrics of *Thalassinoides* and large *Diplocraterion* (Fig. 5). Burrows show a sharp, but not necessarily irregular limit, and are passively filled by coarser-grained sand. The spreiten in *Diplocraterion* is subtle or absent. The heterolithic deposits are composed of intercalations of massive mudstone, parallel-laminated siltstone, and fine- to very fine-grained sandstone forming thin lenticular and wavy bedding with undulate tops (symmetric and asymmetric) and low-angle cross-stratification. These deposits are usually interbedded with medium- to fine-grained sandstone with hummocky cross-stratification and medium- to fine-grained sandstone with bidirectional trough cross-bedding sedimentary facies (Table 1). Softground bioturbation is abundant in these heteroliths (BS 4-5) and is characterized by composite ichnofabrics of *Arenicolites, Asterosoma, Bergaueria, Chondrites, Cylindrichnus, Diplocraterion, Helminthopsis, Lockeia, Ophiomorpha, Palaeophycus, Phycosiphon, Planolites, Rhizocorallium, Rosselia, Skolithos, Teichichnus,* and *Thalassinoides*. The high ichnodiversity, the abundance of burrows, and the preserved ichnotaxa indicate a former substrate occupation by archetypal Cruziana Ichnofacies suites (e.g., Netto, 1994, 2000; Buatois et al., 2007; Gandini et al., 2010) and suggest fair-weather sedimentation below the fair-weather wave base level during periods of low sedimentation rate (e.g., Pemberton et al., 2001; Clifton, 2006).

The burrows in the Glossifungites suite are filled by medium- to coarse-grained quartz sandstone that abruptly overlies the heterolithic deposits, forming erosive surfaces. The presence of a sharp limit indicates that the heterolithic substrate exhumed by erosion was compacted when excavated by the tracemakers, but not firm enough to preserve irregular borders, suggesting stiffgrounds (e.g., Gingras et al., 2001). These occurrences are observed in up to three distinct stratigraphic horizons in the studied area (Fig. 3), suggesting regressive surfaces. In the transition between the Rio Bonito and Palermo successions, however, the heterolithic beds with Glossifungites suite are capped by a ~5 cm-thick bed of very coarse-grained arcosean sandstone while the burrows are filled by fine-grained quartz sandstone (Fig. 5). Coarse- to medium-grained arcosean sandstone with trough cross-stratification, coal intraclasts, phytodetritus, and entire mollusk shells interpreted as tidal bar deposits (e.g., Netto, 1994, 2000; Buatois et al., 2007; Gandini et al., 2010) overlies the ~5 cm-thick very coarse-grained sandstone. These tidal bar deposits indicate the reactivation of the estuarine system over the lower shoreface deposits. The erosive surface that records the shift of the sedimentary facies was interpreted by Netto (2000) and Buatois et al. (2007) as a co-planar surface (e.g., Pemberton et al., 2001), suggesting a forced-regression event and characterizing an erosive surface of marine regression. This forced-regression event was interpreted as a sequence boundary by Netto (1994) and reinforced by Buatois et al. (2007), Kern (2008), and Gandini et al. (2010), using it to separate the sedimentary successions that characterizes the Rio Bonito and the Palermo formations (Fig. 3).

5. Stratigraphic significance of the Glossifungites Ichnofacies

Glossifungites Ichnofacies suites have been recorded throughout the geological time in association with allogenic and autogenic sedimentary surfaces (e.g., Pemberton and Frey, 1985; Yang et al., 2009; Gingras et al., 2001; Dasgupta and Buatois, 2012; Belaústegui et al., 2016; Sedorko et al., 2018). Allogenic sedimentary surfaces occur in a regional scale, demarking major important discontinuities, while autogenic sedimentary surfaces extend laterally only over a few meters, demarking lateral facies variation or normal sea level oscillations (e.g., Pemberton and Frey, 1985; Yang, 2009; Pearson et al., 2012).

5.1. Glossifungites suites demarking autogenic surface

The massive mudstone lithofacies showing Glossifungites suites occur exclusively in the estuarine facies association. These mudstones are spatially limited, showing restricted lateral and geographic continuity, but show abrupt contacts with the overlying sandstone deposits. Thus, the observed characteristics allow interpreting the original surfaces from where the trace fossils descend as autogenic surfaces. Firmground Glossifungites suites with similar features have been registered colonizing autogenic surfaces in marginal marine settings (e.g., Pearson et al., 2012; Abdel-Fattah et al., 2016; Yang et al., 2009).

Several autogenic surfaces with Glossifungites suite were recorded in the upper portion of the Rio Bonito succession, sometimes with a frequency of 4 per linear meter. According to Yang et al. (2009), these omission surfaces are formed by erosion and exhumation by tidal currents, opening the colonization window for firmground burrowers during periods of exposure. Some *Thalassinoides* are slightly deformed by compaction, indicating that the substrate was not fully dewatered during the initial colonization (Fig. 4).

Some of the massive mudstones with Glossifungites suite overlie coal beds and are overlaid by sandstones with rhizobioturbation, suggesting colonization of dewatered mudstone from supratidal settings inner estuarine zone. The firmness of the substrate, in this case, might be caused exclusively by mud dewatering. The hypothesis that some Glossifungites suites preserved in the estuarine facies association from Rio Bonito succession might indicate autogenic surfaces was previously considered by Gandini et al. (2010).

5.2. Glossifungites suites demarking allogenic surfaces

The heterolithic deposits lithofacies showing Glossifungites suites occur exclusively in the lower shoreface facies association. The heterolithic beds have a wide spatial distribution and are laterally associated with the fine-grained sandstone with

HCS lithofacies. Thin beds of the coarse-grained sandstone and arkose sandstone lithofacies overlie the heterolithic deposits with Glossifungites suites, showing an erosive contact. The burrows of Glossifungites suite sometimes extend deep into the substrate and show palimpsest preservation over previous Cruziana Ichnofacies suites. These characteristics allow recognizing the surfaces from which the Glossifungites suites burrows descend as allogenic surfaces.

The Glossifuntes Ichnofacies have been used as an indicator of key allogenic stratigraphic surfaces (e.g., Savrda, 1991; Gingras et al., 2000; Savrda et al., 2001; MacEachern and Hobb, 2004; Carmona et al., 2006; Abdel-Fattah et al., 2016; Sedorko et al., 2018). In the Rio Bonito-Palermo sedimentary succession, most of the allogenic surfaces demarked by the presence of Glossifungites suites represent mostly coplanar surfaces preserved in the Palermo succession. Only one occurrence demarks a sequence boundary (SB), at the base of the Palermo succession (Fig. 3). This SB is characterized by a coplanar surface which encompasses at least three distinct depositional events: (i) a marine forced-regression, which exhumed the heterolithic deposits, (ii) a potential marine transgression that provided the fine-grained sand grains that characterize the burrows infill, and (iii) a posterior marine regression, which brought the coarse-grained sandstone that overlies the heterolithic deposits (Fig. 5). This SB was also recognized by Netto (1994), Buatois et al. (2007), Kern (2008), and Gandini et al. (2010) and can be traced regionally, marking a major break in the record between the Rio Bonito and Palermo successions (Fig. 3).

As a rule, burrows from the Glossifungites suite in the heterolithic deposits are larger than those from the massive mudstones. This difference might be only a taphonomic artifact, as the original thickness of the eroded substrates cannot be estimated. However, the prevalence of larger burrows in the Glossifungites suites formed in lower shoreface settings might also indicate that tracemakers had more time to explore the exhumed substrates in these settings than in the estuarine settings, where erosive events are more frequent.

6. The ability to excavate compacted substrates throughout the geological time

Organisms that interact with stiff- or firmgrounds can be able to penetrate mechanically into these compacted substrates. Thus, they need strong muscles or appendages like limbs, or efficient mouthparts that can remove the sediment grains or particles during the excavation. In some particular cases, biological secretions can help in sediment disaggregation, particularly in calcareous substrates.

Extant arthropods, bivalve mollusks, and some particular sea anemones and polychaetes live in burrows excavated in firm substrates and represent the universe of tracemakers that produced most of the reported ichnotaxa in Glossifungites Ichnofacies (e.g., Carmona et al., 2006; Yang et al., 2009; Buatois and Mangano, 2011; Belaústegui et al., 2016). This universe includes mostly *Arenicolites, Diplocraterion, Gastrochaenolithes, Glossifungites, Rhizocorrallium, Skolithos,* and *Thalassinoides* (e.g., Seilacher, 1964; Pemberton and Frey, 1985; Bromley, 1996; Pemberton, 1998; Uchman et al., 2000; Pemberton et al., 2001; Buatois and Encina, 2006; MacEachern et al., 2007; Netto et al., 2007; Yang et al., 2009; Buatois and Mángano, 2011; Dasgupta and Buatois, 2012; Pearson et al., 2012; Sedorko et al., 2018). MacEachern and Burton (2000) reported *Chondrites* and *Zoophycos* in the Glossifungites Ichnofacies, a curious record considering that the small diameter that normally characterizes these burrows, which suggest a tiny, delicate wormlike organism as tracemaker, does not fit with the biotype expected for reworking firm substrates.

The capability to excavate firm substrates is present in biological programs (*sensu* Seilacher, 2007) since the early Cambrian, revealed by the occurrence of shallow *Diplocraterion paralellum* and *Altichnus foeyni* in the siliciclastic firmgrounds from Norway (Bromley and Hanken, 1991). *Diplocraterion* is common in Glossifungites Ichnofacies suites throughout the Phanerozoic (e.g., Savrda, 1991; Balistieri and Netto, 2002; Carmona et al., 2006; Netto et al., 2007; Yang et al., 2009; Gandini et al., 2010; Sedorko et al., 2018). This capability was expanded in the early Paleozoic, with the record of *Skolithos* since the Ordovician, and *Thalassinoides*, *Rhizocorallium*, and *Arenicolites*, since the Devonian (Driese and Foreman, 1991; Smith and Jacobi, 1998; Tognoli et al., 2003; Sedorko et al., 2018). Except for *Arenicolites*, these trace fossils are the key-ichnotaxa in Glossifungites Ichnofacies, suggesting arthropods and polychaetes as the main colonizers of firm substrates throughout the time (e.g., Rodríguez and Panza, 2003; Rodríguez-Tovar et al., 2007; MacEachern et al., 2007; Buatois et al., 2007).

Thalassinoides is the predominant component of the Glossifungites suites in the Rio Bonito-Palermo sedimentary succession. This ichnogenus is the most ubiquitous trace fossil in the Glossifungites Ichnofacies throughout the Phanerozoic, increasing its record in firmgrounds during the Cretaceous, and in the Neogene (e.g., Pemberton and Frey, 1985; MacEachern et al., 1998; Campbell and Nesbitt, 2000; Gingras et al., 2001, 2002 a,b; Savrda, 2001a,b; Balistiere and Netto, 2002; Buatois et al., 2002; Gandini et al., 2010; Dasgupta and Buatois, 2012; Pearson et al., 2012; Abdel-Fattah et al., 2016; Carmona et al., 2016; Schultz et al., 2016). Although Paleozoic *Thalassinoides* cannot be attributed to a specific group of arthropods with accuracy (Carmona et al., 2004), post-Paleozoic *Thalassinoides* are assumed to be produced by thalassinid crustaceans, which can explore firm substrates in modern settings (e.g., Monaco and Garassino, 2001). According to Carmona et al. (2004), the drop of the *Thalassinoides* record in firm substrates in the Paleogene follows the pattern observed in softgrounds and might reflect the effect of the end-Cretaceous mass extinction. However, the increasing of the *Thalassinoides* record in firm substrates during the Cretaceous could represent a "research" bias caused by the volume of ichnological work carried out on the K-Pg boundary. The increase in the record of *Thalassinoides* in firm substrates in the Neogene reflects the remarkable proliferation of decapod crustaceans in shallow seas and the prevalence of crustacean burrows in shallow-marine ichnofaunas since the Miocene (Carmona et al., 2004).

7. Conclusions

The presence of Glossifungites suites in the Rio Bonito-Palermo sedimentary succession was crucial for recognizing key stratigraphic surfaces and differentiate among autogenic and allogenic surfaces. The recognition of burrows showing sharp irregular borders and sharp, but without irregular borders, allowed differentiating colonization in firmgrounds and stiffgrounds, respectively. Colonization of firmgrounds occurred mostly in barren mudstones from estuarine settings, while the lower shoreface deposits characterized mostly stiffgrounds. The major frequency of large burrows in association with allogenic surfaces was determinant to consider them a potential signature of these surfaces, at least in the studied succession.

The trace fossil assemblages that characterize the Glossifungites suites preserved in the Rio Bonito-Palermo sedimentary succession suggest that crustacean and possibly polychaetes were the main colonizers of firm substrates in the Paraná Basin during the early Permian.

8. Acknowledgements

We thank to F. Tognoli, D. Sedorko, H. Smicht-Neto and R.S. Horodyski for helpful discussions. JVM thanks to CAPES by the Ph.D. grant. RGN thanks the Brazilian National Council for Scientific and Technological Development (CNPq) by the research grants 401826/2010-4 and 303863/2016-1. This study is a contribution to the project CAPES/PVE/88881.062157-2014-01 and was also financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001.

9. References

Abdel-Fattah, Z.A., Gingras, M.K., Caldwell, M.W., Pemberton, S.G., MacEachern J.M. 2016. The *Glossifungites* Ichnofacies and Sequence Stratigraphic Analysis: A Case Study from Middle to Upper Eocene Successions in Fayum, Egypt. Ichnos 3–4, 157–179.

Bann, K. L., Fielding, C. R., MacEachern, J. A., Tye, S. C. 2004. Differentiation of estuarine and offshore marine deposits using integrated ichnology and sedimentology: Permian Pebbly Beach Formation, Sydney basin, Australia. In: McIlory, D. (Ed.), The Application of Ichnology to Palaeoenvironment and Stratigraphic Analysis. Geological Society, Special Publications 228, pp. 179–212.

Balistieri, P., Netto, R.G. 2002. A Glossifungites suite in deposits of the Itararé Group (Upper Carboniferous-Lower Permian of Paraná Basin) at Mafra region, North of

Santa Catarina State, Brazil: ichnotaxonomy, and paleoecological and stratigraphical constraints. Acta Geologica Leopoldensia 55, 91–106.

Belaústegui, Z., Ekdale, A.A., Domènech, R., Martinell, J. 2016. Paleobiology offirmground burrowers and cryptobionts at a Miocene omission surface, Alcoi, SE Spain. Journal of Paleontology 90(4), 721–733.

Bertling, M., Braddy, S.J., Bromley, R.G. 2006. Names for trace fossils: a uniform approach. Lethaia 39, 265–286.

Bocardi, L.B., Rostirolla, S.P., Vesely, F.F., França, A.B. 2009. Diagênese, contexto deposicional e história de soterramento da Formação Rio Bonito, Bacia do Paraná. Revista Brasileira de Geociências 39, 465–478.

Bromley, R.G. 1990. Trace Fossils: Biology and Taphonomy. Unwin Hyman, London.

Bromley, R.G. (Ed.) 1996. Trace Fossils. Biology, Taphonomy and Applications, 2nd ed. Chapman and Hall, London, 361pp.

Bromley, R. G., Hanken, N.M. 1991. The growth vector in trace fossils: Examples from the *Glossifungites* Ichnofacies, Lower Cambrian, Norway. Ichnos 1, 261–276.

Buatois, L.A., Encinas, A. 2006. La icnofacies de Glossifungites en el contacto entre las formaciones Navidad (Miembro Rapel) y La Cueva, Plioceno de la Cordillera de la Costa, Chile: Su significado estratigráfico-secuencial. Ameghiniana 43 (1), 3–9.

Buatois, L. A., Gingras, M. K., MacEachern, J., Mángano, M. G., Zonneveld, J.-P., Pemberton, S. G., Netto, R. G., Martin, A. 2005. Colonization of brackish-water systems through time: Evidence from the trace-fossil record. Palaios 20, 321–347.

Buatois, L. A., Mángano, M.G. (eds.) 2011. Ichnology: Organism-Substrate interactions in Space and Time. Cambridge University Press, 370 pp.

Buatois, L. A., Mangano, M. G., Alissa, A., Carr, T. R. 2002. Sequence stratigraphic and sedimentologic significance of biogenic structures from a late Paleozoic marginal to open-marine reservoir, Morrow Sandstone, subsurface of southwest Kansas, USA. Sedimentary Geology 152, 99–132.

Buatois, L.A., Netto, R.G., Mángano, M.G. 2001a.Reinterpretaciónpaleoambiental de la Formación Rio Bonito (Pérmico de la Cuenca de Paraná) em el yacimiento de carbón de Iruí, Rio Grande do Sul, Brasil: integración de análisis de fácies, icnología y estratigrafia secuencial de alta resolución. Geogaceta 29, 27–30.

Buatois, L.A.; Netto, R.G., Mángano, M.G. 2001b. Paleoenvironmental and sequence-stratigraphic analyses of Lower Permian marginal- to shallow marine coal-bearing successions of the Paraná Basin in Rio Grande do Sul, Brazil, based on ichnological data. Ciência, Técnica, Petróleo, Seção Exploração de Petróleo 20, 171–176.

Buatois, L.A., Netto, R.G., Mángano, M.G. 2007. Ichnology of Permian marginal- to shallow marine coal-bearing successions: Rio Bonitoand Palermo Formations, Paraná Basin, Brazil. In: MacEachern, J.A., Bann, K.L., Gingras, M.K., Pemberton, S.G (Eds.), Applied ichnology. SEPM Short Course Notes 52, pp. 167-178.

Cagliari, J., Lavina, E. L. C., Philipp, R. P., Tognoli, F. M. W., Basei, M. A. S., Faccini, U. F. 2014. New Sakmarian ages for the Rio Bonito formation (Paran a Basin, southern Brazil) based on LA-ICP-MS UePb radiometric dating of zircons crystals. Journal of South American Earth Sciences 56, 265–277.

Cagliari, J., Philipp, R.P., Buso, V,. Netto, R., Klaus, P., Ricardo da Cunha Lopes, R., Miguel Angelo Stipp Basei, M.A.S., Faccini, U.F. 2016. Age constraints of the glaciation in the Paraná Basin: evidence from new U–Pb dates. Journal of the Geological Society 173, 871–874.

Carmona, N.B., Buatois, L.A., Mángano, M.G. 2004. The trace fossil record of burrowing decapod crustaceans: evaluating evolutionary radiations and behavioural convergence. Fossils and Strata 51, 141–153.

Carmona, N.B., Ponce, J.J., Mángano., M.G and Buatois, L.A. 2006. Variabilidad de la icnofacies de Glossifungites en el contacto entre las Formaciones Sarmiento (Eoceno medio -Mioceno temprano) y Chenque (Mioceno temprano) en el Golfo San Jorge, Chubut, Argentina. AMEGHINIANA 43 (2), 413–425.

Clifton, H.E. 2006. A re-examination of facies models for clastic shorelines. In: Walker, R.G., Posamentier, H. (Eds.), Facies Models Revisited. SEPM Spec. Publ., Tulsa, pp. 293–337.

Daemon, R.F., Quadros, L.P. 1970. Bioestratigrafia do Neopaleozóico da Bacia do Paraná. XXIV Congresso Brasileiro de Geologia, Brasília. Anais, Volume 1. Sociedade Brasileira de Geologia, Brasília, pp. 359–412.

Dam, G. 1990. Palaeoenvironmental significance of trace fossils from the shallow marine Lower Jurassic Neill Klinter Formation, East Greenland. Palaeogeography, Palaeoclimatology, Palaeoecology 79, 221–248.

Dasgupta, S., Buatois, L. A. 2012. Unusual occurrence and stratigraphic significance of the *Glossifungites* ichnofacies in a submarine paleo-canyon—Example from a

Pliocene shelf-edge delta, Southeast Trinidad. Sedimentary Geology 269–270, 69–77.

Dolianiti, E. 1945. Descoberta de fósseis na Formação Maricá, Estado do Rio Grande do Sul. Revista Mineração e Metalurgia IX (5), 110.

Driese, S. G., Foreman, J. L. 1991. Traces and related chemical changes in a Late Ordovician paleosol, *Glossifungites* Ichnofacies, southern Appalachians, USA. Ichnos 1, 207–219.

Eyles, C.H., Eyles, N., França, A.B., 1993. Glaciation and tectonics in an active intracratonic basin: The Late Palaeozoic Itararé Group, Paraná Basin, Brazil. Sedimentology 40, 1–25.

Frey, R. W., Seilacher, A. 1980. Uniformity in marine invertebrate Ichnology. Lethaia 13, 183–207.

Gandini, R., Netto, R.G., Kern H.P., Lavina, E.L.C. 2010. Assinaturas icnológicas da sucessão sedimentar Rio Bonito no bloco central da jazida carbonífera de Iruí, Cachoeira do Sul (RS). Gaea– Journal of Geosciences 6, 21– 43.

Gingras, M. K., Pemberton, S. G., Saunders, T. 2000. Firm-ness profiles associated with tidal-creek deposits: The temporal significance of *Glossifungites* assemblages. Journal of Sedimentary Research 70, 1017–1025.

Gingras, M. K., Pemberton, S. G., Saunders, T. D. A. 2001. Bathymetry, sediment texture, and substrate cohesiveness: their impact on *Glossifungites* trace assemblages at Willapa Bay, Washington. Palaeogeography, Palaeoclimatology, Palaeoecology 169, 1–21.

Gingras, M. K., Räsänen, M. E., Pemberton, S. G., Romero, L. P. 2002a. Ichnology and sedimentology reveal depositional characteristics of bay-margin parasequences in Miocene Amazonian foreland basin. Journal of Sedimentary Research 72, 871–883.

Gingras, M. K., Räsänen, M. E., Ranzi, A. 2002b. The significance of bioturbated inclined heterolithic stratification in the southern part of the Miocene Solimoes Formation, Rio Acre, Amazonia Brazil. Palaios 17, 591–601.

Griffis, N.P., Mundil, R., Montañez, I.P., Isbell, J., Fedorchuk, N., Vesely, F., Iannuzzi, R., Yin, Q.-Z., 2017. A new stratigraphic framework built on U-Pb single zircon TIMS ages and implications for the timing of the penultimate icehouse (Paraná Basin, Brazil). Geological Society of America Bulletin, 2018. http://dex.doi.org/10.1130/B31775.1.

Hayward, B. W. 1976. Lower Miocene bathyal and submarine canyon ichnocoenoses from Northland, New Zealand. Lethaia 9, 149–162.

Habekost, N.T. 1978. Paleoambientes da Formação Palermo no Sudeste do Estado de Santa Catarina -Brasil. Acta Geologica Leopoldensia 4, 4–17.

Habekost, N.T. 1983. Paleoambientes da Formação Palermo na região central do Rio Grande do Sul, Brasil. Acta Geologica Leopoldensia 16, 43–113.

Holz, M. 2003. Sequence stratigraphy of a lagoonal estuarine system – an example from the lower Permian Rio Bonito Formation, Paraná Basin, Brazil. Sedimentary Geology 162, 301–327.

Holz M., França A. B., Souza P. A., Iannuzzi R., Rohn R. 2010. A stratigraphic chart of the Late Carboniferous/Permian succession of the eastern border of the Paraná Basin, Brazil, South America. Journal of South American Earth Sciences 29, 381–399.

Hubbard, S., MacEachern, J. A., Bann, K. L. 2012. Slope ichnology. In: Knaust, D., Bromley, R. G. (Eds.), Trace fossils as indicators of sedimentary environments. Developments in Sedimentology, 64, pp. 607–642.

