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TESE DE DOUTORADO

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ANÁLISE ICNOLÓGICA DO INTERVALO SILURIANO-DEVONIANO DA BACIA DO PARANÁ E SUA APLICABILIDADE EM ESTUDOS DE VARIAÇÕES RELATIVAS DO NÍVEL DO MAR

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RESUMO

Esta tese tem como abordagem principal o uso de dados icnológicos como indicadores de assinaturas estratigráficas, parâmetros paleoambientais e paleobatimetria relativa, e almeja, principalmente, diagnosticar alterações nas suítes icnológicas ao longo do Siluro-Devoniano da Bacia do Paraná. Partindo da hipótese de que a análise icnológica permite inferências de oscilações no nível do mar em maior escala (3ª ou 2ª ordem), prospectou-se a sucessão Siluro-Devoniana (formações Furnas e Ponta Grossa) com enfoque na região dos Campo Gerais do Paraná de modo a investigar sua composição faciológica, icnológica e fossilífera. Esta análise integrada possibilitou o diagnóstico de assinaturas estratigráficas-chave (e.g. Glossifungites em limites de sequência, densa ocorrência de *Zoophycos* em trato de sistemas de nível alto ou baixo espaço de acomodação; *Lingulichnus* em trato de sistemas transgressivo ou ciclos de *finning upward*), bem como permitiu a definição de paleoambientes (principalmente reforçando o contexto marinho da Formação Furnas) e zonas icnoestratigráficas (definindo-se idade Siluriano Inferior para as unidades inferior e média da Formação Furnas). Também pautou o reconhecimento de sequências deposicionais em terceira ordem para a Supersequência Paraná. Estudos pontuais ainda foram desenvolvidos na borda noroeste da bacia (Mato Grosso do Sul) para se comparar com os dados da borda sudeste (Paraná), atestando o caráter mais raso dos depósitos setentrionais. Dados paleocológicos inferidos pela análise icnológica auxiliaram na compreensão de eventos paleobiológicos, principalmente relacionados às mudanças faunísticas durante o Devoniano (Evento Basal Zlíchov e declínio de Fauna Malvinocáfrica). Em síntese, esta tese demonstra o potencial da Icnologia para resolver questões de cunho paleoambiental, paleobiológico, icnoestratigráfico e para auxiliar na definição de arcabouços de sequências.

Palavras-chave: Icnologia, Siluriano, Devoniano, Colonização do Ecoespaço, Paleobatimetria Relativa.

APRESENTAÇÃO

A Icnologia é a ciência onde se estuda as interações dos organismos com o substrato (Ekdale et al. 1984). Estas interações podem ocorrer de diversas formas, mas, no geral, são respostas da fauna às condições do meio em que estão inseridas. Deste modo, uma estrutura biogênica reflete um comportamento que foi condicionado pelas características paleoambientais. Sendo assim, e considerando que os icnofósseis são geralmente autóctones, a composição icnológica e o padrão arquitetural preservado no registro sedimentar permitem inferências do contexto paleodeposicional (Netto 2000).

Dentre os principais parâmetros que podem ser inferidos a partir de uma análise icnológica pode-se citar a salinidade, a oxigenação, a taxa de sedimentação, a energia hidrodinâmica, consistência do substrato, fonte de alimentos e a paleobatimetria relativa (Bromley & Ekdale 1984, Ekdale 1988, Beynon & Pemberton 1992, Pemberton & Wightman 1992, Bromley 1996, Martin 2004, Buatois & Mángano 2011). Um estudo icnológico deve ser realizado em conjunto com a análise faciológica, pois fora de seu contexto sedimentar, a informação provinda das estruturas biogênicas perde valor interpretativo. De mesmo modo, os traços fósseis não são meras estruturas sedimentares, mas representam o comportamento de organismos resultante das interações ecológicas (Seilacher 1953). Nesta perspectiva, a Icnologia é uma ciência de interface entre a Sedimentologia e a Ecologia.

Considerando a aplicabilidade da Icnologia para as Geociências, um dos principais paradigmas é seu uso no diagnóstico de parâmetros paleoecológicos. Disso deriva sua utilidade para construção de curvas de oscilação da paleobatimetria relativa, pois mudanças no nível do mar acarretam em alterações nas condições físico-químicas do meio, e assim, proporcionam alterações no padrão etológico preservado em uma sucessão sedimentar. O diagnóstico de variações na composição das suítes icnológicas pode fornecer relevantes dados para balizar interpretações de flutuações no nível relativo do mar (e.g. Bromley & Asgaard 1993, Savrda 1995, Savrda et al. 2001, Fielding et al. 2006). Portanto, esta tese aborda as estratégias de colonização do ecoespaço na sucessão Siluro-Devoniana da Bacia do Paraná (formações Furnas e Ponta Grossa) representadas pelas suítes icnológicas, e sua aplicabilidade em estudos da curva relativa do nível do mar, bem como para a definição do arcabouço de sequências.

DA DEFINIÇÃO DA HIPÓTESE

O paradigma das Icnofácies resulta em certo zoneamento paleoambiental, indicando as condições dominantes à época da deposição. Uma vez que estas condições, de modo geral, apresentam um gradiente para o ambiente marinho, é possível identificar alterações na paleobatimetria relativa considerando mudanças no empilhamento das suítes icnológicas. A partir deste modelo de análise, inúmeros trabalhos apresentam inferências das condições de salinidade, de oxigenação e alterações paleobatimétricas para determinado depósito sedimentar. Contudo, por apresentarem alta resolução, estas abordagens são restritas a escalas de 4ª a 6ª ordem.

Além disso, a litofácies nem sempre é conclusiva na definição do paleoambiente deposicional, enquanto que dados icnológicos podem aportar dados fundamentais nesta determinação. Nesta perspectiva, a partir da sucessão vertical das suítes icnológicas do Siluro-Devoniano e considerando alterações na colonização do ecoespaço, realizou-se inferências de alterações na paleobatimetria relativa ao longo de intervalos de tempo de maior escala (3ª ordem), confrontando com outras fontes de informação (sedimentológicas e tafonômicas), a fim de propor uma metodologia alternativa, de menor custo, ampla aplicabilidade e alta precisão. Assim, esta tese apresenta como principal hipótese de trabalho que a análise icnológica permite inferências de oscilações no nível do mar em intervalos estratigráficos de 3ª ou 2ª ordem.

CAPÍTULOS E ORGANIZAÇÃO DA TESE

O objetivo geral deste estudo foi interpretar as estratégias de colonização do ecoespaço representadas pelas suítes icnológicas na sucessão Siluro-Devoniana da Bacia do Paraná definindo uma curva de paleobatimetria relativa para o intervalo. Para tanto, fez-se necessário atingir alguns objetivos específicos, cada um correspondendo a um capítulo da tese como listados a seguir.

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CAPÍTULO 1

Icnofácies e barreiras preservacionais: das estruturas biogênicas à zona tafonomicamente ativa

Trata-se de um capítulo de livro (Horodyski, R.S. & Erthal, F. orgs. Tafonomia: Métodos, Processos e Aplicações.Curitiba: CRV, p. 115-141) onde se apresentam as bases conceituais da Icnologia e suas implicações para estudos de cunho tafonômico. Esta abordagem foi adotada em todas as camadas que apresentavam icnofósseis e macrofósseis, buscando integrar Icnologia e Tafonomia aos dados sedimentológicos para atingir maior resolução nas interpretações paleoambientais.

ICNOFÁCIES E BARREIRAS PRESERVACIONAIS: DAS ESTRUTURAS BIOGÊNICAS À ZONA TAFONOMICAMENTE ATIVA

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1 Introdução

A Icnologia (do grego *iknos* = vestígio, sinal + *logos* = estudo) é a ciência que estuda a interação dos organismos com o substrato, dando ênfase ao modo que os animais e as plantas deixam o registro de tal atividade, preservadas na forma de estruturas sedimentares biogênicas (Ekdale et al. 1984). Devido a isso, pode ser considerada uma ciência de interface entre a Ecologia e a Sedimentologia, onde é possível realizar estudos das estruturas produzidas em ambientes modernos (Neoicnologia) e no registro fóssil (Paleoicnologia).

Uma estrutura biogênica é qualquer sinal preservado no substrato que resulte de ações comportamentais ou metabólicas. Assim, as pegadas de um animal, a galeria que ele escava, as marcas que deixa quando arrasta partes de seu corpo pela superfície, as estruturas que constrói (e.g., os ninhos ou teias), as escavações que fazem para penetrar em um substrato rígido, e até mesmo suas fezes ou as marcas no solo feitas pelo jato de sua urina, são estruturas biogênicas.

Deste modo, um aspecto importante das estruturas sedimentares biogênicas, tanto fósseis quanto atuais, é que elas constituem evidências do comportamento e até da fisiologia do organismo produtor (Seilacher, 1964; Bromley, 1996; Buatois et al., 2002; Buatois e Mángano, 2011). Mesmo que nem sempre seja possível identificar o organismo responsável pela construção da estrutura, é possível reconhecer a categoria etológica vinculada à sua formação, o que traz relevantes informações das condições ambientais que condicionaram esta atividade (Seilacher, 1964; Bromley, 1996). Por exemplo, escavações verticais produzidas por organismos suspensívoros são bons indicadores da energia hidrodinâmica no meio, condição necessária para manter o alimento em suspensão.

A principal vantagem de se analisar estruturas biogênicas reside em seu caráter autóctone, pois ao contrário de restos de esqueletos e demais partes orgânicas fossilizadas, as estruturas sempre se preservam no substrato onde foram produzidas, indicando as características do meio que induziram o comportamento do animal (Bromley, 1996; Buatois e Mángano, 2011). Portanto, é possível, a partir de dados icnológicos, fazer inferências sobre parâmetros ambientais vigentes no momento da gênese das estruturas biogênicas, tais como salinidade, oxigenação, energia hidrodinâmica, taxa de sedimentação e consistência do substrato. Essas informações contribuem de maneira significativa para a interpretação dos depósitos sedimentares.

Há outras características intrínsecas às estruturas biogênicas, como: (1) a ampla distribuição temporal no registro geológico, sendo assim pouco úteis em bioestratigrafia (exceto no limite Pré-Cambriano/Cambriano e para o Paleozoico com grupos como

Cruziana e arthrophycydeos); (2) preservam-se comumente em rochas aparentemente afossilíferas; (3) refletem o comportamento dos organismos que interagiram como o substrato, em especial os de corpo mole, cujo registro corpóreo é raro; (4) são úteis na caracterização de fácies sedimentares, por serem condicionados por processos deposicionais e (5) são autóctones. Uma lista detalhada dos princípios icnológicos é apresentada por diversos autores (e.g., Bromley, 1996; Buatois et al., 2002; Miller, 2007; Buatois e Mángano, 2011).

As estruturas biogênicas são taxonomicamente nomeadas pelo sistema de nomenclatura binomial lineano, em uma parassistemática, onde se reconhecem duas categorias, icnogênero e icnoespécie, seguindo as regras do Código Internacional de Nomenclatura Zoológica (em alguns casos se reconhecem icnofamílias). Por exemplo, *Skolithos linearis, Palaeophycus striatus, Teichichnus rectus, Asterosoma* isp. (ao referir-se apenas ao icnogênero utiliza-se isp. e não sp.). O principal objetivo da icnotaxonomia é favorecer a identificação das estruturas biogênicas e unificar as bases para os critérios descritivos entre especialistas de diversas partes do mundo. Na ausência de nomes, seria difícil discutir tais estruturas ou reconhecer as descrições anteriores como se referindo ao mesmo objeto.

As várias classificações de Seilacher (1953) forneceram o paradigma dentro do qual os icnólogos trabalham até a atualidade. Em síntese, Seilacher propôs que qualquer estrutura biogênica pode ser classificada simultaneamente de diversas formas: (1) toponomicamente, de acordo com a sua relação de contraste com os materiais do substrato em que estão inseridas; (2) biologicamente, de acordo com a relação com seu produtor; (3) etologicamente, de acordo com a função biológica representada; e (4) de forma sistemática, de acordo com a morfologia. Ainda que Seilacher (1953) tenha se embasado em trabalhos anteriores de outros autores, essas ideias não eram apresentadas de modo tão claro na literatura. Boas classificações refletem relações reais e, portanto, têm poder preditivo, que geralmente é um bom sinal da aplicabilidade de um ramo científico.

As estruturas biogênicas podem ser divididas em três distintos grupos: estruturas sedimentares biogênicas, estruturas de bioerosão e outras evidências de atividade biológica (Bromley, 1996). As estruturas sedimentares biogênicas, por sua vez, se dividem em estruturas de bioturbação (produzidas dentro ou sobre substratos inconsolidados, que envolvem apenas a ação biomecânica do animal), de bioestratificação (por exemplo, estromatólitos produzidos por cianobactérias e tapetes algálicos feitos por esteiras microbianas) e de biodeposição (por exemplo, os coprólitos, as pelotas e as trilhas fecais). As estruturas de bioerosão são aquelas que perfuram substratos duros, como os líticos e xílicos, ou esqueletos mineralizados, como conchas, carapaças e até mesmo ossos. Na classificação de outras evidências de atividade biológica estão ferramentas, ninhos, teias, cápsulas de ovos e estruturas semelhantes, que resultam de padrões biológicos inerentes a determinadas espécies, sendo bem mais fácil a identificação de seu produtor, embora não sejam icnofósseis em sentido estrito. Contudo, como não são produzidas dentro do substrato, facilmente são destruídas ou transportadas, sendo seu registro menos comum.

Considerando que uma estrutura biogênica preservada no registro sedimentar não é um fóssil, a principal aplicabilidade da Icnologia para as ciências históricas está na possibilidade de realizar inferências paleoambientais, complementando e auxiliando a utilização das tafofácies (veja Cap. 2). Este capítulo, entretanto, almeja discutir de que formas as estruturas biogênicas podem se configurar como barreiras para a preservação dos fósseis, sobretudo em processos de dano tafonômico. Assim, será dado destaque para as bioturbações e bioerosões, já que estruturas de biodeposição, de bioestratificação e outras evidências da atividade biológica não apresentam potencial de destruição para os restos esqueléticos.

2 Bioerosão

Estruturas de bioerosão compreendem estruturas biogênicas produzidas mecânica ou bioquimicamente em substratos rígidos por um organismo. Este substrato pode ser clastos, rochas, ossos, dentes, madeira ou conchas (Frey e Wheatcroft, 1989). Por seu caráter destrutivo, constitui-se em um importante agente tafonômico. Dentre os principais organismos bioerodidores estão algas, moluscos bivalves e gastrópodes, fungos, esponjas (principalmente Cliona), polvos, poliquetas, briozoários, foronídeos, ctenostomados e cirripédios (Young e Nelson 1988, Edinger 2003, Taylor e Wilson 2003). Apesar de seu caráter destrutivo, as bioerosões constituem em muitas ocasiões umas das poucas evidências de interação biológica no registro fóssil, e também preservam a ação de organismos de corpo mole (perfuradores).

A principal contribuição no dano tafonômico causado por bioerosão reside no aumento de área disponível para a dissolução, além de favorecer a degradação da matriz orgânica, principalmente em águas temperadas (Young e Nelson 1985, Smith e Nelson 2003). Em casos extremos, a bioerosão pode consumir completamente o substrato, resultando em maior perda de informação tafonômica. Além disso, as características e estilo de preservação da bioerosão preservada no fóssil podem fornecer informações sobre as taxas de soterramento, ambientes deposicionais, tendências evolutivas do comportamento e paleoprodutividade.

As taxas de bioerosão são controladas pela produtividade biológica primária (planctônica), pela taxa de sedimentação, pela profundidade da coluna d’água (zona fótica) e pela densidade/arquitetura do substrato (Edinger 2003, Lecinsky et al. 2002). Embora não se possa estabelecer uma relação linear, a permanência do substrato na interface sedimento-água interfere na intensidade da bioerosão, esta é mais intensa quanto maior for o tempo de exposição e quando há pouco input de bioclastos carbonáticos e clastos sedimentares (Young e Nelson 1985).

De modo geral, a bioerosão pode constituir um evento de morte prematura para muitos organismos com conchas, como resultado de predação (e.g. poliquetos, moluscos bivalves, gastrópodes, entre outros). Posteriormente, a concha se comportaria como uma partícula inerte, um bioclasto, podendo ser transportada pelos mesmos processos que atuam em um depósito sedimentar, aumentando o potencial de fragmentação deste esqueleto, já que a estrutura original do organismo fica mais enfraquecida devido à intensa bioerosão. Além disso, conchas bioerodidas apresentam redução em sua massa, podendo ser mais facilmente transportadas, o que pode acarretar em depósitos com seleção hidrodinâmica.

Macroperfuradores podem perfurar seus substratos para construírem habitações em seu interior, sendo esta atividade comum quando o esqueleto está disponível (pós-morte do organismo) (Buatois e Mángano, 2011). Entretanto, perfurações de predação (no período de vida do organismo), resultam em uma assinatura icnológica distinta. Em ambos os casos, o principal impacto da bioerosão para os danos tafonômicos no material esquelético estará relacionado ao acréscimo da área disponível, facilitando a dissolução.

A maioria das bioerosões é dependente da produtividade primária marinha, pois muitos dos macroperfuradores são filtradores heterotróficos (suspensívoros). Raspadores externos se alimentam de algas nas camadas superficiais de moluscos, corais e rochas sedimentares, e sua atividade está, portanto, limitada necessariamente à zona fótica (Edinger 2003, Lecinsky et al. 2002). Por estas razões, o crescimento de algas endolíticas microperfuradoras sobre as quais bioerodidores externos raspam também é estimulado por nutrientes (Edinger 2003).

A bioerosão pode ser um fator importante na destruição de conchas no meio marinho moderno (Fig. 1), apesar de ser rara em ambientes dulcícolas. Em alguns ambientes intermarés e sublitorais, organismos microperfuradores podem ser os agentes primários de destruição de conchas. Nesses casos, a importância da bioerosão aumenta com a produtividade (e.g., relacionada com a concentração de clorofila), e diminui com a taxa de sedimentação (Fürsich e Flessa 1987, Cutler e Flessa 1995, Lecinsky et al. 2002, Zuschin et al. 2003). Este processo também pode ser responsável por destruição seletiva de informação de organismos aragoníticos em águas temperadas, o que constitui um enviesamento significativo (Young e Nelson 1985).

Ocorrências de bioerosões são agrupadas em icnofácies substrato-controladas, de acordo com suas características nos fósseis corporais, podendo ocorrer principalmente na Icnofácies Trypanites (bancos de conchas, acumulações de ossos ou dentes, paredões rochosos ou bioconstruções) ou na Icnofácies Teredolites (em substrato xílico prolongadamente expostos) (Buatois et al., 2002; Buatois e Mángano, 2011).

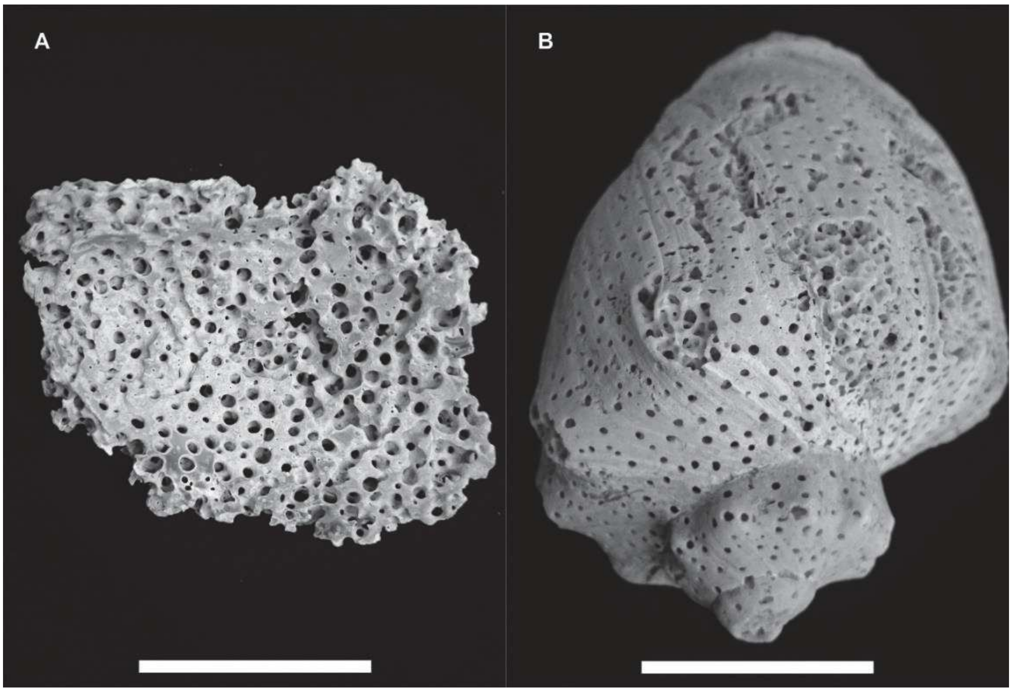

Figura 1. Bioerosões. (a) exemplo de processo de fragmentação acelerado pela intensa bioerosão (e corrosão) em uma concha de molusco coletado no litoral do estado do Rio Grande do Sul (Escala: 2 cm); (b) alto índice de bioerosão em concha de molusco gastrópode do litoral do Rio Grande do Sul. Em ambos os exemplos as bioerosões foram feitas por esponjas endolíticas clionídeas (Escala: 5 cm).

3 Bioturbação

As estruturas de bioturbação resultam da ação mecânica do organismo e são produzidas dentro ou sobre substratos inconsolidados (Buatois e Mángano, 2011). As estruturas de bioturbação mais comuns são escavações, pistas intraestratais rasas, pistas e trilhas epiestratais, marcas de nado e impressões de repouso do animal, que podem ser preservadas em exposições horizontais ou verticais, e visualizadas em três dimensões (3D), ou ainda, em exposições verticais e em testemunhos de sondagem, onde é mais comum a preservação bidimensional (2D).

Escavações são estruturas relativamente permanentes, que são mantidas por seus ocupantes (Bromley, 1996). Pistas são estruturas de deslocamento contínuo, superficial ou subsuperficial, sem a impressão de apêndices. Pegadas são impressões produzidas no sedimento por apêndices locomotores individuais, sejam de vertebrados ou de invertebrados, e trilhas são sucessões de pegadas.

As escavações são as estruturas que mais contribuem para a destruição de bioclastos, embora o pisoteio (*trumpling*) possa ser um importante fator em depósitos continentais. O principal mecanismo de destruição tafonômica desencadeado pelas escavações deve-se à ação de homogeneização do sedimento e destruição das estruturas sedimentares primárias a partir da ação da infauna. Esta ação resulta no aumento do grau de exposição dos bioclastos na interface sedimento-água (SWI, do inglês *sediment water-interface*) e afeta os processos diagenéticos que ocorrem logo abaixo dessa zona, com implicações geoquímicas importantes, incluindo o aprofundamento da zona oxidante, além da ampliação da permeabilidade e porosidade do sedimento. Isso resulta da geração de um mosaico tridimensional de interfaces óxicas/anóxicas no sedimento (Aller 1982, Kristensen 2000, Smith e Nelson 2003). A distribuição vertical e a concentração da água de poro (PW, do inglês *porewater*) são influenciadas pela presença, tipo, espaçamento e tamanho das escavações, já que os organismos bioturbadores afetam o transporte de solutos, taxas de reação e a distribuição de microorganismos no sedimento superficial, ou seja, ampliam a profundidade da TAZ (Aller 1980, Aller e Yingst 1985, Aller 1994).

Um importante processo causador de fragmentação no material esquelético é a bioturbação, pois pode exumar o material previamente soterrado, o qual estará exposto à ações físicas (transporte, intemperismo). Além disso, bivalves da infauna profunda podem ter suas conchas desarticuladas e/ou fragmentadas durante a exumação/inumação (processo de escavamento/soterramento), devido à carga de sedimento. A mobilização também pode gerar perda de informações referentes à posição de vida, ou mesmo produzir misturas espaciais, agrupando organismos ambientalmente distintos. Estes fatores podem gerar dificuldades em reconstruções paleocológicas e em análises estratigráficas de alta resolução. Sedimentos mais grossos podem ainda favorecer a fragmentação de conchas de bivalves infaunais (Parsons e Brett 1991, Zuschin et al. 2003).

Em condições estáveis, a ocupação do substrato pela fauna bioturbadora obedece a certo escalonamento (*tiering*), composto por níveis de ocupação. A análise da sucessão de *tierings* presentes permite a compreensão da evolução dos processos que levaram à distribuição da fauna bentônica (Ekdale e Bromley, 1991). Os níveis mais superficiais são os primeiros a serem colonizados, principalmente por escavadores suspensívoros epiestratais ou endoestratais. Em seguida, níveis inferiores passam a ser explorados, até chegar ao nível dos decompositores (Fig. 2). Assim, a preservação da bioturbação é muito mais significativa em locais onde a sedimentação é baixa e há certa estabilidade nas condições ambientais, o que proporciona exploração de todos os *tiers* (níveis do substrato), já que a alta taxa de sedimentação pode obliterar o efeito da bioturbação.

Estes níveis ou *tiers* podem ser visualizados em duas dimensões, principalmente em análises de testemunho de sondagem. Esta feição é chamada de icnofábrica (ou icnotrama, em tradução literal do inglês, *ichnofabric*) O conceito de icnofábrica é recente na literatura icnológica, tendo surgido principalmente com o reconhecimento da importância da Icnologia na indústria do petróleo, quando os traços fósseis foram analisados em testemunhos de sondagem, gerando as primeiras classificações qualitativas e quantitativas da ocupação do substrato (Ekdale et al., 1984).

Mas muito antes do conceito de icnofábrica surgir, Schäefer (1956), em observações no Mar do Norte, notou que os organismos bentônicos modificam o substrato de várias maneiras distintas, podendo resultar na homogeneização total das estruturas primárias do sedimento e obliteração de traços fósseis anteriores. Reineck (1958) aplicou estas informações para quantificar o retrabalhamento em depósitos de maré. Posteriormente Reineck (1963), a partir de amostras de *box-core* do Mar do Norte, registrou o retrabalhamento das estruturas sedimentares primárias como resultado da ação biogênica. Neste trabalho ele também desenvolveu um esquema semiquantitativo para estimar a quantidade relativa de bioturbação em tais amostras, método que foi posteriormente incorporado e amplamente utilizado nas análises de icnofábricas, por considerar as estruturas sedimentares primárias, que são melhor observadas em fábrica (corte vertical). Reineck (1967) categorizou os sedimentos bioturbados com base no quanto a bioturbação obliterou as estruturas sedimentares primárias. Esta classificação da bioturbação foi a base dos diferentes índices de bioturbação propostos até hoje (e.g. Droser e Bottjer 1986, 1991; Taylor e Goldring, 1993; Miller e Smail, 1997).

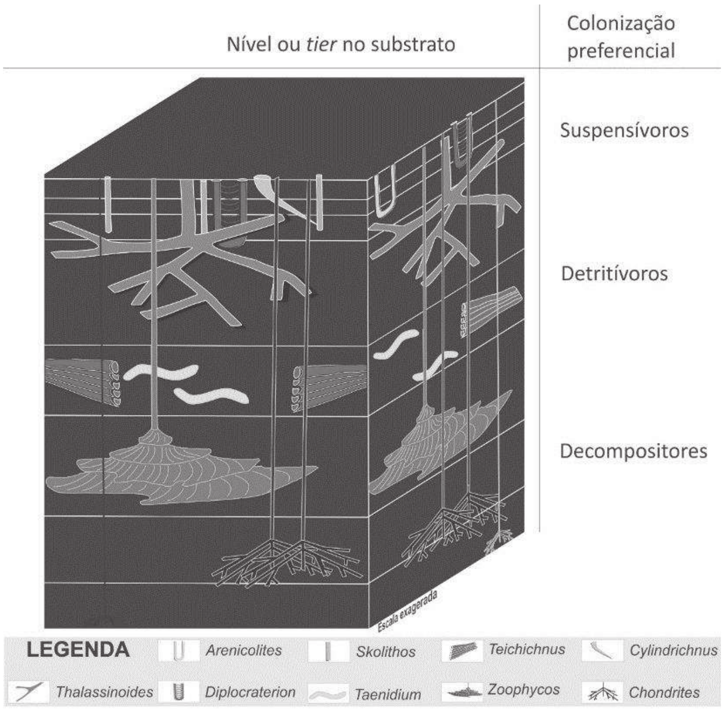

Figura 2. Esquema representativo da ocupação do substrato dependendo da categoria trófica envolvida. Escala exagerada. Inspirado em Bromley (1996).

Droser e Bottjer (1986, 1991), ao introduzir o conceito de índice de icnofábrica, que varia de ii=1 (sem bioturbação) até ii=5 (completamente bioturbado), criaram uma escala visual para várias fácies (como carbonatos marinhos rasos, arenitos ricos em *Skolithos* ou em *Ophiomorpha*, entre outros). Este método não é muito utilizado na literatura icnológica principalmente por ter menos detalhe de resolução que o de Reineck (1963, 1967) (que varia de 0 [sem bioturbação] até 6 [completamente bioturbado]), e por quê "0" é mais representativo de ausência de bioturbação do que "1".

Taylor e Goldring (1993) propuseram uma atualização do índice de Reineck (variando de 0 a 6). Porém, esta atualização foi embasada em testemunhos e junto com ela foi proposta uma metodologia de análise para as icnofábricas, em que o testemunho deve ser analisado da base para o topo, e sua descrição e representação gráfica deve ser do topo para a base, a fim de facilitar a ilustração de amplas seções verticais. Além disso, os autores propõem métodos quantitativos para mensurar a bioturbação, com cálculos da área total bioturbada, viável em análises estatísticas, principalmente em testemunhos, mas que é dificultada em análises de afloramento. Este método preconiza diferenças nos diâmetros da bioturbação e na área analisada, e suas categorias devem ser uniformizadas para correta interpretação estatística. Portanto, embora seja bastante utilizado na literatura icnológica, nem sempre são seguidas todas as preposições propostas pelos autores, principalmente no que concerne aos métodos estatísticos. Em uma análise mais profunda, a proposição de Taylor e Goldring (1993) não difere e não invalida o índice proposto por Reineck, sendo apenas uma atualização deste para contexto de testemunhos.

Miller e Snail (1997) propõem um método de quantificação de bioturbação para amostragens horizontais (visualização em planta). Denominado como "bedding plane bioturbation index" (BPBI) este índice varia de BPBI=0 (sem bioturbação horizontal) até 5 (camada totalmente recoberta por bioturbação). Este método é muito útil em afloramento, principalmente quando se tem predomínio de estruturas espiestratais, que são virtualmente invisíveis em fábrica. Porém, é pouco relevante para análises sedimentológicas, uma vez que a visualização de estruturas sedimentares primárias é dificultada. Este método tem sido pouco utilizado na literatura. Existem ainda os índices de Lockley (1991) para pisoteio sobre o solo ou em substratos sedimentares por dinossauros (dinoturbação) e o índice de Montague et al. (2010) para estimar a extensão de microbioerosões, que não se aplicam à nossa pesquisa.

Com base no exposto, o índice utilizado deve condizer com as necessidades de cada estudo, pois depende principalmente do objetivo e do tipo de amostragem disponível. A seguir, a figura 3 apresenta uma escala visual da quantificação da bioturbação a partir da proposta de Reineck (1967).

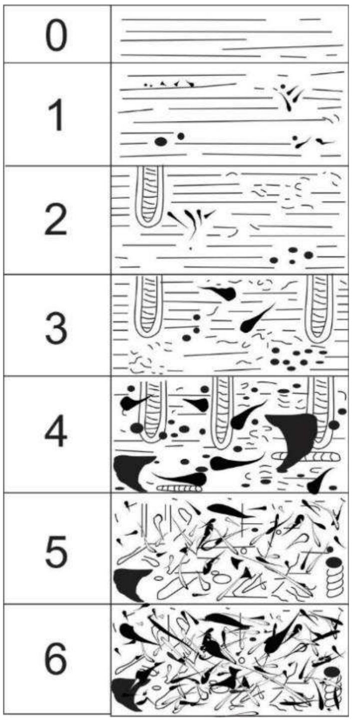

Figura 3. Diagrama representativo do índice de bioturbação (adaptado de Reineck, 1967).

4 Estruturas biogênicas e o processo de perda de informação tafonômica

A seguir serão discutidas as características das estruturas biogênicas, considerando sua contribuição para o processo de perda de informação tafonômica nos ambientes **marinhos** (transicional, raso e profundo) e **continentais**, considerando as respectivas icnofácies.

Uma associação de traços fósseis que sempre corresponde aos mesmos parâmetros ambientais/deposicionais, e que aparece de forma recorrente no registro sedimentar (repetindo-se no tempo geológico) e, ainda, possui caráter global, é caracterizada como icnofácies (Seilacher, 1964; Frey e Pemberton, 1984; Buatois e Mángano, 2011). Deste modo, cada icnofácies possui uma assinatura distinta que pode ser chave para a compreensão dos processos que atuaram em determinado depósito sedimentar.

4.1 Ambientes marinhos

O maior volume de rochas sedimentares provém de ambientes marinhos. Assim, muitos dos modelos para a compreensão da evolução da vida e do planeta são embasados em sucessões marinhas. O registro paleontológico e estratigráfico também é altamente influenciado por interpretações provindas deste tipo de depósito. A partir disso, a seguir se apresentam de modo generalizado as principais características das estruturas biogênicas para os ambientes marinhos, considerando o processo de perda de informação paleontológica e tafonômica. São apresentadas três zonas deposicionais principais para o ambiente marinho, do proximal para o distal: transicional, marinho raso e marinho profundo.

4.1.1 Ambientes transicionais

Os ambientes transicionais, como o nome sugere, englobam a transição de ambientes continentais para marinhos. Deste modo, representa uma mistura de condições marinhas, marginais marinhas e não marinhas, com ambientes subaéreos e subaquáticos. Entre estes ambientes estão presentes as praias, dunas costeiras, leques de *washover*, mangues, pântanos, planícies de maré, entre outros. Devido a essa variedade de ambientes, diversas formas de estruturas biogênicas podem estar preservadas, como por exemplo, estruturas de escavação de caranguejos em forma de J, Y ou U, marcas de raiz, escavações verticais de insetos ou aranhas e pegadas de vertebrados, as quais compõem o conjunto da Icnofácies *Psilonichnus* (Pemberton et al. 2012).

A Icnofácies *Psilonichnus* (Frey e Pemberton, 1987, Netto e Grangeiro, 2009) normalmente apresenta baixas icnodiversidade e abundância. Esta icnofácies pode indicar variações na salinidade e energia hidrodinâmica e evidenciar temporárias exposições subaéreas, dependendo do regime de marés e configuração da costa. Considerando a preservação de fósseis, nesta icnofácies predominam os processos energéticos destrutivos que favorecem a abrasão, fragmentação, corrasão e desarticulação. Devido a essas condições, grande parte das estruturas biogênicas produzidas nesses ambientes possui baixíssimo potencial de preservação, pois podem ser facilmente erodidas (Netto e Grangeiro, 2009). A colonização nesta icnofácies é basicamente composta por organismos oportunistas.

Ainda no ambiente transicional, mas em contexto subaquático da zona intermaré (zonda de *swash*), a diversidade e abundância de bioturbação são baixas, devido às condições altamente energéticas, caracterizando a Icnofácies *Skolithos*. Nesta icnofácies predominam estruturas verticais produzidas por animais suspensívoros, tais como *Arenicolites, Ophiomorpha, Thalassinoides, Skolithos* e *Diplocraterion*, podendo ocorrer também *Macaronichnus* (Buatois e Mángano 2011). Além do ambiente transicional, esta icnofácies pode ocorrer também em zonas de alta energia no shoreface, ou mesmo em camadas de turbidítos e em lobos deltaicos proximais (mais do que a batimetria, as icnofácies são controladas pelos parâmetros ecológicos e ambientais). Nesta icnofácies, o processo de dano tafonômico é desencadeado principalmente pela alta energia do meio.

Deve se considerar também o tempo de residência da infauna bioturbadora no substrato (=Zona Tafonomicamente Ativa, TAZ), seja ela rasa ou profunda. Quanto maior o tempo de residência em um ambiente estável, maior será a taxa de colonização do substrato. Isso acarretará em um maior retrabalhamento dos sedimentos, cujos restos esqueléticos estarão incorporados. Estudos atualísticos demonstram que quanto maior a taxa de bioturbação e consequente oxigenação nas águas intersticiais, maior será a possibilidade de dissolução dos bioclastos mesmo em camadas mais superficiais do substrato. Esta importante observação é válida também para todos os ambientes descritos abaixo.

4.1.2 Ambientes marinhos rasos

Os ambientes marinhos rasos englobam principalmente o *shoreface* (acima do nível de ação de ondas de tempo bom); o *offshore* transicional (entre o nível de ação das ondas de tempo bom e das ondas de tempestade); e o *offshore* (abaixo do nível de ação das ondas de tempestade). Na região do *shoreface* predominam processos de maior energia, tais como ondas e correntes de retorno que geram dunas subaquosas multidirecionais. Geralmente, é representado por camadas compostas de arenito bem selecionado, podendo ocorrer finas camadas pelíticas ou camadas conchíferas.

Predominam estratificações de baixo ângulo, laminações cruzadas por ondas e *wave ripples* (Arnott, 1993). Na porção mais proximal, icnofósseis são localmente comuns, mas raramente abundantes, e pouco diversos. A contínua movimentação das formas de leito representa um grande problema para os organismos endobentônicos. Por conseguinte, pouquíssimos animais são capazes de construir domicílios permanentes sob tais condições (Buatois e Mángano, 2011). Além disso, as estruturas formadas têm potencial de preservação muito baixo devido ao constante movimento hidrodinâmico, que resulta em erosão superficial, preservando apenas estruturas mais profundas (Bromley, 1996). Neste contexto, os principais elementos icnológicos correspondem à Icnofácies *Skolithos*, sendo comum *Skolithos, Conichnus, Diplocraterion, Ophiomorpha, Arenicolites, Bergaueria, Schaubcylindrichnus* e *Palaeophycus* (Pemberton et al. 2012).

À medida que se aproxima do *offshore* transicional a energia hidrodinâmica diminui e as ondas de tempestade passam a ser importante processo físico de controle deposicional (Reading, 1996). Nesta zona predominam depósitos de sedimentos que apresentam estratificação cruzada *hummocky,* estratificação *swaley,* estratificação cruzada de baixo ângulo, laminações cruzadas por ondas e *wave ripples*. A quantidade de bioturbação nestas camadas depende da intensidade de influência dos eventos de alta energia. Eventos de alta intensidade e frequência dificultam a preservação de bioturbação enquanto eventos de baixa intensidade e pouco frequentes permitem que a bioturbação torne os substratos homogêneos (Frey, 1990). Neste caso, a bioturbação pode ser um importante agente causador de dano aos bioclastos disponíveis na Zona Tafonomicamente Ativa (TAZ). Os traços fósseis preservados na zona de transição ao *offsore* tendem a representar um misto das icnofácies *Skolithos* e *Cruziana*, sendo comum a ocorrência de icnogêneros que refletem hábitos suspensívoros, detritívoros e depositívoros, tais como *Asterosoma, Chondrites, Cylindrichnus, Rosselia, Phoebichnus, Planolites, Rhizocorallium, Schaubcylindrichnus, Siphonichnus, Teichichnus* e *Thalassinoides* (Pemberton et al., 2012).

Na Icnofácies *Cruziana* dominam escavações horizontais, com as verticais subordinadas, representativas de várias categorias etológicas, e com predomínio de formas produzidas por depositívoros e detritívoros, alta icnodiversidade e alta abundância de escavações (Buatois et al., 2002). De modo geral, esta icnofácies representa a atividade bioturbadora de comunidades endobentônicas clímax, que possui alto potencial de retrabalhar o substrato, aumentando a oxigenação na TAZ e favorecendo a dissolução de conchas previamente soterradas. Esta icnofácies virtualmente é a que mais pode auxiliar nos processos destrutivos com ação direta da fauna bioturbadora. Eventos de alta energia possuem controle considerável nas características do *shoreface* inferior ao *offshore* transicional (Reading, 1996). Tempestades tendem a exumar, destruir, e/ou soterrar a comunidade bentônica residente (de tempo bom). Na recuperação pós-tempestade a colonização inicial geralmente registra estruturas de moradia de organismos suspensívoros oportunistas, nos níveis mais superiores do substrato, que tipicamente não estão presentes na comunidade residente. Se as condições de tempo bom se mantêm, a suíte original retorna (Pemberton *et al.* 2012).

A distribuição das estruturas biogênicas no *offshore* é amplamente influenciada pela disponibilidade de alimento, oxigenação e pela consistência do substrato (Buatois e Mángano, 2011). Neste contexto, as partículas alimentares estão fundamentalmente depositadas no interior das camadas e os substratos são geralmente coesos, levando ao acréscimo de competição interespecífica e um correspondente acréscimo de especialização nas estratégias alimentares. Isto resulta em comunidades bentônicas altamente diversas e dominadas por organismos de hábito depositívoro e pastador, que irão produzir estruturas frequentemente registradas nas icnofácies *Cruziana* e *Zoophycos* (Pemberton *et al.* 2012).

O *offshore* é dominado por deposição de tempo bom, embora em regimes fortemente dominados por tempestades, areias finas possam ser carreadas para zonas mais distais, preservando delgadas camadas arenosas intercaladas aos sedimentos lamosos que caracterizam o *offshore* (Reading, 1996). Depósitos de tempo bom são caracterizados por grau de bioturbação entre 5 e 6 (ou Índice de Bioturbação, que varia de 0 - sem bioturbação, até 6 – totalmente bioturbado e sem estrutura sedimentar visível), com icnodiversidade alta e icnogêneros característicos de comportamento equilíbrio. Neste contexto, há grande potencial de que a bioturbação homogeneíze o sedimento e favoreça processos de dano tafonômico.

Os depósitos de *offshore* influenciados por tempestades geralmente apresentam grau de bioturbação moderado a alto próximo ao topo de camada, e tipicamente, exibem grau de retrabalhamento alto devido à atividade biogênica, com icnodiversidade alta. Neste contexto, a maior parte das assembleias é composta por escavações produzidas por organismos depositívoros, representada na icnofácies *Cruziana* principalmente por *Asterosoma*, *Chondrites*, *Planolites*, *Rhizocorallium, Teichichnus* e *Thalassinoides.* Subordinadamente podem ocorrer *Arenicolites, Cylindrichnus, Diplocraterion, Gordia, Helminthopsis, Lockeia, Ophiomorpha, Palaeophycus, Phycosiphon, Rosselia, Skolithos, Schaubcylindrichnus, Siphonichnus* e *Zoophycos* (Pemberton et al., 2012).

Também pode dominar neste ambiente a Icnofácies *Zoophycos*, típica de ambientes menos energéticos, com predomínio de estruturas de alimentação com *spreiten*, e de pastagem subordinada, ação de organismos depositívoros ou comportamento de cultivo, principalmente em depósitos pós-Mesozoico (Bromley, 1996). Nesta icnofácies a colonização principal ocorre em níveis mais profundos do sedimento, com icnodiversidade baixa e alta densidade de bioturbação. Esses fatores podem atuar como coadjuvantes nos processos destrutivos, principalmente nesta icnofácies que representa a exploração dos tiers mais profundos. Assim, no offshore é que reside a maior barreira preservacional para os bioclastos a partir da ação da fauna bioturbadora.

Neste contexto, as icnofácies *Cruziana* e *Zoophycos* ocorrem com bioturbações abundantes, dominadas por estruturas de pastagem e forrageio, sendo as principais icnofácies que potencialmente podem reduzir a quantidade e qualidade da informação tafonômica a ser preservada. A figura 4 ilustra a relação entre o grau de bioturbação com a destruição dos restos esqueléticos.

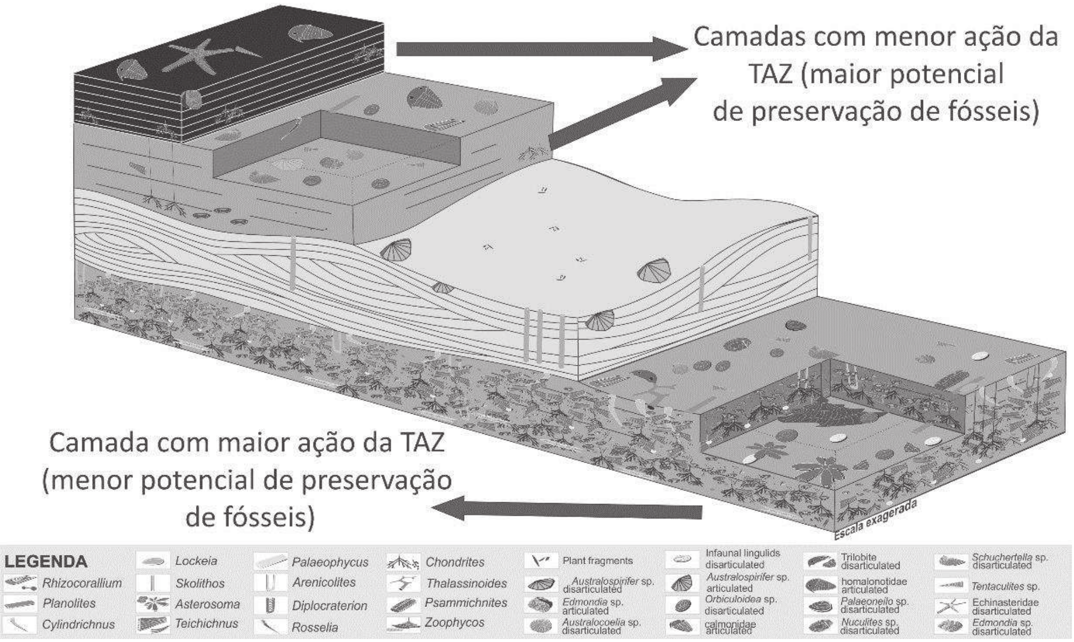

Figura 4. Esquema da relação entre intensidade da bioturbação e destruição dos restos esqueléticos (modificado de Pemberton e Frey, 1984 e MacEachern e Pemberton, 1992).

4.1.3 Ambientes marinhos profundos

Em ambientes distaisocorre a Icnofácies *Nereites* (talude e turbidítos). Pouca ênfase é dada a este ambiente devido às características deposicionais e de suas estruturas biogênicas. Nesta icnofácies predominam estruturas complexas, que refletem o comportamento de pastagem e de cultivo, de *tiers* superficiais, geralmente com baixa icnodiversidade e abundância. A oxigenação do substrato é o principal fator limitante para a fauna bioturbadora, e, deste modo, o predomínio das estruturas biogênicas se dá nas camadas superficiais. O potencial de preservação dos icnofósseis da Icnofácies *Nereites* é baixo, dependendo da ação de eventos deposicionais rápidos (Bromley e Asgaard, 1991; Savrda, 2007). Embora possam apresentar alta abundância, o potencial de destruição na TAZ é reduzido, pois se coloniza principalmente os níveis mais superiores do substrato.

4.2 Ambientes continentais

Os ambientes continentais podem apresentar as icnofácies *Scoyenia, Mermia*, *Coprinisphaera, Termitichnus, Celliforma, Octopodichnus-Entradichnus*. Embora as bioturbações em ambientes continentais possam ser profundas (tocas de vertebrados e bioturbação de invertebrados), elas são geralmente pontuais, deste modo apresentando pouco potencial de destruição. Uma exceção é a Icnofácies *Mermia*, típica de ambientes lacustres, que geralmente apresenta densidade alta de escavações no substrato, podendo atuar como agente de facilitação no processo de perda da informação tafonômica. Os icnogêneros mais comuns nesta icnofácies são *Circulichnis, Cochlichnus, Gordia, Helminthoidichnites, Helminthopsis, Mermia, Palaeophycus, Planolites, Treptichnus, Tuberculichnus, Undichna* e *Vagorichnus* (Buatois e Mángano, 2011). Genise *et al.* (2004) apresentaram um esquema de icnofábricas em paleossolos demonstrando a capacidade de retrabalhamento pela ação de organismos vivos, principalmente insetos.

Uma feição particular que poderia ser classificada como bioturbação exclusiva de ambientes continentais, são os rizólitos ou rizocreções (também conhecidos como calcretes rizogênicos; Klappa, 1980). Estes são o produto do encapsulamento ou mineralização de raízes ou sistemas radiculares, principalmente como consequência da precipitação de carbonato de cálcio, e são usualmente associados a concreções carbonáticas em geral (Kraus & Hasiotis, 2006). Tais concreções são bons indicadores de processos pedogenéticos e são associados à subida do nível freático próximo à superfície do solo, sendo comuns em sedimentos quaternários, principalmente em depósitos sob influência de clima frio e seco (Retallack, 2004; Erthal et al., 2015).

5 Integração da Tafonomia e Icnologia: um exemplo para o Emsiano (Devoniano inferior) da Bacia do Paraná

Em um trabalho que integrou dados icnológicos e tafonômicos, Sedorko *et al.* (no prelo) diagnosticaram que em camadas com grau de bioturbação elevado (5-6), não haviam fósseis corporais preservados. Em camadas sobrepostas e sotopostas, quando o grau de bioturbação diminuía (2 a 4), foram encontrados fósseis de braquiópodes, moluscos e trilobitas.

O grau de bioturbação alto e a icnodiversidade alta, se comparada a outras camadas da seção analisada, além da presença de escavadores de todos os níveis do substrato (*Arenicolites, Cylindrichnus, Diplocraterion, Lockeia, Skolithos* de níveis superficiais, *Asterosoma, Palaeophycus, Planolites, Rhizocorallium, Teichichnus* de níveis intermediários e *Chondrites, Planolites* de níveis inferiores; Fig. 2), sugere que houve estabilidade nas condições do ambiente e melhor oxigenação do substrato, o que deve ter impossibilitado a preservação da fauna fóssil. Assim, a intensa atividade intraestratal provavelmente foi o principal fator responsável pela dissolução dos esqueletos enquanto disponíveis na TAZ, se configurando como uma importante barreira preservacional. A figura 5 ilustra as principais ocorrências icnológicas e a figura 6 sintetiza a interpretação das condições diagnosticadas neste estudo.

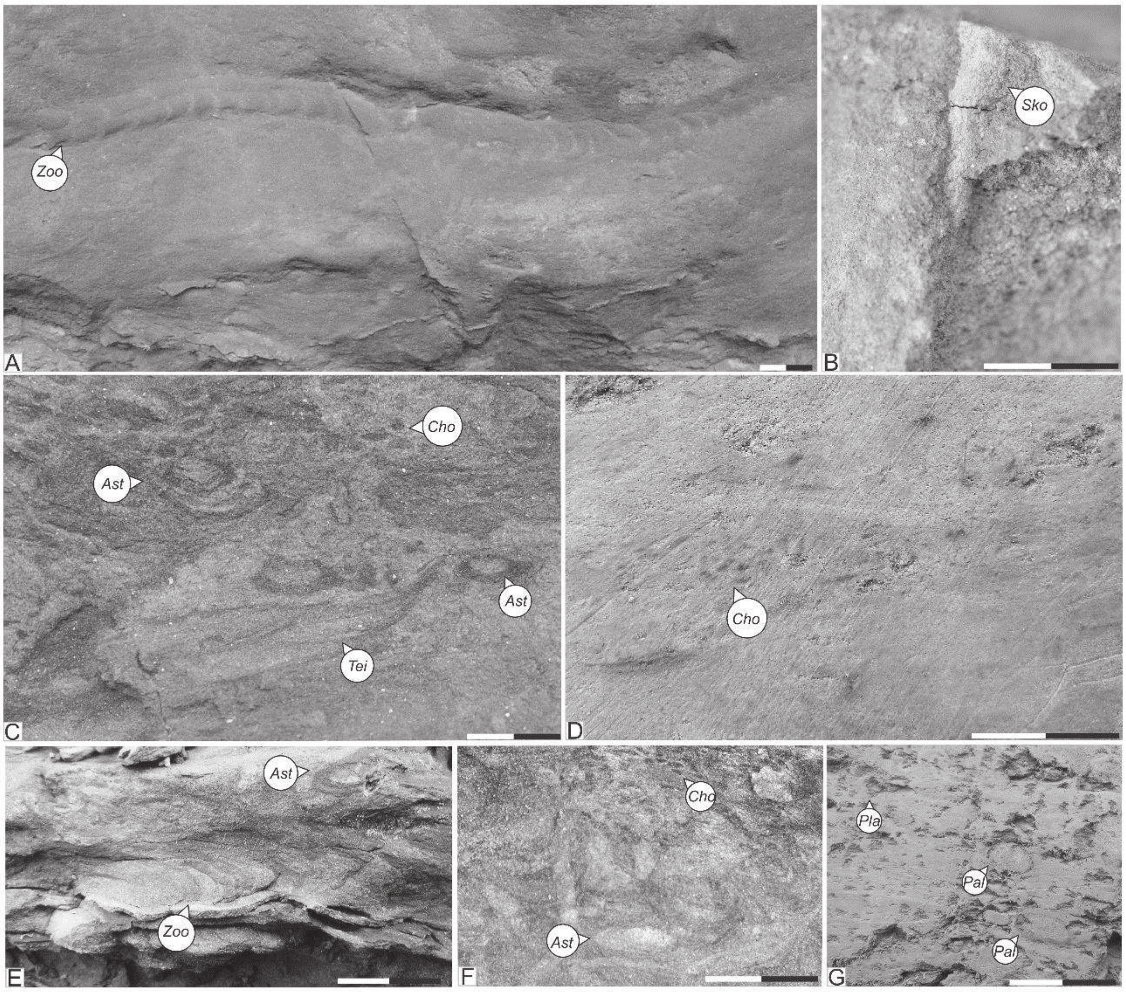

Figura 5. Principais bioturbações da seção analisada por Sedorko *et al.* (no prelo). A. *Zoophycos* em ocorrência monoespecífica. B. *Skolithos* em ocorrência monoespecífica. C. Em destaque, *Asterosoma, Teichichnus* e *Chondrites,* com grau de bioturbação 5-6, onde fósseis corporais são ausentes. D. *Chondrites* em ocorrência monoespecífica. E. Icnofábrica de *Asterosoma* – *Zoophycos*. F. Icnofábrica de *Asterosoma* – *Chondrites*. G. Icnofábrica de *Planolites* – *Palaeophycus*. Escala: 2 cm.

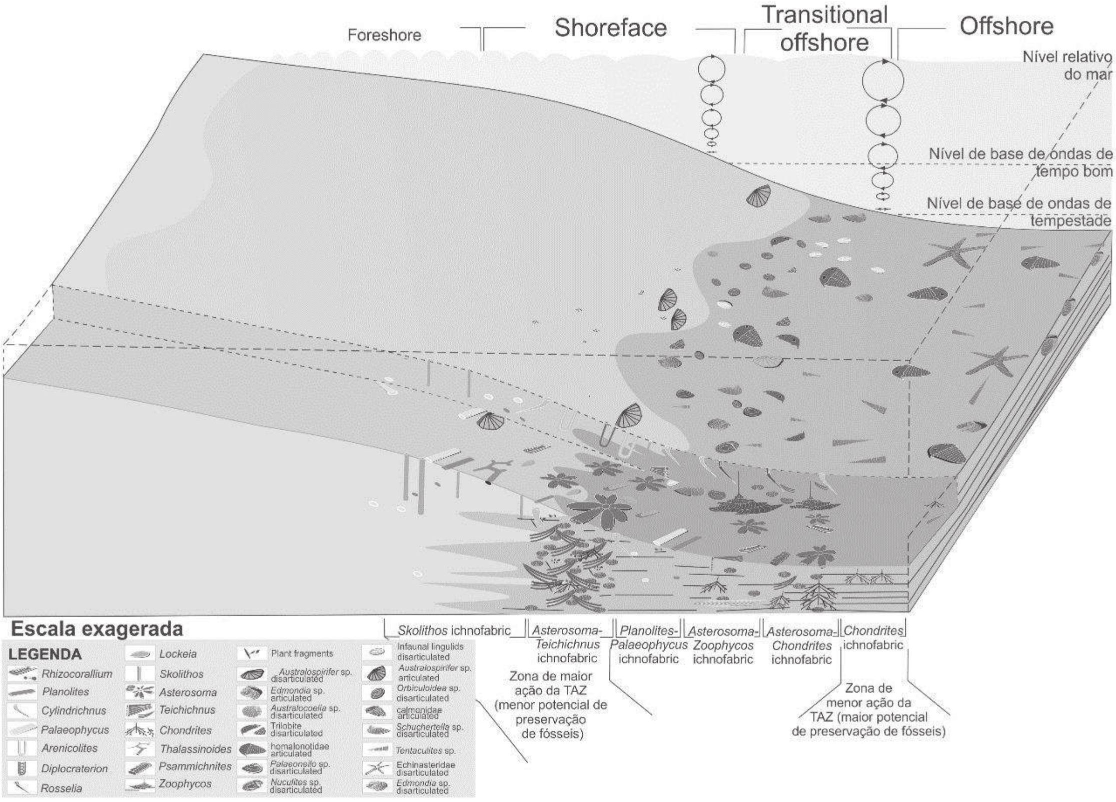

Figura 6. Distribuição paleoambiental das icnofábricas e sua relação com a TAZ a partir de uma seção devoniana da Bacia do Paraná (Sedorko, 2015; Sedorko et al. (no prelo).

6 Tafonomia de uma icnofauna do Carbonífero Superior na região de Trombudo Central (SC): consistência do substrato e esteiras microbianas

Associações de traços fósseis dominadas por trilhas de artrópodes são comuns em sedimentos depositados durante a glaciação do Paleozoico Superior. Um exemplo que recentemente foi alvo de estudos detalhados é a icnofauna da Formação Rio do Sul (Grupo Itararé, Bacia do Paraná) preservada nos ritmitos expostos nas pedreiras da região de Trombudo Central (centro-leste de Santa Catarina). Lima *et al.* (2015) fizeram a revisão taxonômica da icnofauna dessa sucessão, dominada por trilhas produzidas por artrópodes terrestres (*Diplichnites gouldi*) e aquáticos (*Cruziana problematica, Glaciichnium liebegastensis, Protovirgularia dichotoma* e *Umfolozia sinuosa*). Além das trilhas, as estruturas mais comuns são pistas e escavações rasas produzidas por insetos (*Helminthoidichnites tenuis, Mermia carickensis* e *Treptichnus pollardi*). Impressões de repouso (*Gluckstadtella elongata*) e pistas de deslocamento (*Diplopodichnus biformis*) completam a icnofauna da região.

Em Trombudo Central, até o momento não foram registrados fósseis corpóreos, embora os traços fósseis ocupem cerca de 80% das superfícies expostas (Lima et al. 2015). Segundo o autor, os prováveis produtores da icnofauna da Formação Rio do Sul no centro-leste de Santa Catarina são miriápodes (Diplopoda), insetos (Diptera, Coleoptera, Blattodea e Gryloblattodea) e crustáceos (Malacostraca e Branquiópoda). Por razões ainda não esclarecidas, os restos corpóreos desses animais não resistiram às barreiras preservacionais, e virtualmente, não estão preservados nos depósitos portadores de icnofósseis, provavelmente por dissolução. Por sua vez, e apesar do tamanho diminuto, a maioria dos icnofósseis identificados na sucessão sedimentar exposta nas pedreiras está preservada com riqueza de detalhes, que refletem a anatomia do produtor, ou que induzem ao comportamento que resultou na produção do traço. Estes detalhes podem ser observados tanto nos exemplares preservados em epirrelevo (topo da camada) quanto em hiporrelevo (base da camada).

A preservação destes detalhes teria sido favorecida por dois agentes tafonômicos principais: a natureza do substrato – granulometria fina e coesão – e a presença de esteiras microbianas, preservadas na forma de estruturas sedimentares induzidas pela ação microbiana (*microbially induced sedimentary structures* – MISS). A única fácies sedimentar na qual foram registrados traços fósseis em Trombudo Central é a de ritmitos síltico-argilosos (Lima 2015). Essa fácies é caracterizada por um par composto de uma camada centimétrica a decimétrica de siltito e uma lâmina milimétrica de argilito. As formas epiestratais ficaram preservadas no topo do argilito, no topo e na base do siltito. As formas endoestratais são encontradas dentro da camada de siltito, mas muito próximas ao topo ou à base da camada. A granulometria e a plasticidade do substrato naturalmente encontravam-se em condições ideais para a formação e a preservação das pegadas e impressões, produzidas pelos artrópodes, que colonizaram os corpos d'água rasos, preenchidos por água de degelo, em contexto marginal marinho (Lima 2015).

Quase todas as superfícies que contêm traços fósseis em depósitos da Formação Rio do Sul também possuem MISS, cujo tipo mais comum são as *wrinkle structures*. As MISS são a expressão sedimentar de antigas esteiras microbianas que eram compostas, em parte, por cianobactérias filamentosas fotossintetizantes, conforme demonstrado por Netto *et al.* (2009). Além de exercerem o papel de produtoras primárias na sucessão ecológica proposta por Lima (2015) para os registros de Trombudo Central, as esteiras microbianas tiveram grande importância na preservação das estruturas epiestratais da sucessão (Netto *et al.* 2009, Lima *et al.* 2015).

Tal como ocorre em ambientes modernos, em contexto subaquoso as esteiras microbianas teriam reduzido o efeito destrutivo das correntes sobre as trilhas de artrópodes (Lima *et al.* 2015). Além disso, as esteiras são capazes de manter a umidade dos níveis mais rasos de substratos finos, protegendo-os contra o ressecamento durante curtos períodos de exposição (Seilacher 2003). A preservação dos traços fósseis nesses substratos foi provavelmente favorecida pela mucilagem expelida pelos microrganismos (Seilacher 2008). Dessa forma, as esteiras microbianas possibilitaram a colonização do substrato e desempenharam um papel tafonômico imprescindível à preservação da icnofauna de Trombudo Central (Lima *et al.* 2015).

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CAPÍTULO 2

Chronostratigraphy and environment of Furnas Formation by trace fossil analysis: Calibrating the lower Paleozoic Gondwana realm in the Paraná Basin (Brazil)

Artigo publicado no periódico "Palaeogeography, Palaeoclimatology, Palaeoecology" onde almejou-se analisar a Formação Furnas sob a ótica icnológica, fornecendo interpretações relativas aos paleoambientes, idades e superfícies estratigráficas. Os principais resultados obtidos demonstram o caráter marinho da unidade, bem como que as unidades inferior e média foram depositadas ainda no Siluriano Inferior.

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Chronostratigraphy and environment of Furnas Formation by trace fossil analysis: Calibrating the lower Paleozoic Gondwana realm in the Paraná Basin (Brazil)

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ABSTRACT

Ichnology is an important tool for facies and sequence stratigraphic analysis, typically yielding greater resolution than that provided by body fossils. Less commonly, ichnofossils also can be applied to ichnostratigraphy, a variant of biostratigraphy that aids in determining stratigraphic age of sedimentary sequences. Previous publications on the Furnas Formation (Paraná Group, early Paleozoic of the Paraná Basin), have yielded different interpretations of age, depositional environment, and sequence stratigraphic framework. Deposition in fluvial environments has been proposed in many papers, although a tide-influenced marine context has been inferred since the presence of *Cruziana* and *Rusophycus* was reported during the 1990s. Sequence stratigraphic interpretations also differ, mainly regarding the presence or absence of a sequence boundary between the middle and upper units of the Furnas Formation. The absence of body fossils in all but the topmost part of the upper unit, which contains Lochkovian (Lower Devonian) palynomorphs and primitive plants, has precluded age determination for the Furnas Formation in general. Here, we demonstrate the utility of both ichnofacies and ichnostratigraphic analysis to elucidate such questions. The studied sections are located in the cities of Tibagi, Palmeira and Ponta Grossa (Guartelá, Sítio Canei and São Jorge sections, respectively). Seventeen ichnotaxa are recognized, doubling the number of previously known ichnotaxa: *Cruziana acacensis elongata* and *Rusophycus acacensis* n. ichnosp. (in the lower and middle units); *Arthrophycus alleghaniensis*, *A. brongniartii*, *Rhizocorallium commune*, *Didymaulyponomos rowei* and *Heimdallia chatwini* (middle unit only); *Arenicolites*, *Cylindrichnus* and *Diplocraterion* (lower and upper units); *Lockeia siliquaria* and *Psammichnites implexus* (middle and upper units); *Rosselia socialis* (upper unit); and *Palaeophycus tubularis*, *Didymaulichnus lyelli*, *Skolithos*, and *Thalassinoides* (all units). Assemblages of these ichnofossils are assigned to Skolithos and proximal Cruziana ichnofacies. Ichnologic data, combined with associated physical sedimentary facies associations, indicate predominantly tide-influenced marine depositional environments. The presence of ichnotaxa of stratigraphic value (*Arthrophycus alleghaniensis*, *A. brongniartii* and *Cruziana acacensis elongata*) in lower and middle units indicates an Early Silurian age. This, in turn, indicates that a significant unconformity exists between the middle and upper units of Furnas Formation. Although the precise magnitude of this stratigraphic gap is difficult to establish, this break likely is linked to the Late Silurian global regression.

1. Introduction

Ichnology has a broad range of applications in sedimentary geology. Ichnofossils reflect aspects of organism behavior that are responses to physical and chemical conditions in their respective depositional environments. Hence, in conjunction with physical sedimentologic evidence, ichnofossils are important tools for facies analysis (Pemberton and Frey, 1984; Bottjer et al., 1988; Savrda and Bottjer, 1986; Ekdale and Lewis, 1991; Leszczyński et al., 1996; Mángano et al., 1998; Netto et al., 2009, 2014; Srivastava and Mankar, 2012; Mude et al., 2012; Plotnick, 2012), typically yielding greater resolution than that provided by body fossils, including palynofossils and foraminifera (MacEachern et al., 1999).

Ichnofossils are also applied effectively in sequence stratigraphic

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analyses. Key sequence stratigraphic surfaces (e.g., sequence boundaries, transgressive surfaces) are frequently marked by substrate-controlled ichnofossil assemblages (e.g., Glossifungites Ichnofacies; Savrda, 1991a; MacEachern et al., 1992; Pemberton et al., 2000; Buatois and Encinas, 2006; Rodríguez-Tovar et al., 2006; Abdel-Fattah et al., 2016), and vertical changes in ichnofossil assemblages can be used to recognize the signal of sea-level change (e.g., shallowing-upward patterns manifested in parasequences; Savrda, 1991b, 1995; Brett, 1998; Fielding et al., 2006; Rodríguez-Tovar et al., 2010; Paranjape et al., 2014).

Less commonly appreciated among sedimentary geologists, except perhaps those working mainly in the Paleozoic, is the potential use of trace fossils in ichnostratigraphy, a variant of biostratigraphy that aids in determining stratigraphic age of sedimentary sequences (Crimes, 1969, 1970, 1975; Seilacher, 1970, 1992, 1994, 1996, 2000, 2007; Rindsberg and Martin, 2003; Baldwin and Strother, 2004; Mángano et al., 2001; Mángano and Buatois, 2003; Mángano and Droser, 2004; Mángano et al., 2005; Brandt et al., 2010).

The lower Paleozoic siliciclastic Furnas Formation of the Paraná Group in the Paraná Basin of southern Brazil, has been the subject of numerous publications that have yielded conflicting interpretations of depositional environment, age, and sequence stratigraphic framework. In this paper, we use both ichnofacies analysis and ichnostratigraphy to assert a dominant marine environment during deposition and an Early Silurian age for the lower and middle portions of the Furnas Formation. These results indicate the existence of an unconformity within the Furnas succession, which has profound implications for the stratigraphy of the Paraná Basin and for paleogeography of Gondwana during the early Paleozoic.

2. Lower Paleozoic stratigraphy

Lower Paleozoic strata in the Paraná Basin of southern Brazil (Fig. 1) have been grouped into the Ordovician-Silurian Rio Ivaí Group and Devonian Paraná Group (Assine et al., 1994; Assine, 1996), also referred as supersequences (Milani et al., 2007). The Rio Ivaí Group records deposition in fluvial to shallow marine environments (Alto Garças Formation), glacial-marine settings (Iapó Formation), and offshore marine realms (Vila Maria Formation) (Assine et al., 1998a, 1998b). Palynomorphs and marine macroinvertebrate body fossils indicate a Late Ordovician to Early Silurian (early Llandovery) age for the Iapó and Vila Maria formations (Assine et al., 1994; Popp et al., 1981; Burjack and Popp, 1981; Faria, 1982; Gray et al., 1985; Rodrigues et al., 1989; Borghi et al., 1996; Adôrno et al., 2016).

The overlying Paraná Group comprises the Furnas and the Ponta Grossa formations, the later subdivided into three members, from base to top: Jaguariaíva, Tibagi and São Domingos (Lange and Petri, 1967). The Ponta Grossa Formation is very fossiliferous and a Devonian age has been assigned based on macrofossils (brachiopods, trilobites and plants) and palynomorphs (Grahn, 1992 and Grahn et al., 2010, 2013). Paleoenvironments include inner to outer shelf marine settings (Clarke, 1913; Lange and Petri, 1967; Melo, 1988; Grahn, 1992; Rodrigues et al., 2003; Bosetti et al., 2011, 2013; Grahn et al., 2013; Horodyski et al., 2014; Matsumura et al., 2015; Sedorko et al., 2017). The Tibagi Member records a progradational event between the Emsian and Eifelian maximum-flooding surfaces (Assine et al., 1998c).

The Furnas Formation, subject of this research, is a very uniform unit in terms of stratigraphic stacking and thickness. The absence of body fossils and the dominance of cross-bed sets were strong arguments to interpret the Furnas sandstones as products of deposition in fluvial braided systems (Northfleet et al., 1969; Schneider et al., 1974; Popp and Barcellos-Popp, 1986; Melo, 1988; Zalán et al., 1987; Rodrigues et al., 1989; Coimbra et al., 1995; Pereira and Bergamaschi, 1996; Pereira et al., 1998). The unit also has been interpreted as shallow marine (Maack, 1946, 1947; Petri, 1948; Almeida, 1954; Sanford and Lange, 1960; Bigarella et al., 1966; Lange and Petri, 1967; Bigarella and Salamuni, 1967; Petri and Fúlfaro, 1983; Bigarella, 1973; Borghi, 1993; Assine, 1996; Bergamaschi, 1999) based on wide geographic distribution and lithologic uniformity.

A tide-dominated shallow marine environment was interpreted for most of the Furnas succession by Assine (1999) based on the presence of tide-dominated facies associations, numerous levels of conglomerate lag deposits on ravinement surfaces, and many pavements with trace fossils, including *Cruziana* and *Rusophycus*. Marine ichnofacies were confirmed by later investigations (Fernandes et al., 2000; Netto et al., 2012, 2014). Supported by a detailed stratigraphic and sedimentologic approach, Assine (1999) recognized three distinct successive facies associations and subdivided the Furnas Formation into three informal units (lower, middle and upper).

Fossils from primitive plant *Cooksonia* (Rodrigues et al., 1989; Mussa et al., 1996; Gerrienne et al., 2001) and palynomorphs (Grahn et al., 2010) were found in the upper unit, 20–30 m below the contact with the overlying Ponta Grossa Formation, and attest to an Early Devonian age (late Lochkovian) for the uppermost section of the Furnas Formation. However, the age of the lower and middle units remains uncertain because no body fossils or microfossils have been found therein, and different ages have been assumed for those strata; e.g., Late Silurian to Lochkovian (Assine, 1999), Late Silurian (Borghi, 1993) or even Early Silurian (Zalán et al., 1987).

This uncertainty makes it difficult to establish a reliable stratigraphic framework for the Silurian-Devonian sequences of the Paraná Basin (Fig. 1B). Understanding stratigraphic cycles and basin evolution is problematic because different stratigraphic proposals involve age ambiguity and disparate views concerning key surfaces (e.g., presence or absence of unconformities). For example, the entire succession of the Furnas Formation has been considered by some as a single depositional sequence (Bergamaschi, 1999; Grahn et al., 2013), while others split the Furnas into two depositional sequences based on the sharp basal contact between the middle and upper units (Assine, 1996, 1999).

3. Location, material, and methods

Considering the importance of trace fossils to elucidate the above-mentioned questions and uncertainties, we performed an integrated ichnologic and sedimentologic analysis in the Devonian beds exposed in the State of Paraná, southern Brazil. Our studies of the Furnas Formation focused on well-exposed sections at four localities (Fig. 1A), although other localities also were prospected. Data were collected directly in the field, along with samples for further laboratory analysis. Ichnofossils were described in association with sediment textures, physical sedimentary structures and facies geometry for facies analysis. Ichnologic analyses included identification of recurring trace fossils, to the maximum extent possible at the ichnospecies level; and quantification of degree of the bioturbation based on the scheme proposed by Reineck (1963; bioturbation scale, BS, ranging from 0 = no bioturbation through 6 = complete biogenic destruction of primary sedimentary fabric). Collected samples are deposited in the collections of the Museu da História Geológica do Rio Grande do Sul (Unisinos University) with the numbers ULVG-12017, ULVG-12018, ULVG-12019 and ULVG- 21020. The holotype of *Rusophycus acacencis* n. ichnosp. is deposited as a photo, with the number ULVG-12261a, which includes the paratypes ULVG-12261b and ULVG-12261c.

Ichnotaxa are described in alphabetical order. Trace fossil descriptions were based only on field observations, except for *Arthrophycus alleghaniensis*, specimens of which were also examined in detail in the laboratory (samples ULVG-12017, ULVG-12018, ULVG-12019 and ULVG-12020). Trace fossils originally described as *Furnaisichnus langei* Borghi and Fernandes, 2001 were here included in *Didymaulyponomos rowei*. The trace fossil *Rusophycus acacensis* n. ichnosp. were also described, considering that no formal description of these structures has previously been provided in the trace fossil literature. Systematic descriptions of both latter ichnospecies are presented in Appendix A.

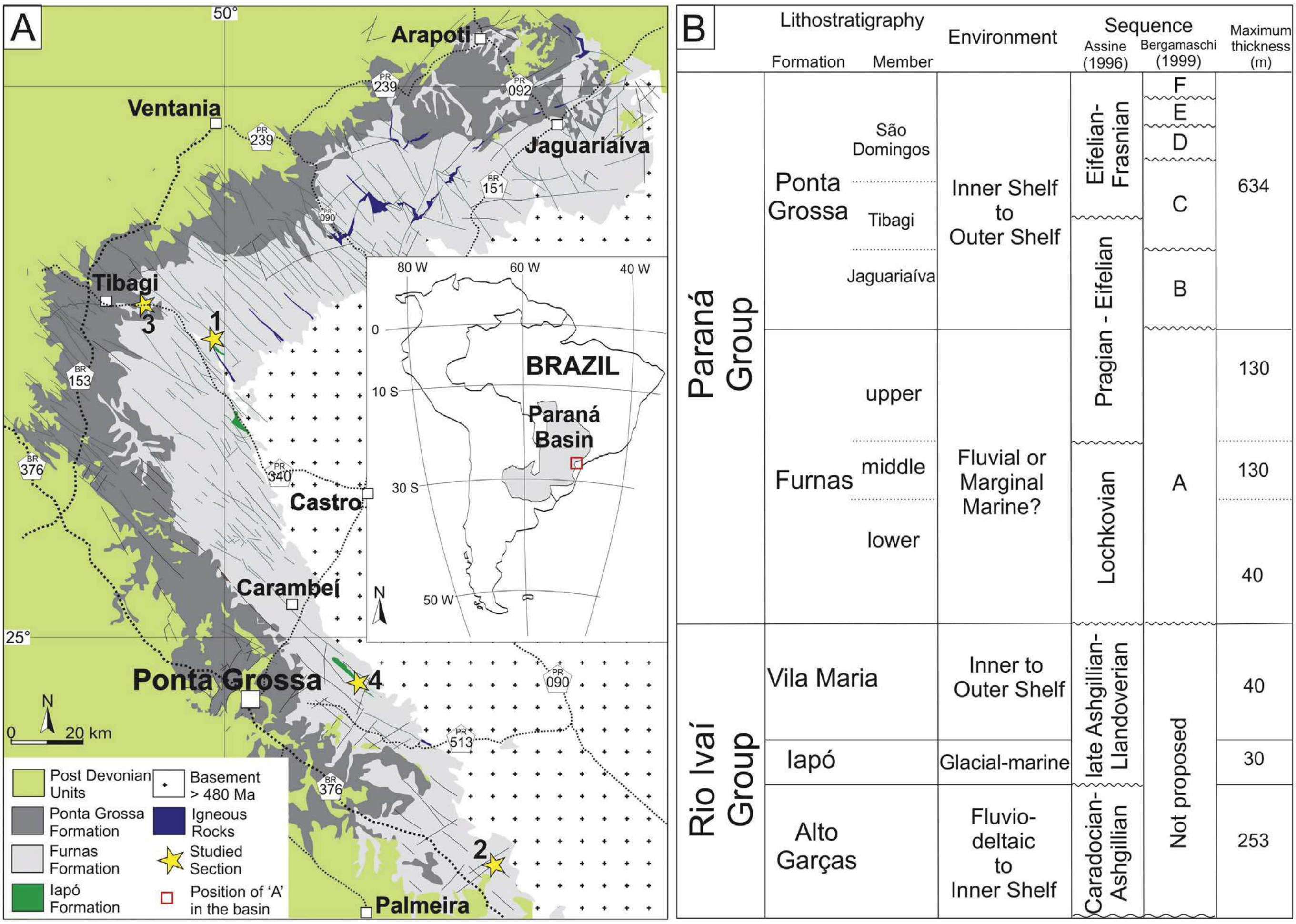

Fig. 1. Location map and stratigraphic context of the study area in Paraná Basin. A. Geological map of Paraná Supersequence in Campos Gerais region, Paraná State, Brazil. Yellow stars numbered 1 through 4 indicate locations of the Guartelá, Sítio Canei, PR340-km 264.5, and São Jorge–Alagados sections, respectively. B. Lithostratigraphy, paleoenvironmental interpretation (based on Lange and Petri, 1967; and Assine et al., 1994), and depositional sequences proposed by Assine (1996) and Bergamaschi (1999). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Ichnofossil and ichnofacies of Furnas Formation

Seventeen ichnotaxa are recognized in the Furnas Formation in the Campos Gerais region, most of them at the ichnospecies level. Associations of two or more ichnospecies in the same bed are common, and some transitional and compound forms locally occur. Recurring assemblages of these ichnotaxa led to the identification of two ichnofacies – Skolithos and proximal Cruziana ichnofacies.

4.1. Trace fossil descriptions

4.1.1. Arenicolites *isp. Salter, 1857 (Fig. 2A)*

Simple, vertical to oblique, U-shaped, unlined, unbranched burrows. *Arenicolites* is manifested on bedding planes as two circular apertures and in cross section by parallel U-limbs with no evidence of a *spreite*. Burrow diameter and limb separation range from 4 to 12 mm and 15 to 45 mm, respectively. *Arenicolites* generally is interpreted as a dwelling structure of filter-, suspension- or deposit-feeding organisms, mainly polychaetes, but also crustaceans and insects (Bromley, 1996).

4.1.2. Arthrophycus alleghaniensis *Harlan, 1831 (Fig. 2B–D)*

Gently recurved, horizontal to slightly inclined, regularly annulated burrows with nearly circular to square cross sections, compacted walls, and fills similar to the host sediment. Apparent lateral branches radiate on both sides of the main axis. In cross section, these palmate structures appear as vertical stacks of crescentic backfill lamellae (i.e., as retrusive spreite structures; Fig. 2B, C). Annulae are pronounced on bottoms of burrows and less discrete on tops. Burrow diameters range from 5 to 15 mm, with an average of 10 mm.

Arthrophycus alleghaniensis was previously reported by Fernandes et al. (2000) from the Sítio Canei section. However, when Neto de Carvalho et al. (2002) commented on this occurrence, they referred to these traces as *Arthrophycus lateralis*, which differs from *A. alleghaniensis* in several aspects. In *A. lateralis*, branches are preferentially arranged to one side of the main axis, crescentic backfill lamellae are horizontal rather than vertical, and the *spreiten* are protrusive rather than retrusive (Seilacher, 2007). Seitz (2010) noted that specimens illustrated and described by Fernandes et al. (2000) correspond to *A. alleghaniensis*, which is supported by the current study. *Arthrophycus* reflects detritus-feeding activity of worm-like organisms or arthropods (Seilacher, 2000; Rindsberg and Martin, 2003; Brandt et al., 2012). McCoy et al. (2012) described a fossil arthropod, *Pleuralata spinosa*, associated with *A. alleghaniensis*, suggesting that the tracemakers of some ichnospecies of *Arthrophycus* could belong to a group of protostome animals known as Ecdysozoa.

4.1.3. Arthrophycus brongniartii *Harlan, 1832 (Fig. 2E)*

Horizontal, straight to sinuous burrows with regularly spaced external lower surface annulae along the main axis and fills similar to the host sediment. Burrows locally exhibit false branching. The specimens found in the deposits of Furnas Formation are preserved in full relief but locally are exposed on bedding-parallel surfaces (Fig. 2E). Burrow axes

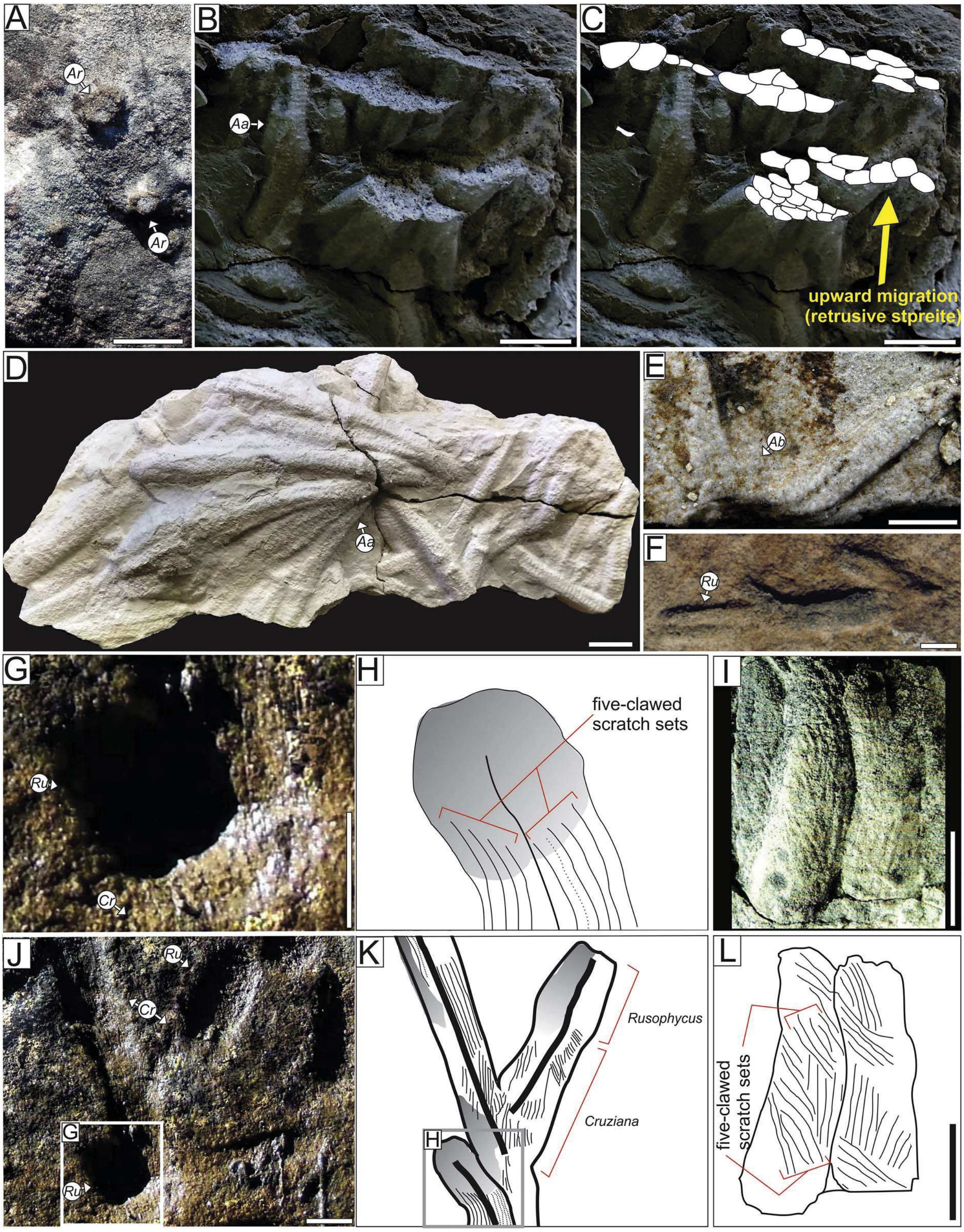

Fig. 2. Trace fossils from Furnas Formation. A. *Arenicolites* isp. (*Ar*) on upper bedding-plane surface. B. *Arthrophycus alleghaniensis* (*Aa*) preserved as convex hyporeliefs on sandstone sole. C. Photo as in B with overlay sketch of retrusive spreite. D. Sample ULVG-12017 with *A. alleghaniensis* in convex hyporelief showing palmate pattern. E. *Arthrophycus brongniartii* (*Ab*) with abrupt turn preserved in full relief along a bedding-parallel surface. F. Holotype of *Rusophycus acacensis* (*Ru*) in concave epirelief (ULVG-12261a). G. Close-up of compound *Rusophycus acacensis*–*Cruziana acacensis elongata* in concave epirelief exhibiting longitudinal scratches. H. Sketch of G highlighting scratch pattern. I. *Cruziana acacensis elongata* (*Cr*) in convex hyporelief. This specimen was identified as "*Rusophycus* ichnosp. 2" by Fernandes (1996; Fig. 41A). J. Detail of scratches in *Rusophycus acacensis* and *Cruziana acacensis elongata.* Box indicates location of photo in G. K. Drawing of traces in J highlighting the scratch pattern. Box indicates drawing in H. L. Sketch of I highlighting scratch pattern. Scale bars = 2 cm.

exhibit abrupt turns with no evidence of parallelism (sensu Rindsberg and Martin, 2003). This ichnospecies differs from *A. alleghaniensis* and *A. lateralis* mainly by the absence of prominent branching. Although *A. brongniartii* is similar in general character to *A. minimus*, the latter ichnotaxon has less pronounced annulae and is smaller (Mángano et al., 2005). *A. parallelus* is characterized by parallel arrangement of traces, which is absent in our occurrences.

4.1.4. Cruziana acacensis elongata *Seilacher, 2007 (Fig. 2F–I)*

Elongate, bilobate symmetric burrows with medial ridges marked by transverse to longitudinal scratches. These bilobed traces are preserved in concave epirelief. Furrows exhibit a discrete median ridge (2 to 5 mm wide) with scratches, which occur in sets of five (Fig. 2H–I). The traces are typically 5–9 cm long, but some reach 16 cm. These structures are aligned with *Cruziana acacensis elongata* based on their straight axes and length/width ratios of ~3 (Seilacher, 2007). Seilacher (2007, p. 198) identified this ichnosubspecies in the Furnas Formation and noted that the same tracemaker made both *Cruziana* and short rusophyciform burrows (compound trace fossils), identified as *Rusophycus* cf. *acacensis* by Netto et al. (2014) (Fig. 2F, G).

The tracemakers of both *Cruziana* and *Rusophycus* are bilaterally symmetrical organisms, most probably arthropods (Donovan, 2010). These ichnogenera have been reported in Triassic continental deposits (Bromley and Asgaard, 1979; Zonneveld et al., 2002). However, in the Paleozoic record, they occur exclusively in marine deposits. With the exception of *Cruziana problematica* and *Rusophycus carbonarius*, Paleozoic *Cruziana* and *Rusophycus* are generally attributed to trilobites (Goldring, 1985; Fortey and Seilacher, 1997).

4.1.5. Cylindrichnus *isp. Toots in Howard, 1966 (Fig. 3A)*

Concentrically laminated, vertical burrows filled with sediments similar to the host sediment. Specimens, observed only on bedding planes, range from 6 to 15 mm in diameter. *Cylindrichnus* is interpreted as a permanent dwelling structure of suspension-feeding organisms (Frey and Howard, 1990). This ichnogenus is common in shoreface to offshore environments, and, thus, represents a common component of the Skolithos and Cruziana ichnofacies (Frey and Howard, 1985; Vossler and Pemberton, 1989).

4.1.6. Didymaulichnus lyelli *Rouault, 1850 (Fig. 3B–C)*

Unbranched, unornamented, smooth-walled, bilobed trails with a narrow median groove (in hyporelief) or crest (in epirelief). *Didymaulichnus lyelli* occurs mainly in Paleozoic strata and is a common facies-crossing trace fossil (Fillion and Pickerill, 1990), possibly produced by mollusks (mainly gastropods; Glaessner, 1969; Hakes, 1976) or trilobites (Crimes, 1970; Bradshaw, 1981).

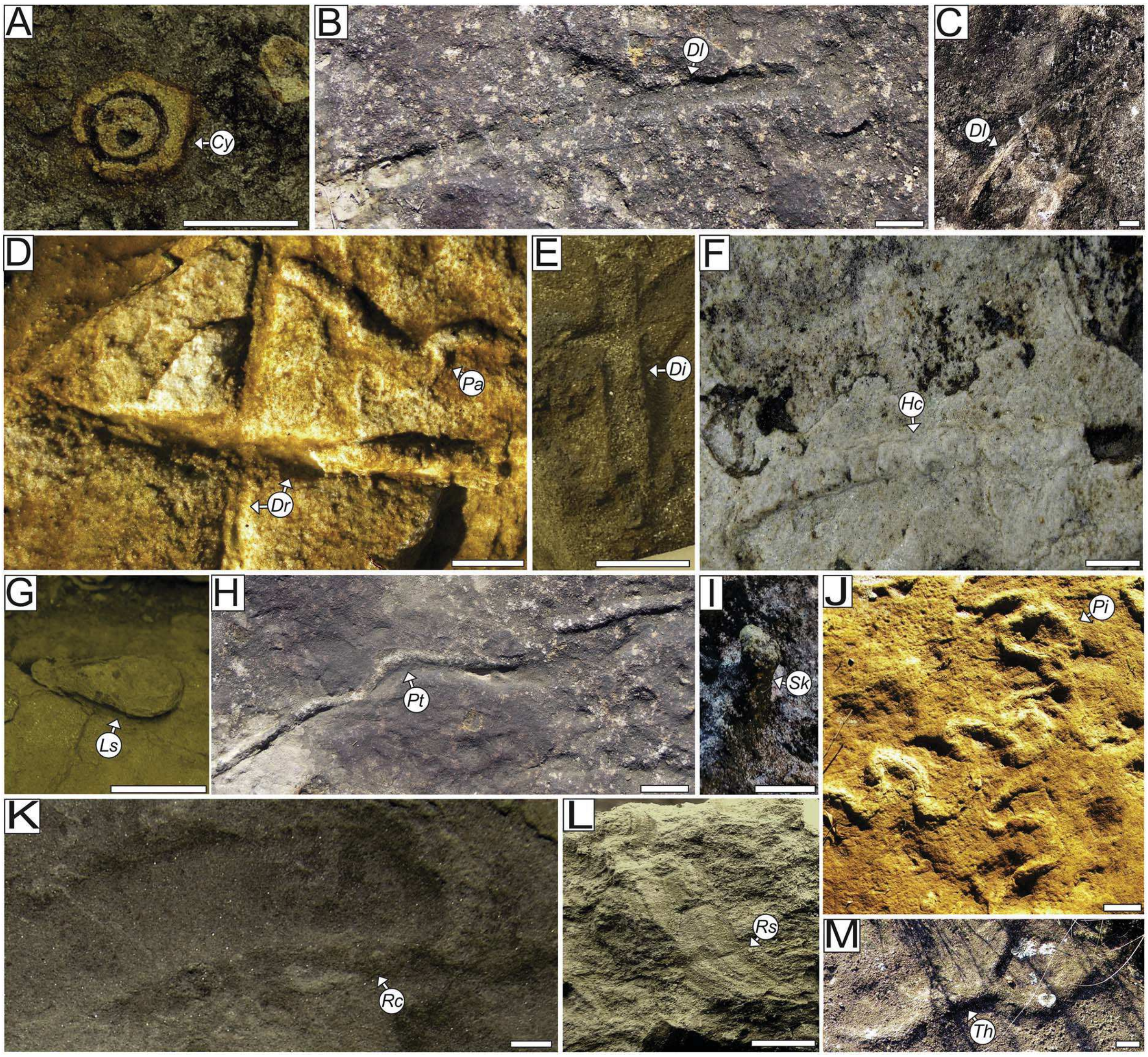

Fig. 3. Trace fossils from Furnas Formation. A. *Cylindrichnus* isp. (*Cy*) in bedding-plane view. B–C. *Didymaulichnus lyelli* (*Dl*) preserved in concave epirelief; D. *Didymaulyponomos rowei* (*Dr*) cross-cutting *Palaeophycus* (*Pa*) and another *D. rowei*. E. *Diplocraterion* isp. (*Di*) in bedding-plane view. F. *Heimdallia chatwini* (*Hc*) in bedding-plane view. G. *Lockeia siliquaria* (*Ls*) in full relief. H. *Palaeophycus tubularis* (*Pt*) preserved in full relief in bedding-plane view. I. Bedding-oblique view of *Skolithos* isp. (*Sk*) preserved in full relief. J. Meandering *Psammichnites implexus* (*Pi*) preserved in convex epirelief. K. *Rhizocorallium commune* (*Rc*) preserved in convex epirelief. L. *Rosselia socialis* (*Rs*) in cross section. M. *Thalassinoides* isp. (*Th*) preserved in full relief in bedding-plane view. Scale bars = 2 cm.

4.1.7. Didymaulyponomos rowei *Bradshaw, 1981 (Fig. 3D; see Appendix A)*

These structures appear as horizontal, straight to sinuous, unbranched, and unornamented endichnial burrows with median furrows in their lower parts. Fills are structureless and similar or locally finer than surrounding sediment. Specimens are generally equidimensional with respect to width and height (10 to 15 mm) and may exceed 1 m in length.

Bradshaw (1981) argued that *Didymaulyponomos* represents feeding or dwelling activity of arthropods below the sediment surface. Trewin and MacNamara (1994) observed that *Didymaulichnus* is quite similar to the bottom half of a *Didymaulyponomos* burrow and suggested that an erosional event may be involved in *Didymaulichnus* preservation. Despite these similarities, both ichnogenera names remain valid. Buatois et al. (2017) placed this trace into their architectural design category "passively filled horizontal burrows", similar to *Palaeophycus.* Coincidentally, occurrences of *D. rowei* in the Furnas Formation are associated with *Palaeophycus.*

4.1.8. Diplocraterion *isp. Torell, 1870 (Fig. 3E)*

Vertical U-shaped, unbranched burrows with *spreiten*; fills are similar to the host sediment. *Diplocraterion* was seen only on bedding planes, permitting identification only at the ichnogenus level. Specimens appear as paired apertures linked by a protrusive *spreite*; apertures are normally 5–15 mm in diameter, and spaced between 25 and 50 mm apart. This ichnogenus represents the dwelling structure of suspension- or detritus-feeding organisms, possibly crustaceans or polychaetes (Turner et al., 1981; Bromley, 1996; Savrda and Nanson, 2003; Goldring et al., 2005; Seilacher, 2007).

4.1.9. Heimdallia chatwini *Bradshaw, 1981 (Fig. 3F)*

Vertical spreite-bearing burrows that appear in bedding-plane view as unbranched ribbons formed of vertical or inclined packets of sediment. This trace fossil was seen mainly in bedding-plane view; vertical *spreiten* are only locally exposed. Packets of sediment resulted from the progressive lateral migration of the tracemaker. Bradshaw (1981) proposed that *Heimdallia* may reflect the activity of a crustacean-like animal in search of food.

4.1.10. Lockeia siliquaria *James, 1879 (Fig. 3G)*

Almond-shaped, unornamented burrows with fills similar to host sediment. *L. siliquaria* includes most of isolated almond-shaped traces (Seilacher and Seilacher, 1994). *L. cordata* differs from *L. siliquaria* by having larger and rounder shape (Rindsberg, 1994). *Lockeia* is interpreted as a resting trace produced by bivalve mollusks (Osgood, 1970).

4.1.11. Palaeophycus tubularis *Hall, 1847 (Fig. 3H)*

Thinly lined, horizontal to slightly inclined, unbranched, straight to slightly curved cylindrical burrows with structureless fills similar to the matrix. *Palaeophycus tubularis* differs from *P. heberti* by having a thinner wall and from other ichnospecies (*P. striatus*, *P. sulcatus*, and *P. alternatus*) by the absence of striae (Pemberton and Frey, 1982). Rindsberg (2012) demonstrated that *P. alternatus* and *P. striatus* may be variants of the same structure, and additional studies are necessary to solve those ichnotaxonomic problems. This ichnogenus is considered to be a dwelling structure produced by suspension-feeding or predaceous organisms, possibly polychaetes. *Glycera* (a glycerid polychaete) was suggested as one potential tracemaker (Pemberton and Frey, 1982; Fillion and Pickerill, 1990).

4.1.12. Psammichnites implexus *Rindsberg, 1994 (Fig. 3J)*

Straight to meandering, horizontal, flat trace with subtriangular to elliptical cross-section, faint meniscate backfill and a dorsal ridge preserved as a groove. The bottom of the trace may be unilobed or bilobed. Burrow width is nearly constant (normally 22 to 28 mm, although forms 10 mm wide are also present), but increases slightly in turns (Fig. 3J), particularly where burrows exhibit phobotactic tendencies similar to those observed by Mángano et al. (2003). Despite phobotactic tendencies, crosscutting is relatively common. *Psammichnites* is attributed to feeding activities of vagile infaunal animals, probably gastropods or other organisms with a siphon device (Seilacher, 1997).

4.1.13. Rhizocorallium commune *Schmid, 1876 (Fig. 3K)*

Horizontal, straight to sinuous, unornamented, unbranched, U-shaped burrows with protrusive spreite. *Rhizocorallium commune* differs from firmground *R. jenense* by the presence of unornamented walls and an actively filled *spreite* (Knaust, 2013). *R. commune* is attributed to suspension- or deposit-feeding activity, probably by polychaetes or crustaceans (Knaust, 2013).

4.1.14. Rosselia socialis *Dahmer, 1937 (Fig. 3L)*

Vertical to inclined, spindle- to funnel-shaped structures with concentrically laminated fine-grained walls surrounding a central shaft. In some levels, *Rosselia* occurs in dense concentrations (i.e., the crowded *Rosselia* ichnofabric of Netto et al., 2014). Nara (1995) described two forms of *R. socialis.* Spindle-shaped forms are the norm, while truncated funnel-shaped forms predominate below erosional surfaces. *Rosselia* is attributed to dwelling or feeding activity of suspension- or detritus-feeding worms, probably terebellid polychaetes (Nara, 1995).

4.1.15. Rusophycus acacensis *n. ichnosp. (Fig. 2F–I; Appendix A)*

Bilobed ovate, symmetrical traces preserved in concave epirelief. Specimens are between 15 and 25 mm wide and 20 to 55 mm long, with a length/width ratio of 3. Furrows exhibit a distinct medial ridge, locally with scratches, and occur either in association with or forming compound trace fossils with *Cruziana acacensis elongata*. Paleozoic *Rusophycus* is generally attributed to trilobite activity, probably reflecting resting behavior (Seilacher, 2007).

4.1.16. Skolithos *isp. Haldeman, 1840 (Fig. 3I)*

Vertical to slightly inclined, cylindrical or subcylindrical, unlined, unbranched burrows with fills similar to the host sediment. Occurrences of *Skolithos* in Furnas Formation are poor preserved or limited to simple apertures on bedding-plane surfaces, precluding identification at the ichnospecific level. *Skolithos* is commonly produced by worm-like organisms, possibly polychaetes (Seilacher, 1967; Pemberton and Jones, 1988; Herringshaw et al., 2010).

4.1.17. Thalassinoides *isp. Ehrenberg, 1944 (Fig. 3M)*

Branched systems of cylindrical, smooth-walled, straight to slightly curved, unlined burrows with enlarged branch junctions and fills similar to host sediment. Burrow diameters average ~30 mm. This ichnogenus is normally attributed to dwelling and feeding activities of decapod crustaceans. However, these burrows also may have been produced by worm-like organisms or small crustaceans during the Paleozoic, as suggested by Myrow (1995).

4.2. Ichnofacies

Based on recurring trace fossil associations, two ichnofacies can be identified in the Furnas Formation: the Skolithos Ichnofacies and proximal Cruziana Ichnofacies.

Trace fossil associations assigned to the Skolithos Ichnofacies are dominated by vertical traces, mainly *Skolithos*, *Arenicolites*, *Diplocraterion* and *Cylindrichnus*, although *Palaeophycus tubularis* and *Thalassinoides* are present locally. This ichnofacies records preferential colonization by suspension feeders in relatively high-energy settings (e.g., Frey, 1990). Trace fossil associations assigned to the proximal Cruziana Ichnofacies are dominated by epigenic and mainly horizontal endogenic structures produced chiefly by deposit feeders. Intervals in the Furnas Formation characterized by this ichnofacies contain one or more (as many as six) of the following ichnotaxa: *Didymaulyponomos*

Table 1
Sedimentary facies and their features in studied section.

Code	Lithology	Sedimentary structures	Trace fossils	Fig
Sm	Pebbly coarse-grained sandstones	Massive	*Arenicolites*, *Cylindrichnus*, *Palaeophycus*, *Rhizocorallium*, *Skolithos*, *Thalassinoides*	4A
Gt	Clast-supported conglomerate	Trough cross-stratification	Absent	4E
Gm	Clast-supported conglomerates	Massive and locally imbricated	Absent	4D, J
Sh	Very fine- to coarse-grained sandstones	Horizontal lamination	*Palaeophycus*, *Thalassinoides*	4G
St	Very fine- to coarse-grained sandstones	Trough cross-stratification	*Arenicolites*, *Arthrophycus brongniartii*, *C. acacensis elongata*, *Cylindrichnus*, *Didymaulichnus lyelli*, *Didymaulyponomos rowei*, *Diplocraterion*, *Heimdallia chatwini*, *Palaeophycus*, *Rhizocorallium commune*, *Rusophycus acacensis*, *Skolithos*, *Thalassinoides*	4C
Sp	Very fine- to coarse-grained sandstones	Planar cross-stratification in tabular sets	*Arenicolites*, *Cruziana acacensis elongata*, *Cylindrichnus*, *Didymaulichnus lyelli*, *Didymaulyponomos rowei*, *Diplocraterion*, *Lockeia siliquaria*, *Palaeophycus*, *Psammichnites implexus*, *Rusophycus acacensis*, *Skolithos*, *Thalassinoides*	4B
Ss	Very fine- to coarse-grained sandstones	Sigmoidal cross-stratification with reactivation surfaces and mud drapes	*Arenicolites*, *Palaeophycus*, *Rusophycus*, *Thalassinoides*	4F
Shc	Very fine- to fine-grained sandstones	Hummocky cross-stratification	*Arenicolites*, *Cylindrichnus*, *Palaeophycus*, *Skolithos*, *Rosselia*	4 K
Sr	Very fine- to fine-grained sandstones	Current ripples	*Arthrophycus alleghaniensis*, *Palaeophycus*	4H
F/Fl	Mudstones to siltstones	Massive to weakly laminated	Absent	4I

rowei, *Heimdallia chatwini*, *Arthrophycus brongniartii*, *A. alleghaniensis*, *Rhizocorallium commune*, *Palaeophycus tubularis*, *Thalassinoides*, *Rosselia socialis*, *Didymaulichnus lyelli*, *Psammichnites implexus*, *Cruziana acacensis elongata*, *Rusophycus acacensis*, and *Lockeia siliquaria*. Taken together, these trace fossil assemblages reflect deposition in overall comparatively low-energy environments. However, localized co-occurrences of *Skolithos* indicate at least periodically enhanced bottom currents, and rare intervals containing stacked *Rosselia* (see below) reflect episodic rapid deposition.

5. Integrated sedimentology and ichnology

Based on detailed field descriptions of rocks, textures, geometry, and physical sedimentary structures, ten lithofacies were recognized in the Furnas Formation exposed at the four study localities (Table 1). The stratigraphic distributions of lithofacies and associated trace fossils through the Furnas Formation at each of the study localities are shown in Fig. 5.

5.1. Lower unit

The lower Furnas Formation is exposed at all localities except the PR 340 section (Fig. 5). This unit is 30–40 m thick and directly overlies Cambrian to Ordovician volcanic rocks of the Castro Group (Assine, 1996) at Guartelá and Sítio Canei, and Ordovician to Silurian diamictites of the Iapó Formation (Rio Ivaí Group; Assine et al., 1998a) at São Jorge-Alagados.

This unit is dominated by thin (< 50 cm), lenticular, massive pebbly coarse-grained sandstones (facies Sm; Fig. 4A), but also includes 0.4 to 2.0 m-thick tabular sets of planar cross-bedded, medium- to coarse-grained sandstones (facies Sp; Fig. 4B) and trough cross-stratification (facies St; Fig. 4C). Subordinate rocks include centimetric, massive, locally imbricated clast pavements (facies Gm; Fig. 4D) and trough cross-bedded clast-supported conglomerates (facies Gt; Fig. 4E).

Trace fossils are present locally in all above-described dominant lithofacies, although the bioturbation in all cases is low to moderate (BS 1 to 3; Fig. 5). Assemblages representing the proximal Cruziana Ichnofacies are dominated by *Palaeophycus*, *Thalassinoides*, and, locally, *Rusophycus*. However, Skolithos Ichnofacies assemblages with *Skolithos*, *Arenicolites*, and *Cylindrichnus* also are common in pebbly sandstones (lithofacies Sm) and are a subordinate component in the cross-bedded sandstones (lithofacies Sp and St) (Fig. 5).

5.2. Middle unit

The middle unit is represented in all sections except for the PR 340 locality. This unit is ~130 m thick at Guartelá and ~95 m thick at São-Jorge-Alagados; the Sítio Canei section exposes only the lower ~20 m of the unit. At all three localities, the transition from the lower to the middle Furnas Formation is gradational and generally reflects a fining-upward trend (Fig. 5).

This unit is dominated by fine- to coarse-grained planar and trough cross-bedded sandstones, 0.3 to 2.5 m thick (facies Sp and St). Subordinate lithofacies include fine- to coarse-grained sandstones with sigmoidal cross-bed sets having reactivation surfaces (facies Ss; Fig. 4F) and horizontal to subhorizontal stratification (facies Sh; Fig. 4G), rippled fine-grained sandstones (facies Sr; Fig. 4H), and 0.2 to 1.8 m-thick massive and crudely laminated mudstones (facies F and Fl; Fig. 4I). Noteworthy is the presence of cross-bed sets up to 4 m thick, exhibiting foreset mud drapes and internal reactivation surfaces.

As in the lower unit, bioturbation is common but of low to moderate intensity (BS 1–3); most intervals (facies St, Sp, Ss, and Sh) are dominated by low-diversity proximal Cruziana Ichnofacies assemblages, and some (facies Sp and St) locally include Skolithos Ichnofacies suites (Fig. 5). Occurrences of proximal Cruziana Ichnofacies assemblages include one or a few of the following ichnotaxa: *Palaeophycus tubularis*,

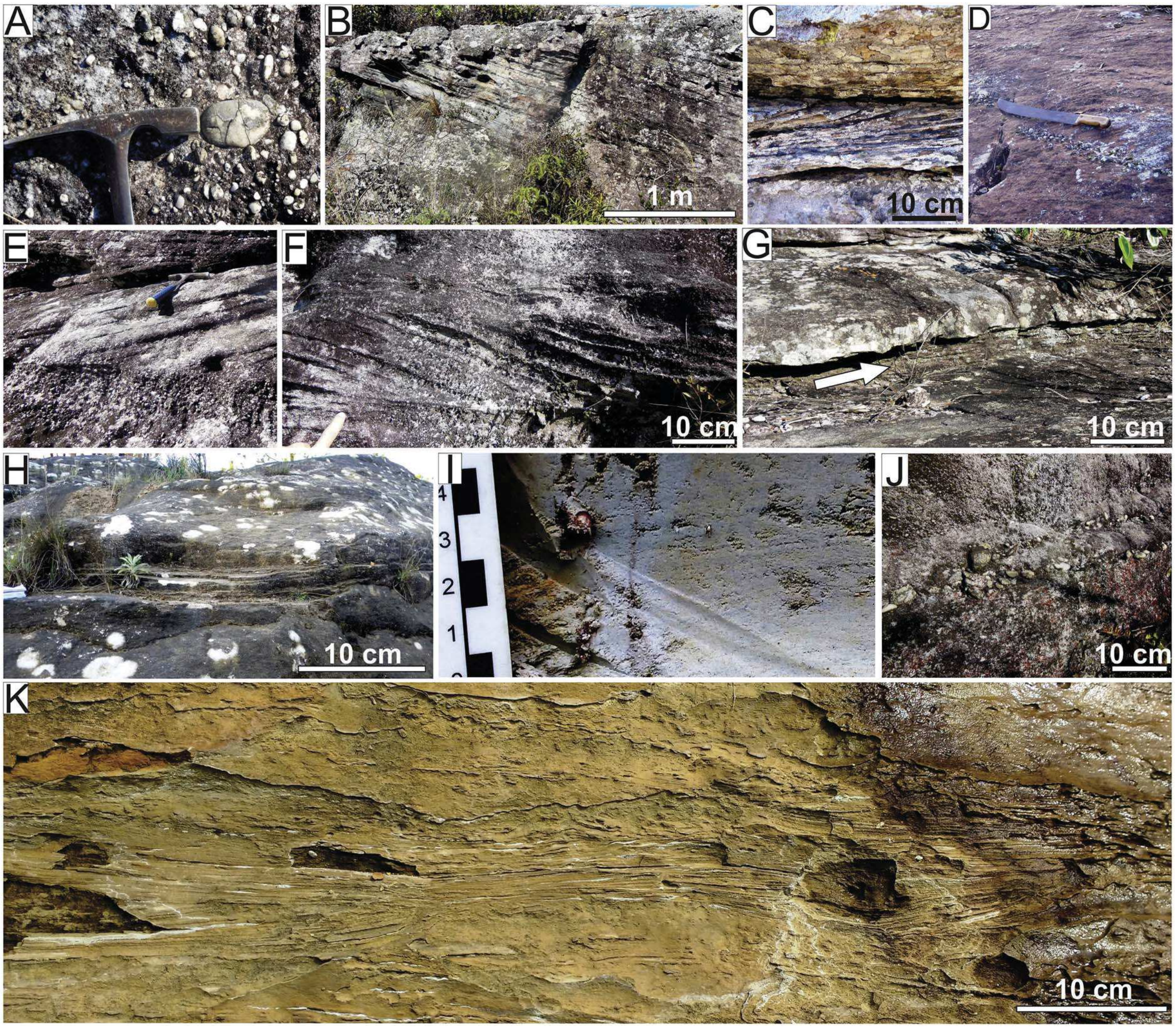

Fig. 4. Sedimentary facies of Furnas Formation (see Table 1). A. Pebbly coarse-grained sandstones (facies Sm). B. Fine- to medium-grained sandstones with tabular sets of planar cross-stratification (facies Sp). C. Fine- to medium-grained sandstones with trough cross-stratification (facies St). D. Structureless and locally imbricate clast pavements (facies Gm). E. Stratified, clast-supported conglomerate (facies Gt). F. Fine- to medium-grained sandstone with trough cross-stratification with reactivation surfaces (facies Ss). G. Medium-grained sandstones with horizontal stratification (arrow; facies Sh). H. Wave ripples in very fine- to fine-grained sandstones (facies Sr). I. Massive mudstones (facies F/Fl). J. Structureless clast pavements (facies Gm at middle–upper units contact). K. Fine-grained sandstones with hummocky cross-stratification (facies Shc).

Didymaulichnus lyelli, *Thalassinoides*, *Cruziana acacensis elongata*, *Didymaulyponomos rowei*, *Heimdallia chatwini*, *Lockeia siliquaria*, *Psammichnites implexus*, *Rhizocorallium commune*, *Rusophycus acacensis*, and *Arthrophycus brongniartii*. Skolithos Ichnofacies assemblages include *Arenicolites*, *Skolithos*, *Cylindrichnus* and *Diplocraterion*. Rippled sandstones (facies Sr) contain *Palaeophycus* and locally *Arthrophycus alleghaniensis*. Massive mudstones and siltstones (facies F/Fl) lack trace fossils altogether.

5.3. Upper unit

The upper unit is represented at all sections except at Sítio Canei. It is ~130 m thick at Guartelá, while only the uppermost 17 m and the lowermost 2 m are exposed at PR 340 and São Jorge-Alagados, respectively (Fig. 5). The base of the upper Furnas Formation is marked by a sharp planar erosive ravinement surface, overlain by thin clast-supported conglomerate beds (Fig. 4J).

This unit is dominated by medium- to coarse-grained sandstones with planar (lithofacies Sp), trough (facies St), or sigmoidal cross bedding (facies Ss) in sets ranging from 0.5 to 5.0 m in thickness. Sandstones with sigmoidal cross bedding contain common mud drapes.

Subordinate facies include thin, locally imbricated clast pavements (facies Gm), massive to weakly graded, conglomeratic sandstones (facies Sm), trough cross-stratified, clast-supported conglomerates (facies Gt), fine- to medium-grained hummocky cross-stratified sandstones (facies Shc; Fig. 4K), and massive mudstones (facies F). The last two lithofacies are generally restricted to the PR 340 section, in the upper parts of the upper unit. Mudstones at that level contain terrestrial fossil remains, including that of the primitive vascular plant *Cooksonia* (Gerrienne et al., 2001).

Most of the lithofacies in this unit are weakly bioturbated (BS = 1–2) and contain trace fossil assemblages representing both the proximal Cruziana and Skolithos ichnofacies (Fig. 5). The former includes *Palaeophycus*, *Thalassinoides*, and locally *Rhizocorallium commune* or *Didymaulichnus lyelli*. The latter includes *Skolithos*, *Arenicolites*, and *Cylindrichnus*.

Hummocky cross-stratified sandstones (facies Shc) occur interbedded with shales at the very top of Unit III, in what Petri (1948) referred to as the “Transitional Beds” to the overlying Ponta Grossa Formation. The Transitional Beds are relatively highly bioturbated (BS 3–4), reflecting the dense emplacement of commonly stacked *Rosselia* (i.e., the Crowded *Rosselia* Ichnofabric, or CRI, of Netto et al., 2014) and localized co-occurrences of *Cylindrichnus*, *Skolithos* and/or *Diplocraterion*.

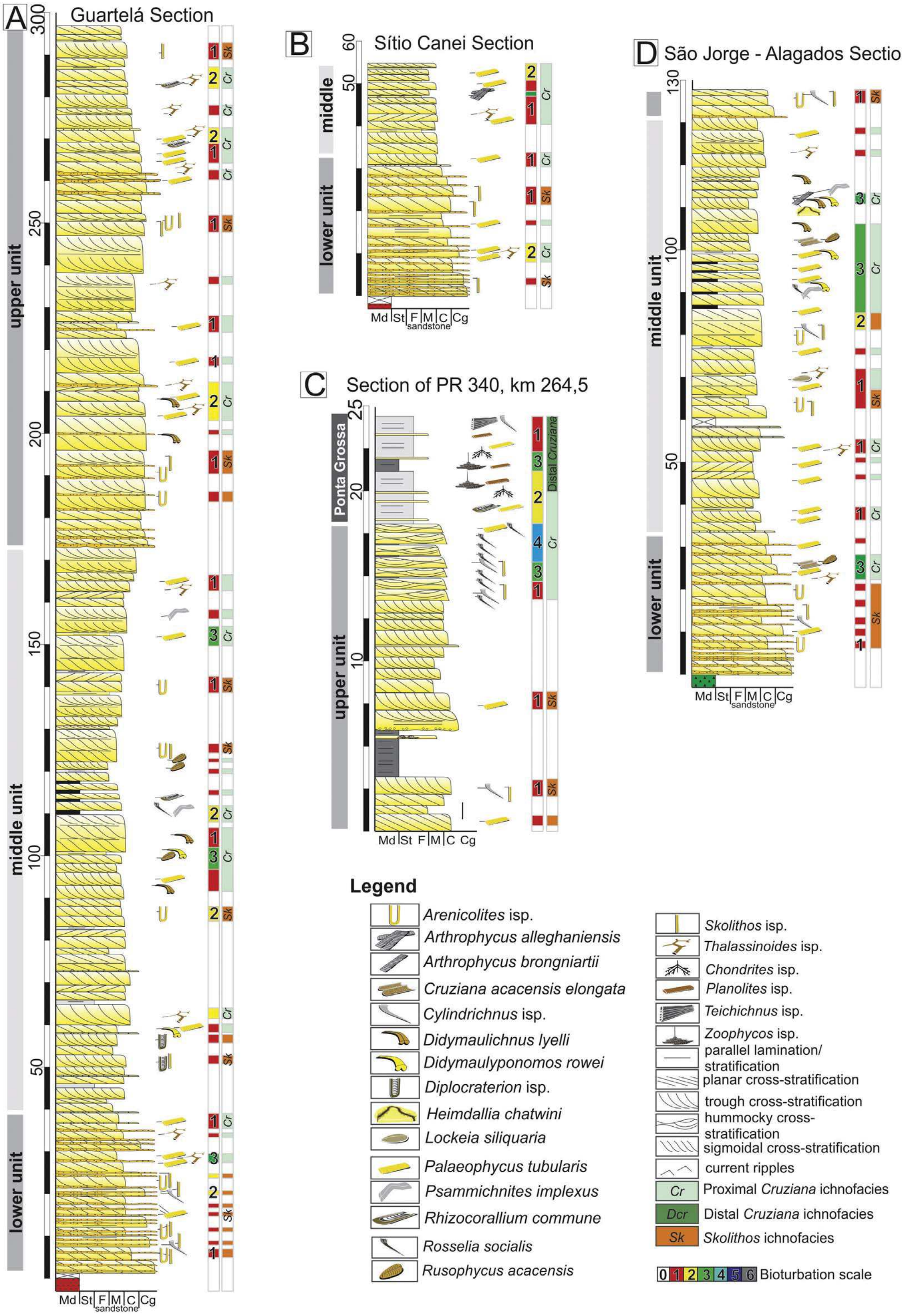

Fig. 5. Distribution of lithofacies, recurring ichnotaxa, degree of bioturbation, and ichnofacies in four sections of Furnas Formation in Campos Gerais region, Paraná State, Brazil. A. Canyon Guartelá section, Tibagi. B. "Sítio Canei" section, Palmeira. C. PR340 section, Tibagi; D. São Jorge–Alagados section, Ponta Grossa.

6. Paleoenvironmental interpretation

Based on detailed stratigraphic and sedimentologic data, supported by the presence of trilobite traces, Assine (1996, 1999) interpreted the Furnas Formation as representing marine environments. Our sedimentologic and ichnologic observations overwhelmingly support that interpretation, particularly the detailed trace fossil analysis, as discussed below.

6.1. Physical sedimentologic evidence

Sedimentary facies associations are consistent with high-energy, tide-dominated and, to a lesser extent, storm-influenced, shallow marine depositional environments. Laterally extensive tabular cross-bed sets, common in sandstones throughout the Furnas Formation (Fig. 4B), are inconsistent with fluvial braided systems. In contrast, tabular sets may be common in tidal regimes, reflecting the migration

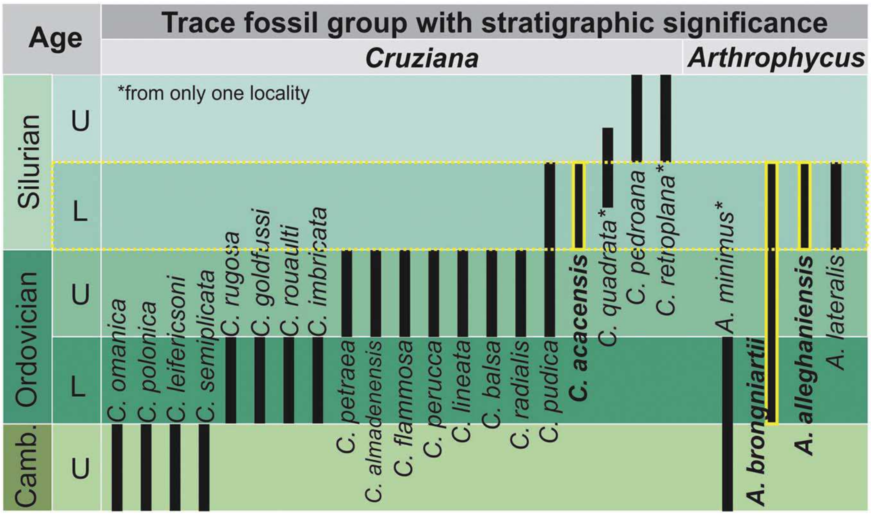

Fig. 6. Chronostratigraphic range of ichnospecies of *Cruziana* and *Arthrophycus* (ichnotaxa present in lower and middle units of Furnas Formation are highlighted in bold) (modified after Seilacher, 2007; Brandt et al., 2010; Buatois and Mángano, 2011).

of elongate, straight-crested, flat-topped subaqueous bars or sandwaves in areas of high tidal asymmetry (Dalrymple and Choi, 2007). Specific lithofacies also provide evidence for significant tidal influence. These include sandstones with sigmoidal cross-bedding (facies Ss; Fig. 4F) and mud drapes, which occur with increasing frequency upward through the middle and upper units (Fig. 5). These sets reflect tide-mediated migration of bedforms in areas of higher tidal asymmetry (Reading, 1996). While a tidal signal is prevalent throughout most of the Furnas Formation, the hummocky cross-stratified sandstones (facies Shc) observed at the top of the section at the PR 340 locality (the aforementioned Transitional Beds of Petri, 1948) reflect a storm-influenced marine setting. As previously suggested by Netto et al. (2014), facies Shc likely reflects deposition in lower shoreface or transitional offshore settings.

6.2. Ichnologic evidence

Ichnofossil assemblages lend further support for the marine interpretation. Some of the recurring ichnotaxa found in the Furnas Formation have been recognized in continental as well as marine deposits, such as *Palaeophycus*, *Didymaulichnus*, and *Skolithos* (Bradshaw, 1981; Buatois et al., 1998; Buatois and Mángano, 2011). Other ichnotaxa, including *Arenicolites*, *Cylindrichnus*, and *Rhizocorallium*, also have been recognized in continental facies, but only in the post-Paleozoic stratigraphic record (Minter et al., 2016). Notably, throughout the Furnas Formation, such potentially facies-crossing ichnotaxa co-occur with other ichnotaxa that are regarded as indicative of marginal marine and marine conditions (e.g., *Thalassinoides*, *Rusophycus*, *Cruziana*, *Arthrophycus*, *Psammichnites*). Hence, ichnofossil assemblages at all levels indicate marine conditions.

The low intensities of bioturbation observed through the Furnas Formation overall reflect high-energy regimes. Ichnofossils likely were only emplaced during periods of relatively quiescence that provided windows for colonization by benthic organisms. Skolithos Ichnofacies assemblages reflect colonization under high-energy environmental conditions, while Cruziana Ichnofacies assemblages record colonization in quieter, deeper-water settings. The latter ichnofacies dominates in the middle unit, which is characterized by finer overall finer grain size and includes common interbedded fine-grained facies. The middle unit contains the most ethologically diverse ichnoassemblages. This likely reflects lower-energy regimes (and, perhaps, somewhat deeper water) than those associated with lower and upper units.

As noted above, the common stacked, funnel-shaped *Rosselia* in hummocky cross-stratified sandstones in "Transitional Beds" record equilibrium responses by stress-tolerant organisms to high-frequency storm depositional events (Netto et al., 2014).

In summary, sedimentologic and ichnologic observations of the Furnas Formation indicate deposition in moderate- to high-energy, strongly tide-influenced but locally storm-influenced marine environments, most likely in the lower shoreface to offshore transition. Depending on energy regime and available colonization windows, sediments were periodically inhabited by varied communities of suspension-, detritus-, deposit-feeding, and/or predaceous organisms.

7. Ichnostratigraphic implications

Aside from plant fossils found in thin, fine-grained facies in the upper unit (Mussa et al., 1996; Gerrienne et al., 2001), body fossils are absent in the Furnas Formation. The lack of body fossils is likely related to persistently high-energy conditions and sandy substrates unfavorable for preservation. These substrates were probably relatively permeable and saturated with oxygenated pore water, factors that are not conducive for body fossil preservation. Regardless of the cause, the absence of body fossils precludes traditional biostratigraphic studies. Fortunately, ichnofossils can assist in establishing age relations and chronostratigraphic framework.

7.1. Furnas Formation ichnofossils as biostratigraphic indicators

One of the commonly stated principles of ichnology is that most trace fossils have rather long geologic ranges and, hence, generally are of limited or no use in biostratigraphic analysis (e.g., Bromley, 1996; Buatois et al., 2002; Buatois and Mángano, 2011). However, for lower Paleozoic strata, certain ichnotaxa preserve morphological features that reflect behaviors and construction strategies that can be linked to specific groups of age-diagnostic trace makers and therefore can be applied as biostratigraphic indicators (Seilacher, 2007). Such trace fossils include *Cruziana* and the arthrophycids (Seilacher, 2000, 2007; Mángano et al., 2005; Buatois and Mángano, 2011) (Fig. 6).

Cruziana and *Rusophycus* were reported in previous investigations of the Furnas Formation (Fernandes, 1996; Assine, 1999; Seilacher, 2007; Netto et al., 2012). Three ichnotaxa with ichnostratigraphic significance are here documented: *Cruziana acacensis elongata*, *Arthrophycus alleghaniensis*, and *A. brongniartii*. Both *Cruziana acacensis elongata* and *Rusophycus acacensis*, which comprise the "*acacensis* group", were recognized here in the middle unit (São Jorge-Alagados section; Fig. 5). Seilacher (2007) recognized this group as a stratigraphic marker of the Lower Silurian (Fig. 6), a relationship corroborated by co-occurrences of ichnofossils and body fossils at other Gondwanan locations, in Benin and Argentina.

Regarding the arthrophycids, Mángano et al. (2005) and Brandt et al. (2010) list five ichnospecies with ichnostratigraphic significance: *A. brongniartii* (= *A. linearis*), *A. alleghaniensis*, *A. lateralis*, *A. minimus* and *A. parallelus* (Fig. 6). Both *A. brongiartii* and *A. alleghaniensis* are present in the middle unit of Furnas Formation (in the São Jorge-Alagados and Sítio sections, respectively; Fig. 5). *A. brongiartii* is an indicator of the Lower Ordovician to Lower Silurian, while *A. alleghaniensis* is used as a guide fossil for the Lower Silurian (Seilacher, 2000, 2007; Buatois and Mángano, 2011). These relations are supported by other occurrences of these ichnospecies in fossiliferous strata reported mostly in Gondwanan terranes from Brazil, Argentina, Falkland/Malvinas Islands, Libya and Chad, with records recently reported from Laurasia (USA; Rindsberg and Martin, 2003; Mángano et al., 2005). Based on the discussion above, a Lower Silurian age can be assigned to the lower and middle units of the Furnas Formation.

The record of the "*acacensis* group" in Paraná Basin (Brazil) fills a geographic gap in Gondwana during the Lower Silurian, corroborating the idea of a possible transcontinental seaway (Seilacher, 2007), since this group was previously reported in Argentina (Jujuy Province) and North Africa. Besides the paleogeographic relevance, this revised sequence stratigraphic framework may have implications for hydrocarbon exploration in the Paraná Basin. Notably, once-contiguous lower Silurian strata in North Africa are important source and reservoir rocks.

7.2. Sequence stratigraphic implications

Two different interpretations have been proposed with regard to the sequence stratigraphy of the Furnas Formation (Fig. 1B). Excluding the uppermost storm-influenced transition beds, Bergamaschi (1999) considered the entire section of the Furnas Formation as a single transgressive-regressive cycle. In contrast, Assine (1996) placed a sequence boundary between the middle and upper units, based on the existence of lag pavements on ravinement surfaces between the middle and upper units, visible in outcrops and traceable in the subsurface using gamma-ray well logs.

Our data also suggest the existence of a significant stratigraphic discontinuity at the base of the upper unit (Fig. 7). During deposition of the lower and middle units (Lower Silurian according the ichnogenera reported here), sedimentation took place under relatively uniform conditions in tidally influenced regimes, and the finer sediment textures and greater ichnological diversity of the middle unit could be interpreted as an indication of transgression.

However, it is not yet possible to accurately determine the magnitude of the gap recognized between the middle and upper unit, owing to the lack of age-constraining fossils through the 100 m-thick upper unit. Palynomorphs and primitive plant fossils have been recovered only near the top of the upper unit (maximum 30 m below the contact with the Ponta Grossa Formation) and these reveal lowest Devonian ages; i.e., Pragian (Dino and Rodrigues, 1995) or Lochkovian (Loboziak and Melo, 2002; Rubinstein et al., 2005; Milagres et al., 2007; Grahn et al., 2010).

The hiatus recognized between the middle and upper Furnas is coincident with the major sea-level fall that occurred during the Late Silurian (Ross and Ross, 1988; Johnson, 1996). However, it is not possible to affirm the time span between deposition of the lower and middle Furnas (Lower Silurian) and the upper Furnas (? Upper Silurian to Pragian) (Fig. 7).

There is no evidence of subaerial exposure in the studied sections, nor the existence of substrate-controlled ichnofacies. The presence of pavements of conglomerate lags is suggestive of sea level fall, fluvial progradation on shelfal environments and subsequent wave reworking and gravel concentration. This sedimentologic information is in accordance with ichnofacies changes, but the temporal significance of this disconformity within the Furnas Formation would not have been established without information provided by age-diagnostic ichnotaxa.

8. Conclusions

1. Seventeen ichnotaxa were identified in the Furnas Formation exposed in the Campos Gerais region of Brazil, doubling the number of ichnotaxa previously recognized in these strata. These traces record feeding, dwelling and/or locomotion activities of various invertebrate organisms (mainly arthropods, polychaetes, and mollusks). Associations of these ichnotaxa define two ichnofacies: Skolithos and proximal Cruziana ichnofacies.
2. In conjunction with evidence provided by suites of physical sedimentary features (e.g., sigmoidal stratification, mud drapes, and rare hummocky cross-stratification), ichnofossils indicate that Furnas deposition took place in a tide-dominated (locally storm-influenced), moderate- to high-energy, shallow marine environment.
3. Ichnotaxa with biostratigraphic significance (*Arthrophycus alleghaniensis*, *A. brongniartii*, *Cruziana acacensis elongata*) indicate an Early Silurian (Llandovery to Wenlock) age for the lower and middle units of the Furnas Formation.
4. Considering the Early Devonian (Lochkovian) age established for the upper unit by microfossil evidence, the contact between the middle and upper units of the Furnas Formation corresponds to a significant hiatus associated with the Late Silurian global sea-level

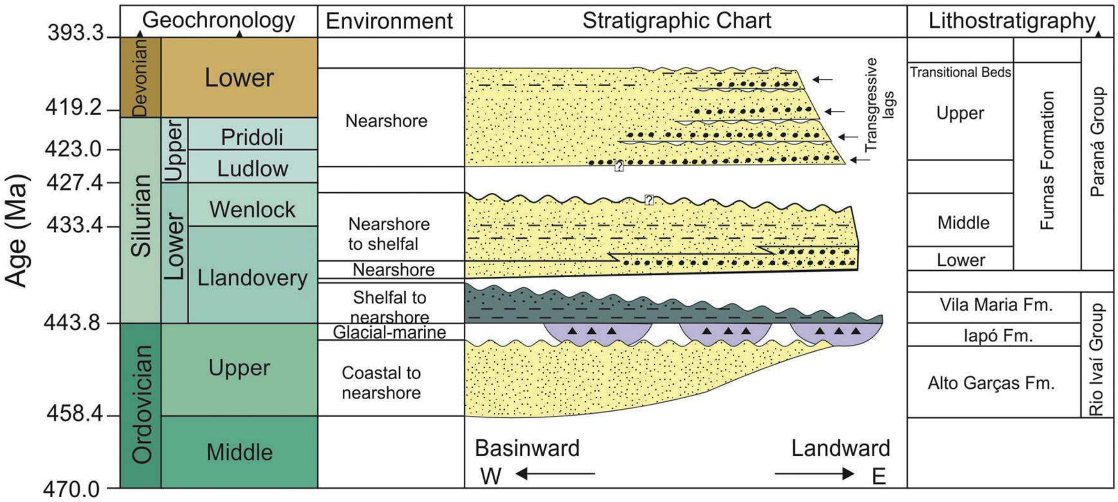

Fig. 7. General chronostratigraphic context of the Rio Ivaí and Paraná groups (supersequences), Paraná Basin, based on the current study (stratigraphic relations for the Ordovician and Devonian are based on Assine et al., 1994, 1998b; Milani et al., 2007; Grahn et al., 2010, 2013; Adôrno et al., 2016; ages are from Cohen et al., 2013).

fall, and may record the Late Silurian (Pridoli) global regression.

5. The recognition of a new Lower Silurian stratigraphic sequence in the Paraná Basin has important implications for Gondwanan palaeogeography and economic resource potential.

Acknowledgments

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Appendix A. Systematic ichnology

Ichnogenus *Didymaulyponomos* Bradshaw, 1981

Didymaulyponomos rowei Bradshaw, 1981

Fig. 3D

2001 *Furnasichnus langei* Borghi and Fernandes, Figs.4, 5

Diagnosis: Horizontal, endichnial burrows with median ridge along the floor and with or without an infill (Bradshaw, 1981).

Material: Observations in situ (São Jorge–Alagados section; Guartelá section).

Description: These structures appear as horizontal, straight to sinuous, unbranched, and unornamented endichnial burrows with median furrows in their lower parts. Fills are structureless and similar or locally finer than surrounding sediment. Specimens are generally equidimensional with respect to width and height (15–20 mm) and may exceed 1 m in length.

Remarks: Recently, Buatois et al. (2017) suggested that *Furnasichnus* is a junior synonym of *Didymaulichnus*, arguing that Borghi and Fernandes (2001) established this new ichnogenus based on the assumption that *Didymaulichnus* is epigenic, while *Furnasichnus* is the product of endogenic activity. In his original description, Young (1972) did regard *Didymaulichnus* as an epigenetic trail. Hence, *Didymaulichnus* does differ from *Furnasichnus* in this regard. However, comparing the original diagnoses of *Didymaulyponomos* Bradshaw, 1981 and *Furnasichnus* Borghi and Fernandes, 2001 (horizontal, straight to sinuous, tubular, unornamented, unbranched burrows, with a median furrow in its lower part; fills with the same type of sediment of the host-rock), it is clear that they describe the same morphology. The only difference is that Borghi and Fernandes (2001) observed fill similar to the host sediment, while Bradshaw (1981) described fill finer than the host sediment. However, this textural difference does not justify ichnotaxonomic separation. Hence, we regard *Furnasichnus* as a junior synonym of *Didymaulyponomos*, a monospecific ichnogenus (*D. rowei*).

Bradshaw (1981) argued that *Didymaulyponomos* represents feeding or dwelling activity by arthropods below the sediment surface. Trewin and MacNamara (1994) observed that the "trail" *Didymaulichnus* is quite similar to the bottom surface of the burrow *Didymaulyponomos*, interpreting that an erosional event may be involved in *Didymaulichnus* preservation. Despite these similarities, both ichnogenera remain valid because it was not proved that they correspond to the same structure. Buatois et al. (2017) included this trace in their architectural design category "passively filled horizontal burrows", similar to *Palaeophycus.* The occurrences of *D. rowei* in the Furnas Formation are associated with *Palaeophycus.*

Ichnogenus *Rusophycus* Hall, 1852

Rusophycus acacensis n. ichnosp.

Fig. 2F, G, J

Diagnosis: Bilobed, ovate, symmetrical traces with furrow exhibiting a distinct medial ridge on the lower surface and sets of five scratches.

Material: Observations in situ (São Jorge-Alagados section; Guartelá section). Holotype: ULVG-12261a (Fig. 2F); paratypes: ULVG-12261b and ULVG-12261.

Description: Short, bilobate burrows with medial ridges, having sets of five heavy and blunt scratch traces. The burrows range from 18 to 32 mm wide and 25 to 60 mm long. These bilobed traces are preserved in concave epirelief, normally with 3 mm depth. Locally, *Rusophycus acacensis* occurs connected with *Cruziana acacensis elongata* (compound trace fossils) (Fig. 2F–G).

Remarks: The name for this ichnospecies comes from the long trace fossil that is preserved connected to *Cruziana acacensis*. Although Seilacher (2007) did not propose *Rusophycus acacensis* as an ichnospecies, he noted that *Cruziana acacensis elongata* frequently is connected with a rusophyciform burrow. Netto et al. (2014) referred to these traces as *Rusophycus* cf. *acacensis*, considering their compound nature, and here we define this new ichnospecies.

The tracemakers of both *Cruziana* and *Rusophycus* are bilaterally symmetrical organisms, most probably arthropods (Donovan, 2010). In Paleozoic strata, they occur exclusively in marine deposits and are generally attributed to trilobites (Goldring, 1985; Fortey and Seilacher, 1997). In the current study, both *C. acacensis* and *R. acacensis* were produced by the same tracemaker in response to different behaviors.

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CAPÍTULO 3

An integrative ichnological and taphonomic approach in a transgressive–regressive cycle: a case study from Devonian of Paraná Basin, Brazil

Artigo publicado no periódico “Lethaia” onde o objetivo foi utilizar análise icnológica, tafonômica e sedimentológica associada à máxima transgressão do Emsiano. Neste estudo se definiram padrões para compreender a colonização do ecoespaço em resposta a ciclos transgressivo-regressivos. Cabe mencionar que o arcabouço estratigráfico utilizado difere daquele apresentado no quarto capítulo (aqui adota-se Bergamaschi 1999) porque foi desenvolvido antes da definição das sequências.

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An integrative ichnological and taphonomic approach in a transgressive–regressive cycle: a case study from Devonian of Paraná Basin, Brazil

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LETHAIA

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The palaeoenvironmental context of a section of the Devonian Ponta Grossa Formation (Paraná Basin) was examined using an integrated ichnological and taphonomic approach. Three taphofacies (T-A, T-B and T-C) and six ichnofabrics are recognized. T-A is mainly composed of disarticulated organisms and is associated with *Chondrites*, *Planolites-Palaeophycus, Asterosoma-Zoophycos* and *Asterosoma-Chondrites* ichnofabrics, representing the *Cruziana* ichnofacies. The upward increase in diversity and abundance of body fossils for Taphofacies A can be explained by changes in sedimentation rates during aggradational to progradational phases. T-B beds, represented by articulated brachiopods, occur in distal tempestites associated with the *Skolithos* ichnofabric (*Skolithos* ichnofacies) and represent higher hydrodynamic energy and oxygenation than in T-A. Taphofacies C, characterized by a mix of articulated and disarticulated organisms, generally lacks bioturbation except for *Chondrites* ichnofabrics occurring only at the bed tops, suggesting low substrate oxygenation and low-energy conditions. T-C indicates the maximum transgression in the T-R cycle, characterizing it as a good indicator of maximum flooding surfaces. The composite *Asterosoma-Teichichnus* ichnofabric (bioturbation degree 5) occurs in layers without body fossils and represents suites of the *Cruziana* ichnofacies. This likely reflects intense intrastratal activity at all substrate levels, which facilitated the oxygenation of the substrate disallowing the preservation of organism remains. This observation indicates that the bioturbation is an important factor controlling the loss of taphonomic information within the TAZ, mainly when associated with detritus-feeding trace fossils. ☐ *Devonian shales, Gondwana, ichnofacies, marine siliciclastic deposits, palaeoenvironmental analysis, taphofacies.*

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The study of trace fossils has been largely increased as the ichnofacies paradigm was proposed by Seilacher (1964). Studies integrating ichnological and sedimentological data sets using the ichnofabric approach (e.g. Ekdale & Bromley 1983; Ekdale *et al.* 1984; Bromley & Ekdale 1986) have become commonplace (e.g. Pollard *et al.* 1993; Taylor & Goldring 1993; Gibert & Martinell 1998; Savrda *et al.* 2001a,b; Droser *et al.* 2002; Netto & Rossetti 2003; Miller & Aalto 2008; Heard *et al.* 2014; Netto *et al.* 2014; Villegas-Martín *et al.* 2014; Leonowicz 2015), and analyses based on trace fossil taphonomy also have been enhanced (e.g. Kotake 1989; Bromley & Asgaard 1991; Bertling 1999; Jensen *et al.* 2005; Monaco 2008; Monaco *et al.* 2012; Good & Ekdale 2014; Bieńkowska-Wasiluk *et al.* 2015). Ichnological and taphonomic data have been used to support sedimentological, stratigraphical, palaeoenvironmental and palaeoecological inferences (e.g. Velbel 1985; Brett & Baird 1986; Speyer & Brett 1986, 1988; Brandt 1989; Frey 1990; Bromley & Asgaard 1991; Radley *et al.* 1998; Savrda & Nanson 2003; Buatois *et al.* 2008; Pak *et al.* 2010; Saneyoshi *et al.* 2011; Good & Ekdale 2014; Kietzmann & Palma 2014), but rarely in an integrate approach. Few studies integrated ichnology and taphonomy to infer palaeoenvironmental contexts (e.g. Henderson & McNamara 1985; Bromley & Asgaard 1991; Reolid *et al.* 2014).

Taphonomy plays an important role in ichnological analyses to evaluate the processes involved in trace fossil preservation (e.g. Gibert & Martinell 1996; Uchman *et al.* 1998; Mángano *et al.* 2002; Genise & Cladera 2004; Dentzien-Dias *et al.* 2008; Genise *et al.* 2009; Marty *et al.* 2009; Boyd 2010; Scott *et al.* 2010; Carmona *et al.* 2011; Monaco 2011; Locatelli 2013). Studies focusing on a more integrative ichnological and taphonomic approach have increased in the last two decades as well (e.g.

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Bromley & Asgaard 1993; Bertling 1999; Sutcliffe *et al.* 2000; Donovan & Jagt 2004; Davies *et al.* 2007; Bressan & Palma 2008; Monaco 2008, 2014; Smith *et al.* 2009; Carmona *et al.* 2010; Marsicano *et al.* 2010; Monaco & Checconi 2010; Carnevale *et al.* 2011; Luo & Chen 2014; Serrano-Brañas & García 2014; Rahman *et al.* 2015; Reolid *et al.* 2015; Tapanila *et al.* 2015), but the majority of them involve three-dimensional, well-preserved trace fossils. Only a few are based on ichnofabrics or embrace both ichnofacies and taphofacies (e.g. Savrda & Ozalas 1993; Giannetti *et al.* 2005; Monaco *et al.* 2012; Belaústegui & Gibert 2013; Buatois *et al.* 2015; Giannetti & Monaco 2015). Notably, all of them occur in substrates of Cenozoic age containing fossil evidence of the post-Mesozoic Marine Revolution (*sensu* Vermeij 1977, 1978).

The Devonian deposits of the Paraná Basin (southern Brazil) are rich in well-preserved body fossils, some of them preserved in life position, as well as trace fossils. These deposits have been target of many taphonomic studies (e.g. Rodrigues *et al.* 2003; Bosetti *et al.* 2009, 2011, 2013; Simões *et al.* 2009; Zabini *et al.* 2010, 2012; Horodyski *et al.* 2014; Comniskey *et al.* 2016) that considered only the body fossil data. However, higher-resolution analyses of associated trace fossil assemblages suggest that they play a relevant role in body fossil preservation in some beds (e.g. Horodyski 2014; Netto *et al.* 2014; Sedorko 2015) and therefore that integrated ichnological and taphonomic analyses can provide more accurate palaeoenvironmental interpretations. Considering that biostratinomic process, associated to diagenesis, tectonics and weathering, may significantly alter the original characteristics of Palaeozoic siliciclastic substrates (resulting in time- and space-averaged assemblages), taphonomic analysis based exclusively on body fossils may underestimate or overestimate some features. Trace fossils, in contrast, are always *in situ* and reflect sedimentary processes, which are responsible for burial. Thus, the objective of this study are twofold: 1, to analyse the ichnological and taphonomy of these Devonian strata using an integrative approach, as a case study; and 2, to evaluate shifts in sedimentary facies that might denote relevant changes in the depositional system, mainly related to storm events and substrate oxygenation, that are not revealed by body fossils.

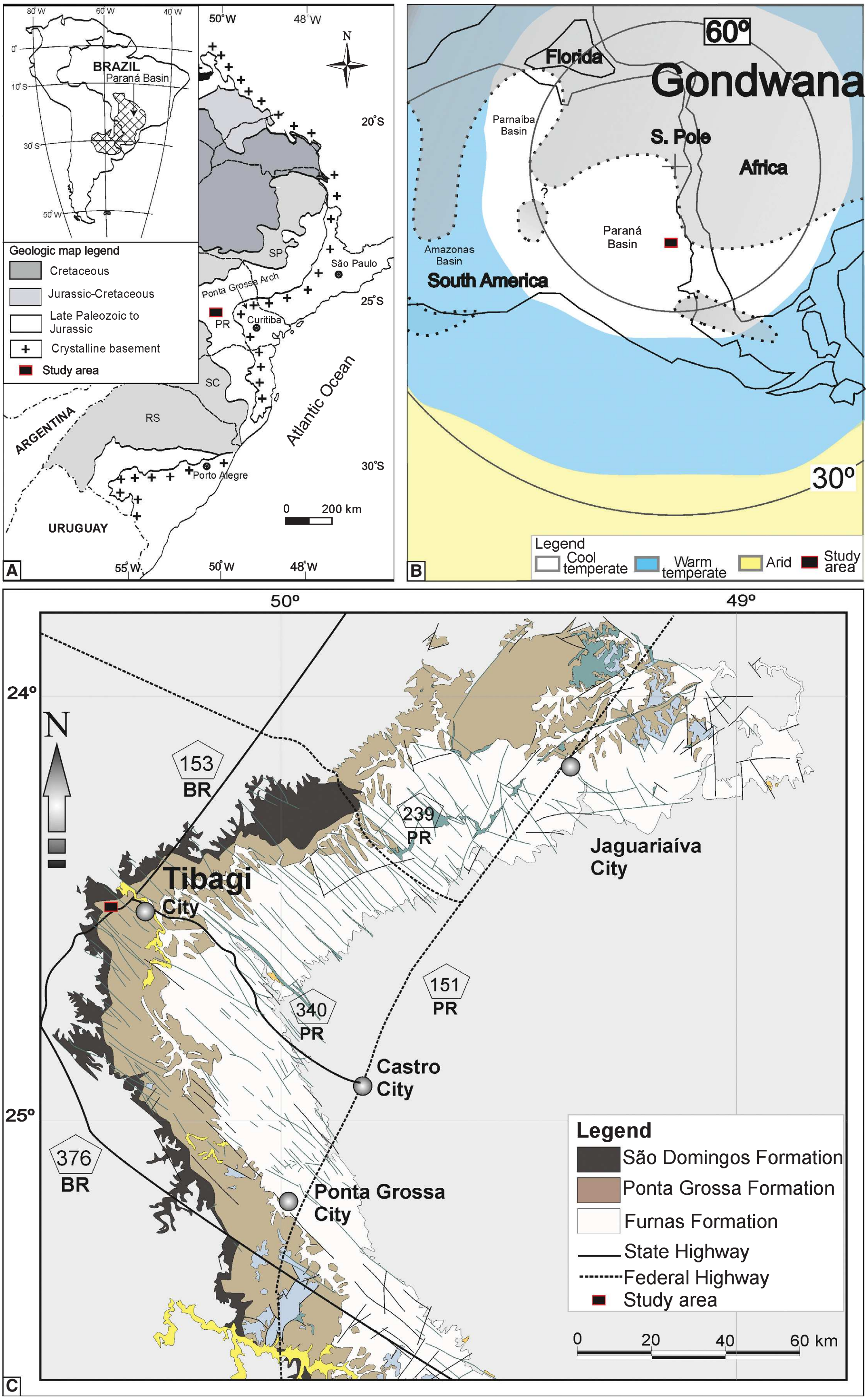
Geological setting

The Paraná Basin is a huge (circa 1.5 × 10^6 km^2) intracratonic basin that covered the southern portion of Brazil and adjacent areas before the Cenozoic (Fig. 1A). Six supersequences comprise the basin sedimentary fill, which was influenced by tectonic-eustatic cycles related to the evolution of western Gondwana from the Late Ordovician to Late Cretaceous (Milani *et al.* 2007). The existence of two depocentres during the Early Palaeozoic allows the differentiation of two sub-basins, Alto Garças (north) and Apucarana (south). Devonian strata occur in both sub-basins and constitute the Paraná Supersequence (Pridoli to Frasnian) that was deposited under marine conditions and a cool temperate climate between 60° and 80° S palaeolatitude (Cooper 1977; Scotese & McKerrow 1990; Matsumura *et al.* 2015; Fig. 1B).

The Paraná Supersequence is composed of six-third-order depositional sequences that correspond to three lithostratigraphical units, the Furnas, Ponta Grossa and São Domingos formations (Fig. 1C), which together are 600 m thick at the surface and almost 1 km thick in the centre of the basin (Grahn *et al.* 2013). The Furnas Formation (300 m thick) contains basal marginal-marine and shallow marine sandy deposits, and its top is composed of sandy heterolithic deposits and fine- to medium-grained sandstones with hummocky cross-stratification (HCS sandstones) strongly bioturbated with a dense *Rosselia* ichnofabric (Netto *et al.* 2014). A transgressive lag, represented by coarse-grained, pebbly sandstone atop the Furnas Formation, marks the transgression manifested in the basal deposits of the Ponta Grossa Formation (~80 m thick). The Ponta Grossa Formation is mostly composed of offshore siltstones, and a thick bed of black shale (approximately 2 m) represents the maximum flooding deposits in the basin during the Emsian (e.g. Bergamaschi 1999; Grahn *et al.* 2013). Siltstones and HCS sandstones forming parasequences overlie the black shale, representing offshore transition and shoreface deposits that characterize a highstand systems tract (*sensu* Grahn *et al.* 2013). These deposits are overlain by sandstones, siltstones and shales of the São Domingos Formation (220 m).

The studied deposits crop out in the Tibagi region (Paraná State, southern Brazil), at the 211-km

Fig. 1. A, location of the study area in the Paraná Basin, southern Brazil (modified of Horodyski *et al.* 2014). B, inferred position of the study area on Gondwana during the Emsian (from Matsumura *et al.* 2015). C, stratigraphical position of Devonian units on east side of the Paraná Basin (modified from Bosetti *et al.* 2012). [Colour figure can be viewed at wileyonlinelibrary.com]


A
80°W
60°W
40°W
0°
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30°S
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BRAZIL
Paraná Basin
Geologic map legend
Cretaceous
Jurassic-Cretaceous
Late Paleozoic to Jurassic
Crystalline basement
Study area
50°W
48°W
N
20°S
SP
São Paulo
Ponta Grossa Arch
25°S
PR
Curitiba
SC
RS
ARGENTINA
Atlantic Ocean
Porto Alegre
30°S
URUGUAY
0 200 km
55°W
50°W
48°W
B
60°
Florida
Gondwana
Parnaíba Basin
S. Pole
Africa
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Amazonas Basin
Paraná Basin
South America
30°
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Cool temperate
Warm temperate
Arid
Study area
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153
BR
239
PR
Tibagi City
Jaguariaíva City
340
PR
151
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Castro City
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São Domingos Formation
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Furnas Formation
State Highway
Federal Highway
Study area
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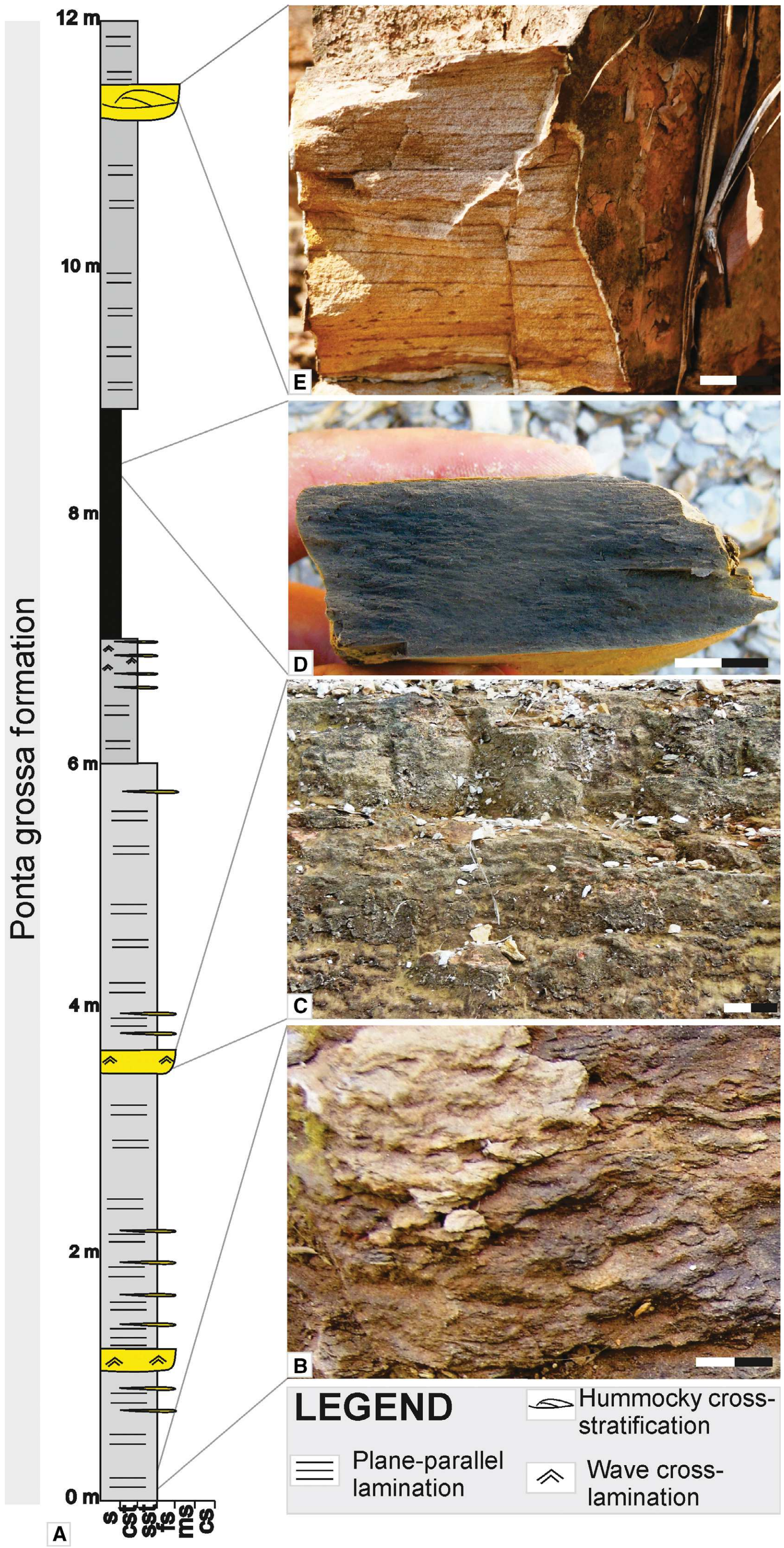

Fig. 2. A, generalized stratigraphical columm of the study interval (s = shale; cst = clayey siltstone; sst = sandy siltstone; fs = fine-grained sandstone; ms = medium-grained sandstone; and cs = coarse-grained sandstone) and photographs of representative lithologies (B–E). B, sandy siltstones with parallel lamination interrupted by fine-grained sandstone lenses. C, fine-grained sandstone beds with wave ripples. D, pyritiferous black shale. E, Fine-grained sandstone with hummocky cross-stratification. Scale bars = 2 cm. [Colour figure can be viewed at wileyonlinelibrary.com]

marker along the BR 153 Highway (geographical coordinates 24°33′50″S, 50°27′14″W; Fig. 1C). The outcrop exposes a 12-m-thick sedimentary succession composed mainly of muddy deposits rich in marine invertebrate fossils of Emsian age representing part of the Malvinokaffric Realm assemblage (*sensu* Richter & Richter 1942) preserved in Lower Devonian strata of the Paraná Basin (Bosetti 2004).

The vertical sequence of lithologies in the study section (Fig. 2) records the transition from a TST to a HST, characterizing a single transgressive–regressive cycle. The transgressive deposits include, in ascending order, siltstones with parallel lamination interrupted by fine-grained sandstone lenses (Fig. 2B) and rare fine-grained sandstone beds with wave ripples (Fig. 2C), mudstones with parallel lamination and a ~1.5-m-thick pyritiferous black shale (Fig. 2D). Black shales signal the retrogradational trend that characterizes the top of the Ponta Grossa Formation (e.g. Bergamaschi 1999; Grahn *et al.* 2013). Aggradational to progradational highstand deposits overlying the black shale include clay-rich siltstones with parallel lamination and fine-grained sandstones with hummocky cross-stratification (Fig. 2E). Facies characteristics are summarized in Table 1.

The studied section was selected because it records sea-level-related palaeoenvironmental changes and it contains an unusual abundance of both trace and body fossils. Trace fossils are represented by *Arenicolites, Asterosoma, Chondrites*, *Cylindrichnus, Diplocraterion*, *Lockeia*, *Palaeophycus*, *Planolites*, *Rhizocorallium, Rosselia, Skolithos, Teichichnus, Thalassinoides* and *Zoophycos* (Fig. 3). Brachiopods (*Orbiculoidea* spp., *Australocoelia palmata*, *Schuchertella* sp., *Australospirifer* spp., infaunal lingulids), trilobites (Homalonotidae and Calmonidae), molluscs (Bivalvia *Edmondia* sp., *Palaeoneilo* sp., *Nuculites* sp. and Tentaculitoidea *Tentaculites* sp.), asteroid echinoderms (Echinasteridae) and plant fragments constitute the body fossil assemblage (Fig. 4).

Material and methods

Trace fossil analysis included characterization of ichnofabrics and quantification of degree of bioturbation, while taphonomic analysis considered the skeletal types preserved in the host rock and their taphonomic signatures (degree of disarticulation, packing, fragmentation, abrasion, corrosion, rounding, reorientation, bioerosion, dissolution and position of fossil within the layer). The amount of bioturbation is expressed based on bioturbation degrees proposed by Reineck (1963), ranging from 0 (without bioturbation) to 6 (homogenized sediment or no apparent sediment structure); the poor preservation permitted identification only at the ichnogenus level. Taphonomic data were acquired by the methodology of Simões & Ghilardi (2000) as adapted by Bosetti (2004), who changed the grid cell size to 3 m wide by 2 m high. Six grid cells were delimited and stacked in the section from which 277 samples were collected containing one or more body fossils. The samples were deposited in the collection of Laboratório de Estratigrafia e Paleontologia at the Universidade Estadual de Ponta Grossa, Brazil, as numbers DEGEO/MPI 1500; 1501; 8596 to 8623; 9695 to 9610; 9636 to 9795; 9883; 9888; 9978 to 9997; 10434 to 10440; 10454 to 10461; 10770 to 10792.

Table 1. Lithologic, ichnologic, and taphonomic character of Ponta Grossa facies and their general paleoenvironmental settings.