Iannuzzi, R., Souza, P.A., 2005. Floral succession in the Lower Permian deposits of the Brazilian Paraná Basin: an up-to-date overview. In: Lucas, S.G., Zigler, K.E. (Eds.) The Non marine Permian: New Mexico. New Mexico Museum of Natural History and Science Bulletin, 30, pp. 144-149.

Jones, B., Pemberton, S.G. 1989. Sedimentology and ichnology of a Pleistocene unconformity-bounded, shallowing-upward carbonate sequence: the Ironshore Formation, Salt Creek, Grand Cayman. Palaios 4, 343–355.

Kern, H.P. 2008. Arquitetura estratigráfica de corpos arenosos gerados por ondas e marés no bloco central da mina de Iruí (Formação Rio Bonito, Eopermiano da bacia do Paraná, RS). (Masters Thesis) Universidade UNISINOS, São Leopoldo, 145 pp.

Lopes, R. da C. 1990. Estudo paleoambiental da Formação Rio Bonito na Jazida do Leão - RS. Uma análise inicial. Acta Geologica Leopoldensia 31, 91–112.

Lopes, R. da. C., Faccini, U.F., Paim, P.S.G., Garcia, A.J.V., Lavina, E.L. 2003. Barras de mare na formação Rio Bonito: elementos arquiteturais e geometria dos corpos (Iruı e Canapee RS). In: Paim, P.S.G., Faccini, U.F., Netto, R.G. (Eds.), Geometria, arquitetura e heterogeneidade de corpos sedimentares: estudo de casos. Ed Unisinos, São Leopoldo, pp. 78–92.

Lavina, E.L., Nowatzki, C.H., Santos, M.A.A., Leão, H.Z. 1985. Ambientes de sedimentação do Super-Grupo Tubarao na região de Cachoeira do Sul. Acta Geologica Leopoldensia 9, 5–75.

Lavina, E.L., Lopes, R.C. 1986. A transgressão marinha do Permiano Inferior e a evolução paleogeografica do Super-Grupo Tubarão no Estado do Rio Grande do Sul. Paula Coutiana1, 51–103.

Limarino, C.O., Césari, S.N., Spalletti, L.A., Taboada, A.C., Isbell, J.L., Geuna, S., Gulbranson, E.L., 2013. A paleoclimatic review of southern South America during the late Paleozoic: a record from icehouse to extreme greenhouse conditions. Gondwana Research 25, 1396–1421.

MacEachern, J. A., Bechtel, D. J., Pemberton, S. G. 1992a. Ichnology and sedimentology of transgressive deposits, trans-gressively related deposits and transgressive systems tracts in the Viking Formation of Alberta. In: Pemberton, S. G. (Ed.), Applications of Ichnology to Petroleum Exploration: A Core Workshop. Society of Economic Paleontologists and Mineralogists, CoreWorkshop,17, pp. 251–290.

MacEachern, J. A., Burton, J. A. 2000. Firmground *Zoophycos* in the Lower Cretaceous Viking Formation, Alberta: A distal expression of the *Glossifungites* Ichnofacies. Palaios 15, 387–398.

MacEachern, J. A., Hobbs, T. W. 2004. The ichnological expression of marine and marginal marine conglomerates and conglomeratic intervals, Cretaceous Western. In: Moslow, T., Zonneveld, J.P. (Eds.), Marine Conglomerates. Bulletin of Canadian Society of Petroleum Geology, 52: 77–104 pp.

MacEachern, J. A., Pemberton, S. G. 1994. Ichnological character of incised valleyfill systems from the Viking Formation of the Western Canada Sedimentary basin, Alberta, Canada. In: Dalrymple, R. W., Boyd, R., Zaitlin, B. A. (Eds.), Incised-Valley Systems: Origin and Sedimentary Sequences. Society of Economic Paleontologists and Mineralogists, Special Publication, 51, pp. 129–157.

MacEachern, J. A., Raychaudhuri, I., Pemberton, S. G. 1992b. Stratigraphic applications of the *Glossifungites* Ichnofacies: Delineating discontinuities in the rock record. In: Pemberton, S.G. (Ed.), Applications of Ichnology to Petroleum Exploration: A Core Workshop. Society of Economic Paleontologists and Mineralogists, Core Workshop, 17, pp. 169–198.

MacEachern, J. A., Gingras, M. K., Bann, K. L, Pemberton, S. G., Dafoe, L.T. 2007. Application of ichnology to high-resolution genetic stratigraphic paradigms. In: MacEachern, J. A., Bann, K. L., Gingras, M. K., Pemberton, S.G. (Eds.), Applied Ichnology. Society of Economic Palaeontologists and Mineralogists, Short CourseNotes, 52, pp. 93–127.

MacEachern, J. A., Zaitlin, B. A., Pemberton, S. G. 1999. Coarse-grained, shoreline-attached, marginal marine para-sequences of the Viking Formation, Joffre Field, Alberta Canada. In: Bergman, K.M., Snedden, J.W. (Eds.), Isolated Shallow Marine Sand Bodies: Sequence Stratigraphic and Sedimentologic Interpretation. Society of Economic Paleontologists and Mineralogists, Special Publication, 64, pp. 273–296.

Martins, E.A., Sena Sobrinho, M. 1950. Novos fósseis e a idade da formação Maricá, Rio Grande do Sul. Boletin Museu Nacional, Geol. 8.

Martins, E.A., Sena Sobrinho, M. 1952. Perfil Geológico de São Gabriel a Cambaí Grande, Rio Grande do Sul. Boletin Museu Nacional, Geol. 16.

Milani, E.J., Melo, J.H.G. de., Souza, P.A. de., Fernandes, L.A., França, A.B. 2007. Bacia Do Paraná. Boletim de Geociências da Petrobras 15, 265–287.

Montañez, I.P., Poulsen, C.J. 2013. The Late Paleozoic Ice Age: An evolving paradigm. Annual Review in Earth and Planetary Sciences 41, 629–656.

Netto, R.G. 1994. A paleoicnologia como ferramenta de trabalho na seqüência sedimentar Rio Bonito/Palermo. (PhD Thesis) Universidade Federal do Rio Grande do Sul, Porto Alegre, 242 pp.

Netto, R.G. 1998. Padrão de icnofábricas da sequência sedimentar Rio Bonito/Palermo no RS e seu valor na diagnose paleoambiental. Acta Geologica Leopoldensia 21, 209–226.

Netto, R.G. 2000. Paleoicnologia do Rio Grande do Sul. In: Holz, M., Fernando, L.F. de. (Eds.), A paleontologia do Rio Grande do Sul. 1ed. Porto Alegre: CIGO/UFRGS, pp. 25-43.

Netto, R.G**.,** Benner, J.S., Buatois, L.A., Uchman, A., Mángano, M.G., Ridge, J.C., Kazakauskas, V., Gaigalas, A. 2012a. Glacial Environments. In: Knaust, D., Bromley, R.G. (Eds.), Trace Fossils as Indicators of Sedimentary Environments. 1ed. Amsterdan. Elsevier, 64, pp. 227–336.

Netto, R.G., Buatois, L.A., Mángano, G., Balistieri, P. 2007. *Gyrolithes* as a multipurpose burrow: an ethologic approach. Revista Brasileira Paleontologia 10(3), 157–168.

Netto, R.G., Tognoli, F.M.W., Gandini, R., Lima, J. H. D., Gibert, J.M. 2012b. Ichnology of the Phanerozoic deposits of southern Brazil. In: Netto, R.G., Carmona, N., Tognoli, F.M.W. (Eds.), Ichnology of Latin America - Selected Papers. 1ed.Porto Alegre, Sociedade Brasileira de Paleontologia, 2, pp. 37–68.

Simões, M.G., Roha-Campos, A.C., Anelli, L.E. 1998. Paleoecology and evolution of Permian bivalve faunas (Paraná Basin) in Brazil. In: Johnston, P.A., Haggart, J.W. (Eds.), Bivalves: An Eon of Evolution. Paleobiological Studies Honoring Norman D. Newell. Calgary University Press, Canada, pp. 443–452.

Pacześna, J. 2001. An application of trace fossils in the facies analysis and high-resolution sequence stratigraphy: An example from the Cambrian of the Polish part of the East European Craton. Przegląd Geologiczny 49, 1137–1146.

Pearson, J.N., Mángano, M.G., Buatois, L.A., Casadío, S., Raising, M. 2012. Ichnology, sedimentology, and sequence stratigraphy of outer-estuarine and coastal-plain deposits: Implications for the distinction between allogenic and autogenic expressions of the *Glossifungites* Ichnofacies. Palaeogeography, Palaeoclimatology, Palaeoecology 333, 192–217.

Pemberton, S. G., Frey, R. W. 1985. The *Glossifungites* Ichnofacies: Modern examples from the Georgia coast, U.S.A. In: Curran, H. A. (Ed.), Biogenic Structures: Their Use in Interpreting Depositional Environments. Society of Economic Paleontologists and Mineralogists, Special Publications, 35, pp. 237–259.

Pemberton, S. G., MacEachern, J. A. 1995. The sequence stratigraphic significance of trace fossils: examples from the Cretaceous foreland basin of Alberta, Canada. In: Van Wagoner, J. C., Bertram, G. (Eds.), Sequence Stratigraphy of Foreland Basins

Deposits: Outcrops and Subsurface Examples from the Cretaceous of North America. American Association of Petroleum Geologists Memoirs, 64, pp. 429–475.

Pemberton, S. G., MacEachern, J. A., Saunders, T. 2004. Stratigraphic applications of substrate-specific ichnofacies: Delineating discontinuities in the rock record. In: MacIlory, D. (Ed.). The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis. Geological Society, Special Publications, 288, pp. 29–62.

Pemberton, S. G., Reinson, G. E., MacEachern, J. A. 1992b. Comparative ichnological analysis of late Albian estuarine valley-fill and shelf-shoreface deposits, Crystal Viking field, Alberta. In: Pemberton, S.G. (Ed.), Applications of Ichnology to Petroleum Exploration, a Core Workshop. Society of Economic Paleontologists and Mineralogists, Core Work-shop, 17, pp. 291–317.

Pemberton, S. G., Spila, M., Pulham, A. J., Saunders, T., MacEachern, J. A., Robbins, D., Sinclair, I. 2001. Ichnology and Sedimentology of Shallow and Marginal Marine Systems: Ben Nevis and Avalon Reservoirs, Jeanne D' Arc Basin. Geological Association of Canada, Short Course Notes, 15, St. John's NF, pp. 343.

Raychaudhuri, I., Brekke, H.G., Pemberton, S.G., MacEachern, J.A. 1992. Depositional facies and trace fossils of a low wave energy shoreface succession, Albian Viking Formation, Chigwell Field, Alberta, Canada. In: Pemberton, S. G. (Ed.), Applications of Ichnology to Petroleum Exploration, a Core Workshop. Society of Economic Paleontologists and Mineralogists, Core Workshop, 17, pp 319–337.

Reineck, H.E. 1963. Sedimentgefüge im Bereich der südliche Nordsee. Abh Senckenb Nat Gesell 505, 1–138.

Santos, R.V., Souza, P.A., Alvarenga, C.J.S., Dantas, E.L., Pimentel, M.M., Oliveira C.G., Araújo, L.M. 2006. Shrimp U–Pb Zircon dating and palinology of bentonitic layers from the Permian Irati Formation, Paraná Basin, Brazil. Gondwana Research 9, 456–463.

Savrda, C. E. 1991. Ichnology in sequence stratigraphic studies: An example from the lower Paleocene of Alabama. Palaios 6, 39–53.

Savrda, C. E., Browning, J. V., Krawinkle, H., Hesselbo, S.P. 2001a. Firmground ichnofabrics in deep-water sequence stratigraphy, Tertiary clinoform-toe deposits, New Jersey slope. Palaios 16, 294–305.

Savrda, C. E., Krawinkle, H., McCarthy, F. M. G., McHugh, C.M. G., Olson, H. C., Mountain, G. 2001b. Ichnofabrics of a Pleistocene slope succession, New Jersey margin: Rela-tions to climate and sea-level dynamics. Palaeogeography, Palaeoclimatology, Palaeoecology 171, 41–61.

Sedorko, D., Netto, R.G., Savrda, C.E. 2018. Ichnology applied to sequence stratigraphic analysis of Siluro-Devonian mud-dominated shelf deposits, Paraná Basin, Brazil. Journal of South American Earth Sciences, 83, 81–95.

Seilacher, A. 1964. Biogenic sedimentary structures. In: Imbrie, J., Newell, N. D. (Eds.), Approaches to Paleoecology. Wiley & Sons, New York, pp. 296–316.

Seilacher, A. 1967a. Bathymetry of trace fossils. Marine Geology 5, 413–428.

Seilacher, A. 1967b. Fossil behavior. Scientific American 217, 72–80.

Schneider, R.L., Mühlmann, H., Tommasi, E., Medeiros R.A., Daemon R.F., Nogueira A.A. 1974. Revisão estratigráfica da Bacia do Paraná. Congresso Brasileiro de

Geologia, XXVIII, 1974, Porto Alegre. Anais, Sociedade Brasileira de Geologia, 1, pp 41–66.

Schmidt-Neto, H. 2010. Diversidade e tafonomia dos fósseis de moluscos da Formação Rio Bonito, Permiano Inferior da Bacia do Paraná, Rio Grande do Sul: proposta de correlação com as camadas de Taió, Santa Catarina. São Leopoldo. (Undergraduate Monograph) Universidade do Vale do Rio dos Sinos, 35 pp.

Schmidt-Neto, H., Netto, R.G., Villegas-Martín, J. 2018. Bioerosion in shells from the early Permian Rio Bonito formation, Brazil: Taphonomic, paleobiological, and paleoecological implications. Palaeogeography, Palaeoclimatology, Palaeoecology 505, 256–264.

Schultz, S., Furlong, C. M., Zonneveld, A.P. 2016. The cooccurence of *Trypanites* and *Glossifungites* substrate-controlled trace-fossil assemblages in a Triassic mixed siliciclastic–carbonate depositional system: Baldonnel Formation, Williston Lake, B.C., Canada. Journal of Sedimentary Research 86, 879–893.

Smith, G.J., Jacobi, R.D. 1998. Fault-induced transgressive incised shoreface model for the Canadaway Group, catskill delta complex. Journal of Sedimentary Research 68, 668–683.

Souza, P.A. 2006. Late Carboniferous palynostratigraphy of the Itararé Subgroup, northeastern Paraná Basin, Brazil. Review of Palaeobotany and Palynology 138, 9–29.

Souza, P.A., Marques-Toigo, M. 2005. Progress on the palynostratigraphy of the Permian strata in Rio Grande do Sul State, Paraná Basin, Brazil. Anais da Academia Brasileira de Ciências 77, 353–365.

Tognoli, F.M.W. 2002. Análise estratigráfica e paleoicnológica do Grupo Guatá no leste paranaense. (Master Thesis) Universidade Estadual Paulista, 90 pp.

Tognoli, F.M.W. 2006. Estratigrafia das Seqüências Deposicionais do Grupo Guatá, Borda Leste da Bacia do Paraná. (PhD Thesis) Universidade Estadual Paulista, Rio Claro, 112 pp.

Tognoli, F.M.W., Assine, M.L., Netto, R.G. 2003. Paleodepositional interpretations based on the integration between ichnology and sedimentology, Ponta Formation, Eastern of the Paraná Basin. Abstract, 3rd Latinamerican Congress of Sedimentology, Brazil, pp. 181–182.

Uchman, A., Bubniak, I., Bubniak, A. 2000. The *Glossifungites* ichnofacies in the area of its nomenclatural archetype, Lviv, Ukraine. Ichnos 7, 183–193.

Villegas-Martín, J., Netto, R. G. 2018. Permian macroburrows as microhabitats for meiofauna organisms: an ancient behaviour common in extant organisms. Lethaia 52, 31–43.

Yang, B.C, Dalrymple, R.W., Gingras, M.K., Pemberton, S.G. 2009. Autogenic occurrence of *Glossifungites* Ichnofacies: Examples from wave-dominated, macrotidal flats, southwestern coast of Korea. Marine Geology 260, 1–5.

Zalan, P.V., Wolff S., Conceiçao, J.C. de J., Marques, A., Astolfia, M.A.M., Vieira, I.S., Appi, V.T., Zanotto, O.A. 1990. Bacia do Paraná. In: Raja Gabaglia, G.P., Milani, E.J. (Eds.), Origem e evolução de bacias sedimentares. Gavea, Rio de Janeiro, pp. 135-168.

10. Figures and table captions

Figure 1. Geographical map with the cores used in this study, Rio Grande do Sul State, south of Brazil.

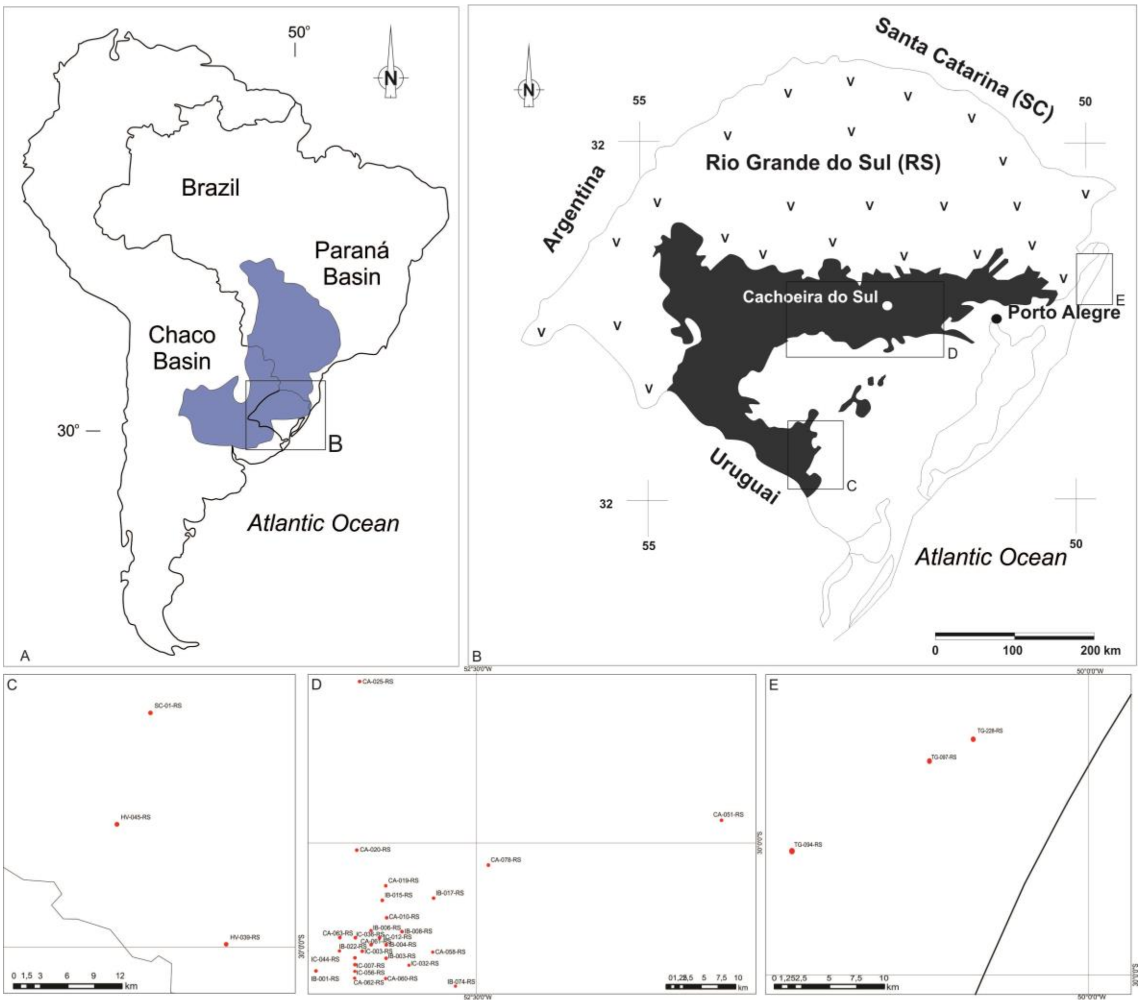
Figure 2. Examples of facies association attributed to the different depositional paleoenvironments identified in the Permian Rio Bonito-Palermo succession. A, Estuarine deposits. B, Lower shoreface deposits bioturbated with Cruziana Ichnofacies. C, Offshore transition deposits bioturbated. D, Offshore deposits with low bioturbation.

Figure 3. Summarized stratigraphic column with the location of the *Glossifungites* suites in the lower shoreface and estuarine deposits.

Figure 4. A-G, Cross section of the firmground substrates showing *Glossifungites* suites demarking autogenic surface, including *Thalassinoides* (Th), *Skolithos* (Sk), *Gyrolithes* (G), and *Diplocraterion* (D) in the estuarine deposits.

Figure 5. A-D, Cross section of the firmground substrates showing *Glossifungites* suites demarking allogenic surface, including *Thalassinoides* (Th), and *Diplocraterion* (D) in the Rio Bonito-Palermo succession. A, *Diplocraterion* and *Thalassinoides* associated to coplanar surface. *Thalassinoides* and *Diplocraterion* associated to coplanar surfaces.

Table 1. Sedimentary facies of the Early Permian deposits (Rio Bonito-Palermo interval) from the Parana Basin.