Code	Facies	Sedimentary structures	Ichnofabrics	Taphofacies	Depositional process	Sedimentary environment
Sts	Sandy Siltstones	Parallel lamination, locally lenticular bedding	*Planolites-Palaeophycus* and *Asterosoma-Teichichnus*	T-A	Suspension emplaced by muddy to sandy gravity flows	Upper offshore storm-dominated
Stc	Clayey Siltstones	Parallel lamination, locally lenticular bedding	*Asterosoma-Zoophycos; Asterosoma-Chondrites;* and *Chondrites*	T-A	Suspension sediments, locally with contribution of muddy to sandy gravity flows	Upper offshore storm-influenced
S	Pyritiferous black shale	Parallel lamination locally with very fine-grained sandstones lenses	*Chondrites*	T-C	Suspension sediments with high organic content, locally with muddy to sandy gravity flows	Lower Offshore
Sw	Very fine- to fine-grained sandstones	Wave cross-lamination	*Skolithos*	T-B	Oscillatory flows	Offshore transition storm-influenced
Shcs	Very fine- to fine-grained sandstones	Hummocky cross-stratification	*Skolithos*	T-B	Oscillatory flows storm generated	Offshore transition storm-dominated

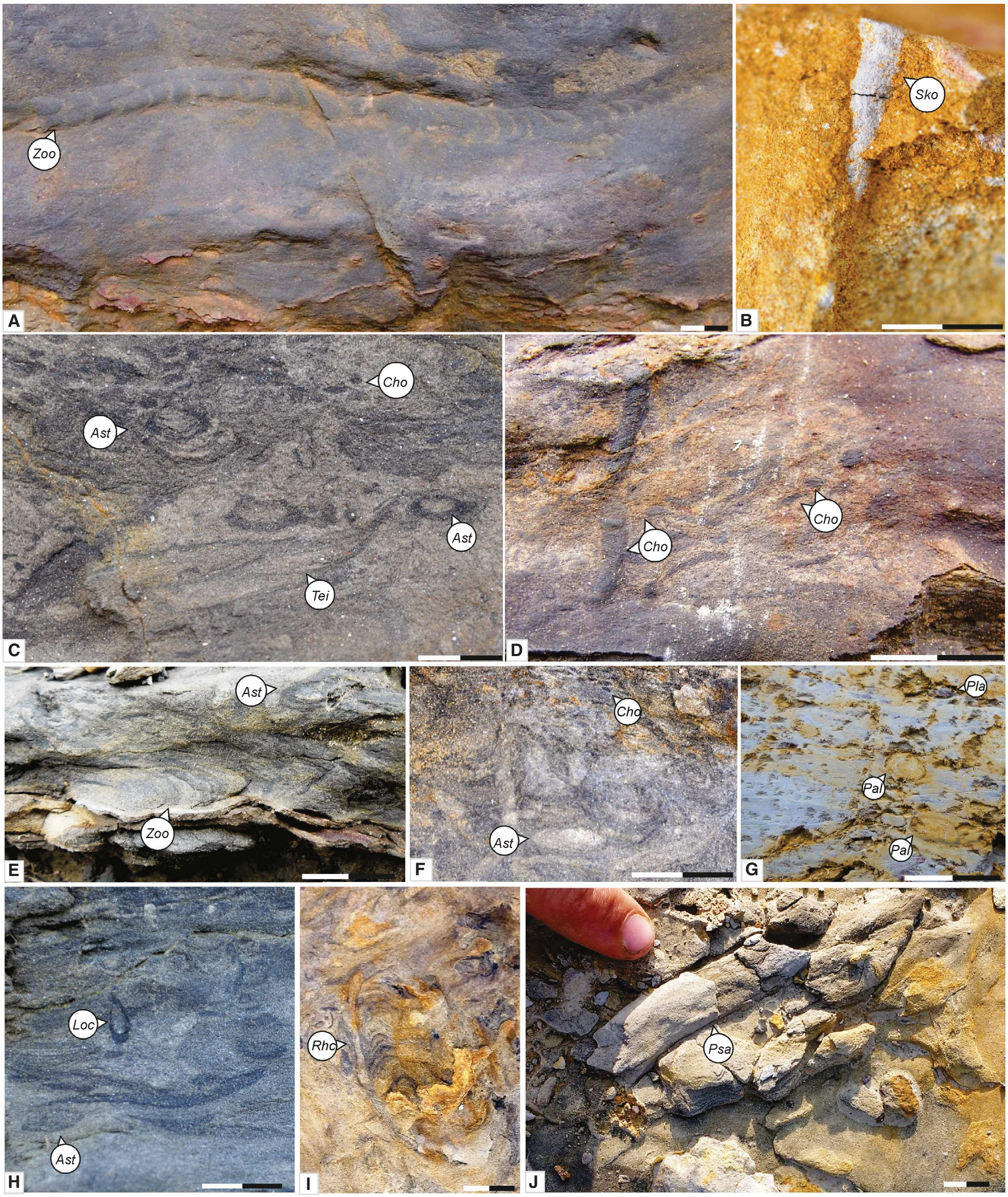

Fig. 3. Ichnofabrics and ichnofossils from the study area. A, *Zoophycos* ichnofabric. B, *Skolithos* ichnofabric. C, composite *Asterosoma-Teichichnus* ichnofabric with *Chondrites*. D, *Chondrites* ichnofabric. E, composite *Asterosoma-Zoophycos* ichnofabric. F, composite *Asterosoma-Chondrites* ichnofabric. G, composite *Planolites-Palaeophycus* ichnofabric. H, I, composite *Asterosoma-Teichichnus* ichnofabric with *Lockeia* (H) and *Rhizocorallium* (I). J, *Psammichnites* as part of composite *Asterosoma-Chondrites* ichnofabric. Scale bars = 2 cm; Zoo = *Zoophycos*; Sko = *Skolithos*; Ast = *Asterosoma*; Tei = *Teichichnus*; Cho = *Chondrites*; Pal = *Palaeophycus*; Pla = *Planolites*, Loc = *Lockeia*; Rhc = *Rhizocorallium*; Psa = *Psammichnites*. [Colour figure can be viewed at wileyonlinelibrary.com]

The collected skeletons were classified in terms of skeletal type as univalved (Mollusca, Tentaculitoidea), bivalved (Brachiopoda and Mollusca, Bivalvia) and multi-element (Trilobita and Echinodermata, Asteroidea). Laboratory analysis of fossil samples allowed identification of taphofacies based

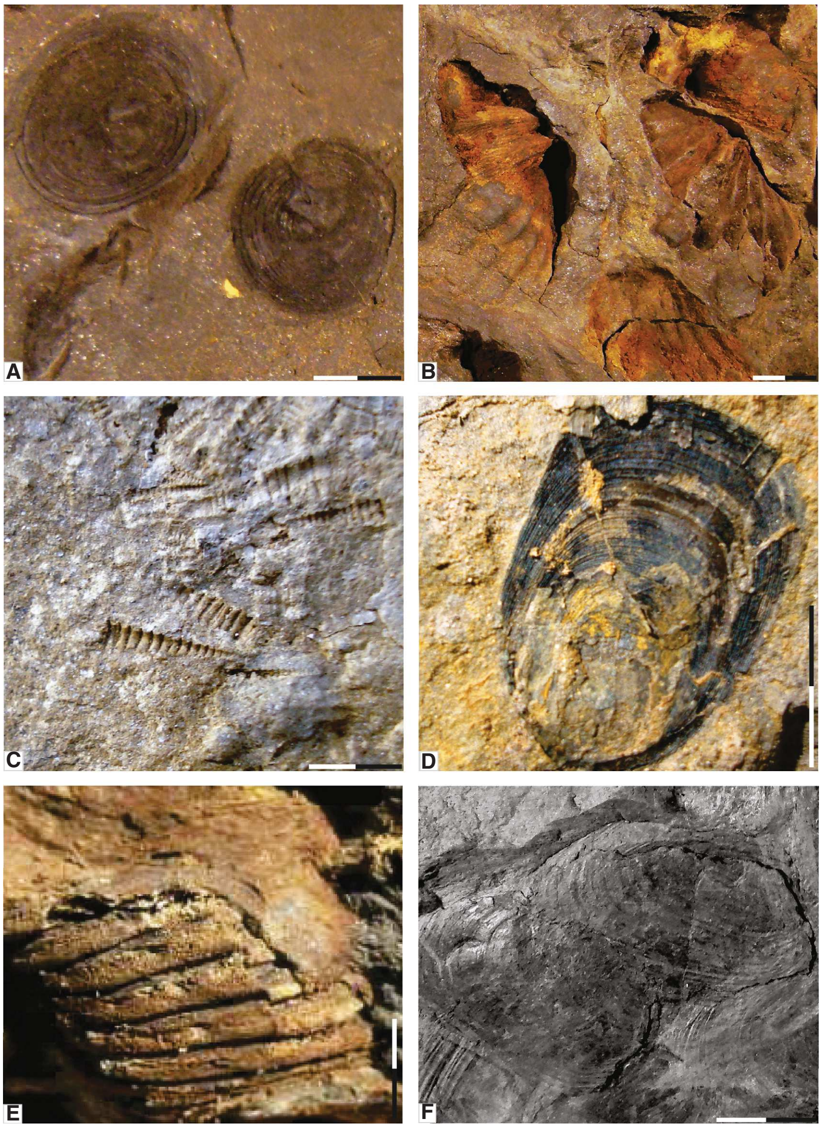

Fig. 4. Body fossils from the study area. A, *Orbiculoidea baini*. B, *Australospirifer* sp. C, *Tentaculites* sp. D, infaunal lingulid. E, trilobite homalonotidae. F, *Edmondia* sp. Scale bar 2 cm. [Colour figure can be viewed at wileyonlinelibrary.com]

on criteria established by Speyer & Brett (1986, 1988). All observable taphonomic signatures were verified, but only articulation, whole-body fossils, reorientation, packing and position relative to bedding planes were diagnosed. Lack of abrasion, corrosion, rounding, bioerosion and dissolution was also considered as relevant data for palaeoenvironmental interpretation.

Ichnofabrics

Bioturbation occurs in most beds in the section, and six distinct ichnofabrics are recognized – the *Asterosoma-Chondrites*, *Asterosoma-Teichichnus*, *Asterosoma-Zoophycos*, *Chondrites*, *Planolites-Palaeophycus*, and *Skolithos* ichnofabrics (Fig. 3). The *Planolites-Palaeophycus*, *Asterosoma-Teichichnus* and *Chondrites* ichnofabrics occur in siltstone beds. The *Skolithos* ichnofabric occurs exclusively in sandstone beds that recur throughout the succession. Except for a discrete occurrence of the *Chondrites* ichnofabric at its top, the shale is devoid of bioturbation (Fig. 5). The *Asterosoma-Zoophycos* ichnofabric is restricted to clayey deposits. The *Skolithos* ichnofabric is a simple ichnofabric formed during short colonization events, while all other ichnofabrics are composite, reflecting long-term overprinting of trace fossils in the host sediment (Bromley & Ekdale 1986).

The *Skolithos* ichnofabric (Fig. 3B) occurs in sandstone beds with wave ripples and hummocky cross-stratification. Although *Palaeophycus* occurs as a

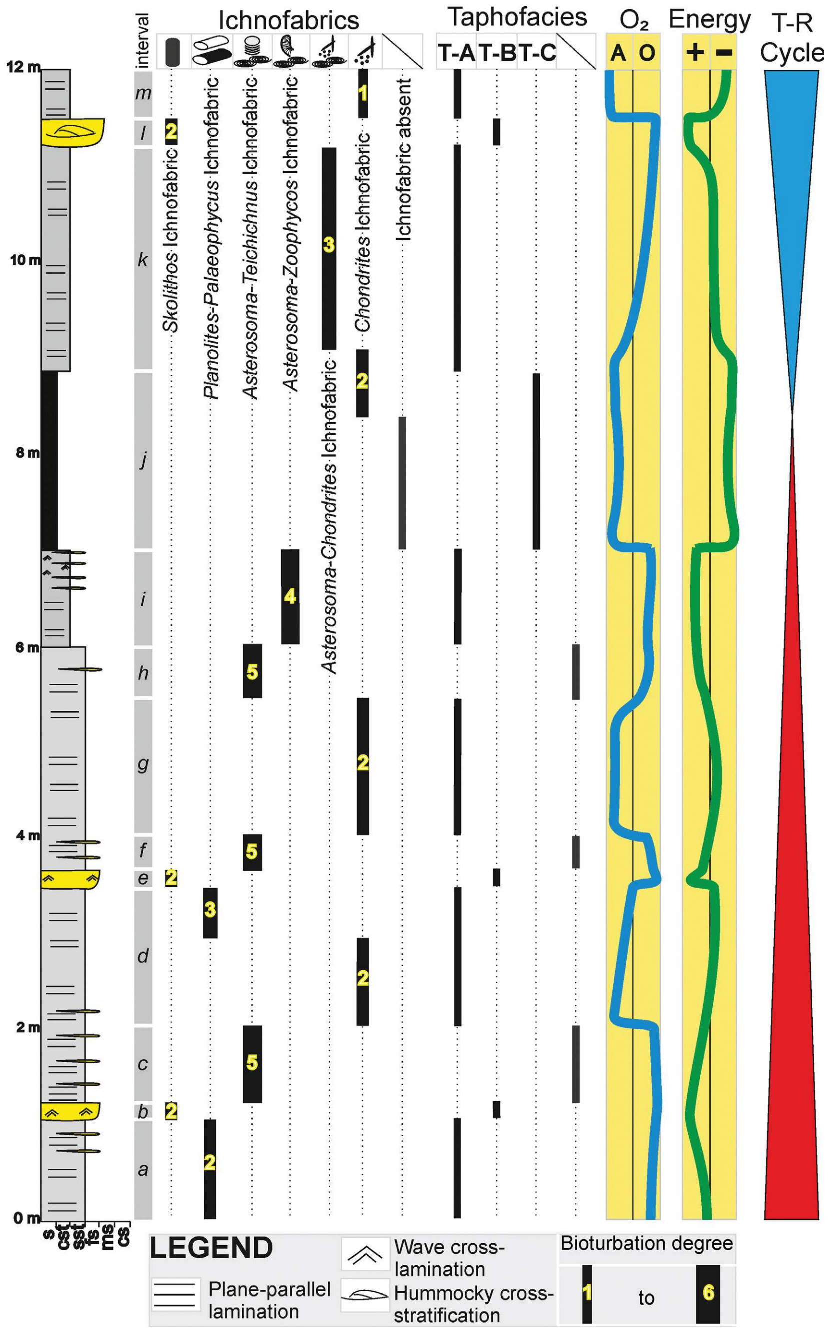

Fig. 5. Ichnofabric and taphofacies characterization in the study area. Fluctuations in oxygenation and hydrodynamic energy through time are inferred from ichnofabric and taphofacies distribution throughout the succession. [Colour figure can be viewed at wileyonlinelibrary.com]

discrete accessory ichnotaxon, the dominant bioturbation consists of simple vertical shafts that express the prevalence of suspension-feeding habit of endobenthic invertebrates. The bioturbation degree is 2 (*sensu* Reineck 1963). The *Planolites-Palaeophycus* ichnofabric (Fig. 3G) is composed mainly of simple horizontal burrows that overprint remnants of vertical shafts. It occurs in sandy siltstone beds in the lower part of the studied succession, preferentially in the upper parts of centimetre-scale fining-upward cycles that are devoid of significant sand (Fig. 5). *Planolites* and *Palaeophycus* dominate the ichnofabric. *Arenicolites*, *Cylindrichnus*, *Lockeia*, *Rhizocorallium*, *Skolithos* and *Thalassinoides* also occur, but are minor components. Most burrows reflect feeding behaviour of deposit- or suspension-feeding invertebrates. Bioturbation degree is 2–3. The *Asterosoma-Teichichnus* ichnofabric (Fig. 3C) also occurs in the

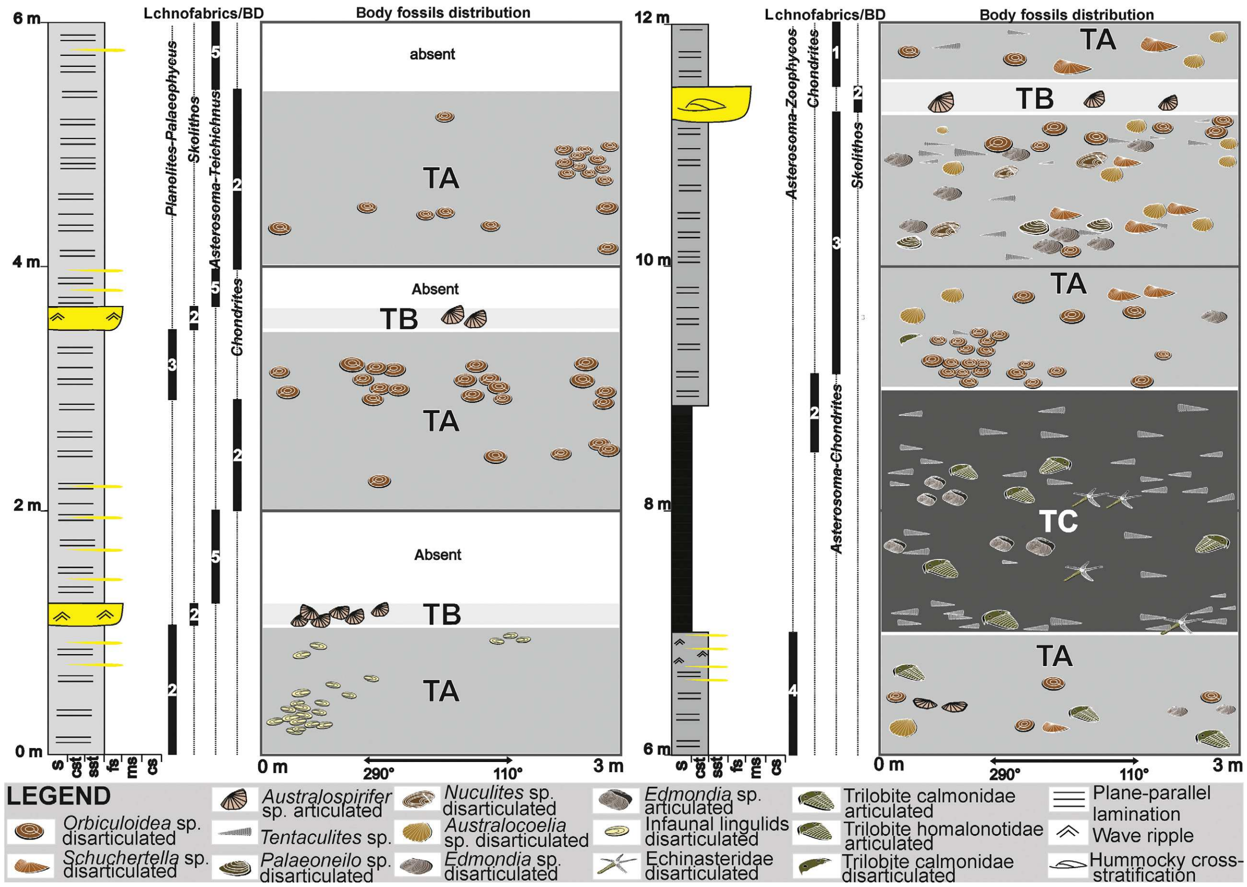

Fig. 6. Spatial distribution of body fossils inside each grid cells, their associated ichnofabric and main taphonomic signatures. [Colour figure can be viewed at wileyonlinelibrary.com]

sandy siltstone beds in the lower part of the section, but exclusively in the sandier parts of the cycles (Figs 5, 6), predominating horizontal burrows of deposit feeders. *Asterosoma* and *Teichichnus* are the dominant ichnotaxa, but other ichnotaxa such as *Chondrites*, *Palaeophycus*, *Planolites*, *Cylindrichnus* and *Rhizocorallium* are also present. Vertical burrows produced by suspension feeders, including *Arenicolites, Diplocraterion, Lockeia and Skolithos* also occur and, where present, are overprinted by other traces, suggesting that they represent the remnants of shallow-tier traces. The *Asterosoma-Teichichnus* ichnofabric reflect the greatest intensity of bioturbation; degree of bioturbation is 5.

The *Asterosoma-Zoophycos* ichnofabric (Fig. 3A, E) occurs only in clayey siltstone beds near the top of the transgressive part of the studied succession (Fig. 5). *Asterosoma* and *Zoophycos* are the dominant ichnotaxa but *Chondrites, Cylindrichnus, Rhizocorallium, Rosselia* and *Teichichnus* are also present. The assemblage is dominated by deposit-feeder burrows, although detritus-feeding habits also are represented. *Zoophycos* normally overprints all other trace fossils, indicating that the *Zoophycos* tracemaker was the last to colonize the substrate. The bioturbation degree is 4. The *Asterosoma-Chondrites* ichnofabric (Fig. 3F) occurs in clayey siltstone beds in the upper regressive part of the section. *Asterosoma* and *Chondrites* dominate the ichnofabric, which also contains *Cylindrichnus, Planolites, Psammichnites, Rhizocorallium, Rosselia, Teichichnus* and *Zoophycos* as accessory ichnotaxa. Horizontal feeding burrows reflecting the activities of mainly deposit and detritus feeders are prevalent. Surface grazing activity also can be inferred by the occurrence of *Psammichnites* (Fig. 3J). Degree of bioturbation is 3. The *Chondrites* ichnofabric (Fig. 3D) occurs in siltstone deposits and in the upper part of the shale bed. Only *Planolites* occurs as an accessory ichnotaxon in this ichnofabric. Limited bioturbation and the low-diversity assemblage of deposit-feeding traces suggest oxygen-deficient substrates. The bioturbation degree is 1-2.

Taphofacies

The fossil distribution in the studied succession and their taphonomic signatures allowed the recognition of three distinct taphofacies that are linked to the substrate type. Whole and disarticulated parautochthonous body fossils dominate the siltstone beds, while whole and articulated autochthonous body fossils dominate the sandstone beds. The shale bed is dominated by whole and articulated autochthonous to parautochthonous body fossils (Fig. 5).

Taphofacies A

Taphofacies A (T-A; Figs 5, 6) is represented at several horizons throughout the siltstone deposits, principally those characterized by parallel lamination and occasional wavy bedding (0–1 m, 2–3.5 m, 4–5.45 m, 6–7.05 m, 8.95–11.15 m and 11.45–12 m). Whole and disarticulated bivalve shells are the predominant body fossils, but whole bodies of univalve or multi-element skeletons (the latter articulated or disarticulated) also occur. Body fossils are preserved parallel to bedding planes and are matrix-supported. Minor evidence of reorientation is observed, mostly in the tentaculitids, suggesting little transport. The body fossil assemblage is dominated by discinid brachiopods such as *Orbiculoidea* (48.5%) and infaunal lingulids (13.17%), followed by *Tentaculites* (10.18%), *Australocoelia* (7.78%), *Edmondia* (6.58%), *Schuchertella* (5.99%), calmonid trilobites (2.4%), *Palaeoneilo* (2.4%) and *Nuculites* (1.8%). This taphofacies is associated with all ichnofabrics except the *Skolithos* ichnofabric.

Taphofacies B

Taphofacies B (T-B; Figs 5, 6) occurs in the sandstone beds with wave ripples and hummocky cross-stratification (1–1.2 m, 3.5–3.7 m and 11–11.45 m). The body fossil assemblage is composed of whole and articulated skeletons of the brachiopod *Australospirifer* (100% of the assemblage) oriented oblique to vertical to bedding and loosely packed in the sediment matrix. Unidentified plant fragments are also present, and this taphofacies is associated with *Skolithos* ichnofabric.

Taphofacies C

Taphofacies C (T-C, Figs 5, 6) occurs in the black shales (7.05–8.95 m). Whole tentaculitids are the predominant body fossil, but whole bivalved (articulated) or multi-element (articulated or disarticulated) skeletons are also present, all of them oriented parallel to bedding and loosely packed in the sediment matrix. The body fossil assemblage is represented by the dominance of *Tentaculites* (70.37%), followed by *Edmondia* (11.11%), echinasterids (7.41%), homalonotid trilobites (7.41%) and calmonid trilobites (3.7%). This taphofacies is associated with *Chondrites* ichnofabric, but only at the top of the shale bed.

Integrated ichnological and taphonomic analysis

The integrated ichnological and taphonomical observations made through the section are summarized in Figure 6 and described in ascending order below.

Interval 0–1 m (a)

This interval is characterized by the occurrence of the Taphofacies A associated with the *Planolites-Palaeophycus* ichnofabric in siltstone beds with parallel lamination and sporadic very fine- to fine-grained sandstone lenses (Sts facies, Table 1). Infaunal lingulids are the unique body fossils in this interval (Fig. 6), and their shells are mostly disarticulated and disposed parallel to bedding planes.

Lingulids are suspension-feeding benthic organisms that live in vertical burrows excavated in soft, fine-grained sandy substrates deposited in the shoreface to offshore transition (Emig 1997; Mergl 2001, 2010; Comniskey 2011). Lingulid shells generally are positioned in the upper parts of their burrows (Emig 1997). According to Emig (1982, 1997) and Kowalewski (1996), the post-mortem deterioration of lingulid shells is rapid, with shells completely disappearing in three weeks. Thus, the absence of fragmentation and corrosion indicates only a short time of exposure at or near the seafloor indicating moderate to high sedimentation rates and the taphonomic signatures suggest a parautochthonous assemblage.

Silty textures suggest quiet water settings, but the presence of parallel lamination and sporadic very fine- to fine-grained sandstone lenses indicates storm-induced turbidity currents or hyperpycnal flows on the bottom. The dominance of horizontal feeding burrows of deposit and detritus feeders in the ichnofabrics (*Planolites, Rhizocorallium, Thalassinoides*) supports the interpretation of quiet water and suggests colonization in offshore transition to offshore settings where the food supply was largely contained within the substrate (Buatois & Mángano 2011). However, the presence of vertical burrows of suspension feeders (*Arenicolites, Skolithos*) or filter feeders (*Lockeia*) indicates that currents and waves episodically impacted these muddy substrates. Distal deposits generated by storm waves and currents may reach the upper offshore (e.g. Pemberton *et al.* 2001). Despite the absence of HCS sandstones at the base of the studied succession, fine-grained sandstone lenses occur sporadically, indicating higher-energy phases. These currents possibly moved the bioclasts into upper offshore settings. Therefore, this interval is characterized by moderate hydrodynamic energy.

Quiet bottom conditions and a food supply that supports different trophic habits are parameters that favour intense bioturbation (Bromley 1996). In fact, upper offshore settings are normally highly bioturbated (bioturbation degree 5–6) and sediment homogenization by bioturbation is common (e.g. Bromley 1996; Pemberton *et al.* 2001; Buatois *et al.* 2002). However, the degree of bioturbation of the *Planolites-Palaeophycus* ichnofabric is low (2). The generally low degree of bioturbation, together with the dominance of burrows of deposit-feeding organisms, suggests periods of low aeration within the substrate (e.g. Ekdale & Mason 1988; Savrda & Bottjer 1989). Nonetheless, the accessory ichnotaxa of the *Planolites-Palaeophycus* ichnofabric are generally present in oxic substrates (e.g. Bromley 1996; Pemberton *et al.* 2001; Buatois *et al.* 2002). Thus, it is possible to assume that the same currents that moved the bioclasts provided not only the food supply for these organisms, but also led to brief periods of bottom oxygenation in a predominately dysoxic substrate.

These features allow the inference of an upper offshore environment with moderate to high sedimentation rates, moderate hydrodynamic energy and dysoxic substrates to the basal interval (interval *a*, Fig. 5).

Interval 1–1.2 m (b)

This interval is marked by a sandstone bed with wave cross-lamination (Sw facies) bearing Taphofacies B and the *Skolithos* ichnofabric. Whole, articulated shells of *Australospirifer* oriented vertical to oblique to bedding are the main taphonomic signatures in these sandstones. These are associated with the dominance of vertical burrows that compose the *Skolithos* ichnofabric.

Taphofacies A beds are periodically interrupted by sandstone beds representing Taphofacies B in the fining-upward cycles (Fig. 5). According to Boucot (1983), the size and relatively large weight, as well as the prominent ribs typical of the genus *Australospirifer,* allowed these organisms to live in more energetic settings. The taphonomic signatures suggest life position (autochthonous) preservation of the body fossils, indicating high sedimentation rates.

The presence of wave ripples indicates oscillatory flows and, in this context, storm-influenced deposits. Based on the thinness and the local occurrence of hummocky cross-stratification, the sandstone beds were deposited in lower shoreface to offshore transition settings. The *Skolithos* ichnofabric is most commonly preserved in shallower shoreface settings where bottom currents and wave action keep the organic particles in suspension within the water column (e.g. Frey 1990; MacEachern & Pemberton 1992; Bromley 1996; Pemberton *et al.* 2001, 2012). Nevertheless, both *Skolithos* and *Palaeophycus* are facies-crossing trace fossils (Bromley 1996; Pemberton *et al.* 2001) and are commonly found in opportunistic assemblages established after storm pulses (Vossler & Pemberton 1988; Frey 1990). Considering that opportunistic tracemakers colonize barren substrates a short period of time, the *Skolithos* ichnofabric represents the opportunistic endobenthic community established in these substrates after storm surges, while the *Planolites-Palaeophycus* ichnofabric observed in the underlying deposits of Taphofacies A corresponds to the resident, fair-weather endobenthic community (e.g. Frey 1990; MacEachern & Pemberton 1992). Thus, compared with Taphofacies A, Taphofacies B represents more energetic and better oxygenated episodes in lower shoreface to transitional offshore.

Interval 1.2–2 m (c)

This interval is characterized by siltstone layers with fine-grained sandstone lenses (Sts facies) with the *Asterosoma-Teichichnus* ichnofabric and lacks body fossils. This ichnofabric is recurrent in the fining-upward cycles (3.6–4 m and 5.4–6 m; Figs 5, 6).

The high bioturbation degree (5), highest ichnodiversity (among all the ichnofabrics preserved in the studied succession) and occurrence of shallow-tier (*Arenicolites, Cylindrichnus, Diplocraterion, Lockeia, Skolithos*), middle-tier (*Asterosoma, Palaeophycus, Planolites, Rhizocorallium, Teichichnus*) and deep-tier (*Chondrites, Planolites*) ichnofabrics suggest more stable and better oxygenated substrates than those reflected by the *Planolites-Palaeophycus* ichnofabric (e.g. Ekdale & Mason 1988; Savrda & Bottjer 1989; Bromley 1996; Buatois *et al.* 2002). The intense intrastratal activity (reflected by bioturbation degree 5) probably exhumed skeletons that were partially buried in the taphonomically active zone (TAZ, *sensu* Olszewski 1999), facilitating the destruction of dead organism skeletal remains (e.g. Bromley & Ekdale 1986; Olszewski 1999). These features allow the inference of low sedimentation rate, moderate hydrodynamic energy and well-oxygenated substrate under upper offshore settings.

Interval 2–3.4 m (d)

This interval is characterized by Taphofacies A in siltstone beds with parallel lamination and sporadic very fine- to fine-grained sandstone lenses (Sts facies). However, the only macrofossil preserved therein is *Orbiculoidea* (discinid brachiopod).

The taphonomic processes in this interval were the same for that previously discussed for the lingulid assemblage (interval *a*); they both represent parautochthonous assemblages under moderate to high sedimentation rates.

The *Chondrites* ichnofabric is associated with Taphofacies A between 2 and 3 m, where sandstone lenses are lacking (Fig. 5). The ichnogenus *Chondrites,* like *Zoophycos* and *Phycosiphon*, has been used as indicator of anoxic conditions within the substrate (e.g. Bromley & Ekdale 1984; Ekdale 1988; Bromley 1996; Martin 2004). However, no such bioturbation is observed in oxygen-deficient substrates in modern seas (Wetzel 1991). Regardless, *Chondrites* is usually the prevalent trace fossil in nearly anoxic substrates (e.g. Bromley 1996; Buatois *et al.* 2002). Thus, the dominance of *Chondrites* and presence of *Planolites* as the sole accessory ichnogenus, along with the low bioturbation degree (2), suggest dysoxic conditions in the substrate. The interval between 3 and 3.4 m is similar to interval *a* and also represents moderate to high sedimentation rates, moderate hydrodynamic energy and dysoxic substrates in upper offshore environments.

Interval 3.4–3.6 m (e)

This interval is similar to interval *b,* containing a sandstone bed (Sw facies) with the *Skolithos* ichnofabric and Taphofacies B representing high energetic and oxygenated conditions in lower shoreface to transitional offshore.

Interval 3.6–4.0 m (f)

This interval is characterized by siltstones (Sts facies) with the *Asterosoma-Teichichnus* ichnofabric, which indicates low sedimentation rate, moderate hydrodynamic energy and well-oxygenated substrates in upper offshore setting. This interval is similar to interval *c.*

Interval 4.0–5.4 m (g)

Taphofacies A associated with the *Chondrites* ichnofabric recurs in the parallel-laminated siltstone with sporadic very fine- to fine-grained sandstone lenses (Sts facies) in this interval. The discinid brachiopod *Orbiculoidea* is the only taxa preserved (Fig. 6). Similar to interval *a*, these beds indicate upper offshore environments under moderate to high sedimentation rates, moderate hydrodynamic energy and dysoxic substrates.

Interval 5.4–6 m (h)

This interval is characterized by the *Asterosoma-Teichichnus* ichnofabric. It lacks associated body fossils as result of intense intrastratal activity under low sedimentation rate, moderate hydrodynamic energy and well-oxygenated substrate in upper offshore settings. This interval is similar to intervals *c* and *f.*

Interval 6.0–7.05 m (i)

This interval is characterized by clayey siltstones with parallel lamination (Stc), with the *Asterosoma-Zoophycos* ichnofabric, and Taphofacies A. Here, this taphofacies is characterized by a more diverse body fossil assemblage than in previous occurrences. *Orbiculoidea, Australospirifer, Australocoelia, Edmondia* and *Schuchertella* occur mainly as disarticulated shells.

Phacopid trilobite sclerites (*Calmonia*) occur both scattered and articulated. Disarticulation in arthropod skeletons is rapid, occurring within two weeks after moulting or death (Brett & Baird 1986; Speyer 1987; Mikulic 1990). Preservation of outstretched articulated phacopid sclerites indicates rapid burial of bodies (not exuviae) in well-oxygenated waters (Babcock & Speyer 1987) and the absence of preburial disturbance (Speyer 1987; Ghilardi 2004). However, the presence of articulated sclerites (Fig. 6) is not enough to justify *in situ* preservation for the trilobite carcasses, as phacopid trilobites were fast-moving, epifaunal, vagile predator-scavenger epibenthic organisms that inhabited shelf environments (Fortey & Owens 1999). Thus, considering all these aspects, the well-preserved trilobites may represent the last generation of organisms caught by a final pulse of sedimentation – i.e. in parautochthonous preservation – but indicating time-averaged slowly deposited shelly sediments (the shells became disarticulated naturally).

Asterosoma and *Zoophycos* are the most conspicuous trace fossils in the clayey siltstone layers. *Zoophycos* overprints all the other burrows in the ichnofabric (even other deep-tier burrows), indicating it was the last emplaced burrow, rather than a simple vertical replacement in response to burial events. The dominance of clayey mudstones indicates prevalence of low hydrodynamic energy and the retention of organic particles in the substrate. These conditions support the dominance of deposit-feeding behaviour reflected by the ichnofauna (*Asterosoma, Chondrites, Rhizocorallium, Teichichnus, Zoophycos*) (Buatois & Mángano 2011). As discussed above, the *Zoophycos* tracemaker was tolerant of low-oxygen conditions mainly in post-Mesozoic deposits, but as the Palaeozoic it could be indicative of moderately dysoxic conditions (e.g. Bromley & Ekdale 1984; Ekdale 1988; Bromley 1996; Martin 2004). Thus, the remarkable overlapping pattern of *Zoophycos* in the *Asterosoma-Zoophycos* ichnofabric is interpreted as a response to decreasing oxygen content within the substrate due to transgression. This event opened the 'colonization window' (*sensu* Pollard *et al.* 1993) for the *Zoophycos* tracemakers, which were able to survive in dysoxic substrates.

According to Miller (1991), the occurrence of burrows characteristic of deeper zones superimposed over burrows produced in shallower zones indicates a flooding trend that is corroborated, in the analysed succession, by the overlapping black shales. Despite being generally reported in deeper marine settings in Mesozoic times, *Zoophycos* was common in shelf deposits during the mid-Palaeozoic (e.g. Bromley 1996; Buatois *et al.* 2002; Seilacher 2007) and also may occur in shallower settings in post-Palaeozoic deposits (e.g. Knaust 2004), in a suggested opportunistic behaviour following marine transgressions. In this way, this interval is representative of moderate to low energy and sedimentation rates and dysoxic substrates in upper offshore settings following transgression episodes.

Interval 7.05–8.9 m (j)

Black shales (S facies) are characterized by Taphofacies C (Fig. 5). Tentaculitids predominate in the body fossil assemblage, but echinasterids (Asteroidea), molluscs (*Edmondia*) and trilobites (calmonids and homalonotids) are also present. Bioturbation is absent except for the *Chondrites* ichnofabric at the top of the shale bed (Fig. 6). Echinasterid arms may be disarticulated from the central axis, but remain whole.

Studies of modern organisms show that total disarticulation of some echinoderms in well-oxygenated water takes a few weeks (e.g. Schaefer 1962; Smith 1984; Kidwell & Baumiller 1990; Donovan 1991). However, the infaunal mollusc *Edmondia* and the trilobite sclerites also are preserved articulated. Enrolled trilobites are indicative of relatively rapid burial (Speyer & Brett 1986, 1988). Thus, autochthonus to parautochthonous preservation is inferred for the body fossils under moderate to low sedimentation rate and low hydrodynamic energy.

The lack of bioturbation in most of the shale beds may be a response to continuous pelagic deposition during a long period of time without interruption by bottom currents. According to Uchman & Wetzel (2011), when organic carbon content is high ($C_{org} > 2\%$), bioturbation is absent. Bergamaschi (1999) identified concentrations of C_{org} near 2% in correlated beds. The presence of the *Chondrites* ichnofabric only at the top of the shale bed suggests that the substrate only became hospitable for chemosymbiotic animals after the improved oxygenation by reactivation of bottom currents. Thus, the occurrence of the *Chondrites* ichnofabric with low bioturbation degree (2) at the top of the shale bed represents the record of bioturbation in a very shallow tier close to the sediment–water interface, where oxygenation was improved. The limited depth of bioturbation in this case was controlled by reducing conditions in pore waters at shallow depths below the sediment–water surface (Wetzel 1991; Uchman & Wetzel 2011).

In this sense, this interval characterizes moderate to low sedimentation rate, low hydrodynamic energy and anoxic to dysoxic substrates, in a lower offshore setting.

Interval 8.9–11.6 (k)

The clayey siltstones (Stc) in this interval are characterized by the Taphofacies A containing the most diverse assemblage of body fossils in the studied section, and by the *Asterosoma-Chondrites* and *Chondrites* ichnofabrics. The body fossil assemblage contains mainly disarticulated shells of *Australocoelia, Edmondia, Schuchertella* and *Orbiculoidea,* disarticulated calmonid trilobites, whole and disarticulated shells of *Palaeoneilo* and *Nuculites,* and whole *Tentaculites* (Fig. 6).

The presence of whole bodies of facultative, mobile, infaunal deposit feeders (molluscs *Palaeoneilo* and *Nuculites*) that preferentially inhabited the lower shoreface (Sepkoski 2002) allows the inference of parautochthonous preservation and moderate sedimentation rate, as predominate in Taphofacies A.

Deposit feeders, represented by *Asterosoma, Planolites, Rhizocorallium* and *Teichichnus,* dominate the infaunal autochthonous assemblages, and bioturbation reflects activity in middle and deep tiers (Bromley & Ekdale 1986; Bromley 1996). *Chondrites* characterizes the deepest bioturbation tier, where decaying organic matter was prevalent. These features allow the inference of moderate hydrodynamic energy and dysoxic to oxic substrates.

Interval 11.6–11.75 m (l)

This interval is characterized by a sandstone bed with hummocky cross-stratification (Shcs), the *Skolithos* ichnofabric and Taphofacies B. Similar to others sandstones beds (intervals *b* and *e*), the unique body fossil preserved is *Australospirifer* (Fig. 6).

The presence of hummocky cross-stratification indicates storm deposition in the lower shoreface to offshore transition zone. High hydrodynamic energy, sedimentation rates and well-oxygenated substrates are inferred.

Interval 11.75–12.0 m (m)

This interval is characterized by clayey siltstones beds (Stc) with Taphofacies A and the *Chondrites* ichnofabric. Similar to interval *k*, these beds represent moderate sedimentation rates and hydrodynamic energy and dysoxic to oxic substrates.

Chondrites is pervasive in the deposits above black shales and is the dominant burrow in both the *Asterosoma-Chondrites* and *Chondrites* ichnofabrics, suggesting prevalence of dysoxic conditions within the substrate during fair-weather phases between storm events. The occurrence of the *Chondrites* ichnofabric after the storm events, with a very low bioturbation degree (1) (Fig. 5), indicates that oxygen deficiency intensified in the pore water, reaching nearly anoxic conditions within substrate and strongly limiting bioturbation. *Orbiculoidea* dominates the levels containing the *Chondrites* ichnofabric, but *Schuchertella* sp., *Australocoelia* sp. and *Tentaculites* sp. also occur. *Orbiculoidea, Australocoelia* and *Schuchertella* individuals were suspension-feeding benthic organisms that lived in zones affected in some way by bottom currents or wave action, while the life habits of *Tentaculites* remain unknown (Wittmer & Miller 2011; Schindler 2012). Evidence of fragmentation, corrosion or bioerosion was not observed in the skeletons, suggesting short transportation, limited exposure at the substrate surface and potentially rapid burial close to living position. These taphonomic signatures suggest parautochthonous preservation for the body fossils (e.g. Boucot & Gill 1956; Emig 1997; Williams *et al.* 2006).

Implications for sea-level change

It is notable that the diversity of body fossils in Taphofacies A increases upward, reaching its highest richness at the top of the studied succession, above the black shales in the early highstand systems tract (Fig. 6). Brett (1998) demonstrated for the marine fossil record of the Middle Palaeozoic that the relative abundance of fossils varies with changes in base level. Burial and preservation of organisms are enhanced during aggradational to progradational phases owing to higher sedimentation rates. Kidwell (1986) postulated two models for increase in fossil concentrations: 'R-sediment', when the decrease in sedimentation rate in relation to bioclastic contribution generates expressive concentration of bioclasts, albeit with a high taphonomic damage; and 'R-hardpart', when occurs combinated increase in bioclastic contribution and sedimentation rate, resulting in low taphonomic damage. Taphofacies A records a context similar to the R-hardpart model.

Overall, our data allow the identification of a main fining-upward sequence (0–8.9 m) reflecting a deepening trend followed by an aggradational to progradational sequence (8.9–12 m) that locally records storm deposition (Fig. 5).

Ichnofacies, taphofacies and palaeoenvironmental inferences

The *Planolites-Palaeophycus, Asterosoma-Teichichnus, Asterosoma-Zoophycos, Asterosoma-Chondrites* and *Chondrites* ichnofabrics present in Taphofacies A (Figs 6, 7) record resident endobenthic invertebrate faunas in shelf deposits and are representative of distinct suites of the *Cruziana* ichnofacies (e.g. Pemberton *et al.* 2001, 2012). In this way, *Asterosoma-Teichichnus* ichnofabric, which is the most diverse and shows the greatest degree of bioturbation, represents optimal ecological conditions in moderate- to low-energy settings between storm and fair-weather wave bases in lower shoreface to offshore transition zones (Fig. 7) (e.g. Frey 1990; MacEachern & Pemberton 1992; Pemberton *et al.* 2001, 2012).

On the other hand, the *Planolites-Palaeophycus* ichnofabric seems to represent colonization of dysoxic upper offshore settings episodically affected by bottom currents derived from the storm surges. Similarly, the moderate to low degree of bioturbation and the presence of dysoxia-tolerant ichnofabrics suggest that the *Asterosoma-Chondrites* and *Asterosoma-Zoophycos* ichnofabric assemblages represent colonization of dysoxic substrates (e.g. Bromley & Ekdale 1984; Ekdale 1988; Martin 2004) in offshore settings, while the *Chondrites* ichnofabric represents colonization of the offshore muds during periods of oxygen deficiency.

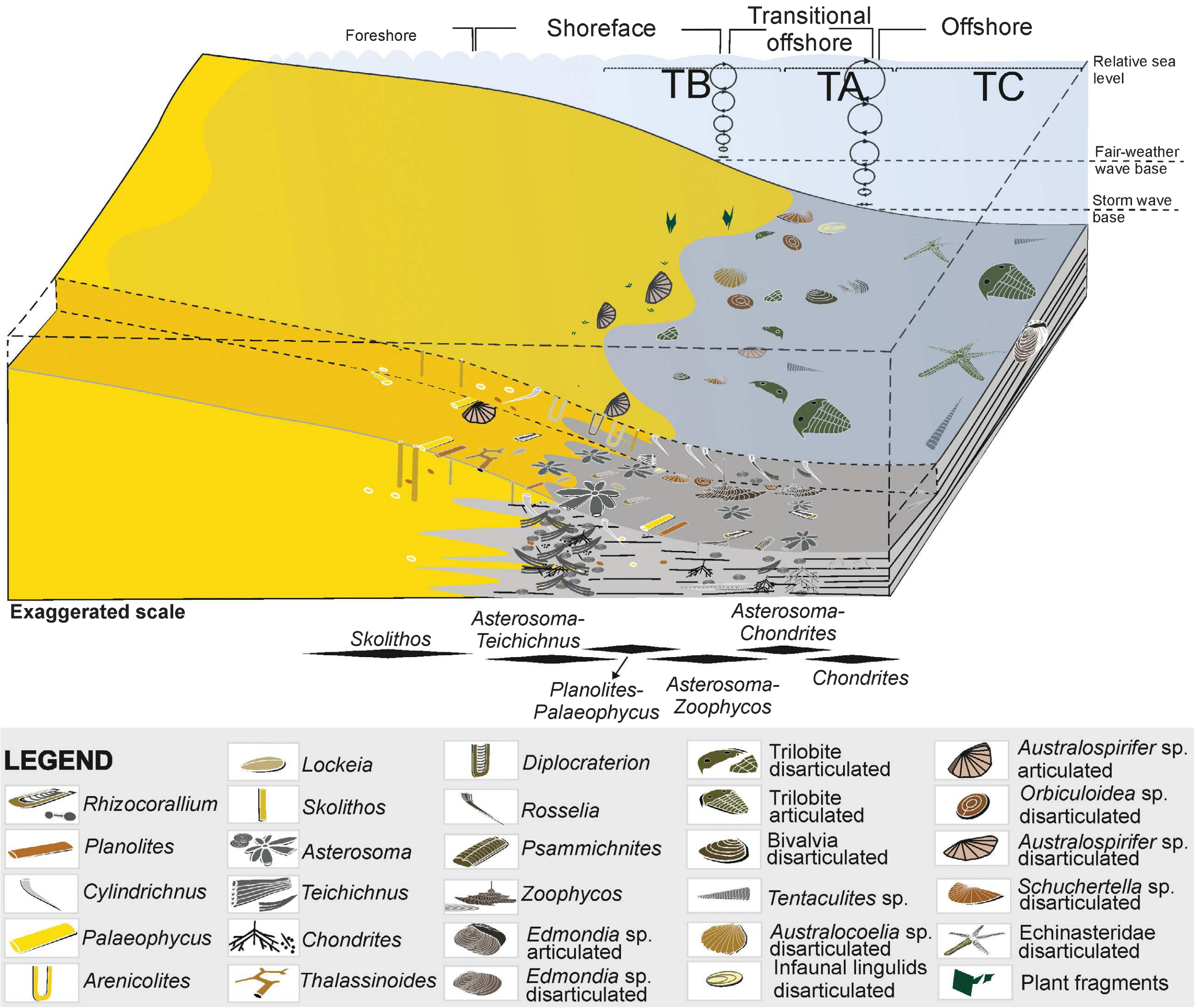

Fig. 7. Palaeoenvironmental reconstruction of the study area with inferred distribution of ichnofabrics and body fossils. [Colour figure can be viewed at wileyonlinelibrary.com]

Considering the sandstones beds, the *Skolithos* ichnofabric in Taphofacies B represents the opportunistic colonization of substrates during higher-energy events and characterizes the *Skolithos* ichnofacies (e.g. Bromley 1996; Buatois *et al.* 2002). Evidence storm-wave action in the sandstone beds that characterize Taphofacies B suggests that storms were chiefly responsible for the sandy accumulations in the offshore transition zone (e.g. MacEachern & Pemberton 1992; Pemberton *et al.* 2001, 2012). In this way, the *Skolithos* ichnofacies record the pioneer post-storm colonization, while the *Cruziana* ichnofacies represents fair-weather colonization between storm surges (Frey 1990).

The black shales present accumulation of undamaged, disarticulated skeletons preserved together with whole articulated skeletons in shales, which is strong evidence of time-averaging (Kidwell 1998). This association suffered only short transport by rapid, episodic, high-energy events that provided relatively rapid burial of these elements (e.g. Brett & Baird 1986, 1993; Speyer & Brett 1986; Speyer 1987). Even events of moderate energy can cause reorientation of univalved skeletons and disarticulation of valves accumulating in the TAZ (Kidwell & Bosence 1991). Muddy deposits in epeiric seas normally occur in distal shelf zones below wave base (Reading 1996). Most fossil concentrations in epeiric seas result from erosion of relatively shallow substrates caused by storm events and subsequent cover by sand or mud (Miller *et al.* 1988; Olóriz *et al.* 2008).

According to Bergamaschi (1999) and Bergamaschi & Pereira (2001), the main agent of sediment transport in the Ponta Grossa Formation (Sequence B for these authors) was storm waves. The dominance of the fair-weather trace fossil assemblages of the *Cruziana* ichnofacies reinforces the idea that deposition occurred below fair-weather wave base in zones affected by storm waves. Thus, the body fossil assemblages preserved in the studied succession are storm-influenced. Moderate sedimentation rates and moderate hydrodynamic energy due to sporadic bottom currents allowed the exposure of invertebrate skeletons at the water/sediment interface for time periods sufficient for disarticulation by necrolysis processes or benthic scavenger activity (e.g. Speyer & Brett 1986). Considering that fossil accumulations occur in almost all layers throughout the succession with predominant parautochthonous preservation and no damage to the skeletons (other than disarticulation), a high frequency of storm events is inferred for all succession.

The high-energy processes generated by storm events accumulated sand bars in lower shoreface to transitional offshore settings and increased oxygenation at the sediment–water interface. The dominance of suspension and filter feeders represented by the trace fossil assemblage in Taphofacies B and the presence exclusively of complete articulated brachiopods in the body fossil assemblage indicate the prevalence of high sedimentation rates during the storm events. Additionally, Taphofacies A is similar to Taphofacies 5 described by Horodyski (2014) in the region, which also has been linked to storm processes.

Taphofacies C deposits characterize pelagic mud accumulation in offshore settings after a major marine flooding (transgressive) event, and the lack of bioturbation in most of the black shale beds that represent Taphofacies C suggests prevalence of anoxic conditions within the substrate (Fig. 5).

Gaillard & Racheboeuf (2006) proposed a zonation from nearshore to offshore considering benthic associations of trace fossils and body fossils for the Lower Devonian Santa Rosa and Icla formations of Bolivia, inferring a deepening event based on the distribution of six trace fossils associations. Although the section described in the current study does not correlate to Santa Rosa or Icla formations, similar trace fossil associations are recognized. The *Palaeophycus* association of Gaillard & Racheboeuf (2006) can be related to the *Planolites-Palaeophycus, Asterosoma-Teichichnus, Asterosoma-Zoophycos* and *Asterosoma-Chondrites* ichnofabrics in terms of depositional conditions, in an offshore transition setting. Similarly, the *Zoophycos* association of Gaillard & Racheboeuf (2006) is analogous to *Chondrites* ichnofabric, corresponding to offshore settings. In contrast, the *Skolithos* association of Gaillard & Racheboeuf (2006) was attributed to fair-weather conditions in nearshore environments, while the *Skolithos* ichnofabric in the current study is attributed to storm deposition in offshore transition to lower shoreface settings.

Fürsich & Oschmann (1993) recognized nine genetic types of fossil concentrations for Bathonian-Oxfordian shallow water sediments of the pericratonic basins of Kachchh and Rajasthan, western India. Considering that, some concentrations of Fürsich & Oschmann (1993) have similar processes in the taphofacies from de current study. The Taphofacies A, particularly in the intervals *a, d* and *g*, has similar signature with the ‘winnowed concentrations – type 7’ of Fürsich & Oschmann (1993). These concentrations can be result of distal storm waves or weak currents that remove finer material, maintaining thin-shelled organisms (infaunal lingulids and *Orbiculoidea* in current study).

The body fossils in taphofacies B can be associated with ‘storm-wave concentrations – type 2’ of Fürsich & Oschmann (1993). These concentrations are characterized by well-preserved skeletal elements in monospecific shell beds; normally with articulated and undamaged body fossils (do not show any signs of abrasion, bioerosion or encrustation).

The body fossils in taphofacies C can be associated with ‘condensed concentrations – type 9’ of Fürsich & Oschmann (1993). Considering that the time involved in this concentration is considerably higher, skeletal elements present different taphonomic signatures, mixed mainly *in situ* reworking rather than by transport. These concentrations tend to be very diverse and highly time-averaged.

Although the brachiopods numerically dominate this fossiliferous association, during the Palaeozoic brachiopods shells were less thick and, thus, more easily fragmented, generating deposits of less than few centimetres (Kidwell 1998).

Conclusions

Integrated analysis of Lower Devonian facies in the Paraná Basin demonstrates that the studied section accumulated at variable rates, and under variable energy and redox conditions influenced by sea-level change.

Taphofacies A and the associated ichnofabrics (*Planolites-Palaeophycus, Chondrites, Asterosoma-Zoophycos* and *Asterosoma-Chondrites* ichnofabrics) represent prevalence of dysoxic conditions within the substrate during fair-weather phases, while Taphofacies B associated with the *Skolithos* ichnofabric indicate higher energetic and well-oxygenated conditions during storm events. The upward increase in diversity and abundance of body fossils for Taphofacies A can be explained by changes in sedimentation rates during aggradational to progradational phases. Taphofacies C lacks bioturbation except for *Chondrites* ichnofabrics occurring only at the bed tops, indicating the maximum transgression in the T-R cycle, characterizing this taphofacies as a good indicator of maximum flooding surfaces.

The *Asterosoma-Teichichnus* ichnofabric, reflecting high degree of bioturbation and high ichnodiversity, contains no associated body fossils. This likely reflects intense intrastratal activity at all substrate levels, which facilitated the oxygenation of the substrate disallowing the preservation of organism remains. This observation indicates that the bioturbation is an important factor controlling the loss of taphonomic information within the TAZ, mainly when associated with detritus-feeding trace fossils.

In contrast, most occurrences of Taphofacies C are associated with unbioturbated sediments, indicating anoxic conditions in the substrate. This study shows that more accurate palaeoenvironmental interpretations can be derivate via an integrated ichnological/taphonomic approach.

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CAPÍTULO 4

Ichnology applied to sequence stratigraphic analysis of Siluro-Devonian mud-dominated shelf deposits, Paraná Basin, Brazil

Artigo publicado no periódico "Journal of South American Earth Sciences" onde buscou-se diagnosticar superfícies estratigráficas-chave a partir de dados sedimentológicos, icnológicos e tafonômicos. Este estudo usa principalmente a Icnologia para calibrar os arcabouços estratigráficos previamente propostos e definir as sequências deposicionais.

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Ichnology applied to sequence stratigraphic analysis of Siluro-Devonian mud-dominated shelf deposits, Paraná Basin, Brazil

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ABSTRACT

Previous studies of the Paraná Supersequence (Furnas and Ponta Grossa formations) of the Paraná Basin in southern Brazil have yielded disparate sequence stratigraphic interpretations. An integrated sedimentological, paleontological, and ichnological model was created to establish a refined sequence stratigraphic framework for this succession, focusing on the Ponta Grossa Formation. Twenty-nine ichnotaxa are recognized in the Ponta Grossa Formation, recurring assemblages of which define five trace fossil suites that represent various expressions of the Skolithos, Glossifungites and Cruziana ichnofacies. Physical sedimentologic characteristics and associated softground ichnofacies provide the basis for recognizing seven facies that reflect a passive relationship to bathymetric gradients from shallow marine (shoreface) to offshore deposition. The vertical distribution of facies provides the basis for dividing the Ponta Grossa Formation into three major (3^{rd}-order) depositional sequences— Siluro-Devonian and Devonian I and II—each containing a record of three to seven higher-order relative sea-level cycles. Major sequence boundaries, commonly coinciding with hiatuses recognized from previously published biostratigraphic data, are locally marked by firmground Glossifungites Ichnofacies associated with submarine erosion. Maximum transgressive horizons are prominently marked by unbioturbated or weakly bioturbated black shales. By integrating observations of the Ponta Grossa Formation with those recently made on the underlying marginal- to shallow-marine Furnas Formation, the entire Paraná Supersequence can be divided into four disconformity-bound sequences: a Lower Silurian (Llandovery-Wenlock) sequence, corresponding to lower and middle units of the Furnas; a Siluro-Devonian sequence (?Pridoli-Early Emsian), and Devonian sequences I (Late Emsian-Late Eifelian) and II (Late Eifelian-Early Givetian). Stratigraphic positions of sequence boundaries generally coincide with regressive phases on established global sea-level curves for the Silurian-Devonian.

1. Introduction

Ichnofossils reflect the behavioral responses of organisms to physical and chemical conditions in their depositional regimes. Consequently, when employed in conjunction with physical sedimentologic evidence, they are important tools for facies analysis (Pemberton and Frey, 1984; Bottjer et al., 1988; Savrda and Bottjer, 1986; Ekdale and Lewis, 1991; MacEachern and Pemberton, 1994; MacEachern et al., 1998, 2005, MacEachern and Bann, 2008; Savrda, 1998; Mángano et al., 1998; Gingras et al., 1999; Netto et al., 2009). Ichnofossils are particularly useful in marine sequence stratigraphic studies. Vertical changes in ichnofossil assemblages can be used to recognize deepening and shallowing trends (e.g., recognition of parasequences; Savrda, 1991b, 1995; MacEachern and Pemberton, 1992, 1994; Pemberton et al., 1992; Pemberton and MacEachern, 1995; MacEachern et al., 1999, Pemberton et al., 2004; Brett, 1998; Fielding et al., 2006; Rodríguez-Tovar et al., 2010; Paranjape et al., 2014), and key sequence stratigraphic surfaces (e.g., sequence boundaries, transgressive surfaces) may be distinctly marked by substrate-controlled ichnofossil assemblages (e.g., Glossifungites Ichnofacies; Savrda, 1991a; MacEachern et al., 1992; Pemberton et al., 2000; Buatois and Encinas, 2006; Rodríguez-Tovar et al., 2006; Abdel-Fattah et al., 2016).

The Devonian Ponta Grossa Formation, part of the Paraná Supersequence in the Paraná Basin of southern Brazil, has been the

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subject of various facies and sequence stratigraphic studies, in part owing to its potential as a hydrocarbon source (Milani et al., 2006). Previous studies concluded that the Ponta Grossa Formation was deposited in marine shelf settings, as demonstrated by sedimentologic character, macro- and microfossils, and trace fossil assemblages (e.g., Campanha, 1985; Melo, 1988; Grahn, 1992; Borghi, 1993; Assine, 1996, 2001; Bergamaschi, 1999; Rodrigues et al., 2006; Milani et al., 2007; Bosetti et al., 2011; Grahn et al., 2013; Horodyski et al., 2014; Sedorko et al., 2018). In contrast, sedimentologic and well-log analyses have yielded a variety of sequence stratigraphic interpretations for this unit (Assine, 1996; Bergamaschi, 1999; Candido and Rostirolla, 2007; Zabini et al., 2011; Horodyski et al., 2014). Notably, previous ichnologic studies of the Ponta Grossa Formation focused mainly on ichnotaxonomic descriptions (*c.f.* Sedorko et al., 2013); ichnological observations previously have not been fully integrated with sedimentologic data in facies and sequence stratigraphic analyses. In the current paper, we (i) describe recurring soft- and firmground ichnofacies in the Ponta Grossa Formation; (ii) translate the vertical distribution of sedimentary facies and ichnofacies to a record of relative sea-level dynamics; and (iii) compare the resulting refined sequence stratigraphic framework to those previously proposed for the Paraná Supersequence and to the Siluro-Devonian global sea-level curve.

2. Paraná Basin and supersequence

The Paraná Basin is a large (~1,500,000 km^2), roughly elliptical sedimentary basin that occupies much of southern Brazil but also extends into adjacent areas of Paraguay, Uruguay, and Argentina (Fig. 1A). The basin infill, which locally reaches 7000 m in thickness, has been divided into six disconformity-bound Paleozoic and Mesozoic supersequences: the Ordovician-Silurian Rio Ivaí, Silurian-Devonian Paraná; Carboniferous-Early Triassic Gondwana I; Triassic Gondwana II; Late Jurassic-Early Cretaceous Gondwana III; and Cretaceous Bauru supersequences (Milani et al., 2007). The basin evolved from a southwest-facing gulf in the early Paleozoic to an intracratonic flexural basin in the late Paleozoic and Mesozoic (Milani et al., 2006, 2007). Strata addressed herein belong to the Paraná Supersequence (hereafter referred to as the Paraná Group).

The Paraná Group contains, in ascending order, the Furnas and Ponta Grossa formations (Fig. 1B). The Furnas Formation, characterized by sandstones with subordinate conglomerates and mudstones, has been divided into three informal units (lower, middle, and upper), based primarily on variations in sediment texture (Assine, 1996). The Ponta Grossa Formation, the focus of the current study, is divided into three members based on relative proportions of mudrock and sandstone (Lange and Petri, 1967). The basal Jaguariaíva Member is ~90 m thick and dominated by mudstones, siltstones, and black shales. The locally overlying sandstone-dominated Tigabi Member is up to 35 m thick in the study area and up to 100 m thick in the subsurface (Candido and Rostirolla, 2007). The upper São Domingos Member includes a thick succession (up to 150 m) of siltstones, fine- to medium-grained sandstones, and subordinate black shales.

3. Location and methods

This ichnological-sedimentological study addressed the Ponta Grossa Formation where it crops out at various localities in the eastern part of the Paraná Basin. These sections are in the Campos Gerais region, which includes the Tibagi and Arapoti municipalities, Paraná State, southern Brazil (Fig. 1A). Focus was on two relatively thick (230–280 m) sections that include all three members of the Ponta Grossa Formation—sections A and B, exposed along Tibagi-

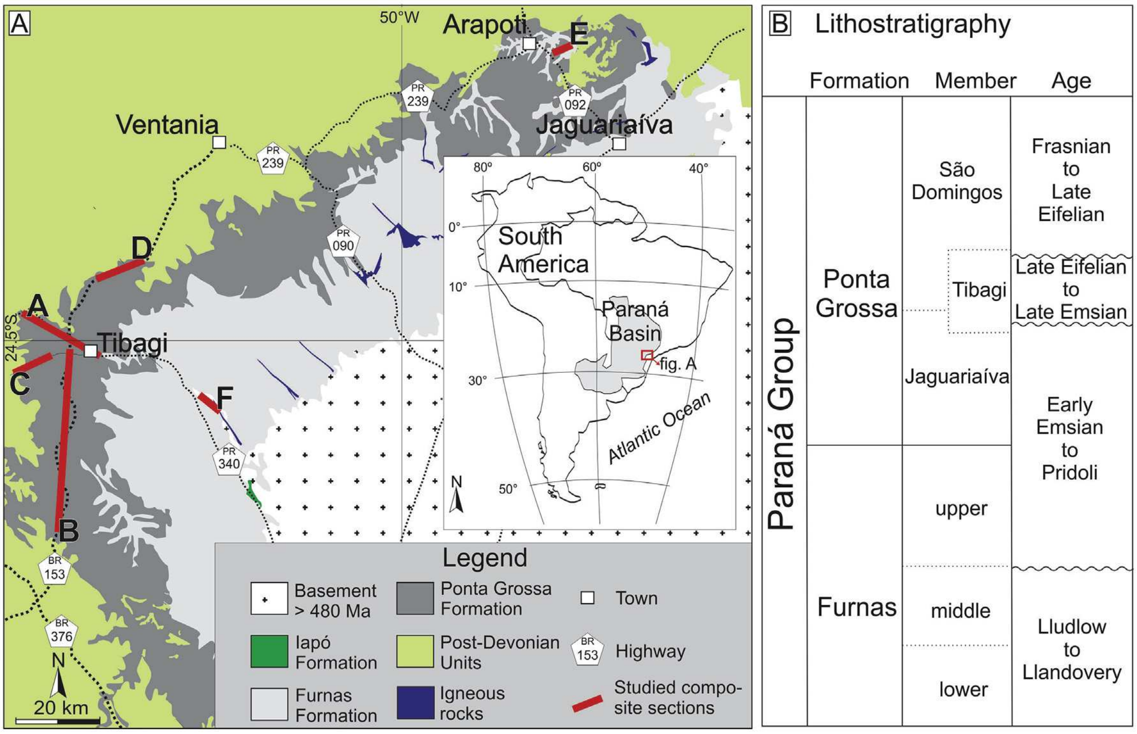

Fig. 1. Location map and stratigraphic context of the study area in Paraná Basin, Brazil. A. Geological map of Paraná Supersequence in Campos Gerais region, Paraná State, Brazil. Red bars indicate locations of studied sections. Section A: Tibagi-Telêmaco Borba; Section B: Tibagi-Alto do Amparo; Section C: Barreiro; Section D: Tibagi-Ventani; Section E: Arapoti; Section F: Furnas Formation, Guartelá (from Sedorko et al., 2017). B. Litho- and chronostratigraphy of the Paraná Supersequence in the Paraná Basin (modified from Milani et al., 2007). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Telêmaco Borba and Tibagi-Alto do Amparo roads, respectively. However, supplementary observations were made at three other sections that include only parts of the formation. Sections at Barreiro (section C) and Tibagi-Ventania (section D) expose the upper and lower parts, respectively, of the São Domingos Member, whereas the Arapoti-CEEP (section E) includes the lower part of the Jaguariaíva Member only. Observations made previously by Sedorko et al. (2017) of the subjacent Furnas Formation exposed near Guartelá (Section F; Fig. 1A) are integrated into later discussion.

At all localities, descriptions were made of general lithologies, sediment textures, physical sedimentary structures, nature of the stratigraphic contacts, and ichnofossils. Ichnologic analysis included identification of recurring trace fossils and quantification of degree of the bioturbation using the scheme of Reineck (1963; bioturbation scale, BS, ranging from 0 = no bioturbation through 6 = complete biogenic destruction of primary sedimentary fabric). All trace fossil descriptions were based on field observations.

4. Ponta Grossa Formation Ichnoassemblages

Twenty-nine ichnotaxa were recognized in the Ponta Grossa Formation, most of them identified to the ichnogenus level (Table 1). Based on recurring trace fossil associations, five suites are recognized, and these are representative of the Glossifungites, Skolithos and proximal, archetypal, and distal expressions of the Cruziana ichnofacies (Fig. 2).

4.1. Glossifungites Ichnofacies suite

The Glossifungites Ichnofacies (Fig. 2A and B) suite is characterized by vertical, irregularly walled, passively-filled burrows (*Arenicolites* and *Skolithos*) that reflect the colonization of firmgrounds substrates (Ekdale, 1984; Pemberton and Frey, 1985; Wetzel and Uchman, 1998). This suite overprints trace fossils representative of proximal Cruziana Ichnofacies or Skolithos Ichnofacies.

4.2. Skolithos Ichnofacies suite

Trace fossil suites assigned to the Skolithos Ichnofacies (Fig. 2C–E) also are dominated by vertical ichnofossils, including *Skolithos, Arenicolites, Rosselia, Diplocraterion, Cylindrichnus*, and *Schaubcylindrichnus*, but also may include mainly horizontal burrows and burrows systems assigned to *Macaronichnus*, *Palaeophycus*, and *Thalassinoides*. Despite the local presence of deposit-feeding structures (e.g. *Macaronichnus*), this ichnofacies records preferential colonization by suspension feeders in relatively high-energy softground substrates (e.g., Frey, 1990).

4.3. Cruziana Ichnofacies suites

Observed variations within the Cruziana Ichnofacies in the Ponta Grossa Formation are similar to those documented by MacEachern et al. (1999, 2007) and MacEachern and Bann (2008). Trace fossil suites assigned to the proximal expressions of the Cruziana Ichnofacies (Fig. 2F–J) are dominated by horizontal endogenic and epigenic structures produced mainly by deposit- and/or suspension-feeders. These may include *Bergaueria, Bifungites*, *Cylindrichnus*, *Diplichnites*, *Heimdallia*, *Laevicyclus, Lingulichnus*, *Lockeia silliquaria*, *Palaeophycus*, *Psammichnites, Rhizocorallium commune*, *Rosselia socialis*, *Rusophycus*, and *Thalassinoides*. Compared to the Skolithos Ichnofacies, these softground associations indicate deposition in lower-energy environments. However, localized co-occurrences of *Skolithos* and *Arenicolites* indicate at least periodically enhanced bottom currents, and some intervals containing *Lingulichnus* reflect periodic episodes of rapid deposition (Horodyski et al., 2015).

Suites attributable to the archetypal Cruziana Ichnofacies suite (Fig. 2K and L) are the most diverse. *Asterosoma, Teichichnus, Zoophycos, Chondrites, Helminthopsis, Cylindrichnus, Planolites*, and *Palaeophycus* dominate these assemblages, but *Skolithos, Arenicolites, Rosselia, Rusophycus, Taenidium satanassi, Diplocraterion, Lockeia, Thalassinoides, Rhizocorallium*, and *Halopoa* are also locally present. This suite is highly bioturbated (BS 5–6), but locally can be moderately bioturbated (BS 3–4), indicating some stress caused by salinity fluctuations in the offshore transition zone, turbidity flows, or low benthic oxygenation. Suites of the archetypal Cruziana Ichnofacies represent deposition mainly between fair-weather and storm wave bases (see MacEachern et al., 1999 for a summary).

Trace fossil associations assigned to the expression of the distal Cruziana Ichnofacies (Fig. 2M–N) suite are dominated by one or more specialized feeding traces, including *Phycosiphon, Helminthopsis, Chondrites, Zoophycos, Planolites*, and *Helicodromites*. Occurrences of this suite can be monospecific and characterized by high trace densities. The distal expressions of the Cruziana Ichnofacies is indicative of lower offshore settings (cf. MacEachern et al., 1999).

As described below, the integration of physical sedimentologic and ichnologic observations allow the recognition of the various sedimentary facies, the vertical distribution of which reflect temporal changes in depositional environments and sea-level dynamics.

5. Facies and trace fossil associations

Based on lithology, textures, physical sedimentary structures, and trace fossil associations, seven sedimentary facies are recognized in the Ponta Grossa Formation exposed at the five study localities (Table 2; Fig. 3). These facies, all of which are linked to marine depositional environments, are described below, from proximal to distal environments.

Facies 1 is represented by wave rippled, very fine- to fine-grained sandstones (Fig. 3A). While some sandstones are unbioturbated (bioturbation scale, BS = 0), many are weakly to moderately bioturbated (BS = 2–3) and are characterized by suites attributable to the Skolithos Ichnofacies and, less commonly, proximal expressions of the Cruziana Ichnofacies (see Table 2).

The interbedding of unbioturbated sandstone and bioturbated sandstone with Skolithos Ichnofacies suites suggests deposition in relatively high-energy settings. The inferred environment for this facies is shoreface above fair-weather wave base.

Facies 2 refers to variably bioturbated, massive to faintly parallel laminated, very fine- to medium-grained sandstones (Fig. 3B) with variable ichnofossil assemblages. Among bioturbated intervals, weakly to moderately bioturbated (BS = 2–3) beds characterized by suites assigned to proximal expressions of the Cruziana Ichnofacies are most common. Moderately to heavily bioturbated (BS = 3–5) intervals with relatively diverse expressions of the archetypal Cruziana Ichnofacies are of secondary importance, whereas weakly bioturbated beds (BS = 0–2) containing low-diversity suites of the Skolithos Ichnofacies are subordinate.

The dominance of suites attributable to proximal and archetypal expressions of the Cruziana Ichnofacies in Facies 2 indicates less energetic conditions than for Facies 1. This context suggests deposition in lower shoreface settings, near to or just below fair-weather wave base.

Facies 3 is characterized by hummocky cross-stratified (HCS), very fine- to fine-grained sandstones (Fig. 3C) containing one of three softground trace fossils associations. In order of increasing

Table 1
Recurring trace fossils in Ponta Grossa Formation.

Ichnotaxa	Description	Inferences from literature
Arenicolites isp. (Fig. 2A, C)	Vertical to oblique, unlined, U-shaped burrows. Diameters range from 0.6 to 24 mm, U-tube widths range from 10 to 48 mm, and burrow depths vary between 20 and 55 mm. Filled with sediment comparable to that of their very fine- to fine-grained sandstone hosts. Locally, burrows exhibit sharp, irregular walls and are filled with darker and finer-grained sediments than the sediment matrix (firmground conditions)	Dwelling structure of suspension- or deposit-feeding worm-like organisms (mainly polychaetes, but also possibly crustaceans or insects)
Asterosoma isp. (Fig. 2K, L)	Systems of horizontal to subhorizontal burrows that radiate outwards from a central shaft; burrows taper towards blind extremities and exhibit concentrically laminated fills. Burrow diameters typically are on the order of ~2.5 cm, but smaller specimens (1 cm) are observed locally	*Asterosoma* is produced by worm-like deposit-feeding animals, most common in shallow marine deposits
Bergaueria perata (Fig. 2J)	Short, vertical, cylindrical burrows with rounded termini, structureless fills, and localized faint radial ridges. *Bergaueria perata* is characterized by the absence of pronounced radial ridges around the central depression. The observed specimens range from 1.8 to 3.2 cm in diameter and from 0.4 to 1 cm in height	This ichnogenus occurs in marine deposits, commonly mudstones, and has been attributed to suspension-feeding organisms (possibly anemones) or deposit-feeding echinoderms (possibly holothurians)
Bifungites isp. (Fig. 2F)	Unornamented, irregular U- or inverted Π-shaped vertical burrows lacking spreiten and with fills similar to or finer than the host sediment. These burrows are preserved as convex hyporeliefs and exhibit characteristic dumbbell-shaped forms ranging from 5.8 to 11.5 cm in width; tube diameter ranges from 0.6 to 1.8 cm	This ichnogenus is diagnostic of marine conditions and is interpreted as a shallow-tier dwelling or feeding structure produced by suspension-feeding, worm-like animals
Chondrites isp. (Fig. 2K)	Complex burrow systems consisting of regularly branched tunnels and shafts of consistent diameter. *Chondrites* are observed in both vertical and bedding-plane views. Branches range from 1 to 12 mm in diameter. Locally, this trace occurs in high densities and heavily cross cuts earlier formed ichnofossils	This facies-crossing marine ichnogenus is regarded as a fodichnian or deep-tier chemichnion produced by worm-like organisms, possibly annelids or sipunculids, that were tolerant of dysoxic conditions
Cylindrichnus isp.	Vertical, cylindrical to subconical burrows with concentrically laminated fills. Specimens observed range from 6 to 15 mm in diameter	*Cylindrichnus* is a permanent dwelling structure of suspension-feeding organisms common in shoreface to offshore environments
Diplichnites isp.	Straight to slight curved trackways exhibiting symmetrical parallel rows of simple tracks. Trackways are normally preserved as concave epireliefs. Tracks are small (1–3 mm wide), with scratches aligned perpendicular to the mid-line. External trackway widths range from 7 mm to 15 mm, while internal widths vary from 4 to 8 mm	*Diplichnites*, likely produced by arthropods, previously has been reported in transitional subaerial to subaqueous, continental to marine deposits
Diplocraterion parallelum (Fig. 2D)	Vertical, U-shaped burrows with spreiten. Width and depths of U-tubes range from 20 to 55 mm and from 28 to 75 mm, respectively, while burrow diameters range between 5 and 15 mm. Spreiten are normally protrusive	Represents the dwelling/equilibrium structure of suspension- or detritus-feeding organisms, possibly crustaceans or polychaetes. typically occurring in marginal and shallow marine deposits
Halopoa isp.	Elongate, horizontal to oblique, unbranched burrows with irregular, longitudinal striations. Burrows are preserved in full relief, range from 15 to 28 mm in diameter, and reach lengths of 120 mm	Produced by worm-like marine animals that expanded their bodies hydraulically to cross the sediment, or by crustaceans that could push against burrow walls with their carapace
Heimdallia isp.	Vertical spreite-like burrows that in bedding-plane views appear as unbranched ribbons with internal structure showing vertical or inclined packets of sediment. Vertical spreiten are rarely exposed. Packets of sediment in the spreiten resulted from progressive lateral migration of the tracemaker, possibly a deposit-feeding crustacean	*Heimdallia* is most frequent in shallow-water marine siliciclastic deposits (Buckman, 1996)
Helicodromites isp. (Fig. 2N)	Horizontal, unbranched, straight to gently curved, smooth-walled, corkscrew-shaped burrow with fills darker than the host sediment. Burrow lengths range up to 20 cm, while diameters vary from 8 to 12 mm, and spiral turns are closed spaced (3–6 mm).	*Helicodromites* is commonly described in marine deposits, and has been interpreted as a relatively deep-tier trace produced by worm-like organisms, possibly capitellid polychaetes or enteropneusts, during feeding or microbial farming activity
Helminthopsis isp.	Horizontal, unbranched, meandering, cylindrical burrows, with fills normally darker than the host sediment; meanders vary in amplitude and are typically U-shaped. Burrows range from 0.8 to 4 mm in diameter	*Helminthopsis* is a facies-crossing marine ichnotaxon attributed to feeding or grazing activity of detritus-feeding worm-like organisms, probably polychaetes
Laevicyclus isp.	Vertical, unbranched, unornamented structures with a central cylindrical burrow extending downward to an enlarged plug-shaped bulb. Burrow and bulb diameters range from 8 to 14 mm and 16 to 30 mm, respectively, while burrow depths vary from 30 to 40 mm	Dwelling structure possibly produced by bivalves or sessile, predaceous sea anemones
Lingulichnus isp. (Fig. 5C)	Vertical to inclined burrows with elliptical to sub-circular cross sections; fills locally exhibit concentric laminae or spreite. Specimens vary from 5 to 15 mm in diameter and are up to 30 mm deep. These specimens are variably allied with the ichnospecies *L. verticalis, L. hamatus* and *L. incinatus*	*Lingulichnus* occurs in open to restricted marine environments characterized by high sedimentation rates and is interpreted as a dwelling structure of infaunal lingulid brachiopods
Lockeia isp.	Almond-shaped burrows with filling similar to the host rock, ranging from 4 to 12 mm in diameter (average = 8 mm)	*Lockeia* is interpreted as a resting trace of bivalve mollusks, and is a facies-crossing ichnotaxa
Macaronichnus isp. (Fig. 2E)	Horizontal or sub-horizontal, straight to meandering, cylindrical burrows with diameters ranging from 3 to 6 mm; and with a mantle and core reflecting grain segregation by the tracemaker	This ichnogenus, attributed to intrastratal deposit-feeding activity of opheliid polychaetes, is an indicator of proximal marine environments, mainly shoreface to foreshore settings
Palaeophycus isp. (Fig. 2G)	Horizontal to slightly inclined, unbranched, smooth-walled, thinly lined, straight to slightly curved, cylindrical burrows filled with structureless sediments similar to the matrix. Diameters range from 5 to 23 mm	This facies-crossing ichnogenus is attributed to dwelling activity by suspension-feeding or predaceous organisms, possibly polychaetes
Phycosiphon incertum (Fig. 2M)	Mainly horizontal, sinuous to meandering burrows with lateral spreiten in areas between the meanders and fills that are darker than the host rock. Diameters range from 0.5 to 2 mm in diameter and reach lengths of 15 mm	*Phycosiphon* is attributed to deposit feeder activity of worm-like organisms, occurs in marine deposits representing continental shelf to submarine fan environments.
Planolites isp.	Horizontal, straight to slightly sinuous, unbranched, unlined, cylindrical burrows commonly filled with sediment that contrasts with the host rock. Diameters range from 8 to 15 mm and the length can reach 12 cm	Deposit-feeding activity of vagile, worm-like organisms in various environments

Table 1 (*continued*)

Ichnotaxa	Description	Inferences from literature
Psammichnites isp.	Horizontal, flat, straight to meandering traces with unilobed or bilobed bases and faint meniscate backfill. Burrow widths are relatively uniform (~15 mm) but increase slightly in meander bends.	*Psammichnites* is generally diagnostic of shallow to marginal marine environments and has been attributed to subsurface feeding activities of vagile organisms, possibly gastropods or other animals equipped with a siphon device
Rhizocorallium commune (Fig. 2I)	Horizontal, straight to sinuous, unornamented, U-shaped burrows with actively filled internal *spreite*. U-tubes range from 15 to 35 mm wide and up to 12 cm long; burrow diameters range from 5 to 14 mm	At least for Paleozoic occurrences, this ichnospecies is restricted to shallow-marine environments and is attributed to suspension- or deposit-feeding activities of polychaetes or crustaceans
Rosselia socialis	Vertical to inclined structures consisting of a concentrically laminated, muddy funnel or bulb surrounding a typically sand-filled central shaft. Burrow diameters and lengths range from 5 to 39 mm and from 9 to 55 mm, respectively	*Rosselia* is a marine ichnogenus attributed to dwelling/feeding activities of suspension- or detritus-feeding worms, probably terebellid polychaetes
Rusophycus isp.	Ovate, bilobed traces with medial ridge and faint scratch traces, ranging from 22 to 30 mm in width and 28 to 35 mm in length	For Paleozoic occurrences *Rusophycus* is an indicator of marine environments and is generally attributed to trilobites
Schaubcylindrichnus coronus	Aggregates of closely-spaced, vertical to subhorizontal, lined tubes that curve upward at both ends and are filled by sediment similar to the host rock. Burrow sheaves contain between 6 and 12 tubes, ranging from 1 to 4 mm in diameter	This ichnogenus is interpreted as a communal domicile of suspension or deposit-feeders organisms, possibly sabellarid polychaetes, and is diagnostic of marine settings ranging from nearshore to slope
Skolithos isp. (Fig. 2B)	Simple, vertical to slightly inclined, unlined, typically unbranched, cylindrical burrows, typically filled with sand comparable to that of the host sediment. *Skolithos* specimens locally exhibit irregular walls and are filled by finer and darker sediment that contrasts markedly with the matrix. These specimens are indicative of firmground colonization	The paleoenvironmental range of *Skolithos* is broad. However, the Ponta Grossa specimens are certainly marine, given their co-occurrence with other strictly marine ichnotaxa. Marine *Skolithos* are generally interpreted as the dwelling structures of polychaetes
Taenidium satanassi	Horizontal to slightly inclined, straight to gently sinuous, unbranched, unlined, unwalled, cylindrical burrows with meniscate backfill composed of alternating sediment packets of roughly equal thickness. Diameters range from 6 to 12 mm and length can reach 95 mm. In the backfill, packets of finer, more carbonaceous sediment alternate with packets of sediments comparable to the host rock	Indicator of shallow water settings, has been attributed to deposit-feeding organisms
Teichichnus isp. (Fig. 2L)	Vertical stacks of horizontal to subhorizontal tubes forming straight or slightly sinuous, generally retrusive spreiten. Burrow diameters and spreiten heights of the observed specimens range from 6 to 12 mm and from 0.9 to 4 cm, respectively	This marine ichnogenus has been attributed to feeding or equilibrium activity of worm-like organisms (mainly annelids) that are tolerant of energy and salinity fluctuations
Thalassinoides isp. (Fig. 2H)	Systems of branched, cylindrical, smooth walled, straight to slightly curved, unlined burrows with commonly Y-shaped and enlarged brunch junctions. Branches are ~15 mm in diameter and up to 11 cm long	This ichnogenus is attributed to dwelling and feeding activities of decapod crustaceans, and is commonly found in shallow-marine environments
Zoophycos isp. (Fig. 3F)	Horizontal to subhorizontal, planar and helical *spreiten* structures, some with marginal tube and/or central shaft preserved. The diameters of marginal tubes are variable, ranging from 3 to 35 mm (average = 12 mm)	*Zoophycos* is a complex trace fossil of a sediment deposit-feeder and has been variably interpreted as a strip mine, refuse dump, cache or cesspit structure, produced by marine worm organisms, possibly sipunculids, echiurids and/or polychaetes

abundance and intensity of bioturbation, these suites are assigned to the Skolithos (BS = 1–3), proximal Cruziana ichnofacies (BS = 2–4), and archetypal Cruziana (BS = 3–4) ichnofacies. However, at two horizons, HCS are truncated and cross-cut by firmground *Skolithos* and *Arenicolites* representing the Glossifungites Ichnofacies.