50°
N
Brazil
Paraná Basin
Chaco Basin
30°
B
Atlantic Ocean
A
Santa Catarina (SC)
N
55
32
50
Rio Grande do Sul (RS)
Argentina
Cachoeira do Sul
Porto Alegre
D
E
C
Uruguai
32
55
50
Atlantic Ocean
0
100
200 km
B
C
SC-01-RS
HV-045-RS
HV-039-RS
30°0'0"S
0 1,5 3 6 9 12
km
D
52°30'0"W
CA-025-RS
CA-051-RS
30°0'0"S
CA-020-RS
CA-078-RS
CA-019-RS
IB-015-RS
IB-017-RS
CA-010-RS
IB-006-RS
IB-008-RS
CA-063-RS
IC-036-RS
IC-012-RS
CA-061-RS
IB-004-RS
IB-022-RS
IC-003-RS
CA-058-RS
IB-003-RS
IC-044-RS
IC-032-RS
IC-007-RS
IC-056-RS
IB-001-RS
CA-060-RS
CA-062-RS
IB-074-RS
01,252,5 5 7,5 10
km
52°30'0"W
E
50°0'0"W
TG-228-RS
TG-097-RS
TG-094-RS
30°0'0"S
0 1,252,5 5 7,5 10
km
50°0'0"W

Fig. 1

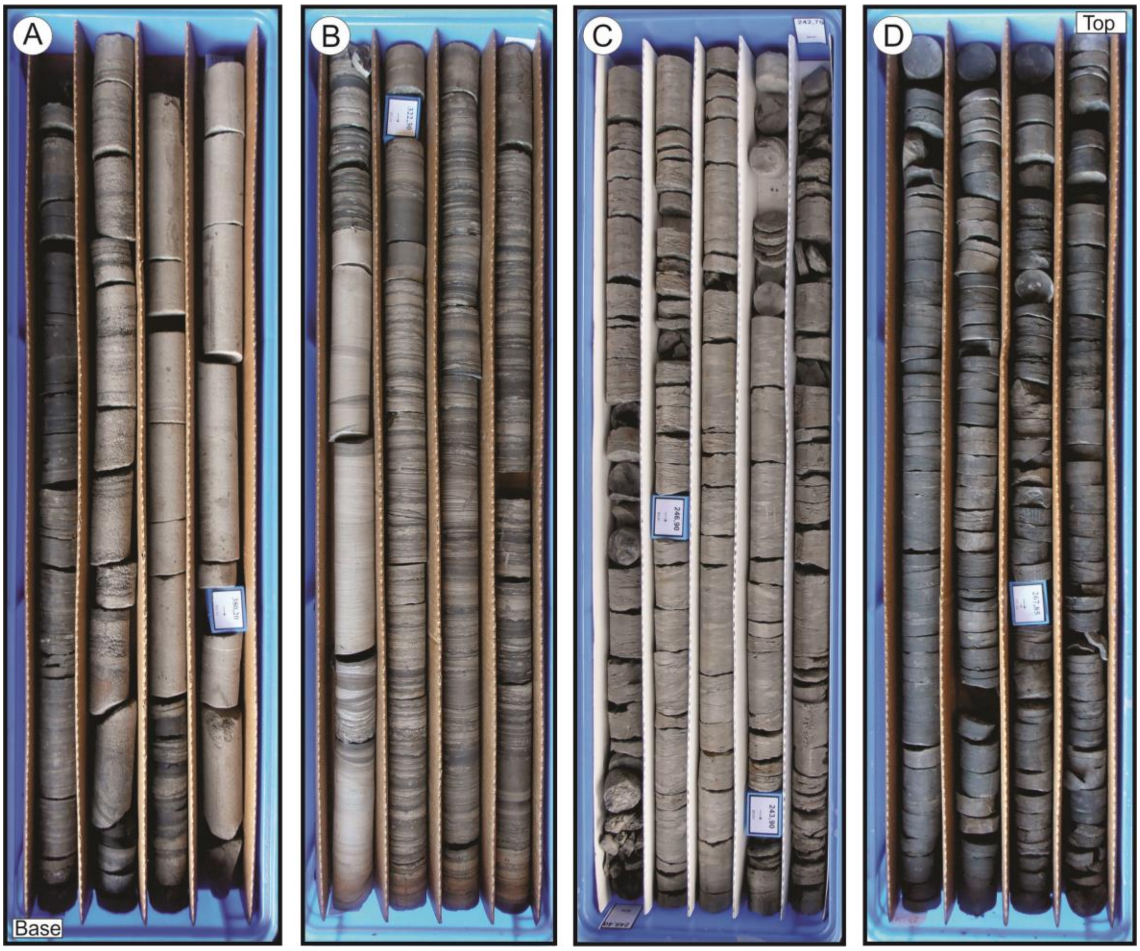


Fig. 2

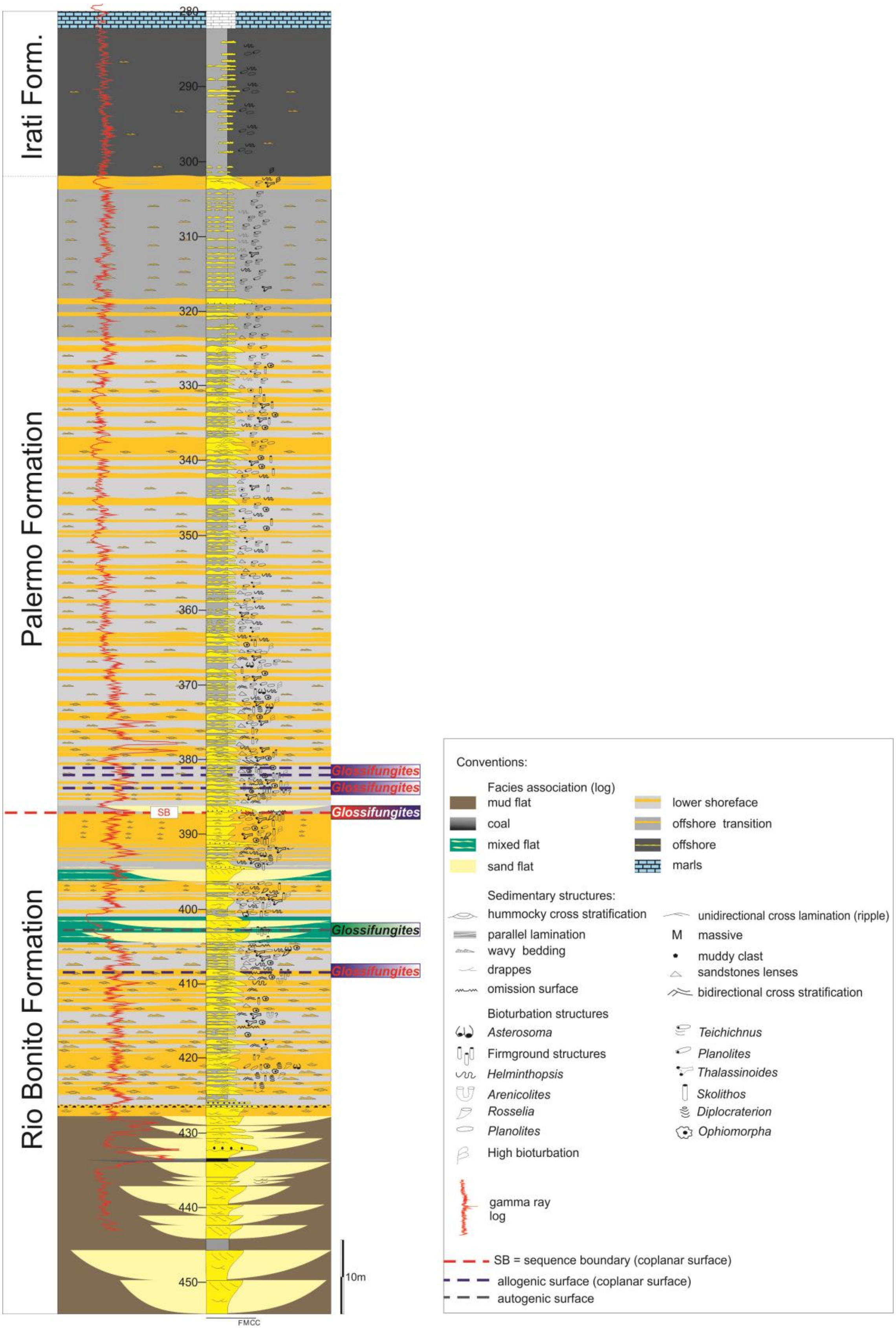

Irati Form.
Palermo Formation
Rio Bonito Formation
280
290
300
310
320
330
340
350
360
370
380
390
400
410
420
430
440
450
Glossifungites
Glossifungites
SB
Glossifungites
Glossifungites
Glossifungites
10m
FMCC
Conventions:
Facies association (log)
mud flat
coal
mixed flat
sand flat
lower shoreface
offshore transition
offshore
marls
Sedimentary structures:
hummocky cross stratification
parallel lamination
wavy bedding
drappes
omission surface
unidirectional cross lamination (ripple)
M massive
muddy clast
sandstones lenses
bidirectional cross stratification
Bioturbation structures
Asterosoma
Firmground structures
Helminthopsis
Arenicolites
Rosselia
Planolites
High bioturbation
Teichichnus
Planolites
Thalassinoides
Skolithos
Diplocraterion
Ophiomorpha
gamma ray log
SB = sequence boundary (coplanar surface)
allogenic surface (coplanar surface)
autogenic surface

Fig. 3

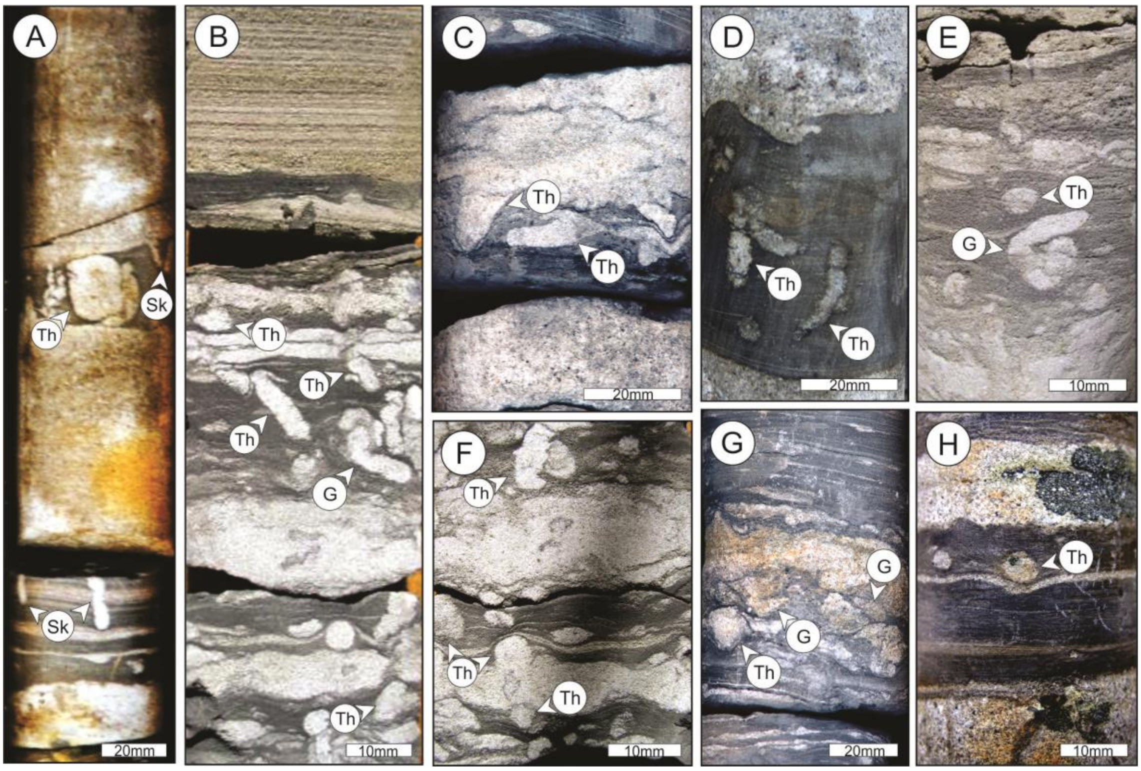

A
Th
Sk
Sk
20mm
B
Th
Th
Th
G
Th
10mm
C
Th
Th
20mm
D
Th
Th
20mm
E
Th
G
10mm
F
Th
Th
Th
10mm
G
G
G
Th
20mm
H
Th
10mm

Fig. 4

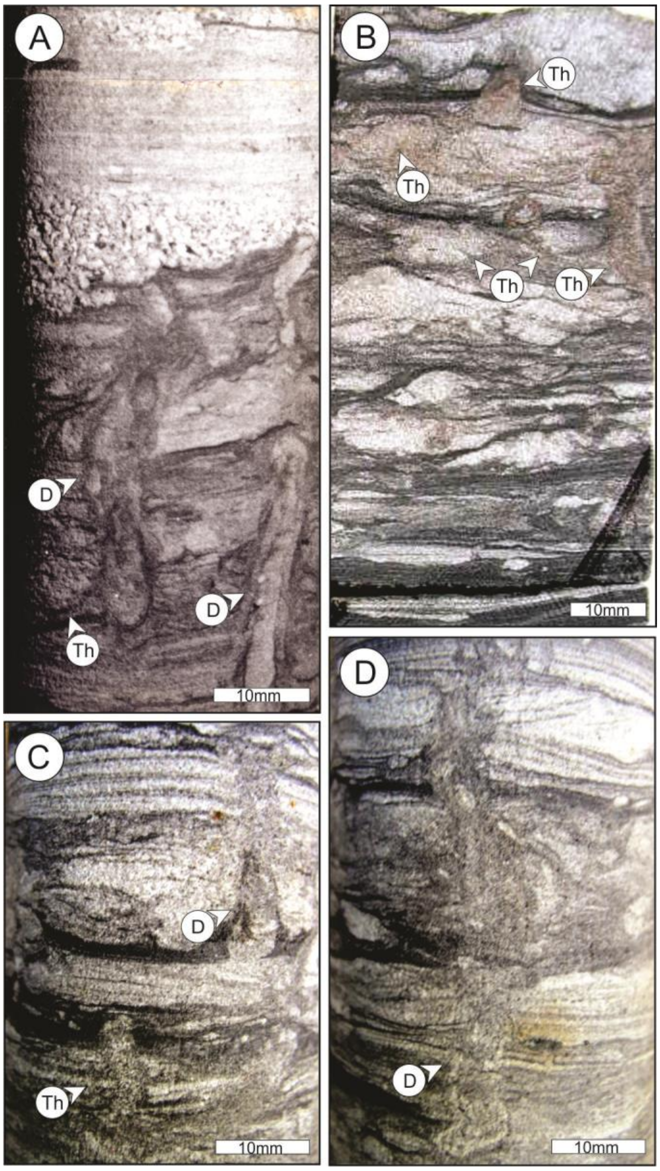


Fig. 5

Facies	Texture	Sedimentary structures	Fossil/trace fossil content (ichnofabrics)
Marl	Carbonate claystone	Massive	Absent
Carbonaceous shales	Carbonaceous shales. Thin lenticular fine-grained sandstones and pyrite nodules, and syneresis cracks occur locally.	Massive	Phytodebris *Thalassinoides*
Coal	Coal	Massive	Absent
Massive mudstone	Muddy deposits formed by mixed clay and silt particles.	Massive	*Thalassinoides*, *Gyrolithes*, *Skolithos*
Laminated siltstone	Siltstone with local occurrences of thin very fine-grained sandstone lenses.	Parallel lamination	Incipient bioturbation; local occurrence of *Planolites*
Heterolithic deposits	Hetherolitic deposits composed of intercalation of organic-rich siltstone, claystone, and very fine- to fine-grained sandstone.	Sandstone beds form wavy and lenticular bedding with symmetric and asymmetric tops; massive mudstones	*Arenicolites, Asterosoma*, *Chondrites, Cylindrichnus*, *Diplocraterion, Gordia*, *Helmintopsis, Planolites*, *Palaeophycus*, *Rhizocorallium*, *Rosselia*, *Skolithos*, *Teichichnus*, *Thalassinoides*, undetermined bioturbation
Very fine-grained sandstone	Very fine-grained sandstone with abundant quartz.	Very low-angle cross-stratification, parallel lamination	Absent
Very fine-grained sandstone with drapes	Very fine-grained sandstone. Drapes of carbonaceous siltstone and carbonate cement occur locally.	Predominantly massive; Low-angle cross-stratification occur locally	*Chondrites*, *Helmintopsis*, *Palaeophycus*, *Planolites*, small unidentified horizontal traces; rhizobioturbation
Fine-grained sandstone	Fine-grained quartz sandstone. Flaser structure, intraclasts of carbonaceous shales, and carbonate cement occur locally.	Low-angle cross-stratification, climbing ripple lamination, parallel lamination, combined-flow ripples; massive when carbonate cement is present	*Chondrites*, *Lokeia*, *Macaronichnus*, *Rosselia*-like burrows, *Skolithos*, rhizobioturbation
Fine-grained sandstone with HCS	Very fine- to fine-grained sandstone.	Hummocky cross-stratification	*Diplocraterion*, *Helminthopsis*, *Ophiomorpha*, *Skolithos*, *Thalassinoides*, *Rosselia*
Medium- to fine-grained sandstone	Fine- to medium-grained sandstone forming fining-upward cycles. Drapes of carbonaceous shales, granule and pebble-sized	Low-angle cross-stratification	Rhizobioturbation

	intraclasts, and pyrite nodules also occur. Erosive base.		
Coarse- to fine-grained sandstone with drapes	Coarse- to fine-grained sandstone forming fining upward cycles. Drapes and intraclasts of carbonaceous shales occur locally. Extraformacional granules occur in the coarse-grained sandstone.	Intercalations of low- and high-angle cross-stratification. Double mud drapes.	*Diplocraterion*, *Lockeia*, *Macaronichnus*, *Planolites*, *Skolithos*, *Thalassinoides*, rhizobioturbation
Arkose sandstone	Coarse to medium-grained arkose sandstone. Mud drapes and pyrite nodules occur locally. Fluidized structures and load casts are frequent. Scarce drapes and laminae of coal.	High-angle trough cross-stratification	Local occurrences of *Ophiomorpha*
Coarse-grained sandstone	Coarse-grained sandstone, poor selected. Quartz, pyritized and oxidized. Intercalated with carbonaceous shale. Carbonaceous shale intraclasts.	Low-angle trough cross-stratification. Double mud drapes occur locally.	Absent in the sandstone; small unidentified horizontal traces in the carbonaceous shale
Ortoconglomerate	Ortoconglomerate composed of intraformational and extraformational clasts of pebble-sized granite, quartz, feldspar, and siltstone. Coarse- to medium-grained sandy matrix. Some clasts are angular. Locally carbonatic cement.	Chaotic	Absent
Diamictite	Diamictite with quartz, feldspar, and granite pebbles and granules. Matrix composed of sandstone and mudstone. Drapes of coal occur locally.	Massive	Absent

Highlights

Subaerial exposure marked by the Glossifungites Ichnofacies in estuarine deposits

Coplanar surfaces marked by the Glossifungites Ichnofacies in lower shoreface deposits

Morphological differences among the Glossifungites assemblages colonizing autogenic and allogenic stratigraphic surfaces

Capitulo 3. Evaluating the resolution of the ichnological record to determine the coastline dynamic: a case study in transgressive post-glacial deposits

Evaluating the resolution of the ichnological record to determine the coastline dynamic: a case study in transgressive post-glacial deposits

Jorge Villegas-Martín, Renata Guimarães Netto, Henrique Parisi Kern , Daniel Sedorko,
Joice Cagliari, Ernesto Luis Correa Lavina
Graduate Program in Geology, UNISINOS University, Av. Unisinos, 950, 93022-000 Sao Leopoldo, RS, Brazil.

Abstract

A few studies used ichnofabrics as a relative proxy for determining shoreline variation and coastal dynamics. In addition, most of these few studies demonstrated the efficiency of the ichnologic analysis for determining relative sea-level variations in 4th or 5th order cycles. However, the accuracy of trace fossils for determining shoreline variation and the coastal dynamics in cycles of higher orders is still poorly tested. In this work is analyzed and discussed the ichnology of the Early Permian deposits (Rio Bonito, Palermo and Irati formations) of the Paraná Basin to discuss the reliability of the ichnological record for determining the coastal dynamic variations in 2nd and 3rd order cycles and to trace bathymetric curves that reflect regional eustatic cycles and coastal dynamics. The ichnological and sedimentological data correspond to different cores located in the SSE border of the Paraná Basin. The vertical distribution of the trace suites and facies association vary from impoverishes Cruziana (estuarine) –Skolithos– archetypical Cruziana (lower shoreface) – distal Cruziana (offshore transition-offshore) ichnofacies from base to top suggest a transgressive tendency well marked during the

Early Permian in the Paraná. In the 3rd order cycle this transgressive event is disrupted by a forced regression–transgressive event (SB, coplanar surface) marked by a Glossifungites suite at the base of the Palermo Formation. The bathymetric curve traced for the Asselian-Artinskian interval studied has no correspondence with the global sea-level curve and illustrate local processes associated to a particular subsidence and basin restriction during the deposition of the Godwana I Supersequence in the early Permian.

Keywords: Ichnological record, coastline relative dynamic, Paraná Basin, early Permian, Brazil

1. Introduction

Sedimentary sequences record the fluctuations of sea level dynamics, sedimentation, and other related environmental parameters (Brett, 1998). The ichnological data contribute significantly to refine paleoecological and paleoenvironmental interpretations in these sequences, serving as indirect signatures of relative sea-level variations (Sarvda, 1991, 1995; Brett, 1998). Trace fossil assemblages provide evidence of the relative paleobathymetry, salinity, substrate consistency, sedimentation rate, and bottom-water oxygenation, which vary according to the coastal dynamics in shallow marine environments (e.g., Rhoads et al., 1972; Fürsich,1978; Brett, 1998, Buatois et al., 1992; Savrda, 1991; Sarvda and King, 1993; Savrda, 1993; Netto and Rossetti, 2003; Buatois et al., 2007; Villegas-Martin et al., 2014; Sedorko et al., 2017).

Despite ichnology has been used in many studies to infer sedimentary processes and key stratigraphic surfaces (e.g., Buatois et al., 2007; Gandini et al., 2010; Sedorko et al., 2018), only a few have used ichnofabrics as a relative proxy for determining shoreline variation and coastal dynamics. Most of these few studies demonstrated the utility of the ichnologic analysis for determining relative sea-level variations in 4th or 5th order cycles (e.g., Savrda, 1991; Fielding et al., 2006; Rodríguez-Tovar et al., 2010; Paranjape et al., 2014). However, the accuracy of trace fossils for determining shoreline variation and the coastal dynamics in cycles of higher orders is still poorly tested.

The Permian deposits of the Paraná Basin were interpreted as a 2nd order transgressive-regressive cycle (Milani et al., 2007), in which the transgressive cycle is represented by the Early Permian Rio Bonito, Palermo, and Irati formations, and the Late Permian Serra Alta, Teresina, and Rio do Rasto formations characterize the regressive cycle. The Rio Bonito and Palermo formations are well-known for possessing a continue, extensive, and rich ichnological record (Netto, 1994, 1995, 1997; 1998; Buatois et al., 2001a,b; Netto et al., 2007; Buatois et al., 2007; Gandini et al., 2010). Some of these studies were successful in recognizing 3rd order regressive-transgressive cycle using trace fossils. However, these analyses were mostly restricted to the transition between the wave-dominated estuarine deposits that characterize the top of the Rio Bonito Formation and the shallow marine deposits preserved at the lower half of the Palermo Formation. The ichnology of the basal and middle deposits of the Rio Bonito Formation have been poorly explored for stratigraphic purposes (e.g., Buatois et al., 2001a,b, 2007; Gandini et al., 2010) and the ichnofabrics present in both the upper portion of the Palermo Formation and the Irati Formation have been never considered in this analysis. In this contribution, we analyze the ichnology of the Early Permian deposits of the Paraná Basin with two main purposes: to discuss the reliability of the ichnological record as a relative proxy to determining coastal dynamics in 2nd and 3rd order cycles and to trace curves that reflect regional eustatic cycles and coastal dynamics.

2. Geological context

The trace fossils studied herein occur in deposits of the Rio Bonito, Palermo and Irati formations that represent the Early Permian succession of the Paraná Basin (state Rio Grande do Sul), southern Brazil (e.g., Habekost, 1978, 1983; Lavina et al., 1985; Lavina and Lopes, 1986; Lopes, 1990; Santos et al., 2006) (Fig. 1).

The Paraná Basin is a Gondwanan intracratonic basin that covers a territory of approximately 1.5×10^6 km^2 in the southeast of South America and is mostly preserved in the central-southern Brazil (Zálan et al., 1990; Milani et al., 2007). The basin infill reaches a maximum thickness of ~8000 m in its depocenter (Zalan et al., 1990) and consists mainly of Late Ordovician to Late Cretaceous sedimentary deposits with minor participation of volcanic rocks (Milani et al., 2007). The tectonic and depositional evolution of the Paraná Basin originated uplift and subsidence cycles that coincided with the major orogenic phases in the history of southwestern Gondwana, originating regional unconformities that allowed delimitat six supersequences (Milani et al., 2007). The sedimentary succession of the Rio Bonito, Palermo, and Irati formations is included in the basal part of the Gondwana I Supersequence and represents the transgressive basal Permian deposits (Milani et al., 2007). These deposits are part of a 2nd order transgressive-regressive cycle and represent the transgressive trend that characterizes the post-glacial deposition that demarks the demise of the Gondwana glaciation in southwestern Gondwana (e.g., Eyles et al., 1993; Milani et al., 2007; Bocardi et al., 2009; Limarino et al., 2013; Montañez and Poulsen, 2013; Cagliari et al., 2016, Griffin et al., 2017; Isbell et al., 2018).