Facies 3 is composed of storm-derived sandstones inferred to have been deposited between fair-weather wave base and storm wave base. As addressed further below, firmground surfaces demarcate important sequence stratigraphic horizons.

Facies 4 is characterized by interbedded very fine-grained sandstones and siltstones (Fig. 4D). Highly bioturbated intervals (BS = 3–6) characterized by suites of the archetypal Cruziana Ichnofacies are most common, but some beds are more weakly bioturbated (BS = 1–2) and host suites assigned to proximal expressions of the Cruziana Ichnofacies.

The heterolithic character of Facies 4 reflects a mix of suspension and tractive processes. This facies is interpreted to reflect deposition in inner shelf settings above storm-wave base.

Facies 5 is characterized by parallel laminated and locally lenticular bedded siltstones/fine-grained sandstones (Fig. 3E). Beds are moderately to intensely bioturbated (BS = 2–5) and host relative diverse suites of the archetypal Cruziana Ichnofacies.

Facies 5 reflects the predominance of suspension over traction; coarser beds reflect only periodic higher energy events. This facies is interpreted to reflect deposition in inner shelf settings close to storm wave base.

Facies 6 is represented by massive, locally parallel laminated mudstones (Fig. 3F). Some moderately to highly bioturbated intervals (BS = 3–6) are characterized by suites of the archetypal Cruziana Ichnofacies. However, intensely bioturbated (BS = 5–6), lower-diversity assemblages representing distal expressions of the Cruziana Ichnofacies are prevalent.

Facies 6 mudstones reflect deposition in relatively quiet environments characterized by moderately to well-oxygenated substrates. This facies indicates deposition in outer shelf settings.

Facies 7 is dominated by laminated black shales with rare very fine-grained sandstone lenses (Fig. 3G). Localized intervals within the shale are moderately to intensely bioturbated (BS = 2–5) with *Phycosiphon*, representing the distal Cruziana Ichnofacies. Virtually all other ichnotaxa (*Chondrites, Heliocodromites*, and *Zoophycos*) observed in these carbonaceous shales pipe downward from overlying facies (typically Facies 5).

Facies 7 records deposition in generally low-energy, dysoxic outer shelf settings. Locally preserved very fine-grained sandstone lenses record storm-induced, distal turbidity flows.

6. Depositional sequences

Small -scale lithologic variability in the studied sections can be attributed to autocyclic processes, mainly storm-related erosional and depositional events. However, longer-term changes in facies indicate changes in accommodation space that reflect relative sea-level changes mediated by allocyclic processes (e.g., tectonism, climate change, and/or eustacy). Based on the general vertical distributions of facies and associated trace fossil suites established

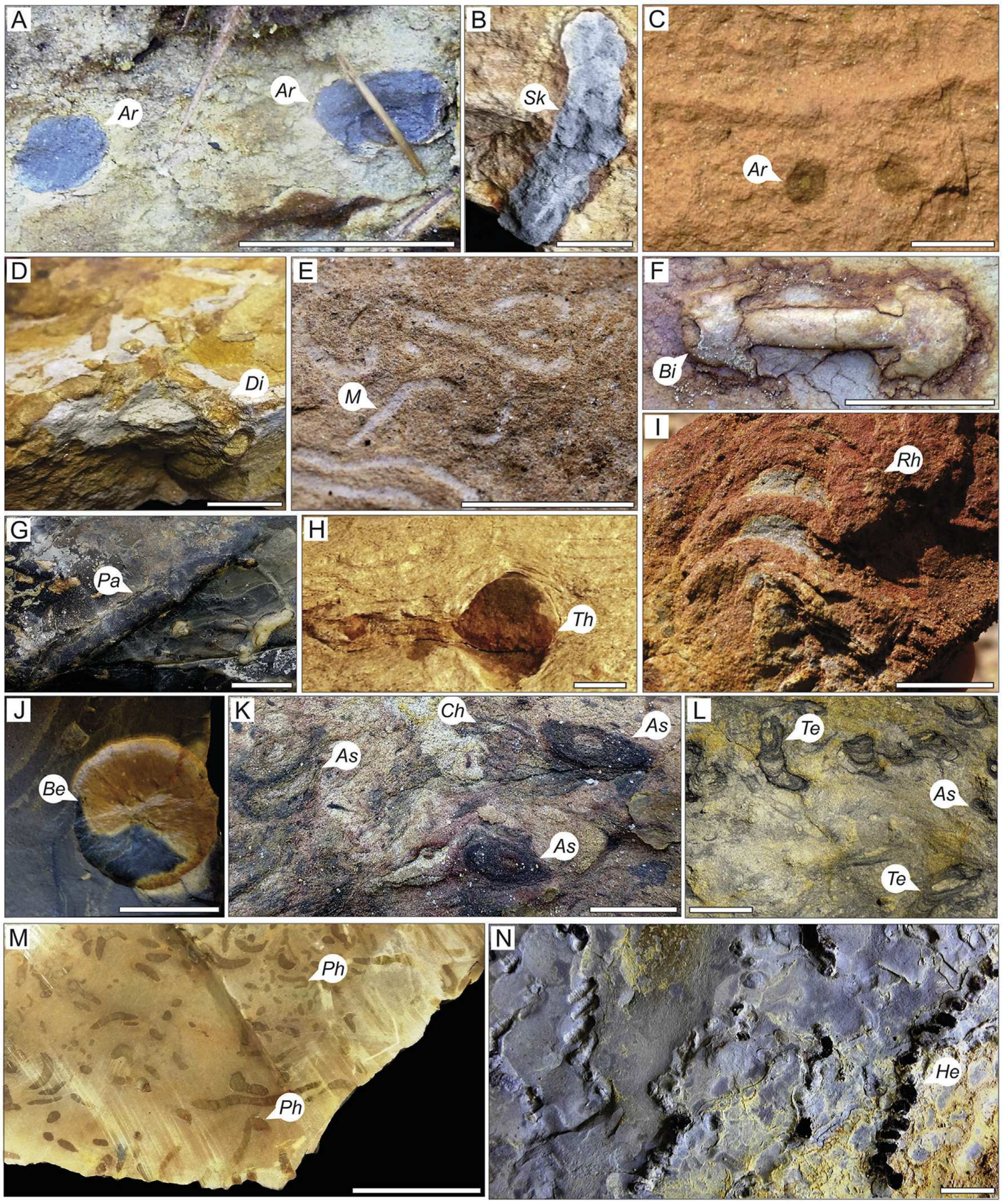

Fig. 2. Photographs exemplifying recurring trace fossils and trace fossil suites in the Ponta Grossa Formation. A-B. Firmground trace fossils representing the Glossifungites Ichnofacies: *Arenicolites* (*Ar*) in bedding-plane view (A) and *Skolithos* (*Sk*) in vertical section exhibiting irregular walls and clayey filling (B); C-E. Trace fossils representing Skolithos Ichnofacies: *Arenicolites* in bedding-plane view (C), *Diplocraterion* (*Di*) in vertical and horizontal section (D), and *Macaronichnus* (*Ma*) in bedding-plane view (E); F-J. Trace fossils representing proximal expressions of the Cruziana Ichnofacies: *Bifungites* (*Bi*) in convex hyporelief (F), *Palaeophycus* (*Pa*) in convex hyporelief (G), *Thalassinoides* (*Th*) in vertical section (H), *Rhizocorallium* (*Rh*) in bedding-plane view (I), and *Bergaueria* (*Be*) in convex hyporelief (J); K-L. Trace fossils representing archetypal expressions of the Cruziana Ichnofacies: *Asterosoma* (*As*) associated with *Chondrites* (*Ch*) (K) and *Asterosoma* (*As*) with *Teichichnus* (*Te*) (L) in vertical section; M-N. Trace fossils indicating distal expressions of Cruziana Ichnofacies: *Phycosiphon* (*Ph*) in bedding-plane view (M) and monospecific occurrences of *Helicodromites* (*Hc*) in bedding-plane view (N). All scale bars are 2 cm long.

for the sections A and B, three third-order depositional sequences—referred herein as Siluro-Devonian and Devonian I and II sequences—are recognized in the Ponta Grossa Formation (Figs. 4–6).

All three sequences are characterized by transgressive deposits (transgressive systems tract, TST) that directly overlie a coplanar sequence boundary (SB)/transgressive surface (TS). Coplanar SB/TS are marked by a broad transition from coarser-grained, shallower-water facies to finer-grained, deeper-water facies, paralleled by the general passage from suites assigned to proximal, through archetypal, to distal expressions of the Cruziana Ichnofacies. Regressive phases (highstand systems tracts, HST) are marked by reversals in these trends; coarsening- and shallowing-upward facies successions are marked by transitions from suites attributable to distal

Table 2
Lithologic and ichnologic character of Ponta Grossa facies and their general paleoenvironmental settings. Ichnofacies in each facies are listed in order from most (top) to least (bottom) common.

Facies	Lithology	Ichnofacies	BS	Dominant Traces	Subordinate Traces	Environment
1	Wave ripled, very fine- to fine-grained sandstone	Skolithos	0–3	*Ar, Di, Sk*	*Cy, Li, La, Ma*	Shoreface (above fair-weather wave base)
		Proximal Cruziana	0–3	*Pa, Rh, Sk*	*Cy*	
2	Massive to faintly stratified, very fine- to medium-grained sandstone	Proximal Cruziana	2–3	*Cy, Pa, Ro, Sk*	*Bi, Di, Rh, Sc, Th, Li*	Lower shoreface, at or near fair-weather wave base
		Archetypal Cruziana	3–5	*As, Te, Zo*	*Be, Cy, Ha, Pa, Pl, Rh, Ro, Sc, Ta, Di*	
		Skolithos	0–2	*Ar, Sk*	*Pa, Di, Sc*	
3	Hummocky cross-stratified, very fine- to fine-grained sandstone	Skolithos	1–3	*Ar, Sk*	*Di, Ma, Pa, Cy, Sc*	Inner shelf between storm and fair-weather wave base
		Proximal Cruziana	2–4	*Pa, Rh, Ro, Th*	*Di, Pl, Sc, Sk, Cy*	
		Archetypal Cruziana	3–4	*As, Ch, Te*	*Pa, Rh, Ro, Zo, Hm, Os, Sk, Th*	
		Glossifungites	–	*Ar, Sk*	-	Transgressive surfaces
4	Interbedded very fine-grained sandstone and siltstone	Archetypal Cruziana	3–6	*As, Ch, Pl, Te, Zo*	*Cy, Dp, Pa, Rh, Ru, Ta*	Inner shelf above storm wave base
		Proximal Cruziana	1–2	*Pa, Rh*	*Ar, P, Be, Cy, Dip, Ro, Di, Th, Bi, Sc, Sk*	
5	Parallel laminated, locally lenticular bedded fine-grained sandstone/siltstone	Archetypal Cruziana	2–5	*As, Ch, Pl, Te, Zo*	*He, Lo, Pa, Ps, Rh, Ro, Sk*	Inner shelf at or near storm wave base
6	Massive to parallel laminated mudstone	Distal Cruziana	5–6	*Ch, Zo*	*Pl*	Outer shelf
		Archetypal Cruziana	3–6	*Pl, Rh, Te*	*He, As, Zo, Ta, Ch*	
7	Laminated black shale with rare, very fine-grained sandstone lenses	No ichnofacies	0	-	–	Dysoxic to anoxic outer shelf
		Distal Cruziana	2–5	*Ph*	*Ch, Hc, Zo* (piped from facies 5)	

BS = bioturbation scale. *Ar- Arenicolites,As- Asterosoma,Be- Bergaueria,Bi- Bifungites, Ch- Chondrites, Cy- Cylindrichnus, Di- Diplocraterion, Dp- Diplichnites, Ha- Halopoa, Hm-Heimdallia, Hc- Heliocodromites, He- Helminthopsis, La- Laevicyclus, Li- Lingulichnus, Lo- Lockeia, Ma- Macaronichnus, Pa- Palaeophycus, Ph- Phycosiphon, Pl- Planolites, Ps-Psammichnites, Rh- Rhizocorallium, Ro- Rosselia, Ru- Rusophycus, Sc- Schaubcylindrichnus, Sk- Skolithos, Ta- Taenidium, Te- Teichichnus, Th- Thalassinoides, Zo- Zoophycos.*

expressions of Cruziana Ichnofacies through those of the archetypal Cruziana Ichnofacies (sequence Devonian II) or the Skolithos Ichnofacies (sequences Siluro-Devonian and Devonian I). In detail, each of the three sequences contain three to nine smaller-scale alternations in sedimentary and ichnofacies, which are inferred to record higher-frequency (4th-order) relative sea-level cycles and may define parasequences (Fig. 4).

Sequence boundaries are variably manifest between sequences and localities. The base of the Siluro-Devonian sequence corresponds to the boundary between the middle and upper units of the Furnas Formation (Fig. 5A), which, according to ichnostratigraphic evidence presented by Sedorko et al. (2017), represents a significant hiatus between lower and uppermost Silurian (see below).

The base of sequence Devonian I in section B is marked by an irregular contact that is cut by a firmground trace fossil suite (*Skolithos* and *Arenicolites*) representing the Glossifungites Ichnofacies (Fig. 2A). The overlying deposits represent the TST; low-accommodation prograding forms characteristic of Falling Stage System Tracts (FSST) or Lowstand Systems Tracts (LST) in proximal areas of low-gradient basins (e.g., Lindsay et al., 1993) are absent. In section A, this boundary is marked by an erosional contact between a hummocky cross-stratified sandstone (Facies 3) and an overlying mudstone (Facies 6) (Fig. 6). *Lingulichnus* containing *in situ* lingulids in the upper part of the sandstone and sharply overlain by mudstones suggests that this contact is an omission surface (Fig. 5B and C). Notably, Grahn et al. (2013) inferred the presence of a hiatus at or near this boundary (between their sequence B and C; see below) based on the absence of several palynomorph-based zones.

The boundary between Devonian I and II sequences in section A (Fig. 5D) is characterized by a firmground *Glossifungites* suite (Fig. 2B) similar to that at the base of sequence Devonian I in section B. In contrast, the boundary between Devonian I and II in section B is marked by an irregular, erosional contact overlain by coarser-grained sandstones within an amalgamated hummocky cross-stratified sandstone interval (Facies 3; Fig. 5D).

The top of sequence Devonian II is not exposed in section A (Fig. 6). In section B, it is truncated at the contact between the Ponta Grossa Formation and the overlying Gondwana I Supersequence (Fig. 5E).

Maximum flooding surfaces (MFS) mark the boundaries between transgressive and regressive intervals and are characterized by unbioturbated to weakly bioturbated, black shales (Facies 7) in all three sequences at both sections A and B (e.g., Fig. 5F and G). These black shales are rich in organic material (TOC = 2.28%, 2.13%, and 0.92% in the Siluro-Devonian, Devonian I and II sequences, respectively) and variably fossiliferous. Black shales marking these MFS, characterized by time-averaged body fossil assemblages indicative of relative sediment starvation, previously have been linked to transgressive episodes (e.g., Bosetti et al., 2013; Horodyski, 2014; Sedorko et al., 2018) and these may correspond to global Devonian events (see section 7.4 below).

7. Comparison with previous sequence stratigraphic interpretations

Several sequence stratigraphic interpretations previously have been proposed for the Ponta Grossa Formation or the Paraná Supersequence as a whole (Assine, 1996; Bergamaschi, 1999; Candido and Rostirolla, 2007; Zabini et al., 2011) (Fig. 7). These interpretations differ from our proposed sequence stratigraphic framework to varying degrees, in part related to differences in analytical approach (geophysical log interpretation vs. sedimentologic observations in outcrop) and/or the sequence stratigraphic models employed.

7.1. Ponta Grossa sequences

The sequence stratigraphic framework for the Ponta Grossa Formation established by Bergamaschi (1999) and revised by Grahn et al. (2013), which is based on both gamma-ray log and outcrop analyses, matches most closely the framework derived in the current study. Placement of most key surfaces (e.g. sequence boundaries, maximum flooding surfaces) and systems tract designations for Bergamaschi's sequences closely correspond with those for our Devonian sequences; our interpretations of this part of the Ponta Grossa Formation differ only in the precise placement of the intervening sequence boundary.

Bergamaschi (1999) placed his sequence A-B boundary beneath

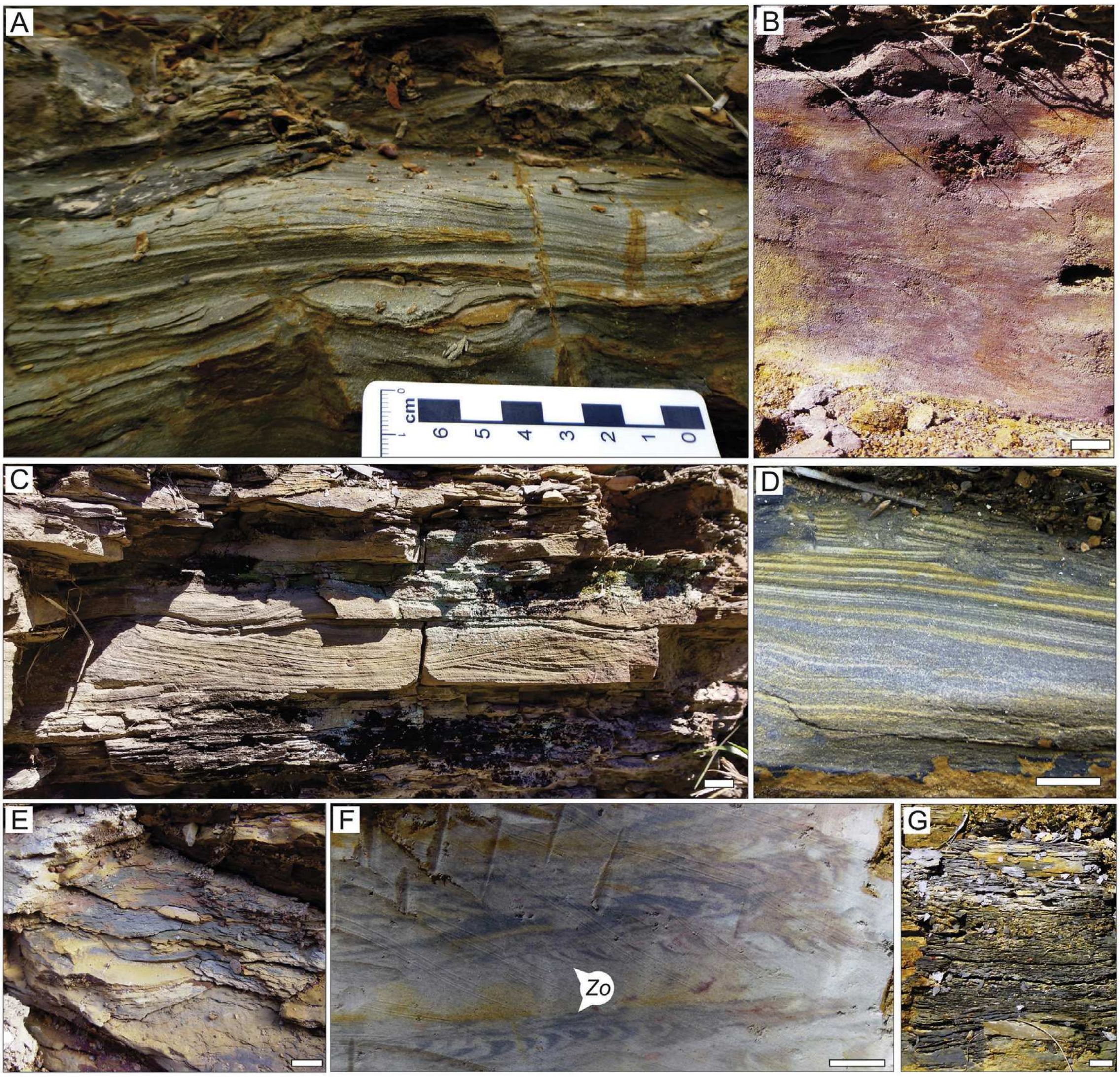

Fig. 3. Sedimentary facies in studied sections. A. Very fine-grained sandstones with wave-ripple lamination (facies 1). B. Massive fine-grained sandstones (Facies 2). C. Fine-grained sandstones with hummocky cross-stratification (Facies 3). D. Wavy bedded fine-grained sandstones/siltstones (Facies 4). E. Siltstones with parallel lamination (Facies 5). F. Mudstones (Facies 6) with *Zoophycos* (*Zo*). G. Black shale (Facies 7).

hummocky cross-stratified sandstones of the Transition Beds (topmost Furnas Formation), based on an interpreted regressive context for upper unit of Furnas Formation. However, our ichnologic observations suggest a progressive trend of transgression upward through the middle and upper units of the Furnas Formation (Fig. 7).

The upper boundary of our Siluro-Devonian sequence was placed by Bergamaschi (1999) at the base of the hummocky cross-stratified (HCS) sandstones of the Tibagi Member, which he interpreted to record an abrupt transition to shoreface conditions. In contrast, we place this boundary above the HCS deposits because our observations document a more gradual progradation upward and through the HCS interval (i.e., the HCS interval is part of an underlying HST; Fig. 7). Notably, Zabini et al. (2011) divided Bergamaschi's sequence B into three sequences, which likely correspond to the higher-frequency (4th-order) cycles we recognize in our Siluro-Devonian sequence (Fig. 4).

For the upper part of the Ponta Grossa Formation, Bergamaschi (1999) divided the interval corresponding to our Devonian sequence II into two thinner sequences (his sequences D and E), based on the presence of a shale in his sequence D that he inferred to reflect an earlier-formed marine flooding event. However, ichno-sedimentologic observations made in the current study (Fig. 4) provide no evidence for a significant stratigraphic break at this level. Thus, Bergamaschi's (1999) sequence D is interpreted here as a parasequence in the TST of our Devonian sequence II.

Bergamaschi (1999) recognized a fifth sequence at the top of the Ponta Grossa Formation (his sequence F) in the subsurface. However, this uppermost interval is not exposed in our study area and may have been removed by the erosion that preceded glacial deposition of the overlying Gondwana I supersequence.

Assine (1996) recognized only two sequences in the Ponta Grossa Formation based on gamma-ray logs and outcrop observations. His Pragian-Eifelian sequence includes our Siluro-Devonian sequence. Notably, however, he assigned part of the upper unit of the Furnas Formation to a lowstand systems tract, based on the presence of conglomeratic sandstones representing deltaic

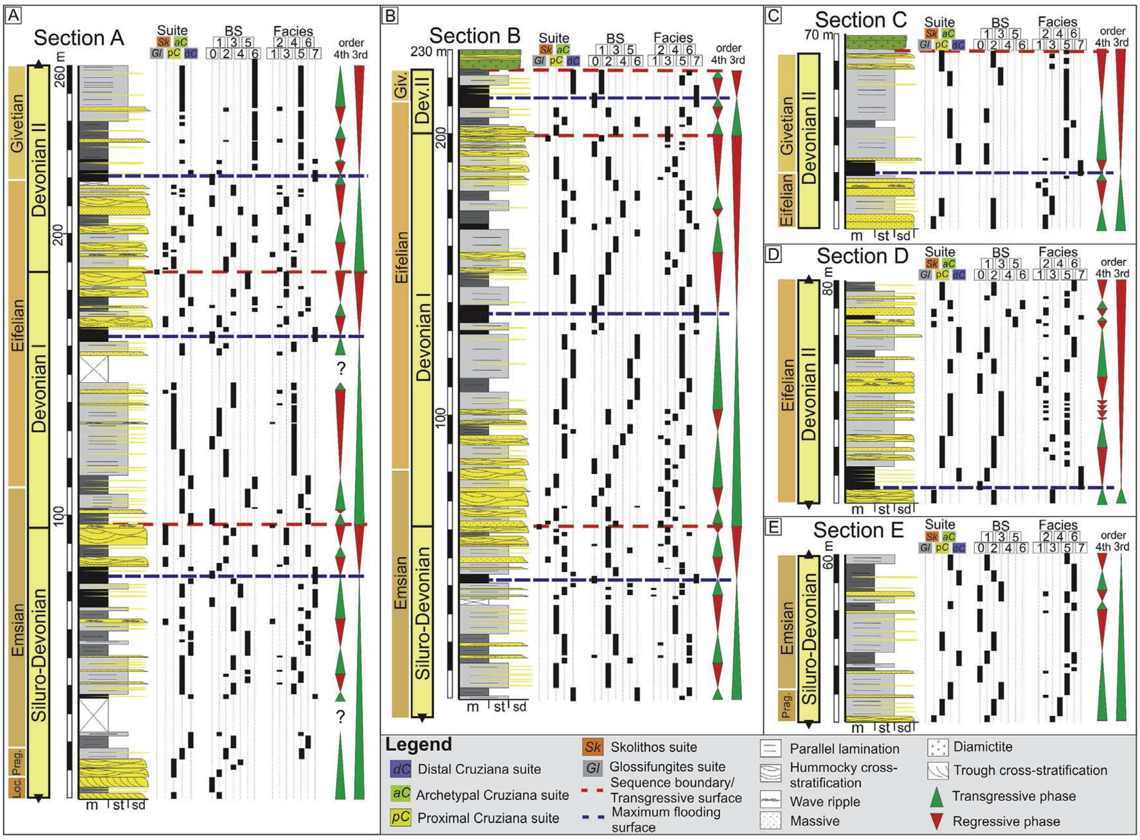

Fig. 4. Lithologic and ichnologic character of the Ponta Grossa Formation in the studied sections. Section A. Tibagi-Telêmaco Borba. Section B. Tibagi-Alto do Amparo. Section C. Barreiro Section. Section D. Tibagi-Ventania Section. Section E. Arapoti CEEP Section. BS = Bioturbation scale; m = mudstones; st = siltstones; s = sandstones. Ages are based on Grahn et al. (2013) and Horodyski et al. (2014).

progradation; his transgressive and highstand systems tracts roughly correspond to the Jaguariaíva and Tibagi members of the Ponta Grossa Formation. In contrast, we include the upper unit of the Furnas Formation in our TST. This unit, exposed at section F, exhibits a general transgressive trend. Given that this section accumulated relatively close to the margin of this low-gradient intracratonic basin, the presence of LST deposits would not be expected (e.g. Lindsay et al., 1993; Vecsei and Duringer, 2003; Santos et al., 2017).

The base of Assine's (1996) Eifelian-Frasnian sequence coincides with the boundary between our Siluro-Devonian and Devonian I sequences. However, we recognize evidence for significant omission within his Eifelian-Frasnian sequence (occurrence of the Glossifungites Ichnofacies in section B and *in situ* lingulids in section A; see above) and thus divide his Eifelian-Frasnian sequence into two sequences—Devonian I and II.

Candido and Rostirolla (2007) also recognized two sequences in the Ponta Grossa Formation (Fig. 7). Their Inferior sequence includes part of our Siluro-Devonian and Devonian I sequences, while their Superior sequence coincides with our Devonian II sequence. These authors suggested the presence of shelf-margin systems tract (SMST) deposits due to absence of erosive features overlying HST deposits, while transgressive surfaces (TS) were recognized in the lower parts of both of their sequences. Considering that SMST deposits are generated during regressive low-accomodation phases (similar to LST) and that prograding trends are diagnosed only in low-scale intervals (equivalent to parasequences), we regarded those levels as part of the transgressive systems tract.

7.2. Furnas Formation sequences

While the current manuscript focuses on the Ponta Grossa Formation, the sequence stratigraphic framework of the underlying Furnas Formation and its implications for reconstructing the sea-level history of the Paraná Supersequence overall are worthy of note here. Bergamaschi (1999) placed virtually all of the Furnas Formation into a single transgressive-regressive cycle (his sequence A; Fig. 7). In contrast, Assine (1996, 1999) proposed that the Furnas includes all or part of two sequences; his Lochkovian sequence corresponds to the lower and middle units of the Furnas, whereas his Pragian-Eifelian sequence encompasses the upper unit of the Furnas and the lower part of the Ponta Grossa Formation (Fig. 7). His placement of a sequence boundary between middle and upper units of the Furnas was based on the relatively abrupt coarsening above the sharp basal contact of upper unit and a coincident drop in gamma-ray signatures seen in well logs.

Most recently, Sedorko et al. (2017) divided the Furnas Formation into two sequences – a Lower Silurian and a Siluro-Devonian sequence – based on new ichnostratigraphic evidence and previously published paleobotanical data that indicate the presence of significant hiatuses within the Furnas Formation (Figs. 7 and 8). The boundary between these sequences is placed at the contact between middle and upper units of the Furnas Formation. Rare primitive plant fossils and palynomorphs recovered from the upper part of the Furnas indicate earliest Devonian ages, i.e., Pragian (Dino and Rodrigues, 1995) or Lochkovian (Loboziak and Melo, 2002; Rubinstein et al., 2005; Milagres et al., 2007; Grahn et al., 2010). By contrast, the presence of trace fossils with ichnostratigraphic

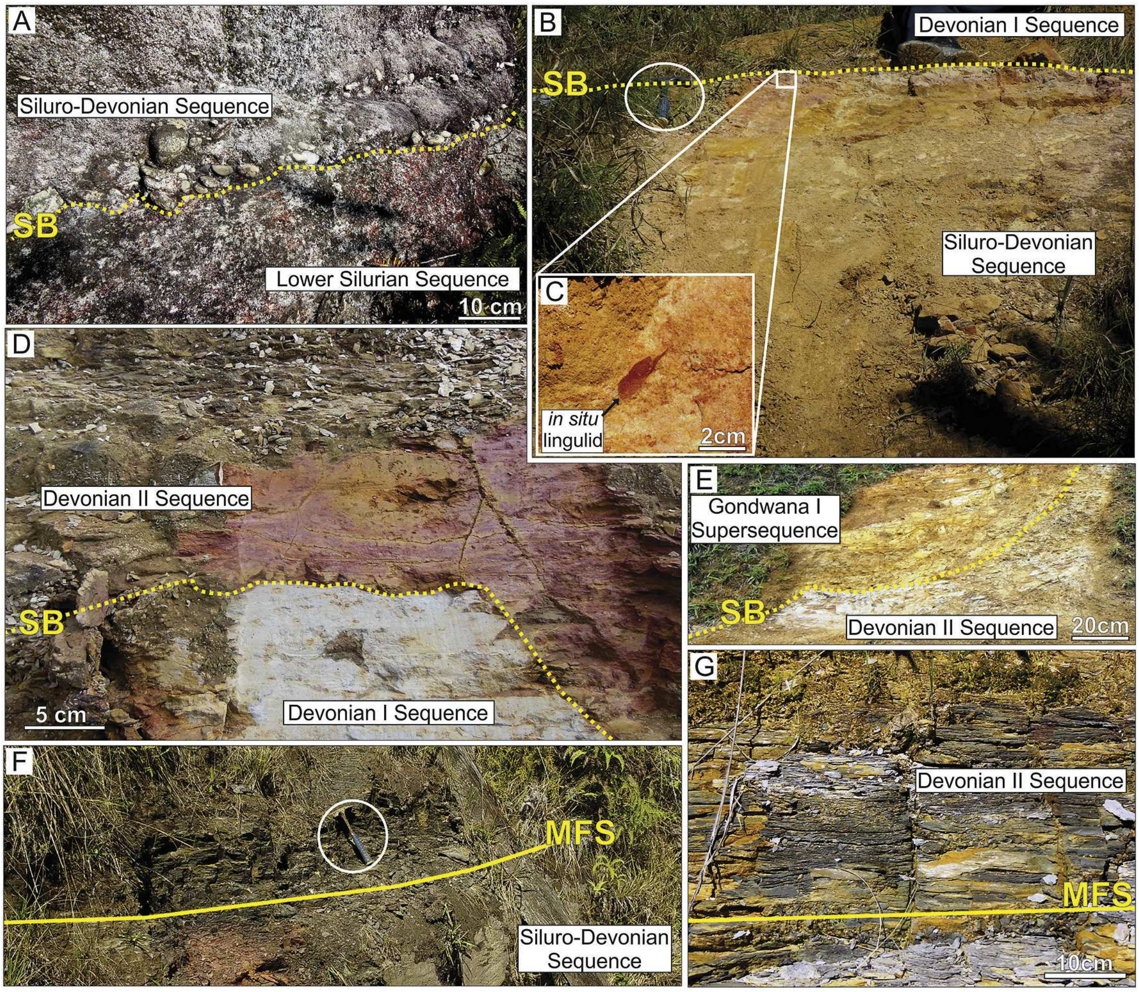

Fig. 5. Sequence boundaries (SB) and maximum flooding surfaces (MFS) expressed in the studied sections. A. Base of Siluro-Devonian sequence (Furnas middle-upper unit contact). B. Boundary between Siluro-Devonian and Devonian I sequences with *in situ* infaunal lingulids in the top of the bed (C). D. Boundary between Devonian sequences I and II marked by erosive contact. E. Erosive contact between Devonian sequence II and overlying glacial deposits of Gondwana I Supersequence. F-G. Black shales marking maximum flooding horizons (MFS) within Devonian sequences I (F) and II (G).

value (e.g., *Arthrophycus alleghaniensis*, *Cruziana acacensis*; e.g., see Seilacher, 2007) indicates a Lower Silurian age (Llandovery-Wenlock) for the lower and middle units of the Furnas. Hence, despite the predominance of marginal and shallow marine depositional facies throughout the Furnas Formation (see Sedorko et al., 2017), these observations indicate a significant hiatus at the boundary between the middle and upper Furnas units. Consequently, we infer that the upper unit of the Furnas Formation represents the earliest formed part of the TST in our Siluro-Devonian sequence (Fig. 8).

7.3. Paraná sequences and the global Silurian-Devonian sea-level curve

Based on the current study of the Ponta Grossa Formation and the companion study of the Furnas Formation by Sedorko et al. (2017), four sequences are recognized in the Paraná Supersequence: (1) a Lower Silurian (Llandovery-Wenlock) sequence, corresponding to lower and middle units of Furnas Formation; (2) a Siluro-Devonian sequence (?Pridoli-Lower Emsian), encompassing the upper Furnas, the Jaguariaíva Member, and part of the Tigabi Member of the Ponta Grossa Formation; (3) Devonian sequence I (Upper Emsian-Upper Eifelian), which includes the upper part of the Tibagi Member and lower part of the São Domingos Member of the Ponta Grossa; and (4) Devonian sequence II (Upper Eifelian-Lower Givetian), comprising the upper part of the São Domingos Member of the Ponta Grossa Formation.

Boundaries separating these sequences generally compare favorably with the global sea-level curves of Haq and Schutter (2008), as depicted in Fig. 7. The basal boundaries of our sequences are generally coincident with major regressive phases. For example, the hiatal boundary between the Lower Silurian and Siluro-Devonian sequence is tentatively linked to Upper Silurian (Pridolian) sea-level fall (Fig. 7). Similarly, the basal hiatal boundary of the Devonian I sequence may be related to regressive phases during the Emsian. By contrast, the base of Devonian sequence II, for which a biostratigraphic break has yet to be recognized, is less confidently tied to the global sea-level curve. This boundary could be linked to a relatively minor global regression in the Eifelian. Alternatively, the regression inferred for this boundary may reflect regional, tectonically-mediated changes in the Paraná Basin.

7.4. Possible correlations with global Devonian events

Numerous (~20) widespread biotic events previously have been

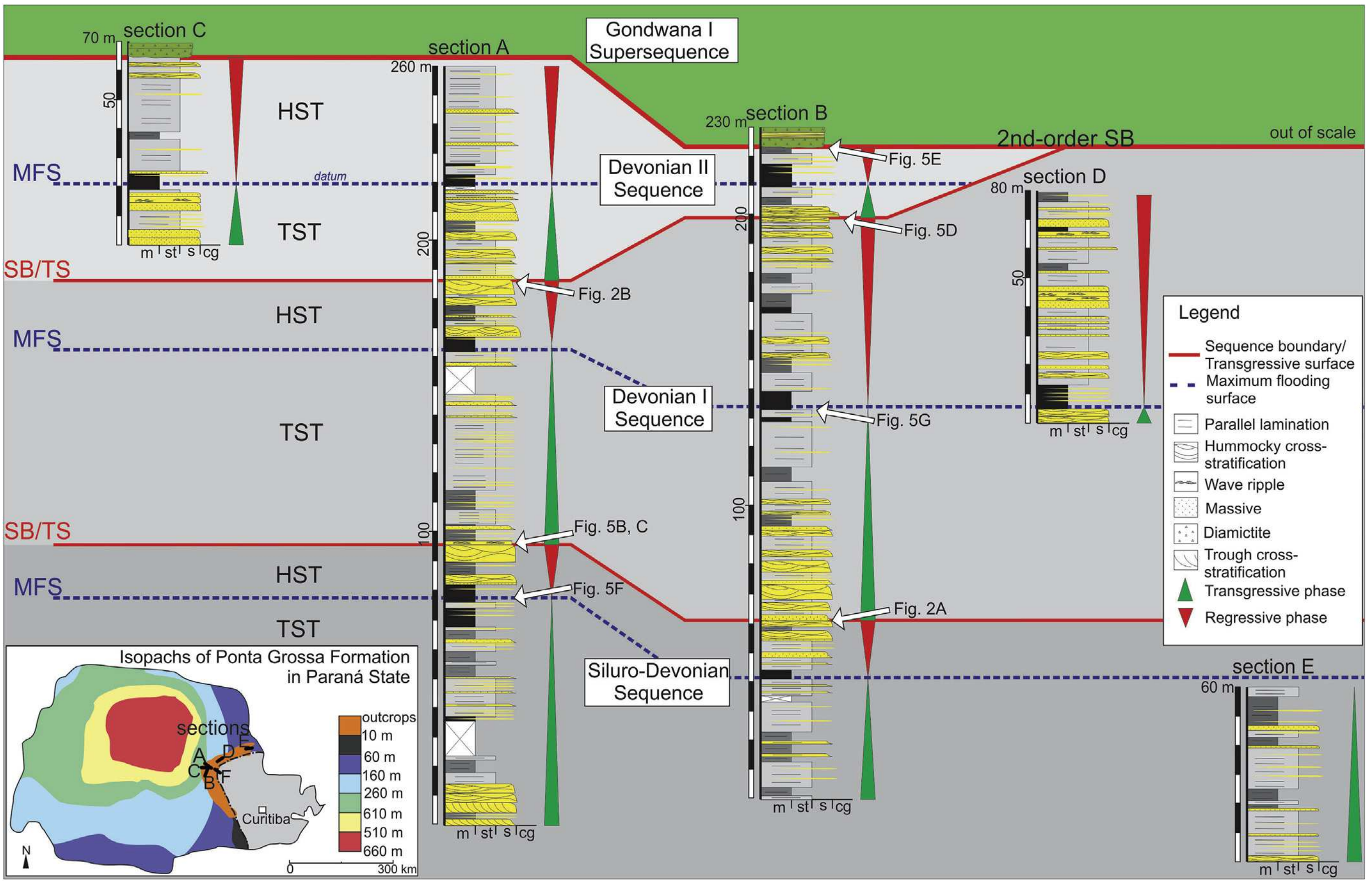

Fig. 6. Cross-section based on studied composite sections showing key stratigraphic surfaces (MFS, SB/TS). The map indicates the studied sections' position with respect to the isopach map of Ponta Grossa Formation. Arrows indicate stratigraphic positions of surfaces depicted in Fig. 2 and 5.

recognized in the Devonian System (e.g., House, 1983, 2002; Walliser, 1984a,b). These events, marked by faunal changes of variable magnitude, commonly are represented by thin, widespread dark mudrock intervals that reflect dysoxic or anoxic conditions and are typically associated with transgressive episodes. Events most pertinent to the Lower-Middle Devonian Ponta Grossa Formation are the Emsian Zlíchov-Daleje events, and the Kačák event at the Eifelian-Givetian transition.

The Kačák event, associated with moderate extinction rates, represents a period of global anoxia marked by the deposition of marine black shales. Based on their biostratigraphic studies in the Paraná Basin, Bosetti et al. (2011) and Horodyski et al. (2014) linked this event to the black shale interval that defines the MFS of our Devonian II sequence. Accordingly, these black shales likely correlate with the transgressive Kačák-Obershausen black shales of Europe and the North American Appalachian Basin (Brett et al., 2011).

The Emsian Zlíchov-Daleje events are associated with low-level extinctions. The earliest of these, the Zlíchov event, is reflected by a gradual reduction in biodiversity and is linked to deepening. Horizons associated with this event are marked by significant changes among the conodonts, pelagic graptolites and coiled ammonoids and, in North America, by gradual replacement of endemic brachiopod genera by Old World genera (Johnson, 1986). The subsequent Daleje event is linked to transgression and associated with benthic oxygen-deficiency. Emsian reduction in faunal diversity documented by Bosetti et al. (2012) within Ponta Grossa Formation suggests that the black shale at the MFS of our Siluro-Devonian sequence may be tied to the Zlíchov event. However, given the general absence of conodonts, pelagic graptolites, and ammonoids in Devonian strata of the Paraná Basin, confirmation of this link will require further investigation. Similarly, further study is needed to further explore the potential link between the Daleje event and the sequence stratigraphic framework of the Ponta Grossa Formation.

8. Summary

(1) Marine sandstones and mudrocks of the Devonian Ponta Grossa Formation in the Paraná Basin of southern Brazil contain twenty-nine ichnotaxa, recurring assemblages of which define five suites attributable to Skolithos, Glossifungites, and proximal, archetypal, and distal expressions of the Cruziana ichnofacies.
(2) Physical sedimentologic characteristics and associated softground trace fossils suites provide the basis for recognizing seven facies that reflect relative bathymetric gradients from shallow marine (shoreface) to offshore environments.
(3) The vertical distribution of facies provides the basis for dividing the Ponta Grossa Formation into three major (3^{rd}-order) depositional sequences— Siluro-Devonian, Devonian I, and Devonian II—each containing a record of three to seven higher-order sea-level cycles. Major sequence boundaries, commonly coinciding with hiatuses recognized from previously published biostratigraphic data, are locally marked by firmground trace fossil suites attributable to Glossifungites Ichnofacies. Maximum flooding horizons are prominently

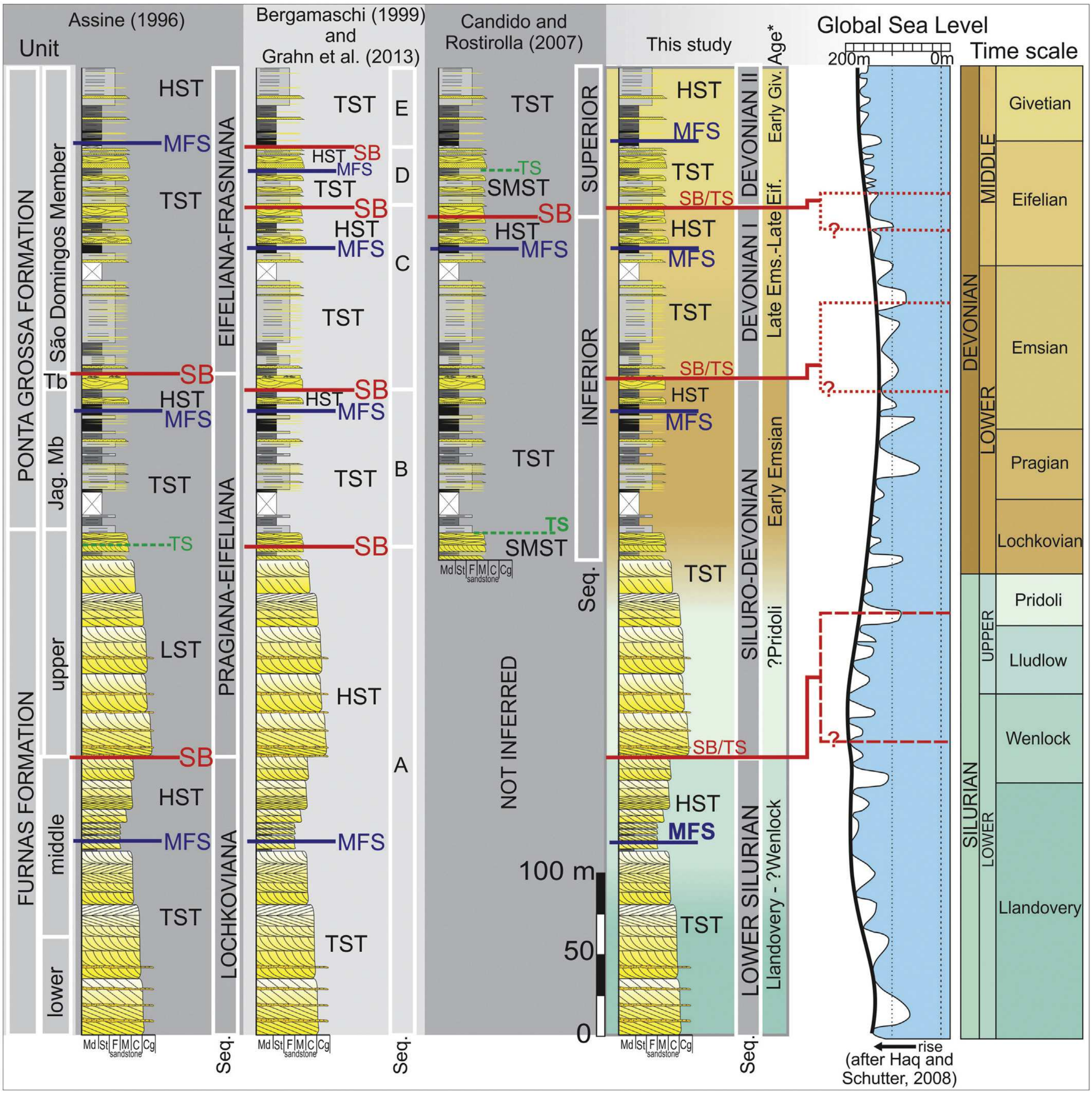

Fig. 7. Comparison of previously and currently proposed sequence stratigraphic frameworks for the Paraná Supersequence. Composite section is based on the Guartelá section of the Furnas Formation (section F, Fig. 1A; Sedorko et al., 2017) and Tibagi-Telêmaco Borba section of the Ponta Grossa Formation (Section A, Fig. 1A). SB= Sequence Boundary; MFS = Maximum flooding Surface; TST = Transgressive Systems Tract; HST=Highstand Systems Tract; TS = Transgressive surface; LST = Lowstand Systems Tract; SMST=Shelf Margin Systems Tract; Jag Mb = Jaguariaíva Member; Tb= Tibagi Member. *Ages are based on Grahn et al. (2013) and Sedorko et al. (2017).

marked by unbioturbated or weakly bioturbated black shales.

(4) By integrating observations of the Ponta Grossa Formation with those recently made on the underlying marginal- to shallow-marine Furnas Formation, the entire Paraná Supersequence can be divided into four disconformity-bound sequences: a Lower Silurian (Llandoverian-Wenklockian) sequence, corresponding to the lower and middle Furnas Formation; a Siluro-Devonian sequence (?Pridoli-Lower Emsian) encompassing the upper Furnas and the lower part of the Ponta Grossa Formation, and Devonian I (Upper Emsian-Upper Eifelian) and Devonian II (Lower Givetian) sequences, comprising the remainder of the Ponta Grossa.

(5) Our sequence stratigraphic framework, based on integrated sedimentologic and ichnologic observations, differs to varying degrees from those previously proposed for the Paraná Basin. Notably, boundaries separating our sequences compare favorably with regressive phases on established

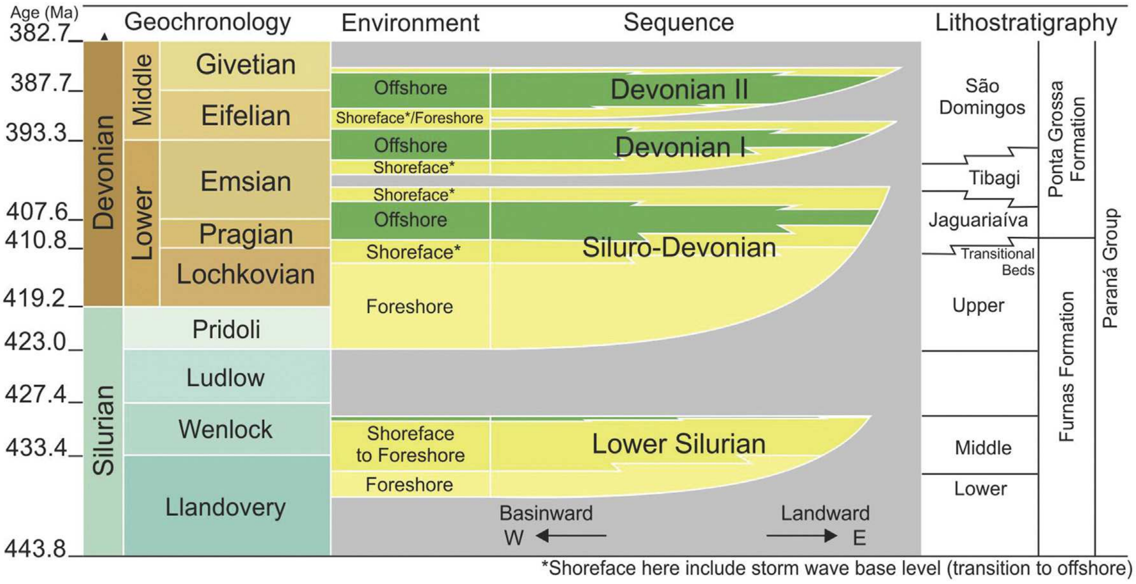

Fig. 8. General stratigraphic context of the Paraná Group (Supersequence) from Paraná Basin, based on the current study (biostratigraphic data are based on Grahn et al., 2010, 2013; Sedorko et al., 2018; ages are from Cohen et al., 2013).

global sea-level curves for the Silurian-Devonian. Nonetheless, regional tectonics cannot be discounted as an additional control over transgressive-regressive cycles manifested in the Paraná Supersequence.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jsames.2018.02.008.

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CAPÍTULO 5

A *Zoophycos* carnival in Devonian beds: Paleoecological, paleobiological, sedimentological, and paleobiogeographic insights

Artigo publicado no periódico “Palaeogeography, Palaeoclimatology, Palaeoecology” onde analisou-se densas ocorrências de *Zoophycos* em depósitos da Formação Ponta Grossa, indicando sua aplicabilidade para reconhecimento de vieses preservacionais e assinaturas em contextos de baixo espaço de acomodação (i.e., depósitos de tratos de sistemas de nível alto).

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A *Zoophycos* carnival in Devonian beds: Paleoecological, paleobiological, sedimentological, and paleobiogeographic insights

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ABSTRACT

Devonian occurrences of *Zoophycos* are often observed in successions representing shelfal deposits and have been interpreted as the first expansion of this trace fossil during the Paleozoic. Dense *Zoophycos* occurrences in storm-generated Paleozoic beds have been interpreted as the result of ecological opportunist strategy when the tracemaker exploited quiet, nutrient garden substrates after storms. In the Devonian Ponta Grossa Formation (Pragian to Frasnian) of the Paraná Basin (Brazil), *Zoophycos* is both preserved in storm-generated strata indicating oxyc substrates, and in association with *Chondrites* and *Phycosiphon* suggesting dysoxic offshore deposition. This study focuses on the analysis of *Zoophycos* observed in the Devonian strata to understand the depositional context reflected by paleoecologic strategies and taphonomic signatures. We analyzed the ichnofabrics and sedimentary facies of Devonian sections from the Paraná Basin, focusing on the occurrences of *Zoophycos*. The tiering structure involving dense *Zoophycos* ichnofabrics demonstrated that shallower burrows (e.g., *Asterosoma*, *Palaeophycus*, *Cylindrichnus*, *Schaubcylindrichnus*, *Skolithos*) reworked deep-tier burrows (*Chondrites*, *Phycosiphon*, and *Zoophycos*), indicating erosion of surficial levels. The dense *Zoophycos* ichnofabric representing the fair-weather suite obliterated primary sedimentary structures of storm deposits, which favored the visibility of deep-tier structures in a lam-scram pattern. In this sense, dense *Zoophycos* ichnofabric from Paraná Basin cannot be linked to an opportunistic behavior, but to an over-represented occurrence in space and time, being a taphonomic artifact related to low accommodation space in prograding context. The association with other trace fossils allowed the attribution of *Zoophycos* as a component of distal and archetypal expressions of Cruziana Ichnofacies rather than Zoophycos Ichnofacies. Concerning the vertical distribution of *Zoophycos* in the Paraná Basin, this trace appears in strata related to the first occurrence of land plants, being common in the Pragian–Eifelian interval, and declining in upper strata. This decline might be related to a potential structural change of the Paraná Basin during Middle Devonian.

1. Introduction

Zoophycos is characterized by different morphologies of helical or tongue-shaped spreiten burrows produced by endobenthic worm-like organisms (e.g., Seilacher, 1967; Simpson, 1970; Ekdale, 1977; Wetzel and Werner, 1981; Kotake, 1989; Ekdale and Lewis, 1991; Olivero, 1994, 2007; Knaust, 2009; Zhang and Zhao, 2015; Zhang et al., 2015a). Although being preserved in a variety of sedimentary facies throughout Phanerozoic, a general trend was recognized, from shallow-marine settings in pre-Jurassic deposits to deep-marine environments in post-Cretaceous rocks (Seilacher, 1986; Bottjer et al., 1987, 1988; Zhang et al., 2015b). An increase in the morphological complexity is also identifiable, from simple, helical morphologies to lobed tongue-shaped forms, following the shift of the bathymetric distribution to more in-depth settings after Cretaceous (Seilacher, 1986; Olivero, 2003; Zhang et al., 2015b). In this sense, monospecific occurrences of *Zoophycos* suggest low-oxygen slope to deep-sea environments in post-Cretaceous deposits, while in Paleozoic and Mesozoic rocks *Zoophycos* can be found both in well-oxygenated shelf and, less frequent, in dysoxic deep-sea environments (Bottjer et al., 1988; Zhang et al., 2015b).

Devonian *Zoophycos* are often preserved in successions representing shelfal deposits (Zhang et al., 2015b) and have been considered as the first bloom of this trace fossil during the Paleozoic (Miller, 1991; Neto de Carvalho and Rodriguez, 2003; Gaillard and Racheboeuf, 2006; Seilacher, 2007; Zhang, 2014; Zhang et al., 2015b). Dense *Zoophycos* occurrences are relatively common in Devonian beds, being preserved in several localities (e.g., Bolivia – Gaillard and Racheboeuf, 2006; USA – Marintsch and Finks, 1982; Miller, 1991; Senglaub, 2004; Australia –

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Ellenor, 1970). Other occurrences of dense *Zoophycos* from Paleozoic strata are preserved in storm beds (Lower Devonian, China – Zhang, 2014; Zhang and Zhao, 2016; Li et al., 2017; Upper Devonian, USA – Miller, 1991; Upper Pennsylvanian–Lower Permian, China – Hu et al., 2010; Middle Permian [Guadalupian], Oman – Knaust, 2009), which has been attributed to an opportunistic strategy exploiting quiet, nutrient garden substrates after storms (Gaillard et al., 1999; Zhang, 2014; Zhang and Zhao, 2016; Li et al., 2017).

In Devonian strata of the Paraná Basin (Brazil), *Zoophycos* is both preserved in storm-generated and in offshore beds, having different signatures that can help to understand the evolutionary trends related to ecospace colonization. These occurrences are mostly positioned in Lower Devonian beds (Pragian to Emsian age), which correspond to the first bloom of this trace fossil worldwide (e.g., Zhang et al., 2015b). In this sense, this study aims (i) to interpret distinct occurrences of *Zoophycos* in Devonian strata from Paraná Basin; (ii) to infer paleoecologic strategies and taphonomic context represented by *Zoophycos* in these strata; and (iii) to analyze the trends related to the vertical distribution of *Zoophycos* throughout the Ponta Grossa Formation.

2. Geological setting

The Paraná Basin is a vast intracratonic basin (circa $1.5 \times 10^6\,\text{km}^2$) that covers the southern portion of Brazil and adjacent areas (Fig. 1A). The sedimentary fill is divided into six second-order sequences influenced by tectonic-eustatic cycles related to the evolution of the Western Gondwana, from Late Ordovician to Late Cretaceous (Milani et al., 2007). The Devonian beds characterize the upper portion of the Paraná Supersequence (Silurian-Devonian) and are superimposed by the Gondwana I Supersequence in a slightly angular unconformity (Assine, 1996). The sedimentary succession was deposited under marine conditions and cold temperate climate, between 60° and 80°S paleolatitude (Cooper, 1977; Scotese and McKerrow, 1990; Matsumura et al., 2015).

Four third-order sequences were identified in surface sections from Paraná Supersequence, named Lower Silurian, Siluro-Devonian, Devonian I and Devonian II, and they were associated in part with Furnas and Ponta Grossa Formations, sensu Lange and Petri (1967) (Sedorko et al., 2018a; Figs. 1B, 2). The deposits of the Lower Silurian sequence (lower and middle Furnas Formation) contains fine- to coarse-grained sandstones and conglomerates from marginal-marine and shallow marine environments, besides sandy-dominated heterolithic deposits and fine- to medium-grained sandstones with tidal influence at the top (Sedorko et al., 2017). Tidal-influenced marginal-marine and shallow marine environments also occur at the base of the Siluro-Devonian sequence (Fig. 2A). These deposits are overlaid by sandstones with hummocky cross stratification (HCS), which are capped by the *Zoophycos*-rich siltstones and shales (Fig. 2), mostly representing lower shoreface to offshore settings. A bed of black shales represents the top of this sequence and characterizes the maximum flooding deposits during the Emsian (e.g., Grahn et al., 2013; Sedorko et al., 2018a). The Devonian I and II sequences contain sandstones, siltstones, shales, and locally conglomerates representing dominantly offshore and locally shallower marine conditions (Sedorko et al., 2018a). As further presented, in those beds the *Zoophycos* intensity declines in comparison with the Siluro-Devonian sequence.

3. Material and methods

The trace fossils studied herein are exposed in Tibagi municipality, Paraná State, southern Brazil (Fig. 1A). Data acquisition was conducted at centimeter scale and consisted of a description of sedimentary facies and trace fossil content. Trace fossils were described and photographed in place, and some samples were collected for morphological analyses in the laboratory. Those samples are deposited in the collections of the Museu da História Geológica do Rio Grande do Sul (Unisinos University) with the numbers ULVG-12474, ULVG-12475, and ULVG-12476. The trace fossil analysis included the ichnofabric characterization and the quantification of the bioturbation. This quantification was based on the bioturbation scale (BS) proposed by Reineck (1963), ranging from 0 (without bioturbation) to 6 (homogenized sediment or no apparent primary sedimentary structures). The dense *Zoophycos* occurrence was analyzed in detail (Fig. 3), while the vertical distribution of *Zoophycos* was analyzed on two surface sections (i.e., Sections A and B, Fig. 1A) as presented by Sedorko et al. (2018a).

4. Ichnofabrics and sedimentary facies

Two main sections were prospected to analyze the vertical distribution of *Zoophycos* in the Ponta Grossa Formation: Section A (Tibagi-Telêmaco Borba section) and Section B (Tibagi-Alto do Amparo

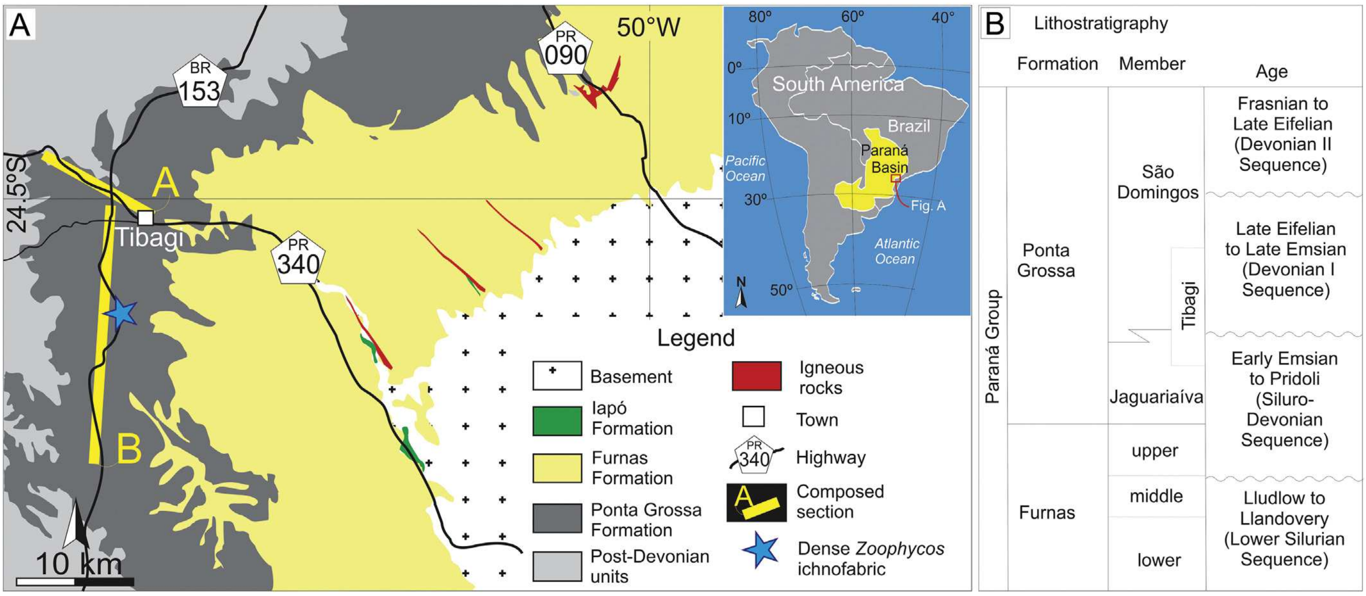

Fig. 1. Location map and stratigraphic context of the study area in Paraná Basin, Brazil. A. Geological map of Paraná Group in Campos Gerais region, Paraná State, Brazil. Blue star indicates the location of dense *Zoophycos* ichnofabric at road BR 153 km 214. B. Lithostratigraphy and ages of the Paraná Group in the Paraná Basin (sensu Lange and Petri, 1967). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

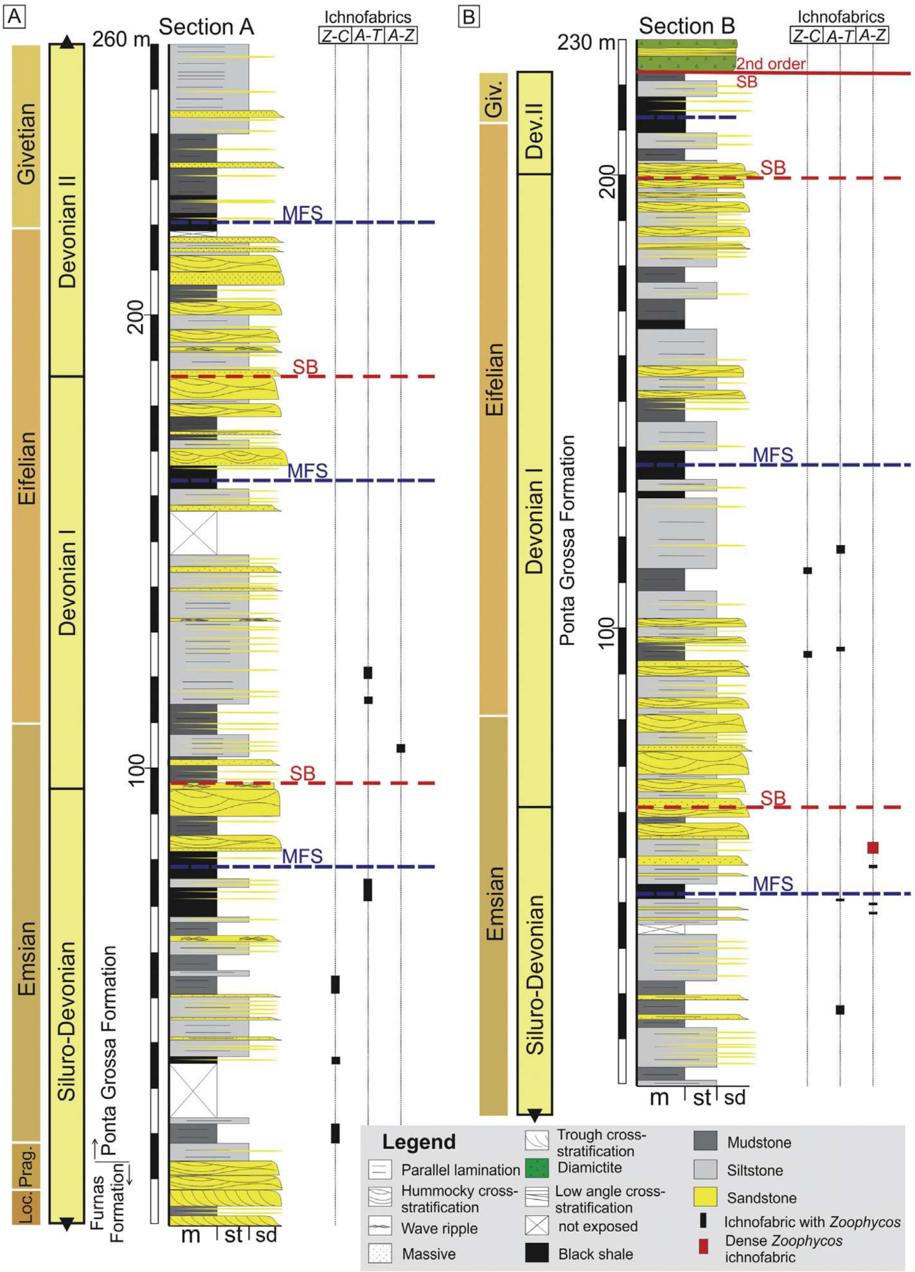

Fig. 2. Studied sections and vertical distribution of ichnofabrics with *Zoophycos* in Ponta Grossa Formation. Geographic position in Fig. 1. *Z* = *Zoophycos* ichnofabric; *Z-C* = *Zoophycos-Chondrites* ichnofabric; *A-Z* = *Asterosoma-Teichichnus* ichnofabric; *A-T* = *Asterosoma-Zoophycos* ichnofabric; m = mudstone; st = siltstone; sd = sandstone.; SB = sequence boundary; MFS = maximum flooding surface. Modified from Sedorko et al. (2018a).

section) (Figs. 1A, 2). *Zoophycos* is preserved mainly in fine-grained beds of the Siluro-Devonian and Devonian I sequences (Figs. 2, 3). In those beds, *Zoophycos* is a component of three ichnofabrics: *Zoophycos-Chondrites*, *Asterosoma-Teichichnus*, *Asterosoma-Zoophycos*, and ichnofabrics.

The *Zoophycos-Chondrites* ichnofabric has *Phycosiphon* as accessory ichnogenus (Fig. 4A, E). This ichnofabric is preserved in gray to dark mudstones (Table 1; Fig. 5D), and the bioturbation scale (BS) is low to moderate, between 2 and 4.

The *Asterosoma-Teichichnus* ichnofabric (Fig. 4B) has *Zoophycos* as accessory, as well *Chondrites*, *Cylindrichnus*, *Rhizocorallium*, and *Rosselia*. This ichnofabric is preserved in heterolithic sandstones with mudstones beds (Table 1) or in mudstones (Facies 4, Table 1), and the bioturbation intensity is moderate, with BS 3–4.

The *Asterosoma-Zoophycos* ichnofabric (Fig. 4C) is more diverse than the *Zoophycos-Chondrites* ichnofabric, presenting *Arenicolites*, *Bifungites*, *Chondrites*, *Cylindrichnus*, *Diplocraterion*, *Lockeia*, *Palaeophycus*, *Phycosiphon*, *Planolites*, *Rhizocorallium*, *Rosselia*, *Skolithos*, and *Teichichnus* as accessories. This ichnofabric is preserved in Facies 3 (Table 1, Fig. 5C), composed of heterolithic, lenticular bedded very fine-grained sandstone and siltstone, and exhibits a high intensity of bioturbation, with BS 4–6. A variation of this ichnofabric is named as dense *Zoophycos* ichnofabric (Fig. 4D–E) because *Zoophycos* is the most evident trace fossil, but all other ichnogenera are present. This variation occurs associated with sandstone lenses eroding heterolithic beds (Fig. 6A), in some places also truncating previous *Zoophycos* (Fig. 6B). *Zoophycos* truncates and is truncated by other trace fossils, such as *Asterosoma*, *Chondrites*, *Cylindrichnus*, *Palaeophycus*, *Planolites*, *Schaubcylindrichnus*, *Skolithos*, and other *Zoophycos* (Figs. 6C–F, 7D).

Two other ichnofabrics occur associated within the interval with

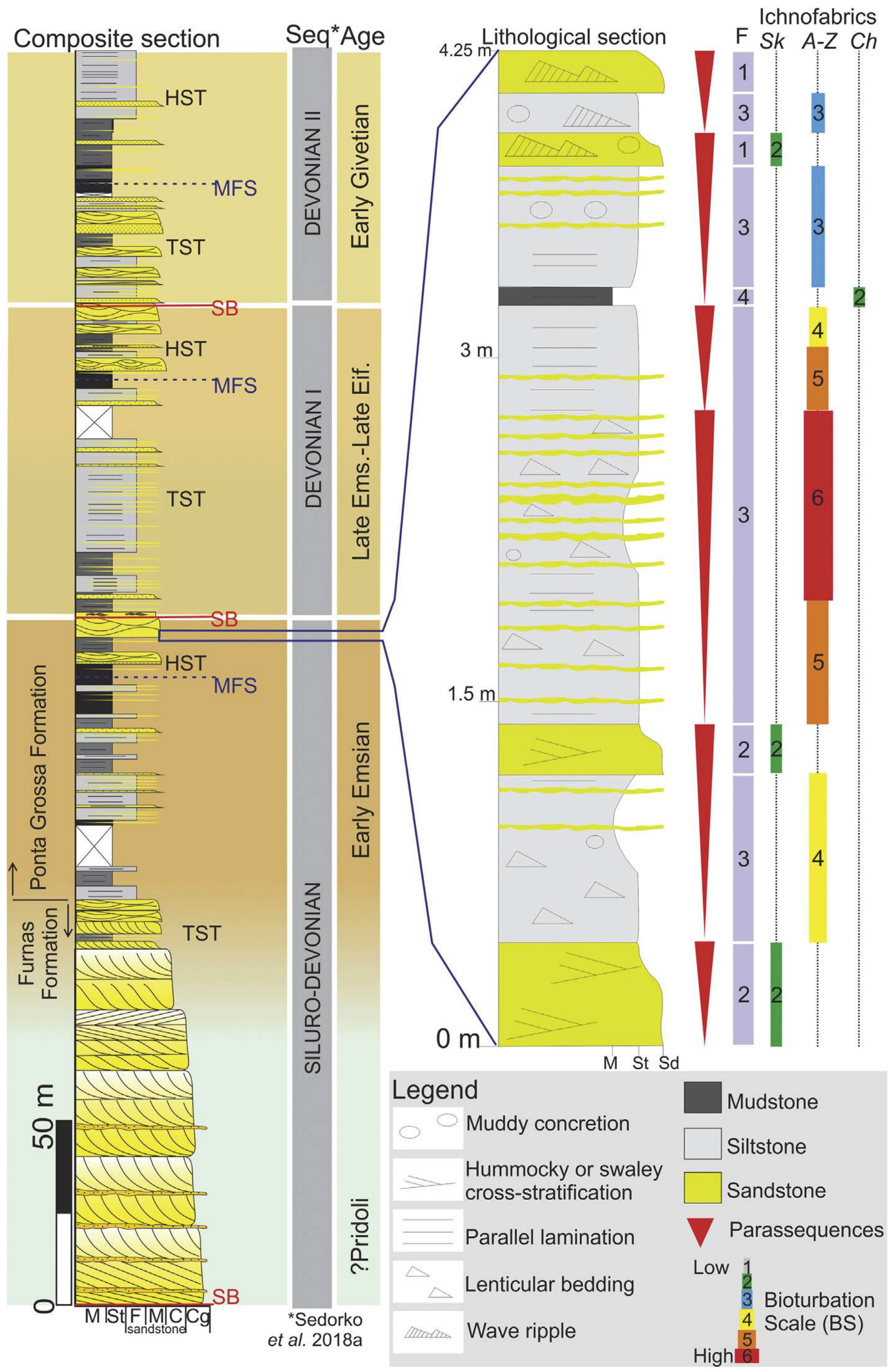

Fig. 3. Sedimentary profile and ichnofabrics associated to dense *Zoophycos* ichnofabric, and its position in the Siluro-Devonian sequence (sequences and composed section modified from Sedorko et al., 2018a); Lower Silurian sequence was excluded from this composed section. *Sk* = *Skolithos* ichnofabric; *A-Z* = *Asterosoma-Teichichnus* ichnofabric; *Ch* = *Chondrites* ichnofabric; F = facies (details in Table 1); m = mudstone; st = siltstone; sd = sandstone.

dense *Zoophycos* ichnofabric: the *Skolithos* and *Chondrites* ichnofabrics (Fig. 3). The *Skolithos* ichnofabric presents *Palaeophycus*, *Lockeia*, *Arenicolites*, and *Rhizocorallium* as accessories and occurs in sandstone beds (Facies 1 and 2; Table 1), with BS 2–3. The *Chondrites* ichnofabric is monospecific and is exclusive of the shale bed (Facies 4; Table 1).

4.1. Morphology of *Zoophycos*

The most common morphology in the Ponta Grossa Formation is a planar U-shaped form; however, helical and lobed forms (Fig. 7A–D) are also preserved in association with the dense *Zoophycos* ichnofabric. The helical structures commonly present two whorls and were produced downward (Fig. 7E). *Spreiten* thickness varies from 0.6 to 2.2 cm, and the width of *spreiten* oscillates from 11 to 44.6 cm (Fig. 7G) (details in Table 2). Some *Zoophycos* specimens show a passive filling by sandy material from upper layers (Fig. 7G), and can present macrofossils burrowing *Zoophycos* (Fig. 7F–G).

Few structures exhibit variations in *spreiten* thickness (Fig. 8A), and locally, different diameters are preserved at the same level (Fig. 8B) demonstrating the different size of tracemakers. Some *Zoophycos* filled

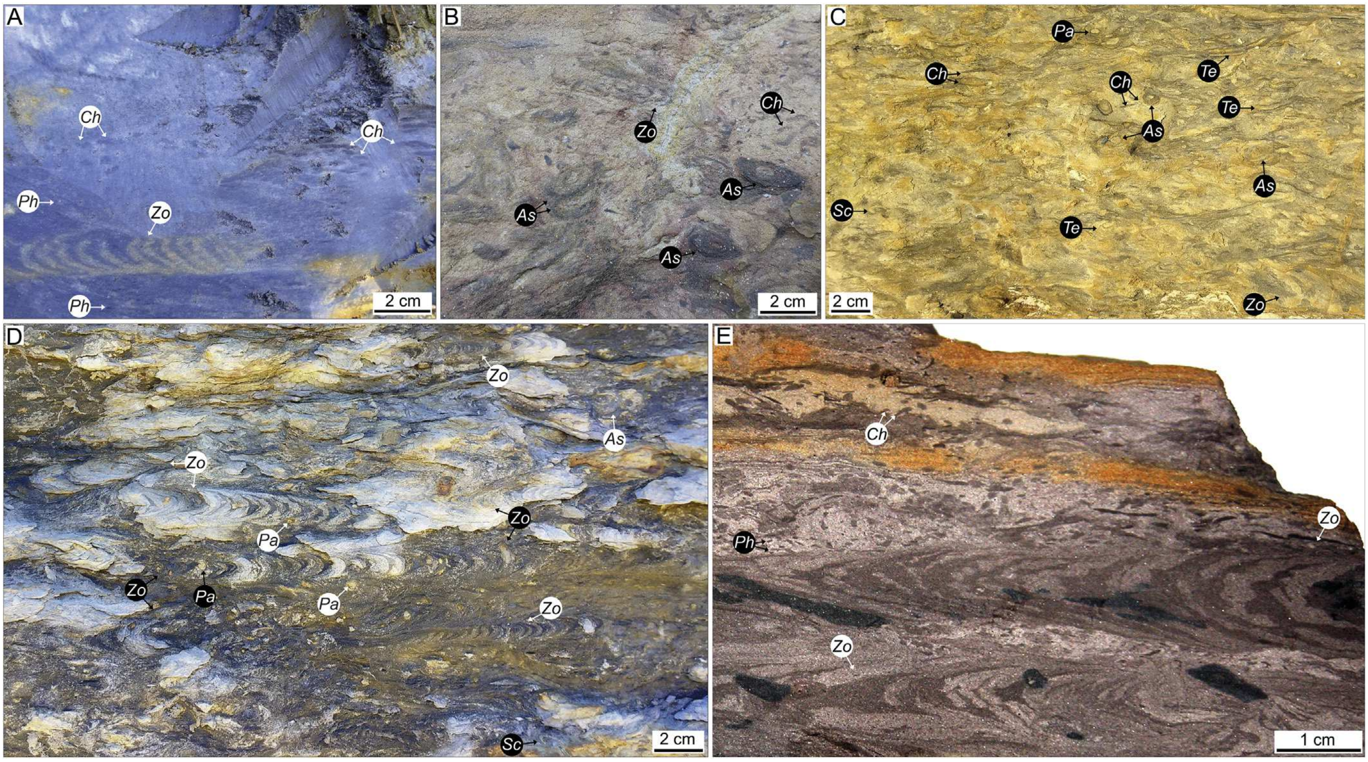

Fig. 4. Ichnofabrics from the studied section. A. *Zoophycos-Chondrites* ichnofabric in dark mudstones. B. *Asterosoma-Zoophycos* ichnofabric in heterolithic sandstones with mudstones beds. C. *Asterosoma-Teichichnus* ichnofabric in siltstones beds. D. Dense *Zoophycos* ichnofabric in heterolithic sandstones with mudstones beds. E. *Zoophycos-Chondrites* ichnofabric with *Phycosiphon* as accessory. *As* = *Asterosoma*, *Ch* = *Chondrites*, *H* = *Helminthopsis*, *Lo* = *Lockeia*, *Pa* = *Palaeophycus*, *Pl* = *Planolites*, *Sc* = *Schaubcylindrichnus*, *Te* = *Teichichnus*, *Zo* = *Zoophycos*.

with sand material appear penetrating at least 8 cm below an erosive surface (disregarding compaction), from where the sand comes from (Fig. 8C).

4.2. Macrofossil content

Although body fossils are well distributed throughout the studied section, we only mention the macrofossils associated with dense *Zoophycos* ichnofabric, exclusively preserved in Facies 3 (Table 1). An extended analysis of the macrofossil content from the Ponta Grossa Formation is available in Bosetti et al. (2012) and Horodyski et al. (2014). The body fossils association in Facies 3 is represented by brachiopods (Lingulida, Rhynchonellida, and Spiriferida), trilobites (Homalonotidae), echinoderms (Crinoidea), and mollusks (*Tentaculites* sp.).

The brachiopods are whole, both articulated (Fig. 8E) and disarticulated (Fig. 8H), being chaotically distributed in relation to the bedding-plane (Fig. 8J), while the trilobites are whole, articulated and winding or extended-contorted. Isolated columnals of crinoids occur vertically to the bedding plane with no crown and holdfast fossils evidence (Fig. 8F–G). Univalved bioclasts (*Tentaculites*) are whole and parallel to the bedding plane (Fig. 8I) or can occur oblique in relation to the bedding-plane (Fig. 7F).

5. Paleoenvironmental implications

The *Zoophycos-Chondrites* ichnofabric is preserved in mudstones facies presenting a low-diversity assemblage of deposit-feeding traces. Comparing to other ichnofabrics bearing *Zoophycos*, this ichnofabric has trace fossils with minor dimensions (Table 2). A limiting factor to the growth of the tracemaker is the oxygenation within the substrate, and it is observed that ichnological suites in dysoxic settings present low diversity and diminutive trace fossils (Savrda and Bottjer, 1986; Boyer and Droser, 2011).

The consensus for Paleozoic *Zoophycos* is that they do not represent deep-water colonization as preconized by the Zoophycos Ichnofacies (Miller, 1991; Kotake, 2014). Although Zoophycos Ichnofacies have been reported in Ponta Grossa Formation (Campanha, 1985; Fernandes, 1996; Abelha et al., 2007), those occurrences were not associated with deep-waters or slope settings. Thus, ichnofabrics bearing *Zoophycos* in Paleozoic strata are common component of distal expressions of the

Table 1
Lithofacies, trace fossils and sedimentary processes in the study section.

Code	Facies	Associated trace fossils	Sedimentary processes	Fig.
1	Wave rippled very fine- to fine-grained sandstone	*Skolithos*, *Palaeophycus*, *Lockeia*	Lower shoreface dominated by oscillatory flows	5A
2	Swaley or hummocky cross-stratified, very fine- to fine-grained sandstone	*Skolithos*, *Palaeophycus*, *Arenicolites*, *Rhizocorallium*	Lower shoreface to offshore transition dominated by oscillatory flows	5B
3	Lenticular bedded very fine-grained sandstone and siltstone or locally mudstone	*Asterosoma*, *Teichichnus*, *Zoophycos*, *Chondrites*, *Planolites*, *Lockeia*, *Skolithos*, *Rhizocorallium*, *Rosselia*, *Bifungites*, *Palaeophycus*, *Phycosiphon*, *Arenicolites*, *Diplocraterion*	Offshore transition (below storm wave base) alternating oscillatory flows and decantation	5C
4	Parallel laminated mudstone	*Chondrites*, *Zoophycos*, *Planolites*, *Helminthopsis*, *Asterosoma*, *Rhizocorallium*, *Cylindrichnus*, *Rosselia*, *Teichichnus*	Offshore dominated by decantation	5D

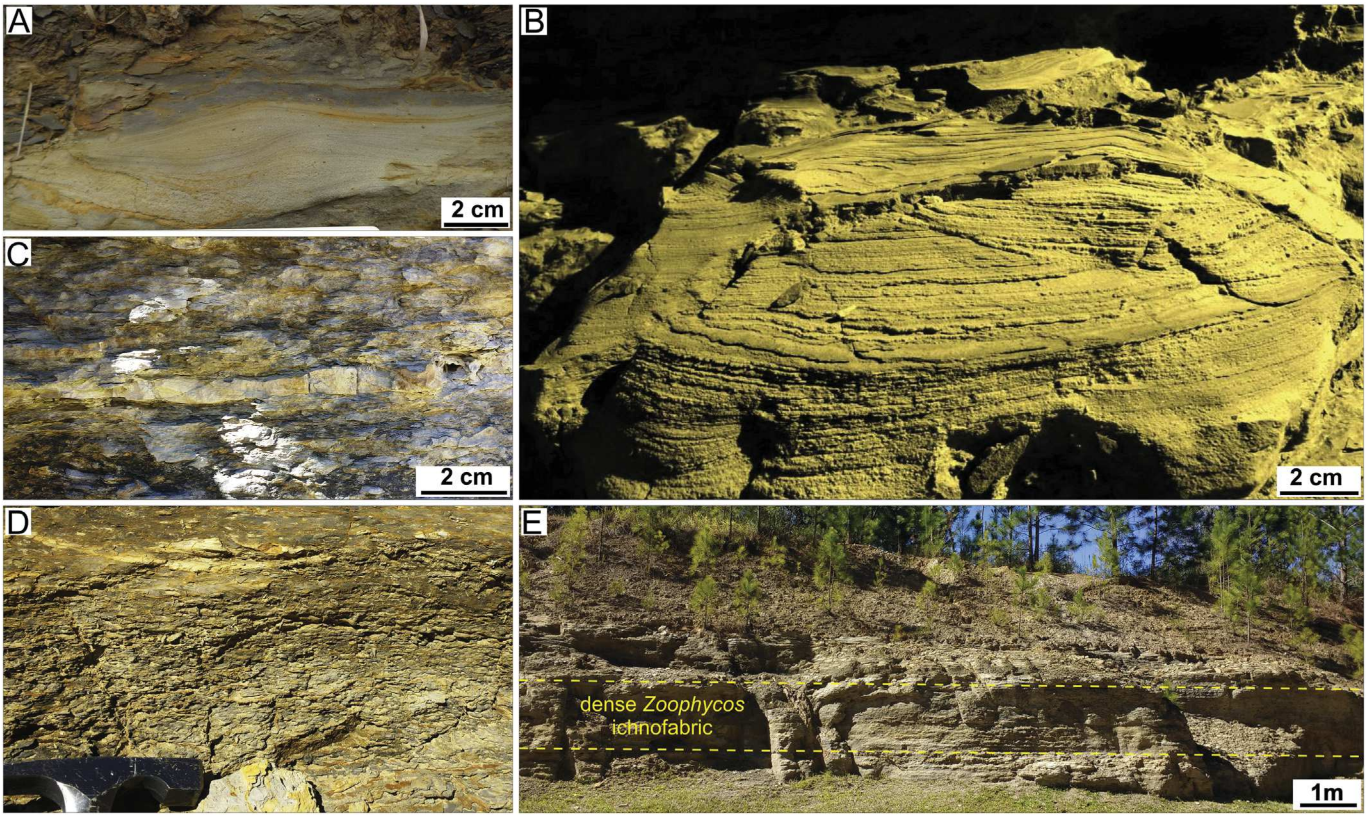

Fig. 5. Sedimentary facies from the studied section. A. Very fine-grained sandstones with wave ripples (Facies 1). B. Fine-grained sandstones with hummocky cross-stratification (Facies 2). C. Lenticular bedded very fine-grained sandstone and siltstone (Facies 3). D. Laminated mudstones (Facies 4). E. Outcrop view; dashed lines indicate the level with dense *Zoophycos* ichnofabric.

Cruziana Ichnofacies (e.g., Miller, 1991; Seilacher, 2007; Kotake, 2014; Zhang et al., 2015b; Sedorko et al., 2018b).

The *Asterosoma-Teichichnus* ichnofabric is dominated by deposit-feeder burrows. *Zoophycos* overprints all other trace fossils, indicating that *Zoophycos* was the deeper structures or its producer was the last to colonize the substrate (Sedorko et al., 2018b). This ichnofabric and associated sedimentary facies indicate deposition in upper offshore settings, below storm wave base.

The *Asterosoma-Zoophycos* ichnofabric is preserved in siltstone interbedded with very fine-grained sandstone. This mixture of textures is typical in the zone between storm wave base and fair-weather wave base. The moderate to high bioturbation degree (3–6), the highest ichnodiversity among the all ichnofabrics in the sections, and the occurrence of shallow-tier (*Arenicolites*, *Diplocraterion*, *Lockeia*, *Skolithos*, *Rosselia*), middle-tier (*Asterosoma*, *Palaeophycus*, *Planolites*, *Rhizocorallium*, *Teichichnus*) and deep-tier (*Chondrites*, *Phycosiphon*, *Zoophycos*) burrows in the trace fossil assemblage led to infer moderate hydrodynamic conditions close to the fair-weather wave base. The trace fossil composition associated with dense *Zoophycos* ichnofabric (Fig. 3) indicates more stable, organic-rich substrates than those reflected by the underlying *Skolithos* ichnofabric (e.g. Ekdale and Mason, 1988; Savrda and Bottjer, 1989; Bromley, 1996; Buatois et al., 2002), and more oxygenated substrates than the covering mudstones with *Chondrites* ichnofabric (Fig. 3).

The variation of *Asterosoma-Zoophycos* ichnofabric (i.e., dense *Zoophycos* ichnofabric) is related to sedimentary structures indicating storm-generated oscillatory flows (Facies 1 and 2, Table 1). Also, the occurrences of wave-laminated erosive lenses (Fig. 6A–B) indicate a predominance of storm-induced flows under low accommodation space in the highstand systems tract, precluding preservation of the whole tempestite structure. The tiering structure also presents signatures of erosive processes, with shallow-tier (*Lockeia*, *Schaubcylindrichnus*, *Skolithos*) and middle-tier structures (*Asterosoma*, *Palaeophycus*, *Planolites*, *Teichichnus*) truncating *Zoophycos* (Fig. 6C–F). Occasionally, *Zoophycos* also truncates other structures (*Chondrites*, *Phycosiphon*, *Zoophycos*, *Palaeophycus*, *Skolithos*) in the vertical migration of the suite.

The taphonomy of macrofossil assemblage evidences in situ organisms associated to disarticulated, chaotic orientated remains, representing mixture of transported and autochthonous assemblages. This context indicates reworking before final burial, as result of high energetic flows related to storm-generated processes. The presence of *Tentaculites* burrowing a *Zoophycos* indicate that low level benthonic organisms could access previously bioturbated strata, corroborating the prevalence of erosive processes. This in situ occurrence indicate fair-weather colonization intervals interspersed with storm events.

6. General characteristics of the *Zoophycos* from Ponta Grossa Formation

The dominant morphology of Paleozoic *Zoophycos* is represented by unlobed *spreiten* planar or helicoidal structures with pronounced primary lamellae, circular tunnel and a marginal tube (Zhang et al., 2015b). Strongly lobed forms of *Zoophycos* were associated to starvation periods that induced the intense exploitation of the substrate (Olivero, 1996, 2003; Savary et al., 2004); while unlobed forms would develop in environments with higher and constant sedimentation rates and amounts of benthic food (Giannetti et al., 2017).

The beds with dense *Zoophycos* ichnofabric (BS 5–6) are characterized mostly by unlobed forms (Fig. 7A–B), representing a specialized behavior under constant parameters (Olivero and Gaillard, 2007). Besides the general assumption that lobed forms are not common in Paleozoic (Zhang et al., 2015b), it occurs subordinated in the section (Fig. 7C), suggesting famine periods. No feces or fecal pellets were found in the studied structures, indicating that the tracemaker

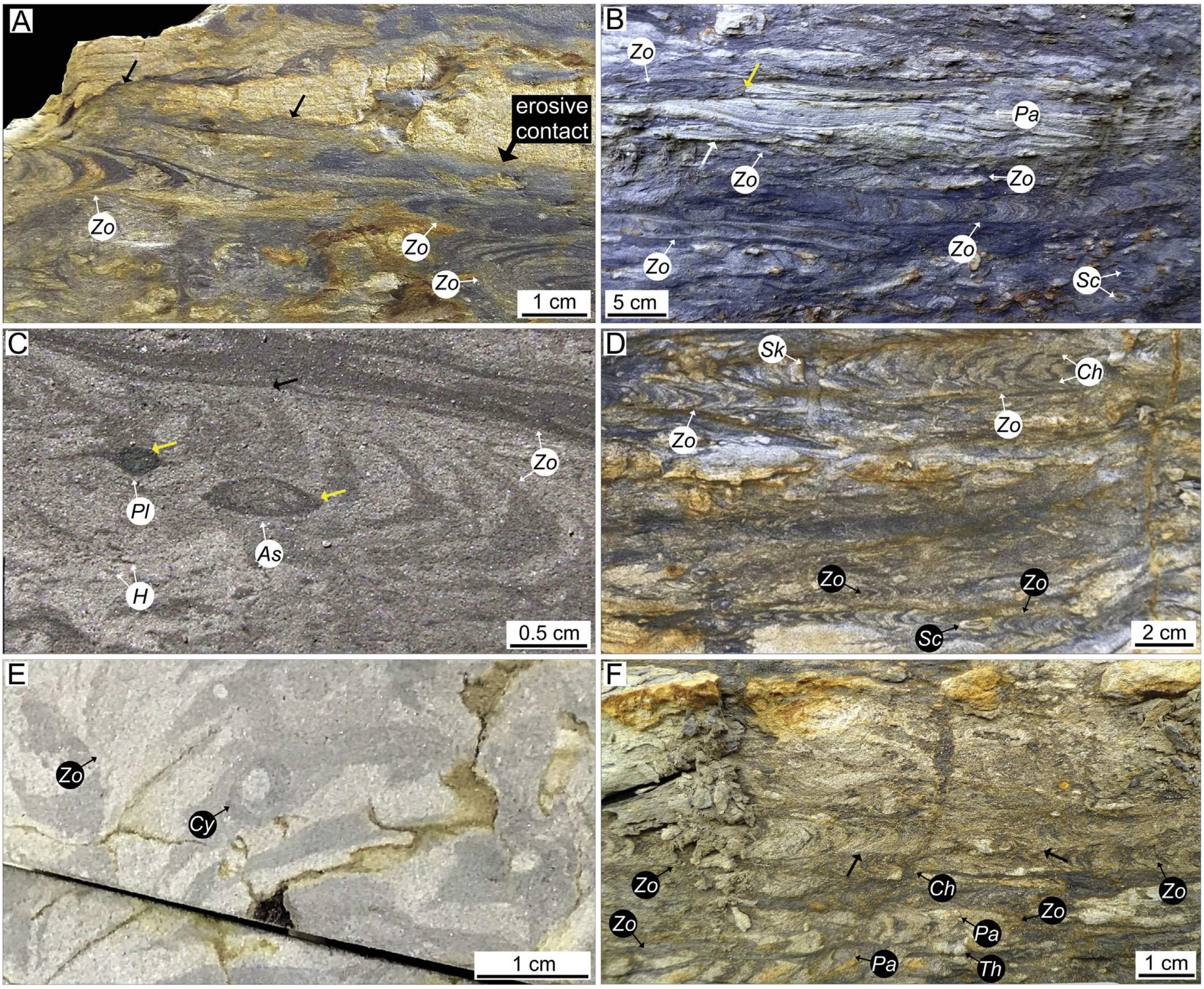

Fig. 6. Dense *Zoophycos* ichnofabric and its tier relations. A–B. Heterolithic sandstones and mudstones beds bearing *Zoophycos* ichnofabric truncated by erosive wave-rippled sandstone; black narrows indicate erosive surface, white narrow indicate erosion of *Zoophycos*, and yellow arrow indicates *Zoophycos* reworking sandy lenses. C. *Zoophycos* truncating other *Zoophycos* (black arrow) and being truncated by shallower-tier structures, such as *Asterosoma* and *Planolites* (yellow arrows). D. *Zoophycos* truncated by shallow-tier structures such as *Schaubcylindrichnus* and *Skolithos* and deep-tier structures (*Chondrites*). E. Polished sample of *Zoophycos* in bedding-plane view truncated by *Cylindrichnus* (shallow-tier structure). F. *Zoophycos* truncating other *Zoophycos*, besides *Thalassinoides* and *Palaeophycus* and being truncated by *Chondrites*; black narrow indicates the contact between two *Zoophycos*. *Ch* = *Chondrites*, *Cy* = *Cylindrichnus*, *He* = *Helminthopsis*, *Pa* = *Palaeophycus*, *Sc* = *Schaubcylindrichnus*, *Sk* = *Skolithos*, *Th* = *Thalassinoides*, *Zo* = *Zoophycos*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

homogenized the feces in the sediment or keep the feces outside the burrow (unlike the *Zoophycos* reported by Kotake, 1992).

Although *Zoophycos* have been largely studied, its construction and associated behavior are still misunderstood. The general hypothesis interprets *Zoophycos* as a feeding burrow, characterizing a strip-mining deposit-feeding behavior (Seilacher, 1967; Wetzel and Werner, 1981; Ekdale and Lewis, 1991; Gaillard and Olivero, 1993; Olivero and Gaillard, 1996). Otherwise, some studies have demonstrated that the *Zoophycos* tracemaker could introduce surface material into the burrow in downward constructed *Zoophycos*, allowing the interpretation of a detritus-feeding strategy (Kotake, 1989, 1991, 1992). In this sense, the *spreiten* would result from feces deposition within the sediment. Some models were listed to explain the downward deposition (sensu Bromley, 1991): (i) the refuse-dump model—that explain the deposition of surface material as result of the filling in the cavity caused by deposit feeding; (ii) the cache model—that consider this deposition as a store strategy for posterior use; and (iii) the gardening/chemosymbiosis model—that speculate the introduced organic material as condition to create favorable environment for sulfide-oxidizing bacteria, resulting in cultivation of microorganisms for food (Bromley et al., 1999; Bromley and Hanken, 2003).

The occurrence of large *Zoophycos* specimens and *spreiten* with different dimensions in the study area suggest maintenance of stable conditions, allowing the exploitation of large volumes of nutrient-rich sediments by tracemakers at different ontogenetic stages or even different groups (Wu, 1982; Kotake, 1989, 2014). Few specimens present an increase in *spreiten* thickness toward its margin, suggesting that *Zoophycos* could be the result of a lifelong activity (e.g., Bromley, 1990). The dominance of planar morphologies in the study area suggests that the primary ethologic activity was to exploit food in the substrate rather than organic matter storage. Also, *Zoophycos* is preserved exclusively in organic-rich heterolithic beds, being absent in

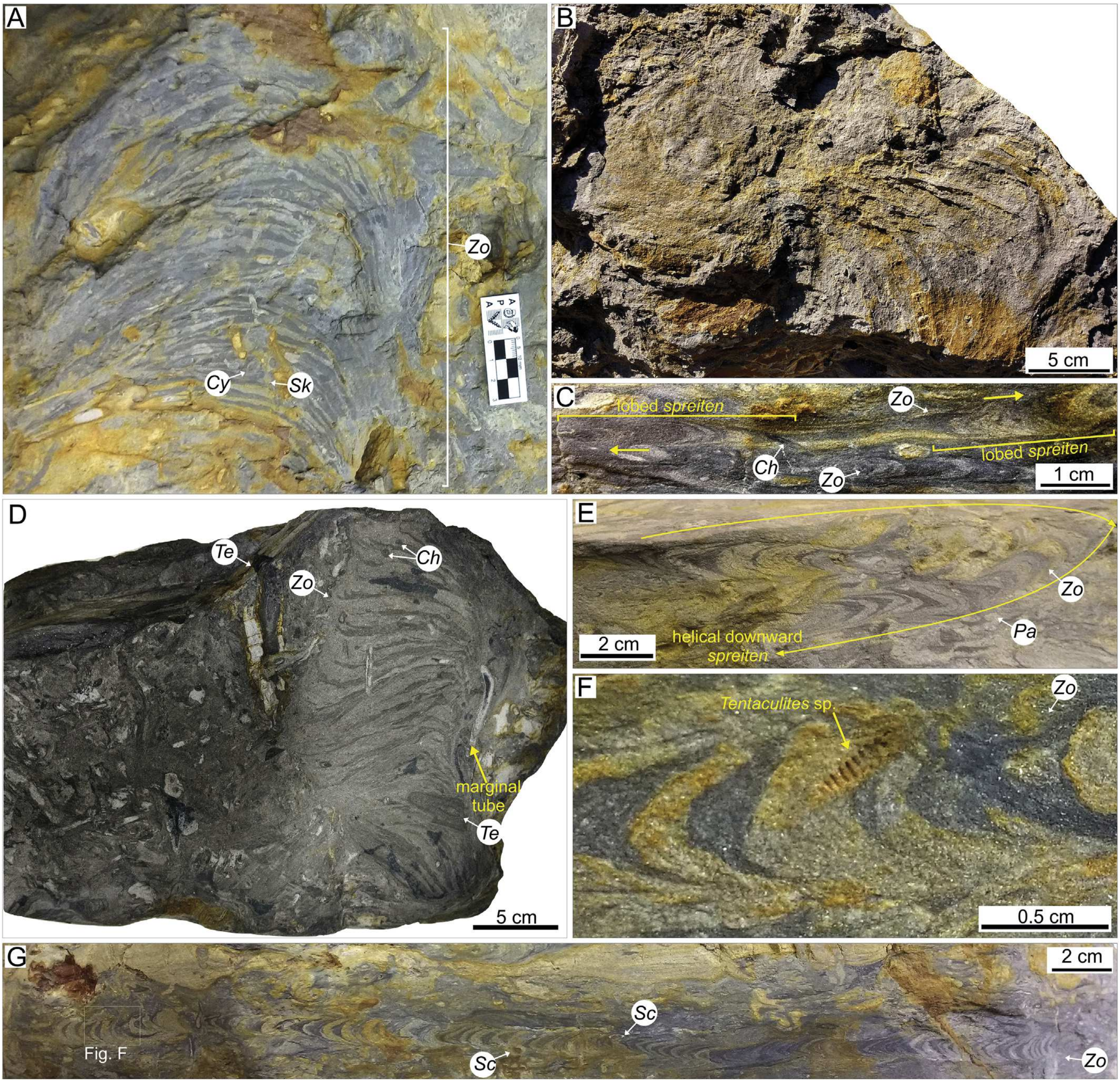

Fig. 7. Morphologies of *Zoophycos* in studied sections. A. U-shaped planar form in bedding-plane view. B. Helical *Zoophycos* in bedding-plane view. C. Lobed *Zoophycos* in vertical view; yellow arrows indicate the constructional direction of the lobes. D. Lobed *Zoophycos* in bedding-plane view. E. Vertical view of a helical downward *Zoophycos*. F. Detail of a macrofossil (*Tentaculites* sp.) truncating the *Zoophycos* (Fig. G). G. Vertical view of a large planar *Zoophycos*; this structure has at least 45 cm length. *As* = *Asterosoma*, *Ch* = *Chondrites*, *Pa* = *Palaeophycus*, *Te* = *Teichichnus*, *Sc* = *Schaubcylindrichnus*, *Zo* = *Zoophycos*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Relation of *Zoophycos* dimensions and accessories ichnogenera by the sedimentary facies. *Recording style: e.g. 0.6–1.0 (7.6 n9) represents that the diameter oscillates from 0.6 to 1.0 cm in 9 analyzed specimens and that 7.6 cm is its average.

Facies	Spreiten height (cm)*	Spreiten width (cm)*	Number of whorls*	Ichnogenera accessories
Heterolithic (Facies 3)	0.6–2.2 (1.32 n24)	12.6–44.6 (20.89 n24)	1–2 (1.37 n24)	*Asterosoma*, *Teichichnus*, *Chondrites*, *Planolites*, *Lockeia*, *Rhizocorallium*, *Helminthopsis*, *Arenicolites*, *Palaeophycus*, *Thalassinoides*, *Rosselia*, *Cylindrichnus*, *Schaubcylindrichnus*, *Diplocraterion*, *Bifungites*
Mudstones (Facies 4)	0.6–1.0 (0.76 n9)	11–23 (16 n9)	1–2 (1.22 n9)	*Phycosiphon*, *Chondrites*

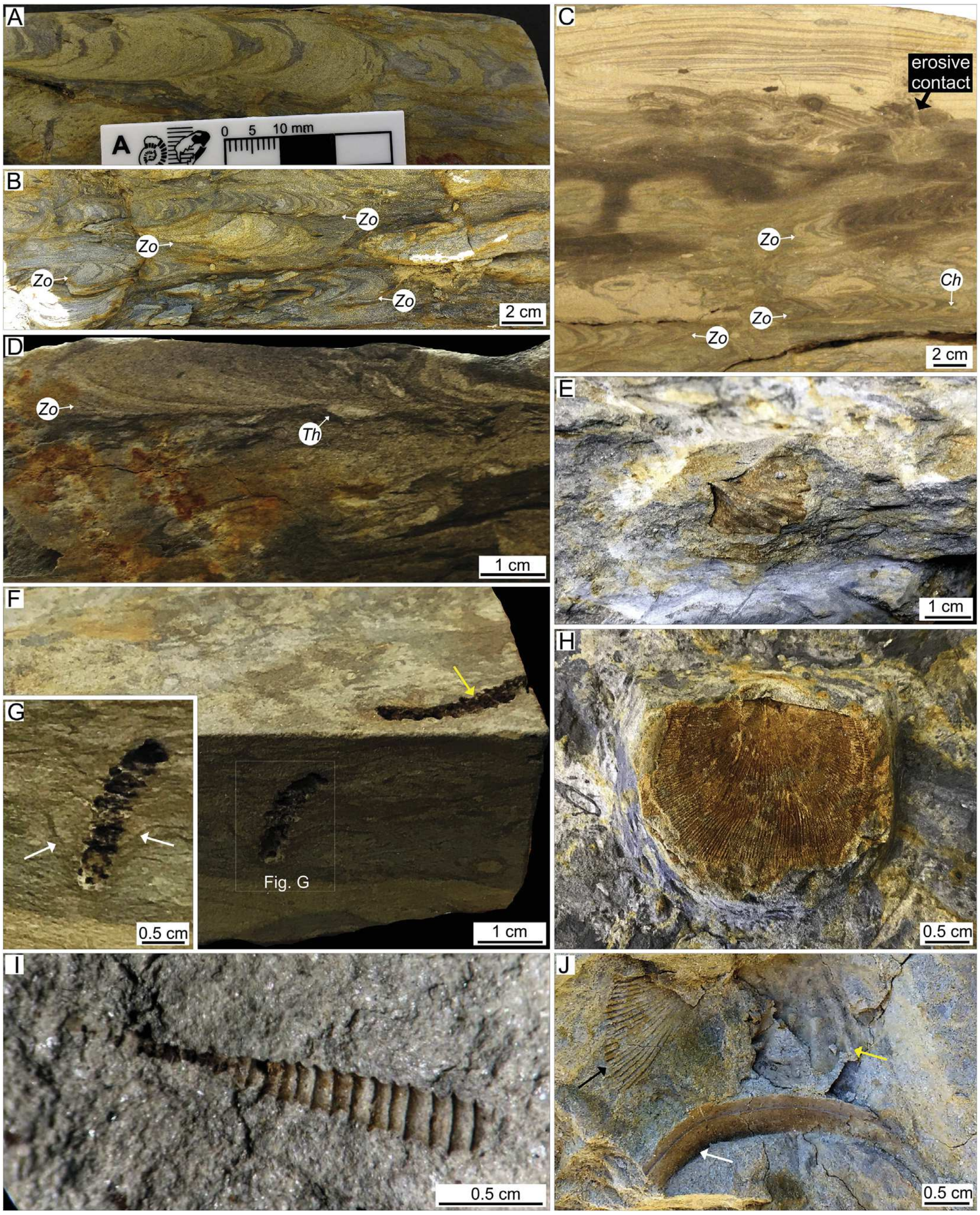

Fig. 8. Dense *Zoophycos* ichnofabric and associated macrofossils. A. *Zoophycos* with an increase in *spreiten* thickness in the same structure. B. Different *spreiten* thickness in the same level. C. *Zoophycos* filled with sandy material at least 8 cm below an erosive surface. D. *Zoophycos* with an increase in *spreiten* thickness and truncating *Thalassinoides*. E. Brachiopod *Derbyina* sp. in an oblique position in relation to the bedding plane. F. Bended column of Crinoidea (yellow arrow). G. Detail of "F" with the column disturbing the lamination (white arrow). H. Disarticulated *Schuchertella* sp. in bedding-plane view. I. *Tentaculites* sp. in bedding-plane view. J. Chaotic distribution of fossils, with homalonotidae trilobite (white arrow) and *Schuchertella* sp. (black arrow) oblique to bedding-plane, besides *Australospirifer* sp. (yellow arrow) concordant with bedding-plane. *Ch* = *Chondrites*, *Th* = *Thalassinoides*, *Zo* = *Zoophycos*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

clean, ripple-laminated event layers, corroborating the deposit-feeding strategy (e.g., Seilacher, 2007).

According to Gaillard and Racheboeuf (2006), Devonian forms composed of thin planar *spreiten* usually occur in shallow-tiers. However, *Zoophycos* has been found associated to deep-tier structures since Devonian, for example, with *Chondrites* in the Devonian Kettle Point Formation (Bingham-Koslowski et al., 2016), or overlapping shallower structures, such as *Asterosoma*, *Rosselia*, *Rhizocorallium*, and *Teichichnus* (Sedorko et al., 2018b). Some *Zoophycos* reported here are filled by sand from a surface at least 8 cm above (Fig. 8C). Thus, it is probable that *Zoophycos* tracemakers might have explored middle- to deep-tiers since Devonian.

The *Zoophycos* tracemaker might be a marine worm-like sediment-feeder with a proboscis, like sipunculid worms (Wetzel and Werner, 1981), a group that has the mouth and anus located at the same anterior extremity of the body. For Olivero and Gaillard (2007), this feature would be crucial in *Zoophycos* tracemakers for producing the secondary lamellae. However, other potential tracemaker groups were proposed, such as Polychaeta (Ekdale and Lewis, 1991; Knaust, 2009) and Echiurida (Kotake, 1992). The *Zoophycos* from Ponta Grossa Formation

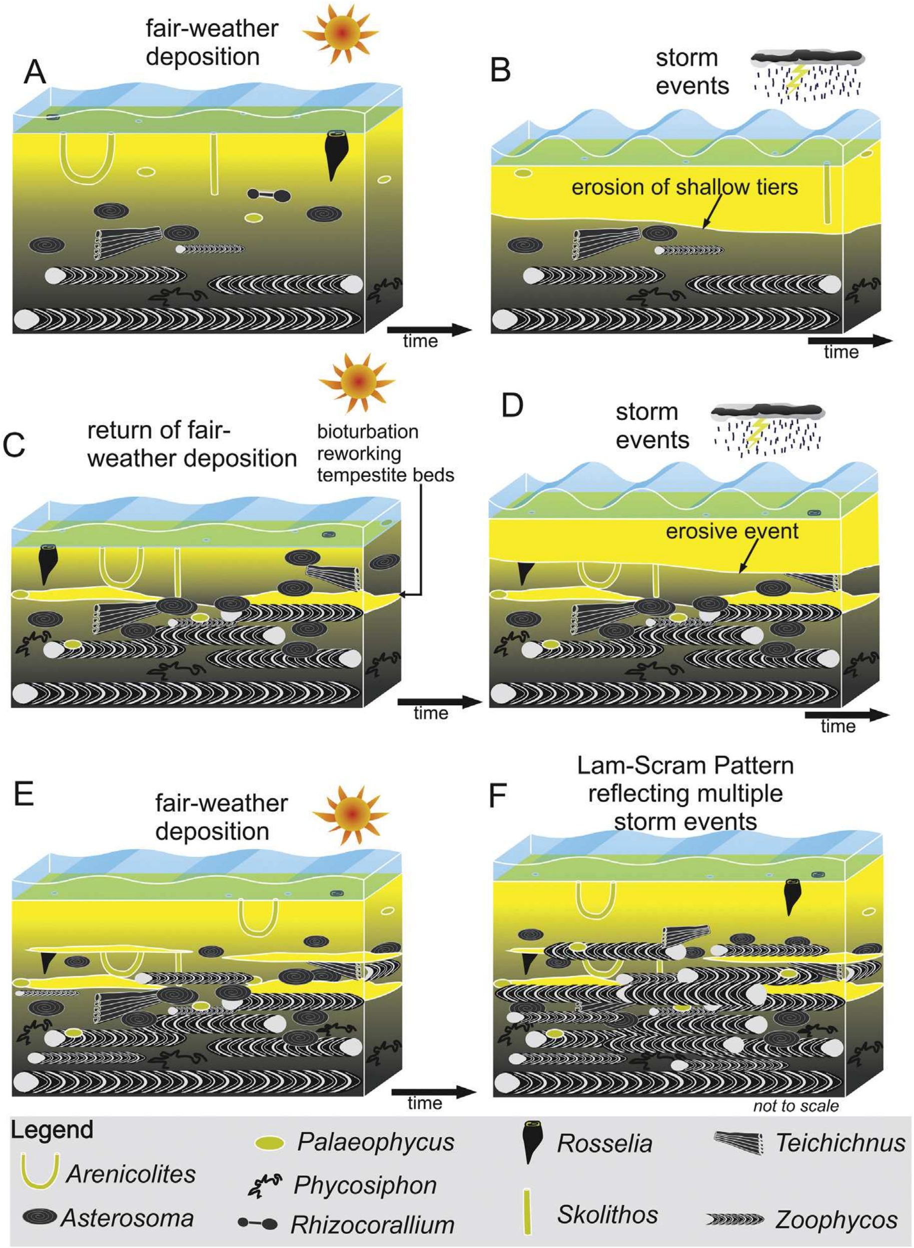

Fig. 9. Schematic illustration of the inferred sequence of colonization during high-frequency deposition caused by storms based on the data from Ponta Grossa Formation. A. Fair-weather suite of Ichnofacies Cruziana with a normal distribution of shallow-, middle- and deep-tiers. B. Erosion of shallow-tier after a storm event associated with the short colonization of opportunistic organisms (e.g., *Skolithos* and *Palaeophycus*). C. Fair-weather conditions with the vertical migration of an Ichnofacies Cruziana suite reworking storm-deposits; trace fossils from middle-tier (e.g., *Asterosoma* and *Palaeophycus*) overlap previous trace fossils from deep-tier, such as *Zoophycos*. D. Other storm event illustrating erosion of shallow-tier. E. Fair-weather conditions with middle-tier trace fossils (e.g., *Asterosoma*, *Teichichnus*, and *Palaeophycus*) overlapping previous deep-tier structures (*Zoophycos*). F. After multiple storm events, the deep tier structure *Zoophycos* is taphonomically biased by a higher potential for preservation, generating a "lam-scram" pattern.

was probably produced by some polychaeta or a similar worm-like organism. Signatures as secondary lamella or fecal pellets are absent, precluding the attribution to sipunculans or echiurans, respectively.

Zoophycos is a middle- to deep-tier structure that reworked more significant amount of sediments than other deep-tier structures (compared to *Chondrites* and *Phycosiphon*). When multiple erosive events (as evidenced by erosive sandy lenses and tiers relations – Figs. 6, 9A–B) acted in substrates removing shallow-tier structures, middle- to deep-tier structures as *Zoophycos* increases its representation (Fig. 9C–E), generating a dense *Zoophycos* ichnofabric (Fig. 9F). This taphonomic artifact (or "elite trace fossils" sensu Bromley, 1996) results in a long-term colonization window, obliterating the background suite and generating a "Lam-Scram Pattern" (Howard, 1978; MacEachern and Pemberton, 1992). Except by the dominance of *Zoophycos*, this suite has the same components as the fair-weather suite.

In this sense, the dense *Zoophycos* ichnofabric in some strata of the Ponta Grossa Formation does not reflect an ecologic dominance, but the recurrent erosion of shallower tiers under regimes of low-accommodation space. Thus, this ichnofabric indicates a higher frequency of storms and higher hydrodynamic rates than those represented by other ichnofabrics bearing *Zoophycos*.

Dense occurrences of *Zoophycos* in tempestites have been reported to Devonian beds, mostly in China (e.g., Zhang, 2014; Zhang and Zhao, 2016; Li et al., 2017), but also in USA (Miller, 1991). Those occurrences were interpreted as evidence of an opportunist behavior, corresponding to the exploitation of the large volume of mud deposited after storms. The argument for an opportunistic interpretation is that *Zoophycos* represents the first colonization in new substrates, indicating lack of specialization and inefficient use of resources as expected in r-selected species. In this sense, *Zoophycos* would reflect stressful, changeable environments.

In contrary, the dense *Zoophycos* ichnofabric reported herein is not monospecific, being part of a fair-weather suite exploiting post-storm substrates, in which *Zoophycos* truncates (Figs. 6F, 7D–E) and is truncated (Fig. 6) by other burrows from the *Asterosoma-Zoophycos* ichnofabric. The occurrence of diverse and complex traces is more consistent with k-selected equilibrium species using resources efficiently and presenting specialized feeding behavior or long-term activity (Ekdale, 1985; Bromley, 1990). Moreover, the apparent dominance of *Zoophycos* in Ponta Grossa Formation should not be related to an opportunistic behavior.

The small-sized *Zoophycos* preserved with low-diverse ichnofabrics in Silurian-Devonian and Devonian I sequence beds might be indicating a tolerant behavior to dysoxic conditions (e.g., in *Zoophycos-Chondrites* ichnofabric). A similar context was reported as "*Zoophycos* Association" from Devonian of Bolivia, where *Zoophycos* also present small dimensions (Gaillard and Racheboeuf, 2006). This suite is commonly associated with *Chondrites* and *Planolites* and was interpreted as indicator of dysoxic substrates.

7. Paleoecological trends of a non-opportunist behavior

Zoophycos is well distributed throughout the Siluro-Devonian Sequence of the lower Ponta Grossa Formation sedimentary succession and is a standard component of the resident suite (Bosetti et al., 2013; Sedorko et al., 2018a, 2018b). Kotake (2014) inferred that the main bathymetrical distribution of *Zoophycos* during the Paleozoic was in shelf context and that during Devonian the marine substrates suffered an increase in land-based nutrients, mainly as result of acritarch abundance and the origin of real soil by the development of plants in land areas. The distribution of *Zoophycos* throughout Phanerozoic was possibly controlled by the disposition of food within substrates. The first bloom of *Zoophycos* was related to the appearance of land plants during Devonian, while the second bloom during Cretaceous was associated to an increase in benthic food content on the deep seafloor (Kotake, 2014; Zhang et al., 2015b).

The basal occurrence of *Zoophycos* in Paraná Basin is ~5 m above the first record of primitive land plants (e.g., *Cooksonia*; Mussa et al., 1996, 2002), which seems to corroborate the general control by food supply. If the occurrence of *Zoophycos* is directly related to the appearance of land plants and the consequent increase of organic matter on the sea floor, then the *Zoophycos* might be an expression of deposit-feeding strategy (Kotake, 2014). However, if *Zoophycos* appearance in Devonian beds of the Paraná Basin might be controlled by the input of phytodetritus coming from land plants, this factor does not seem to be the one that controls *Zoophycos* decline. While the land plants diversify and increase in abundance throughout the Devonian (e.g., Matsumura et al., 2015), the *Zoophycos* occurrence declines in the Eifelian, being virtually absent in upper strata.

Recently, Dorador et al. (2016), based on cyclicity analysis in Neogene deposits from the Iberian Peninsula, reinforced the hypothesis erected initially by Wetzel (1981, 1991) that *Zoophycos* represents a cache behavior of an animal that collects food particles during periods of seasonal primary productivity into the sea. This strategic behavior is assumed to have been enhanced during the Cretaceous, due to the increase of phytodetritus input into hemipelagic settings. The Paraná Basin, however, is an intracratonic basin, and *Zoophycos* occur mostly in heterolithic and muddy facies that characterizes lower shoreface and offshore settings. Even that it could mimic for long periods the calm conditions found in hemipelagic zones, the phytodetritus input apparently did not control the distribution of *Zoophycos* into the basin. Moreover, the decline of *Zoophycos* in Paraná Basin after the Eifelian might be related to a reduction in the primary paleoproductivity (e.g., Kotake, 2014). Bosetti et al. (2011) observed a reduction in acritarchs and chitinozoans above the Eifelian beds, which can be related to changes in oceanic circulation caused by a restriction in the basin.

Besides the food availability, another factor that seems to control the *Zoophycos* distribution and preservation is the need for open marine conditions. Zhang et al. (2015b) presented a bibliographic revision of *Zoophycos* reports worldwide, demonstrating its affinity with marine facies since Cambrian. The presence of a climax fauna of the Malvinokaffric Realm in the beds of the Jaguariaíva Member, composed of brachiopods, trilobites calmoniids and homalonotids, echinoderms crinoids and asteroids, mollusks bivalves and gastropods, conularids, bryozoans, among others (Clarke, 1913; Melo, 1988; Bosetti et al., 2012) provides clear evidence of the prevalence of open marine conditions in the *Zoophycos*-bearing beds.

The mudstones and shales in the upper part of the studied succession (MFS Devonian II sequence) represent the main flooding during Devonian in Paraná Basin and were correlated with the Kačák Event (Bosetti et al., 2011; Horodyski et al., 2014). The dominance of *Phycosiphon* and lilliputian macrofossils (Bosetti et al., 2011) is an indicator of low oxygenation rates, and a general absence of trace fossils due to anoxic conditions corroborated this hypothesis (Sedorko et al., 2018a). The relatively low TOC in MFS of Devonian II sequence (0.92%; Sedorko et al., 2018a) might also be related to the reduction in biomass, caused by this deepening event (Kačák Event) associated to a basin restriction.

It is possible that tectonic activity associated to the Asunción Arch caused the restriction of the basin during Eifelian (Northfleet et al., 1969; Ramos, 1970; Ferreira et al., 1981; Andrade and Camarço, 1982; Fulfaro et al., 1982). This activity could have restricted the epeiric sea, resulting in a decrease in biodiversity of Malvinokaffric Realm, as observed by Bosetti et al. (2012) in Emsian to Eifelian deposits. Other evidence for this restriction can be the decline of *Zoophycos* abundance after Eifelian. The Paraná Basin remained restricted since then (Milani and Ramos, 1998; Milani et al., 2007), and *Zoophycos* is a rare component in the post-Devonian basin strata (Netto et al., 2012).

Olivero (1996) reported dense slope to basin *Zoophycos* occurrences preserved in parasequence sets of lowstand systems tract (Jurassic–-Cretaceous) due to optimal conditions by an increase in surface planktonic productivity and by increasing supplies from the nearby continent during prograding phases. He argued that during retrogradational regimes the landward migration resulted in starved sedimentation on the slope, reducing *Zoophycos* abundance and dimensions. For Olivero (1996), *Zoophycos* would be better preserved in the prograding phases (lowstand systems tract and upper part of the HST), and, in small-scale, in the top of parasequences.

In Ponta Grossa Formation (Devonian) the dense *Zoophycos* ichnofabric is preserved in beds representing highstand systems tracts of the Siluro-Devonian Sequence (Fig. 2). During Devonian *Zoophycos* was a common component of the Cruziana Ichnofacies, being preserved in shallower depositional environments than Mesozoic to Cenozoic forms. This fact favored the preservation of dense *Zoophycos* ichnofabrics in storm beds, as discussed above. The predominance of erosive processes associated with amalgamed hummocky beds indicates low accommodation space, as expected by prograding clinoforms in highstand systems tract. Thus, dense *Zoophycos* ichnofabrics in storm beds can be a good indicator of low accommodation space and a signature of prograding clinoforms.

Non-dense *Zoophycos* occurrences mostly characterize deposits representing transgressive systems tract, as also observed in other basins (e.g., Knaust, 2009; Hu et al., 2010; Zhang, 2014). In these cases, *Zoophycos* specimens are normally small-sized and occur in low diverse ichnofabrics preserved in strata representing dysoxic offshore settings or being a signature of maximum flooding surfaces.

8. Conclusions

Zoophycos in Ponta Grossa Formation is a standard component of the fair-weather trace fossil suites, being preserved both in storm-related and muddy offshore beds. When *Zoophycos* occurs associated with *Phycosiphon* and *Chondrites* in low-diverse and low-bioturbated context, it represents dysoxic substrates, precluding colonization by other tracemakers. In contrary, when *Zoophycos* is part of a more diverse suite (e.g., *Asterosoma-Zoophycos* or *Asterosoma-Teichichnus* ichnofabrics), it represents more stable substrates.

The tiering structure involving dense *Zoophycos* ichnofabrics demonstrated that shallower burrows (e.g., *Asterosoma*, *Palaeophycus*, *Cylindrichnus*, *Schaubcylindrichnus*, *Skolithos*) reworked deep-tier burrows (*Chondrites*, *Phycosiphon*, and *Zoophycos*), indicating erosion of surficial levels. Due to the high intensity of bioturbation, primary sedimentary structures are obliterated, and the dense *Zoophycos* ichnofabric resulted from the total reworking of storm deposits by the fair-weather suite, which favored the visibility of deep-tier structures in a lam-scram pattern. In this sense, dense *Zoophycos* ichnofabric from Paraná Basin cannot be linked to an opportunistic behavior, being a preservational artifact related to low accommodation space in prograding sections. In Siluro-Devonian and Devonian I sequences, the absence of monospecific occurrences and the associated ichnofabrics allowed the attribution of *Zoophycos* as a component of distal and archetypal expressions of Cruziana Ichnofacies rather than Zoophycos Ichnofacies.

The basal occurrence of *Zoophycos* seems to be related to the first irradiation of land plants in the Paraná Basin, which had increased the food-supply in shallow sea environments. The reduction in macrofossil diversity and *Zoophycos* abundance seems to be associated with tectonic activity in the basin during Eifelian, generating a restriction in the paleo-sea.

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CAPÍTULO 6

Paleoenvironments of a regressive Devonian section from Paraná Basin (Mato Grosso do Sul state) by integration of ichnologic, taphonomic and sedimentologic analyses

Artigo aceito para publicação no periódico “Brazilian Jounal of Geology” focado em uma sucessão devoniana da borda noroeste da bacia, onde foram usados dados sedimentológicos, icnológicos e tafonômicos para demonstrar que a subdivisão em duas sub-bacias (Apucarana e Alto Garças) não é evidente, ao menos para o intervalo Pragiano-Emsiano.

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ARTICLE

Paleoenvironments of a regressive Devonian section from Paraná Basin (Mato Grosso do Sul state) by integration of ichnologic, taphonomic and sedimentologic analyses

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ABSTRACT: *Studies that integrate ichnologic, taphonomic and sedimentologic data result in more accurate paleoenvironmental inferences than isolated approaches. Most of paleontological studies regarding Devonian from Paraná Basin were conducted in the southern part of the basin (Paraná state), precluding taphonomic or ichnologic studies to the northern part, and even its macrofossils content is understudied. This study analyzes paleoecologic and depositional conditions represented by trace fossils, macrofossils and sedimentary facies in a regressive Devonian section from Paraná Basin, Mato Grosso do Sul state, Brazil. Seven ichnofabrics (Macaronichnus, Psammichnites, Arenicolites-Skolithos, Cylindrichnus-Skolithos, Zoophycos, Rhizocorallium-Palaeophycus, and Chondrites ichnofabrics) and three taphofacies (T1: parautochthonous to allochthonous preservation; T2: Autochthonous preservation; and T3: time-averaged autochthonous to allochthonous association) were diagnosed. The studied sections are positioned in a highstand systems tract (HST) exhibiting dominance of sandy facies, and four sub-environments were defined: foreshore; shoreface; storm-dominated shoreface to transitional offshore; and offshore. The dominance of foreshore to shoreface settings in a HST corroborates a shallower context in relation to the southern part. However, similarities in the facies and ichnofacies stacking, as well in the macrofossil content suggest that the hypothetical division between two sub-basins (Apucarana and Alto Garças Sub-basins) was not complete until early Emsian.*

KEYWORDS: *Ichnofacies; Taphofacies; Tempestites; Devonian; Sub-Basins.*

INTRODUCTION

The distribution of the trace fossil associations is controlled by biologic and environmental parameters, making them useful for paleoecologic, depositional and paleoenvironmental analyses (*e.g.*, Pemberton & Frey 1984, Bottjer *et al*. 1988, Savrda & Bottjer 1986, Ekdale & Lewis 1991, Savrda 1998). In the same way, taphonomic signatures are controlled by environmental processes, allowing inferences regarding depositional regimes (*e.g.*, Brett & Baird 1986, Speyer & Brett 1986, 1988). The integration of these tools result in more accurate depositional inferences. However, studies integrating ichnological and taphonomic analysis applied to sedimentological, stratigraphical, palaeoenvironmental and palaeoecological inferences are still rare (*e.g.*, Henderson & McNamara 1985, Bromley & Asgaard 1991, Reolid *et al*. 2014, Sedorko *et al*. 2018a).

The Devonian macrofossils from Paraná Basin have been widely studied under different approaches, such as taxonomy (*e.g.*, Clarke 1913, Kotzian 1995, Leme *et al*. 2004, Scheffler & Fernandes 2007a, 2007b, Scheffler *et al*. 2013, Richter *et al*. 2017), biogeography (Melo 1988) and

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taphonomy (Simões *et al.* 2009, Rodrigues *et al.* 2003, Bosetti *et al.* 2011, 2012, 2013, Zabini *et al.* 2010, Horodyski *et al.* 2014). However, most of those studies were developed in the south part of the Paraná Basin (Paraná State, Brazil, Fig. 1A), and ichnologic studies were conducted under ichnotaxonomic approach (see Sedorko *et al.* 2013 for a synthesis). The strata from the northern basin preclude taphonomic or ichnologic studies, and even the macrofossils content is understudied, especially in Mato Grosso do Sul state, Brazil (see Scheffler *et al.* 2010 for a synthesis). In this sense, this study aims to:

1. infer the paleoecologic and depositional conditions to Devonian strata in the northern Paraná Basin;
2. record the Malvinokaffric fauna in this regressive succession;
3. compare the stratigraphic stacking and macrofossil content represented by coeval deposits from south part of the basin (Paraná state).

MATERIALS AND METHODS

Two sections (referred as MS14 [19º24'41.91"S; 54º58'59.92"W; datum WGS84] and MS 18/19 [19º26'16.37"S; 55º0'2.41"W; datum WGS84] were prospected considering their sedimentologic, ichnologic and taphonomic features. These sections crop out at Rio Negro municipality (Mato Grosso do Sul state, Brazil; Figs. 1A and 1B).

The sedimentologic analysis considered textures, primary sedimentary structures, geometry of beds and macrofossil content. The trace fossil analysis took into account the ichnofabric characterization and the quantification of the bioturbation. The amount of bioturbation was expressed based on bioturbation scale (BS), as proposed by Reineck (1963), ranging from 0 (no bioturbated) to 6 (completely bioturbated). Finally, taphonomic analysis followed the techniques as proposed by Simões & Ghilardi (2000), with vertical control of the fossil content, as well their taphonomic signatures. The collected skeletons were classified as univalved, bivalved or multielement, and all observable taphonomic signatures were verified according to the criteria established by Speyer & Brett (1986, 1988), but only articulation and fragmentation were diagnosed. Lack of abrasion, corrosion, rounding, bioerosion, encrustation, and partial dissolution were also considered for paleoenvironmental interpretation, as well packing and relative position to the bedding plane (Suppl. Tab. A1).

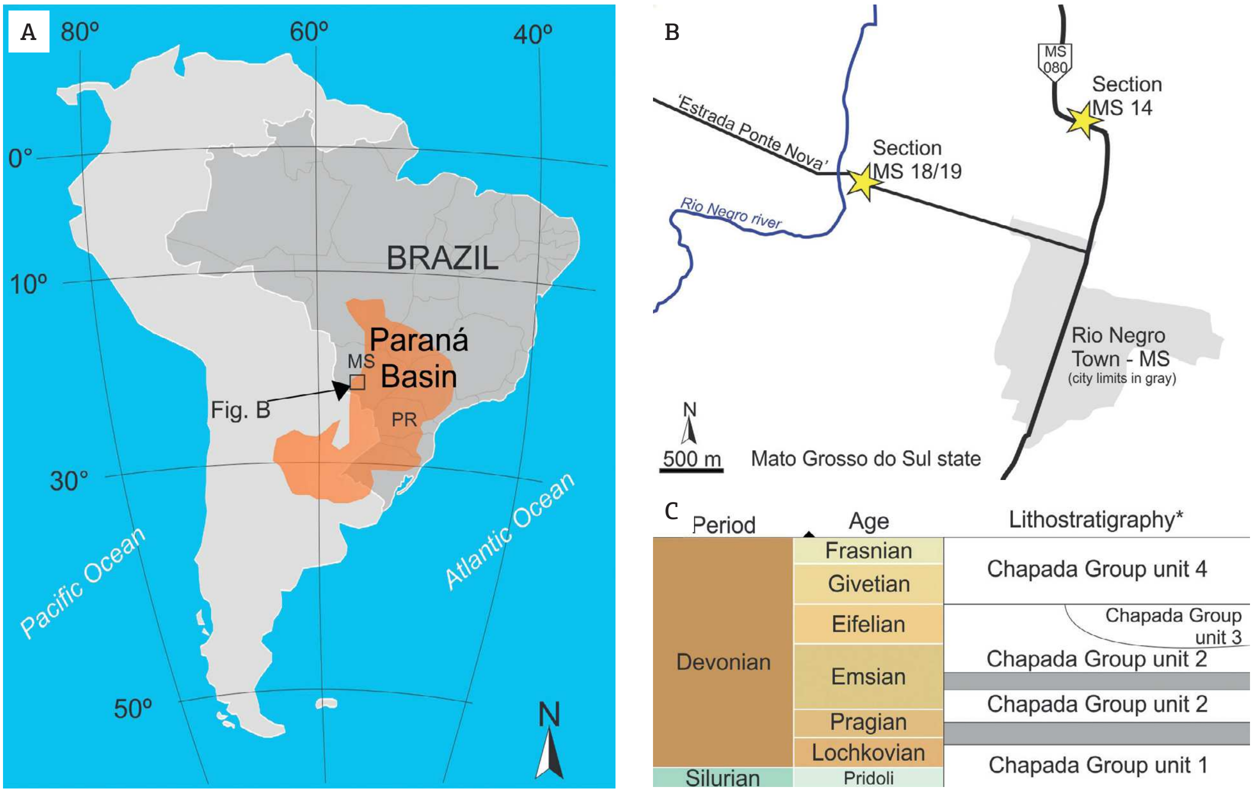

Figure 1. Geographic and stratigraphic context of studied sections. (A) Position of studied sections in the Paraná Basin; (B) geographic position of studied outcrops close to Rio Negro Town (MS); (C) general lithostratigraphy, ages and sequences of Devonian strata in northern basin; studied sections are positioned in the lower Chapada Group unit 2.

GEOLOGICAL SETTING

The Paraná Basin is a huge intracratonic basin that covered the southern portion of Brazil and adjacent areas during the pre-Cenozoic eras. This basin was originally a gulf opened to the Panthalassa (Zalán *et al.* 1990, Milani 1992), changing to an intracratonic depression in the interior of Gondwana probably during Upper Devonian (Milani 1997). Six supersequences compose the basin sedimentary fill, which was influenced by tectonic-eustatic cycles related to the evolution of the Western Gondwana, from Late Ordovician to Late Cretaceous (Milani *et al.* 2007). Ramos (1970) and Pereira *et al.* (1998) proposed the existence of two depocenters during the Early Paleozoic and the differentiation of two sub-basins, Alto Garças (north) and Apucarana (south). However, Milani *et al.* (1998, 2006, 2007) argued that the difference in thickness of Devonian strata are product of differential preservation beneath the sub-Pennsylvanian unconformity.

At least in the south part of the basin, the Paraná Supersequence spans in age from Lower Silurian (Sedorko *et al.* 2017) to Middle Devonian (Grahn *et al.* 2013) in outcrops, with Upper Devonian ages preserved only in subsurface (Bergamaschi 1999, Grahn *et al.* 2013, Sedorko *et al.* 2018c). Grahn *et al.* (2013) used microfossil zonation to correlate the ages of the lithostratigraphic units from southern basin (referred by them as Apucarana sub-basin) and northern (Alto Garças sub-basin). There is no consensus in relation to the exact position of south pole during Emsian, but during Emsian the basin was possibly positioned between 70 and 80º South (Isaacson & Sablock 1990, Isaacson & Diaz Martinez 1994, Witzke & Heckel 1988, Scotese & McKerrow 1990, Kent & Van Der Voo 1990, Torsvik & Cocks 2013).

In Mato Grosso do Sul state (northern basin), Brazil, the Paraná Supersequence is composed of four lithostratigraphic units, named Chapada Group units 1, 2, 3 and 4 (Grahn *et al.* 2013, Fig. 1C).

The Chapada Group unit 1 contains the basal marginal-marine and shallow marine sandy deposit and is mostly correlated with Furnas Formation from southern part of the basin (Grahn *et al.* 2013). The lower and middle units of Furnas Formation were deposited during Lower Silurian, based on its trace fossils with ichnostratigraphic value (Sedorko *et al.* 2017).

The Chapada Group unit 2 is composed by a basal conglomerate capped by purple-red sandstone interbedded with siltstones and shales, overlapped by fine- to medium-grained grayish to reddish sandstones, ranging from Early Pragian to Eifelian (Grahn *et al.* 2010). Pioneering descriptions of the macrofossil content in this unit attributed affinities to the Malvinokaffric Realm (Melo 1988). Grahn *et al.* (2013) identified a gap within Chapada Group unit 2, dividing this unit in lower and upper parts. The lower part was correlated with Ponta Grossa Formation (*sensu* Grahn *et al.* 2010, 2013, or Jaguariaíva Member *sensu* Lange & Petri 1967), while the upper part corresponds to lower São Domingos Formation (*sensu* Grahn *et al.* 2013, or São Domingos Member *sensu* Lange & Petri 1967). Outcrops here studied are inserted in lower Chapada Group unit 2 (Ponta Grossa Formation or Jaguariaíva Member; Pragian to Early Emsian) considering their stratigraphic relations overlapping the Chapada Group unit 1 and the macrofossil content.

The Chapada Group unit 3 crops out only in the northeast border of the basin (Andrade & Camarço 1980, Melo 1988). This unit is characterized by reddish medium- to coarse-grained sandstones interbedded with conglomeratic sandstones, interpreted as shallow marine to wave-dominated deltaic environments (Andrade & Camarço 1980, Grahn *et al.* 2010). This unit was deposited during Early Emsian to Eifelian and was interpreted as the proximal equivalent of the upper Chapada Group unit 2, correlated to São Domingos Formation and its Tibagi Member from southern part of the basin (*sensu* Grahn *et al.* 2010, 2013).

Finally, the Chapada Group unit 4 consists of dark-gray shales interbedded with sandstones and siltstones. The base of this unit is related to the maximum flooding surface in the Eifelian-Givetian boundary (Assine 2001, Grahn *et al.* 2010). This unit is correlated with the upper São Domingos Formation (*sensu* Grahn *et al.* 2013) from southern part of the basin.

RESULTS

Six sedimentary facies, seven ichnofabrics, and three taphofacies were diagnosed in the studied section. Their vertical disposition characterizes regressive pattern, as suggested by the dominance of sandy facies to the top of the sections and the ichnofabrics stacking, as further presented (Figs. 2 and 3).

Macaronichnus ichnofabric (Fig. 4A) is characterized by horizontal to sub-horizontal, straight to meandering, cylindrical burrows with a mantle and core reflecting grain segregation by the tracemaker. Only few plant fragments occur associated with this ichnofabric (no defined taphofacies), and the bioturbation scale is low to moderate (BS 2-3). *Macaronichnus* occurs as simple ichnofabric, reflecting the activity of a single ichnocoenosis, and is preserved in horizontal stratified (Fig. 5A) or wave cross-laminated (Fig. 5B), well sorted, fine- to medium-grained sandstones (Sw and Sh facies; Tab. 1).

Psammichnites ichnofabric (Fig. 4B) is characterized by straight to meandering, horizontal, flat traces preserved in negative epirelief (trail preservation) on bedding

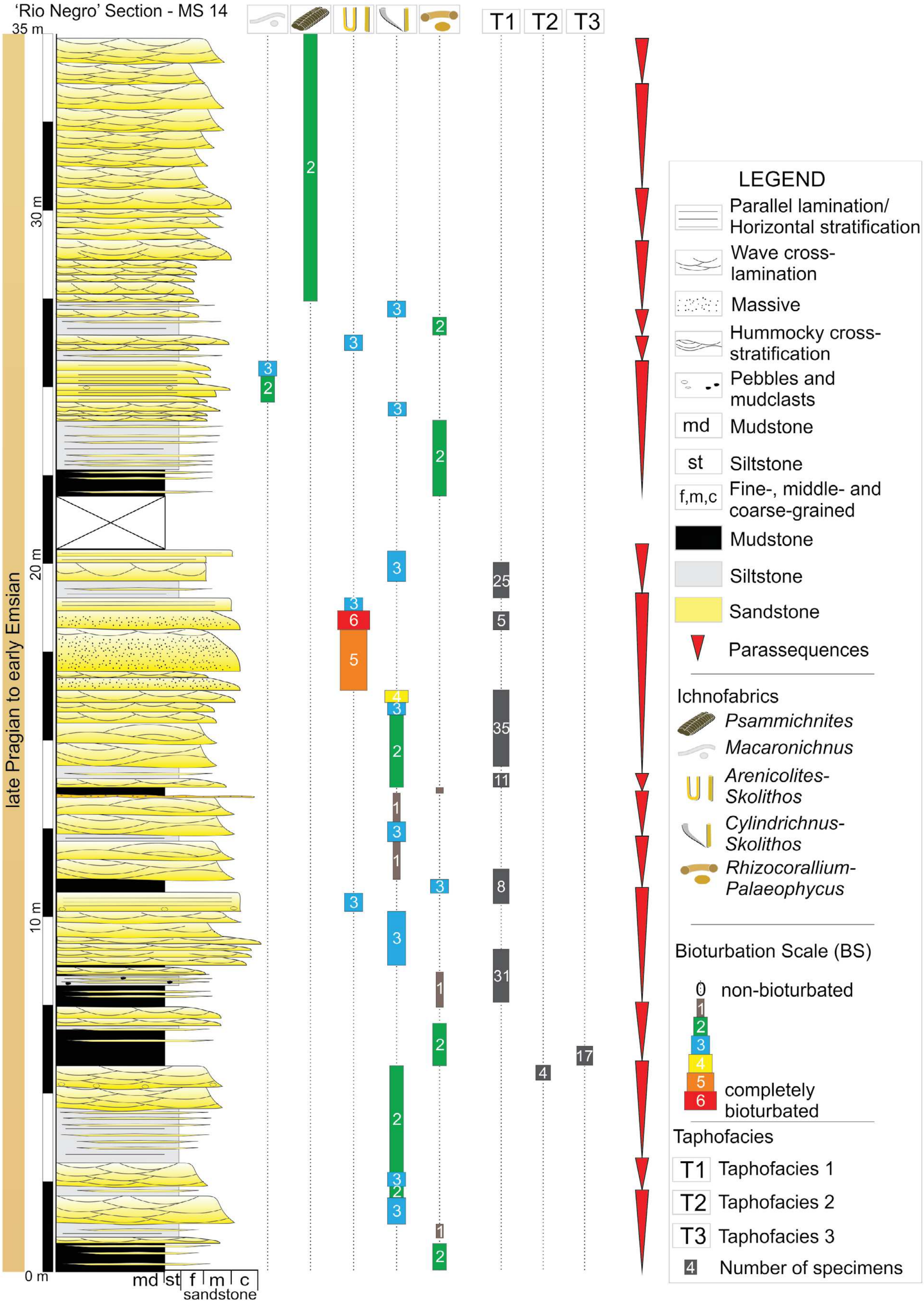

Figure 2. Sedimentologic profile, ichnofabric distribution and taphofacies from outcrop MS 14.

planes, internally ornamented by a faint meniscate backfill. *Skolithos*, *Arenicolites*, *Diplocraterion*, *Palaeophycus*, and *Macaronichnus* are locally preserved, characterizing this ichnofabric as composite, and with no associated macrofossils. The *Psammichnites* ichnofabric is preserved at wave cross-laminated fine-grained sandstones (Sw facies; Tab. 1), with low bioturbation scale (BS 2).

The *Arenicolites-Skolithos* ichnofabric (Fig. 4C) is composed by vertical burrows, simple or U-shaped, locally with *Cylindrichnus*, *Rosselia*, *Rhizocorallium*, *Diplocraterion*, and

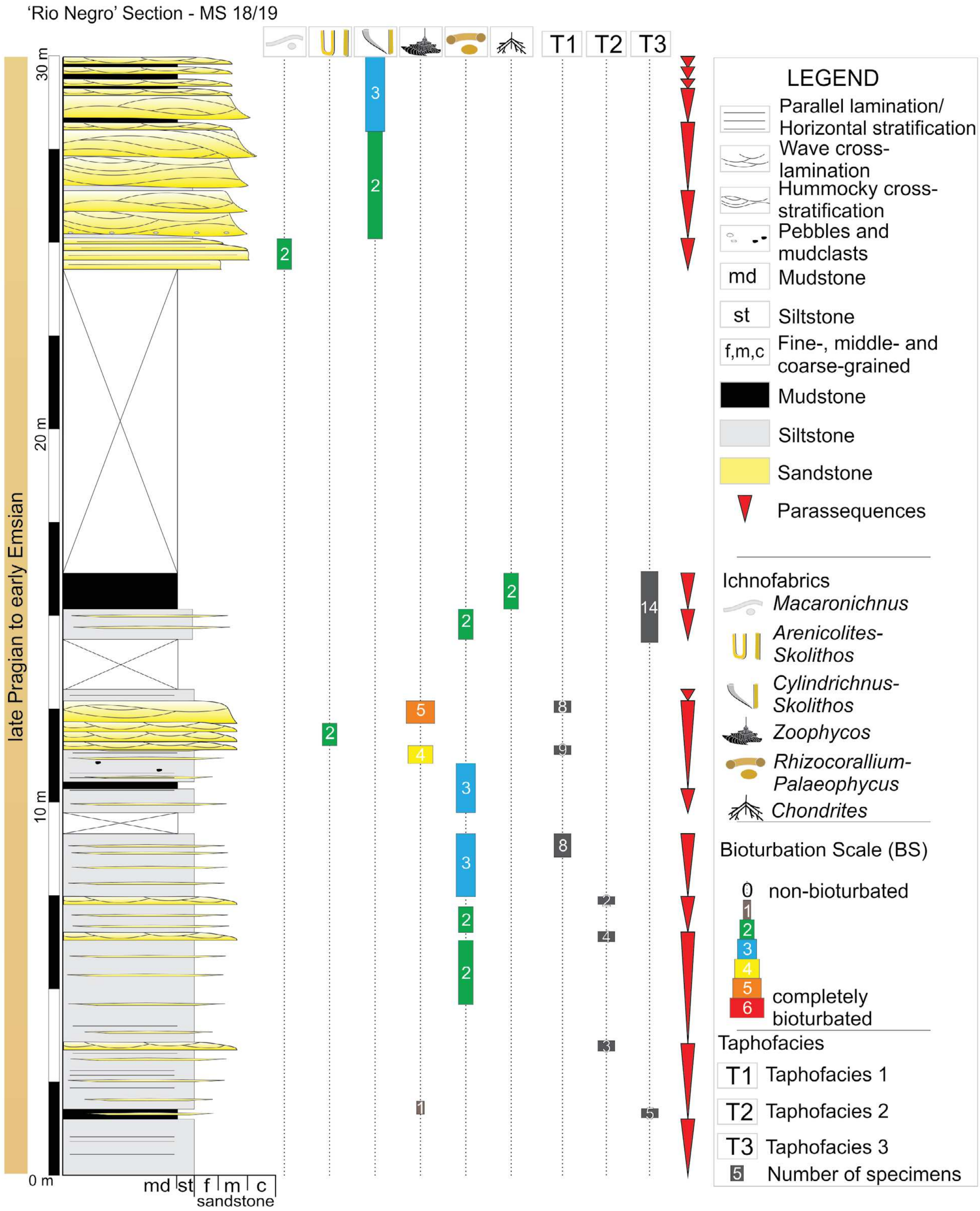

Figure 3. Sedimentologic profile, ichnofabric distribution and taphofacies from outcrop MS 18/19.

Palaeophycus, with bioturbation scale variably expressed, being normally low to moderate (BS 3-4), but occasionally high (BS 5-6). In the rare levels with macrofossils, they occur disarticulated, few fragmentated, parallel or oblique in relation to bedding-plane, being composed of conulariids and mollusks bivalves, which characterizes the Taphofacies 1 (Tabs. 2 and 3). This composite ichnofabric is preserved in several sandstones facies (Shcs, Sm, Sw, and Sh; Fig. 5 and Tab. 1).

The *Cylindrichnus-Skolithos* ichnofabric (Fig. 4D) is dominated by vertical structures, with funnel-shape or circular apertures, locally with *Arenicolites*, *Diplocraterion*, *Rhizocorallium*, *Palaeophycus*, *Lingulichnus*, and *Rosselia*, presenting low bioturbation scale (BS 1-3), to locally moderated (BS 4). The associated macrofossils are predominantly disarticulated, few fragmented, parallel or oblique in relation to bedding-plane. In this association, two preservation modes occurs, which were grouped in two taphofacies. The most recurrent association of macrofossils is characterized by dominance of disarticulated (bivalved) and predominantly parallel-oriented fossils in relation to the bedding-plane. This association is characterized by the presence of brachiopods infaunal lingulids (Fig. 6A) *Orbiculoidea* (Fig. 6C), *Australocoelia*, *Australospirifer*, conulariids, *Tentaculites* and

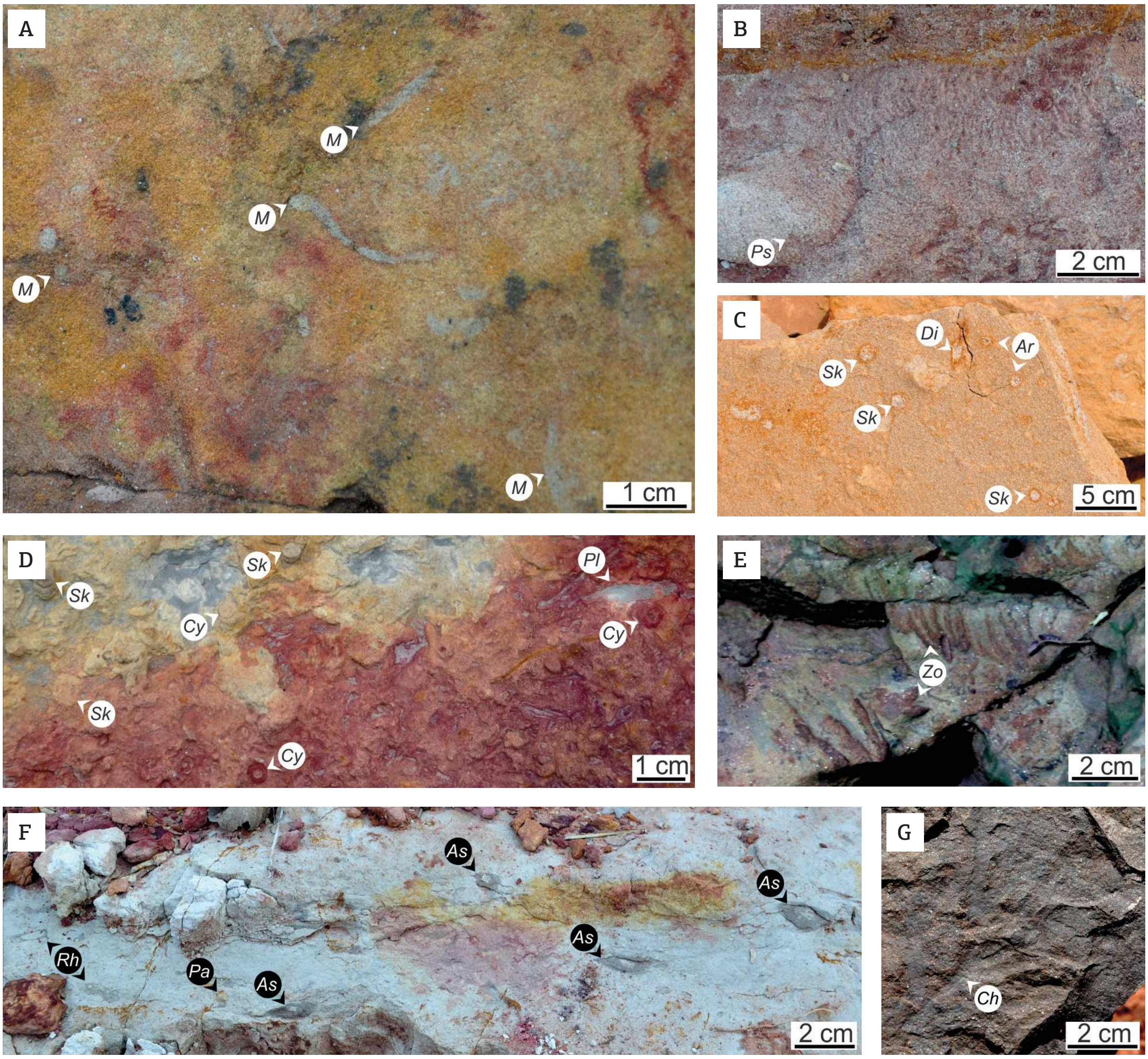

Figure 4. Ichnofabrics from lower Chapada Group unit 2 in Rio Negro (MS). (A) *Macaronichnus* (*M*) ichnofabric in bedding-plane view. (B) *Psammichnites* (*Ps*) ichnofabric in bedding-plane view. (C) *Arenicolites-Skolithos* (*Ar* and *Sk*) ichnofabric with *Diplocraterion* (*Di*) in bedding-plane view. (D) *Cylindrichnus-Skolithos* (*Cy* and *Sk*) ichnofabric with *Planolites* (*Pl*) and other indistinct trace fossils in bedding-plane view. (E) *Zoophycos* (*Zo*) ichnofabric in bedding-plane view. (F) *Rhizocorallium-Palaeophycus* (*Rh* and *Pa*) ichnofabric with *Asterosoma* (*As*) in oblique view in relation to the bedding-plane. (G) *Chondrites* (*Ch*) in bedding plane view.

trilobites, which were grouped as Taphofacies 1. In the other hand, the occurrences of whole and articulated fossils, vertically oriented in relation to bedding plane indicating *in situ* position, is composed of *Australospirifer* (Figs. 6D and 6E) and infaunal lingulids (Fig. 6F). This association was grouped as Taphofacies 2 and is preserved in sandy facies (Tab. 2). The *Cylindrichnus-Skolithos* ichnofabric is very frequent in the MS 14 section, being preserved in all facies, but mudstones (Fig. 2).

The *Zoophycos* ichnofabric (Fig. 4E) is characterized by planar U-shaped morphology or few helical *spreiten* burrows, parallel to inclined in relation to bedding-plane, with marginal tube and central shaft occasionally preserved. *Palaeophycus*, *Asterosoma* and *Rhizocorallium* are subordinate structures, characterizing a composed ichnofabric. The bioturbation scale is moderate (BS 4-5), or locally low (BS = 1), and the associated shelly fauna occurs in two preservation modes. The fossil content is characterized by disarticulated, no fragmentated fossils, parallel or oblique in relation to bedding-plane, being composed of infaunal lingulids, *Orbiculoidea* and *Australospirifer*, which was grouped as Taphofacies 1. In the other hand, occurrences of conulariids and *Orbiculoidea* (Fig. 6H) with a mixture of articulated and disarticulated brachiopods, without signal of fragmentation, dissolution or abrasion, both inclined- and parallel-oriented in relation to the bedding-plane were grouped as Taphofacies 3. In the level T3 is preserved, *Zoophycos* occurs as monospecific ichnofabric with low intensity (BS = 1). *Zoophycos* ichnofabric is preserved in siltstones or in fine-grained sandstones with hummocky cross-stratification (F and Shcs facies; Tab. 1).

The *Rhizocorallium-Palaeophycus* ichnofabric (Fig. 4F) is characterized by dominance of U-shaped horizontal traces with spreiten and unbranched horizontal cylindrical burrows. The associated structures are *Asterosoma*, *Rosselia*, *Diplocraterion*, *Cylindrichnus*, *Chondrites*, *Planolites*, and *Skolithos*. Although the relatively high ichnodiversity, this ichnofabric has low bioturbation scale (BS 1-3). The macrofossils are also preserved in two patterns. The dominance

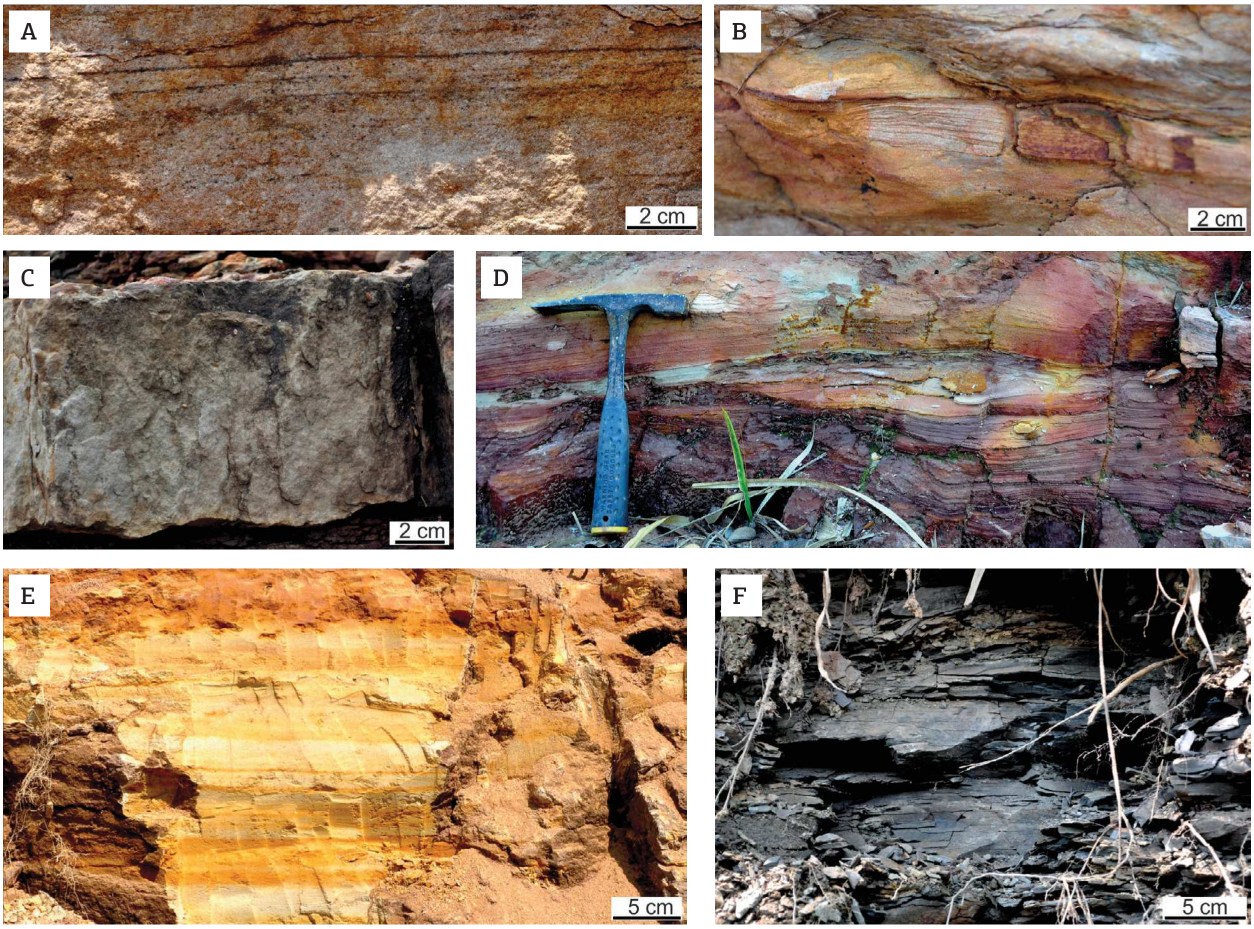

Figure 5. Facies and macrofossils from lower Chapada Group unit 2 in Rio Negro (MS). (A) Middle-grained sandstone with horizontal stratification (Sh facies). (B) Wave cross-laminated fine-grained sandstone (Sw facies). (C) Massive middle-grained sandstone (Sm facies). (D) Hummocky cross-stratified very fine-grained sandstone (Shcs facies). (E) Parallel laminated siltstone interbedded with very fine-grained sandstones (F facies). (F) Mudstone with high organic content (M facies).

of disarticulated and non-fragmented macrofossils, oblique or parallel to the bedding plane, mostly composed of *Orbiculoidea*, *Tentaculites*, trilobites, infaunal lingulids, *Australocoelia*, *Derbyina* (Fig. 6B), brachiopods and mollusks bivalves were grouped as Taphofacies 1. In the other hand, a mixture of articulated and disarticulated brachiopods *Schuchertella*, *Orbiculoidea*, infaunal lingulids, crinoids (Fig. 6I) and *Craniops* with no fragmentation, dissolution or abrasion, both vertical- and parallel-oriented in relation to the bedding-plane were grouped as Taphofacies 3. This ichnofabric is preferentially preserved in siltstones and mudstones (F and M facies; Tab. 2).

Finally, the *Chondrites* ichnofabric (Fig. 4G) is characterized by a branched system of small excavations, mostly vertically oriented and filled by darker material than the host rock, associated to simple horizontal excavations (*Planolites*).

Table 1. Sedimentary facies and inferred processes from studied sections.

Facies code and figure	Texture	Sedimentary structures	Geometry	Sedimentary process	Ichnofabrics	Taphofacies
Sh (Fig. 5A)	Middle-grained sandstone	Horizontal lamination	Lenticular	High energetic unidirectional flows above fair-weather wave-base	*Macaronichnus*, *Arenicolites-Skolithos*	Absent
Sw (Fig. 5B)	Fine- to coarse-grained sandstone	Wave cross-lamination	Lenticular	Oscillatory flows generated above fair-weather wave-base	*Psammichnites*, *Cylindrichnus-Skolithos*	T1 and T2
Sm (Fig. 5C)	Coarse- to middle-grained sandstone	Massive to faint wave cross-stratification	Lenticular	Oscillatory flows with fast deposition storm-generated above fair-weather wave base	*Arenicolites-Skolithos*	Absent
Shcs (Fig. 5D)	Very fine- to fine-grained sandstone	Hummocky cross-stratification	Lenticular	Oscillatory flows storm-generated, between storm and fair-weather wave-base	*Zoophycos*	T1
F (Fig. 5E)	Siltstone locally interbedded with very fine-grained sandstones	Parallel lamination	Tabular	Decantation episodically disrupted by storm flows below storm wave-base, in outer shelf context	*Rhizocorallium-Palaeophycus*	T1 and T3
M (Fig. 5F)	Mudstone locally interbedded with very fine-grained sandstones	Parallel lamination	Tabular	Decantation episodically disrupted by storm flows below storm wave-base, in outer shelf context	*Chondrites*	T3

Table 2. Composition of recurrent ichnofabrics from studied sections.