The Rio Bonito Formation consists principally of conglomerate, very fine- to very coarse-grained sandstone, fine-grained heterolithic deposits, mudstone, and coal seams. In its type area, the unit has been divided, from base to top, into the Triunfo, Paraguaçu, and Siderópolis Members (e.g., Schneider et al., 1974; Lavina et al., 1985; Lavina and Lopes, 1986; Buatois et al., 2001a, 2007; Tognoli, 2002; Gandini et al., 2010; Holz et al., 2010). U-Pb radiometric analyses made by Cagliari et al. (2014, 2016) and zircon provenance analysis by Griffins et al. (2017) indicate an Asselian–Sakmarian ages for its deposits. The fauna fossil of the Rio Bonito Formation is composed mainly of bivalves, inarticulated brachiopods, asteroid and ophiuroid echinoderms, gastropods, and plant fragments (e.g., Dolianiti, 1945; Martins and Sena Sobrinho, 1950, 1952; Schmidt-Neto et al., 2018a,b). The basal deposits of the Rio Bonito Formation had been assumed as accumulated in fluvial-deltaic settings (e.g., Lavina et al., 1985; Lavina and Lopes, 1986; Holz et al., 2010), and the median and upper portions were interpreted as tide- and wave-dominated shallow marine and estuarine deposits (e.g., Netto, 1994, 1998; Buatois et al., 2001a,b; Tognoli, 2002, 2006; Lopes et al., 2003a,b).

The Palermo Formation consists principally of very fine- to fine-grained sandstone and mudstone deposited during the Artinskian, based on palynological content and paleoflora associations (e.g., Daemon and Quadros, 1970; Souza and Marques-Toigo, 2005; Iannuzzi and Souza, 2005; Souza, 2006). The fossils fauna of the Palermo Formation is composed principally of wood (*Dadoxylon* sp.), amphibian teeth (*Loxomma* sp.), and bivalves (Schneider et al., 1974). The Palermo Formation records deposition in open marine environments, ranging from lower shoreface to offshore (e.g., Netto, 1994; Buatois et al., 2007; Holz et al., 2010).

Trace fossils of mesohaline and fully marine invertebrate organisms are common in the Rio Bonito (median and upper portions) and Palermo formations (Netto 1994, 1995, 1998; Buatois et al., 2001a,b; 2007; Gandini et al., 2010; Villegas-Martín and Netto, 2018). In addition, bioerosion structures occur in bivalve shells from shell beds preserved in the median portion of the Rio Bonito Formation (Schmidt-Neto et al., 2018a). The boundary between the Rio Bonito and Palermo formations marks the establishment of shelf deposits over coal-rich coastal deposits (e.g., Netto, 1994; Buatois et al., 2007; Holz et al., 2010).

The Irati Formation consists mainly of shales, bituminous shales, sandstones, marls, and carbonates. In its type area, this unit has been divided, from base to top, into the Taquaral (inferior) and Assistência members (Milani et al., 1994, 2007). These deposits were dated from Late Artiskian, based on U-Pb radiometric (Santos et al., 2006). The fauna of the Irati Formation is composed principally of invertebrates such as insects (Mecoptera, Neuroptera e Homoptera), crustaceans, and microfossils (foraminifers and palynomorphs) (Daemon and Quadros, 1970; Röster et al., 1981; Pinto and Ornellas, 1981). Among the vertebrates, these deposits are worldwide known by the richness in Mesosauridae reptiles (*Mesosaurus*, *Stereosternum,* and *Brazilosaurus*) (Oelofsen and Araújo, 1987; Lavina, 1991; Soares, 2003). Swimming trace fossils attributed to mesosaurids have also been recorded by Sedor and Silva (2004) and Silva et al. (2009). Paleoenviromental reconstructions based on facies association and fossil content considered deposition in transitional marine settings (Taquaral Member) and in marine settings (Assistência Member) (Lavina et al., 1985;

Aboarrage and Lopes, 1986; Lavina and Lopes, 1986; Albuquerque, 1990; Lopes, 1990; Santos et al., 1990).

3. Materials and methods

The sedimentological and ichnological data of the studied interval came from subsurface deposits expressed in cores TG-94-RS, TG-97-RS, TG-228-RS, HV-39-RS, HN-45-RS, HV-54-RS, SC-01-RS, CA-25, CA-51-RS, CA-61-RS, and CA-74-RS drilled by the Brazilian Geological Survey (CPRM) and housed in Caçapava do Sul (Rio Grande do Sul State, Brazil). The sedimentological and ichnological data from cores TG-97-RS, TG-228-RS, HV-39-RS, HN-45-RS, and CA-74-RS were used herein as originally described by Netto (1994). Supplementary ichnological and sedimentological data were obtained on cores CA-74-RS, CA-25-RS, CA-51-RS, and CA-61-RS as described and analyzed originally by Netto (1994), and cores IB-01-RS, IB-03-RS, IB-04-RS, IB-06-RS, IB-08-RS, IB-15-RS, IB-17-RS, IB-22-RS, IB-74-RS, IC-20-RS, IC-32-RS, IC-36-RS, IC-56-RS, CA-10-RS, CA-19-RS, CA-20-RS, CA-58-RS, CA-60- RS, CA-62-RS, CA-63-RS, CA-78-RS, IC-03-RS, IC-07-RS, IC-12-RS, and IC-44-RS originally studied by Buatois et al. (2001, 2007) and Gandini et al. (2010).

Trace fossil are preserved mostly as ichnofabrics, which were described through direct observations in the different cores. Trace fossil description was based on the main general ichnotaxobases (*sensu* Bromley, 1990) applicable to ichnofabrics: burrow infill, burrow limit, branching pattern, and presence/absence of spreiten. The criteria for ichnofacies analysis followed the principles stated by Seilacher (1967). In addition, detailed information such as cross-cutting relationships, burrow trajectory, and external surface features were also considered. The bioturbation was quantified using the scale (bioturbation scale, BS) proposed by Reineck (1963), ranging from 0 (without bioturbation) to 6 (sediment totally homogenized) and taking in account an average diameter of 4 cm for the cores.

The facies description followed the general description made by Netto (1994) for the Rio Bonito-Palermo sedimentary succession. For stratigraphic purposes, the base of Palermo and Irati formations was delimited by the establishment of massive storm deposits represented by very fine- to fine-grained sandstone with hummocky cross stratification interbedded with moderate to high bioturbated heterolithic deposits, following the criteria used by Lavina et al. (1985), Netto (1994), and Buatois et al. (2007).

The shoreline variation and bathymetry in the studied section was determined by the vertical variation in the ichnological signatures (considering ichnodiversity, degree of bioturbation, and composition of the trace fossil suites), paying special attention to the significant vertical shifts in the trace fossil assemblages (ichnofacies) and lithofacies, and the evidence of key stratigraphic surfaces.

4. Trace fossils, lithofacies, and facies association

The distribution of the sedimentary facies throughout the sedimentary succession (Rio Bonito-Irati interval) allowed recognized three main facies association: estuarine, shoreface, and offshore. These main facies associations were also recognized in the studied interval in previous studies (e.g., Netto, 1994; Buatois et al., 2007; Gandini et al., 2010; Holz et al., 2010), and show local variations, according to the studied area in the SSE border of the Paraná Basin.

The bioturbation scale (BS) vary throughout the studied succession from low (BS 1-2), locally moderate to high (BS 3-5), in the Rio Bonito Formation, to moderate to high (BS 4-5), locally high (BS 6) in the Palermo Formation, dropping to non-bioturbated to locally low in the Irati Formation. The ichnodiversity is low, locally moderate in the Rio Bonito Formation, high to locally moderate in the Palermo Formation, and moderate to monotypic in the Irati Formation (Fig. 2, 4, legend Fig.3).

4.1. Estuarine facies association

The estuarine deposits are preserved at the base of the sedimentary succession and is better represented by the deposits of the Rio Bonito Formation. These deposits include conglomerate, amalgamated and stratified sandstones with drape and flaser bedding, intercalated with heterolithic deposits, marls and mudstones including coals (Table 1). Two types of estuary have been recognized in the Rio Bonito Formation: a tide-dominated estuary that characterizes the basal Rio Bonito deposits, and a wave-dominated estuary that characterizes the middle and upper portions of the Rio Bonito Formation in the study area (e.g., Buatois et al., 2001a,b, 2007; Gandini et al., 2010; Netto et al., 2012).

4.1.1. Tide-dominated estuary

The tide-dominated estuary facies association is composed of fluvio-estuarine and intertidal deposits that correspond to conglomerate (Or and D lithofacies), stratified sandstone (As, Cgs, Csd, Fs, and Ms lithofacies), and fine-grained deposits (C, Cs, He,Ls, Mm lithofacies) (Table 1). The conglomerates are observed exclusively at the very base of the sedimentary succession in the northeast section (Fig. 2) and compose fining-upward cycles together with lithofacies As (Fig. 4). A thick pack of muddy deposits from Ls and Mm lithofacies overlies these fining-upward cycles. Bioturbation is absent in the coarser-grained deposits and is represented exclusively by rhizobioturbation in the muddy beds, which are rich in phytodebris (Fig. 2, 3). These deposits characterize the inner estuary fluvio-estuarine settings (e.g., Netto, 1994; Buatois et al., 2007).

The Csd lithofacies is dominant in the lower and middle portion of the Rio Bonito succession in the southwest section, and represents sand flat channels and bars (e.g., Allen, 1982; Buatois et al., 2007). The absence of wave-generated structures indicates prevalence of tidal processes in these sand flats. The trough cross-bedded sandstone resulted from unidirectional tractive flows and show thicker and thinner bundles ascribed to spring- and neap-tidal cycles locally (e.g., Houbolt, 1968, Boersma and Terwindt, 1981). The sandstones with bidirectional trough cross bedding indicate tidal reworking. The accumulation of abundant muddy debris forming drape and flaser bedding would be associated with slack-water conditions (McCave, 1972, Allen, 1982).

Non-bioturbated deposits of the He lithofacies with a high content of phytodebris occur intercalated with deposits of the Ls and Mm lithofacies in the northeast section (Fig. 2). In the southwest section, however, the deposits of the He lithofacies occur intercalated with the lithofacies Csd and locally with lithofacies Cgs (Fig. 4, 5). The He lithofacies in the tidal-dominated estuarine system deposits consists of millimetre- to decimetre-scale beds composed of very fine-grained sandstone with current ripples and mud drapes alternated with centimetre- to decimetre-scale beds of laminated siltstone and/or claystone. Bioturbation occurs in lithofacies He in the southwest section and is represented by the low diverse *Palaeophycus-Planolites-Helminthopsis* ichnofabric (Table 2) (Fig. 4-5). The burrows generally show small diameter (≤ 5 mm) and the intensity of bioturbation is moderate (BS 3-4). These characteristics and the trace fossil content indicate colonization of softgrounds possibly stressed by salinity fluctuations (e.g., Buatois et al., 2005). Thus, *Palaeophycus-Planolites-Helminthopsis* ichnofabric characterizes a brackish-water trace fossil suite (BW suite; Table 2) and is an expression of the impoverished Cruziana Ichnofacies in the tide-dominated estuarine settings.

Mm, C, and Cs lithofacies (Table 1) occur locally interbedded with or capping the Csd lithofacies, representing lateral deposits of mud flats accumulated in muddy-mixed intertidal (mudstones and heterolithic strata) and supratidal (coal seams) settings (e.g., Reineck, 1980).

4.1.2. Wave-dominated estuary

The wave-dominated estuary facies association is composed of intertidal, beach, and storm-influenced deposits that correspond to medium- to fine-grained cross-stratified sandstone (As, Cgs, Csd, Fs, and Sw lithofacies), fine-grained parallel-laminated sandstone (Vfs lithofacies) and fine-grained deposits (C, Cs, He, Ls, M, and Mm lithofacies) (Table 1, Fig. 5). Storm-influenced deposits, represented by amalgamated beds of lithofacies Sw_1, mark the transgressive surface that flood the tide-dominated estuarine system in the studied succession. These deposits are better represented in the northeast section (Fig. 2) and show an erosive base. Marine mollusk-dominated shell beds are common in Sw1 lithofacies (Schmidt-Neto et al., 2018 a, b) and are better preserved in the central-western portion of the Rio Grande do Sul State.

Bioturbation is represented by the crowded *Rosselia* ichnofabric (BS 4-5), which are dominated by funnel-shaped *Rosselia* with average diameter ≥ 2 cm (Table 2). Deposits of the Sw_2 and He lithofacies occur in close association with the lithofacies Sw_1 and represent, respectively, sand bars formed by wave and currents in outer estuary settings during fair-weather conditions and a laterally disposed bay or lagoon. In the He lithofacies the bioturbation is represented by crowded *Palaeophycus* ichnofabric (CPI)(Villegas-Martín and Netto, 2018), which are dominated by *P. tubularis* subcylindrical to horizontally flattened in cross-section with range from 3.0 to 7.6 mm (Villegas-Martín and Netto, 2018).

Wave-dominated sandstone (Fs lithofacies) occurs locally and characterizes the subtidal deposits in the estuarine mouth. Tidal bars and channels are also preserved in the outer estuarine zone and are represented by the deposits of the As, Csd, Cgs, and Ms lithofacies (Table 1). These deposits include very fine- and fine-grained sandstone with abundant quartz and bidirectional trough cross-stratification (Csd lithofacies) produced by tractive, unidirectional flow giving rise to 3D dune (e.g., Harms et al., 1982; Walker and Plint, 1992; and Clifton, 2006). Low-angle cross-stratification is the main sedimentary structure in the sandstones in Cgs and Ms lithofacies. Lithofacies Vsf represents beach deposits and, like Ms lithofacies, is observed exclusively in the southwest section (Fig. 4).

Bioturbation is absent in Cgs, Fs, and Vsf deposits, and is represented exclusively by rhizobioturbation (BS 2) in Ms and Fs lithofacies. A monotypic *Ophiomorpha* ichnofabric with low bioturbation degree (BS 2) occurs locally in lithofacies As. The *Macaronichnus* ichnofabric (BS 4), with local occurrence of *Diplocraterion, Lockeia*, *Planolites*, *Skolithos, Thalassinoides* characterizes the bioturbation in lithofacies Csd. Rhizobioturbation occurs locally, in palimpsest preservation over the previous bioturbation. The monotypic *Palaeophycus* ichnofabric occurs in the Sw_2 lithofacies with low bioturbation scale (BS 2) while the *Thalassinoides-Teichichnus* ichnofabric (BS 2-3) occurs in the heterolithic deposits (Table 2; Fig. 5, 6).

The set of ichnofabrics registered in the outer estuary settings points to a polyhaline trace fossil suite (PH suite; Table 2). They are characterized by the low ichnodiversity and the low amount of bioturbation, which might reflect stressing conditions caused by the prevalence of high energy and potentially high frequency sedimentary processes. Thus, the PH trace fossil suite is an impoverished expression of the mixed Skolithos-Cruziana Ichnofacies (e.g., Pemberton et al., 2001; Buatois et al., 2005) in the studied deposits.

The supratidal-intertidal deposits preserved in the inner portion of the estuary are mostly represented by the fine-grained deposits, which include carbonaceous shales, coal beds, and massive mudstones containing abundant plant fragments (Cs, C, Mm lithofacies), heterolithic beds (He), and marls (M) (Table 1; Fig. 5).

Lithofacies He show a similar composition observed in the tide-dominated estuary system, except for the presence of wavy bedding and the poorness in phytodebris (Fig. 2). Bioturbation in these settings is represented by the *Palaeophycus-Planolites-Helminthopsis* ichnofabric of BW suite (Table 2), suggesting deposition in estuarine bay.

Lithofacies C, Cs, Ls, M, and Mm compose the mud flats. Thick coal beds occur in this portion of the Rio Bonito sedimentary succession. Together with the carbonaceous shale, they comprise the richest record of the Glossopteris Flora in the southern portion of the Paraná Basin (e.g., Aboarrage and Lopes, 1986; Iannuzzi and Souza, 2005). Fining-upward cycles composed of carbonaceous shales (Cs) containing lenses of very fine-grained sandstone and syneresis cracks on the base and massive mudstones (Mm) on the top occur locally. Marls deposits occur locally capping massive mudstones or interbedded with Sw_1 deposits (Fig. 2, 4), suggesting quiescence periods in shallow lagoons.

Except for the Mm lithofacies, bioturbation is absent in the mud flat deposits. In Mm deposits, it is characterized by the *Thalassinoides-Gyrolithes* ichnofabric (BS 2-3) and represents colonization of firmgrounds and stiffgrounds formed in muddy intertidal and supratidal settings. This assemblage had been previously reported in the estuarine facies of the Rio Bonito sedimentary succession (e.g., Buatois et al., 2007; Netto et al., 2007, 2012b; Gandini et al., 2010). The Mm deposits bearing the *Thalassinoides-Gyrolithes* ichnofabric intercalate with thin (≤ 10 cm) sandstone beds of Csd and Ms lithofacies, sometimes suggesting a cyclic repetition. According to Villegas-Martín et al. (submitted), these cyclic occurrences characterize autogenic stratigraphic surfaces controlled by variations in the coastal dynamics in these estuarine settings. The *Thalassinoides-Gyrolithes* ichnofabric represents colonization of firm, denuded substrate, characterizing a substrate-controlled Glossinfungites suite (G suite; Table 2). In this sense, the G suite is the expression of the Glossifungites Ichnofacies in the studied succession.

4.2. Shoreface facies association

The shoreface facies association is composed of fair-weather wave- and storm wave-generated sandy deposits and fair-weather heterolitic deposits of the lithofacies

Hcs, He, and Sw1 (Table 1; Fig. 5) and characterize the lower portion of the Palermo Formation in the study area (Fig. 2,3). The hummocky and swaley cross-stratified sandstones of the Hcs and Sw_1 lithofacies represent storm deposits (e.g., Walker, 1979; Walker and Plint, 1992; Clifton, 2006) and usually conform amalgamated beds. Fair-weather deposits are expressed by the Sw_2 lithofacies, deposited above the everyday wave base (e.g., Raaf et al., 1977; Clifton, 2006), and He lithofacies, and occur in close association with the storm deposits (Fig. 2, 3). Bioturbation is sparse in the cross-stratified sandstones and is more frequent in non-amalgamated beds. It is characterized by the *Thalassinoides-Skolithos* ichnofabric (BS 2-3, eventually 4), with local occurrences of *Diplocraterion*, *Ophiomorpha*, and *Palaeophycus* (Fig. 6; Table 1). The dominance of vertical burrows and the amount of bioturbation suggest colonization of softgrounds in high-energy shallow marine settings and characterizes a high-energy stenohaline suite (HS suite; Table 2) (e.g., Ekdale et al., 1984; Bromley, 1996; Pemberton et al., 2001; Buatois and Mángano, 2011). The HS suite is an expression of the Skolithos Ichnofacies in the studied succession.

The heterolithic deposits from the shoreface facies association are composed of intercalations of massive mudstone, parallel-laminated siltstone, and fine- to very fine-grained sandstone forming thin lenticular and wavy bedding with undulate tops (symmetric and asymmetric) and low-angle cross-stratification. Bioturbation is abundant and is characterized by the *Thalassinoides-Asterososma* ichnofabric (BS 4-5). Although *Thalassinoides* and *Asterosoma* (Fig. 6) are the most frequently observed burrows, this composite ichnofabric is highly diverse and also contains *Arenicolites, Bergaueria, Chondrites, Cylindrichnus, Diplocraterion, Gordia, Helminthopsis,Ophiomorpha, Palaeophycus, Phycosiphon, Planolites, Rhizocorallium,* *Rosselia*, *Skolithos,* and *Teichichnus* (Fig. 6, Table 2). The high ichnodiversity, the abundance of burrows produced in softgrounds by stenohaline organisms, and the diversity of trophic habits represented in the trace fossil assemblage suggest colonization of stable substrates during fair-weather conditions. This stability is reinforced by the presence of dwelling burrows, fecal trails, spreiten formed by filtering activity or by burrow enlargement due animal growing, and galleries of chemosymbiont organisms, which suggest the prevalence of optimum or quasi-optimum conditions in the benthos. Thus, the *Thalassinoides-Asterososma* ichnofabric characterizes a moderate- to low-energy stenohaline suite (MLS suite; Table 2) and is an expression of the archetypal Cruziana Ichnofacies in the studied succession (e.g., Netto, 1994, 2000; Pemberton et al., 2001; Buatois et al., 2005, 2007).

In some intervals of the Palermo Formation succession, the He lithofacies also contains large vertical burrows, like *Diplocraterion*, and deep galleries like *Thalassinoides*. The amount of bioturbation is low to moderate (BS 2-4) and the burrows are characterized by the presence of irregular borders and passive infill by medium- to coarse-grained quartz sandstone that overlie abruptly the heterolithic deposits, forming erosive surfaces. This trace fossil assemblage represents the Glossifungites suite (Table 2) and occur in palimpsest preservation over the MLS suite (Fig. 7). They indicate forced-regression and transgressive events in the studied succession (e.g., Gingras et al., 2000; Pemberton et al., 2001; Carmona et al., 2006; Preasor et al., 2009; Yang et al., 2009; Sedorko et al., 2018) and mark allogenic stratigraphic surfaces that represent sequence boundaries in 4th and 3rd order stratigraphic cycles (Netto, 1994; Gandini et al., 2012; Villegas-Martín et al., submitted).

The alternance of trace fossil suites representing the Skolithos and Cruziana ichnofacies is an ichnological signature of deposition in the upper-lower shoreface transition zone. The trace fossil composition of the MLS suite, however, indicates the prevalence of an archetypal Cruziana Ichnofacies, which suggests preferential colonization of lower shoreface substrates. In addition, the fading of the Sw_2 deposits towards the top of the Palermo Formation succession reinforces the lower shoreface character of these deposits.

4.3. Offshore facies association

Offshore-transition and offshore deposits are represented by He, Mm, and Bs lithofacies (Table 1) preserved on the top of the Palermo Formation and the Irati Formation succession (Fig. 2-3). They occur in all the study area and comprise predominantly fine-grained lithologies, including silty to sandy heterolithic beds and muddy deposits.

The offshore transition deposits encompass mainly heterolithic deposits (He lithofacies; Table 1). These deposits record mostly periods of quiet water, in which the suspended sediment fall-out is the predominant sedimentary process during fair-weather conditions. Episodic deposition of thin beds of fine-grained sandstone or siltstone caused by combined-flow and storm wave action may occur (Clifton, 2006; Buatois et al., 2007). The bioturbation is characterized by the *Thalassinoides-Asterosoma* ichnofabric with a high degree of bioturbation (BS 5, locally 6). The occurrence of the MLS suite in these deposits indicates the prevalence of the stable conditions observed in the lower shoreface deposits, suggesting colonization of the offshore transition zone. The occurrence of the MLS suite indicates the distribution of the archetypal Cruziana

Ichnofacies throughout the lower shoreface to the offshore-transition zone, in accordance with the record of this ichnofacies in shallow marine settings (e.g., Buatois et al., 2007; Buatois and Mángano, 2011; Villegas-Martin et al., 2014).