Ichnofabric	BS	Accessory ichnogenus	Associated taphofacies
Macaronichnus	1-2	Absent	Absent
Psammichnites	1-3	*Skolithos*, *Palaeophycus*, *Arenicolites*, *Diplocraterion*, *Macaronichnus*	Absent
Arenicolites- Skolithos	3-4, locally 5-6	*Cylindrichnus*, *Rosselia*, *Rhizocorallium* *Diplocraterion*, *Palaeophycus*	T1
Cylindrichnus-Skolithos	1-3, locally 4	*Arenicolites*, *Diplocraterion*, *Rhizocorallium*, *Palaeophycus*, *Lingulichnus*, *Rosselia*	T1, T2
Zoophycos	3-4	*Palaeophycus*, *Asterosoma*, *Rhizocorallium*	T1
Rhizocorallium, *Palaeophycus*	1-3	*Rosselia*, *Asterosoma*, *Diplocraterion*, *Cylindrichnus*, *Chondrites*, *Planolites*, *Skolithos*	T1, T3
Chondrites	2	*Planolites*	T3

The bioturbation scale is low (BS 2), and the associated shelly fauna is composed of *Orbiculoidea*, infaunal lingulids, trilobites (Fig. 6G), *Tentaculites*, *Craniops*, and *Cryptonella*. This association is characterized by articulated and disarticulated skeletons, few fragmented, both vertical- and parallel-oriented in relation to the bedding-plane, which were grouped as Taphofacies 3. This ichnofabric is preserved in mudstones with parallel lamination rarely disrupted by thin lenses of very-fine grained sandstones (M facies, Fig. 5F; Tab. 1).

DISCUSSION

Integrated sedimentologic, ichnologic and taphonomic analysis resulted in recognition of four main depositional contexts, named from proximal to distal paleoenvironments: foreshore, shoreface, storm-dominated shoreface to transitional offshore, and offshore (Fig. 7).

5.1 Foreshore

This sub-environment is characterized by high energetic flows, which is corroborated by the dominance of sandstones with horizontal cross-stratification. In this sub-environment, the erosion or non-preservation of shallow-tiers is common. High energetic conditions also difficult the colonization of the upper levels of the substrates, and only deep-tiers structures are preserved, for example, *Macaronichnus* (Howard & Frey 1984, Saunders 1989). This ichnogenus is common near the upper shoreface/foreshore contact (Pemberton *et al.* 2001, Saunders 1989, Saunders & Pemberton 1986, Saunders *et al.* 1994) and has been used as indicator of cold waters (Quiroz *et al.* 2010). The presence of this ichnogenus in high paleolatitude of the Paraná Basin during Lower Devonian corroborates the affinity by cold waters.

Although less common, other ichnofabric associated to sandstones with horizontal cross-stratification is *Arenicolites*-*Skolithos* with moderate bioturbation scale

Table 3. Taphofacies and their main characteristics from studied sections.

Characteristic	Taphofacies 1	Taphofacies 2	Taphofacies 3
Macrofossil content (number)	*Orbiculoidea* (40), *Australospirifer* (21), infaunal lingulids (17), *Conularia* (11), *Australocoelia* (8), *Tentaculites* (8), *Schuchertella* (7), Bivalvia (7), Trilobite (4), *Derbyina* (4), Crinoids (2), Brachiopod (2), Gastropoda (1) = 132 (total)	*Australospirifer* (11), *Australocoelia* (1), infaunal lingulids (1) = 13 (total)	infaunal lingulids (15), *Orbiculoidea* (13), trilobites calmonids (4), conularids (3), crinoids (3), *Craniops* (2), *Tentaculites* (2), *Schuchertella* (1), *Cryptonella* (1) = 44 (total)
Percentage of articulated skeletons	33.6% (113D/38A/19U)	92.3% (1D/12A)	38.6% (27D/17A)
Percentage of fragmented	17.4% (23F)	7.7% (1F)	15.9% (7F)
Abrasion	Absent	Absent	Absent
Corrosion	Absent	Absent	Absent
Rounding	Absent	Absent	Absent
Bioerosion	Absent	Absent	Absent
Encrustation	Absent	Absent	Absent
Partial dissolution	Absent	Absent	Absent
Position in relation to the bedding plane	Parallel 84.8% (112P), inclined 12.9% (17I), vertical 2.3% (3V)	Parallel 7.7% (1P), inclined 7.7% (1I), vertical 84.6% (11V)	Parallel 72.7% (32P), inclined 6.8% (3I), vertical 20.5% (9V)
Packing density	Dispersed	Dispersed	Dispersed
Inferred sedimentation rate	Low	High	Low
Genetic process	Onshore fair-weather deposition	Onshore storm-deposition	Offshore fair-weather deposition

D: disarticulated; A: articulated; U: univalved skeleton; F: fragmented; P: parallel-oriented in relation to the bedding-plane; I: inclined-oriented in relation to the bedding-plane; V: vertical-oriented in relation to the bedding-plane. Obs.: *the numbers inside parenthesis indicate the number of macrofossils.*

(BS 3) and low ichnodiversity (*Skolithos*, *Arenicolites* and *Diplocraterion*). This ichnofabric attests the preservation of shallow-tier structures in high energetic conditions, allowing the inference of less erosive processes or higher depositional frequency if compared to *Macaronichnus* ichnofabric (*e.g.*, MacEachern & Pemberton 1992). The presence of conulariids and mollusks bivalves also indicates lesser residence time in the taphonomically active zone (*e.g.*, Olszewski 1999) than that represented in the *Macaronichnus* ichnofabric.

The general absence of macrofossils in foreshore deposits is interpreted to be result of destructive processes associated to high energetic conditions, the high residence time of the organisms, and to the nature of coarse-grained substrates, commonly permeable and saturated with oxygenated pore water, factors that are not conducive for body fossil preservation. The subordinated presence of plant fragments corroborates the interpretation of reworking by waves in proximal areas.

Shoreface

This sub-environment is characterized by dominance of oscillatory flows, as expressed by the occurrence of sandstones with wave cross-lamination. In those beds, *Psammichnites* ichnofabric is preserved, with shallow-tier structures (*Arenicolites*, *Skolithos*, *Diplocraterion*, *Palaeophycus*, and *Psammichnites*) in low intensity and low ichnodiversity. Although highly

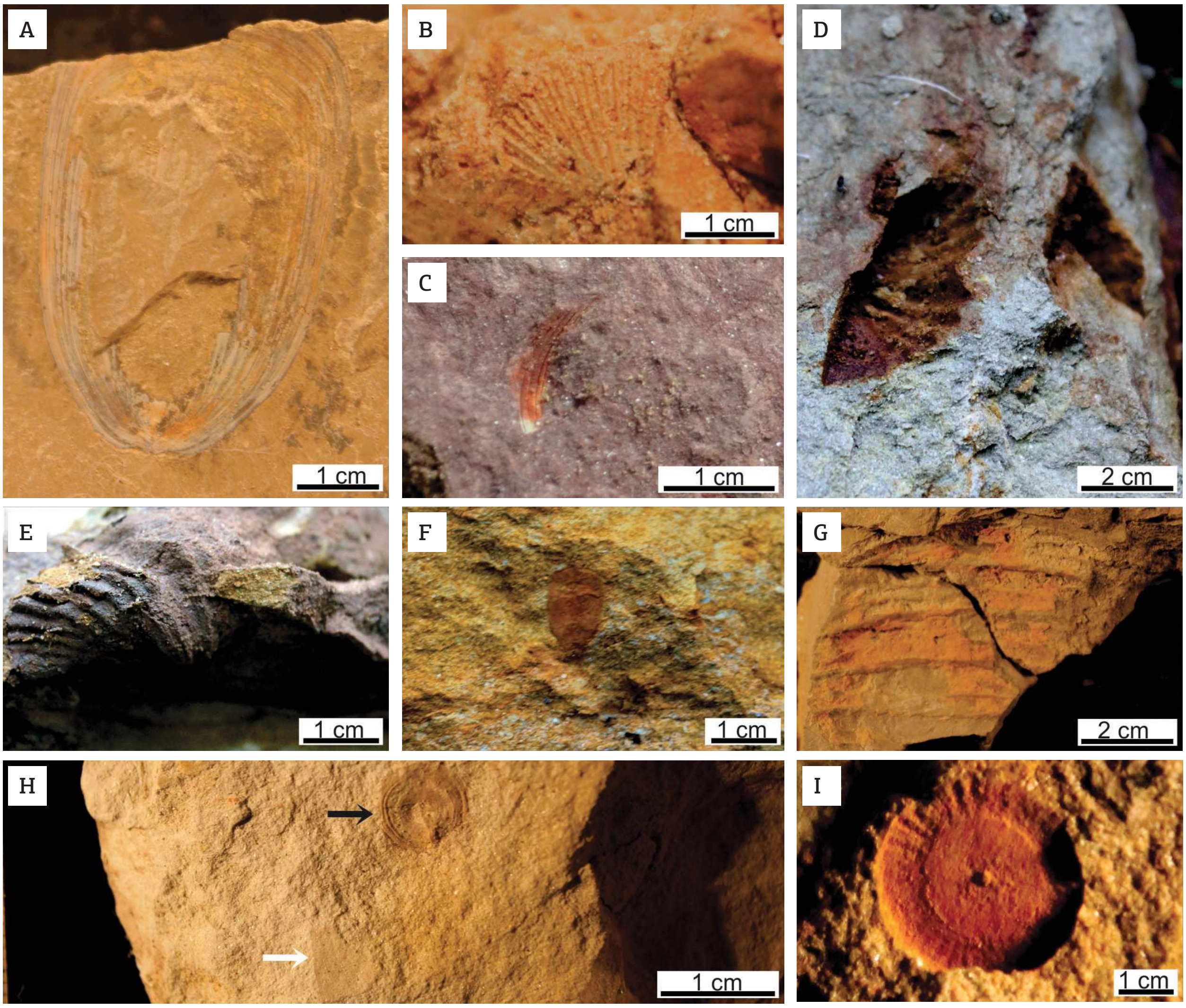

Figure 6. Macrofossil content of studied sections representing Taphofacies 1: (A) whole, disarticulated lingulid parallel-oriented in relation to the bedding-plane; (B) whole, disarticulated *Derbyina* parallel-oriented in relation to the bedding-plane; (C) fragmented *Orbiculoidea* parallel-oriented in relation to the bedding-plane; Taphofacies 2: (D-E) *in situ Australospirifer* vertically oriented in relation to the bedding-plane; (F) *in situ* infaunal lingulid inclined in relation to the bedding-plane); Taphofacies 3: (G) thorax of trilobite parallel-oriented in relation to the bedding-plane; (H) whole, articulated *Orbiculoidea* (black arrow) and fragmented infaunal lingulid (white arrow) parallel-oriented in relation to the bedding-plane; (I) disarticulated crinoid columnal parallel-oriented in relation to the bedding-plane).

energetic, this sub-environment is less erosive than the foreshore, allowing preservation of few shallow-tier structures. *Macaronichnus* locally overprint the shallow-tier structures, which is interpreted as the result of the vertical migration of the ichnocoenosis (autocomposite ichnofabric *sensu* Savrda 2016). The absence of macrofossils probably is consequence of high energetic conditions and low sedimentation rates resulting from fair-weather conditions, which increase the residence time in the interface water-sediment, as discussed to the foreshore setting.

Other ichnofabric preserved in this context is *Cylindrichnus-Skolithos* ichnofabric. Although vertical forms produced by suspension-feeder organisms are the main signature of this ichnofabric, there are some detritus-feeding structures preserved (*e.g.*, *Rhizocorallium* and *Rosselia*), indicating short moments of lesser energetic conditions. This ichnofabric expresses the alternation of the Skolithos and the Cruziana ichnofacies in lower shoreface zone (*e.g.*, MacEachern & Pemberton 1992, Buatois *et al.* 2007).

In some levels, massive sandstones with faint wave cross-stratification (Sm facies) are preserved. The massive characteristic can be both caused by high biogenic activity within the substrate, marked by *Arenicolites-Skolithos* ichnofabric, as well by fast deposition after storm events. The dominance of suspension-feeding habits associated to high bioturbation scale indicate low depositional rates under energetic conditions in shoreface environment (Pemberton *et al.* 2001). Depending on the depositional rates, two taphofacies can be associated to these sandstones with wave cross-lamination:

1. T1, with disarticulated organisms indicating a reworked assemblage under minor sedimentation rates;
2. T2, represented by *in situ* organisms recording rapid burial (*Australospirifer*) associated to storm events close to the fair-weather wave base.

The T1 is here representing relatively longer resident period in the taphonomic active zone under lower accommodation rates, as expected in prograding trends. In this sense, it is hard to infer if either the different taphonomic modes associated in a single bed is result of variable hydrodynamic flows or if they are indicating a time-averaged assemblage (*e.g.*, Kidwell 1997). In the other hand, the T2 is representing rapid deposition, as expected when the accommodation space is relatively higher or during intense storm events and higher sedimentation rates

To western India, Fürsich & Oschmann (1993) recognized nine genetic types of fossil concentrations in Jurassic deposits of the pericratonic basins of Kachchh and Rajasthan. Although from different basin type and age,

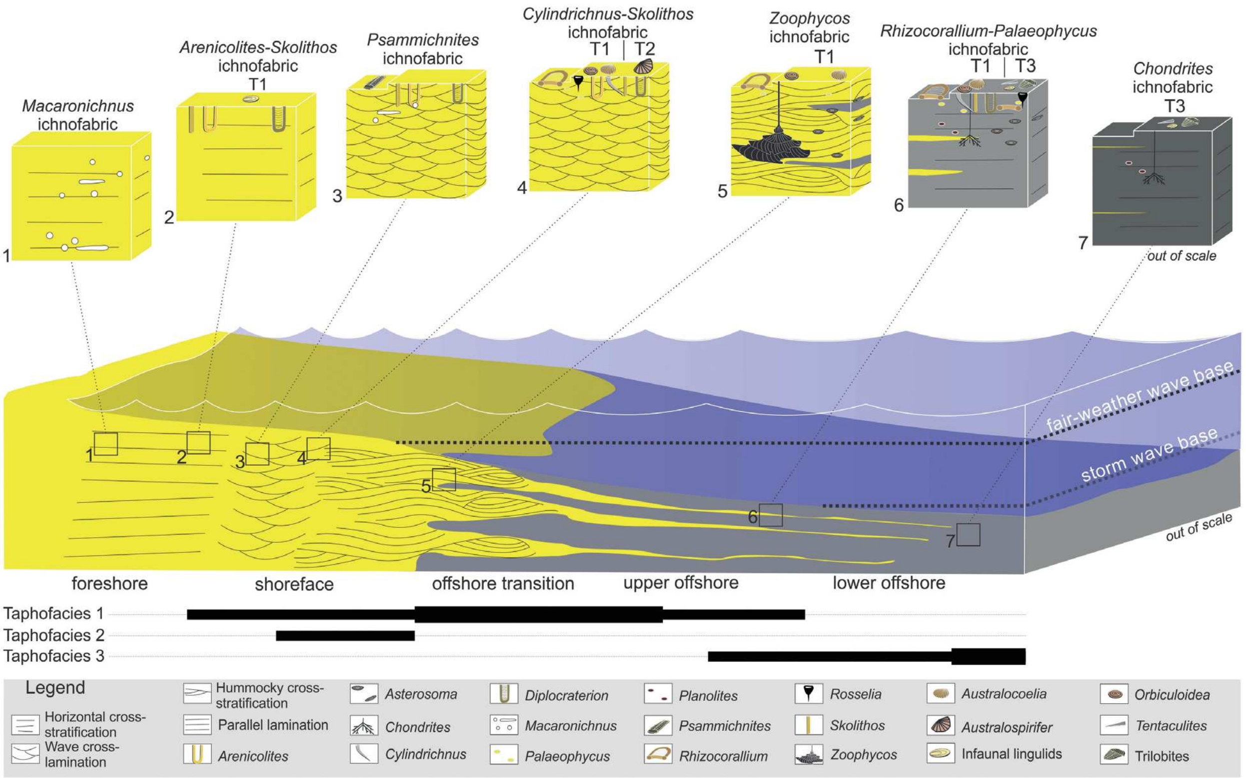

Figure 7. Paleobathymetric context of high-stand systems tract (HST) deposits in northern Paraná Basin, Brazil, inferred by integrated ichnofabric, taphofacies and sedimentologic analyses.

these concentrations have similar signatures with the here identified taphofacies. Thus, the Taphofacies 1 has similarities with the "distal tempestites (type 4)" (*sensu* Fürsich & Oschmann 1993), showing evidences of transport, moderate sorting, and dominance of small-sized fossils. In the other hand, the Taphofacies 2 has common signatures with the so-called "storm-wave concentrations (type 2)" (*sensu* Fürsich & Oschmann 1993), grouping well-preserved, monospecific *in situ* fossils associations. A similar taphofacies was also diagnosed to coeval strata in the southern Paraná Basin (Taphofacies B of Sedorko *et al*. 2018a), representing storm-generated fossil assemblages.

Storm-dominated shoreface to transitional offshore

This sub-environment is the most recurrent in the studied section, characterized by a mixture of decantation and traction in the sea bottom, expressed by sandstones with hummocky cross-stratified interbedded with siltstones, or mudstones disrupted by thin sandstones lenses (Shcs, F and M facies). Due to this mixture, different ichnofabrics are associated to this context, such as *Cylindrichnus-Skolithos*, *Zoophycos* and *Rhizocorallium-Palaeophycus* ichnofabrics.

As previous discussed, *Cylindrichnus-Skolithos* ichnofabric indicates the mixture of suspension- and detritus-feeding strategies, in this case possibly resulting from the alternation of storm and fair-weather conditions. The *Zoophycos* ichnofabric expresses preferential deposit-feeding strategies, but the unexpected depleted character of this ichnofabric (low diversity: *Asterosoma*, *Rhizocorallium*, *Palaeophycus* and *Zoophycos*) indicates some stressful condition, possibly related to storm events. Recently, a similar context of *Zoophycos* dominance was reported in the south part of the basin, which was interpreted as differential preservation of deep-tier structures due to high frequency storms and erosion of shallow tiers under low accommodation space regimes (Sedorko *et al*. 2018b).

Rhizocorallium-Palaeophycus ichnofabric is the most diverse, although presenting low bioturbation scale (BS 1-3). The variability of feeding strategies (*i.e.*, suspension-feeding: *Diplocraterion*, *Skolithos* and *Cylindrichnus*; detritus-feeding: *Rhizocorallium*, *Rosselia*, and *Asterosoma*; and deposit-feeding: *Chondrites* and *Planolites*) indicates environmental stable conditions, allowing colonization of all tiers (*e.g.*, Ekdale & Mason 1988, Savrda & Bottjer 1989). The scarcity of bioturbation can be explained by relatively high sedimentation rates or because some taphonomic filter, such as the predominance of soup substrates, precluding visibility of previous structures (*e.g.*, Ekdale 1985).

The macrofossils associated to this sub-environment were grouped as Taphofacies 1, with disarticulated and few fragmented fossils indicating minor reworking before final burial in transitional offshore settings. In siltstones and mudstones, the macrofossil assemblage is more diverse (T3; Tab. 3), with a mixture of *in situ* (*Orbiculoidea* and infaunal lingulids) and transported organisms (*Schuchertella*, *Craniops*, and infaunal lingulids), suggesting a time-averaged assemblage, at least in 5th or 6th order. Time-averaging is the process that accumulates organic remains from different time intervals, sometimes expressing repeated burial/exhumation cycles as result of sediment reworking (Kidwell 1997). In this sense, the apparent diversity can be a taphonomic artifact resulting from accumulation of different biocoenosis, but the magnitude of this time-averaging is not accessible by this study.

Offshore

This sub-environment is characterized by dominance of decantation, expressed by gray to dark mudstones only locally disrupted by very-fine grained sandstones (M facies). In this sub-environment, both *Chondrites* and *Zoophycos* ichnofabric occur with low density of trace fossils and representing deposit-feeding habits (*e.g.*, *Chondrites*, *Zoophycos*, and *Planolites*), which allow the interpretation of stressed conditions, possibly associated to dysoxic substrates (Savrda & Botjer 1989). The associated macrofossils (Taphofacies 3) might be representing a time-averaged assemblage, as suggested by the dominance of disarticulated shells, which can be linked to long residence time as consequence of starvation periods (Kidwell 1997).

The Taphofacies 3 has similar signatures of the "condensed concentrations (type 9)" of Fürsich & Oschmann (1993), or with the "Taphofacies C" of Sedorko *et al*. (2018a), the last identified to coeval strata from southern Paraná Basin. These concentrations are described as grouping different taphonomic signatures in the skeletal elements due to *in situ* reworking and the highest time involved. These concentrations tend to be very diverse and highly time-averaged, even that the magnitude of time is not accessible to that Devonian strata.

STRATIGRAPHICAL CORRELATIONS WITH SOUTH PART OF THE PARANÁ BASIN

The studied sections are inserted in the lower Chapada Group 2 (Pragian-Emsian), correlated in age with Ponta Grossa Formation from southern basin (*sensu* Grahn *et al.* 2013), based on the macrofossil content and palynological data. The prograding pattern observed in the studied sections is characterized by upward dominance of shoreface to foreshore environments, which allows to correlate these sections with the high-stand systems tract (HST) of the Siluro-Devonian Sequence from Paraná state (Sedorko *et al*. 2018c). As previously discussed, in the studied sections predominate shoreface to foreshore settings, in a general onshore setting. In the other hand, even the HST in the southern basin (Paraná state; Fig. 1A) is represented mostly by transitional offshore to lower shoreface deposits (e.g. Sedorko *et al*. 2018a, 2018b, 2018c). These strata in Paraná state exhibit dominance of expressions of the Cruziana ichnofacies (Sedorko *et al*. 2018c), while in Mato Grosso do Sul state dominates expressions of the Skolithos ichnofacies (this study).

The shallower character of the north part might be a passive response to its position in the basin, closer to the border (Ramos 1970, Assine 1996). To Goiás state, Assine (1996) reported the absence of fine-grained rocks covering the sandstones of the Furnas Formation, which conducted him to infer that the Tibagi Member overlays the Furnas Formation. In studied region, late Pragian to early Emsian mudstones were previously reported in Rio Verde do Mato Grosso, overlaying the sandstones of Chapada Group unit 1 (Furnas Formation) (*e.g.*, Carvalho *et al*. 1987, Melo 1988, Becker-Kerber *et al*. 2017). Some palynological studies in "Paleosul-02-RV-MT" corroborate a late Pragian to early Emsian age for the rocks in this region (Mendlowicz Mauller 2007, Mendlowicz Mauller *et al*. 2009, Grahn *et al*. 2010). These data support the inference of a similar stacking of the Pragian to Emsian strata in the whole basin, but in a general shallower setting to the northern basin.

The Lower Devonian macrofossil content is also similar both in Mato Grosso do Sul and Paraná states. Except by fish remains only preserved in southern part of the basin (*e.g.*, Richter *et al*. 2017), all groups are distributed in the basin, corresponding to the typical association of the Malvinokaffric Realm (dominance of brachiopods *Orbiculoidea*, lingulids, *Australospirifer*, *Australocoelia*, *Schuchertella*, with subordinated mollusks bivalves and gastropods, tentaculitids, conulariids and crinoids). The decline in diversity during the Middle Devonian (Eifelian), as observed by Bosetti *et al*. (2012), was not yet observed in Mato Grosso do Sul state.

Thus, the dominance of proximal environments in Devonian strata of the Mato Grosso do Sul region, especially in Rio Negro municipality, is related to its proximal context in the border of the basin. The presence of the Três Lagoas, Campo Grande Arch (*c.f.* Northfleet *et al*. 1969), geographically close to the study area, was not clear in our study. However, the virtual absence of middle Devonian strata in the study region do not allow to conclude that this high was not active in posterior times. The similarities in the facies and ichnofacies stacking in Paraná and Mato Grosso do Sul states and the similar macrofossil content suggest that the division between two sub-basins was not complete during late Pragian to early Emsian. However, the problem regarding the division of the Paraná Basin in two sub-basins during Devonian needs more detailed studies to be elucidated.

CONCLUSIONS

Seven ichnofabrics (*Macaronichnus*, *Psammichnites*, *Arenicolites-Skolithos*, *Cylindrichnus-Skolithos*, *Zoophycos*, *Rhizocorallium-Palaeophycus*, and *Chondrites* ichnofabrics) and three taphofacies (T1: parautochthonous to allochthonous preservation with evidence of moderate transport; T2: autochthonous preservation, indicating rapid burial; and T3: time-averaged association with autochthonous to allochthonous preservation) were diagnosed in Devonian strata from lower Chapada Group unit 2 (Ponta Grossa Formation, *sensu* Grahn *et al*. 2013), in Rio Negro (MS). The studied sections are positioned in a HST and exhibit upward dominance of sandy facies representing shoreface to foreshore settings, with local occurrences of transitional offshore to offshore context.

Four sub-environments were defined by integration of ichnologic, taphonomic and sedimentologic analyses: foreshore (*Macaronichnus* and *Arenicolites-Skolithos* ichnofabrics); shoreface (*Psammichnites*, *Arenicolites-Skolithos*, *Cylindrichnus-Skolithos*, associated to T1 and T2); storm-dominated shoreface to transitional offshore (*Cylindrichnus-Skolithos*, *Zoophycos* and *Rhizocorallium-Palaeophycus* ichnofabrics associated to T1 and T3); and offshore (*Chondites* and *Zoophycos* ichnofabric associated to T3). The dominance of foreshore to shoreface settings in HST of the Pragian to Emsian strata in northern basin corroborates a shallower context in relation to the south part. Similarities in the facies and ichnofacies stacking, as well in the macrofossil content, suggest that the division between two sub-basins was not complete during late Pragian to early Emsian. Additional studies are needed to evaluate the stratigraphic distribution of the macrofossils in middle Devonian strata in the northern Paraná Basin, as well the existence of two sub-basins during this time.

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SUPPLEMENTARY DATA

Supplementary data associated with this article can be found in the online version: Suplementary Table A1.

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CAPÍTULO 7

Tracking Silurian-Devonian Events and paleobathymetric curves by ichnologic and taphonomic analyzes in the southwestern Gondwana

Manuscrito submetido no periódico “Global and Planetary Change” que teve como objetivo avaliar a distribuição das suítes icnológicas na Supersequência Paraná. Este manuscrito integra os dados abordados no escopo da tese para analisar a evolução das suítes icnológicas ao longo do Siluro-Devoniano da bacia, definindo curvas de paleobatimetria relativa e atestando mudanças que culminaram no declínio da fauna Malvinocáfrica durante o Devoniano Médio.

Estes estudos corroboram a hipótese formulada no escopo da tese ao demonstrar a utilidade da análise icnológica para resolver questões paleoambientais, paleobiológicas, paleocológicas, paleogeográficas, tafonômicas e estratigráficas. Os capítulos posteriores (8 e 9) foram desenvolvidos em coautoria e complementam as discussões apresentadas nesta tese.

To Global and Planetary Change

Tracking Silurian-Devonian Events and paleobathymetric curves by ichnologic and taphonomic analyzes in the southwestern Gondwana

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Abstract

Trace fossils have been used worldwide to access paleoecologic data in sedimentary sections. In Paraná Basin (southern Brazil), trace fossils are stratigraphically well distributed; however, they are understudied if compared to macrofossils or microfossils. Only few studies applied Ichnology to the Silurian-Devonian strata, and mostly focused in a ichnotaxon. This comprehensive study aims to analyze the ecospace colonization represented by trace fossils in a Silurian-Devonian section from Paraná Basin, and to associate the paleoenvironmental data provided by trace fossils with the decline of the Malvinokaffric Realm. In this sense, trace fossils were analyzed in six sedimentary sections to encompass the whole outcropping supersequence. The vertical distribution of trace fossils (Glossifungites, Skolithos and Cruziana ichnofacies) was compared with the distribution of the Malvinokaffric macrofossils. Paleoecologic and ichnodisparity analyzes allowed to infer dominance of stable conditions throughout the Silurian-Devonian section; however, some levels express dysoxic to anoxic conditions, and in others the high energetic conditions biased the ichnologic record. The stratigraphic distribution of *Zoophycos* suggests a change in the basin configuration during Eifelian, which might be the cause of the decline in the diversity of the Malvinokaffric fauna.

Keywords: Silurian events; Devonian events; Ichnodisparity; *Zoophycos*; Malvinokaffric Realm.

1. Introduction

The record of Devonian extinctions, in variable scales, results of many efforts of researches in the last decades, with a set of events recognized in different basins from the world (synthesis in House, 2002; Becker et al., 2016; Brett et al., 2018). The fossil record is useful to infer paleoenvironmental and evolutionary changes even considering the possibility of some preservational bias (e.g., Signor-Lipps Effect; Signor and Lipps, 1982). Given the frequent body fossil evidence in Devonian beds, the abovementioned studies were focused on body fossils distribution rather than trace fossils.

Although trace fossils are evidence of behavioral strategies as a response to biotic and environmental parameters (e.g., Seilacher, 1967; Pemberton and Frey, 1984; Bottjer et al., 1988; Savrda, 1998; Mángano et al., 1998), the tracemakers are rarely recognized. In other hand, trace fossils can be the unique evidence of some groups, such as cnidarians, polychaetes, annelids, and other invertebrates (Buatois and Mángano, 2011). In this scenario, the applicability of trace fossils to infer paleoenvironmental settings is a paradigm, but the applicability as evidence of biodiversity, extinctions or faunal turnovers are underexplored (with few exceptions, as Mangano and Buatois, 2016). Also, the application of trace fossil analysis to infer oxygenation rates and paleobthymetric curves are very useful to understand the ecospace colonization throughout the time.

In this study, we analyzed the ichnologic signatures of the Silurian-Devonian interval in Paraná Basin (southern Brazil) to track paleobathymetric curves and their relationship with paleobiologic events. The fossil content in those strata represents the Malvinokaffric Realm, a cold-water fauna that inhabited medium to high latitude settings in Gondwana during Devonian. Despite the extensive and detailed paleobiologic (e.g., Bosetti et al., 2011, 2012) and taphonomic (e.g., Simões et al., 2000; Rodrigues et al., 2003; Zabini et al., 2010, 2012; Bosetti et al., 2013; Horodyski et al., 2014, 2018) studies concerning the macrofossils from this interval in Paraná Basin, trace fossils were lesser considered to infer paleoecologic trends and paleoenvironmental changes. Also, the association between trace fossils and macrofossils is yet understudied, and these strata offer excellent exposures to perform such integrated analysis. Thus, the present study aims (i) to discuss the vertical distribution of trace fossils from Silurian-Devonian strata (Paraná Basin); (ii) to analyze the paleoecologic parameters and paleobathymetric curve provided by trace fossils analysis; and (iii) to infer paleoecological events considering the vertical distribution of trace fossil and macrofossils.

2. Geological setting

The huge intracratonic Paraná Basin (circa 1.5x10^6 km²) covers the southern portion of Brazil and adjacent areas (Fig. 1A) and has its sedimentary fill divided into six second-order sequences influenced by tectonic-eustatic cycles related to the evolution of the Western Gondwana. This basin was deposited from Late Ordovician to Late Cretaceous (Milani et al., 2007) and this study focuses on the Paraná

Supersequence, which characterizes the Silurian-Devonian interval (Fig. 1B-C). During this time, the basin was positioned in cold-temperate regions, between 60° and 80°S paleolatitude (Cooper, 1977; Scotese and McKerrow, 1990; Matsumura et al., 2015).

Lithostratigraphically, these strata are divided in Furnas and Ponta Grossa formations (*sensu* Lange and Petri, 1967), the last divided in Jaguariaíva, Tibagi, and São Domingos members. These units comprise four third-order sequences, named Lower Silurian (lower and middle Furnas), Siluro-Devonian (upper Furnas, Jaguariaíva Member and part of Tibagi Member), Devonian I (upper Tibagi Member and lower São Domingos Member), and Devonian II (upper São Domingos Member) (Sedorko et al., 2018a; Figs. 1B-C).

The non-fossiliferous Lower Silurian sequence onlaps the basement or Ordovician deposits from the Rio Ivaí Supersequence (Milani et al., 2007). This sequence is composed of fine- to coarse-grained sandstones and conglomerates from marginal-marine and shallow marine environments, as well as tidally-influenced sandy heterolithic deposits and sandstones (Sedorko et al., 2017). The Siluro-Devonian sequence also contains non-fossiliferous tidal-influenced shallow marine environments, which are overlaid by sandstones with hummocky cross stratification (HCS) capped by *Zoophycos*-rich siltstones and shales (base of the Jaguariaíva Member; Sedorko et al., 2018c). The upper levels of Siluro-Devonian sequence represent lower shoreface to offshore settings bearing a rich fauna characteristic of the Malvinokaffric Realm (e.g., Simões et al., 2009; Rodrigues et al., 2003; Bosetti et al., 2009, 2011, 2012, 2013; Sedorko et al., 2018a).

The Devonian I sequence is marked at the base by the Glossifungites Ichnofacies (Sedorko et al., 2018b) and contains sandstones, siltstones, and shales representing a transgressive trend from shoreface to offshore settings. This sequence registers the first decline in biodiversity of the Malvinokaffric Realm (Bosetti et al., 2012; Horodyski et al., 2018) and, coincidently, also registers a decline in *Zoophycos* abundance, which might be related to a basin restriction (Sedorko et al., 2018c).

Finally, the Devonian II sequence contains sandstones, siltstones, shales, and locally conglomerates also representing a transgressive trend from shoreface to offshore settings. The maximum transgressive surface of this section was correlated to the global anoxic Kačák event (Horodyski et al., 2014) and corresponds to the main flooding event of the 2nd-order sequence (Milani et al., 2007; Sedorko et al., 2018b). In surface sections, these strata are capped by the erosive glacial deposits related to the Late Paleozoic Ice Age.

3. Material and Methods

The trace fossils studied herein are exposed in Campos Gerais region, corresponding to Ponta Grossa, Tibagi, Arapoti, Palmeira, and Jaguariaíva municipalities, Paraná State, southern Brazil (Fig. 1). Data acquisition was conducted at centimeter scale and consisted of description and photographic record of the sedimentary facies and trace fossils in place. The majority of the trace fossils encompassed in this study was previously discussed by Sedorko et al. (2017, 2018a, b, c).

The sedimentological analysis was based in texture, physical sedimentary structures, composition, relations of contact, trace fossils, and macrofossil content. The ichnofabric characterization involved analysis of ichnotaxa, tiers composition, ichnodiversity, ichnodisparity, and the quantification of the bioturbation. This quantification was based on the bioturbation degree of the substrate as originally proposed by Reineck (1963), ranging from 0 (without bioturbation) to 6 (homogenized sediment or no apparent primary sedimentary structures). To avoid repetition, “bioturbation scale” throughout the text was shortened as BS.

Ichnodisparity analysis followed the main morphological plans as proposed by Buatois and Mángano (2013). Ichnofossils were usually accessed in outcrops with vertical and horizontal exposures, while in those with preferential vertical or horizontal exposures the trace fossil assemblages are represented mostly by ichnofabrics.

Taphonomic analyzes were based in the characterization presented by Horodyski et al. (2018), which identified six taphofacies in a general onshore to offshore trend. The macrofossil distribution in the section follows Bosetti et al. (2012) and the adopted ages are based on Grahn et al. (2013).

4. Facies and trace fossils of Silurian-Devonian from Paraná Basin

The trace fossil assemblage of the Paraná Supersequence is represented both by ichnofossils and ichnofabrics, being grouped in twelve trace fossils suites. These suites are described below associated to the sedimentary facies, according to a general onshore-offshore trend.

4.1 Glossifungites suite

This suite is characterized by *Skolithos* (Fig. 2A) and *Arenicolites* (Fig. 2B) with signatures of colonization in firmground substrates (burrows with irregular borders and passively filled by clay), and is preserved in fine-grained sandstones presenting hummocky cross-stratification or wave ripples (S-hc and S-w facies, Table 1). The BS is low (1), and the suite is dominated by vertical and sub-vertical dwelling burrows of inferred suspension-feeding organisms. The Glossifungites suite-bearing beds present irregular contact between sandstones.

4.2 Macaronichnus *suite*

This monospecific suite contains *Macaronichnus* (Fig. 2C), preserved in S-w facies with full relief preservation. The BS is 2-4, and locally 5 (where it reworks another suite). Locally, *Macaronichus* superimposed traces from *Skolithos-Diplocraterion* suite, mainly *Arenicolites*, *Diplocraterion, Palaeophycus, Cylindrichnus* and *Lingulichnus* (palimpsest preservation). This suite shows preferential preservation of horizontal traces fossils representing deposit-feeding activity.

4.3 Arenicolites-Skolithos *suite*

This suite is dominantly composed of *Arenicolites* and *Skolithos* (Fig. 2D-E), with subordinate *Cylindrichnus, Palaeophycus,* and *Diplocraterion*. They are preserved in full relief, show low to moderate BS (1-3), and represent dominantly dwelling structures of suspension-feeding organisms. This suite is present in S-p, S-t, S-s, and rarely in S-m facies (Table 1), and *Skolithos* occur as simple ichnofabric in some beds.

4.4. Skolithos-Diplocraterion *suite*

This suite is dominated by *Skolithos* and *Diplocraterion* (Fig. 2F), although *Arenicolites*, *Cylindrichnus*, and *Lingulichnus* are also frequent. *Schaubcylindrichnus, Palaeophycus, Rosselia,* and *Thalassinoides* occur subordinately. This suite shows full relief preservation, low to locally high BS (1-3 and locally 5), and is present in S-hc and S-w facies (Table 1). Phytodetritus occur locally associated with the burrow openings or aligned to the external border of the burrow in Ponta Grossa Formation. Dwelling structures of suspension-feeding organisms and subordinated detritus-feeding structures characterize this suite.

4.5 Palaeophycus *suite*

This suite is characterized by the dominance of *Palaeophycus* (Fig. 2G), although *Thalassinoides* and *Didymaulichnus* are also frequent. *Psammichnites, Didymauliponomos, Rhizocorallium, Arthrophycus, Rusophycus,* and *Cruziana* are less frequent. The BS is low (1-2), although some beds can present high concentrations in bedding plane view (equivalent to BPBI 3-4 of Miller and Smail, 1997). The *Palaeophycus* suite mainly occurs in S-p, S-t, S-s facies, and, rarely, in S-h, S-m, and S-w facies and its components can be preserved in full relief, concave epirelief, or convex hyporelief.

This suite occurs associated with biomat structures, and another potential microbially induced sedimentary structures (MISS), such as the pseudoichnofossils *Protospiralichnus* (concentric microfault systems, Fig. 4A) and *Kinneyia* (Fig. 4C-D) (*sensu* Seilacher, 2007). In the beds with MISS evidence, *Didymauliponomos* and *Thalassinoides* dominate (Fig. 4B). The *Palaeophycus* suite is chiefly composed of dwelling structures produced by worm-like suspension-feeder or predaceous organisms (*Palaeophycus, Thalassinoides*). Locomotion/feeding structures of detritus-feeding organisms (*Didymaulichnus, Arthrophycus, Heimdallia*), and trilobite resting/feeding activity (*Rusophycus, Cruziana*) also occur.

4.6 Didymaulichnus *suite*

This suite is dominated by *Didymaulichnus* (Fig. 2H), although *Heimdallia* and *Didymauliponomos* are also frequent. Subordinately, *Palaeophycus, Arthrophycus,* and *Psammichnites* occur. Burrows of detritus- or deposit-feeding organisms are dominant. The trace fossils are preserved in S-t and S-s facies (Table 1) and show full relief, concave epirelief or convex hyporelief preservation, and moderate BS (3). This suite is the most diverse from Furnas Formation.

4.7 Psammichnites *suite*

Psammichnites (Fig. 2I) is the dominant ichnotaxon in this suite, with accompanying *Rhizocorallium, Rosselia, Palaeophycus,* and *Didymauliponomos,* the last in minor expression and restricted to Furnas Formation. Detritus-feeding burrows dominate in this suite. These traces are preserved in full relief, concave epirelief or convex epirelief, and show a moderate BS (3). They occur in S-p or S-s facies, interbedded with unbioturbated mudstones (facies M; table 1).

4.8 Rosselia *suite*

This suite is characterized by the dominance of *Rosselia* (Fig. 2J) with high BS (4-5), frequently presenting a stacked pattern, preserved in S-hc facies. *Cylindrichnus, Skolithos*, and *Palaeophycus* occur locally, all of them in full relief preservation. *Rosselia* is the most frequent burrow, forming a monospecific ichnofabric in some beds. It was originally reported in these beds by Netto et al. (2014) and interpreted as a response of a tolerant behavior to storm events. In this suite dominates dwelling structures of detritus-feeding organisms.

4.9 Rhizocorallium-Palaeophycus *suite*

This suite is dominated by *Rhizocorallium* (Fig. 2K) and *Palaeophycus*, but other ichnogenera such as *Arenicolites, Cylindrichnus, Rosselia, Diplocraterion, Lingulichnus, Thalassinoides, Planolites,* and *Skolithos* are also frequent. *Teichichnus, Rusophycus, Chondrites, Heimdallia, Laevicyclus, Bergaueria,* and *Bifungites* can be also present as subordinated ichnotaxa. These traces occur in full relief, concave epirelief or convex epirelief preservation in S-hc, S-w or F-p facies showing a low to moderate BS (1-4). Although this suite presents the dominance of horizontal burrows produced by detritus-feeding or predaceous organisms, vertical burrows of suspension-feeding animals are also frequent.

4.10 Asterosoma-Teichichnus *suite*

This suite is characterized by the dominance of *Asterosoma* and *Teichichnus* (Fig. 2L), but other traces such as *Chondrites, Zoophycos, Planolites, Palaeophycus, Rhizocorallium, Taenidium satanassi, Helminthopsis, Rosselia, Cylindrichnus, Lockeia, Psammichnites, Halopoa, Heimdallia,* and *Phycosiphon* are also present. This association characterizes dominance of detritus- and deposit-feeding habits in the original biocenosis; however, burrows produced by suspension-feeders like *Arenicolites, Diplocraterion, Lockeia, Schaubcylindrichnus, Lingulichnus,* and *Skolithos* were also preserved. All trace fossils present full relief preservation, and this suite is the most diverse in the studied succession (ichnodiversity up to 20, Table 2), also presenting the higher variation in bauplans (ichnodisparity up to 15, Table 2). The BS is high (BS 4-6), and locally low to moderate (2-3). *Asterosoma-Teichichnus* suite occurs in W, F-p, or F-l facies (table 1), and phytodetritus is locally abundant. The high diversity in food exploitation ways reflects stable conditions for tracemakers, characterized by oxygenated substrates, low to moderate energetic conditions and variable food source.

4.11 Planolites-Chondrites *suite*

This suite is characterized by the dominance of *Planolites* and *Chondrites* (Fig. 2M) and subordinated *Palaeophycus* and *Rhizocorallium*, being frequent in F-l and F-p facies (Table 1) with full relief preservation. The BS for this suite is 5 and in some levels 6, due to the homogenized aspect in the rock, although in some beds only few trace fossils are discernible, resulting in a low diversity suite (both ichnodiversity and ichnodisparity are up to 3; Table 2). This suite is associated with high intrastratal activity in the mixed-layer, where the previous burrows are obliterated by the latest and deepest colonizers. In this sense, the dominance of soupground condition would have precluded morphologic distinction, generating aspect of unbioturbated strata.

4.12 Chondrites *suite*

The *Chondrites* suite is characterized by the dominance of *Chondrites, Zoophycos,* and *Phycosiphon* (Fig. 2N-O), and discrete accessories ichnogenera such as *Planolites* and *Teichichnus*. These burrows usually occur as monospecific ichnofabric, with full relief preservation in F-l or F-p facies, in low (BS 1-3) to moderate intensity (BS 3-4). Considering the relations between the strata, a monospecific occurrence of *Helicodromites* was attributed to this suite. In some levels, *Chondrites* and *Zoophycos* superimposed burrows of the *Asterosoma-Teichichnus* suite, resulting in a dense ichnofabric (BS 5-6). This suite has dominance of feeding activity of detritus-feeding and chemosymbiont worm-like animals, reflecting the high concentration of food into the substrate in low energetic and dysoxic substrates.

5. Taphonomy of Malvinokaffric Realm in Paraná Basin

The following descriptions are mostly based on the data presented by Horodyski (2014) and Horodyski et al. (2018), complemented by new data. The fossils found throughout the section are skeletons classified taphonomically, as bivalved shells (Mollusca: Bivalvia; and Brachiopoda), univalved shells (Mollusca: Gastropoda and Tentaculitoidea), multi-element skeletons (Trilobita; Echinodermata: Crinoidea and Stylophora; Annelida: Polychaeta) and flexible thecae (Cnidaria: Conulatae).

In the Furnas Formation strata (Lower Silurian and basal Siluro-Devonian sequences) there is no macrofossil preserved, except few beds bearing plant remains in uppermost unit, 20–30 m below the contact with the overlying Ponta Grossa Formation. These plants were identified as the primitive plant *Cooksonia* (Rodrigues et al., 1989; Mussa et al., 1996; Gerrienne et al., 2001; Martins et al., 2018).

The climax of faunal biodiversity of the Malvinokafrric Realm, with eighty-five taxa (Bosetti et al., 2012) is preserved in the Jaguariaíva Member of the Ponta Grossa Formation (upper Siluro-Devonian sequence; upper Pragian to lower Emsian). This climax assemblage is replaced by a depauperate assemblage in beds younger than the upper Emsian, showing a reduction in biodiversity to only fifteen species, representing ~17.5% of all Malvinokaffric fauna (Horodyski et al., 2018).

The preservation of taxa varied in terms of the degree of disarticulation (whether complete or partial, judging the type of skeleton), fragmentation (if high when more than 90%, intermediate between 50% and 90%, or low if less than 50% of the original), and bedding-plane position (vertical, oblique or parallel). The taphofacies were numbered T1-T6, in relation to relative onshore-offshore position, from proximal to distal settings (Horodyski et al., 2018) and are indicated in the composite stratigraphic section of the Fig. 5 and Table 3.

6. Ichnofabric and ichnofossils: a palaeoecological approach

Based in the suites and facies features it was possible to identify three ichnofacies, one of them with three different expressions: (i) Glossifungites Ichnofacies, representing substrate exposition; (ii) Skolithos Ichnofacies, suggesting high energy, oxygenated and softground substrates colonization; and (iii) Cruziana Ichnofacies, with (iii-a) proximal expressions, indicating colonization under moderate energy, and in oxygenated softground substrates; (iii-b) archetypal expressions, characterizing moderate to low energy, in oxygenated softground substrates; and (iii-c) distal expressions, representing low energetic, dysoxic to anoxic soft- to soupground substrates.

6.1 Glossifungites Ichnofacies

This ichnofacies is expressed by the Glossifungites suite, representing colonization in firmground substrates. When associated with stratigraphic surfaces, these deposits are overlaid by fine-grained sandstones of the S-hc and S-w facies containing *in situ* lingulids and *Lingulichnus* (*Skolithos-Diplocraterion* suite). Although Glossifungites Ichnofacies may be present in a wide range of environments, the related facies (S-hc and S-w facies) indicate a marginal marine context for these occurrences. Considering the dark clay filling in *Skolithos* and *Arenicolites* preserved in sandstones, it is possible to infer that this suite is characterizing an omission surface. In fact, expressions of this suite were used as a marker of sequence boundaries (e.g., Sedorko et al., 2018b), but other levels seem to be indicating autogenic processes, as in the HST of Siluro-Devonian sequence.

6.2 Skolithos Ichnofacies

This ichnofacies is composed of three suites representing colonization in high energetic softground substrates: *Macaronichnus, Arenicolites-Skolithos,* and *Skolithos-Diplocraterion* suites.

Macaronichnus suite occurs as monospecific ichnofabric, representing the activity of deep-tier deposit-feeder organisms. The monospecific character possibly results from erosional processes in proximal environments (due to the action of fair-weather waves), which acted as a taphonomic barrier to preserve shallow-tier burrows. This suite is common in upper shoreface to foreshore settings (Pemberton et al., 2001), and is more common in Devonian strata from northern Paraná Basin (Sedorko et al., 2018d). In some occurrences from studied sections, *Macaronichus* superimposed trace fossils of *Skolithos-Diplocraterion* suite, representing moments of minor erosional rates, which had allowed preservation of shallow-tiers.

The record of *Macaronichnus* has been mostly reported to post-Paleozoic deposits, and opheliid polychaetes are assumed as tracemakers (Clifton and Thompson, 1978). This trace fossil has been used as an indicator of cold waters and medium to high paleolatitudes (Quiroz et al., 2010). Vagile epibenthic annelids like opheliid polychaetes are present in the fossil record since the Early Cambrian, but infaunal polychaetes apparently diversified much later than the vagile forms (Dzik, 2004). Considering that opheliid or opheliid-like polychaetes might be the producer of early Paleozoic *Macaronichnus*, this occurrence suggests that the trace fossil record of infaunal polychaetes precedes its fossil record. In addition, Paraná Basin was under high paleolatitudes during Devonian (Cooper, 1977; Scotese and Mckerrow, 1990; Isaacson and Sablock, 1990), corroborating that the palaeolatitudinal constraint might reflect a strategic behavior present in opheliid and opheliid-like polychaetes biological program since Devonian.

The *Arenicolites-Skolithos* suite is present only in facies associated with tidal processes and exhibits low diversity and density (Furnas Formation). Comparatively, transgressive marginal-marine deposits, within a tide-dominated estuary in the Silurian Shawangunk Formation (New Jersey) are characterized by general low diversity, however with high density of suspension- and deposit-feeding structures, such as *Skolithos, Monocraterion, Arenicolites, Rosselia, Palaeophycus, Arthrophycus, Planolites, Protovirgularia*, and *Chondrites* (Metz, 1998). In this way, low diversity is a commonplace to Silurian tidal environments (Buatois et al., 2005). These features can be twofold explained, by the high energetic conditions in proximal tide environments, preventing intense colonization of the substrate, and by the possible low amount of adapted tracemakers to high energetic environments, mainly during Lower Silurian (post-Late Ordovician extinction; Sepkoski, 1986). In fact, the general ichnodiversity and ichnodisparity are low for the whole Furnas Formation (Fig. 5), even in beds representing low energetic conditions (for example close to the MFS of the Lower Silurian sequence; Fig. 5). Thus, besides the energetic constraint, the general biodiversity was low during Silurian in Paraná Basin.

Finally, *Skolithos-Diplocraterion* suite dominates Ponta Grossa sandstones, in storm deposits (S-hc facies). In that beds, the amount of bioturbation is higher compared with the *Arenicolites-Skolithos* suite, indicating optimum ecological conditions for tracemakers in lower shoreface to transitional offshore settings during Devonian. This context of high density and relatively high ichnodiversity is frequently observed in proximal environments bearing Skolithos Ichnofacies (e.g., Frey, 1990).

6.3 Proximal Cruziana Ichnofacies

This ichnofacies is composed of five suites representing colonization in softground substrates with moderate to low energetic conditions, which are: *Palaeophycus, Didymaulichnus, Psammichnites, Rosselia,* and *Rhizocorallium-Palaeophycus* suites.

Besides the relatively high diversity in *Palaeophycus* suite, only two or three ichnogenera represent the suite in most of the beds in which it occurs (Fig. 5), characterizing a recurrent low diverse suite. Horizontal trace fossils are common, mostly related to arthropods activity (*Rusophycus, Cruziana, Arthrophycus, Didymauliponomos, Didymaulichnus, Thalassinoides*), mollusks or worm-like organisms (*Psammichnites, Rhizocorallium*).

In some beds, *Didymaulyponomos* is associated with morphologies indicative of microbially induced sedimentary structures (MISS; Fig. 4) such as the pseudoichnofossils *Protospiralichnus* (concentric microfault systems) and *Kinneyia* (Seilacher, 2007). The presence of MISS and *Didymaulyponomos* just below finer-grained facies are indicating that the development of an ecologic succession was conditioned to decrease in hydrodynamic energy. This scenario could attract small organisms to feed in the microbial mats, favoring predation by the *Didymaulyponomos* tracemakers. The absence of active filling in this trace fossil argues against the interpretation of a detritus-feeding habit, but the hypothesis of locomotion associated with predaceous habits is plausible. These features allow the inference that the search for food was the primary colonization control in tidal settings during the Silurian of

Paraná Basin. Thus, considering that the first land plants are from Lower Devonian strata (uppermost Furnas Formation), the microbial mats may have provided a source of nutrients for the pioneer ichnofauna.

The *Didymaulichnus* and *Psammichnites* suites are characterized by a local high density of horizontal trace fossils, with low diversity (*Didymaulichnus* suite with *Heimdallia, Didymauliponomos, Arthrophycus, Psammichnites,* and *Psammichnites* suite with *Rhizocorallium, Rosselia, Didymauliponomos,* and *Palaeophycus*). These suites are also restricted for Furnas strata (Lower Silurian) and characterize moderate energetic conditions. The low diversity, like to *Arenicolites-Skolithos* suite, can be explained by the low diversified post-extinction fauna (Late Ordovician Extinction) and stressed conditions in proximal high energetic environments.

The *Rosselia* suite occurs in moderate to high densities (Netto et al., 2014). This suite is indicating a tolerant behavior to relatively high energetic conditions. *Rosselia* frequently occurs in a stacked pattern, proving the constant repositioning within the substrate as a response to the increase in sedimentation rate. This suite is interpreted as the signature of transgressive shallow-water settings with high sedimentation rates (Nara, 2002; Miller and Aalto, 2008; Netto et al., 2014), and in the study area is indicating shoreface conditions.

Rhizocorallium-Palaeophycus suite is common in Ponta Grossa Formation and records a higher ichnodiversity than previous “energetic suites” (i.e., Skolithos and proximal Cruziana ichnofacies). The dominance of vertical forms (e.g., *Arenicolites, Skolithos, Diplocraterion, Cylindrichnus, Laevicyclus, Rosselia*), associated with trace fossils typically present in lower energetic settings (e.g., *Chondrites, Teichichnus, Heimdallia, Bergaueria, Planolites*) characterize the environment close to fair-weather or storm wave base. The presence of *Lingulichnus* with infaunal lingulids at the end of the structure and a retrusive *spreiten* in *Diplocraterion* indicate a high sedimentation rate. Thus, *Rhizocorallium-Palaeophycus* suite represents colonization of mostly suspension- and detritus-feeders during the prevalence of high energy conditions and seasonal high sedimentation rates.

6.4 Archetypal Cruziana Ichnofacies

This ichnofacies is composite of *Asterosoma-Teichichnus* and *Planolites-Chondrites* suites, representing colonization in moderate to low energetic conditions and in softground to soupground substrates.

The *Asterosoma-Teichichnus* suite is characterized by high ichnodiversity, ichnodisparity, and bioturbation intensity, representing exploitation of all tiers. These features are indicating stable paleoenvironmental conditions and low sedimentation rates, which allowed the full exploitation of substrate. This suite frequently is devoided of associated body fossils (Sedorko et al., 2018a), possibly as a result of intense intraestratal activity that would facilitate the destructive processes. Although *Asterosoma* and *Teichichnus* are the most common trace fossils, *Zoophycos* or *Chondrites* overlaps these structures in some beds, indicating vertical tier replacement. Sedorko et al. (2018c) demonstrated that this vertical replacement associated with the high frequency of erosive events under low accommodation space generate a dense *Zoophycos* ichnofabric.

In this sense, the trace fossils and the sedimentological features (indicating a mixture of suspension and traction) suggest stable and more well-oxygenated conditions in the substrate than those reflected by the other suites (e.g. Ekdale and Mason, 1988; Savrda and Bottjer, 1989a; Bromley, 1996; Buatois et al., 2002). The presence of *Asterosoma-Teichichnus* suite in correlated areas far apart for almost 45 km (Arapoti and Tibagi municipalities) indicate that these stable conditions acted in extensive areas, characterizing the transitional offshore to offshore zone.

The *Planolites-Chondrites* suite represents a variation of the archetypal Cruziana Ichnofacies, where trace fossils preservation was limited by the mixed-layer soupy-substrates. The homogenized aspect in the mudstones and siltstones, associated with preferential preservation of deeper-tier structures (*Planolites* and *Chondrites*) suggest that shallow-tier structures were obliterated. The faint preservation of *Rhizocorallium* and *Palaeophycus* indicates that middle tiers were also colonized, characterizing an archetypal expression of Cruziana Ichnofacies. Both *Asterosoma-Teichichnus* and *Planolites-Chondrites* suites indicate preferential colonization under low sedimentation rates, moderate to low energetic conditions, and oxygenated substrates in transitional offshore deposits.

6.5 Distal Cruziana ichnofacies

This ichnofacies is expressed by *Chondrites* suite, representing colonization of low energetic, dysoxic, softground substrates. Bromley and Ekdale (1984) pointed out that *Chondrites* can be an indicator of dysoxia to anoxia, generally in chemically reducing conditions. Although bioturbation is absent in oxygen-deficient substrates in modern seas (Wetzel, 1991), *Chondrites* is usually the prevalent trace fossil in nearly anoxic substrates (e.g., Bromley, 1996; Buatois et al., 2002). In this way, *Chondrites* and the recurrent accessories *Phycosiphon* and *Zoophycos* were considered oxygen-related ichnocoenosis (ORI). Savrda and Bottjer (1986; 1989a; b) postulated a scheme for analyzing ORIs, where the depth, size, and diversity of burrows decrease following the declining oxygen gradient. This suite can be expressed by local monospecific ichnofabrics (mainly with *Chondrites*, but also *Phycosiphon*, *Zoophycos* or locally

Helicodromites), with small diameter burrows (~1 mm), which are good proxies to infer anoxic conditions within the substrate (Bromley, 1996).

Besides *Chondrites* and *Phycosiphon, Zoophycos* also has been used as a proxy to anoxic conditions, and by analogy in the context of the section, distal environments. However, during Devonian, *Zoophycos* is reported from nearshore to offshore and is not well stated if the tracemaker would have supported dysoxic conditions (Miller, 1991; Gaillard and Racheboeuf, 2006; Seilacher, 2007). Considering the monospecific character and small diameter in mudstones beds from the study area, this ichnofabric possibly is indicating a decrease in oxygenation conditions following a paleobathymetrical deepening, which was enabling *Zoophycos* tracemaker to explore the substrate with no competition. In this sense, *Zoophycos* represents a tolerant behavior in offshore setting from Devonian of Paraná Basin.

Thus, deposit-feeder and chemosymbiont habits occur in this suite, in lower offshore setting, under dysoxic to anoxic conditions. These conditions allowed preservation of a rich invertebrate fossils assemblage in offshore settings (Bosetti et al., 2013, Horodyski et al., 2014, Sedorko et al., 2018a).

7. The absence of trace fossils: a taphonomic barrier

The absence of trace fossil in some beds is also relevant to taphonomical and paleoecological analyses. It was possible to infer three reasons to lacking bioturbation, considering the associated sedimentary features. The most common context of trace fossil absence (BS=0) is observed in sandstone layers of the Furnas Formation but also occurs in some sandstone facies of the Ponta Grossa Formation. In this case, two related agents acted as a taphonomic barrier to trace fossil preservation: high hydrodynamic energy and erosion of shallow tiers. The first parameter limited food supply into the substrate, enabling colonization only by suspension-feeders (Buatois and Mángano, 2011), which colonized shallow-tiers. Additionally, high hydrodynamic rates resulted in the erosion of shallow-tier structures, disabling preservation of those excavations.

The second scenario is related to structureless mudstones facies, occurring both in Ponta Grossa and Furnas formations. In those beds, the limiting factor for trace fossil preservation was the consistency of substrate. Associated beds bearing *Planolites-Chondrites* ichnofabric suggest the dominance of soupy substrate conditions, precluding preservation of the bioturbation due to the lack of sediment plasticity, resulting in structureless beds (Ekdale, 1985).

Finally, the third scenario of BS=0 is restricted to Ponta Grossa Formation and is related to oxygen decrease within the substrate. These beds occur interspersed with the so-called oxygen-relates ichnocoenosis, such as *Chondrites, Zoophycos*, and *Phycosiphon* (ORI; Savrda and Bottjer, 1986; 1987; 1991). In this case, dysoxic conditions limited the substrate colonization, configuring a relevant taphonomic barrier.

8. Ichnodiversity and ichnodisparity

Ichnodiversity is directly related to the number of ichnotaxa, and this concept has mainly been used as a proxy for environmental stress and stability, commonly quantified in ichnogenera diversity (Ekdale, 1985; Mángano and Buatois, 2004b; MacEachern et al., 2007). In general, ichnodiversity can be used as an indicator of richness, but not directly of the diversity of the original community (Buatois and Mángano, 2013). In this sense, Buatois and Mángano (2011, 2013) proposed the concept of ichnodisparity, which measures the morphologic plans variability (trace-fossil bauplans, *sensu* Bromley 1990, 1996).

Ichnodiversity and ichnodisparity were defined to each bioturbated bed in the studied section, and it resulted in 25 morphological plans (listed in Table 2), as defined in Buatois and Mángano (2013). The main difference between the ichnodiversity and ichnodisparity curves is related to intervals in which some morphologic plan was favored, as can be observed, for example, in the basal peak representing the best expression of archetypal Cruziana ichnocoenoses (favoring detritus-feeder habits).

In general, the rates between ichnodiversity and ichnodisparity throughout the section are almost the same, reflecting that the diversity in ichnogenera corresponds to the diversity in architectural plans. However, a pattern of decrease in those values is observed in transgressive trends, culminating in low values in maximum-flooding surfaces. Contrary, the regressive phases exhibit a general increase in ichnodiversity and ichnodisparity due to the prevalence of optimum conditions in onshore settings. This oscillation is expected in the stacking of systems tracts and variations in this pattern can be very informative in relation to environmental changes. For example, the peak just below the MFS of the Siluro-Devonian sequence (Fig. 5) is unusual in deepening settings, and probably is indicating the community climax during lower Devonian in Paraná Basin.

9. Paleobathymetric trend and events in Paraná Basin by trace fossils

The distribution of ichnologic suites throughout Paraná Supersequence was strongly influenced by paleoecological parameters in response to variations in the relative paleobathymetry. A general transgressive pattern is observed in the whole succession, from Furnas Formation strata dominated by Skolithos and proximal Cruziana ichnofacies to Ponta Grossa Formation strata exhibiting prevalence of archetypal and distal Cruziana Ichnofacies (Fig. 5).

Ichnostratigraphic data (*Cruziana acacensis, Rusophycus acacencis, Arthrophycus alleghaniensis,* and *A. brongniartii*) evidenced that deposition of Furnas Formation started during Early Silurian (Sedorko et al., 2017). At this time, the fauna began to colonize non-marine environments (Gray and Boucot, 1994). However, the diversity in those environments was very low, and the main colonization of non-marine facies occurred only near Silurian–Devonian boundary (Buatois et al., 1998). In this way and supported by typically marine traces (such as *Rusophycus, Cruziana, Arthrophycus, Rosselia*), the ichnologic content from Furnas Formation correspond to marine conditions in all intervals where trace fossils are preserved.

The dominant trace fossils in early Paleozoic tidal-influenced environments result of arthropods activity, principally trilobites (Durand, 1985; Mángano and Buatois, 2004a). In another hand, during the late Paleozoic, mollusks (mainly bivalves) started to be dominant in tidal environments (Rindsberg, 1994; Buatois and Mángano, 2011). In addition, tidal flats commonly presented microbial mat grounds during early Paleozoic times (Hagadorn and Belt, 2008).

In most Furnas Formation, there is a predominance of proximal Cruziana Ichnofacies, although Skolithos Ichnofacies also occur. This colonization scenario exhibits a significant change when *Rosselia* suite (proximal Cruziana Ichnofacies) is preserved, being the signature of the transgressive trend in the basin. This ichnofabric can be recognized in different outcrops (at least 100 km apart from each other, in Tibagi and Jaguariaíva), corroborating the relevance of this event in the basin scale. In the same way, it reflects a tolerance behavior to storm-dominated events (Netto et al., 2014). The mudstones that overlay Furnas Formation have dominance of distal

Cruziana Ichnofacies, with local archetypal Cruziana and Skolithos ichnocoenoses (Jaguariaíva Member). In some beds, trace fossils are absent, and the main limiting factor in this interval was oxygenation of the substrate, as observed in the main inundation (MFS-SD) of this interval (Fig. 5).

The sandstones that superimposed these facies bearing Skolithos Ichnofacies represent a change in sedimentation pattern (Tibagi Member), indicating the establishment of a regressive phase. The sequence boundary in this interval is marked by the Glossifungites Ichnofacies. Above these strata, the interval of São Domingos Member (Fig. 5) shows the dominance of distal Cruziana Ichnofacies, represented mainly by the *Planolites*-*Chondrites* suite. Soupgrouds are more common than in previous intervals, resulting in the absence of discernible trace fossils and even body fossils. In sandstones that overlay this interval, the Skolithos Ichnofacies and the archetypal Cruziana Ichnofacies are present, and beds with *Macaronichnus* suite represent the most proximal marine settings during the regressive phase. The Glossifungites Ichnofacies is also present in these sandstones (near 485 m; Fig. 5), indicating a sequence boundary.

Overlaying these sandstones, a 510 m-thick bed of the shale facies (Fig. 5) represents the main flooding event occurred in Paraná Basin during Devonian, which is correlated with the Kačák Event (Bosetti et al., 2011; Horodyski et al. 2014). In this interval, trace fossils are absent or are represented by sparse *Phycosiphon,* which corroborates dysoxic to anoxic conditions within the substrate. The upper strata are characterized by distal to archetypal expressions of the Cruziana Ichnofacies, attesting the establishment of well-oxygenated substrates.

In general, hydrodynamic energy and oxygenation rates controlled the ichnofauna distribution, mostly linked to the global sea-level curve. An exception is evidenced in the transgressive phase of the Siluro-Devonian sequence, that is contrary to the global regressive tendency (Fig. 6). Milani and Ramos (1998) pointed out that the tectonic stability reflected by Furnas deposition was followed by accelerated subsidence in foreland setting during the Pragian-Emsian (Juaguariaíva Member), induced by the Pre-cordillera Orogeny in the western Gondwanan margin.

Considering the Devonian events as summarized by House (2002), only two of them have expressions in the Paraná Basin. Sedorko et al. (2018b) suggested that the basal Zlíchov event is correlated with the maximum flooding observed in the basin during the Emsian. This event is globally associated with deepening evidence and faunal changes, especially for conodonts and as well as a gradual loss of the pelagic graptolites. In North America, the changes included a slow replacement of endemic brachiopod genera by Old World genera (Johnson, 1986). In the Paraná Basin, Emsian reduction in faunal diversity documented by Bosetti et al. (2012) within Ponta Grossa Formation suggests that the black shale at the MFS of the Siluro-Devonian sequence may be tied to the Zlíchov event.

A particularity is expressed by *Zoophycos* distribution in the Ponta Grossa Formation. The basal occurrence of *Zoophycos* in Paraná Basin is preserved in associated strata bearing primitive land plants (e.g., *Cooksonia*; Mussa et al., 1996, 2002). Considering that this is the basal occurrence of plants and *Zoophycos* in the basin, it seems to corroborate a control of *Zoophycos* by food supply in shelfal settings. However, in middle Devonian strata from Ponta Grossa Formation, where the land plants were very abundant and diversified (Matsumura et al., 2015), the *Zoophycos* occurrence declines, being virtually absent in upper strata (Sedorko et al., 2018c). Thus, this decline of *Zoophycos* in upper Eifelian strata might be related to a reduction in the primary paleoproductivity (e.g., Kotake, 2014). Bosetti et al. (2011) observed a reduction in acritarchs and chitinozoans abundance above the Eifelian beds, which can be related to changes in oceanic circulation caused by a restriction in the basin. In this sense, the *Zoophycos* decline (Fig. 6) probably is a response to a basin restriction associated to the Asunción Arch, what probably played a relevant role in the decline of Malvinokaffric fauna (Sedorko et al., 2018c).

The mudstones and shales in the upper part of the studied succession (MFS Devonian II sequence) represent the main flooding during Devonian in Paraná Basin and were correlated with the Kačák Event (Bosetti et al., 2011; Horodyski et al., 2014). The Kačák event was associated with moderate extinction rates and a period of global anoxia, as indicated by worldwide marine black shales. In Paraná Basin, this event is related to the Lilliput effect as diagnosed in groups as brachiopods, trilobites, and conulariids (Bosetti et al., 2011; Horodyski et al., 2014). The dominance of *Phycosiphon* and lilliputian macrofossils (Bosetti et al., 2011) is an indicator of low oxygenation rates, and a general absence of trace fossils due to anoxic conditions corroborated this hypothesis (Sedorko et al., 2018a). Thus, the final extinction of the Malvinokaffric Realm probably occurred as a response to changes in basin configuration and predominance of high relative sea-level during Middle Devonian.

10. Summary

The vertical distribution of trace fossils from Silurian-Devonian strata (Paraná Basin) indicate a dominance of tide-marine settings during Silurian, followed by high subsidence rates in the Pragian-Emsian interval, culminating with the higher diversity of the Malvinokaffric Realm and higher ichnodiversity in this succession. The main controlling parameters to trace fossil distribution were hydrodynamic energy and oxygenation rates, as a passive response to relative paleobathymetric changes. Facies and ichnofacies indicative of onshore settings predominate in Furnas Formation while offshore settings are more recurrent to Ponta Grossa strata. By the vertical distribution of trace fossil and macrofossils, the decline in biodiversity identified to Emsian-Eifelian of the Paraná Basin was probably a consequence of basin restriction and flooding anoxic events in the basin during Middle Devonian.

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Code	Lithology	Sedimentary structures	Trace fossil suite	Fig
S-m	Pebbly coarse-grained sandstones	Massive	*Arenicolites-Skolithos Palaeophycus*	3A
G-t	Clast-supported conglomerate	Trough cross-stratification	Absent	3B
G-m	Clast-supported conglomerates	Massive and locally imbricated	Absent	3C
S-h	Very fine- to coarse-grained sandstones	Horizontal lamination	*Palaeophycus*	3D
S-t	Very fine- to coarse-grained sandstones	Trough cross-stratification	*Arenicolites-Skolithos, Palaeophycus, Didymaulichnus*	3E
S-p	Very fine- to coarse-grained sandstones	Planar cross-stratification in tabular sets	*Arenicolites-Skolithos, Palaeophycus, Psammichnites*	3F
S-s	Very fine- to coarse-grained sandstones	Sigmoidal cross-stratification with reactivation surfaces and mud drapes	*Arenicolites-Skolithos, Palaeophycus, Didymaulichnus, Psammichnites*	3G
S-hc	Very fine- to fine-grained sandstones	Hummocky cross-stratification	Glossifungites, *Skolithos-Diplocraterion, Rosselia, Rhizocorallium-Palaeophycus*	3H
S-w	Very fine- to fine-grained sandstones	Wave ripples or faint massive	Glossifungites, *Macaronichus, Skolithos-Diplocraterion, Palaeophycus, Rhizocorallium-Palaeophycus*	3I
W	Interbedded siltstones/very	Wavy bedding	*Asterosoma-Teichichnus*	3J

	fine-grained sandstones			
F-p	Siltstones often interspersed with thin sand lenses	Parallel lamination and lenticular and locally lenticular sand bedding	*Rhizocorallium-Palaeophycus, Asterosoma-Teichichnus, Planolites-Chondrites, Chondrites*	3K
F-l	Claystones, interspersed with thin sand lenses	Massive, laminated	*Asterosoma-Teichichnus, Planolites-Chondrites, Chondrites*	3L

Table 1. Descriptions of the facies of the studied section.

Suite	Associated Facies	Trace Fossils	Architectural design	Ichnofacies
Glossifungites	Shcs (firmground)	*Skolithos*	Vertical simple burrows	Glossifungites
		Arenicolites	Vertical U- and Y-shaped burrows	
Macaronichnus	Sw, Sm	*Macaronichnus*	Activelly filled (massive) horizontal burrows	Skolithos
Arenicolites-Skolithos	Cmm, Sp, St, Ss, Shb	*Arenicolites*	Vertical U- and Y-shaped burrows	Skolithos
		Diplocraterion		
		Skolithos	Vertical simple burrows	
		Cylindrichnus	Vertical concentrically filled burrows	
		Palaeophycus	Passively filled horizontal burrows	
Skolithos-Diplocraterion	Shcs, Sw, Sm	*Skolithos*	Vertical simple burrows	Skolithos
		Lingulichnus		
		Schaubcylindrichnus		
		Diplocraterion	Vertical U- and Y-shaped burrows	
		Arenicolites		
		Cylindrichnus	Vertical concentrically filled burrows	
		Rosselia		
		Palaeophycus	Passively filled horizontal burrows	
		Thalassinoides	Mazes and boxworks	
Palaeophycus	Sp, St, Ss, and Shb, rarely in Sh, Cmm, and Sw	*Palaeophycus*	Passively filled horizontal burrows	Proximal Cruziana
		Thalassinoides	Mazes and boxworks	
		Psammichnites	Activelly filled (complex meniscate) horizontal burrows	
		Didymauliponomos	Bilobated trails and paired groves	
		Didymaulichnus		
		Cruziana		

		Rhizocorallium	Burrows with horizontal spreiten	
		Arthrophycus	Branched annulated burrows	
		Rusophycus	Bilaterally symmetrical short, shallow to deep scratched impressions	
Psammichnites	Sp, Ss	*Psammichnites*	Actively filled (complex meniscate) horizontal burrows	Proximal Cruziana
		Rhizocorallium	Burrows with horizontal spreiten	
		Rosselia	Vertical concentrically filled burrows	
		Didymauliponomos	Bilobated trails and paired groves	
		Palaeophycus	Passively filled horizontal burrows	
Didymaulichnus	St	*Didymaulichnus*	Bilobated trails and paired groves	Proximal Cruziana
		Didymauliponomos		
		Heimdallia	3D spreiten traces	
		Arthrophycus	Branched annulated burrows	
		Psammichnites	Actively filled (complex meniscate) horizontal burrows	
Rosselia	Shcs	*Rosselia*	Vertical concentrically filled burrows	Proximal Cruziana
		Cylindrichnus		
		Skolithos	Vertical simple burrows	
		Palaeophycus	Passively filled horizontal burrows	
Rhizocorallium - Palaeophycus	Shcs, Sw, Sm, Sts	*Rhizocorallium*	Burrows with horizontal spreiten	Proximal Cruziana
		Palaeophycus	Passively filled horizontal burrows	
		Arenicolites	Vertical U- and Y-shaped burrows	
		Diplocraterion		
		Cylindrichnus	Vertical concentrically filled burrows	
		Rosselia		
		Thalassinoides	Mazes and boxworks	
		Planolites	Actively filled (massive) horizontal burrows	
		Skolithos	Vertical simple burrows	
		Lingulichnus		
		Teichichnus	Burrows with vertical spreiten	
		Rusophycus	Bilaterally symmetrical short, shallow to deep scratched impressions	
		Chondrites	Dicotomically branched burrows	
		Heimdallia	3D spreiten traces	
		Laevicyclus	Plug-shaped burrows	
		Bergaueria		
		Bifungites	Dumbbell-shaped trace fossils	
Asterosoma-Teichichnus	Sts, W, Sm, M	*Asterosoma*	Horizontal, branched concentrically filled burrows	Archetypal Cruziana
		Halopoa		
		Teichichnus	Burrows with vertical spreiten	
		Chondrites	Dicotomically branched burrows	
		Zoophycos	Burrows with horizontal spreiten	
		Rhizocorallium		

		Planolites	Activelly filled (massive) horizontal burrows	
		Palaeophycus	Passively filled horizontal burrows	
		Taenidium	Activelly filled (simple meniscate) horizontal burrows	
		Arenicolites	Vertical U- and Y-shaped burrows	
		Diplocraterion		
		Helminthopsis	Simple horizontal trails	
		Cylindrichnus	Vertical concentrically filled burrows	
		Rosselia		
		Lockeia	Isolated and serial almond-shaped burrows	
		Psammichnites	Activelly filled (complex meniscate) horizontal burrows	
		Skolithos	Vertical simple burrows	
		Lingulichnus		
		Schaubcylindrichnus		
		Phycosiphon	Branching, spreiten burrows	
		Heimdallia	3D spreiten traces	
Planolites-Chondrites	M, Sts	*Planolites*	Activelly filled (massive) horizontal burrows	Archetypal Cruziana (mixed layer)
		Chondrites	Dicotomically branched burrows	
		Palaeophycus	Passively filled horizontal burrows	
		Rhizocorallium	Burrows with horizontal spreiten	
Chondrites	S, M, Sts	*Chondrites*	Dicotomically branched burrows	Distal Cruziana
		Zoophycos	Burrows with horizontal spreiten	
		Phycosiphon	Branching, spreiten burrows	
		Teichichnus	Burrows with vertical spreiten	
		Planolites	Activelly filled (massive) horizontal burrows	
		Helicodromites	Horizontal helicoidal burrows	

Table 2. Ichnologic suites, ichnodiversity and ichnodisparity from Paraná Supersequence.

Taphofacies	**Facies**	**Stratigraphic distribution**	**Skeleton type**	**Disarticulation**	**Fragmentation**	**Bedding-plane position**	**Common components**
T1	Sf	D-II	Bivalved	high	low	inclined to vertical	Brachiopods *Schuchertella, Australocoelia* and lingulides

T2	SS-hcs	SD	Bivalved	low	low	vertical to inclined	lingulides, *Australospirifer*
T3	SL-hcs	SD, D-I, D-II	Multielement	moderate to high	low	horizontal	trilobite *Metacryphaeus* and crinoid *Marettocrinus*
T4	SL-p	SD, D-I, D-II	Bivalved, Multielement, Univalved	moderate	low	horizontal	lingulides, trilobites, brachiopods *Orbiculoidea, Australocoelia,* mollusks bivalves and gastropods, tentaculitids
T5	SS	SD, D-II	Flexible tecae	-	moderate	chaotical	conulariids
T6	SH-L	SD, D-I, D-II	Bivalved, Multielement, Univalved	moderate	moderate	horizontal	lingulides, trilobites, brachiopods lingulides and *Orbiculoidea, Australocoelia,* tentaculitids, bivalve *Edmondia,* Asteroid Echinasteridae

Table 3. Characteristics of the recurrent taphofacies from Devonian of Paraná Basin (Modified from Horodyski et al., 2018).

CAPTIONS

Fig. 1. General context of the study area. (A) Location map in Paraná Basin and its supersequences; (B) Lithostratigraphic chart of the Silurian-Devonian interval of the Paraná Basin (simplified after Sedorko et al., 2018b); (C) Sequence framework proposed to the study area.

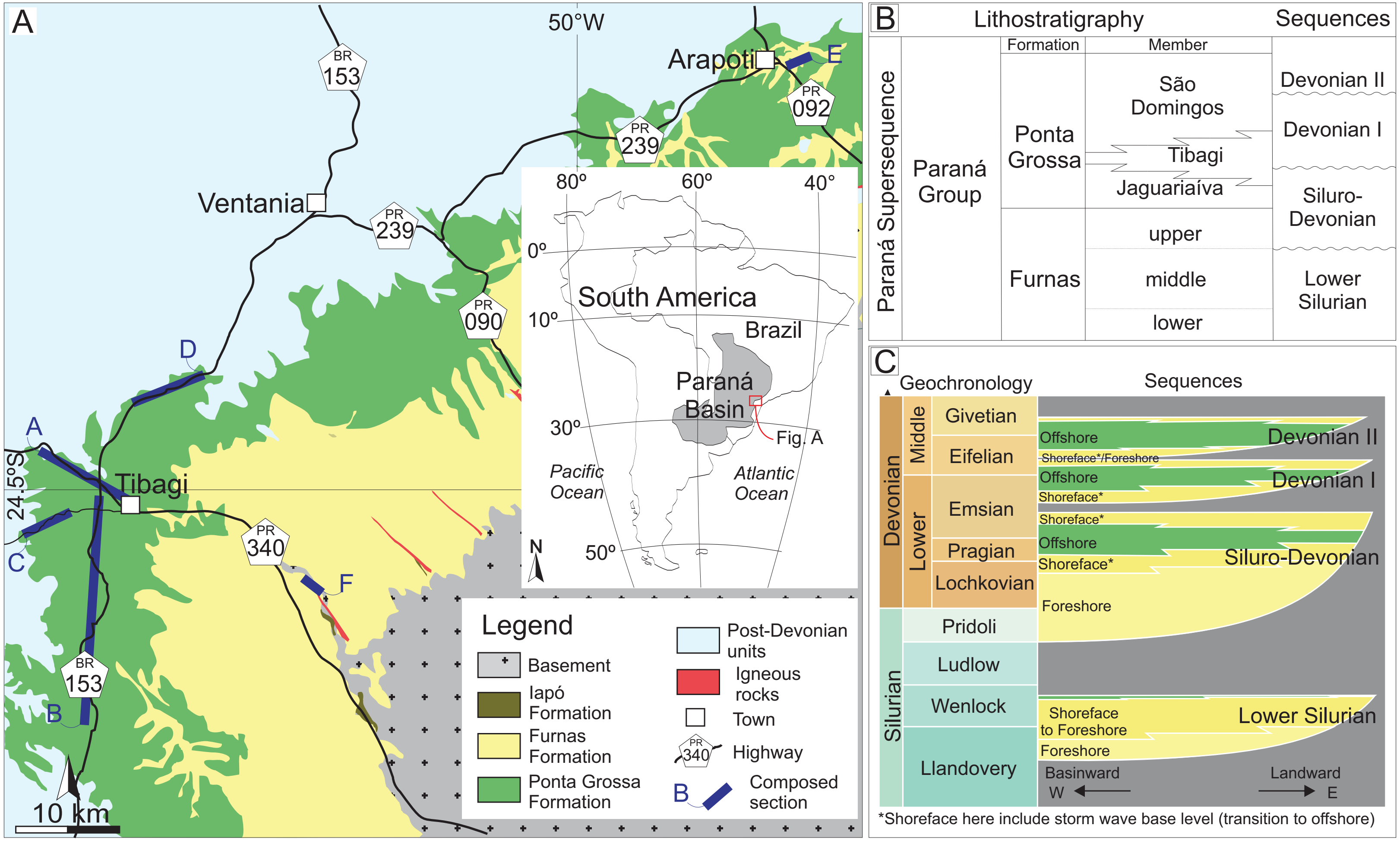
Fig. 2. Trace fossil suites from studied area. A-B. Glossifungites suite represented by *Skolithos* (*Sk*) and *Arenicolites* (*Ar*) in S-w facies of Ponta Grossa Formation; C. Monospecific *Macaronichnus* (*M*) suite in well-sorted fine-grained sandstone representing S-w facies in Ponta Grossa Formation; D-E. *Arenicolites-Skolithos* suite in S-t and S-m facies of Furnas Formation; F. *Skolithos-Diplocraterion* (*D*) suite in very fine-grained sandstones representing S-hc facies in Ponta Grossa Formation. G. *Palaeophycus* (*Pa*) suite with associated *Didymaulichnus* (*Di*) and *Diplocraterion* (*D*) in S-h facies of Furnas Formation; H. *Didymaulichnus suite* with associated *Heimdallia* (*He*) in Ss facies of Furnas Formation; I. *Psammichnites* (*Ps*) suite in S-t facies of Furnas Formation; J. *Rosselia* (*Ro*) suite in S-hc facies in transitional beds of Furnas to Ponta Grossa formations; K. *Rhizocorallium-Palaeophycus* (*Rh*) suite in W facies of Ponta Grossa Formation; L. High bioturbated *Asterosoma-Teichichnus* (*As* and *Te*) suite with *Chondrites* (**Ch**) as accessory in F-p facies of the Ponta Grossa Formation; M. High bioturbated *Planolites-Chondrites* suite evidencing the homogenized aspect in the F-l facies of the Ponta Grossa Formation; N. *Zoophycos* (*Zo*) as a component of *Asterosoma-Teichichnus* suite in W facies. and O. *Phycosiphon* (*Ph*) as a component of the *Chondrites* suite in F-l facies of Ponta Grossa Formation.

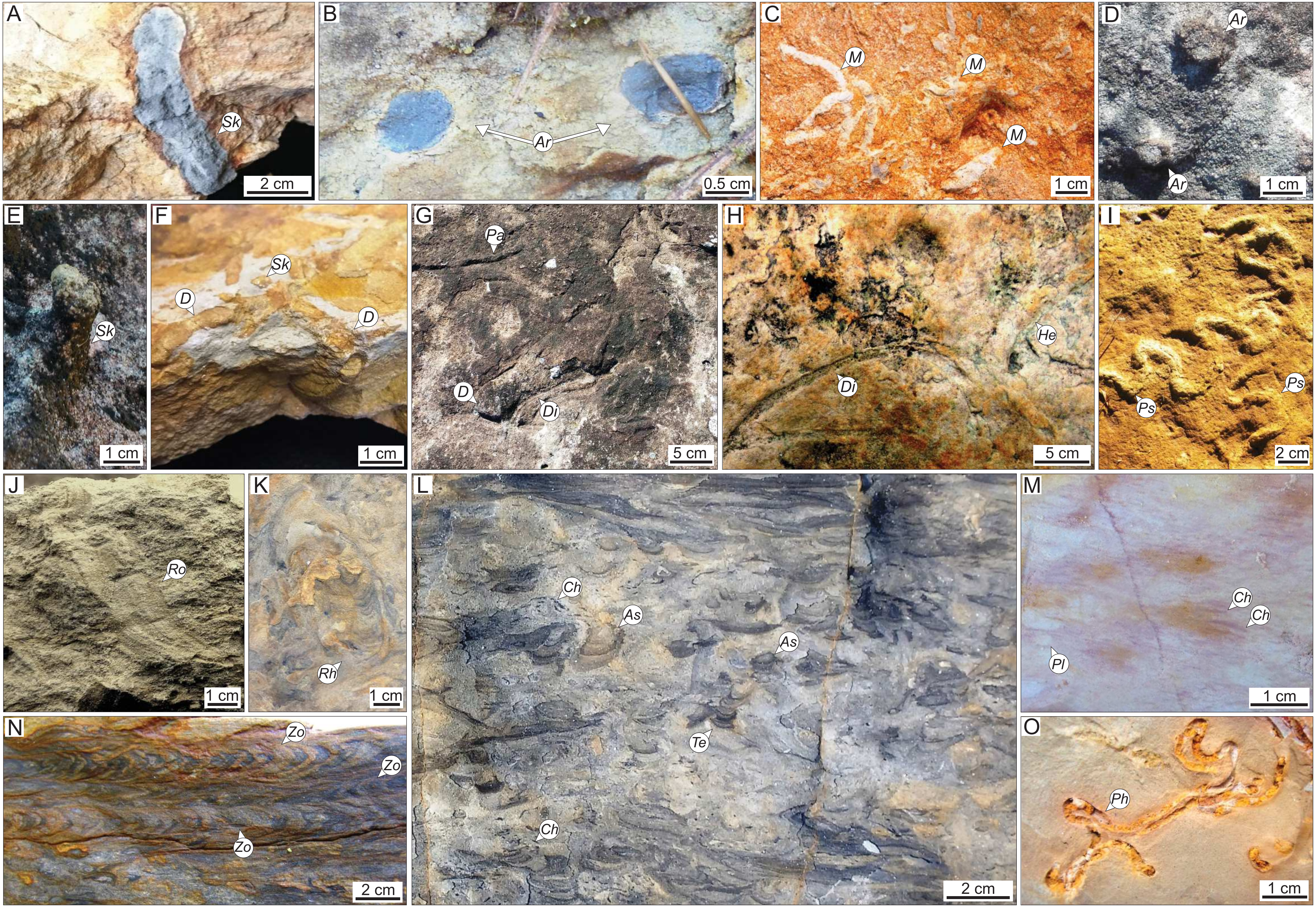
Fig. 3. Facies from studied succession. A. Massive pebbly coarse-grained sandstones (S-m facies); B. Trough cross-stratified clast-supported conglomerates (G-t facies); C. Massive and locally imbricated clast-supported conglomerates (G-m facies); D. Horizontal laminated very fine- to coarse-grained sandstones (S-h facies); E. Trough cross-stratified very fine- to coarse-grained sandstones (S-t facies); F. Planar cross-stratified very fine- to coarse-grained sandstones (S-p facies); G. Very fine- to coarse-grained sandstones with sigmoidal cross-stratification showing reactivation surfaces and mud drapes (S-s facies); H. Hummocky cross-stratified very fine- to fine-grained sandstones (S-hc facies); I. Wave rippled very fine- to fine-grained sandstones (S-w facies); J. Wavy bedding, interbedded siltstones/very fine-grained sandstones (W facies); K. Parallel laminated siltstones often interspersed with thin sand lenses (F-p facies); and L.Laminated claystones, interspersed with thin sand lenses (F-l facies).

Fig. 4. Biomat structures in association with *Didymauliponomos* ichnofabric in S-t and S-s facies from Furnas Formation. A. *Kinneyia* (*Ki*) structure and *Protospiralichnus* (Pr). B. Wrinkle structures recovering *Didymauliponomos* ichnofabric. C, D. Wrinkle structures and *Kinneyia* (*Ki*) structures in beds associated with *Didymauliponomos*.

Fig. 5. Composite section of Paraná Supersequence grouping data of ichnofacies, taphofacies, ichnodiversity, ichnodisparity, bioturbation scale, and total organic content. It is also presented the inferred paleobathymetric curve (blue line), oscillation in the substrate consistency as well the anoxic intervals. Note the decreasing tendency in ichnodiversity/ichnodisparity associated to maximum flooding surfaces (red arrow) and the increase in regressive patterns (green arrow).

Fig. 6. Comparison of the Global sea-level curve with the inferred paleobathymetric curve to Paraná Basin and the main bio-events (events recognized in Paraná Basin are in bold). Note that during the Pragian-Emsian interval the global regressive pattern has no correspondence in the Paraná Basin due to high subsidence rates.


A
50°W
BR 153
Arapoti
E
PR 092
PR 239
Ventania
PR 239
PR 090
D
A
24.5°S
Tibagi
C
PR 340
F
BR 153
B
10 km
80°
60°
40°
0°
10°
South America
Brazil
Paraná Basin
30°
Fig. A
Pacific Ocean
Atlantic Ocean
N
50°
Legend
Basement
Iapó Formation
Furnas Formation
Ponta Grossa Formation
Post-Devonian units
Igneous rocks
Town
PR 340
Highway
B
Composed section
B
Lithostratigraphy
Sequences
Formation
Member
Paraná Supersequence
Paraná Group
Ponta Grossa
São Domingos
Tibagi
Jaguariaíva
Furnas
upper
middle
lower
Devonian II
Devonian I
Siluro-Devonian
Lower Silurian
C
Geochronology
Sequences
Devonian
Middle
Lower
Givetian
Eifelian
Emsian
Pragian
Lochkovian
Silurian
Pridoli
Ludlow
Wenlock
Llandovery
Offshore
Devonian II
Shoreface*/Foreshore
Offshore
Devonian I
Shoreface*
Shoreface*
Offshore
Siluro-Devonian
Shoreface*
Foreshore
Shoreface to Foreshore
Lower Silurian
Foreshore
Basinward
W
Landward
E
*Shoreface here include storm wave base level (transition to offshore)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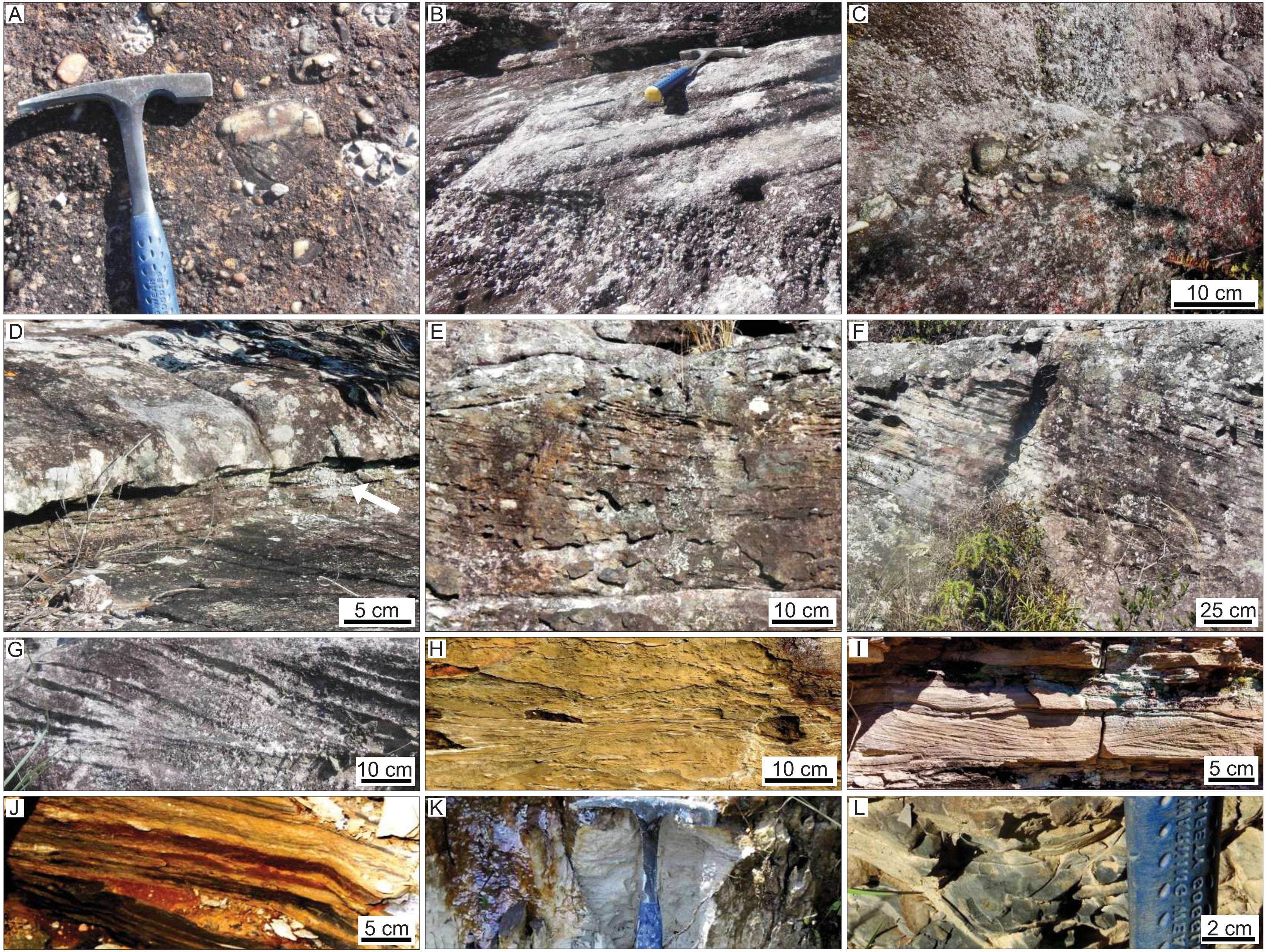
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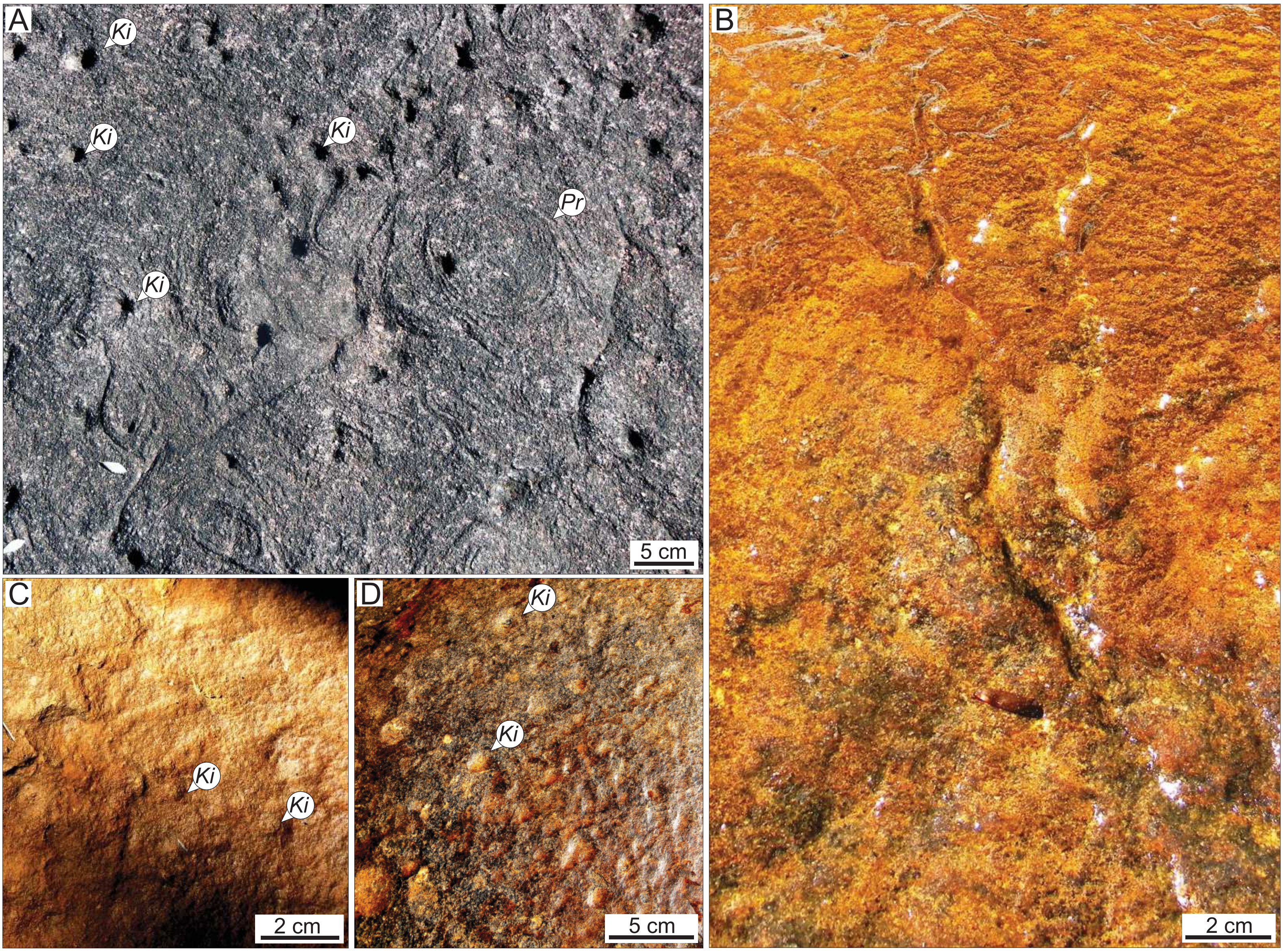
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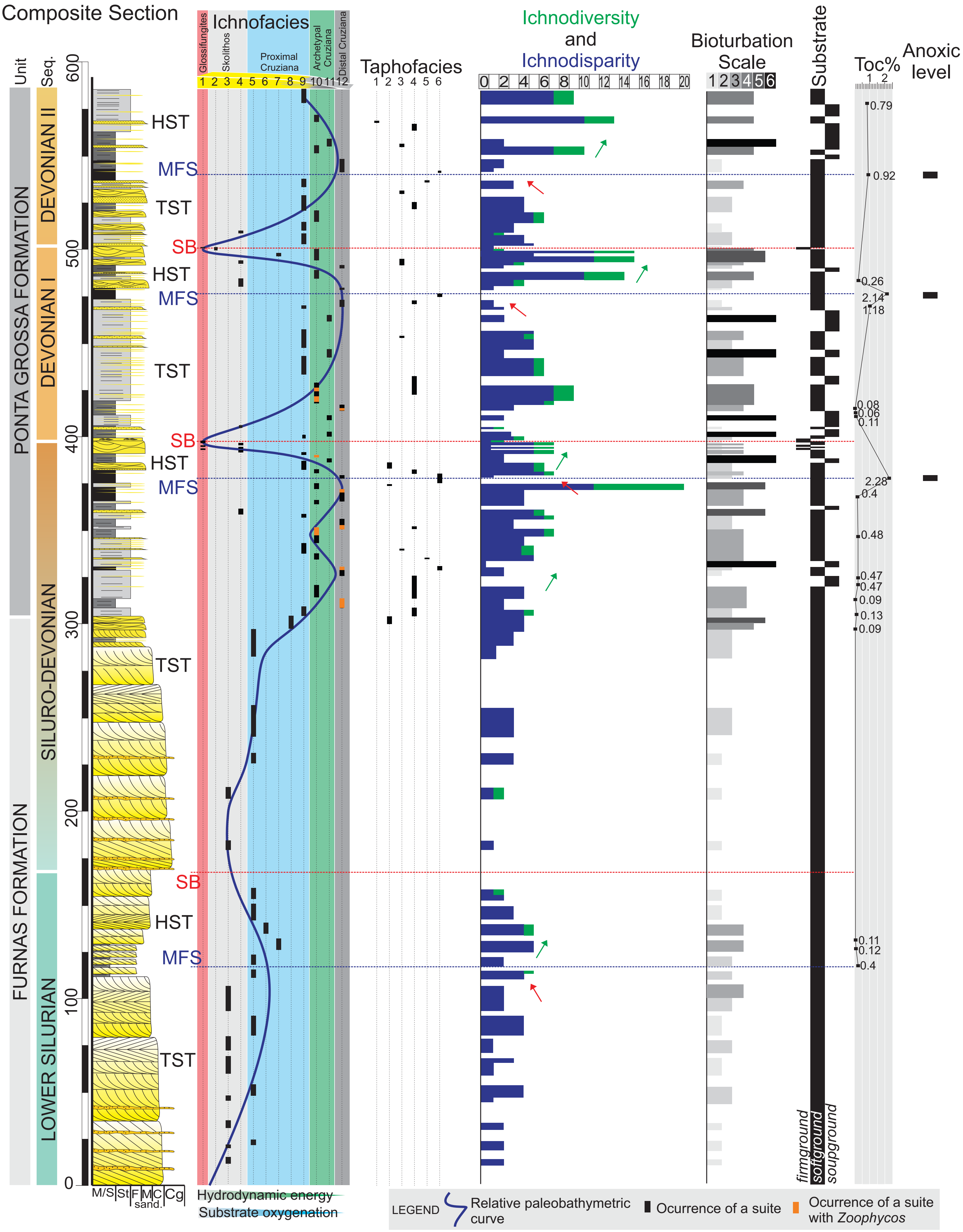
Composite Section
Unit
Seq.
PONTA GROSSA FORMATION
FURNAS FORMATION
DEVONIAN II
DEVONIAN I
SILURO-DEVONIAN
LOWER SILURIAN
600
500
400
300
200
100
0
HST
MFS
TST
SB
HST
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SB
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MFS
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SB
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MFS
TST
M/S St F M C Cg
sand.
Ichnofacies
Glossifungites
Skolithos
Proximal Cruziana
Archetypal Cruziana
Distal Cruziana
1 2 3 4 5 6 7 8 9 10 11 12
Hydrodynamic energy
Substrate oxygenation
Taphofacies
1 2 3 4 5 6
Ichnodiversity
and
Ichnodisparity
0 2 4 6 8 10 12 14 16 18 20
Bioturbation Scale
1 2 3 4 5 6
Substrate
firmground
softground
soupground
Toc%
1 2
Anoxic level
0.79
0.92
0.26
2.14
1.18
0.08
0.06
0.11
2.28
0.4
0.48
0.47
0.47
0.09
0.13
0.09
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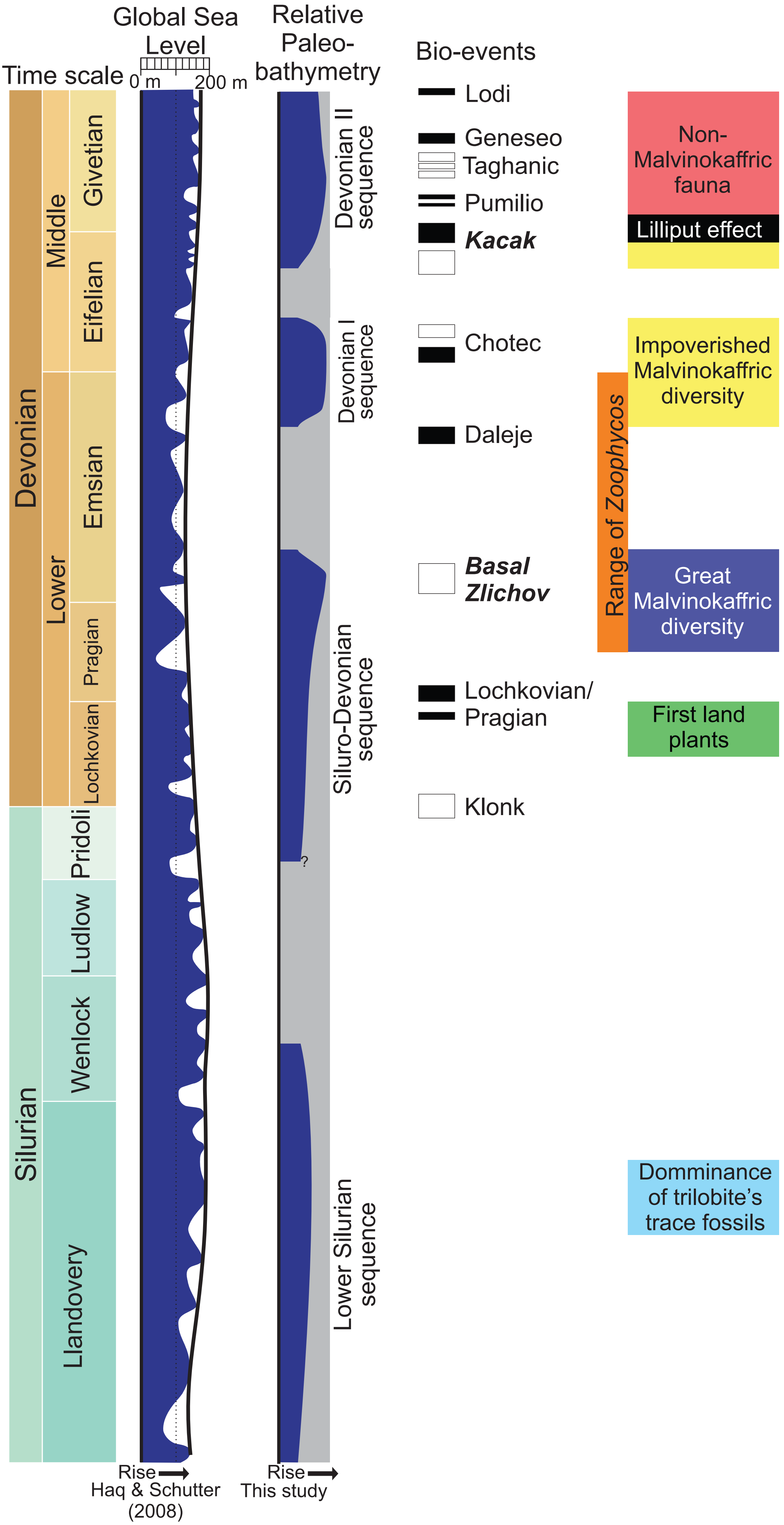
0.12
0.4
LEGEND
Relative paleobathymetric curve
Ocurrence of a suite
Ocurrence of a suite with *Zoophycos*


Time scale
Global Sea Level
0 m
200 m
Relative Paleo-bathymetry
Bio-events
Devonian
Middle
Lower
Givetian
Eifelian
Emsian
Pragian
Lochkovian
Silurian
Pridoli
Ludlow
Wenlock
Llandovery
Devonian II sequence
Devonian I sequence
Siluro-Devonian sequence
?
Lower Silurian sequence
Lodi
Geneseo
Taghanic
Pumilio
Kacak
Chotec
Daleje
Basal Zlichov
Lochkovian/ Pragian
Klonk
Non-Malvinokaffric fauna
Lilliput effect
Impoverished Malvinokaffric diversity
Range of Zoophycos
Great Malvinokaffric diversity
First land plants
Domminance of trilobite's trace fossils
Rise
Haq & Schutter (2008)
Rise
This study

HIGHLIGHTS

Trace fossils analysis allowed paleoecologic interpretations regarding oxygenation and paleobathymetric curves

Paleobathymetryc trends suggest high subsidence rates during Pragian-Emsian in Paraná Basin

The decline both of Malvinokaffric fauna and *Zoophycos* seems to be related to a basin restriction

Global events influenced the marine biota in the southern Gondwana

CAPÍTULO 8

***Lingulichnus* and *in situ* lingulides assemblage from Devonian event beds (Paraná Basin)**

Manuscrito submetido ao periódico “Palaios” que teve objetivo de investigar a distribuição paleoambiental e estratigráfica de *Lingulichnus* e lingulídeos *in situ* usando-os como biomarcadores de ciclos de alta taxa de sedimentação em contextos transgressivos.

To Palaios

LINGULICHNUS AND *IN SITU* LINGULIDES ASSEMBLAGE FROM DEVONIAN EVENT BEDS (PARANÁ BASIN)

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RRH: LINGULICHNUS AND LINGULIDES

LRH: R.S. HORODYSKI ET AL.

Abstract: Infaunal lingulides are common in Lower to Middle Devonian beds from Paraná Basin (Brazil) and *Lingulichnus* associated with *in situ* lingulides are restricted to offshore, transitional offshore to lower shoreface settings. This study aims to analyze the *Lingulichnus* and *in situ* lingulides in event beds and to demonstrate its implication to stratigraphy. Four taphonomic modes were identified within beds containing lingulides and *Lingulichnus* and include: (i) autochthonous - *in situ*, isolated lingulides normally associated with *Lingulichnus verticalis* or *L. inclinatus*; (ii) allochthonous - lingulides with reworking evidences (e.g. disarticulated or fragmented shells); autochthonous sub-primary position - *in situ* lingulides associated to *Lingulichnus hamatus*; (iv) temporary sub-primary position - *in situ* lingulides, isolated or associated to *Lingulichnus hamatus* or *L. verticalis*. Except the former, these taphonomic modes present high paleoecological resolution, and therefore, paleobiological implications can be interpreted. Isolated *in situ* lingulides or associated with *Lingulichnus* can be a good indicator of high

sedimentation rates, characterizing bases of fining-upward cycles, and, therefore, it can be useful to stratigraphic correlations.

Keywords: taphonomy, ichnology, sequence stratigraphy, trace fossil, *Lingulichnus*.

INTRODUCTION

The Devonian succession of the Paraná Basin contains the most complete fossil record of the so-called Malvinokaffric Realm in Gondwana (*sensu* Boucot 1971; Melo 1988), represented by endemic, cold water marine faunas composed mostly of brachiopods and trilobites. The organisms included in the Malvinokaffric Realm colonized high paleolatitude seas in Southern Hemisphere during the Early Devonian (Boucot 1971; Melo 1988) and in Paraná Basin (Brazil) lingulides are a common component (Zabini et al. 2010). Infaunal lingulides had been able to colonize different marine and marginal-marine environments, supporting adverse salinity, oxygenation, and energetic conditions since the Early Cambrian (Paine 1963; Emig et al. 1978; Pollard 1981; Hammond 1983; Pickerill et al. 1984; Emig 1986; Kammer et al. 1986; Wignall and Hallam 1992; Schubert and Bottjer 1995). In this way, lingulides were suggested as a disaster taxon (associated with mass extinctions), because they could live under stressed environmental conditions and colonize different environments (Fischer and Arthur 1977; Schubert and Bottjer 1995; Rodland and Bottjer 2001). In other hand, data from Early Triassic marine successions from western Canadian evidenced that lingulides occupied the same environmental settings before and after the Permian-Triassic extinction, thus, in that case, lingulides were interpreted as ecological opportunists rather post extinction disaster taxa (Zonneveld et al. 2007).

The trace fossil *Lingulichnus* is one of the few cases that can be closely associated to a tracemaker. The burrow morphology and construction indicate similarities with life style of lingulide brachiopods, and in some cases, the producer is preserved in the top of the burrow (Hakes, 1976; Szmuc et al., 1976; Zonneveld and Pemberton, 2003; Zonneveld et al., 2007), corroborating this interpretation.

In Devonian event beds from the Paraná Basin, lingulides are preserved in situ predominantly in sedimentary facies that suggest shelfal deposits, being a common component of shoreface to foreshore zones (Zabini et al. 2010, 2012; Zabini and Boseti 2011; Bosetti et al. 2011; Horodyski et al. 2014, Sedorko et al. 2018a). If *in situ* conditions are taphonomically recognized, then the recurrences of the biofacies assemblage (*sensu* Brett et al. 2007) have a strong significance for Stratigraphy and Taphonomy. Considering the widespread occurrence of lingulides, this study aims (i) to test the preferential environment for lingulides in the Paraná Basin during the Devonian, and (ii) to associate *Lingulichnus* occurrences with the systems tracts stacking.

MATERIAL AND METHODS

The studied fossil material was collected in four outcrops located in the Tibagi and Ponta Grossa regions (Paraná State, Brazil), and are housed in the paleontological collection of the Stratigraphy and Paleontology Laboratory at Ponta Grossa University (Paraná State) under the numbers MPI-11141, MPI-11142, MPI-11143, MPI-11144, MPI-11145. These sections crop out between Tibagi and Telêmaco Borba cities, in the PR 340 (outcrop 5) km 279 and (outcrop 3) km 271 (24°28'31.10"S, 50°30'56.72"O), between Tibagi and Ventania cities in the BR 153 (outcrop 4) km 208 and (outcrop 1) km 200,5 (24°29'1.91"S, 50°26'23.08"O) (Fig. 1A), and also Ponta Grossa city at (outocrop 2) Fazenda Rivadávia (25°17’35.92”S, 50°01’28.91”O).

The body fossils were collected following the taphonomic protocol of Simões and Ghilardi (2000) which provides that the paleoecological analysis stratigraphic position must be precise enough (bed-to-bed, centimeter-to-centimeter) to generate taphonomic signatures showed by each individual fossil from the same bedding plane. The taphofacies analysis was made using Speyer and Brett (1986, 1988) criteria.

Fossil concentration and sedimentological features classifications followed methods of Kidwell et al. (1986) and Kidwell and Holland (1991). For the bioturbation measurement we used the bioturbation scale (BS) of Reineck (1963), which ranging from 0 (with no bioturbation present) to 6 (homogenized sediment or no apparent sediment structure). *Lingulichnus* ichnotaxonomy identification was based on Hakes (1976) and Zonneveld and Pemberton (2003).

The facies analysis was based on previous studies (Zabini et al. 2010; Horodyski et al. 2014; Sedorko et al. 2018b). This study focuses only on the fossil-bearing and trace fossil-bearing facies and beds.

GEOLOGICAL SETTING

The Paraná Basin is a large intracratonic basin (~1,500,000 km²) disposed with a NE-SW preferential orientation on the southern area of South American platform (Fig. 1A). In the Brazilian portion, the sedimentary fill of the basin was influenced by eustatic-tectonic cycles linked to the evolution of the Western Gondwana during Paleozoic and Mesozoic times (Milani and Ramos 1998; Milani et al. 2007). These eustatic-tectonic cycles generated a stratigraphic record composed of six second-order depositional sequences, from Late Ordovician to Late Cretaceous (Milani and Ramos 1998; Milani et al. 2007). The stratigraphic interval studied herein includes the Ponta Grossa Formation (*sensu* Lange and Petri 1967; Fig. 1B) and is part of the Paraná

Group, ranging from the Lower Silurian to Middle Devonian. In Brazil, the Paraná Basin is represented by two sedimentary depocenters, the northern Alto Garças Sub-basin and the southern Apucarana Sub-basin, which are separated by the Três Lagoas and Campo Grande Archs (Northfleet et al. 1969; Ramos 1970; Assine 2001; Bergamaschi and Pereira 2001; Grahn et al. 2010, 2013).

The study area is in the Apucarana Sub-Basin and consists of fine-grained sandstone and siltstone, with subordinated shale, which have been interpreted to have been deposited in shelfal zone by storm waves and currents (Bergamaschi 1999; Simões et al. 2000; Rodrigues et al. 2003). A marine fossil assemblage representative of the Malvinokaffric Realm occurs throughout the succession, with lingulides being the most abundant body fossil in the studied outcrops (Zabini 2010). These outcrops correspond to the Siluro-Devonian, Devonian I, and Devonian II sequences of Sedorko et al. (2018b) (Fig. 2) and were deposited probably from Pridolian to Givetian (Grahn 1992; Grahn et al. 2000; Mendlowicz Mauller et al. 2009; Grahn et al. 2013; Sedorko et al., 2017).

The basal limit of the Sequence Siluro-Devonian (SS-D) is marked by a transgressive surface evidenced by lags observed at the base of the upper unit of Furnas Formation (Sedorko et al. 2018b). The basal deposits of SS-D characterize the transgressive systems tract (TST) and are composed primarily of fine-grained sandstone with hummocky cross-stratification (HCS) and heterolithic beds with wavy and lenticular structures, indicating the prevalence of storm and fair-weather wave action influencing deposition. Bioturbation is common, being represented by a fully marine Cruziana Ichnofacies suite in the heterolithic beds and a crowded *Rosselia* ichnofabric (CRI) in the HCS sandstones, with moderate to high degree of bioturbation (BS= 4-6) (Netto et al. 2014). *Lingulichnus* occurs in equivalent storm beds in the study area but in a monospecific preservation. These deposits are capped by siltstones and mudstones, and black shale that make up the Jaguariaíva Member and are characterizing the finning-upward cycle of the TST that represents the offshore settings. The highstand systems tract (HST) of SS-D is not expressive, being represented in outcrop as a slight coarsening-upward cycle with a diversified ichnofauna that characterizes a fully marine Cruziana Ichnofacies, mostly represented by *Asterosoma, Teichichnus, Zoophycos, Planolites, Thalassinoides, Palaeophycus, Chondrites, Phycosiphon, Rosselia, Schaubcylindrichnus,* and *Cylindrichnus* (Sedorko et al. 2018b), which corresponds, in part, to the Tibagi Member of Ponta Grossa Formation. The HST succession is capped by a sequence boundary, in which *Lingulichnus* and *in situ* lingulides occur. These beds are locally covered by mudstone, siltstone and shale beds or is marked by Glossifungites Ichnofacies (Sedorko et al. 2018b). Sequence boundaries can be marked by substrate-controlled trace fossils, which indicate erosive processes in the substrate (e.g. MacEarchern et al. 1992), which is the case of Glossifungites in Ponta Grossa strata (Sedorko et al. 2018b).

The basal beds bearing *Lingulichnus* and *in situ* lingulides in the SD I also represent basal stage of a TST (Sedorko et al. 2018b). These deposits are characterized by sandstone packages with abrupt or erosive contact, that overlain the HCS sandstone beds of the top of SS-D where *Lingulichnus* occurs. Siltstone, mudstone, and shale occur at the top of the basal sandstone and represent the fine-grained deposits of the transgressive phase. The HST deposits of SD I exhibit a diversified ichnofauna that characterizes a Cruziana Ichnofacies, mostly represented by *Asterosoma, Teichichnus, Schaubcylindrichnus, Planolites, Thalassinoides, Palaeophycus, Chondrites, Phycosiphon, Rosselia* and *Cylindrichnus* (Sedorko et al. 2018b).

Finally, the basal limit of Sequence Devonian II (SD II) is characterized by shoreface sandstone with an erosional contact in its basal portion. In the studied section, firmground suites of Glossifungites Ichnofacies overprint pre-omission softground ichnofabrics (*Macaronichnus* ichnofabric, Sedorko et al. 2018b). Thus, *Skolithos* and *Arenicolites* sharply walled and filled with muddy content (i.e. Glossifungites Ichnofacies) are marking the sequence boundary in fine to medium-grained sandstone with very low-angle cross-laminae. This surface bearing Glossifungites Ichnofacies also correspond to a transgressive surface of erosion, being overlaid by fine-grained massive sandstone beds or sandstone beds with HCS and wave ripples containing *in situ* lingulides, *Lingulichnus hamatus* and *L. verticalis*, which marks the establishment of the TST. The TST is not expressive in the SD II, being covered by black shale deposits that characterize the maximum flooding surface. A global anoxic event was identified in this level (Kačák Event, for details see Horodyski et al. 2014).

THE TAPHONOMIC *STATUS QUO* OF THE DEVONIAN LINGULID FAUNA OF THE PARANÁ BASIN

According to Zabini et al. (2010, 2011, 2012) and Zabini and Bosetti (2011), two lingulid taphofacies, Tf1 and Tf2, can be recognized in the Devonian beds of the Paraná Basin. The Tf1 is characterized by disarticulated shells, shell fragments and lingulid debris disposed parallel to the bedding plane and showing chaotic, string or rosette types of geometry in the same pavement (Zabini et al., 2010, 2011, 2012; Zabini and Bosetti, 2011). Such type of assemblage is generally recorded in medium- to fine-grained sandstone, siltstone, and mudstone beds deposited in shallow marine environments by normal and storm waves or currents. These sedimentary processes promote exhumation and reworking of the buried shells, normally between the middle shoreface and the offshore zones. The Tf2 is represented by articulated lingulides with complete valves disposed vertically or obliquely to the bedding plane and preserved in sandstone and shale beds deposited in proximal shoreface or offshore-transition zones (Zabini et al., 2010, 2011, 2012; Zabini and Bosetti, 2011).

The *in situ* lingulides preserved in association with *Lingulichnus* in Devonian beds exposed in Tibagi region (Paraná State) were also discussed by Horodyski (2014), who included them in his Taphofacies 3 (from a set of 7 taphofacies established by the whole succession of Devonian beds), which is equivalent to the Tf2 of Zabini (2010). Abrasion, corrosion, and bioerosion were not detected in any lingulid shell in this taphofacies, indicating rapid skeleton burial. The presence of HCS in the fine-grained sandstone beds provides evidence of episodic storm surges, which resulted in rapid sandy accumulation burying completely the infauna.

RESULTS

Taphonomy and Ichnology of the lingulid-dominated taphofacies

In the studied sections, fine-to medium-grained sandstone with HCS (SS-hcs; Fig. 3A) and fine-grained sandstone with wave ripples (SS-f; Fig. 3B) are the predominant sedimentary facies (Table 1). SS-hcs facies represents deposition in lower shoreface settings below the storm wave base (SWB) whereas SS-f facies is indicative of lower shoreface deposits above fair-weather wave base (FWWB). Black shale (S facies, Fig. 3C) represent deposition below storm wave base. These deposits characterize the very base of the TSTs of the SD I and SD II and the base of the finning-upward cycles of SS-D (Sedorko et al., 2018b; Fig. 3C).

The fossil assemblage preserved in SS-hcs facies is composed of complete, articulated lingulid bioclasts vertically or obliquely oriented in relation to the bedding plane, plant debris and vertically-oriented trace fossils. The bioturbation intensity is low (BS= 2-3) and biogenic activity is represented by a composite ichnofabric formed by *Diplocraterion* isp. (Fig. 3I), *Lingulichnus hamatus* (Fig. 3D)*, Cylindrichnus* isp.*,* and funnel-shaped *Rosselia* (Fig. 3J). Lingulid shells are preserved in a dispersed packing (floating in a matrix), and there is no evidence of fragmentation, abrasion, incrustation, or bioerosion. The lingulides are normally small (≤1cm) and the characteristics of the fossil assemblage represent *in situ* preservation, configuring an autochthonous pattern (derived from local community; *sensu* Kidwell et al., 1986)

The fossil assemblage preserved in SS-f facies is composed of complete, articulated, and disarticulated lingulid bioclasts with no preferential orientation in relation to the bedding plane (vertical, oblique, and horizontal lingulides can be observed in the same bed). Disarticulated bioclasts occur exclusively on the bedding plane, in horizontal disposition, and can appear isolated or grouped forming rosette-polymodal geometries. Vertically-oriented trace fossils (mainly *Skolithos* isp. and *Arenicolites* isp.) and plant fragments occur associated with the lingulides in SS-f facies. Bioturbation Scale is low to moderate (BS= 2-3) and the biogenic activity primarily composed of *Lingulichnus verticalis* (Fig. 3E, F). Like SS-hcs facies, the bioclasts are dispersed in the matrix, with no evidence of fragmentation, abrasion, incrustation, or bioerosion. The lingulides show the same average size that those preserved in SS-hcs facies (≤1cm).

The fossil assemblage preserved in S facies is composed of complete, articulated lingulid bioclasts parallel, vertically, or obliquely oriented in relation to the bedding plane (Fig. 3C, G). Like in the other occurrences, the bioclasts are dispersed in the matrix, with no evidence of fragmentation, abrasion, incrustation, or bioerosion. The body fossils show the same average size that in the other occurrences (≤1cm).

Bioturbation Scale is low to moderate (BS= 2-3) and the *Lingulichnus hamatus* and *Lingulichnus verticalis* (Fig. 3C, H) are the dominant traces present within S facies.

INTERPRETATION AND DISCUSSION

Taphonomic and paleobiological implications

Taphonomic and ichnologic characteristics observed in SS-f lithofacies suggest that colonization and deposition occurred within lower shoreface settings (Fig. 4). In this way, *Lingulichnus* likely being preserved when sedimentation rate is high and as hydrodynamic energy dissipates (to not exhume the buried traces). Such conditions commonly occur at the base of finning-upward cycles, which are found at the base of the transgressive systems tract (Fig. 2).

The preservation of *in situ* lingulides in SS-hcs facies reflects rapid burial caused by increase in the sedimentation rate during storm surges in lower shoreface. Additionally, re-excavation behavior expressed by *Lingulichnus hamatus* associated with lingulides preserved in their burrows, and the occurrence of funnel-shaped (top eroded) *Rosselia,* suggest intense turbulence (re-burrowing structure) and bottom erosion caused by stormy waves (Nara 1995, 1997; Zonneveld and Greene 2009; Netto et al. 2014).

The zone between lower shoreface and offshore transition commonly presents high ichnodiversity and abundance of trace fossils (MacEachern and Pemberton 1992; Buatois et al. 2002, 2003; Carmona et al. 2007). However, the *Lingulichnus* occurrences in the Devonian event beds in Paraná Basin are restricted to low bioturbated intervals with generally monospecific trace fossil assemblages. The dominance of a suspension-feeding assemblage indicates waters rich in suspended nutrients, which is observed in proximal shelf settings.

Transported lingulides are preserved associated with *Lingulichnus hamatus* in storm-influenced offshore transition zone (S-facies), being characterized by well-preserved bioclasts (Figs. 3C, 4B). Sparsely occurrences of *Lingulichnus verticalis* in S-facies deposits indicate that the lingulides could survive at least for a short period in offshore zones. Zonneveld and Greene (2009) demonstrated that part of the lingulides from the Triassic of Western Canada had ability to survive after exhumation and transport and re-inhabit the storm-modified substrate. The concept of "doomed pionner" was proposed to infer a causal relation and attribute the importation of thalassinidean crustacea to the influx events of allochthonous sediments (Föllmi & Grimm, 1990). This may be an alternative interpretation for the presence of *Lingulichnus verticalis* in such facies, since offshore conditions might limit the lingulides activity out of their habitat precluding development of subsequent generations.

In this sense, four taphonomic modes were identified when investigating the relationship between lingulides and *Lingulichnus* occurrences (Fig. 4C):

Autochthonous— *In situ*, isolated lingulides normally associated with *Lingulichnus verticalis* or *L. inclinatus*. This taphonomic mode is preserved at the base of finning-upward cycles, frequently marking the early stage of transgressive systems tract in offshore transition to shoreface settings. Exceptionally, this taphonomic mode can coincide with sequence boundaries.

Allochthonous— This preservation is characterized by lingulides with reworking evidences such as disarticulated or fragmented shells from shoreface to offshore settings (Zabini et al. 2012). Alloctonous assemblages preserved in transitional offshore to offshore settings are the main fossiliferous record in the Devonian event beds in Paraná Basin (e.g., Zabini et al. 2010, 2012; Sedorko et al., 2018d);

Autochthonous sub-primary position— This taphonomic mode includes *in situ* lingulides associated to *Lingulichnus hamatus*. However, considering that *L. hamatus* does not indicate the original terrier, but the re-excavation strategy it is referred as sub-primary position. In the study area, this context is preserved in tempestites in the bases of finning-upward cycles (or TSTs);

Temporary sub-primary position— This mode is characterized by *in situ* lingulides, but not in its main habitat, isolated or associated to *Lingulichnus hamatus* or *L. verticalis* (Zabini and Bosetti 2011; Zabini et al. 2013). In the studied strata, lingulides occur in storm-influenced offshore settings, associated to flooding surfaces (Horodyski 2014; Zabini et al. 2013).

Taphonomic event beds are characterized by stratigraphic intervals with unusual taphonomic features (e.g. obrution deposits, tempestites, and others; Brett et al. 2008). The four taphonomic modes here diagnosed can be considered as taphonomic event beds. However, considering the high paleoecological resolution, three are the main ones (i.e. autochthonous, autochthonous sub-primary position, and temporary sub-primary position) because they present paleobiological implications. Storm beds with *in situ* lingulides, represented by HCS sandstones with “autochthonous” and “autochthonous sub-primary position”, and obrution deposits represented by black shales with “temporary sub-primary position” allow to assign a *status* of “event concentration” (*sensu* Kidwell 1991). The “allochthonous” taphonomic mode is characterized by lingulides that have been reworked and possibly time-averaged and represent low paleobiological resolution. On the logical context of time-averaging magnitude scale, those three taphonomic modes correspond to event beds with a reliable ecological sample from the Devonian Malvinokaffric Realm.

Influence of the Taphonomically active zone on preservation

The preservation of the trace fossil associated to its tracemaker is rare and depends of positive taphonomic phenomena (Cummins et al. 1986; Davies et al. 1989; Cutler and Flessa 1995; Meldahl et al. 1997; Olszewski 1999). *Lingulichnus* with no associated lingulides are relatively common in the fossil record (Hakes 1976; Szmuc et al. 1976, 1977; Pemberton and Kobluk 1978; Emig 1983; Savazzi 1991; Zonneveld and Pemberton 2003; Zonneveld et al. 2007, Bromley and Gaillard 2016). This preservational pattern likely is related to the ability of the tracemaker to escape from being completely buried.

The presence of *in situ* lingulides with its trace fossil (Fig. 3E, F) in the Devonian event beds of the Paraná Basin indicates rapid burial, possibly caused by large masses of sediment deposited in a short-lived event, characterizing an autochthonous pattern. According to Morse (1902), upon dying, a lingulide protrudes its body from the burrow and lie down horizontally at full length in the substrate surface. Thus, vertically-oriented lingulides reflect *in situ* preservation. However, the occurrence of bioclasts on the bedding plane forming rosette-polymodal geometry suggests post-mortem reworking of some valves, revealing some parautochthonous preservation (reworked autochthonous specimens, but not transported out of the original life habit; *sensu* Kidwell et al., 1986). The dominance of *Lingulichnus verticalis* in the trace fossil assemblage suggests continuous but moderate sedimentation rates above the FWWB (e.g., Zonneveld and Pemberton, 2003; Zonneveld et al., 2007).

Substrate erosion, promoted by fair-weather waves (SS-f facies) and more predominantly by storm waves (SS-hcs facies), in lower shoreface settings exhume and dispose living lingulides on the sediment-water interface (or, in the taphonomically active zone; TAZ) (Aller, 1982). The exhumed lingulides tried to re-excavate, generating J- or U-shaped burrows that are characteristic of *Lingulichnus hamatus* (Zonneveld and Pemberton 2003). If sedimentation rate rises, or just after the re-excavation attempt and the sediment mass accumulated is bigger than the escape capacity, the burrow is immediately buried and the lingulide can be preserved inside the burrow (Miller et al. 1988). The same is valid for lingulides that were not exhumed: if the amount of sediment deposited by rapid, episodic events is thicker than the capacity of vertical escape, then the chance of preservation of the lingulide in the burrow is enhanced. Thus, under such conditions, complete, articulated lingulide shells in life position or in escape trajectory may be preserved inside or associated with *Lingulichnus.*

Infaunal lingulides inhabit muddy or sandy bottoms preferentially in shallow marine settings (e.g., Morse 1902; Penseler 1930; Over 1988). They live anchored by the pedicle in vertically-oriented mucus-lined burrows excavated in soft sediments (e.g., Savazzi 1991), being well-adapted to high-energy hydrodynamic conditions, frequent sediment reworking, and oscillation of sedimentation rates (Hakes 1976; Szmuc et al. 1976, 1977; Emig 1983; Savazzi 1991; Zonneveld and Pemberton 2003; Zonneveld et al. 2007). Lingulides also support salinity fluctuations and low oxygenation rates, being able to live in brackish water settings and in waters rich in decomposing organic matter (Schuchert 1911). If low oxygenation rates are not a limiting factor for the establishment of lingulides in protected settings, the input of plant debris in more energetic settings may impact in the settlement of lingulid populations.

Stratigraphic bias and significance

The vertical distribution of macrofossils and its taphonomic features in a stratigraphic succession is controlled by differences between the systems tracts and the filling of the basin (e.g., Kidwell 1991a, 1991b; Holland 1996, 2000; Brett 1995; Scarponi and Kowalewski 2007; Sedorko et al. 2018a). For example (Fig. 4), in a third-order transgressive systems tract, the preservation potential is higher than in other phases because the accommodation space overcomes the sedimentation rates, resulting in less action of erosive processes during the costal onlap (Catuneanu et al. 2009, 2010). In minor scale cycles, this principle may be also observed (Fig. 4); however, its distribution depends of the higher order context (accommodation space *versus* sedimentation rates; Catuneanu et al. 2009, 2010). In the progradational phase (LST and HST), the preservational potential is relatively lower due to intense erosion caused by low accommodation space in proximal areas (Fig. 4). In other hand, in agradational phases, this potential is slight higher because the accommodation and sedimentation rates are equivalent. Thus, in LST and HST, shallow waters communities (foreshore to shoreface) generally are not preserved *in situ*. Besides those expected occurrences, *in situ* lingulides can be preserved in sequence boundaries due to intense erosion that might expose and erode part of previous buried deposits, generating omission surfaces (e.g., between Siluro-Devonian and Devonian I sequences; Sedorko et al., 2018b).

Trace fossils are commonly applied as an auxiliary tool in sequence stratigraphy. For example, *Zoophycos* is better represented in prograding phases (lowstand systems tract and upper part of the HST), and, in small-scale, in the top of parasequences (Olivero, 1996). Dense *Zoophycos* ichnofabric in highstand systems tracts of the Siluro-Devonian Sequence was associated to storm-related erosive processes, as indicated by amalgamed hummocky beds indicating low accommodation space (e.g. Sedorko et al., 2018c). In other hand, storm-related strata under increasing accommodation space tend to be well preserved and might include in situ macrofossils. Thus, it is expected that *Lingulichnus* preserved associated to its tracemaker can be an indicator of high depositional rates or high accommodation space, being preferentially preserved in the base of finning upward cycles.

CONCLUSIONS

This study described *Lingulichnus* occurrences that can be associated to lingulides within Lower to Middle Devonian beds in Brazil. The lingulides can occur in four taphonomic modes, which are allochtonous, autochthonous, autochthonous sub-primary position and temporary sub-primary position. Excluding allochtonous pattern, all of them present high paleoecological resolution, and therefore, paleobiological implications. The main habit life of lingulides preserved in Devonian strata of the Paraná Basin was in the shelfal zone, concentrated above fair-weather wave base. Lingulides preserved in offshore settings associated to *Lingulichnus verticalis* and *L. hamatus* suggests that few organisms could survive in distal environments, but this was not the main site of the group.

The integration of taphonomy, ichnology and sequence stratigraphy demonstrated that analyzing the trace fossils associated with their tracemakers and interpreting its genetic signature, can provide important clues for the interpretation of system tracts. On the other hand, the high-resolution paleoecology here demonstrated, provide important information about taphonomic bias in the stratigraphic controls of infaunal lingulides by evidencing stratigraphic information about the fossiliferous horizons.

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Table Captions

Table 1. — Lithologic and ichnologic character of facies studied and their interpreted paleoenvironmental settings.

Figure Captions

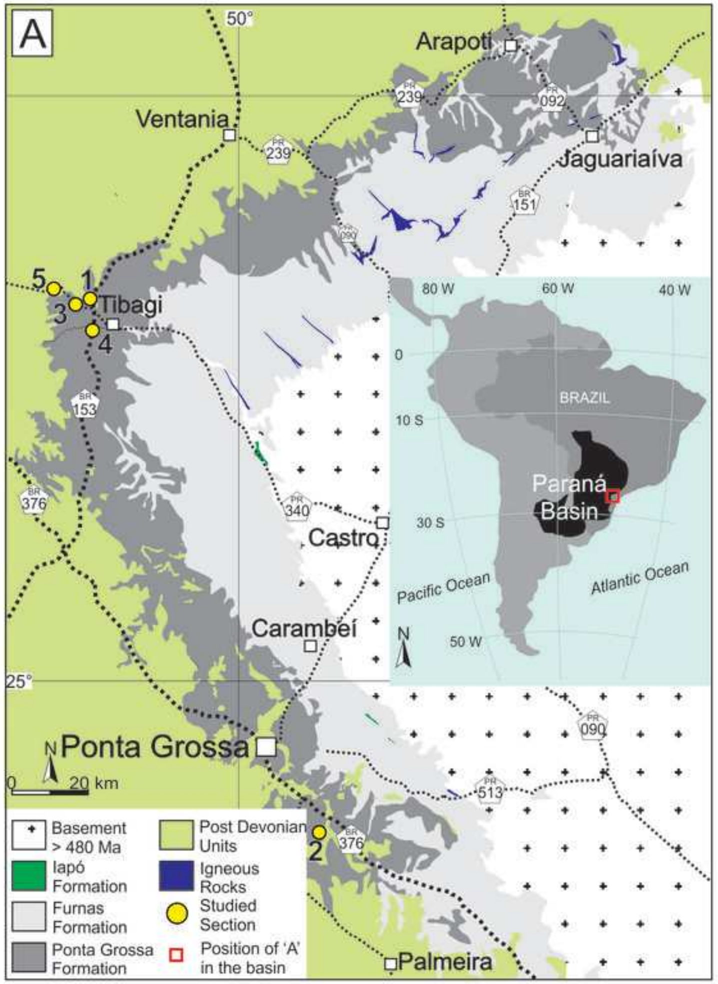
Fig. 1. — Location map and stratigraphic context of the study area in Paraná Basin, Brazil. A. Map of South America with the Paraná Basin identified as the shaded region and geological map of Paraná Group in Campos Gerais region, Paraná State, Brazil. B. Localities of outcrops in Tibagi region (PR). C. Stratigraphy of the Siluro-Devonian successions in the Apucarana sub-Basin (Paraná Basin) and distribution of lingulides and *Lingulichnus* are identified in the generalized log for the Devonian of the basin. Modified from Sedorko et al. (2018b).

Fig. 3. — Sedimentary facies and trace fossils from studied sections. A. Fine-grained sandstone with hummocky cross-stratification; B. Fine-grained sandstone with wave ripples; C. Black shale bearing *Lingulichnus hamatus* (*Lh*) associated to *in situ* lingulides and *L. verticalis* (*Lv*)*;* D. Fine-grained sandstone with *Lingulichnus hamatus* (*Lh*); E. Fine-grained sandstone with lingulides in oblique position (OP) associated to *Lingulichnus verticalis* (*Lv*); F. Very-fine grained sandstone with *Lingulichnus verticalis* (*Lv*). G. Black shale with lingulides in different orientation (vertical [VP], oblique [OP], and parallel [PP] position; H. *Lingulichnus hamatus* (*Lh*) in fine-grained sandstones; I. *Diplocraterion* (*Di*) in fine-grained sandstones, preserved in same level of fig. H; J. *Rosselia* (*Ros*) associated to a lingulid in vertical position (VP). All scale bars are 1 cm long.

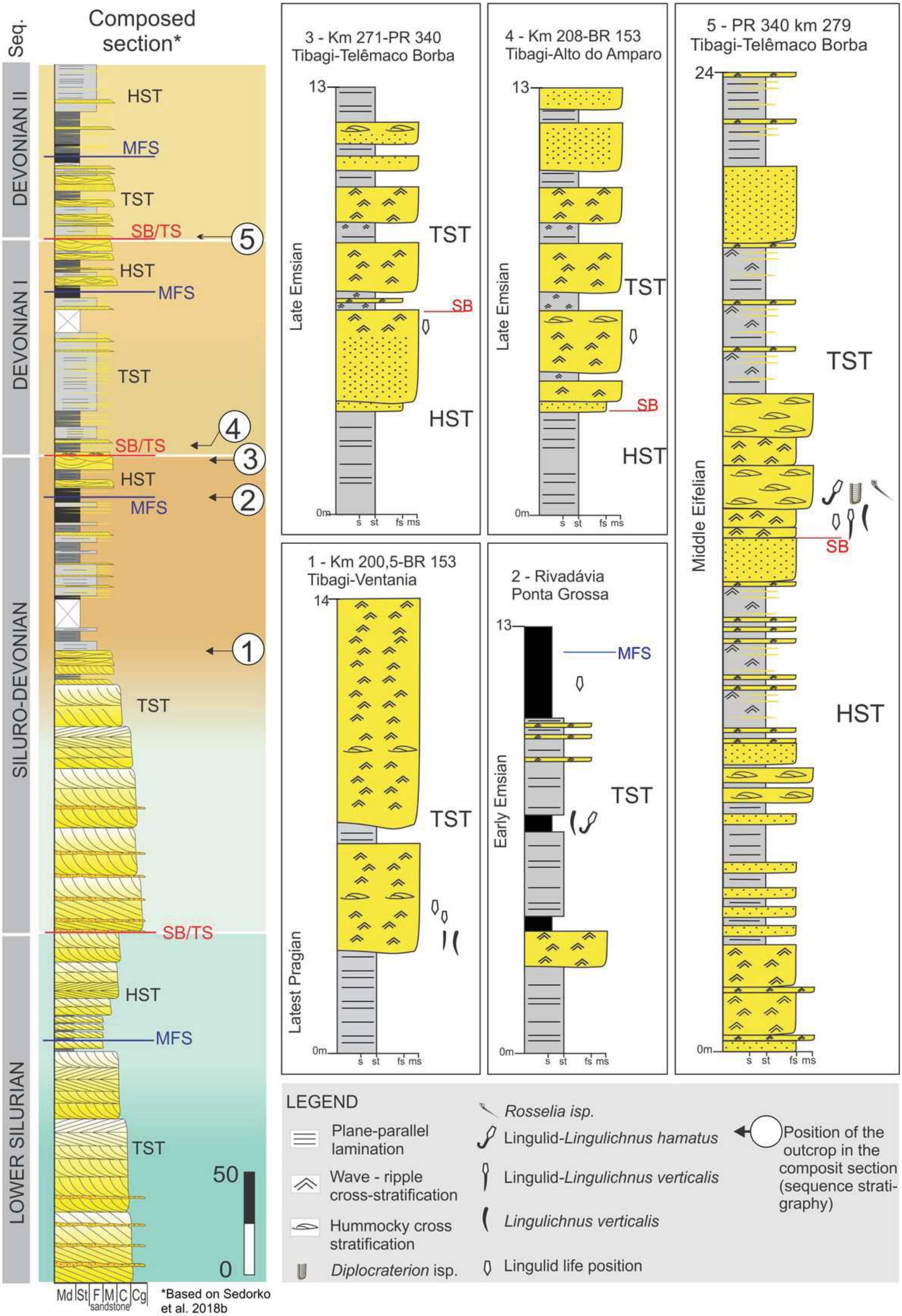
Fig. 4. — Four taphonomic modes were diagnosed considering the lingulides and *Lingulichnus* occurrences in the Devonian event beds, *i.e.,* autochthonous, allochthonous, autochthonous sub-primary position and temporary sub-primary position. The diagram A shows different occurrences of lingulides under no taphonomic analysis. The B is interpretative and consider the taphonomic processes (B) that can have biased (C) the fossil record. The B and and C shows the interpretation of taphonomic bias when living lingulides was transported in distal zones by storm waves and currents. RSL = relative sea level; FWWB = fair weather wave base; SWB = storm wave base.

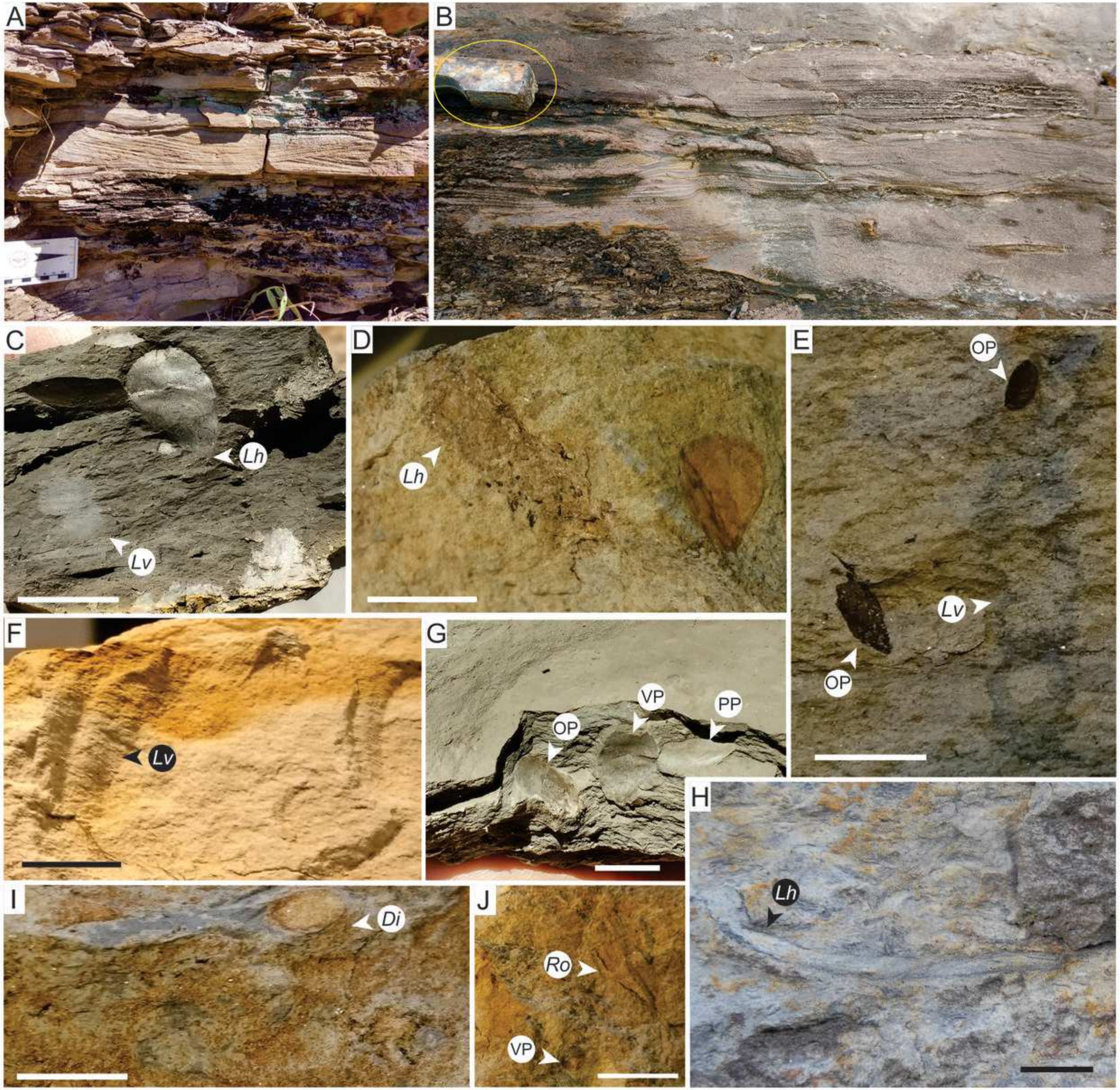
Code	**Facies**	**Sedimentary structure**	**Biogenic Structure**	**Sedimentary processes**	**Depositional system**
Shcs	Fine-to medium-grained sandstone	Hummocky cross-stratification	*Diplocrateriun*, *Lingulichnus hamatus*, *Rosselia, Arenicolites, Palaeophycus, Schaubcylindrichnus, Macharonichnus, Skolithos*	Oscillatory flows storm generated	Lower Shoreface to offshore-Transition
SSf	Fine sandstones	Wave ripples	*Lingulichnus verticalis, Palaeophycus, Diplocraterium*	Oscillatory flows	Lower Shoreface
SSm	Fine-to medium-grained sandstone	Massive	*Lingulichnus verticalis, Glossifungites*	Sediment-gravity flow deposits	Lower Shoreface to offshore-Transition

Table. 1



B	Formation	Member	Age
Paraná Group	Ponta Grossa	São Domingos	Givetian to Late Eifelian
			Late Eifelian to Late Emsian
		Tibagi	
		Jaguariaíva	Emsian to ?Pridoli
	Furnas	upper	
		middle	?Lludlow to Llandovery
		lower	


Seq.
Composed section*
DEVONIAN II
DEVONIAN I
SILURO-DEVONIAN
LOWER SILURIAN
HST
MFS
TST
SB/TS
HST
MFS
TST
SB/TS
HST
MFS
TST
SB/TS
HST
MFS
TST
5
4
3
2
1
50
0
Md St F M C Cg
sandstone
*Based on Sedorko et al. 2018b
3 - Km 271-PR 340
Tibagi-Telêmaco Borba
13
Late Emsian
TST
SB
HST
0m
s st fs ms
4 - Km 208-BR 153
Tibagi-Alto do Amparo
13
Late Emsian
TST
SB
HST
0m
s st fs ms
5 - PR 340 km 279
Tibagi-Telêmaco Borba
24
Middle Eifelian
TST
SB
HST
0m
s st fs ms
1 - Km 200,5-BR 153
Tibagi-Ventania
14
Latest Pragian
TST
0m
s st fs ms
2 - Rivadávia
Ponta Grossa
13
MFS
Early Emsian
TST
0m
s st fs ms
LEGEND
Plane-parallel lamination
Wave - ripple cross-stratification
Hummocky cross stratification
Diplocraterion isp.
Rosselia isp.
Lingulid-Lingulichnus hamatus
Lingulid-Lingulichnus verticalis
Lingulichnus verticalis
Lingulid life position
Position of the outcrop in the composit section (sequence stratigraphy)


A
B
C
Lh
Lv
D
Lh
E
OP
Lv
OP
F
Lv
G
OP
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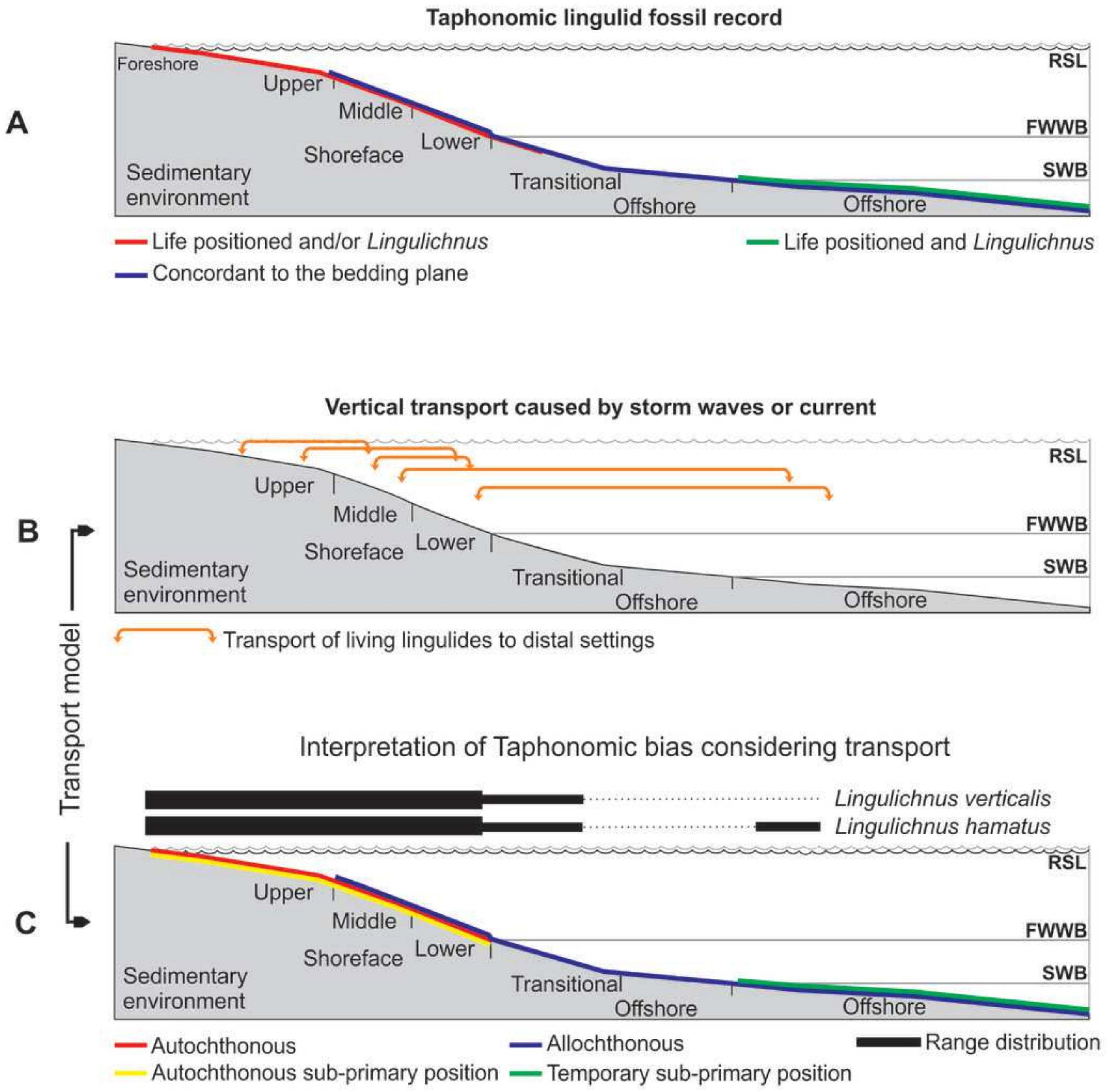
A
Taphonomic lingulid fossil record
Foreshore
Upper
Middle
Lower
Shoreface
Sedimentary environment
Transitional
Offshore
Offshore
RSL
FWWB
SWB
Life positioned and/or *Lingulichnus*
Concordant to the bedding plane
Life positioned and *Lingulichnus*
B
Vertical transport caused by storm waves or current
Upper
Middle
Lower
Shoreface
Sedimentary environment
Transitional
Offshore
Offshore
RSL
FWWB
SWB
Transport of living lingulides to distal settings
Transport model
C
Interpretation of Taphonomic bias considering transport
Lingulichnus verticalis
Lingulichnus hamatus
Upper
Middle
Lower
Shoreface
Sedimentary environment
Transitional
Offshore
Offshore
RSL
FWWB
SWB
Autochthonous
Autochthonous sub-primary position
Allochthonous
Temporary sub-primary position
Range distribution

CAPÍTULO 9

Storm-related taphofacies and paleoenvironments of Malvinokaffric assemblages from the Lower/Middle Devonian in southwestern Gondwana

Artigo publicado no periódico “Palaeogeography, Palaeoclimatology, Palaeoecology” que teve como objetivo utilizar dados tafonômicos e icnológicos para a compreensão dos depósitos de tempestade de inverno no contexto de altas paleolatitudes na Formação Ponta Grossa e sua relação com outros depósitos devonianos (e.g. África do Sul, Marrocos e Estados Unidos).

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Storm-related taphofacies and paleoenvironments of Malvinokaffric assemblages from the Lower/Middle Devonian in southwestern Gondwana

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ABSTRACT

Taphofacies of Malvinokaffric macroinvertebrate-bearing rocks from the uppermost Pragian to lower Givetian in southwestern Gondwana are evaluated. During the Lower/Middle Devonian, the Paraná Basin (southern Brazil) was positioned at high latitudes in southwestern Gondwana (60° to 80°S). Integrated litho- and taphofacies interpretations in siliciclastic environments presented here provide paleoecological and paleoenvironmental insights. The six taphofacies recognized here showed changing depositional conditions in paleoenvironments ranging from shoreface to offshore shelf settings. They vary in recurrence and abundance, but all facies exhibit evidence of storm events. Winter storms are to be expected at latitudes 60° to 80° S under cool climate zone. Storm-related taphofacies recurrence during the latest Pragian to early Givetian points to two agents of sedimentation, direct wave erosion by winter storms and sedimentary processes related to combined flow during deposition (*e.g.* turbidity currents and oscillatory flow). Winter storms are considered more capable of affecting sediment transport than hurricanes, due to longer duration and larger coverage area in higher latitudes. Therefore, winter storms of high latitudes should generate more persistent currents in space and time. Finally, the taphofacies, lithofacies and high-latitude paleogeographic context of the Paraná Basin suggest the action of storm-influence in the genesis of all Lower/Middle Devonian Malvinokaffric assemblages here recognized.

1. Introduction

The taphofacies concept was originally developed from the detailed study of Paleozoic fossil associations (Brett and Baird, 1986; Speyer and Brett, 1986, 1988). A taphofacies consists of a fossil assemblage, with distinctive taphonomic signatures that reflect the depositional history of the skeletal remains under study (Speyer and Brett, 1986, 1988).

Studies of fossil preservation dynamics, such as sedimentation rates, sea-level changes (*e.g.* Brett et al., 2007), and storm events (*e.g.* Miller et al., 1988) allowed a better understanding of the taphonomic patterns of various taxonomic groups through depth gradients in a sedimentary basin (Speyer and Brett, 1988; Brett and Seilacher, 1991; Brett, 1995; Brett et al., 1997).

Taphonomic studies from the Malvinokaffric Realm in Paraná Basin are mainly limited to Lower/Middle Devonian invertebrate fossil assemblages (*e.g.* Rodrigues et al., 2003; Zabini et al., 2010, 2012; Sedorko et al., 2018a). These provide an understanding of marine environments during the middle Paleozoic and included documentation of *in situ* occurrence of some specific invertebrate taxa such as conulariids (Simões et al., 2000; Rodrigues et al., 2003) and infaunal lingulids (Zabini et al., 2010, 2012). Therefore, it is important to emphasize that taphofacies studies can aid in understanding the distributional ecology of taxa, as well as the dynamics of ancient environments (*i.e.* paleoenvironmental reconstruction).

Here we address the Early to Middle Devonian invertebrate Malvinokaffric fauna *sensu* Melo (1988). This fauna inhabited cold

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epeiric seas of the Paraná Basin (and elsewhere) during Devonian, where it faced severe environmental changes during late Emsian (Bosetti et al., 2012), especially associated with the rapid global marine transgression that occurred during the Middle Devonian (latest Eifelian-Givetian) Kačák Event (House, 1996; Bosetti et al., 2011; Horodyski et al., 2014). Important biogeographic, taphonomic and ecological shifts occurred in the post-Kačák sedimentary layers in the Paraná Basin (Bosetti et al., 2011; Horodyski et al., 2014), with an occurrence of opportunistic faunas, characterized by diminutive taxa that putatively display the Lilliput Effect (*sensu* Urbanek, 1993; see also Bosetti et al., 2011).

In this study, we evaluate the taphofacies present in a sedimentary section of latest Pragian to early Givetian age (Paraná Basin) but with an emphasis on the Givetian. This provides an opportunity to compare taphofacies of siliciclastic-dominated cool water facies of approximately the same age in the Cape Basin of South Africa, Emsian of southwestern Morocco (Mdaouer-el-Kbir Formation), as well as the lower latitude warmer water settings, the classic Hamilton Group taphofacies of the Appalachian Basin studied by Brett and Baird (1986) and Speyer and Brett (1986, 1988, 1991). Thus, using the comparative taphonomic approach, we partially test the generalizations made from the Brazilian samples and highlight some differences with other settings that may lead to further understanding of processes. Our approach was to determine how different energy levels of storm and normal waves controlled the generation of the several taphofacies. From this study, it was possible to recognize scales of time-averaging (Kidwell and Bosence, 1991) in parautochthonous as well as some *in situ* fossil occurrences, to reconstruct the Devonian biota and environment.

2. Geological setting

The intracratonic Paraná Basin (about 1,700,000 km^2) is located in southernmost Brazil and north/northwestern Uruguay, parts of Paraguay and Argentina (Fig. 1A). The basin has a NE-SW elongated oval shape and its sedimentary fill was influenced by tectonic-eustatic cycles linked to the evolution of Western Gondwana during Paleozoic and Mesozoic times. Six second-order depositional sequences or supersequences (Late Ordovician to Late Cretaceous) compose the basin filling (Milani and Ramos, 1998; Milani et al., 2007). The stratigraphic interval studied herein corresponds to the second supersequence, named “Paraná Supersequence” (Lower Silurian to Late Devonian) (Milani et al., 2007; Grahn et al., 2013; Sedorko et al., 2017). This succession is divided into three units, the Furnas, Ponta Grossa and São Domingos formations (Fig. 1B; Grahn et al., 2013). Stratigraphic and paleontological data presented herein were acquired from one of the composite sections located in Tibagi County, Paraná State (Fig. 1C). The stacking of stratigraphic columns from successive outcrops resulted in a composite section, herein referred to as Tibagi-Ventania section (Fig. 2).

The Ponta Grossa and São Domingos formations were dated by Grahn et al. (2013) and correlated to the 3rd order sequence framework of Bergamaschi (1999) and Bergamaschi and Pereira (2001). Based on different approaches other sequences were also proposed to these strata (*e.g.* Assine, 1996; Candido and Rostirolla, 2007; Zabini et al., 2012; Horodyski et al., 2014). Recently, Sedorko et al. (2018b) presented a synthesis of these interpretations based on ichnological data and dividing the Paraná Supersequence in four 3rd order sequences (named Lower Silurian, Siluro-Devonian, Devonian I and Devonian II sequences; Fig. 1B). The Furnas facies was not included in the present study due to its absence of macrofossils (*i.e.* Lower Silurian and basal part of Siluro-Devonian sequences). Fossiliferous facies of Siluro-Devonian, Devonian I and II sequences (uppermost Pragian to lower Givetian) are representative of environments ranging from shoreface to offshore (Bergamaschi, 1999; Bergamaschi and Pereira, 2001; Sedorko et al., 2018b).

The five oldest fossil-bearing intervals that were used in this taphonomic study are derived from the lower 22.4 m of the Ponta Grossa Formation (Fig. 2), which constitutes a transgressive systems tract (TST of the Siluro-Devonian sequence *sensu* Sedorko et al., 2018b). This fossiliferous interval (late Pragian to early Emsian; Grahn et al., 2013) is composed of fine-grained sandstone beds in the base of the section with upward replacement for finer sands and siltstones, culminating in a flooding event of dark sandy shales. Fossiliferous assemblages are found throughout these intervals, providing a spectrum from relatively shallow to deep water facies.

The Devonian I sequence in studied section presents basal transgressive sandy mudstones (upper Emsian; Grahn, 2005). A 2-m-thick dark shale occurring above (151 to 151.7 m; Fig. 2) record maximum flooding zone. Based on its estimated age, this shale may record the earliest Eifelian Choteč event, a global interval of deepening and anoxia (*e.g.* House, 2002). Above the dark shale, the facies coarsen upward into siltstones and sandy mudstones. Just two fossiliferous samples were derived from this sequence, one from the lower dark, fissile shales and one from about 10 m above.