In the upper portion of the Palermo Formation succession, however, the sedimentary and ichnological patterns in He lithofacies deposits changes. The heterolithic beds show a high frequency of thin layers of fine-grained sandstone with carbonate cement interbedded with non-carbonaceous mudstones. The ichnodiversity decreases, but the abundance of trace fossils is still high (BS 4-5, locally 6). The bioturbation is characterized by the *Teichichnus* ichnofabric (BS 3-5) (Fig. 6). *T. zig zag* and *T. rectus* are the main ichnotaxa observed in this ichnofabric, with *Palaeophycus* and *Thalassinoides* as accessory burrows. *Chondrites, Helminthopsis*, and *Rhizocorallium* may occur locally. The dominance of prospecting burrows made by sediment filtering-feeders in the trace fossil assemblage suggest a high frequency in the sedimentary input, but a reduction in the amount of organic content into the substrate. Thus, the *Teichichnus* ichnofabric represents the colonization of high-frequency oderate-energy softgrounds in stenohaline settings (HMS suite; Table 2). The HMS suite is an impoverished expression of the Cruziana Ichnofacies. Impoverished suites of Cruziana Ichnofacies have been registered in deposits affected by stress caused by estabilization of environmental parameters that control the distribution of the biota, such s high sedimentation and erosion rates, salinity and oxygen fluctuations, unbalancing in food supply, and abrupt changes in substrate consistency (e.g., Bromley, 1990; Netto, 2001; Buatois et al., 2005; Buatois and Mángano, 2011). In the case of the HMS suite, the stress factors seem to be related to the high frequency of sedimentation and to an abrupt change in the food supply into the basin.

The offshore deposits are represented by the finer-grained expression of the He lithofacies, the Mm, and the Bs. The heterolithic deposits are composed of thin intercalations of laminated siltstone and claystone, with sporadic lenses of very fine-grained sandstone. They occur in the very top of the Palermo Formation succession (Fig. 2,3) and characterizes the upper offshore deposits. Bioturbation is characterized by the *Helminthopsis* ichnofabric (Fig. 6), which also contains *Palaeophycus, Planolites* and local occurrences of *Thalassinoides* and *Teichichnus* (Table 2). The amount of bioturbation remains high (BS 5-6), suggesting that the reduction in ichnodiversity is a taphonomic artifact, preserving only the last-emplaced burrows made by sedimentophagous/detritivorous organisms in deep tiers (e.g., Bromley and Ekdale, 1986). Thus, the *Helminthopsis* ichnofabric represents colonization of low-energy quiet, stable soft- to soupgrounds by stenohaline burrowing communities (LS suite; Table 2) and is a distal expression of the Cruziana Ichnofacies (Table 2).

The Mm and Bs lithofacies characterize the lower offshore deposits (Table 1; Fig. 5). Bioturbation is poorly preserved in these settings and restricted to the occurrences of the *Helminthopsis* ichnofabric with BS 6, locally 4-5 in the Mm lithofacies, and the monotypic ichnofabric of *Chondrites* (BS 5) in the Bs lithofacies (Table 2). The occurrence of the *Helminthopsis* ichnofabric in Mm lithofacies extends the LS suite towards the lower offshore deposits. The massive aspect of these mudstones are due to the homogenization by bioturbation activity, and trace fossils are clearly observed only in intervals in which the amount of bioturbation is lower. The presence of the monotypic *Chondrites* ichnofabric in Bs lithofacies reinforces the anoxic or quasi-anoxic character of the black shales that characterize the top of the Irati Formation succession in the study area. These bituminous shales characterize nonconventional hydrocarbon source rocks. The prevalence of shelfal conditions suggest that the monotypic *Chondrites* ichnofabric represents substrate colonization of oxygen-depleted soft- to soupgrounds by chemosymbiont organisms (e.g., Bromley and Ekdale, 1984) in a restricted basin.

5. Shoreline variation and changes in coastal dynamics based on trace fossils

Chronostratigraphic data calibrate the Lower Permian deposits of the Paraná Basin in the Asselian–Artinskian interval: 298.8 ± 1.9 Ma is the age of the oldest tonstein deposits ever dated in the Rio Bonito Formation (Cagliari et al., 2016) and 278.4±2.2 Ma is the age of the youngest tonstein known in the Irati Formation (Santos et al., 2006). The transgressive tendency of these deposits during the Early Permian has been associated to the Gondwana deglaciation (Milani, 1997). The vertical distribution of trace fossil suites and ichnofacies throughout the Lower Permian sedimentary succession of the Paraná Basin was strongly influenced by ecological parameters, such as hydrodynamic energy, salinity and oxygenation rates, food supply, substrate consistency, which controlled the ichnofauna distribution in response to the sea-level oscillations and shoreline variations caused by deglaciation. A general transgressive attern is observed in the whole succession, from the Rio Bonito Formation strata dominated by impoverished suites of the Cruziana Ichnofacies and suites of the mixed Skolithos-Cruziana Ichnofacies to the Irati Formation strata exhibiting dominance of distal suites of Cruziana Ichnofacies, passing through Skolithos and archetypal Cruziana ichnofacies suites in the Palermo Formation (Fig. 2,3,7).

The estuarine deposits expressed in the Rio Bonito Formation sedimentary succession exhibit a great variability of depositional settings formed during the original paleovalley infill (e.g., Buatois et al., 2007). Tides were the main coastal processes that influenced these estuarine systems at their initial phase. The evidence of wave action in the upper part of the Rio Bonito Formation sedimentary succession and the establishment of well-developed subtidal bars in the outer estuarine settings evidence the change in the coastal dynamics and the wave influence in the sedimentary processes into these estuaries. This change is well marked by the impact of storm deposits into the estuarine settings but also by the shift in trace fossil suites. Ichnofabrics are locally observed in the tide-dominated estuarine facies association, show low ichnodiversity and low intensity of bioturbation in general, and, except for local evidence of the brackish water (BW) suite, trace fossils cannot be assigned to a saline context. In the wave-dominated estuarine facies association, however, ichnofabrics are commonly observed in finer-grained deposits and is represented by the BW suite and the polyhaline (PH) suite. As expressions of the impoverished Cruziana and mixed Skolithos-Cruziana ichnofacies, these suites reveal substrate colonization of marginal marine settings (e.g., Pemberton et al., 2001; Buatois et al., 2005).

The occurrence of the crowded *Rosselia* ichnofabric (e.g., Schmidt Neto et al., 2018b) in the storm deposits that affected the estuarine system indicates that high-energy and high-frequency marine sedimentary processes took place in these settings for a relative time interval (e.g., Nara, 1995; Netto et al., 2014), and reflects a major transgressive event. The erosive character of these deposits, the prevalence of storm deposits signatures and the change in the estuarine regime allow establishing the post-glacial transgressive surface (TS) at the base of the storm-influenced facies association in the Rio Bonito Formation (Fig. 8). Conversely, the occurrence of crowded *Palaeophycus* ichnofabric (CPI) in the heterolithic deposits intercalated to the storm deposits suggest deposition in quiet environments for a relative time interval (Villegas-Martín and Netto, 2018). The density of *Palaeophycus* (absence of other macroburrows) suggest ecologically stressing conditions during substrate colonization (e.g. Buatois et al., 2005), which associated to dense shell pavements suggest depleted oxygen conditions established in quiet settings in the estuarine system.

The wave-dominated estuarine deposits are marked by the presence of thick coal beds and frequent intercalations of massive mud and coarser-grained deposits. Marls occur locally, sometimes showing stromatolite growing (e.g., Netto, 1994). Sediment biostabilization are frequent (e.g., Schmidt-Neto et al., 2018b). Rhizobioturbation is common and Glossifungites (G) suites are more frequent, locally showing cyclic occurrences and marking autogenic surfaces (Villegas-Martín et al., submitted). These features suggest frequent lateral facies variation and a shoaling upward tendency.

An important change in the coastal dynamics is recognized in the lower portion of the Rio Bonito Formation, when the intercalations between Skolithos and Cruziana ichnofacies suites, with the predominance of the latter, mark the overall flooding of the estuarine systems and the establishment of shelf deposits (Fig. 8). The flooding surface (FS) that marks this change is better observed in core CA-74-RS, and compose a coplanar surface (FS/SB_1) that marks the transition between the Rio Bonito and Palermo formations in almost all analyzed cores (Fig. 2-3). Intercalations of storm and fair-weather deposits characterizes the basal expression of the shoreface facies association.

The common presence of fair-weather wave sand bars in association with the storm deposits suggest deposition in upper-lower shoreface transition settings. The dominance of high, moderate, and moderate to low-energy stenohaline trace fossil suites (HS, MS, and MLS suites, respectively) in these deposits points to alternance between Skolithos and Cruziana ichnofacies, which are expected in shallow marine environments. The dominance of the Cruziana Ichnofacies suites to the top indicates the general transgressive trend of the Lower Permian succession in Paraná Basin. However, an abrupt change marked by the occurrence of G suites reworking lower shoreface heterolithic beds containing the MSL suite and capped by estuarine deposits of the lithofacies As and Cgs (Fig. 6, 7) broke this tendency and reactivated deposition in marginal marine settings. These G suite occurrences were assumed as resultant of allogenic events in the basin and a biomarker of the sequence boundary observed in the transition of Rio Bonito and Palermo sedimentary succession in many cores (Villegas-Martín et al., submitted) (Fig. 2-3, 6). This sequence boundary represented by a coplanar surface (SB_1/FS) involves not only the forced-regressive surface, but also at least two erosive surfaces, considering the difference between the sandstones in the burrow fill and those that overly the heterolithic deposits, and a flooding surface (e.g., Netto, 1994; Buatois et al., 2007; Gandini et al., 2010; Villegas-Martín et al., submitted). The recurrence of the Glossifungites Ichnofacies also demarks regressive-transgressive events in high frequency in the lower shoreface deposits (Fig. 8). This general change is recognized in all the sections (e.g., Netto, 1994; Buatois et al., 2007; Gandini et al., 2010), indicating the relevance of this event in the basin scale.

Shelfal deposition dominates in the Paraná Basin after this change, in which shoreline variations are discretely preserved throughout the sedimentary succession that characterizes the Palermo Formation and the base of the Irati Formation. The dominance of Cruziana Ichnofacies suites, with a prevalence of the MSL suite that represents the archetypal expression of this ichnofacies is a potent signature of stable sea-level conditions in offshore-transition and upper offshore settings. The record of the HMS suite, however, points to another change in the coastal dynamics that affected these offshore settings. The low content of organic matter in mudstones and the significant amount of carbonate cement in the fine-grained sandstones that compose the heterolithic bedding, associated to the increase in the frequency of sandstone and the change in the ichnofabric pattern, pointing to colonization of more energetic substrates in the upper portion of the Palermo Formation. These features suggest a drastic change in the basin, potentially related to climatic changes, in which the predominantly humid conditions gave place to more dry conditions. Thus, the impoverished character of the Cruziana Ichnofacies represented by the HMS suite is a biomarker of this change in the coastal dynamics as reflect in offshore-transition settings.

The distal expression of the Cruziana Ichnofacies represented by the LS suite preserved in the offshore deposits from the top of the Palermo Formation succession characterizes a condensed section (e.g., Netto, 1994; Buatois et al., 2007). This section records the maximum flooding interval in the second-order transgressive sequence represented by the Rio Bonito-basal Irati sedimentary succession. The shift of ichnofabrics from HS suite to LS suite as observed at the base of these beds might be used as a biomarker of the maximum flooding surface (MFS_2) of this sequence (Fig. 8).

The thick carbonate deposits that occur at the base of the Irati Formation lack bioturbation. They have been interpreted as evaporitic deposits (e.g., Hachiro, 2000; Cassel, 2017) with evidence of a microbial origin (e.g., Calça, 2014; Warren et al., 2017). The occurrences of this carbonate deposits on the top of the Lower Permian sedimentary succession marks another remarkable change in the coastal dynamics of the Paraná Basin and signalizes a forced-regression event (SB_2) and the reactivation of the marginal marine settings under dry climate conditions. A remarkable flooding event was responsible for the establishment of the Bs lithofacies deposits on the very top of the succession. The shift of M and Bs lithofacies in this portion of the succession demark a new maximum flooding surface, which configures the maximum flooding surface (MFS$_2$; Fig. 8) of the 2nd order Supersequence Gondwana I in Paraná Basin (Milani et al., 2007). Bioturbation is represented by the CS suite, which attests the restricted character of the marine deposits of the Paraná Basin at the end of the Early Permian (Milani and Ramos, 1998).

The shoreline variations and changes in coastal dynamics of the southern border of the Paraná Basin during the Early Permian as measured by the vertical distribution of ichnofabrics and the shifts of trace fossil suites and ichnofacies allowed tracing a relative palobathymetric curve that can be compared with the global sea-level change record during this time interval. The 3rd-order curve as proposed by Haq and Schutter (2008) evidenced a trend of sea-level fall in the Asselian interval. Contrary, in the studied section it was diagnosed a relative sea-level rise in that interval, materialized by Rio Bonito deposits (Fig. 8). This discrepancy can be explained by high subsidence rates in the basin during Asselian. Milani and Ramos (1998) had diagnosed a prolonged subsiding phase during the early Permian in Paraná Basin.

In the global sea level curve (Haq and Schutter 2008), the Sakmarian-Artinskian interval is marked by a stillstand phase in 3rd order, but in 4th order some sea level falls are often observable (Fig. 9). In the studied section a slight sea level rise is observable, attesting minor subsidence rates than the Asselian interval. Only in the top of the Artinskian interval a stillstand pattern is observable in the studied section (Fig. 9). However, the absence of accurate ages and biomarkers in the sequence boundaries precludes an exact correlation between those curves in 4th order. Milani and Ramos

(1998) also pointed that the main global peaks during the early Permian diagnosed by Vail et al. (1977) has not expression in the stratigraphic record of the Paraná Basin, as result of regional subsidence. In addition, the curve established by Haq and Shutter (2008) did not considered intracratonic basins and few data were collected in the Gondwana Realm, which can be a bias on the global curve. Thus, this paleobathymetric curve constructed for the early Permian of the Paraná Basin illustrated principally local processes associated to a particular subsidence and basin restriction during the deposition of the Godwana I Supersequence.

6. Conclusions

The vertical distribution of the ichnofacies and suites in the early Permian reflects changes controlled principally by relative bathymetric and bottom water oxygenation and suggested a deepening of the basin evidenced of base to top by (1) Skolithos– arquetipic Cruziana– distal Cruziana (lower ichnodiversity) ichnofacies, and (2) distinctive sedimentologic signatures characteristic, which vary principally of estuarine – shoreface (upper and lower) – offshore transition– offshore subenvironments.

The vertical distribution of ichnofabrics and the shifts of trace fossil suites and ichnofacies constituted a useful tool for the identification of the shoreline variations and changes in coastal dynamics in regional scale. Futhermore, these vertical distribution of the traces permitted traced bathymetric curves for the Paraná Basin in 4ta, 3or, and 2da order cycles.

The bathymetric curve of 3rd-order traced for the Permian sequence is predominantly discrepant with the sea level change global curve and illustrated principally local processes associated to a particular subsidence and basin restriction during the deposition of the Godwana I Supersequence.

7. Acknowledgments

We thank to F. Tognoli, D. Sedorko, H. Smicht-Neto and R.S. Horodyski for helpful discussions. JVM thanks to CAPES by the Ph.D. grant. RGN thanks the Brazilian National Council for Scientific and Technological Development (CNPq) by the research grants 401826/2010-4 and 303863/2016-1. This paper is a contribution to the project CAPES/PVE/88881.062157-2014-01.

8. Reference

Aborrage, A.M., Lopes, R.C. 1986. Projeto A Borda Leste da Bacia do Paraná: integração geológica e avaliação econômica. Ministério das Minas e Energia, Departamento Nacional da Produção Mineral, Convênio DNPM-CPRM, SUREG/Porto Alegre. 18. Relatório Final.

Allen, J.R.L. 1982. Mud drapes in sand-wave deposits: a physical model with application to the Folkestone Beds (Early Cretaceous, Southeast England). *Philosophical Transactions of the Royal Society*, 306, 291-345.

Bertling, M., Braddy, S.J; Bromley, R.G. 2006. Names for trace fossils: a uniform approach. *Lethaia*, 39, 265–286.

Boersma, J.R., Terwindt, J.H.J. 1981. Neap-spring sequences os intertidal shoal deposists in a mesotidal estuary. *Sedimentology*, 28, 151-170.

Brett, C. E. 1998. Sequence Stratigraphy, Paleoecology, and Evolution: Biotic Clues and Responses to Sea-Level Fluctuations. *Palaios*, 13, 241–262.

Bromley R.G. (ed.) 1996. Trace Fossils. Biology, Taphonomy and Applications, 2nd ed.Chapman and Hall, London, 361pp.

Bromley, R.G., Ekdale, A.A. 1984. Chondrites: a trace fossil indicator of anoxia in sediments. *Science*. 25; 224.

Buatois, L.A., Gingras, M., MacEachern, J.A., Mángano, M.G., Zonneveld, J.P., Pemberton, S.G., Netto, R.G., Martin, A. 2005. Colonization of brackish water systems trough time: Evidence from the trace-fossil record, *Palaios*, 20, 321-347.

Buatois, L.A., López Angriman, A.O. 1992. Evolución de sistemas deposicionales en el Cretácico del Grupo Gustav, Isla James Ross, Antártida. In Rinaldi, C.A. (eds.), Geología de la isla James Ross, Publicación del Instituto Antártico Argentino, Buenos Aires, 263–297 pp.

Buatois, L. A., Mángano, M.G. (eds.) 2011. Ichnology: Organism-Substrate interactions in Space and Time, Cambridge University Press, 370 pp.

Buatois, L.A.; Netto, R.G., Mángano, M.G. 2001a. Reinterpretación paleoambiental de la Formación Rio Bonito (Pérmico de la Cuenca de Paraná) en el yacimiento de carbón de Iruí, Rio Grande do Sul, Brasil: integración de análisis de fácies, icnología y estratigrafia secuencial de alta resolución. *Geogaceta*, 29, 27–30.

Buatois, L.A., Netto, R.G., Mángano, M.G. 2001b. Paleoenvironmental and sequence-stratigraphic analyses of Lower Permian marginal- to shallow marine coal-bearing successions of the Paraná Basin in Rio Grande do Sul, Brazil, based on ichnological data. *Ciência, Técnica, Petróleo, Seção Exploração de Petróleo*, 20, 171–176.

Buatois, L.A., Netto, R.G., Mángano, M.G. 2007. Ichnology of Permian marginal- to shallow marine coal-bearing successions: Rio Bonito and Palermo Formations, Paraná Basin, Brazil. In MacEachern, J.A., Bann, K.L., Gingras, M.K., Pemberton, S.G (eds.) Applied ichnology. SEPM Short Course Notes 52, 167–178 pp.

Cagliari, J., Lavina, E. L. C., Philipp, R. P., Tognoli, F. M. W., Basei, M. A. S., Faccini, U. F. 2014. New Sakmarian ages for the Rio Bonito formation (Paraná Basin, southern Brazil) based on LA-ICP-MS UePb radiometric dating of zircons crystals. *Journal of South American Earth Sciences*, 56, 265–277.

Cagliari, J., Philipp, R.P., Buso, V.V., Netto, R.G., Hillebrand, P.K., Lopes, R.C., Basei, M.A.S., Faccini, U.F., 2016. Age constraints of the glaciation in the Paraná Basin: evidence from new U-Pb dates. *Journal Geological Society*, 173, 871–874.

Calça, C.B. 2014. Abordagem micropaleontológica e geoquímica da formação assistência (subgrupo Irati, Permiano, Bacia do Paraná, Brasil). PhD Theses, Universidade de São Paulo, 53 pp.

Carmona, N.B., Ponce, J.J., Mángano, M.G., Buatois, L.A. 2006. Variabilidad de la icnofacies de *Glossifungites* en el contacto entre las Formaciones Sarmiento (Eoceno medio -Mioceno temprano) y Chenque (Mioceno temprano) en el Golfo San Jorge, Chubut, Argentina. *Ameghiniana*, 43 (2), 413–425.

Cassel, M.C. 2017. Implicações paleoambientais dos folhelhos negros na rampa carbonática da Formação Irati. Master Theses, Unisinos University, 39 pp.

Clifton, H.E. 2006. A re-examination of facies models for clastic shorelines. In Walker, R.G., Posamentier, H (eds.). Facies Models Revisited, SEPM Spec. Publ., Tulsa, 293–337 pp.

Daemon, R.F., Quadros, L.P. 1970. Bioestratigrafia do Neopaleozóico da Bacia do Paraná. Congresso Brasileiro de Geologia, XXIV, Brasília. Anais, vol. 1. Sociedade Brasileira de Geologia, Brasília, p. 359–412.

Desjardins, P.R., Buatois, L.A., Mangano, M.G. 2012. Tidal flats and subtidals and bodies. Trace fossils as indicators of sedimentary environments. *Developments in Sedimentology*, 64, 529–562.

Fielding, C.R., Bann, K.L., Maceachern, J.A., Tye, S.C., Jones, B.G. 2006. Cyclicity in the nearshore marine to coastal, Lower Permian, PebbleyBeach Formation, southern Sydney Basin, Australia: a record of sea-level fluctuations at the close of the Late Palaeozoic Gondwanan ice age. *Sedimentology*, 53, 435–463.

Fürsich, F.T. 1978. The influence of faunal condensation and mixing on the preservation of fossil benthic communities. *Lethaia*, 11, 243–250.

Gandini, R., Netto, R.G., Kern, H.P., Lavina, E.L.C. 2010. Assinaturas icnológicas da sucessão sedimentar Rio Bonito no bloco central da jazida carbonífera de Iruí, Cachoeira do Sul (RS). *Gaea– Journal of Geosciences*, 6, 21–43.

Gingras, M. K., Pemberton, S. G., Saunders, T. 2000. Firm-ness profiles associated with tidal-creek deposits: The temporal significance of *Glossifungites* assemblages. *Journal of Sedimentary Research*, 70, 1017–1025.

Habekost, N.T. 1978. Paleoambientes da Formação Palermo no Sudeste do Estado de Santa Catarina -Brasil. *Acta Geologica Leopoldensia*, 4, 4–17.

Habekost, N.T. 1983. Paleoambientes da Formação Palermo na região central do Rio Grande do Sul, Brasil. *Acta Geologica Leopoldensia*, 16, 43–113.

Hachiro, J. 2000. Occurrences of evaporites in the Irati Subgroup (late Permian, Paraná Basin). *Anais da Academia Brasileira de Ciências*, 72(4), 600.

Haq, B.U., Shutter, S.R. 2008. A Chronology of Paleozoic Sea-Level Changes. *Science*, 322, 64–68. http://dx.doi.org/10.1126/science.1161648.

Holz, M., França, A. B., Souza, P. A., Iannuzzi, R., Rohn, R. 2010. A stratigraphic chart of the Late Carboniferous/Permian succession of the eastern border of the Paraná Basin, Brazil, South America. *Journal of South American Earth Sciences*, 29, 381–399.

Iannuzzi, R., Souza, P.A., 2005. Floral succession in the Lower Permian deposits of the Brazilian Paraná Basin: an up-to-date overview. In Lucas, S.G., Zigler, K.E. (eds.). The Nonmarine Permian: New Mexico. New Mexico Museum of Natural History and Science Bulletin, 30, 144-149 pp.

Knaust, D. 2018. The ichnogenus *Teichichnus* Seilacher, 1955. *Earth-Science Reviews*, **177:** 386–403.

Lavina, E.L., 1991. Geologia sedimentar e paleogeografia do Neopermiano e Eotriássico (Intervalo Kazaniano-Scythiano) da Bacia do Paraná. PhD These, Universidade Federal do Rio Grande do Sul, Instituto de Geociências, Porto Alegre, 333 pp.

Lavina, E.L., Lopes, R.C. 1986. A transgressão marinha do Permiano Inferior e a evolução paleogeográfica do Super-Grupo Tubarão no Estado do Rio Grande do Sul. *Paula Coutiana1*, 51–103.

Lavina, E.L., Nowatzki, C.H., Santos, M.A.A., Leão, H.Z. 1985. Ambientes de sedimentação do Super-Grupo Tubarao na região de Cachoeira do Sul. Acta *Geologica Leopoldensia*, 9, 5–75.

Lopes, R. da C. 1990. Estudo paleoambiental da Formação Rio Bonito na Jazida do Leão - RS. Uma análise inicial. *Acta Geologica Leopoldensia*, 31, 91–112.