The Devonian II Sequence (*sensu* Sedorko et al., 2018b) represents the late Eifelian to early Givetian stages (Grahn et al., 2013), is represented by lower sandstones and sandy mudstones, and culminates in a black shale, which may correspond to the widespread eustatic deepening recorded in the Kačák-Odershausen black shales of Europe and the upper Marcellus subgroup of the Appalachian Basin (Brett et al., 2011). This sequence records a major global transgression and highstand identified by Johnson et al. (1985) as sequence If. This interval probably correlates with Eif-Giv sequence, *i.e.* the Oatka Creek Formation of the classic Hamilton Group in New York. Unfortunately, no usable fossiliferous samples were obtained from the TST of this sequence.

Most of our samples (6 intervals) were derived from highstand systems tract (HST) of the Devonian II Sequence (early Givetian; Grahn, 2005; Mauller et al., 2009). This interval can be used to develop a model of approximately contemporaneous taphofacies that reflect a variety of environments. This model is then applied to other intervals and analogous taphofacies are recognized in the Pragian to Eifelian sequences Siluro-Devonian and Devonian I of the Tibagi-Ventania Section.

3. Materials and methods

Fossil samples were collected from newly discovered outcrops (based on a single composite section), located between Tibagi and Ventania municipalities (Paraná state, Brazil; Fig. 1) and are stored in the collections of the *Laboratório de Estratigrafia e Paleontologia, Universidade Estadual de Ponta Grossa* (Paraná State, Brazil). The samples were obtained following field observations of outcrops by clearing of certain stratigraphically documented bedding planes. Intervening intervals apparently were barren. Approximately 500 hand samples were analyzed, each sample displaying one or more fossils. The macrofossils were processed by means of fine brushes and needles.

Fossil data were collected according to the taphonomic/paleoautecological protocol developed by Simões and Ghilardi (2000), which was also used to permit the taphofacies analysis, using criteria established by Speyer and Brett (1986, 1988). The taphonomic observations recorded for each skeleton type (univalve, bivalve, multielement, and flexible thecae) included disarticulation, fragmentation degree, position and orientation of the skeletons relative to bedding planes (1). We used lithological criteria to subdivide the facies, and then assessed taphonomic criteria for all the samples that were preserved within each of these lithofacies. The ichnofacies data followed the studies of Sedorko et al. (2018a, 2018b).

4. Lithofacies interpretations

Conglomeratic and coarse to fine-grained sandstones, siltstones and

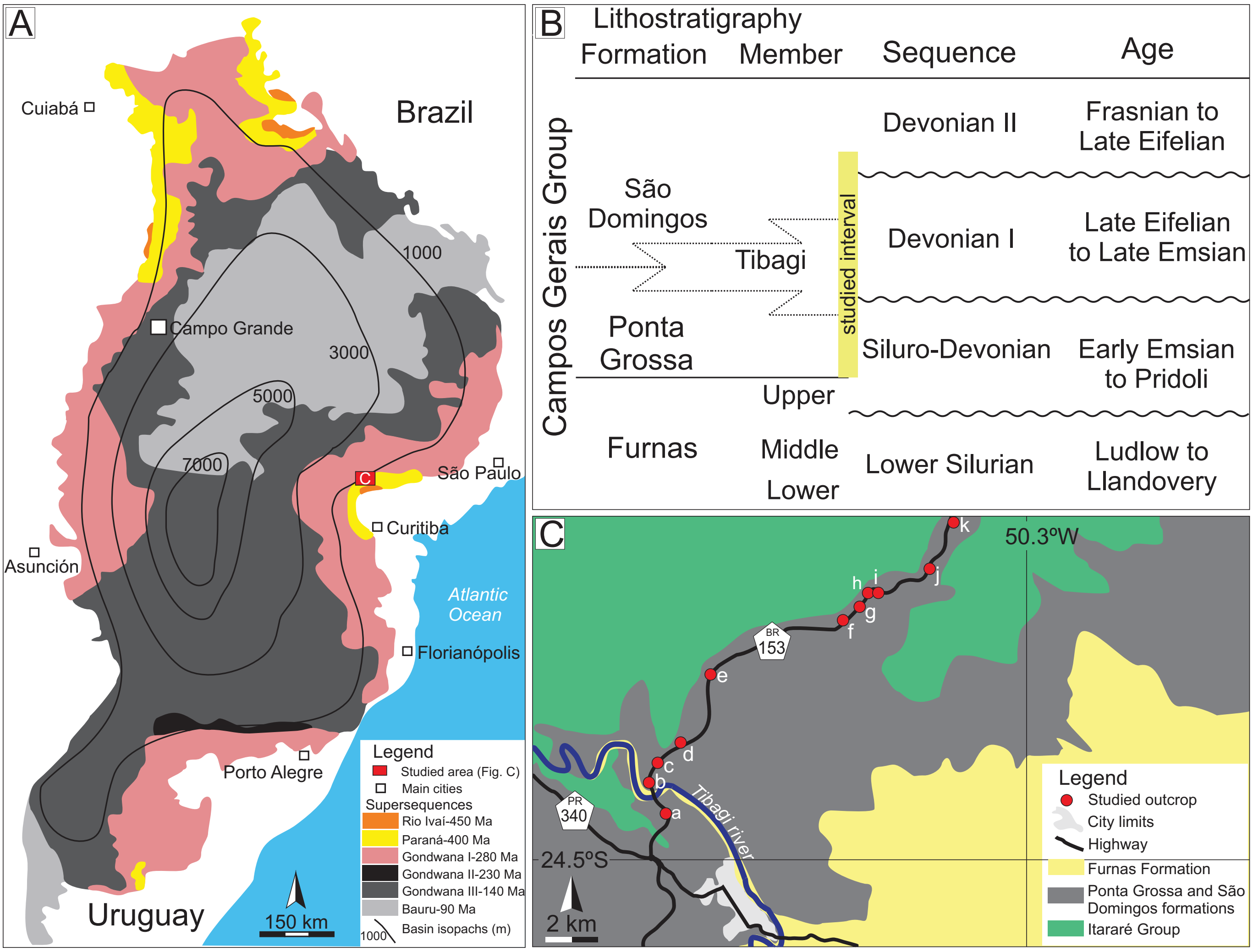


Fig. 1. (A) Location map of the study area in Paraná Basin and its supersequences; (B) stratigraphic chart showing the Lochkovian to lower Givetian stratigraphy of the Paraná Basin (simplified after Grahn et al., 2013 and Sedorko et al., 2018a); (C) the outcrops are distributed along of road BR-153, in between of Tibagi and Ventania municipalities, Paraná State, southern Brazil.

shale dominate the rocks from the Lower and Middle Devonian in the studied region. Palynofacies analysis and geochemical studies were not conducted; therefore, the facies analysis is based only on composition, texture and structure, either syn- and post-depositional. Here we describe only fossil-bearing facies, which were subject to taphofacies analysis. The facies summarized in Table 1 (Fig. 3) show three depositional systems, which were studied.

The most proximal facies, Sf, are fine-grained quart-rich sandstones. These sands are interpreted to have been deposited in regions above fair-weather wave base (FWWB), associated with the lower shoreface zone and represent combined oscillatory flows with sediment-gravity flows deposits. The SS-hcs, fine-grained sandstone, and SL-hcs record fine-grained sandstones to coarse siltstones, with thin interspersed sand lenses. These sands display hummocky cross-stratification and indicate a transition between lower shoreface to offshore settings, *i.e.*, transition zone, because of evidence for the interaction of fair-weather and frequent storm waves. Facies SL-p consists of siltstones often interspersed with thin, centimeter-scale, sand lenses. These sediments indicate the offshore transitional zone, below FWWB and are interpreted as deposits emplaced by muddy to sandy storm-generated gradient currents. This region was located between the FWWB and the storm wave base level (SWB), representing dominance of low energy settings, but influenced by episodic storm flows. SS facies (massive coarse- to medium-grained sandstones) indicates sediment-gravity flow deposits in the offshore shelf zone, above SWB.

The deepest water environments are recorded by lithofacies SH-L, black shales with minor silt laminae. These facies are interpreted as representative of offshore deposits, formed by gravitative settling of suspended fine-grained sediments after storm flows. This portion of the seafloor was located below SWB.

5. Taphofacies descriptions

The fossils found throughout the section (Table 2 and Supplementary Table 1) are skeletons classified taphonomically, as bivalved shells (Mollusca: Bivalvia and Brachiopoda), univalved shells (Mollusca: Tentaculitoidea), multi-element skeletons (Trilobita, Echinodermata: Crinoidea and Stylophora; Annelida: Polychaeta) and flexible thecae (Cnidaria: Conulatae) types.

The uppermost Pragian to lower Givetian invertebrates assemblages studied here are rather depauperate, represented by fourteen species, *i.e.*, 16.5% of approximately eighty-five taxa of all Malvinokaffric fauna (see a synthesis in Bosetti et al., 2012). According to Bosetti et al. (2012), Horodyski et al. (2014), Grahn et al. (2016) and Richter et al. (2017), the highest diversity of Malvinokaffric taxa occurs in the Ponta Grossa Formation, and represents the climax of faunal biodiversity in the Lower Devonian times. However, only about six taxa make up most of the studied assemblages in the latest Pragian to Emsian (*Edmondia*

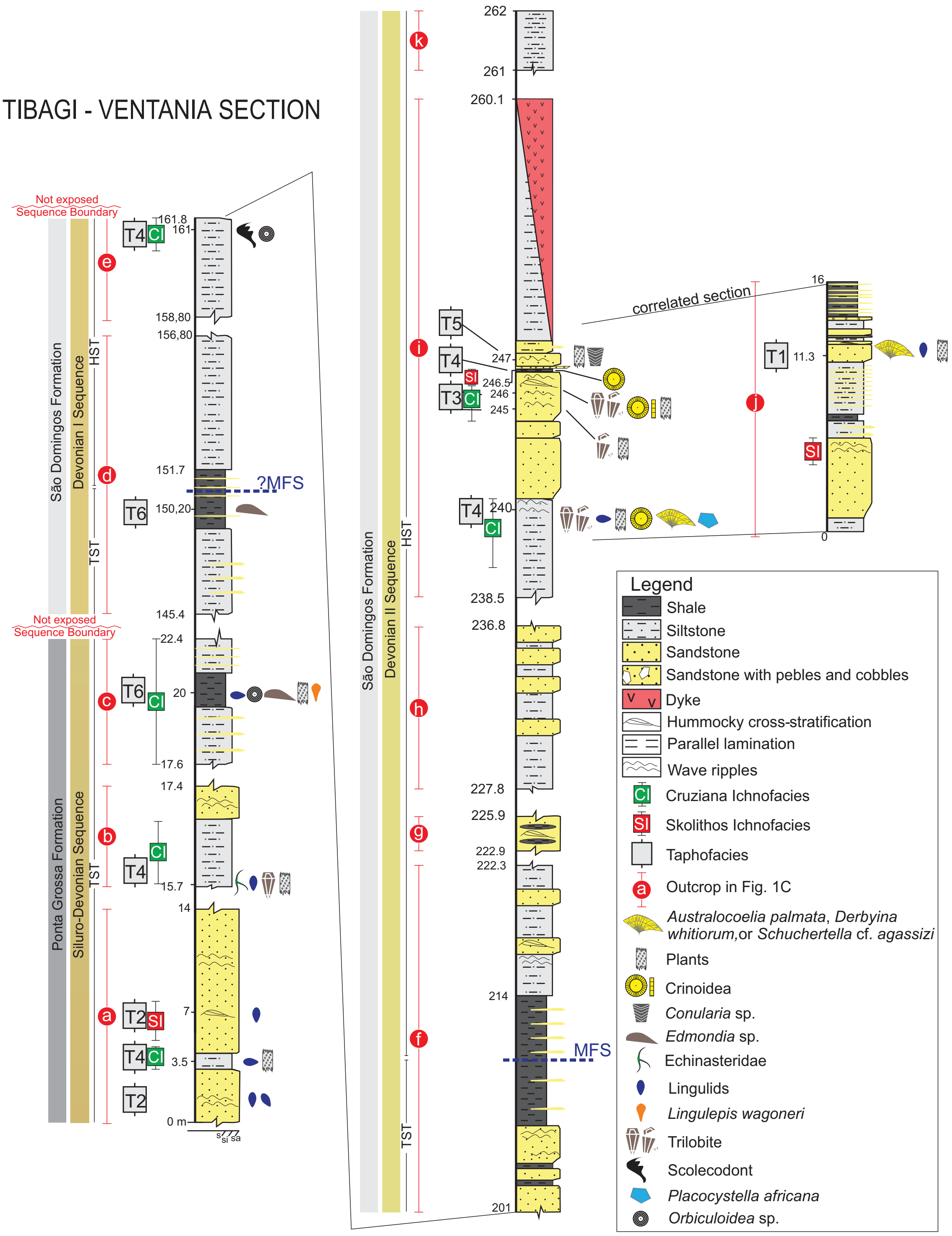


Fig. 2. Stratigraphic profile of the Tibagi-Ventania section showing the distribution of lithologies, main sedimentary structures, taxa, taphofacies recognized and stratigraphic position (letter T with taphofacies number within the rectangle), and ichnofacies. MFS = Maximum Flooding Surface.

sp., *Lingulepis wagoneri*, *Orbiculoidea* sp., ophiuroidea and two calmonid trilobites). Considering the current distribution of fauna (see Bosetti et al., 2012), a greater abundance and diversity would be expected in these basal beds. However, low diversity of provincial taxa of lower Devonian in this study may reflect a sampling bias as the Tibagi-Ventania section is not complete vertically.

Species richness is more than doubled in the Middle Devonian samples, *i.e.*, about 15 taxa. The fauna collected in the main studied section (HST of Devonian II Sequence, Givetian) is composed mostly of rhynchonelliforme brachiopods *Derbyina* sp., *Australocoelia* sp. and *Schuchertella* sp., and the lingulate *Lingulepis wagoneri*, *Orbiculoidea* sp.; the bivalves *Edmondia* sp.; the conulariids Conulatae; the scolecodont *Paulinites paranaensis*; the trilobites *Metacryphaeus* sp. and *Calmonia* sp.; the stylophoran *Placocystella langei*; and the columnal-based crinoid parataxon *Marettocrinus* aff. *M. hartti* (Table 2). The preservation of taxa varied throughout the section in terms of the degree of disarticulation (whether complete or partial, judging the type of skeleton given in percentage) and fragmentation (if high, > 90%, intermediate (50–90%)

Table 1
Descriptions of the facies of the fossiliferous levels of the studied section.

Code	Facies	Sedimentary structure	Interpretation
SS	Coarse to medium sandstones	Massive	Sediment-gravity flow deposits
Sf	Fine to medium sandstones	Wave ripples or faint massive	Combined oscillatory flows with sediment-gravity flow deposits
SS-hcs	Fine sandstones	Hummocky cross-stratification and wave ripples	Oscillatory flows storm generated
SL-hcs	Fine sandstones to coarse siltstones, with thin interspersing of sand lenses	Hummocky cross-stratification and wave ripples	Oscillatory flows storm generated
SL-p	Siltstones often interspersed with thin sand lenses	Parallel lamination and lenticular and locally lenticular sand bedding	Suspension emplaced by muddy to sandy turbidity currents
SH-L	Claystones, interspersed with thin sand lenses	Massive, laminated	Suspension sediments, locally with muddy to sandy turbidity currents

Fig. 3. Sedimentary facies in studied section. (A) Massive coarse to medium sandstones (facies SS). (B) Fine to medium sandstones with wave ripples or massive (facies Sf). (C) Fine sandstones with hummocky cross-stratification and wave ripples (facies SS-hcs). (D) Fine sandstones to coarse siltstones, with thin interspersing of sand lenses, hummocky cross-stratification and wave ripples (facies SL-hcs). (E) Siltstones often interspersed with thin sand lenses, parallel lamination and lenticular and locally sand bedding (facies SL-p). (F) Claystones, interspersed with thin sand lenses, massive, laminated (facies SH-L).

or low, < 50% of the original preservation of the taxon) and position relative to the bedding plane (vertical, oblique or parallel). Based on this information, taphofacies are characterized as described below, and are indicated in the stratigraphic section (Fig. 2).

The taphofacies are numbered T1–T6, in relation to relative onshore-offshore position based upon sedimentological features that permit reconstruction of position in relation fair weather wave base (FWWB) and storm wave base (SWB). Taphofacies in analogous positions in various sequences are designated with letters corresponding to those of the sequences. Thus, the late Pragian to early Emsian Sequence (previously called Silurian-Devonian sequence *sensu* Sedorko et al., 2018b) representative of Taphofacies 2 is denoted T2-PE, that in the Givetian a T2D-II (Devonian II Sequence).

Taphofacies 1 facies Sf—T1 (Table 3; Fig. 4). This taphofacies is characterized by disarticulated lingulate and rhynchonelliform brachiopods that occur on bedding planes of fine to medium grained

Table 2
Skeletal types and feeding habits of taxa found within the taphofacies recognized in the stratigraphic profile here analyzed.

Taxa	Feeding habit	Life style inferred	Skeletal type	Total composition
Lingulidae	Infaunal suspension feeder	Emig (1997), Zabini et al. (2012)	Bivalve	110
Lingulepis wagoneri	Stationary low-level epifaunal suspension feeder	Williams et al. (2000)	Bivalve	6
Derbyina	Stationary epifaunal suspension feeder	Williams et al. (2002)	Bivalve	12
Australocoelia	Stationary epifaunal suspension feeder	Boucot and Gill (1956)	Bivalve	19
Schuchertella	Stationary epifaunal suspension feeder	Williams et al. (2006)	Bivalve	3
Orbiculoidea sp.	Epifaunal attached by pedicle, suspension feeder	Mergl (2001), Mergl and Massa (2005), Comniskey (2011)	Bivalve	49
Edmondia sp.	Facultatively mobile infaunal deposit feeder chemosymbiotic	Runnegar and Newell (1971), Kotzian and Simões (1997), Williams et al. (2000)	Bivalve	21
Conulatae	Sessile epifaunal	Van Iten (1991), Van Iten et al. (2013), Simões et al. (2000), Rodrigues et al. (2003)	Flexible thecae	5
Paulinites paranaensis	Epifaunal detritivore	Eriksson et al. (2011)	Multielement	12
Metacryphaeus sp.	Mobile detritivore benthic epifauna	Fortey and Owens (1999), Ghilardi (2004)	Multielement	31
Calmonia sp.	Mobile detritivore benthic epifauna	Fortey and Owens (1999), Ghilardi (2004)	Multielement	9
Placocystella sp.	Active mobile epifaunal suspension feeder	Ruta and Theron (1997)	Multielement	1
Marettocrinus aff. *M. hartii*	Sessile epifaunal	Le Menn (1985), Scheffler (2010), Scheffler et al. (2015)	Multielement	26
Encrinasteridae	Epifaunal detritivore suspension feeder	Shackleton (2005)	Multielement	3

quartzose sandstones. The unique occurrence of this proximal taphofacies, T1D-II, is in early Givetian Devonian II Sequence. It is well represented in an interval of 11 m in a supplementary section that is laterally correlative with interval 240 m to 247 m of the main section (Fig. 2). Bivalve-type skeletons (brachiopods *Schuchertella* sp. (Fig. 4A and B), *Australocoelia* sp. (Fig. 4C), and infaunal lingulids) are present. The fossils are complete, disarticulated and distributed horizontally in relation to bedding planes, associated with *Spongiophyton* spp. plant microfragments (Fig. 4D). At present, no analog of Taphofacies1 was found in sequences older than Givetian.

Taphofacies 2 facies SS-hcs—T2 (Table 3; Fig. 5). This taphofacies consists of disarticulated as well as articulated bivalved skeletons (*e.g.* lingulids), including some in life position in fine-grained sandstones and siltstones. The only example of this taphofacies (T2SD) occurs in latest Pragian to Emsian strata of the Siluro-Devonian Sequence, in intervals 1 m and 7 m above the base of the section (Fig. 2). No analogs were found higher in the section; however, Taphofacies T3 may represent a somewhat analogous position in the onshore-offshore gradient.

In T2 all fossils are representatives of infaunal lingulid brachiopods (Fig. 5A and B), which occur as complete and articulated shells. These may occur obliquely and/or vertically in relation to the bedding planes, with sparse parallel-oriented occurrences. Associated with them, the vertical excavation of *Lingulichnus* isp. is also present, in some cases containing lingulid shells at the top of the burrow. The associated trace fossils correspond to expressions of Skolithos Ichnofacies (Sedorko et al., 2018b), mostly represented by *Skolithos*, *Cylindrichnus*, *Lingulichnus* and *Arenicolites*. A few microscopic fragments of unidentified plants are present. The skeletons occur loosely packed in sandstones.

Taphofacies 3 facies SL-hcs—T3 (Table 3; Fig. 6) occurs in hummocky bedded sandstone and siltstone in the interval of 245 m to 246 m of early Givetian Devonian II Sequence (Fig. 2). The remains include mainly multielement skeletons of the trilobite *Metacryphaeus* sp. (Fig. 6A) and crinoid columnals, *Marettocrinus* aff. *M. hartii* (Scheffler et al., 2015) (Fig. 6B). The trilobites display three taphonomic grades, which co-occur in these facies: (a) whole, articulated and extended exoskeletons, positioned parallel to bedding planes, (b) articulated thorax and pygidium, and (c) isolated cephala, thoracic segments and pygidia. Crinoids occur as disarticulated, isolated columnals or small pluricolumnals, occurring as a weakly-packed fabric. Horizontal and vertical burrows are present, mostly *Teichichnus*, *Planolites*, *Asterosoma*, *Rusophycus*, *Thalassinoides*, *Phycosiphon* and *Bifungites* representing expressions of the Cruziana Ichnofacies (Sedorko et al., 2018b). Microfragments of plants (*Spongiophyton* spp.) are also present (Fig. 6C).

Taphofacies 4 facies SL-p—T4 (Table 3; Fig. 7) occurs at five different stratigraphic intervals (Fig. 2). It is characterized by variably disarticulated complete valves of lingulids, together in most cases with variably articulated trilobite material in thinly bedded siltstones and fine-grained sandstone lenses.

In the first interval of 3.5 m, in latest Pragian to Emsian strata (Siluro-Devonian Sequence; T4SD) skeletal remains are of bivalved type (infaunal lingulids; Fig. 7F). Remains are complete, disarticulated, and concordant with bedding planes. The fossils occur loosely-packed in the sedimentary matrix, associated with horizontal and secondarily vertical burrows corresponding to expressions of Cruziana Ichnofacies, represented by *Planolites*, *Asterosoma*, *Teichichnus*, *Rosselia*, *Rhizocorallium*, *Chondrites*, and *Zoophycos*. Plant fragments are also present.

The fauna of the second interval (15.70 m) of T4SD, also in late Pragian to early Emsian strata (Siluro-Devonian Sequence), is composed of brachiopods (infaunal lingulids) and multielement skeletons (Trilobita: Calmonidae and Echinodermata: Echinasteridae). The lingulid valves are complete, disarticulated and oriented parallel to

Table 3
Percentage of taphonomic signatures from each taphofacies.

Taphofacies	Skeletal type				Articulation			Preservation			Bedding position			*n*
	Univalved	Bivalved	Multielement	Flexible thecae	Articulated	Partial articulated (thorax/ pygidium)	Disarticulated	Whole	Fragmented	Torn	Parallel	Inclined	Vertical	
T1	–	100%	–	–	–	–	100%	100%	–	–	–	58.3%	41.7%	12
T2	–	100%	–	–	94.1%	–	5.9%	94.1%	5.9%	–	5.9%	41.2%	52.9%	34
T3	–	–	100%	–	23.8%	38.1%	38.1%	100%	–	–	100%	–	–	21
T4	11.5%	55.7%	32.8%	–	17.2%	7.4%	75.4%	100%	–	–	99.2&	–	0.8%	122
T5	–	–	–	100%	–	–	–	–	–	100%	100%	–	–	5
T6	–	100%	–	–	38.8%	–	61.2%	78.6%	21.4%	–	100%	–	–	103

Conventions: *n* = sample number.

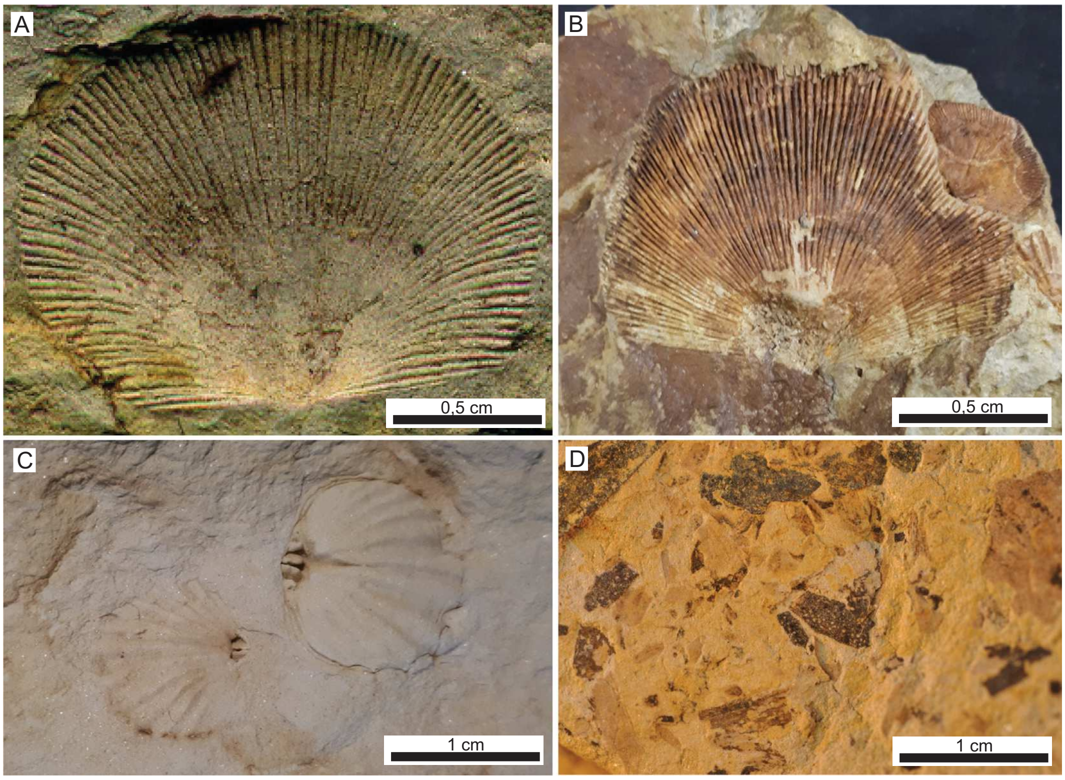


Fig. 4. Examples of Taphofacies 1 - Facies Sf. (A) and (B) Entire and disarticulated valves of *Schuchertella* sp. (U-1549); Two disarticulated valves of *Australocoelia* sp. (U-1293); fragments of *Spongiophyton* spp.

bedding planes. All carcasses of trilobites are extended, entire and articulated (cephalon-thorax-pygidium) and oriented parallel to bedding plane. The brittle stars are disarticulated, occurring as isolated complete arms. The skeletal remains are horizontal, and the association is loosely packed in the sedimentary matrix with slightly bioturbated beds representing expressions of the Cruziana Ichnofacies (ichnogenera *Planolites*, *Rhizocorallium*, *Schaubcylindrichnus*, and *Teichichnus*), besides fragments of plants.

In the third interval (161 m), T4D-I (Devonian I Sequence) occurs in the São Domingos Formation (Emsian) with the skeletal remains including brachiopods (Discinidae *Orbiculoidea* sp.) and scolecodonts (*Paulinites paranaensis*). Whole discinids are positioned parallel to bedding planes; 45% brachiopod shells are articulated (with dorsal-ventral flattening). Scolecodonts occur totally disarticulated and scattered in the sedimentary layer, all of them loosely packed in the matrix. Isolated trace fossils, including *Palaeophycus*, *Planolites*, *Asterosoma*, *Teichichnus*, *Diplocraterion*, and *Cylindrichnus* also represent the Cruziana Ichnofacies.

The remainders of the examples fall in the Givetian (HST of the Devonian II Sequence) and are assigned to taphofacies T4D-II. In comparison to older examples these samples show an abundance of crinoid columnals, as well as lingulids and trilobites. They also occur in siltstones.

The fourth interval (232.8 m) is characterized by isolated tentaculitids (*Uniconus crotalinus*), complete and parallel-oriented in relation to the bedding-plane. Few plant fragments occur associated and the fossil content occur loosely packed in the matrix.

The fourth interval (240 m) contains multielement skeletons (Trilobita *Metacryphaeus* sp. (Fig. 7C and D), *Calmonia* sp., and Crinoidea *Marettocrinus* aff. *M. hartii* (Scheffler, 2010; Scheffler et al.,

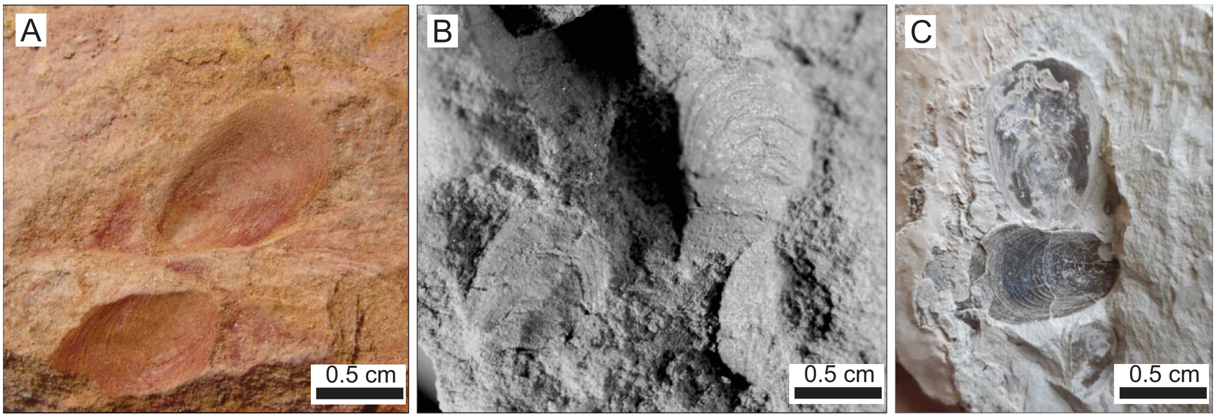


Fig. 5. Examples of Taphofacies 2 - Facies SS-hcs. (A) Infaunal lingulids distributed parallel to the bedding plane (MPI-8484); (B) Infaunal lingulids preserved *in situ*, oriented perpendicularly to the bedding plane (MPI-8484).

Fig. 6. Examples of Taphofacies 3 - Facies SL-hcs. (A) Partial disarticulation (thorax-pygidium) of *Metacryphaeus* sp. (MPI-13000); (B) Columnals of *Marettocrinus* sp. (MPI-13001); (C) Fragments of *Spongiophyton* spp.

2015; Fig. 7B) and Stylophora Mitrata *Placocystella langei*; Fig. 7G), and bivalved shells (infaunal lingulids, epifaunal *Derbyina* sp. (Fig. 7H), *Australocoelia* sp.). Trilobite remains exhibit three taphonomic classes (Fig. 7A, D and E): (I) 30% are completely articulated, bent or extended, parallel to the bedding plane, (II) 45% are articulated thorax and pygidium, and (III) 25% isolated pygidia (Fig. 7E).

Disarticulated crinoids occur in the form of columnals or small pluricolumnals, parallel to the bedding plane without preferential hydrodynamic orientation. The stylophorans occur partially disarticulated (with the two spines and the aulacophore missing) and entire and positioned parallel to the bedding plane. The brachiopods occur as entire, disarticulated valves, oriented parallel to the bedding plane. This fossil association is loosely packed. Plant fragments (*Spongiophyton* spp.) are present and the trace fossils association present a dominance of *Teichichnus* and *Diplocraterion* with protrusive and retrusive spreiten, as well *Rusophycus*, *Planolites*, and *Cylindrichnus* corresponding to Cruziana Ichnofacies (Sedorko et al., 2018b).

In the fifth sedimentary interval (246.50 m), tentatively placed in T4 based on association, loosely packed, skeletons of multielement type (crinoid columnals *Marettocrinus* aff. *M. hartii* (Scheffler et al., 2015)) are present. The skeletons are disarticulated, occurring as isolated and entire columnals, distributed parallel to the bedding plane. Trace fossils also occurs as expressions of the Cruziana Ichnofacies, marked by dominance of *Planolites* and localized *Teichichnus* and *Rusophycus*.

Taphofacies 5 facies SS—T5 (Table 3; Fig. 8). This taphofacies occurs in fine-grained, thin bedded sandstones with small scale HCS, interbedded with shales. This taphofacies has only been identified in Devonian II Sequence. T5D-II (Table 3) occurs in the interval around 247 m (Fig. 2) of the Tibagi-Ventania section (early Givetian). The skeletal remains of the flexible thecae of conulariids (Cnidaria: Conulatae) are recorded (Fig. 8A). The conulariids are intensely damaged (< 20% of the original size of the body) and chaotically positioned relative to bedding. Associated indeterminate plant microfragments also occur.

Taphofacies 6 facies SH-L—T6 (Table 3; Fig. 9) occurs in two intervals in the section. In the first interval (T6SD, 20 m, Siluro-Devonian Sequence; Fig. 2), skeletons of bivalved type occur (infaunal lingulids (Fig. 9A and C), *Orbiculoidea* sp. (Fig. 9B), the bivalve *Edmondia* sp. (Fig. 9D) and *Lingulepis wagoneri* (Fig. 9E)). *Orbiculoidea*, *Lingulepis* and *Edmondia* remains are complete valves, with moderate disarticulation (45%), which are oriented parallel to the bedding plane.

Infaunal lingulids are preserved as disarticulated, complete valves as well as fragmented bioclasts parallel to bedding (Fig. 9C). The association is loosely packed in the matrix. Trace fossils occurs as distal expressions of the Cruziana ichnofacies, characterized by *Chondrites, Phycosiphon* and locally *Planolites* and *Helicodromites* (Sedorko et al., 2018b). Indeterminate plant remains are present. In the second interval (Devonian I Sequence) of the São Domingos Formation (150.20 m) analogous facies contains bivalves (*Edmondia* sp.), which are dispersed and entire, mostly with articulated valves, oriented parallel to the bedding plane.

6. Discussion

Taphofacies 1—T1 and Sf facies indicate lower shoreface, above fair-weather wave base (FWWB; Fig. 10). The T1 assemblages display no *in situ* preservation, despite the skeletons being located within their life habitats (no out of habitat transport). The sedimentation rate and the degree of turbulence may be moderate, with no breakage of skeletal elements but high levels of disarticulation. The absence of features such as fragmentation, abrasion, corrosion and bioerosion indicates low residence time at the sediment-water interface despite relatively high energy conditions. Necrolysis and turbulence associated with fair weather waves might have been responsible for disarticulating the skeletal remains. The presence of fragments of land plants is consistent with the influence of storm events near shorelines. The nature of the depositional events and rate of burial for facies T1 includes proximal storm waves and storm-generated submarine flows, as evidenced by large scale hummocky cross stratification formed by combined oscillatory flows and local sediment-gravity flow deposits (Fig. 6).

Taphofacies 2—T2 and SS-hcs facies indicate offshore-transition zone to lower shoreface zone, from the lower end of FWWB to the level of average SWB (Fig. 10). These layers preserve taphofacies T2, with *in situ* infaunal lingulids. Vertical or oblique occurrences associated with hummocky cross-stratification (HCS; SS-hcs facies) and wave ripples on the tops of beds suggest rapid skeletal burial by storm waves/currents (Fig. 10). The ichnological association is dominated by vertical burrows, which in some cases are *Lingulichnus* isp. The facies indicate oxygenated water, rich in suspended organic matter, which is also indicated by the inferred life habits of the preserved taxa (suspension-feeding infauna and shallow burrowers). Some *Lingulichnus* burrows are preserved with articulated lingulid remains at the top, suggesting a failed escape attempt by the brachiopods after pulses of burial. This also indicates that the final burial occurred very rapidly (Speyer and Brett, 1988; Olszewski, 2004), during storm events. In this sense, the infaunal lingulids were disrupted by the large mass of sediment deposited in a short-lived event and were buried *in situ* or in escape positions; very similar occurrences have been reported by Harris and Gess (2018) from the Emsian of South Africa. Local occurrences of Skolithos Ichnofacies are in accordance with high energetic processes and short colonization of the substrate.

According to MacEachern and Pemberton (1992), lower shoreface to offshore-transition deposits generally show strong ichnological variability because of contrasting regimes in terms of intensity and

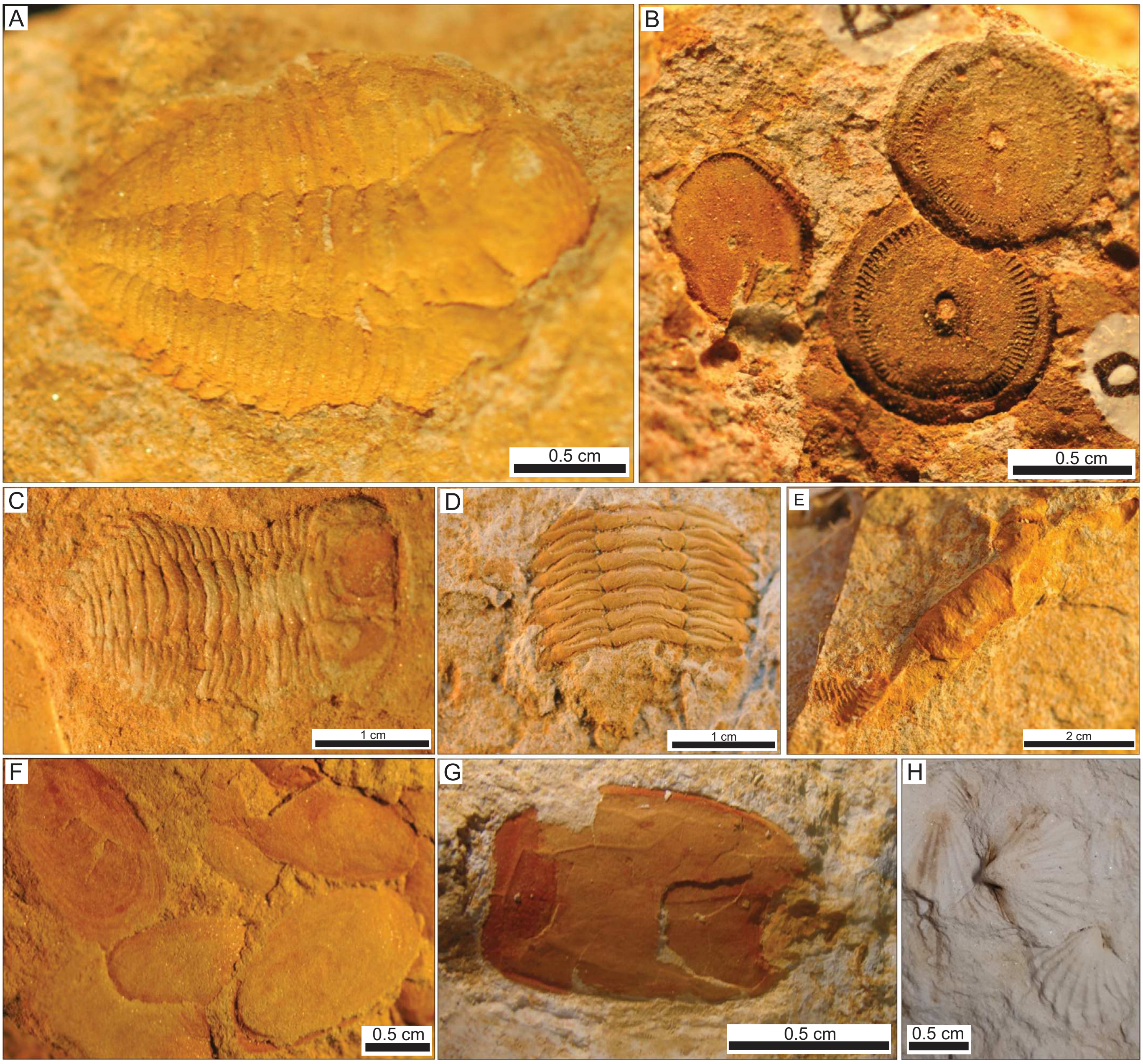


Fig. 7. Examples of Taphofacies 4 - Facies SL-p. (A) Extended carcass of a complete trilobite *Metacryphaeus* sp. (MPI-8234A); (B) Columnals of *Marettocrinus* sp. (MPI-8268); (C) Complete, bent carcass of *Metacryphaeus* sp. (MPI-8215A); (D) Articulated thorax of *Metacryphaeus* sp. (MPI-8225); (E) Horizontal bioturbation (*Planolites* isp.) intersecting a bedding plane containing a calmonid pygidium (MPI-1494A); (F) Infaunal lingulids distributed parallel to the bedding plane (MPI-8410); (G) Echinoderm Mitrata *Placocystella langei* (MPI-9088) well preserved, oriented parallel to the bedding plane; (H) Disarticulated valves of *Derbyina* sp. (U-1232) distributed parallel to the bedding plane.

frequency of normal waves (FWWB) and storm events (SWB) (SS-hcs facies). Two distinct situations occur during storm events. The first occurs with sedimentation pulses followed by the vertical migration of infaunal organisms to compensate for the high sedimentation rates (Zonneveld and Pemberton, 2003; Zonneveld et al., 2007; Horodyski et al., 2015). The second takes place during higher energy events when substrate erosion, exhumation and local transport of the fauna take place.

Taphofacies 3—The T3 and SL-hcs facies also indicate offshore-transition zone to lower shoreface deposits (Fig. 10). The facies (SL-hcs) and taphonomy of multielement fossil skeletons indicates a mixture of bioturbated background and HCS sandstones representing storm event deposits. The partial to complete disarticulation in trilobites (higher percentage of moults than complete specimens), and nearly complete disarticulation in crinoids (higher percentage of columnals than pluricolumnals), indicates that the skeletal remains were disarticulated after death by necrolysis, and/or, scavenging organisms, as evidenced by some horizontal bioturbation (*Planolites*; Fig. 7E). Environmental energy was moderate during background conditions as indicated by levels of bioturbation, but most of the sandy sediments accumulated during storm episodes with high sedimentation rate (Fig. 10). Crinoid and trilobite debris beds are parautochthonous, despite significant disarticulation, and indicate time-averaged accumulations during conditions of low background sedimentation. Burrowing scavengers acted during low energy background conditions in the TAZ, *i.e.* when the waves were weaker (in intervals between storms) and sedimentation rates were low. The final burial of the skeletal remains (in the association as a whole) took place when sedimentation rates increased

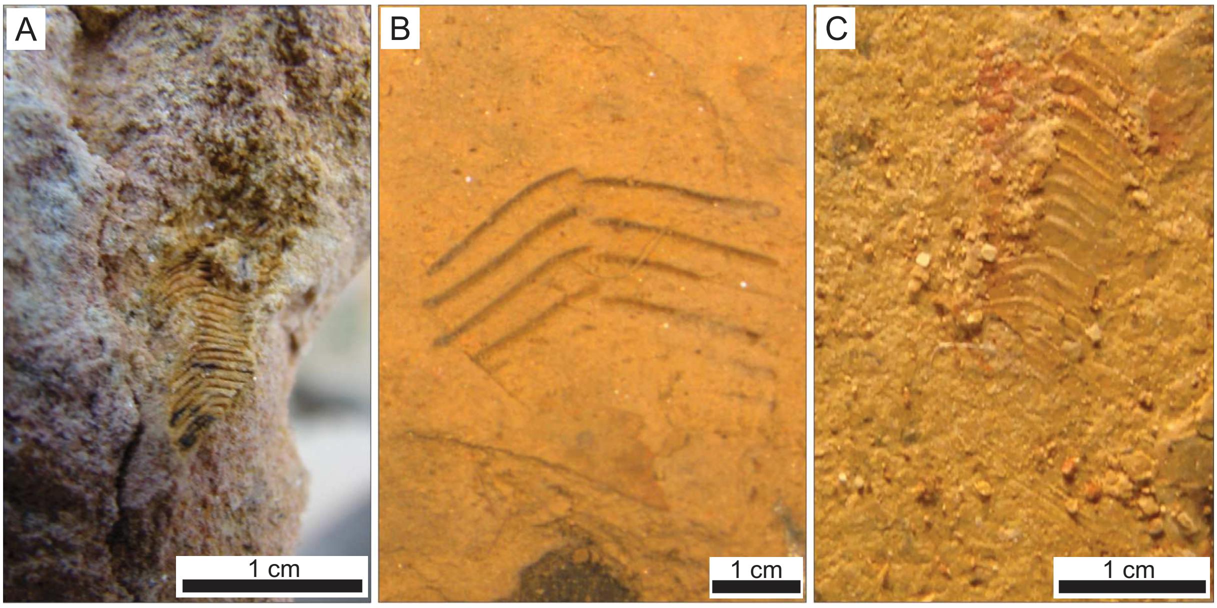


Fig. 8. Example of Taphofacies 5 - Facies SS. (A) Conulariid torn (MPI-13003).

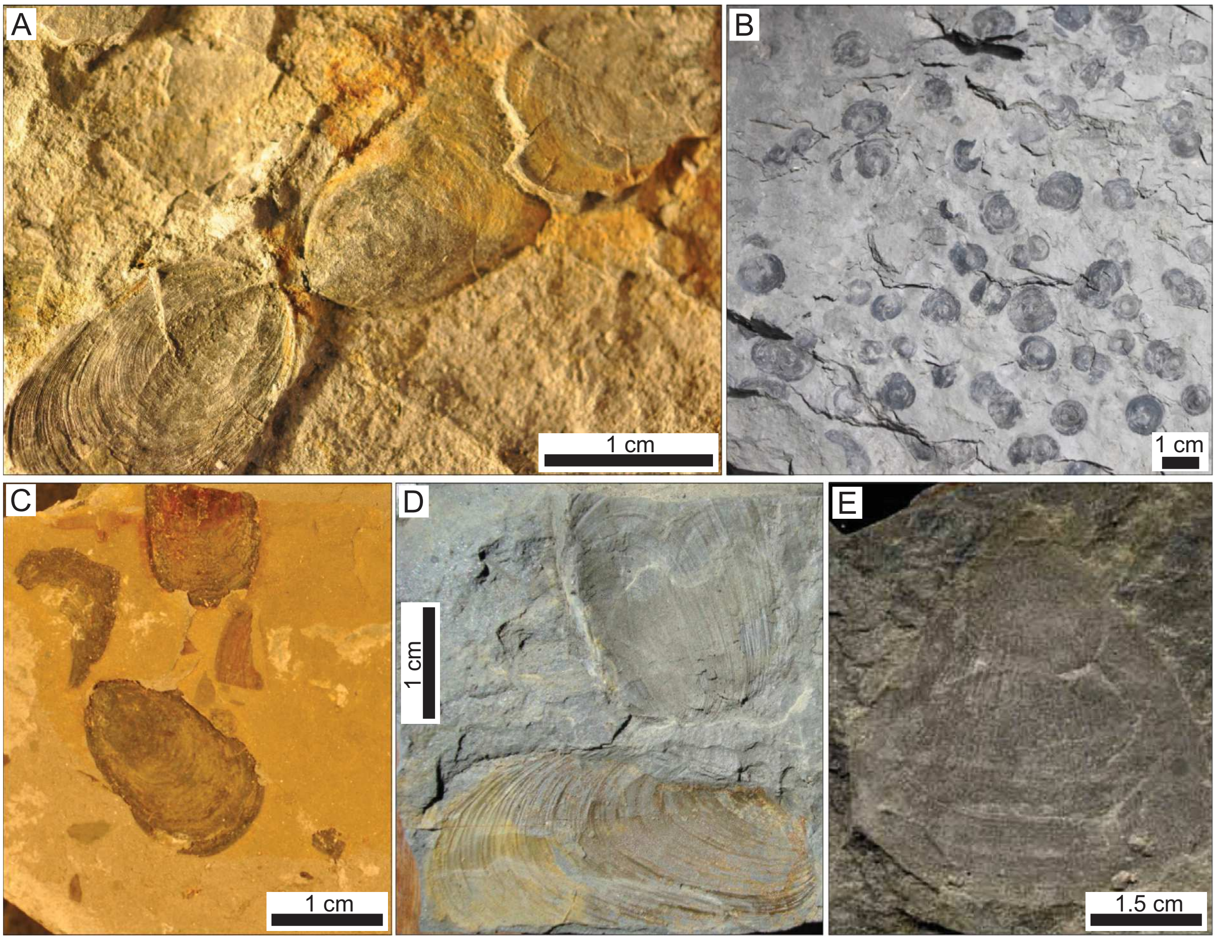
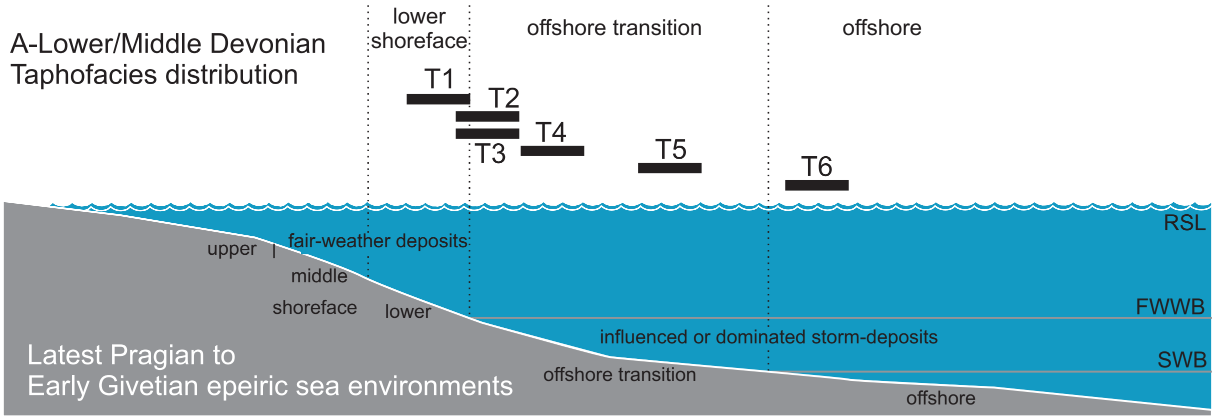


Fig. 9. Examples of Taphofacies 6 - Facies SH-L. (A) A bimodal stringer arrangement of lingulids (MPI-13002); (B) valves of *Orbiculoidea* sp. (MPI-13002C) on the bedding plane; Disarticulated (C) Fragments of lingulids (MPI-13002); (D) Disarticulated valves of *Edmondia* sp. (MPI-13002A); and (E) Disarticulated valve of *Lingulepis* sp. (MPI-13002B) on the bedding plane.



B-Paleoenvironmental inferences of biostratinomic parameters

T	Taphonomic processes
T1	High disarticulation caused by necrolysis and/or oscilatory flows in the TAZ above FWWB; moderate energy
T2	Rapid burial caused by episodic sedimentation during storm events with fair weather waves interbedded. Re-excavation burrows associated
T3	Low exposure in the TAZ; mixed of background and events deposits (HCS); benthic scavenger disturbance;
T4	High residence time in the TAZ; final burial by storm flows; environmental condensation and biodiversity richness timing-averaging
T5	Low exposure in the TAZ; reworking by storm wave currents; minor transport in offshore transition
T6	Rapid burial below storm wave base in dysaerobic substrate; obrution deposits; reworked linguliforms bioclasts associated for episodic flows.

Fig. 10. (A) Distribution of the six taphofacies here recognized of the Lower/Middle Devonian. (B) Paleoenvironmental inferences of taphonomic processes.

because of storm events. Deposition of thin layers of silt without substantial bottom disruption may also account for the absence of articulated crinoids as these events may not have been lethal to elevated stalked crinoids, although further search may yield some articulated remains.

Semi-articulated moults suggest abrupt burial by silt or sand, which preserved these delicate exuviae intact but in layers sufficiently thin to permit escape by live trilobites. Similar molt beds were reported by Speyer and Brett (1986) from distal mudstones in the Appalachian Basin. In an analysis of trace fossils, Sedorko et al. (2018c) also document analogous facies of mixed-events represented by storm and fair-weather waves suites from Early Emsian beds (Paraná Basin), evidenced by dense *Zoophycos* occurrences. The associated macrofossils are characterized by both articulated and disarticulated, chaotically distributed in the matrix, univalved *Tentaculites* whole and parallel to the bedding plane, whole trilobites, and isolated vertically-oriented columnals of crinoids.

Taphofacies 4—The T4 and SL-p facies characterizes distal regions of the basin (Fig. 10), in this sense it is analogous to several of the taphofacies reported by Speyer and Brett (1986). The facies represent offshore shelf environments, between FWWB and SWB (Fig. 10). This taphofacies is dominated by horizontal bioturbation, with a smaller proportion of vertical burrows, characterizing expressions of the Cruziana Ichnofacies (Sedorko et al., 2018b). Locally, equilibrium trace fossils (*e.g. Diplocraterion*) suggest relocation of the tracemakers into the substrate as response to erosion and/or high sedimentation rates. These features, as well as the taphonomy suggest high residence time and low turbulence interrupted by episodic sedimentation events (SL-p).

Disarticulation was a result of bacterial decay processes or benthic scavengers (see Speyer and Brett, 1986 for discussion of scavenger mediated disarticulation); bioturbation may have increased the input of skeletons into the TAZ during low sedimentation background conditions characterized by high residence times. Considering the differential preservation with mostly disarticulated remains mixed with a few articulated skeletons, the assemblage demonstrates within habitat time averaging (*cf.* Kidwell, 1986; Kidwell and Bosence, 1991), which may have increased and biased the apparent relative richness as consequence of the mixing of local patches of differing species composition (Tomašových and Kidwell, 2009).

The occurrence of complete trilobite carcasses, as well as moults, and ophiuroid arms indicates episodic pulses of silt burial. It should be remembered that ophiuroids can escape thinner pulses, up to 10 cm of sediment accumulated over the course of a few hours (Schaefer, 1972). However, these delicate echinoderms may also autotomize some rays as part of their response to physical disturbances; hence leaving arm fragments behind in buried seafloors (*e.g.* Clements et al., 1994; Oji and Okamoto, 1994; Sköld and Rosenberg, 1996; Gorzelak and Salamon, 2013). In similar age sediment in the Devonian of South Africa, Reid et al. (2015) observed an obrution deposit in which large numbers of disarticulated ophiuroid arms were overlain by sediment containing largely articulated ophiuroids in escape positions but missing some arms. This setting suggests partial autotomy associated with stress prior to burial.

Taphofacies 5—T5 and SS facies indicates distal environments in the offshore-transition zone (Fig. 10). In this interval, skeletons were composed exclusively of flattened and torn conularian thecae. After death, these cnidarians were subject to taphonomic loss at the sediment-water interface, for they are easily destroyed given their relatively soft skeletal periderm (Van Iten, 1991). Simões et al. (2000) and Rodrigues et al. (2003) reported this occurrence for the Brazilian Devonian. It has been suggested that conularians (Conulatae) lived mainly in relatively deep waters, at or below the level of storm wave base level

(SWB), and were preserved in obrution deposits (Van Iten, 1991; Van Iten et al., 2013; Simões et al., 2000; Rodrigues et al., 2003). However, Bosetti (2004) and Bosetti et al. (2009, 2014) recorded the occurrence of these organisms in vertical position (*in situ*) in thick siltstones, representative of shallower water settings (offshore-transition zone). The latter are represented by two inclined specimens, with their bases converging to a common center (taphonomic class II of Rodrigues et al., 2003). According to Rodrigues et al. (2003), the facies indicate that skeletal remains were preserved above SWB. These two interpretations offer different bathymetric ranges. We suggest that the bathymetric range of conularians may reach shallower levels of the transition zone below FWWB. However, we also suggest that these skeletal remains suffered local reworking during sediment-gravity flow (SS facies) by storm-generated deposition. These environmental factors contributed to the increase of torn skeletal remains. This occurrence is considered to represent a parautochthonous assemblage (Kidwell, 1986; Kidwell and Bosence, 1991).

Taphofacies 6—The T6 and the SH-L indicate the most distal environments of the section (Fig. 10); this taphofacies was not recognized in the Givetian where environments may have been largely shallower than those favoring T6 assemblages, as expected in a progradational stacking pattern. The facies showed that the offshore zone, although generally of low hydrodynamic energy, was affected by the sporadic action of gradient currents caused by storm events, given the presence of (thin) lenses of sand.

This environment was much less well oxygenated than those discussed above, with lower oxic to dysoxic bottom waters and anoxic conditions somewhat below the sediment-water interface, as indicated by the occurrence of pyrite within the layers, locally filling *Phycosiphon*. Bioturbation is characterized mostly by *Phycosiphon* and small *Chondrites*, which can indicate low oxygen levels and low energy environments (Bottjer et al., 1988). The taphonomic and paleoecologic features demonstrate an association of indigenous taxonomic groups, such as *Edmondia* sp. in life position, with locally transported skeletons *i.e.*, fragments of reworked infaunal lingulids, and disarticulated *Orbiculoidea* and *Lingulepis*, preserved in the very fine sandy lenses below storm wave base (SWB). The *Edmondia* remains are usually articulated specimens but these are associated with a few disarticulated valves. Kotzian and Simões (1997) suggested that this group lived in deep environments, out of direct wave action. The taphonomic and paleoecologic features observed herein suggest that they were buried *in situ* in deeper dysoxic settings and thus, probably lived below FWWB. A similar context was reported by Sedorko et al. (2018a), but with more diverse macrofossil assemblage (their Taphofacies TC).

According to Mergl (2001, 2010) and Comniskey (2011), *Orbiculoidea* sp. are a group that preferred shallow waters (shoreface to offshore transition). However, numerous other studies have shown that orbiculoids were abundant organisms in offshore, typically dysoxic facies (Campbell, 1946; Brett et al., 1991; Boyer and Droser, 2009; Sedorko et al., 2018a). Isolated skeletons buried in transitional offshore to offshore sediments are thus considered to be autochthonous to parautochthonous. The preservation of shells in this taphofacies indicates that inputs of distal gradient currents, related to storm events, locally fragmented the very fragile skeletons of orbiculoids, but also produce obrution deposits of molluscan fauna (*Edmondia*). Similar deposits including both fragmented thin shelled brachiopods and some *in situ*, articulated, and rarely, pyritized bivalves occur in distal basinal dark shales in the Hamilton Group (Speyer and Brett, 1986, 1988; Brett et al., 1991).

6.1. Storm-related taphofacies from Paraná Basin

Storm disturbances, typically associated with tropical storms-hurricanes, have been considered as obvious agents on the preservation of benthic communities (*e.g.* Speyer and Brett, 1988; Fürsich and Oschmann, 1993; Brett et al., 1997; Fursich and Pandey, 2003; Parras and Casadío, 2005). Winter storms (storms of higher latitudes) are to be expected at latitudes 60° to 80° S under a cool-temperate climate zone, of the Paraná Basin during Early to Middle Devonian times (Cooper, 1977; Melo, 1988; Isaacson and Sablock, 1990; Scotese et al., 1999; Torsvik and Cocks, 2013; Matsumura et al., 2015). Storm-related taphofacies recurrence during the latest Pragian to early Givetian points to two sedimentation agents: direct wave erosion by winter storms and related sedimentary processes related to combined flow during deposition (*e.g.* turbidity currents and oscillatory flow). Winter storms are considered more capable of affecting sediment transport than hurricanes, due to longer duration and larger coverage area in higher latitudes (Swift and Nummedal, 1987). Therefore, winter storms of high latitudes should generate more persistent currents in space and time (Swift et al., 1983; Swift and Niedoroda, 1985; Duke, 1985; Lavina et al., 1991; Peck et al., 1999).

The lithofacies (facies SS, Sf, SS-hcs, SL-hcs, SL-p, SH-L; Table 1) and taphofacies recurrence show the persistence of storm events (sediment-gravity and oscillatory flows, suspension sediments and turbidity currents) during the prolonged interval (~20 million years) studied here. During the action of storm-generated waves in shallow marine environments, not only erosion and transport take place, but a large volume of fine-grained sediments must be brought into suspension and transported to offshore. The latter can improve the quality of the fossil record by fostering obrution deposits (Brett and Seilacher, 1991).

Fossils preserved in life position from Taphofacies 2, 4, and 6 (Facies SS-hcs, SL-p and SH-L), for instance, indicate high mortality related to high sedimentation in response to such events. The T1 (Sf), T3 (SL-hcs) and T5 (SS) show storm-influenced deposition. However, much accumulation seems to be time-averaged because most skeletal material is strongly disarticulated (Table 3). Features of T5 indicate turbulent processes (SS) and reworking caused by storm currents below storm wave base, as evidenced by intensely damaged conulariids. The impoverished expressions of the Cruziana Ichnofacies and the recurrence of Skolithos Ichnofacies also suggest a general high energetic regime and moderate to high sedimentation rates (Sedorko et al., 2018b), corroborating the interpretations provided by the taphofacies analysis.

6.2. Comparative taphonomy of Malvinokaffric and other Devonian faunas

Similar taphonomic evaluations in shoreface to offshore transitions in the Paraná Basin ranging in age from Pragian to Givetian (*e.g.* Simões et al., 2000; Rodrigues et al., 2003; Ghilardi, 2004; Zabini et al., 2010, 2012; Bosetti et al., 2012; Horodyski et al., 2014; Comniskey et al., 2016; Richter et al., 2017; Sedorko et al., 2018a, 2018c) indicate the importance of episodic storm events as a key taphonomic control on preservation of marine benthic Malvinokaffric communities. In this sense, the recurrence of similar suites of facies indicate that seasonal winter storms in this cool climate zone exerted a strong influence in the sedimentation and taphonomy on the shelves of Paraná Basin during the Pragian-Givetian interval (~20 million years).

The cycles and their taphofacies can also be compared to previously described facies from other settings to partially test the generality of the patterns observed in the Paraná Basin. Here we can compare with examples first from the Lower-Middle Devonian of another depositional basin within the Malvinokaffric Realm and second from a lower latitude clastic dominated setting of comparable age (Givetian) from the Appalachian (Tables 4–6). In this sense, generalities may emerge that provide insight into the similarities and differences in processes.

Penn-Clarke et al. (2018) discussed the facies and sequence stratigraphic context from onshore to offshore settings from Emsian-Eifelian facies of Bokkeveld Group (South Africa). Only lower shoreface to offshore settings are comparable with our study (Table 4). Proximal lower shoreface paleoenvironments in the Clanwilliam Basin are comparable to SL-hcs facies of the Paraná Basin. The trace fossil assemblage presents a mixture of Cruziana and Skolithos ichnofacies with low

Table 4
Comparison of Emsian-early Givetian shoreface zone-transitional offshore taphofacies.

Paraná Basin, Brazil (Emsian Early Givetian)	Cape Basin, South Africa (Emsian-Eifelian)	Anti-Atlas, Morocco (Emsian)	Appalachian Basin, NY (Givetian)
Facies/SED structures			
Poorly sorted, fine-grained sandstone	Poorly sorted fine-grained sandstone		
Trough cross bedding	Trough cross bedding	Trough cross bedding	Trough cross bedding
HCS, SCS	HCS/SCS	HCS/SCS	HCS/SCS
Wave, current interf. ripples	Wave, current interf. ripples	Wave, current interf. ripples	Wave, current interf. ripples
	Rip-up clasts	Rip-up clasts	Rip-up clasts
Faunal composition			
Lingulids	Lingulids (*in situ*)	?	Rare lingulids
Australospirifer	*Australospirifer*	*Euryspirifer*	Mucrospirifer, Spinocyrtia
	Derbyina	Nests of *Meganteris*	*In situ* spiriferids
Abundant bivalves	Abundant bivalves	Abundant bivalves	Abundant bivalves
Metacryphaeus, Calmonids	*Metacryphaeus*	Dalmanitids	Greenops
Calmonids	Calmonids	Homalonotids	Homalonotids
Plant fragments	Plant fragments	Plant fragments	Rare plant fragments
Ichnofacies/trace fossils			
Skolithos ichnofacies	Cruziana-Skolithos Ichnofacies	Cruziana-Skolithos Ichnofacies	Cruziana-Skolithos Ichnofacies
Traces scattered	Traces scattered	Traces rare	Traces rare
Schaubcylindrichnus, *Palaeophycus*, *Lingulichnus*, *Diplocraterion*, *Cylindrichnus*, *Rusophycus*, *Arenicolites*	*Cruziana/Rusophycus*, *Diplocraterion*, *Planolites*, *Palaeophycus*, *Skolithos*	*Cruziana/Rusophycus*, *Planolites*, *Palaeophycus*	*Cruziana/Rusophycus*, *Planolites*, *Palaeophycus*
Taphonomic features			
Disarticulated shells	Disarticulated shells	Disarticulated shells	Disarticulated shells
Little or no fragmentation	Fragmented	Fragmented	Fragmented
Crinoid columnals	Crinoid columnals	Crinoid columnals	Crinoid columnals
Rare *in situ* lingulids	*In situ* lingulid	*In situ* lingulids	Rare *in situ* lingulids
Mainly disarticulated trilobite	Disarticulated trilobites	Disarticulated trilobites	Disarticulated trilobites

Table 5
Comparison of Emsian-early Givetian transition zone-offshore taphofacies

Paraná Basin, Brazil (Emsian early Givetian)	Cape Basin, South Africa (Emsian-Eifelian)	Anti-Atlas, Morocco (Emsian)	Appalachian Basin, NY (Givetian)
FACIES/SED STRUCTURES			
	laminated, massive clays		
	silt to fine grained sand		
	plane to ripple laminated		
lenses of graded sandstone	lens of graded sandstonne	lenses of graded sandstone	
FAUNAL COMPOSITION			
Australocoelia, Derbyina, Schuchertella	*Astralocoelia, Derbyina, Schuchertella*	*Meganteris, Schuchertella*	*Schuchertella*
abundant bivalves	abundant bivalves	abundant bivalves	abundant bivalves
Metacrypheus, calmonids	*Metacrypheus*	dalmanitids	*Greenops, Eldredgeops*
calmonids	Calmoinia	homalonotids	homalonotids
Tentaculites	*Tentaculites*	*Tentaculites*	*Tentaculites*
Mitrate: *Placocystella*	Mitrate: *Placocystella*		
plant fragments	plant fragments	plant fragments	rare plant fragments
ICHNOFACIES/TRACE FOSSILS			
Cruziana Ichnofacies	Cruziana Ichnofacies	Cruziana Ichnofacies	Cruziana Ichnofacies
Teichichnus, Planolites, Asterosoma, Rusophycus, Thalassinoides, Phycosiphon, Bifungites, Rosselia, Rhizocorallium, Chondrites, Zoophycos, Schaubcylindrichnus, Palaeophycus, Cylindrichnus	*Diplocraterion*	*Zoophycos*	*Zoophycos*
Skolithos Ichnofacies	*Zoophycos* (rare)	*Zoophycos* (common)	*Zoophycos* (common)
Palaeophycus, Diplocraterion, Cylindrichnus, Rusophycus, Schaubcylindrichnus			
TAPHONOMIC FEATURES			
entirely disarticulated	mainly disarticulated shells	mainly disarticulated shells	mainly disarticulated shells
little or no fragmentation	minor fragmentation	minor fragmentation	minor fragmentation
crinoid columnals	crinoid columnals	crinoid columnals	crinoid columnals
fully articulated trilobites	fully articulated trilobites	fully articulated trilobites	disarticulated trilobites
moults	moults	moults	moults
semiarticulated mitrates	articulated mitrates	none	none
ophiuroid arms	ophiuroid arms/complete	??	rare artic asteroids
disart. crinoid columnals	disart, crinoid columnals	disartic crinoid columnals	disartic. Crinoid columnals
crinoid pluricolumnals	crinoid pluricolumnals	crinoid pluricolumnals	crinoid pluricolumnals
	articulated crowns	??	articulated crowns

Table 6
Comparison of Emsian-early Givetian.

Deeper dysoxic facies	
Paraná Basin, Brazil (Eifelian-Early Givetian)	Appalachian Basin, NY (Givetian)
Facies/SED structures	
Dark gray-black shale	Dark gray to black shale
Laminated; some sand lenses	Laminated; thin silt lenses
Faunal composition	
Orbiculoids	Orbiculoids (rare)
Lingulepis	Lingulids (rare)
Edmondia, nuculid bivalves	Nuculid bivalves, *Paleoneilo*
	Leiorhynchid brachiopods
	Ambocoeliid and chonetids
Trace fossils	
Chondrites	*Chondrites*
Phycosiphon	
Helicodromites	
Taphonomic features	
Med disarticulation ~45%	Moderate disarticulation > 45%
Complete valves	Complete & fragmented valves
Fragmented orbiculoid valves	Fragmented brachiopods
Rare *in situ Edmondia*	Articulated nuculids
Rare *in situ* lingulids	Rare *in situ* lingulids
Pyrite present	Pyrite present

diversity in amalgamated sandstones, which may reflect high sedimentation rates or frequent reworking by storm activity.

The modes of macrofossil preservation are equivalent to the here identified Taphofacies 1, indicating high energy storm processes. Abundant articulated lingulid brachiopods in life position associated with *Lingulichnus* were also reported in coeval strata from South Africa (Harris and Gess, 2018), which is similar to Emsian taphofacies T2 herein. The more distal transition and offshore zone from the Clanwilliam Basin are interpreted as storm influenced offshore deposits, comparable to the SL-p or SL-hcs facies of the Paraná Basin. These strata present similarities in the faunal assemblages and taphonomy to taphofacies 3 and 4 of Paraná Basin.

In South Africa the distal facies includes beds with three grades of trilobite preservation, with fully disarticulated material being typical, but presenting completely articulated dalmanitid trilobites and thoracopygidia (Reid et al., 2015; C. Brett personal observations). Molt beds suggest rapid burial as in taphofacies T4D-II herein. In the Emsian Voorstehoek Formation occurs some obrution deposits composed of fully articulated ophiuroids, mitrates (*Placocystella* and *Paranacystis*), and trilobites. These deposits overlie levels with disarticulated crinoid columnals and brachiopod valves, as well as disarticulated complete arms of ophiuroids (Reid et al., 2015). These obrution deposits are similar to bedding planes preserved in taphofacies T4D-II in the highstand of late Eifelian-Givetian sequence II in the Paraná Basin, which, likewise, include examples of partially articulated ophiuroids and mitrates of the same genera.

Overall, the similarities of sedimentology and taphofacies in shoreface to shallow offshore settings in the late Early to Middle Devonian of South Africa and Brazil suggest that a similar taphofacies and environmental model can be applied for high latitude Malvinokaffric assemblages that accumulated along the southern part of Gondwana. This comparison indicates a remarkable degree of lateral and temporal persistence of facies.

In other hand, the Emsian siliciclastic facies from Morocco corresponds to lower latitude areas of Gondwanaland (Mdaouer-el-Kbir Formation - formerly Rich 3, Hollard, 1967; Jansen et al., 2004). The skeletal component of the capping shell beds consists of disarticulated often fragmented shells of spiriferids (*e.g. Euryspirifer*) and strophomenid brachiopods, crinoid debris, bryozoans, and homalonotid trilobites. They have sharp to abruptly gradational contacts with underlying sandstones. These beds form a distinctive taphofacies, representing siliciclastic starved open shelf conditions during transgressions, that seemingly have no counterpart in the TSTs of coarsening upward cycles of the Paraná or Clanwilliam basins of southern Gondwana. The shell beds are overlain by shale mudstones heavily bioturbated, silty, calcareous mudstones, commonly with *Zoophycos*. Where observed, no dark shaly facies comparable to T6 of the Paraná Basin was found at the bases of the cycles. Upper portions of these cycles consist of hummocky cross-bedded siltstone and sandstone with local clusters of articulated, *in situ* terebratulid brachiopods (*Meganteris*; closely related to *Derbyina*). In two cycles are obrution beds possibly comparable to the well preserved *in situ* lingulids seen in the Paraná and Clanwilliam Basins.

Despite some similarities of the Moroccan and southern Gondwanan litho-, bio, and taphofacies, especially in the upper middle and upper (offshore-transition zone to shoreface) parts of the cycles there are key differences in the overall suite of taphofacies. Most notable, thicker shell beds at the bases of the Moroccan cycles are absent in the southern basins and there appears to be a stronger degree of bioturbation, especially by *Zoophycos* in more distal facies. In Paraná Basin, *Zoophycos* is very abundant in tempestites, which was interpreted as a taphonomic artifact resulting from erosion of shallow-tiers and preferential preservation of deep-tiers structures, while in distal zones *Zoophycos* common occurs in low to moderate bioturbation degree (*e.g.* Sedorko et al., 2018c).

Finally, the Middle Devonian Hamilton Group taphofacies has some similarities to the Paraná Basin facies, but they are not comparable to the siliciclastic dominated facies of the latter. Much stronger comparison can be made with shale-mudstone-siltstone cycles, which are well represented in the Middle Devonian (Givetian) of central New York. These cycles, like those in the Emsian of Morocco, begin with a sharply based skeletal debris bed ranging from silty and muddy packstones to grainstones, with abundant full valves to highly fragmented brachiopods, crinoidal debris, bryozoans, and corals. Basal shell rich facies grade abruptly into dark gray shales with dysoxic faunas and skeletal beds are sharply overlain by dark gray to black shales with scattered small and brachiopods, especially thin shelled orbiculoids, rhynchonellids ("*Leiorhynchus*", *Eumetabolotoechia*), ambocoeliids, and chonetids, as well as small mollusks. Most fossils are disarticulated and may be fragmentary and partially decalcified. Despite differences in the brachiopod genera these facies are similar to the most distal taphofacies, T6, of the Paraná Basin. The fragmentation of more fragile thin-valved brachiopods is similar in both cases despite a lack of evidence for out of habitat transport. Medial portions of cycles are heavily bioturbated, especially by *Zoophycos*, and pass gradationally into amalgamated silty to sandy mudstones. Body fossils may be scarce but occur in local lenses or as *in situ* well preserved, articulated and often closed-valved brachiopods (*e.g. Spinocyrtia*, *Tropidoleptus*, chonetids, strophomenids) and clams (*Grammysia*, *Modiomorpha*, pterioids); diversities can be moderate, but fossil densities are low. There do not appear to be strictly comparable to offshore such as taphofacies T-4, in the Paraná Basin successions.

A major difference with the Paraná and Clanwilliam basin offshore facies, involves the abundance of *Zoophycos* in such environments in the Appalachian Basin, while in Paraná Basin the abundance of *Zoophycos* is related to high frequency of storms and erosion of shallow-tier structures (Sedorko et al., 2018c). *Zoophycos* in distal facies from Paraná Basin occur in low densities, associated with *Chondrites* or *Phycosiphon* (Sedorko et al., 2018c). These facies shallow upward into increasingly silty to sandy mudstones, which are typically sparsely fossiliferous, but include lenses of skeletal debris, primarily of disarticulated valves of brachiopods and bivalves, plus crinoid ossicles. Intercalated silty beds exhibit hummocky cross-stratification and may be locally amalgamated. Occasional obrution beds show perfectly preserved trilobites and moults, especially asteropygids (*Greenops*) and homalonotids, crinoids or even starfish. These beds are comparable to those of taphofacies T-3 of the Paraná basin, but trilobites tend to be less common.

In proximal areas trace fossils are not prominent but may include rare *Planolites*, *Palaeophycus* and *Skolithos*. Articulated fossils are rare, but occasional crinoid crowns and even asteroids (starfish) occur within these sandy facies. This facies, interpreted as lower shoreface environments, differs in specifics of taxonomic composition from those in the Givetian of the Malvinokafric Province. However, there are strong analogies in terms of sedimentary structures, in the scarce trace fossils, lack of extensive bioturbation, lenses and stringers of probably transported crinoid ossicles. These intervals may be abruptly overlain by shell beds, or even coral biostromes and other skeletal rich beds associated with the base of the next cycle. Again, there do not appear to be any analogs to these facies in the Paraná or Clanwilliam basin facies.

7. Conclusions

The six taphofacies recognized here show changing depositional conditions in paleoenvironments ranging from shoreface to offshore shelf settings. The taphofacies, lithofacies and high-latitude paleogeographic context of the Paraná Basin atest the importance of storm-influence in the genesis of all Lower/Middle Devonian Malvinokaffric assemblages here recognized. These assemblages are result of winter storms, characterized by recurrence of storm-related taphofacies during the latest Pragian to early Givetian. A comparative taphonomic approach shows that the taphofacies of the late Early to Middle Devonian Paraná and Clanwilliam Basin are similar to one another. The Malvinokafric taphofacies of Brazil and South Africa also bear resemblances to the taphofacies of the Emsian in Morocco and those originally recognized in the Middle Devonian of New York, mostly in the coarser proximal facies representing shoreface to shallow offshore transition zone despite differences in fauna. The processes in shallow shoreface to transition zone environments were affected by storm deposition and show a similar spectrum of storm related sedimentary structures. The Malvinokafric assemblage storm preservation may have been controlled by winter storms whereas the comparable storm sedimentation was probably related to tropical storms. This appears to have had little influence on difference on the aspect of facies; if anything, there may have been a greater frequency and thickness of hummocky to swaley bedded event deposits in Paraná Basin which could indicate a more prolonged or stronger effects of storm waves.

However, there are also major differences between the overall spectrum of taphofacies in the two provinces that may be related to climate and production of skeletal material. The most obvious is that even in the coarser siliciclastic sections of central New York, there are still substantial shell and coral beds that apparently accumulated in shallow shelf environments during transgressions. Somewhat similar shell rich beds are present in the Emsian of Morocco but appear to be lacking in the southern Gondwana basins. We postulate that this may result from substantially lower rates of production of skeletal material in the cool water Malvinokaffric fauna.

Preliminary comparisons are based mainly on observational data, and point up strong similarities of preservational process in analogous environments in the Devonian, but also some apparently significant differences in similar environments in different latitudinal settings. Such comparisons are critical in developing hypotheses of depositional processes, which will require further field testing and more abundant and quantitative data.

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CONSIDERAÇÕES FINAIS

Esta tese demonstra o potencial da Icnologia para elucidar questões de cunho paleoambientais, paleobiológicos, paleogeográficos, estratigráficos e icnoestratigraficos. A abordagem icnológica demonstrou que a Formação Furnas teve suas unidades inferior e média depositadas ainda no Siluriano Inferior, enquanto que dados palinológicos atestam idade Devoniano Inferior para a unidade superior. As três unidades apresentam traços fósseis característicos de contexto deposicional marinho influenciado por maré.

Os demais trabalhos focaram na Formação Ponta Grossa, por exemplo, com a integração de fósseis com macrofósseis para inferir contextos deposicionais e controle tafonômico nas assinaturas icnológicas e tafonômicas. A partir da distribuição das associações icnológicas 4 Sequências Deposionais foram definidas para a Supersequência Paraná, sendo elas *Lower Silurian, Siluro-Devonian, Devonian I* e *Devonian II.*

Também se analisou densas ocorrências de *Zoophycos* na Formação Ponta Grossa, se demonstrando a distribuição deste icnogênero em contextos marinho raso a distal, atestando a variabilidade morfológica das estruturas e inferindo um viés preservacional que favoreceu a preservação de estruturas de *tiers* profundos sob regimes com baixo espaço de acomodação (*elite trace fossil*).

Para a borda noroeste (Mato Grosso do Sul) da bacia, a análise sedimentológica, icnológica e tafonômica demonstrou contexto deposicional mais raso do que na borda leste/sul (Paraná), devido à maior proximidade com a borda da bacia. O contexto progradacional em camadas de idade Pragiano/Emsiano associado a similaridades na composição da macrofauna não permite a inferência de que a Bacia do Paraná estaria subdividida em duas sub-bacias neste intervalo.

A distribuição das suítes icnológicas na Supersequência Paraná também permitiu traçar curvas paleocológicas e paleobatimétricas para o Siluro-Devoniano. Destas curvas evidenciou-se contexto transgressivo em camadas do Membro Jaguariaíva, quando a curva do nível do mar global demonstra tendência regressiva, evidenciando altas taxas de subsidência como já assinalado na bibliografia. A distribuição de *Zoophycos* no intervalo, restrito ao Pragiano-Eifeliano, evidencia mudanças paleogeográficas que poderiam estar associadas ao declínio da fauna Malvinocáfrica.

Dois estudos de caso complementam esta tese. No primeiro se analisou a distribuição de *Lingulichnus* com lingulídeos associados, o que permitiu análises da distribuição deste grupo nos sub-paleoambientes e possibilitou reconhecer esta associação como indicativa de contextos de alto espaço de acomodação. O segundo estudo analisou as tafofácies de uma seção da Formação Ponta Grossa correlacionando-as às tempestades de inverno. A comparação com depósitos coevos demonstrou que as tafofácies são fator-chave para reconhecer fatores que controlaram o acúmulo de macrofósseis.

Deste modo, confirma-se a hipótese elencada nesta tese, onde demonstrou-se a utilidade da Icnologia para análises nos parâmetros paleoambientais e paleobatimétricas, bem como no auxílio a inferências estratigráficas, bioestratigráficas e paleobiogeográficas. A análise integrada aos dados sedimentológicos e tafonômicos também se mostrou profícua para fornecer maior acurácia nas interpretações paleobiológicas.