Lopes, R. da C., Faccini, U.F., Paim, P.S.G., Garcia, A.J.V., Lavina, E.L. 2003a. Barras de mare na formação Rio Bonito: elementos arquiteturais e geometria dos corpos (Iruí e Canape e RS). In Paim, P.S.G., Faccini, U.F., Netto, R.G. (eds.) Geometria, arquitetura e heterogeneidade de corpos sedimentares: estudo de casos. Unisinos, São Leopoldo, 78-92 pp.

Lopes, R. da C., Lavina, E.L., Paim, P.S.G., Goldberg, K., 2003b. Controle estratigrafico e deposicional da genese dos carvoes da regiao do Rio Jacuí (RS). In Paim, P.S.G., Faccini, U.F., Netto, R.G. (eds.), Geometria, arquitetura e heterogeneidade de corpos sedimentares: estudo de casos. Unisinos, São Leopoldo, 187–206 pp.

Lopes, R. da C., Paim, P.S.G., Lavina, E.L. 2003c. Modelo de reservatorio em arenitos litorâneos: ilha de barreira Permiana na Formação Rio Bonito (Minas do Leao e RS). In Paim, P.S.G., Faccini, U.F., Netto, R.G. (eds.) Geometria, arquitetura e heterogeneidade de corpos sedimentares: estudo de casos. Unisinos, São Leopoldo, 60–77 pp.

McCave, I.N. 1972. Transport and escape of fine-grained sediment from shelf areas. In Swift, D.J.P., Duane, D., Pilkey, O.H. (eds.). Shelf Sediment Transport, Dowden Hutchinson and Ross, Stroudsburg, PA, 225-248 pp.

MacEachern, J.A., Bann, K.L. 2008. The role of ichnology in refining shallow marine facies models. In Hampson, G., Steel, R., Burgess, P., R. Dalrymple, R. (eds.). Recent Advances in Models of Siliciclastic Shallow-Marine Stratigraphy, SEPM Spec. Publ., 90, 73–116 pp.

MacEachern, J.A., Raychaudhuri, I., Pemberton, S.G. 1992. Stratigraphic application of the *Glossifungites* Ichnofacies: delineating discontinuities in the rock record. In Pemberton, S.G (ed.). Applications of Ichnology to Petroleum Exploration, Calgary, SEPM Core Workshop No 17, 169–198 pp.

Miall, A.D. 1996. The Geology of Fluvial Deposits: Sedimentary Facies, Basin Analysis and Petroleum Geology. Springer-Verlag, Berlin, 852 pp.

Milani, E.J., França, A.B., Schneider, R.L. 1994. Bacia do Paraná. *Boletim Geociências da Petrobrás*, 8(2), 69–82.

Milani, E.J., Melo, J.H.G. de, Souza, P.A. de, Fernandes, L.A., França, A.B. 2007. Bacia Do Parana. *Boletim de Geociencias da Petrobras*, 15, 265–287.

Milani, E. J., Ramos, V. A. 1998. Orogenia paleozoicas no domínio sul-ocidental do Gondwana e os ciclos de subsidência da Bacia do Paraná. *Revista Brasileira de Ciências*, 28(4), 473–484.

Netto, R.G. 1994. A paleoicnologia como ferramenta de trabalho na sequência sedimentar Rio Bonito/Palermo. PhD These, Universidade Federal do Rio Grande do Sul, Porto Alegre, 242 pp.

Netto, R.G. 1998. Padrão de icnofábricas da sequência sedimentar Rio Bonito/Palermo no RS e seu valor na diagnose paleoambiental. *Acta Geologica Leopoldensia*, 21, 209–226.

Netto, R. G**.** 2001. Icnologia e Estratigrafia de Seqüências. In Ribeiro, H.J.P.S. (ed.).Estratigrafia de Sequências – Fundamentos e aplicações, Universidade do Vale do Rio dos Sinos – UNISINOS. 219-259 pp.

Netto, R.G**.,** Benner, J.S., Buatois, L.A., Uchman, A., Mángano, M.G., Ridge, J.C., Kazakauskas, V., Gaigalas, A. 2012a. Glacial Environments. In Knaust, D., Bromley, R.G (eds.). Trace Fossils as Indicators of Sedimentary Environments.1ed. 630 Amsterdan: Elsevier, 64, 227–336 pp.

Netto, R.G., Buatois, L.A., Mángano, G., Balistieri, P. 2007. *Gyrolithes* as a multipurpose burrow: an ethologic approach. *Revista Brasileira Paleontologia,* 10 (3), 157–168.

Netto, R.G, Rossetti, D.F. 2003. Icnhology and saliniti fluctuations: A case study from the Early Miocene (Lower Barreiras Formations) of São Luis Basin, Maranhão, Brazil. *Revista Brasileira de Paleontologia*, 6, 5–18.

Paranjape, A. R., Kulkarni, K. G., Kale, A. K. 2014. Sea level changes in the Upper Aptian-lower/middle(?) Turonian sequence of Cauvery Basin, India- An ichnological perspective. *Cretaceous Research*, 1–14.

Pemberton, S., MacEachern, J.A., Dashtard, K.L.B., Gingras, M.K., Zonneveld, J.P**.** 2012. Shallow-Marine Siliciclastic Systems - Shorefaces. Trace fossils as indicators of sedimentary environments. *Developments in Sedimentology*, 64, 563–603.

Pemberton, S.G., Spila, M.V., Pulham, A.J., Saunders, T., MacEachern, J.A., Robbins, D., Sinclair, I. 2001. Ichnology and Sedimentology of Shallow and Marginal Marine Systems: Ben Nevis and Avalon Reservoirs, Jeanne D'Arc Basin, Geological Association of Canada, St. John’s Newfoundland, Short Course Notes, 15, 353 pp.

Pinto, I.D., Ornellas, L.P. 1981. Permian insects from Paraná Basin, South Brazil. III Homoptera -1-Pereboridae. Congresso Latino–Americano de Paleontologia, 2, Porto Alegre, vol. 1. Anais, 209–219 pp.

Premaor, E., Fischer, T.V., Souza, P.A. 2006. Palinologia da Formação Irati (Permiano inferior da bacia do Paraná), em Montevidiu, Goiás, Brasil. *Revista del Museo Argentino de Ciencias Naturales*, 8(2), 221–230.

Raaf, J.F.M., Boersma, J.R., Van Gelder, A. 1977. Wave-generated structures and sequence from a shallow marine succession, Lower Carboniferous, Couny Cork, Ireland. *Sedimentology*, 24, 451–483.

Reineck, H.E. 1963. Sedimentgefüge im Bereich der südliche Nordsee. *Abh Senckenb Nat Gesell*, 505, 1–138.

Rhoads, D.C., Speden, I.G., Waage, K.M. 1972: Trophic group analysis of Upper Cretaceous (Maestrichtian) bivalve assemblages from South Dakota. *American Association of Petroleum Geologists Bulletin*, 56, 1100–1113.

Rodríguez-Tovar, F. J., Uchman, A., Payros, A., Orue-Etxebarria, X., Apellaniz, E., Molina, E. 2010. Sea-level dynamics and palaeoecological factors affecting trace fossil distribution in Eocene turbiditic deposits (Gorrondatxe section, N Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 285, 50–65.

Rösler, O., Rohn, R., Albamonte, L. 1981. Libélula permiana do Estado de São Paulo, Brasil (Formação Irati): Gondvanoptilon Brasiliensegen. et sp. nov. Congresso Latino–Americano de Paleontologia, 2, Porto Alegre. Anais, 1, 221–232 pp.

Santos, R.V., Souza, P.A., Alvarenga, C.J.S., Dantas, E.L., Pimentel, M.M., Oliveira, C.G., Araújo, L.M. 2006. Shrimp U–Pb Zircon dating and palinology of bentonitic layers from the Permian Irati Formation, Paraná Basin, Brazil. *Gondwana Research*, 9, 456–463.

Savrda, C.E. 1991. Ichnology in sequence stratigraphic studies: an example from the Lower Paleocene of Alabama. *Palaios*, 6, 39–53.

Savrda, C.M. 1993. Ichnosedimentologic evidence for a non catastrophic origin of Cretaceous-Tertyari boundary sands in Alabama. *Geology*, 21, 1075–1078.

Savrda, C. H. 1995. Ichnologic applications in paleoceanographic, paleoclimatic, and seal level studies. *Palaios*, 10, 565–577.

Savrda, C.E., Hannelore, K., Mccarthy, F.M.G., Mchugh, C.M.G., Olson, H.C., Mountain, G. 2001. Ichnofabrics of a Pleistocene slope succession, New Jersey margin: relations to climate and sea-level dynamics. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 171, 41–61.

Savrda, C.E., King, D.T. JR. 1993. Log-ground and *Teredolites*. Lagerstätte in a transgressive sequence, Upper Cretaceous (Lower Campanian) Mooreville Chalk, central Alabama. *Ichnos*, 3**,** 69–77.

Schneider, R.L., Mühlmann, H., Tommasi, E., Medeiros, R.A., Daemon, R.F., Nogueira, A.A. 1974. Revisão estratigráfica da Bacia do Paraná. Congresso Brasileiro de Geologia, XXVIII, 1974, Porto Alegre. Anais, Sociedade Brasileira de Geologia, vol. 1, 41–66 pp.

Schmidt-Neto, H., Netto, R.G., Villegas-Martín, J. 2018a. Bioerosion in shells from the Early Permian Rio Bonito Formation, Brazil: Taphonomic, paleobiological, and paleoecological implications. *Palaeogeography Palaeoclimatology Palaeoecology*, 505, 256-264.

Schmidt-Neto, H., Netto, R.G., Dasgupta, S. 2018b. Storm-related taphofacies in estuarine settings: An integrated analysis on the Early Permian deposits of the Rio Bonito Formation (Paraná Basin, S Brazil). *Journal of South American Earth Sciences*, 85, 263–277.

Sedor, F. A., Silva, R.C. 2004. Primeiro registro de pegadas de Mesosauridae (Amniota, Sauropsida) na Formação Irati (Permiano Superior da Bacia do Paraná) no Estado de Goiás, Brasil. *Revista Brasileira de Paleontologia*, 7(2), 269–274.

Sedorko, D., Netto, R.G., Savrda, C.E. 2018. Ichnology applied to sequence stratigraphic analysis of Siluro-Devonian mud-dominated shelf deposits, Paraná Basin, Brazil. *Journal of South American Earth Sciences*, 83, 81–95.

Sedorko, D**.**, Netto, R.G., Savrda, C. E., Assine, M. L., Tognoli, F.M.W. 2017. Chronostratigraphy and environment of Furnas Formation by trace fossil analysis: Calibrating the lower Paleozoic Gondwana realm in the Paraná Basin (Brazil). *Palaeogeography Palaeoclimatology Palaeoecology*, 487, 307–320.

Seilacher, A. 1964. Biogenic sedimentary structures. In Imbrie, J., Newell, N. D. (eds.). Approaches to Paleoecology. Wiley & Sons, New York, 296–316 pp.

Silva, R. C., Sedor, F. A., Fernandes, A. C. S. 2009. Ichnotaxonomy, functional morphology and paleoenvironmental context of Mesosauridae tracks from Permian of Brazil. *Revista Brasileira de Geociencîências*, 39, 705–716.

Soares, M.B. 2003. A taphonomic model for the Mesosauridae assemblage of the Irati Formation (Paraná Basin, Brazil). *Geologica Acta*, 1(4), 349–361.

Souza, P.A. 2006. Late Carboniferous palynostratigraphy of the Itararé Subgroup, northeastern Paraná Basin, Brazil. *Review of Palaeobotany and Palynology*, 138, 9–29.

Souza, P.A., Marques-Toigo, M., 2005. Progress on the palynostratigraphy of the Permian strata in Rio Grande do Sul State, Paraná Basin, Brazil. *Anais da Academia Brasileira de Ciências*, 77, 353–365.

Tognoli, F.M.W. 2002. Análise estratigráfica e paleoicnológica do Grupo Guatá no leste paranaense. Master These, Universidade Estadual Paulista, 90 pp.

Vail, P.R.; Mitchum, R.M.; Thompson, S. 1977. Scismic straligraphy and global changes of sca level, part 3: relative changes of sea level from coastal onlap. In Payton, C.E (ed.). Seismic stratigraphy - applications to hydrocarbon exploration.Tulsa: American Association of Petroleum Geologists Memoir 26, 63-81 pp.

Villegas-Martín, J., Netto, R. G. 2018. Permian macroburrows as microhabitats for meiofauna organisms: an ancient behaviour common in extant organisms. *Lethaia*, 52, 31–43.

Villegas-Martín, J., Netto, R.G., Lavina, E.L.C., Rojas-Consuegra, R. 2014. Ichnofabrics of the Capdevila Formation (early Eocene) in the Los Palacios Basin (western Cuba): Paleoenvironmental and paleoecological implications. *Journal of South American Earth Sciences*, 56, 214–227.

Warren, L.V., Quaglio, F., Simões, M.G., Assine, M.L., Alessandretti, L., Luvizotto, G.L., Riccomini, C., Stríkis, N.M. 2017. A Permian methane seep system as a paleoenvironmental analogue for the pre-metazoan carbonate platforms. *Brazilian Journal of Geology*, 47(4), 722–733.

Walker, R.G**.** 1979. Shallow marine sands. In Walker, R.G. (ed.). Facies Models, Geol. Assoc. Can. Spec. Pap. 75–89 pp.

Walker, R.G., Plint, A.G. 1992. Wave- and storm-dominated shallow marine systems. In Walker, R.G., James, N.P. (eds.). Facies Models: Response to Sea Level Change, Geological Association Canada. Spec. Pap., 219–238 pp.

Yang, B. C., Dalrymple, R. W., Gingras, M. K., Pemberton, S. G. 2009. Autogenic occurrence of *Glossifungites* Ichnofacies: Examples from wave-dominated, macrotidal flats, southwestern coast of Korea. *Marine Geology*, 260, 1–5.

Zalan, P.V., Wolff, S., Conceiçao, J.C. de J., Marques, A., Astolfia, M.A.M., Vieira, I.S., Appi, V.T., Zanotto, O.A. 1990. Bacia do Paraná. In Raja Gabaglia, G.P., Milani, E.J. (eds.). Origem e evolução de bacias sedimentares. Gavea, Rio de Janeiro, 135-168 pp.

9. Figures and Table captions

Figure 1. A, Regional map of the Paraná Basin extension in South America (grey shading). B, Map demarking the Paraná Basin in Rio Grande do Sul state showing the rock ages and geographical location of the cores correspondent to two sections. C, D, Detail of the cores included in each one of the sections.

Figure 2. Regional stratigraphic section of the Early Permian deposits, signalling the levels with the *Glossifungites* suite and the vertical distribution of the softground ichnofauna.

Figure 3. Legends of the figures 2,4 and 8.

Figure 4. Regional stratigraphic section of the Early Permian deposits, signalling the levels with the Glossifungites suite and the vertical distribution of the softground ichnofauna.

Figure 5. Lithofacies identified in the deposits studied. A, Medium- to fine-grained sandstone with Low-angle cross-stratification and flaser structure. B, Laminated siltstone dark gray. C, Heterolithic deposits bioturbated composed of intercalation of organic-rich siltstone, claystone, and very fine-to fine grained sandstone. D, Shale and massive mudstone. E. Medium- to fine-grained sandstone with high-angle cross-stratification. F, Very fine- to fine-grained sandstone with hummocky crosss tratification. G, Fine- to medium-grained sandstone with low-angle cross-stratification and mud drapes to the top. H, Betuminosos shales. I. Siltsones with very fine-grained sandstone intercalated. J, Q, Coarse-grained sandstone, quartz with low-angle cross-stratification. K, Heterolithic with very fine grained sandstones with symmetric and asymmetric tops and ripples. L, Very fine-grained sandstone with abundant quartz. M, Medium- to fine-grained sandstone with low-angle cross-stratification and granules. N, Paraconglomerate. O, Ortoconglomerate. P, Medium-to fine-grained sandstone with mud drapes capped the low-angle cross-stratification. R. Marl. Scale: 2 cm.

Figure 6. Traces fossils identified in the ichnofabrics of the Rio Bonito-Irati interval from the Early Permian. A , Structures produced in firmground substrate attributed to *Thalassinoides* (Glossifungites Ichnofacies). B-M, Bioturbation structures included in the Skolithos and Cruziana Ichnofacies. F, Ichnofabric with predominance of *Teichichnus* in heterolithic deposits. G, Trace attributed to *Rosselia* in sandstone. E., J–M. Ichnofabrics with predominance of horizontal traces. Pa=*Palaeophycus,*

Pl=*Planolites*, Cy=*Cylindrichnus*, D=*Diplocraterion*, He=*Helminthopsis*, Th=*Thalassinoides*, As=*Asterosoma*, R=*Rosselia*, Ch=*Chondrites*, Lo=*Lockeia*. Scale: 2cm.

Figure 7. A, B, Cross section of the firmground substrates showing Glossifungites suite demarking allogenic (A) and autogenic (B) surface. A Note the Glossifungites suite preserved in palimpsest over the MLS suite in Scale 1 cm.

Figure 8. Inferred paleobathymetric curves (blue line) grouping data of lithofacies, traces suítes, and using the core CA-74-RS as example.

Figure 9. Comparison of the Global sea-level curve with the inferred bathymetric curve to Paraná Basin during the early Permian.

Table 1. Sedimentary facies of the Early Permian deposits (Rio Bonito, Palermo, Irati formations) from the Paraná Basin.

Table 2. Ichnofabrics, Ichnologic suites, and Ichnofacies identified in the early Permian deposits (Rio Bonito, Palermo, Irati formations) from the Paraná Basin.

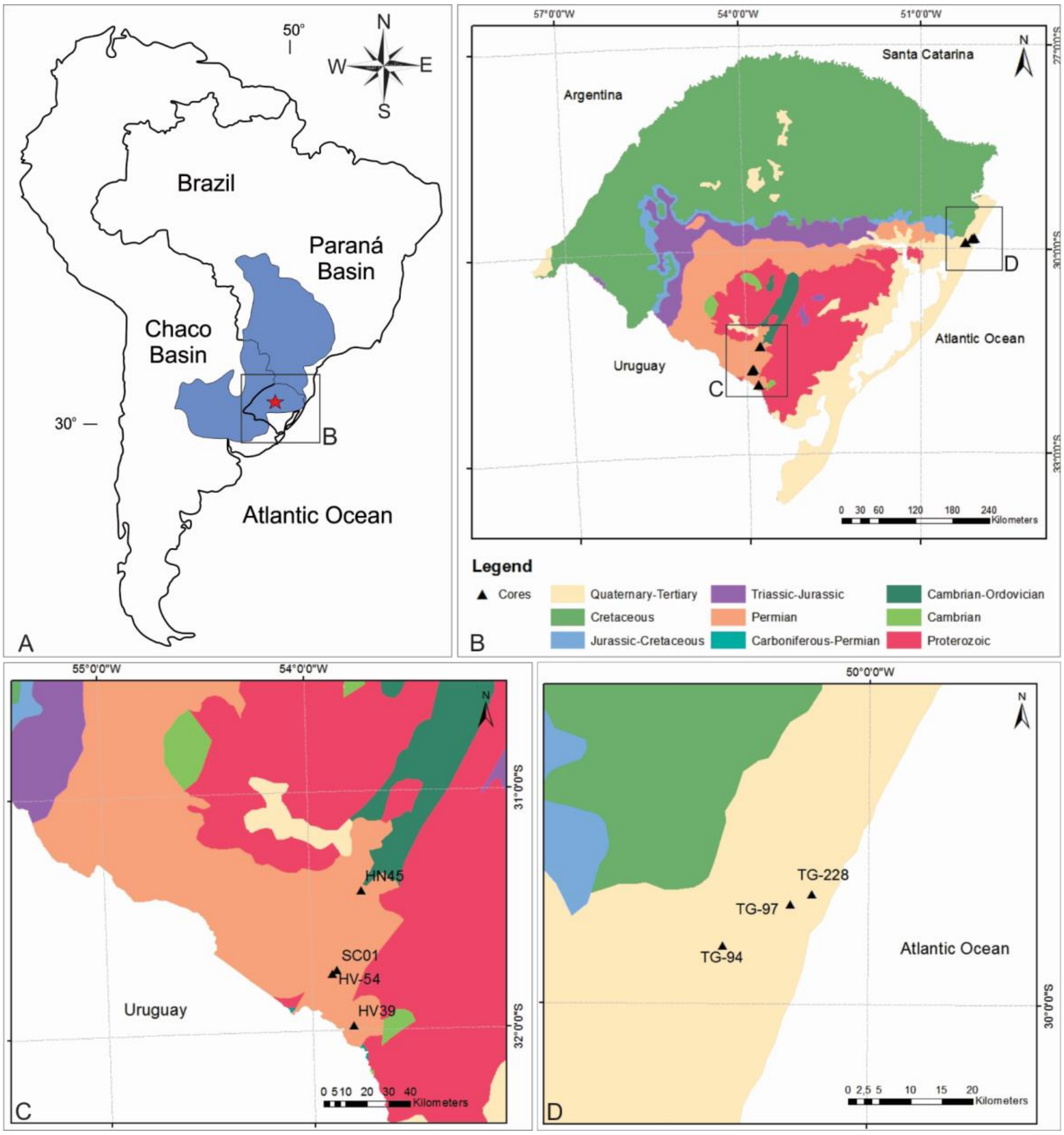

A
50°
N
W
E
S
Brazil
Paraná Basin
Chaco Basin
30°
B
Atlantic Ocean
57°0'0"W
54°0'0"W
51°0'0"W
27°0'0"S
30°0'0"S
33°0'0"S
Santa Catarina
Argentina
Uruguay
Atlantic Ocean
C
D
0 30 60 120 180 240 Kilometers
Legend
Cores
Quaternary-Tertiary
Cretaceous
Jurassic-Cretaceous
Triassic-Jurassic
Permian
Carboniferous-Permian
Cambrian-Ordovician
Cambrian
Proterozoic
55°0'0"W
54°0'0"W
31°0'0"S
32°0'0"S
HN45
SC01
HV-54
HV39
Uruguay
0 5 10 20 30 40 Kilometers
C
50°0'0"W
30°0'0"S
TG-228
TG-97
TG-94
Atlantic Ocean
0 2,5 5 10 15 20 Kilometers
D

Fig. 1

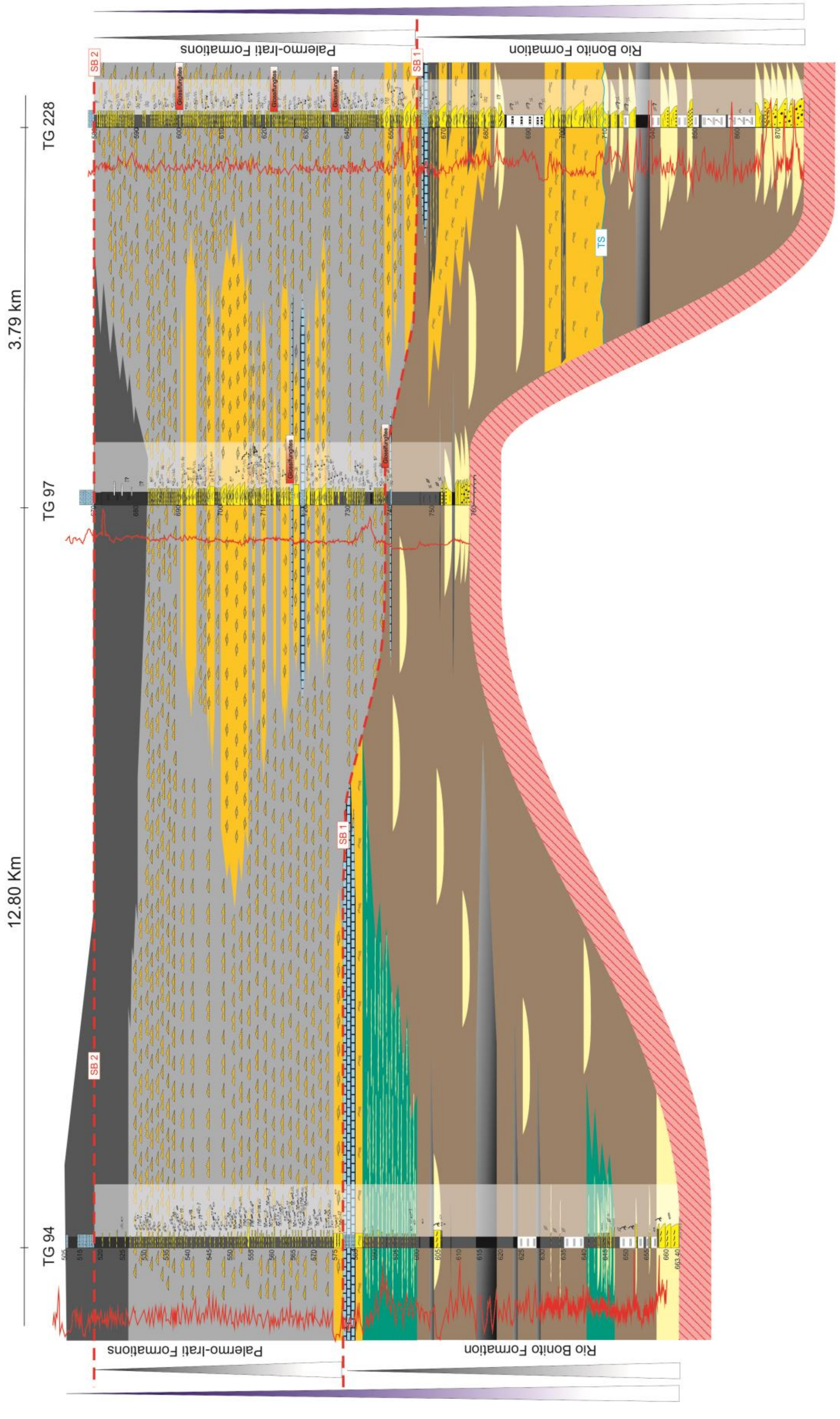

TG 94
12.80 Km
TG 97
3.79 km
TG 228
SB 2
SB 1
TS
Glossifungites
Palermo-Irati Formations
Rio Bonito Formation
663.40

Fig. 2

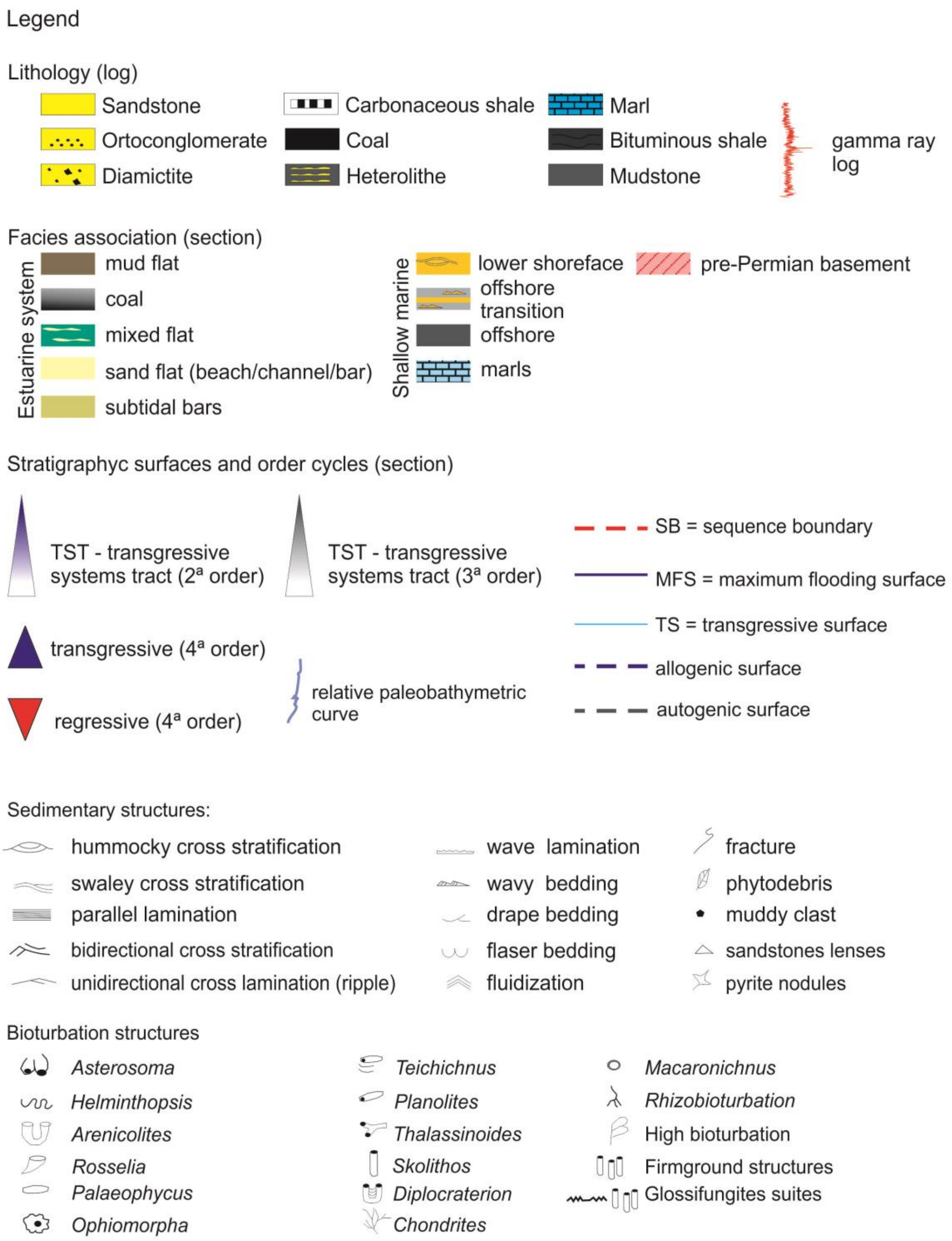
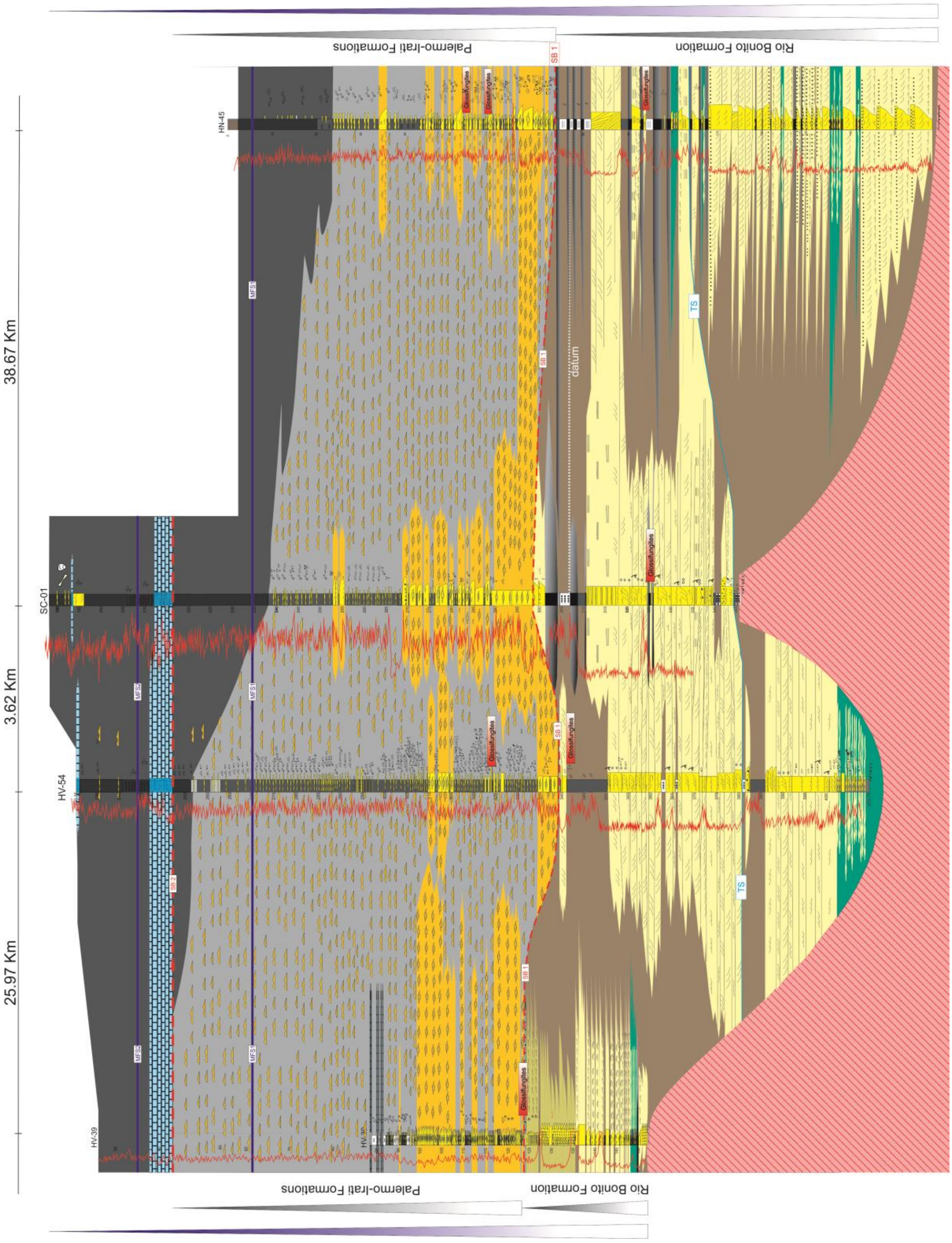

Legend
Lithology (log)
Sandstone
Ortoconglomerate
Diamictite
Carbonaceous shale
Coal
Heterolithe
Marl
Bituminous shale
Mudstone
gamma ray log
Facies association (section)
Estuarine system
mud flat
coal
mixed flat
sand flat (beach/channel/bar)
subtidal bars
Shallow marine
lower shoreface
offshore transition
offshore
marls
pre-Permian basement
Stratigraphyc surfaces and order cycles (section)
TST - transgressive systems tract (2ª order)
TST - transgressive systems tract (3ª order)
transgressive (4ª order)
regressive (4ª order)
relative paleobathymetric curve
SB = sequence boundary
MFS = maximum flooding surface
TS = transgressive surface
allogenic surface
autogenic surface
Sedimentary structures:
hummocky cross stratification
swaley cross stratification
parallel lamination
bidirectional cross stratification
unidirectional cross lamination (ripple)
wave lamination
wavy bedding
drape bedding
flaser bedding
fluidization
fracture
phytodebris
muddy clast
sandstones lenses
pyrite nodules
Bioturbation structures
Asterosoma
Helminthopsis
Arenicolites
Rosselia
Palaeophycus
Ophiomorpha
Teichichnus
Planolites
Thalassinoides
Skolithos
Diplocraterion
Chondrites
Macaronichnus
Rhizobioturbation
High bioturbation
Firmground structures
Glossifungites suites

Fig. 3



HV-39
HV-30
HV-54
SC-01
HN-45
25.97 Km
3.62 Km
38.67 Km
Palermo-Irati Formations
Rio Bonito Formation
MFS1
MFS2
SB 1
SB 2
TS
datum
Glossifungites

Fig. 4

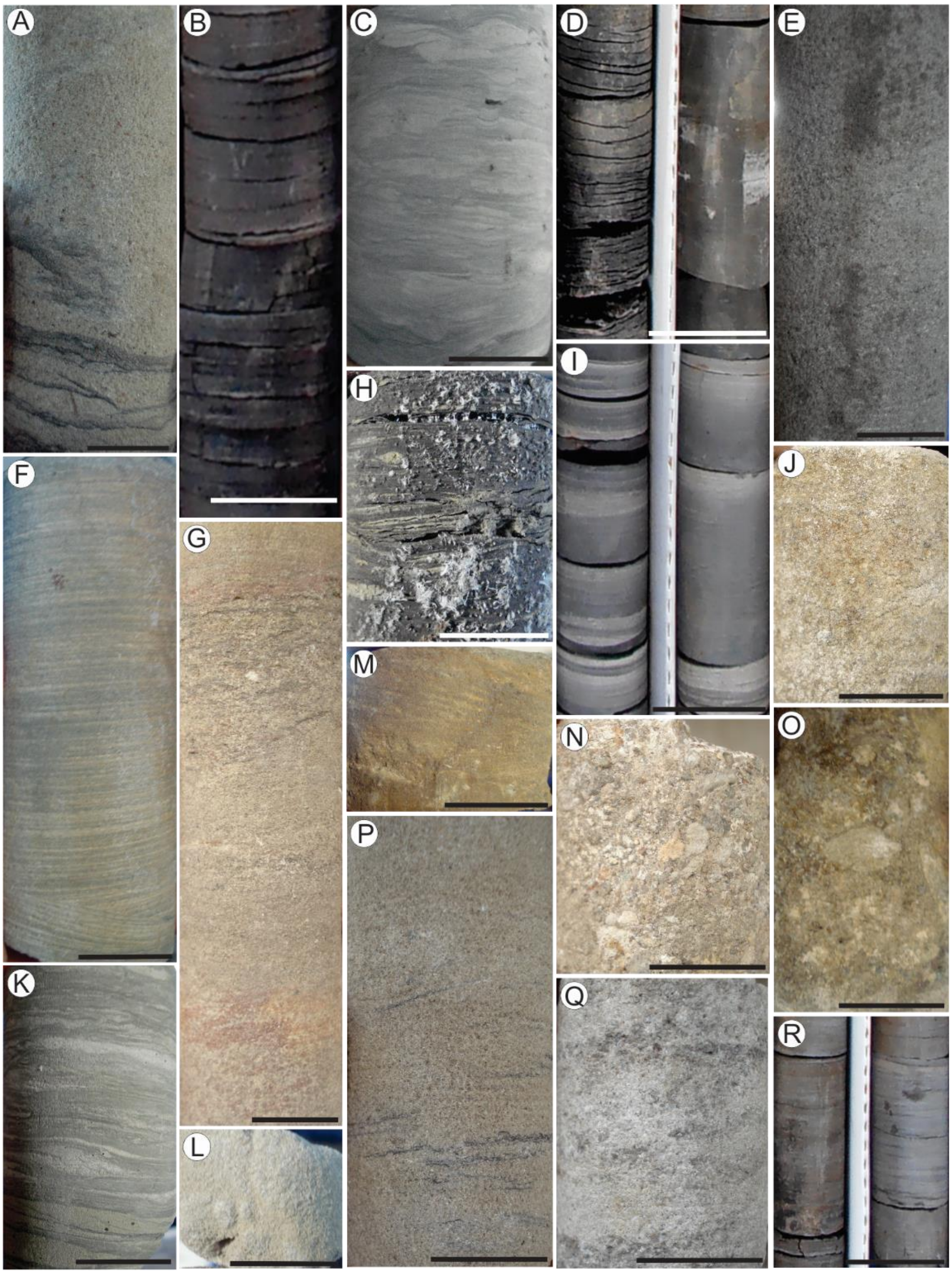


Fig. 5

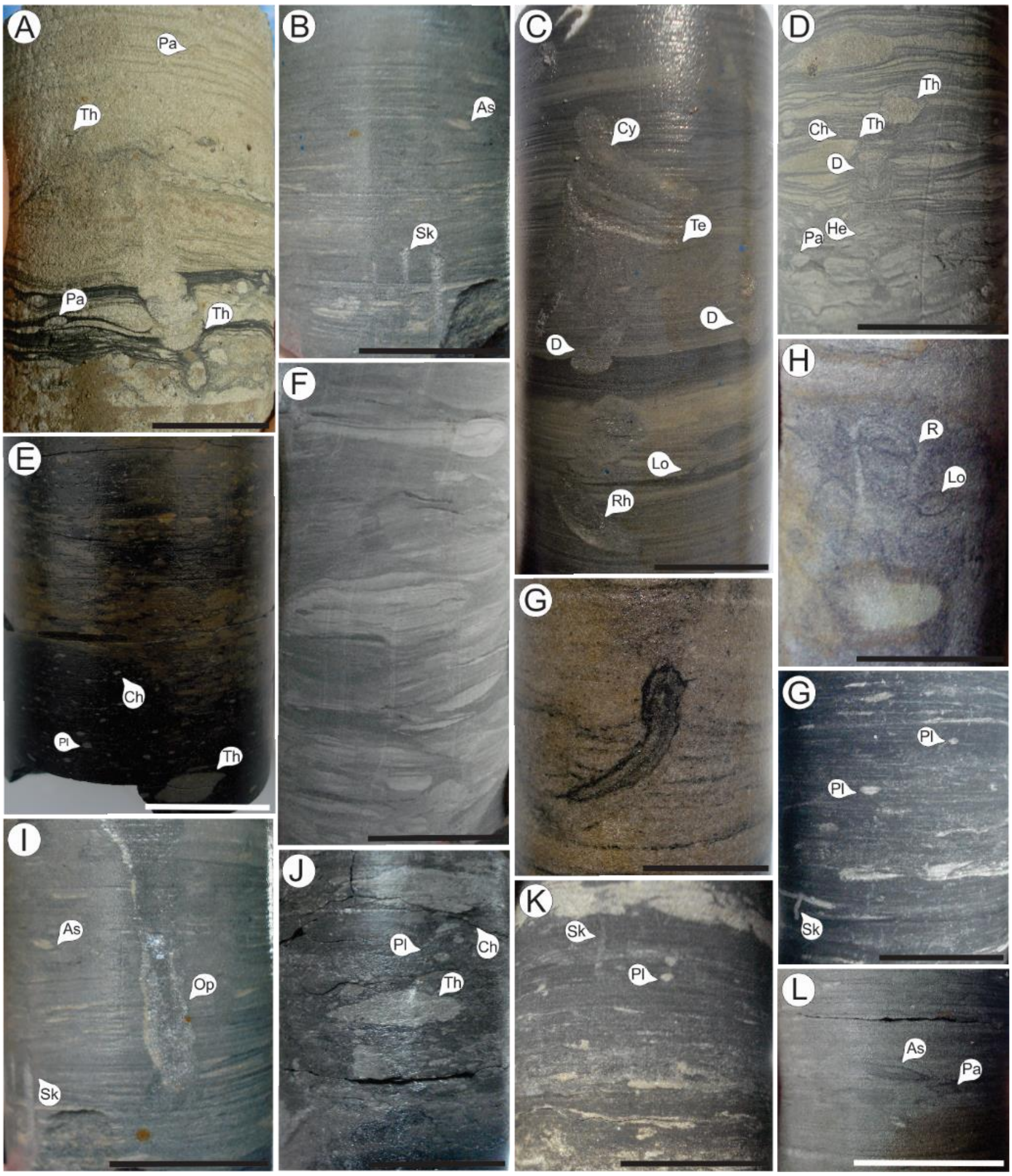

A
Pa
Th
Pa
Th
B
As
Sk
C
Cy
Te
D
D
Lo
Rh
D
Th
Ch
Th
D
He
Pa
E
Ch
Pl
Th
F
G
H
R
Lo
G
Pl
Pl
Sk
I
As
Op
Sk
J
Pl
Ch
Th
K
Sk
Pl
L
As
Pa

Fig. 6

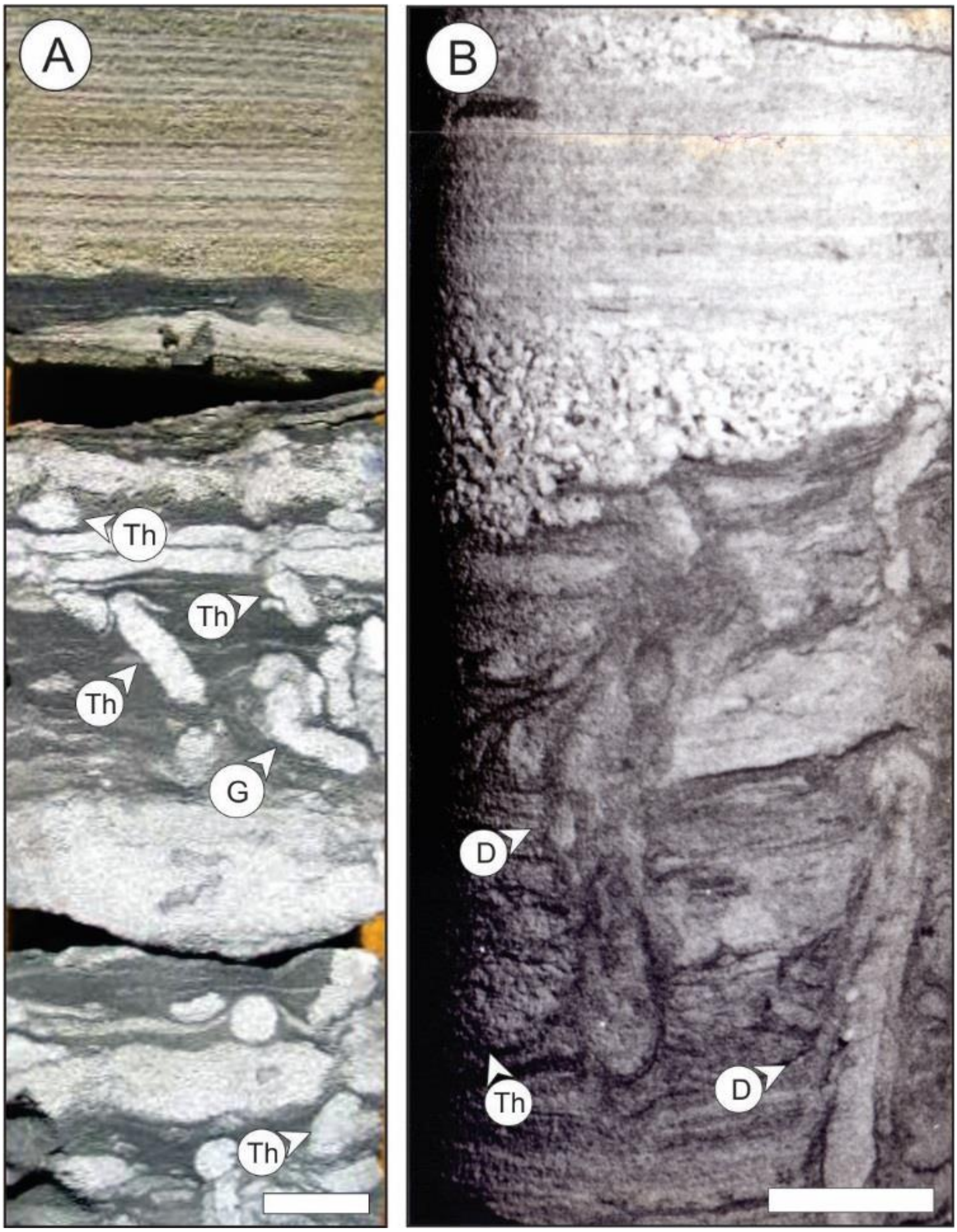


Fig. 7

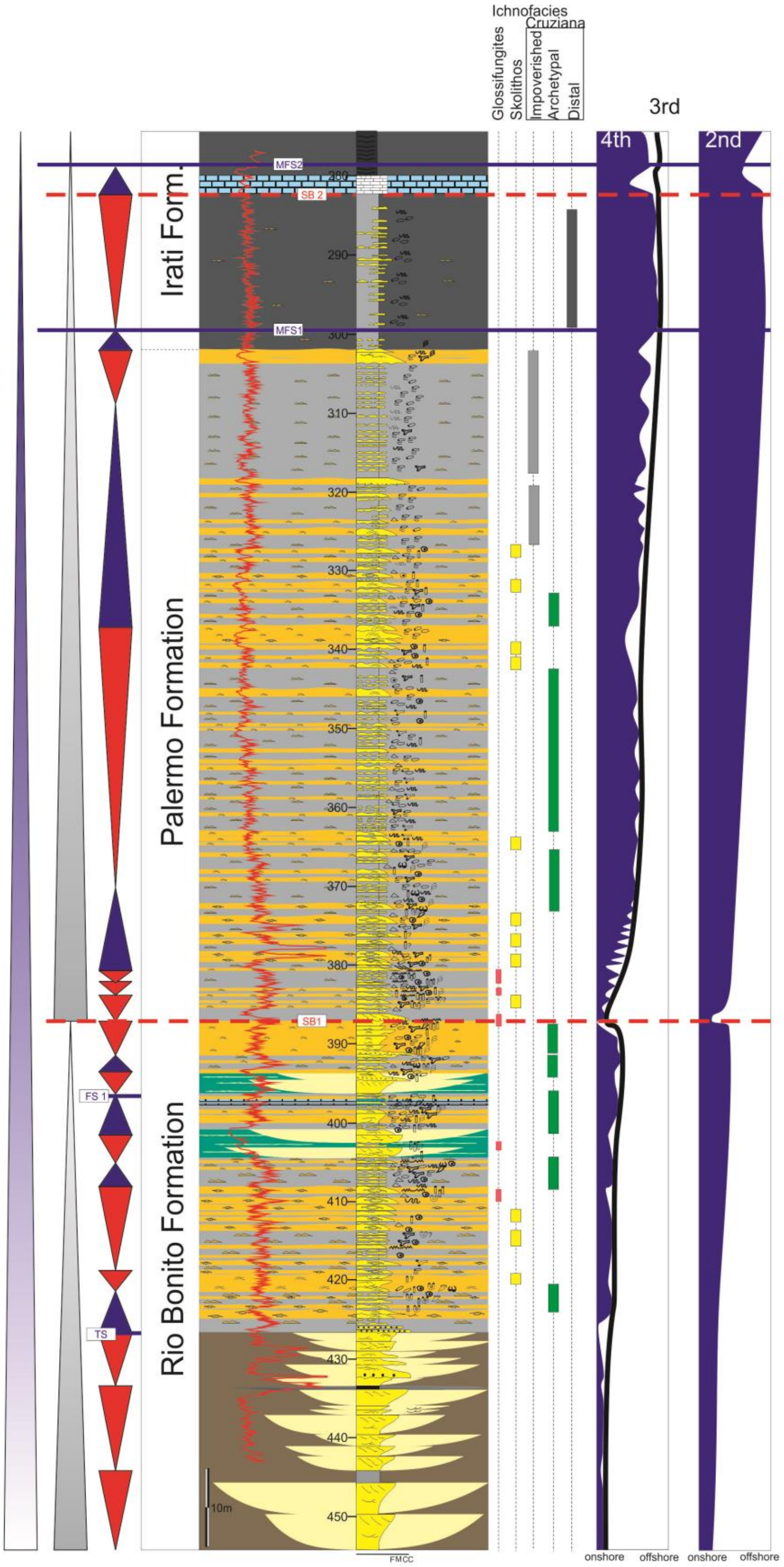
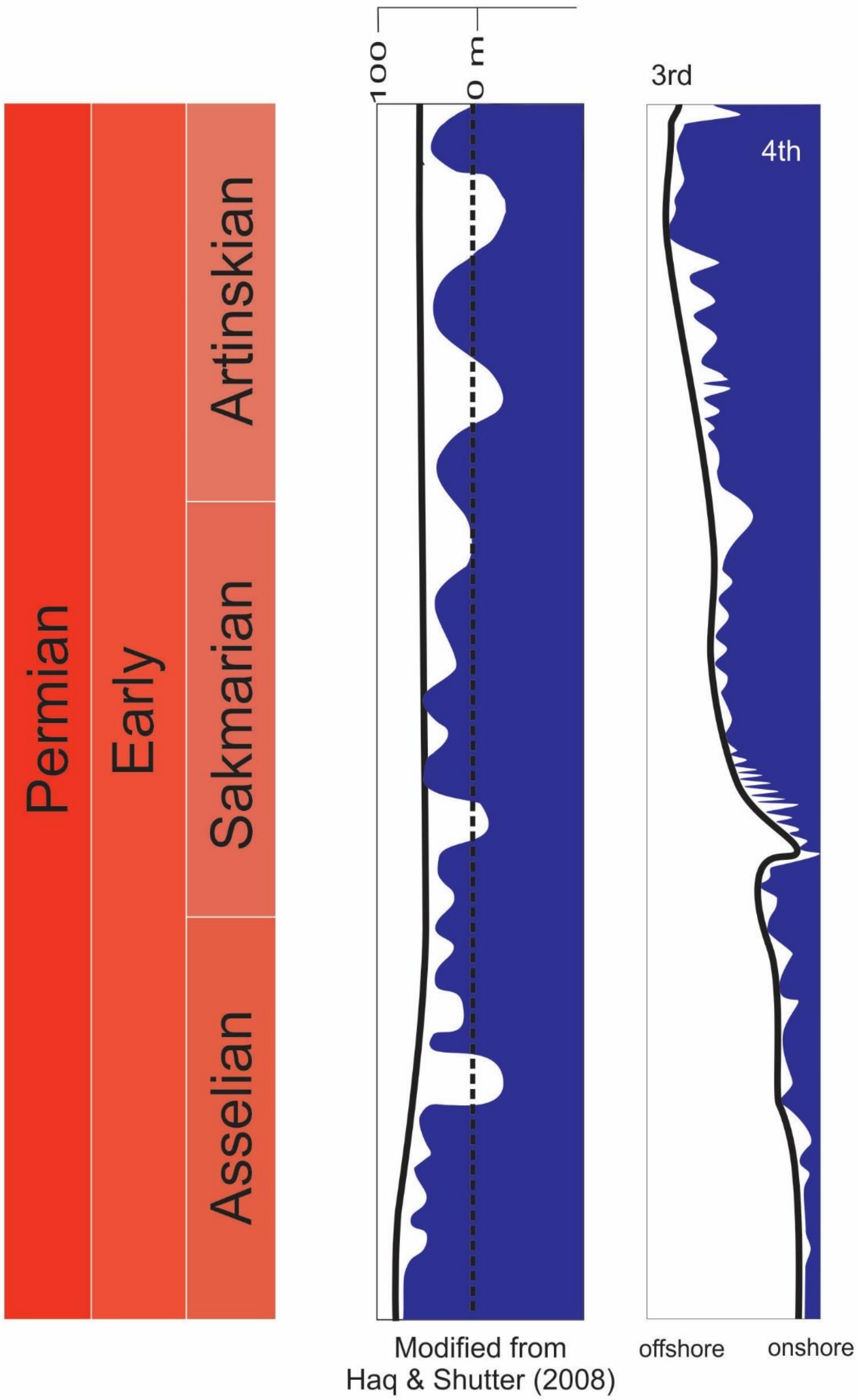

Ichnofacies
Glossifungites
Skolithos
Cruziana
Impoverished
Archetypal
Distal
3rd
4th
2nd
MFS2
SB 2
MFS1
SB1
FS 1
TS
Irati Form.
Palermo Formation
Rio Bonito Formation
280
290
300
310
320
330
340
350
360
370
380
390
400
410
420
430
440
450
10m
FMCC
onshore
offshore
onshore
offshore

Fig. 8



Modified from Haq & Shutter (2008)

Fig. 9

Code	Lithofacies	Texture	Sedimentary structures	Fossil/trace fossil content (ichnofabrics)
M	Marl	Carbonate claystone	Massive	Absent
Cs	Carbonaceous shales	Carbonaceous shales. Thin lenticular fine-grained sandstones and pyrite nodules, and syneresis cracks occur locally.	Massive	Phytodebris *Thalassinoides*
Bs	Bituminous shales	Bituminous shales	Fissility	Absent, locally *Chondrites*
C	Coal	Coal	Massive	Absent
Mm	Massive mudstone	Muddy deposits formed by mixed clay and silt particles.	Massive	*Helmintopsis*, *Planolites*, *Palaeophycus*, *Thalassinoides*, *Teichichnus*
Ls	Laminated siltstone	Siltstone with local occurrences of thin very fine-grained sandstone lenses.	Parallel lamination	Incipient bioturbation; local occurrence of *Planolites*
He	Heterolithic	Heterolithic deposits composed of intercalation of organic-rich siltstone, claystone, and very fine-to fine-grained sandstone.	Sandstone beds form wavy and lenticular bedding with symmetric and asymmetric tops; massive mudstones	Phytodebris, *Palaeophycus-Planolites-Helmintopsis*, *Helmintopsis*, *Planolites-Palaeophycus*, *Teichichnus*, *Teichichnus-Thalassinoides*, *Planolites*, *Diplocraterium-Planolites-Palaeophycus*, undetermined bioturbation
Vfs	Sandstone	Very fine-grained sandstone with abundant quartz.	Very low-angle cross-stratification, parallel lamination	Absent
Vfsd	Sandstone	Very fine-grained sandstone. Drapes of carbonaceous siltstone and carbonate cement occur locally.	Predominantly massive; low-angle cross-stratification occur locally	*Chondrites*, *Helminthopsis*, *Palaeophycus*, small unidentified horizontal traces; rhizobioturbation
Fs	Sandstone	Fine-grained quartz sandstone. Flaser	Low-angle cross-stratification,	rhizobioturbation

		structure, intraclasts of carbonaceous shales, and carbonate cement occur locally.	climbing ripple lamination, parallel lamination, combined-flow ripples; massive when carbonate cement is present	
Sw1	Sandstone	Fine- to medium-grained sandstone with wave cross stratification.	Swaley cross stratification	*Rosselia*
Sw2	Sandstone	Very fine- to medium-grained sandstone.	Bidirectional trough cross stratification.	*Thalassinoides*, *Skolithos*, *Ophiomorpha*, *Palaeophycus*
Hcs	Sandstone	Very fine- to fine-grained sandstone.	Hummocky cross-stratification	*Thalassinoides*, *Skolithos*, *Ophiomorpha*, *Palaeophycus*
Ms	Sandstone	Fine- to medium-grained sandstone forming fining-upward cycles. Drapes of carbonaceous shales, granule and pebble-sized intraclasts, and pyrite nodules also occur. Erosive base.	Low-angle cross-stratification	*Thalassinoides*, Rhizobioturbation
Csd	Sandstone	Coarse- to fine-grained sandstone forming fining upward cycles. Drapes and intraclasts of carbonaceous shales occur locally. Extraformacional granules occur in the coarse-grained sandstone.	Intercalations of low- and high-angle trough cross-stratification. Double mud drapes.	*Palaeophycus*, *Macaronichnus*, *Diplocraterium*, *Macaronichnus-Planolites*, rhizobioturbation
As	Arkose sandstone	Coarse to medium-grained arkose sandstone. Mud drapes and pyrite nodules occur locally. Fluidized structures and load casts are frequent. Scarce drapes and laminae of	High-angle trough cross-stratification	Local occurrences of *Ophiomorpha*

		coal.		
Cgs	Sandstone	Coarse-grained sandstone, poor selected. Quartz, pyritized and oxidized. Intercalated with carbonaceous shale. Carbonaceous shale intraclasts.	Low-angle trough cross-stratification. Double mud drapes occur locally.	Absent in the sandstone
Or	Ortoconglomerate	Ortoconglomerate composed of intraformational and extraformational clasts of pebble-sized granite, quartz, feldspar, and siltstone. Coarse- to medium-grained sandy matrix. Some clasts are angular. Locally carbonatic cement.	Chaotic	Absent
Di	Diamictite	Diamictite with quartz, feldspar, and granite pebbles and granules. Matrix composed of sandstone and mudstone. Drapes of coal occur locally.	Massive	Absent

Ichnofabrics	Components	BS	Lithofacies	Suite	Ichnofacies
Palaeophycus-Planolites-Helmintopsis,	*Helminthopsis, Planolites, Palaeophycus, Thalassinoides,* short spreiten *Teichichnus, Asterososma, Chondrites*	3-4	He	Brakish suite (BW)	Impoverishes Cruziana Ichnofacies
Palaeophycus	*Palaeophycus, Helmintoidichnites*		He	Impoverished	
Macaronichnus	*Macaronichnus, Diplocraterion, Lockeia, Planolites, Skolithos, Thalassinoides*	4	Csd	Polihyaline suite	Impoverishes mixed Cruziana and Skolithos Ichnofacies
Thalassinoides-Teichichnus,	*Thalassinoides, Teichichnus, Planolites, Palaeophycus*	2-3	He		
Palaeophycus	*Palaeophycus*	2	Sw_2		
Rosselia	*Rosselia*	4	Sw_1	High energy suite (HE)	Impoverishes Skolithos Ichnofacies
Thalassinoides-Gyrolithes	*Thalassinoides, Gyrolithes, Skolithos*	2-3	Mm	Glossifungites suite (G)	Glossifungites Ichnofacies
Thalassinoides-Skolithos	*Thalassinoides, Skolithos, Ophiomorpha, Palaeophycus*	2-3, locally 4	Hcs, Sw2	High energy stenohaline suíte (HS)	Skolithos Ichnofacies
Thalassinoides-Astersomas	*Diplocraterium, Planolites, Cylindrichnus, Skolithos, Thalassinoides, Asterosoma, Lockeia, Helminthopsis, Rosselia, Teichichnus, Ophiomorpha, Chondrites, Gordia, Bergaueria, Phycosiphon, Rhizocorallium*	4-5, locally 6	He	Moderate to low energy stenohaline suite (MLS)	Arquetypal Cruziana Ichnofacies
Thalassinoides-Ophiomorpha	*Thalassinoides, Ophiomorpha, Diplocraterion,*	4	He	Moderate energy stenohaline (MS)	Proximal Cruziana Ichnofacies

Diplocraterion-Thalassinoides	*Diplocraterion, Thalassinoides*	3-4	He	Glossifungites suite	Glossifungites Ichnofacies
Teichichnus	*Teichichnus, Planolites, Palaeophycus, Skolithos, Thalassinoides, Diplocrateriom, Helminthopsis, Rhizocorallium*	3-5	He	High frequency moderate energy stenohaline suite (HMS)	Impoverishes Cruziana Ichnofacies
Helmintopsis	*Helmintopsis, Planolites, Palaeophycus, Thalassinoides, Teichichnus*	5-6	He, Mm,	Lower energy stenohaline suite (LS)	Distal Cruziana Ichnofacies
Chondrites	*Chondrites*	4-5	Bs	chemosymbiont suite (CS)	Impoverishes Cruziana Ichnofacies

CONSIDERAÇÕES FINAES

Esta tese demonstrou o potencial da Icnologia para elucidar questões de cunho paleoambientais, paleobiológicos e estratigráficos. Analisou-se densas ocorrências de *Palaeophycus* nos depósitos marinhos transgressivos na Formação Rio Bonito demonstrando uma situação de estresse ambiental produzida por escassez de oxigênio num ambiente restrito de baixa energia. Também a preservação de pequenas escavações (*Helminthoidichnites tenuis*) preservadas nas paredes de *Palaeophycus* demonstrou relações de comensalismo ou mutualismo entre poliquetas e nematoides da meiofauna desde o Permiano inferior.

A presença de suítes de Glossifungites na sucessão Rio Bonito-Palermo foi importante para reconhecer superfícies estratigráficas importantes e diferenciar entre superfícies autogênicas e alogênicas. O predomínio de escavações maiores foi associado a superfícies alogênicas em comparação com as superfícies autogênicas. As características dos icnofósseis representantes da Icnofacies Glossigungites sugerem crustáceos e vermes como principais colonizadores dos substratos “*firmground*” no Permiano inferior da Bacia do Paraná.

A variação na distribuição vertical das associações icnológicas e associações de litofácies da base para o topo atestam o caráter transgressivo da sucessão. A distribuição das suítes icnológicas também permitiu traçar curvas paleobatimétricas relativas para o Permiano inferior da Bacia do Paraná. Destas curvas evidenciou-se um contexto transgressivo, quando a curva do nível do mar global demonstra um nível de mar estável para este período, evidenciando provavelmente efeitos da subsidência na Bacia do Paraná além do caráter intracratônico e restrito da bacia durante o Permiano inferior. Deste modo, confirma-se a hipótese elencada nesta tese demonstrando-se a utilidade da Icnologia para análises paleobatimétricas.

REFERÊNCIAS

Boeira J.B. & Netto R.G. 1987. Novas considerações sobre os icnofósseis da Formação Rio Bonito, Cachoeira do Sul, RS. Acta Geologica Leopoldensia, 11:105-140.

Bromley R.G. (ed.) 1996. Trace Fossils. Biology, Taphonomy and Applications, 2nd ed. Chapman and Hall, London, 361pp.

Bromley R.G. & Asgaard U. 1993. Two bioerosion ichnofacies produced by early and later burial associated with sea-level change. Geologische Rundschau, 82: 872-874.

Bromley, R.G., Ekdale A.A., 1984. Chondrites: a trace fossil indicator of anoxia in sediments. Science, 224: 872–874.

Buatois L. A. & Mángano M.G. (eds.) 2011. Ichnology: Organism-Substrate interactions in Space and Time, Cambridge University Press, 370pp.

Buatois L. A., Mángano M. G., Aceñolaza F (eds.) 2002. Trazas fósiles. Arsa Gráfica, 382 pp.

Buatois L.A.; Netto R.G., Mángano M.G. 2007. Ichnology of Permian marginal- to shallow marine coal-bearing successions: Rio Bonito and Palermo Formations, Paraná Basin, Brazil. In: MacEachern J.A., Bann K.L., M.K. Gingras M.K., Pemberton S.G (eds.) Applied ichnology. SEPM Short Course Notes 52, p. 167-178.

Ekdale, A.A., 1988. Pitfalls of paleobathymetric interpretations based on trace fossil assemblages. Palaios, 3: 464–472.

Ekdale A.A., Bromley R.G., Pemberton S.G. 1984. Ichnology: Trace Fossils in Sedimentology and Stratigraphy. Society of Economic Paleontologists and Mineralogists. Short Course.

Fernandes A. C. S., Carvalho I.S., Agostinho S. 2007. Icnofosseis: conceitos gerais. In: Carvalho I.S. & Fernández A. S (eds). Icnología, Sociedade Brasileira de Geologia. IBEP Gráfica. São Paulo, p. 8-23.

Fielding C.R., Bann, K.L., Maceachern J.A., Tye S.C., Jones B.G. Cyclicity in the nearshore marine to coastal, Lower Permian, Pebbley Beach Formation, southern Sydney Basin, Australia: a record of sea-level fluctuations at the close of the Late Palaeozoic Gondwanan ice age. *Sedimentology*, 53: 435–463.

Gandini R., Netto R.G., Kern H.P., Lavina E.L.C. 2010. Assinaturas icnológicas da sucessão sedimentar Rio Bonito no bloco central da jazida carbonífera de Iruí, Cachoeira do Sul (RS). Gaea– *Journal of Geosciences*, 6:21-43.

Lima J.H.D. 2010. Icnologia de depósitos marinhos regressivos: o exemplo da Formação Teresina (Permiano, bacia do Paraná) no Rio Grande do Sul. Dissertação de Mestrado, Universidade Vale do Rio dos Sinos, São Leopoldo, 102 p.

Martin K.D. 2004. A re-evaluation of the relationship between trace fossils and dysoxia. In: McIlroy D. (ed.) The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis. Geological Society, London, Special Publications.

Martínez N. & Santoja J. (eds.) 1994. Paleontología. Colección Ciencias de la tierra. Síntesis, SA, España, 334 p.

Meléndez B. 1989. Paleofisiología y Paleoicnología. In: E. Aguirre (ed.) Paleontología, colección. Nuevas tendencias. Consejo Superior de Investigaciones Científicas (CSIC), Madrid, p. 179-203.

Netto R.G. 1987. Sobre a ocorrência de Neonereites Seilacher 1960 no Permiano do Rio Grande do Sul. In: Congresso Brasileiro de Paleontologia, 10, Anais, 1: 285-290.

Netto R.G. 1992. Paleoecology of ichnocoenoses in the Cruziana Ichnofacies, Serrinha Member, Rio do Rasto Formation, (Upper Permian) from the Parana Basin, Rio Grande do Sul, Brazil. *Acta Geologica Leopoldensia*, 36:67-82.

Netto R.G. 1994. *A paleoicnologia como ferramenta de trabalho na seqüência sedimentar Rio Bonito/Palermo*. Tese de Doutorado, Universidade Federal do rio Grande do Sul, Porto Alegre, 242 p.

Netto R.G. 1998. Padrão de icnofábricas da sequência sedimentar Rio Bonito/Palermo no RS e seu valor na diagnose paleoambiental. *Acta Geologica Leopoldensia*, 21:209-226.

Netto, R.G. & Gonzaga, T.D. 1985. Paleoicnologia do Grupo Guatá (Supergrupo Tubarão) nos sedimentitos da Mina do Iruí, Cachoeira do Sul, RS. *Acta Geologica Leopoldensia*, 9:77-104.

Nogueira M.S. & Netto R.G. 2001a. A presença de Cruziana nos sedimentos da Formação Rio do Sul (Grupo Itararé, Permo carbonífero da bacia do Paraná) na pedreira Itaú-Itaúna, Santa Catarina, Brasil. *Acta Geologica Leopoldensia*, 52/53: 387-396.

Nogueira M.S. & Netto R.G. 2001b. Icnofauna da Formação Rio do Sul (Grupo Itararé, Permiano da bacia do Paraná) na pedreira Itaú-Itaúna, Santa Catarina, Brasil. *Acta Geologica Leopoldensia*, 52/53: 397-406.

Paranjape A. R., Kulkarni K. G & Kale A. K. 2014. Sea level changes in the upper Aptian-lower/middle(?) Turonian sequence of Cauvery Basin, India- An ichnological perspective. *Cretaceous Research*, 1-14.

Pemberton S.G. & Wightman D.M. 1992. Ichnological characteristics of brackish water deposits. In: PEMBERTON S.G. Applications of ichnology to petroleum exploration – A core workshop. Society of Economic Paleontologists and Mineralogists, Core workshop 17.

Rodríguez-Tovar F. J., Uchman A., Payros A., Orue-Etxebarria X., Apellaniz E., Molina E. 2010. Sea-level dynamics and palaeoecological factors affecting trace fossil distribution in Eocene turbiditic deposits (Gorrondatxe section, N Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 285: 50–65.

Savrda C. H. 1995. Ichnologic applications in paleoceanographic, paleoclimatic, and seal level studies. *Palaios*, 10: 565-577.

Savrda C.E., Hannelore K., Mccarthy F.M.G., Mchugh C.M.G., Olson H.C., Mountain G. 2001. Ichnofabrics of a Pleistocene slope succession, New Jersey margin: relations to climate and sea-level dynamics. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 171: 41–61.

Tognoli F.M.W. & Netto R.G. 2003. Ichnological signature of Paleozoic estuarine deposits from the Rio Bonito-Palermo succession, eastern Paraná Basin, Brazil. Publicación Especial de la Asociación Paleontológica Argentina, 9:141-155.