DOI: 10.5212/TerraPlural.v.15.2118495.033

Ichnological Research of Silurian–Devonian Strata and the *Zoophycos* Distribution in the Paraná Basin

Pesquisas icnológicas dos estratos Siluro-Devonianos e a distribuição de *Zoophycos* na Bacia do Paraná

Investigación icnológica de estratos del Siluro-Devónico y distribución de *Zoophycos* en la Cuenca de Paraná

Kevin William Richter
https://orcid.org/0000-0002-2576-4117
kevinwilliamrichter@gmail.com
Universidade Estadual de Ponta Grossa, UEPG, Ponta Grossa, PR

Elvio Pinto Bosetti
https://orcid.org/0000-0003-1120-4933
elviobosetti@gmail.com
Universidade Estadual de Ponta Grossa, UEPG, Ponta Grossa, PR

Daniel Sedorko
https://orcid.org/0000-0002-9324-3460
sedorko@ufu.br
Universidade Federal de Uberlândia, UFU, Monte Carmelo, MG

Abstract: The Silurian–Devonian strata of the Paraná Basin (southern Brazil) have a wide variety of ichnofossils. The first records date from the beginning of the last century, with pioneering studies in 1912 addressing the Furnas and Ponta Grossa formations. Significant advances in the ichnological knowledge of these units occurred between the 1980s and 1990s, emphasizing ichnotaxonomic characterizations. These ichnological studies were important for better understanding and describing the main depositional environments, ecological strategies, biostratigraphy, and the relation with the preserved paleofauna. In this contribution, we review this knowledge and analyze the distribution and paleoecological significance of *Zoophycos*, the most remarkable ichnotaxon in the Lower Paleozoic beds of the Paraná Basin.

Keywords: Ichnofossils, Silurian, Devonian, Paraná Basin.

Resumo: Os estratos siluro-devonianos da Bacia do Paraná (sul do Brasil) apresentam grande variedade de icnofósseis. Os primeiros registros datam do início do século passado, com estudos pioneiros em 1912 abordando as formações Furnas e Ponta Grossa. No entanto, avanços significativos no conhecimento icnológico dessas unidades ocorreram entre as décadas de 1980 e 1990, com ênfase nas caracterizações

icnotaxonômicas. Os estudos icnológicos foram importantes para o entendimento e caracterização dos principais ambientes deposicionais, estratégias ecológicas, bioestratigrafia e relação com a paleofauna preservada. Nessa contribuição, faz-se uma revisão do conhecimento icnológico do Paleozoico inferior da Bacia do Paraná e uma análise da distribuição e do significado paleoecológico de *Zoophycos*, que configura o mais destacado icnotáxon nesses depósitos.

Palavras chaves: Icnofósseis, Siluriano, Devoniano, Bacia do Paraná.

Resumen: Los estratos siluro-devónicos de la Cuenca de Paraná (sur de Brasil) presentan una gran variedad de trazas fósiles. Los primeros registros datan de principios del siglo pasado, con estudios pioneros en 1912 acerca de las formaciones Furnas y Ponta Grossa. Sin embargo, entre los años 1980 y 1990 se produjeron avances significativos en el conocimiento icnológico de estas unidades, con énfasis en las caracterizaciones icnotaxonómicas. Los estudios icnológicos fueron importantes para el conocimiento y caracterización de los principales ambientes depositacionales, estrategias ecológicas, bioestratigrafía y relación con la paleofauna preservada. El presente estudio consiste en una revisión de la icnología del Paleozoico inferior de la Cuenca de Paraná y un análisis de la distribución y de la importancia paleoecológica de *Zoophycos*, el más destacado icnotaxón en estos depósitos.

Palabras clave: Traza fósiles, Silúrico, Devónico, Cuenca del Paraná.

INTRODUCTION

The early records of trace fossils for the Silurian–Devonian strata of Paraná State were made by Oliveira (1912), Clarke (1913), and Lange (1942), with references to the presence of "tubes of worms" for the Furnas and Ponta Grossa formations. However, ichnologic studies in that units were more frequent in the literature between the 1980s and 1990s (Ciguel & Aceñolaza, 1986; 1989; Campanha, 1985; Fernandes & Melo, 1985; Assine, 1996; 1999; Fernandes, 1996), although recent studies are available in the literature (Netto, Tognoli, Assine & Nara, 2014; Sedorko et al., 2017, Sedorko, Bosetti & Netto, 2018a; Sedorko, Netto & Savrda 2018b; Sedorko, Netto & Horodyski, 2018c, 2019; Sedorko et al., 2021).

A particular ichnogenus, *Zoophycos* Massalongo, 1855, has been reported by several authors for Ponta Grossa Formation (Campanha, 1985; Diniz, 1985; Castro, 1988; Fernandes, 1996; Simões et al., 2000; Sedorko, Bosetti & Netto, 2018a). *Zoophycos* is a conspicuous trace fossil in marine deposits from Phanerozoic, with a well-established distribution trend from shallow-marine facies during Paleozoic to deep water in post-Mesozoic strata (Zhang, Fan & Gong, 2015). This trace fossil was initially identified as a plant (Massalongo, 1855) in the fucoid age of Ichnology, but after, an animal origin was evidenced even that its ethology and mode of production are still a debated topic (Kotake, 1989, 1992; Bromley, 1991; Oliveiro, 2007; Löwemark, 2012). Although the tracemaker and the ethologic class represented by Zoophycos are open questions in Ichnology, the paleoenvironmental distribution is well-established for the so-called *Zoophycos* Group.

Considering that the Paraná Basin preserves important geologic and biologic events from Ordovician to Cretaceous (Milani et al., 2007), we aimed in this study to (i) analyze the advances that ichnological studies had provided for the understanding of the

Silurian–Devonian deposits in the state of Paraná; and (ii) analyze the *Zoophycos* distribution in the Paraná Basin (southern Brazil) focusing in its paleoecological significance.

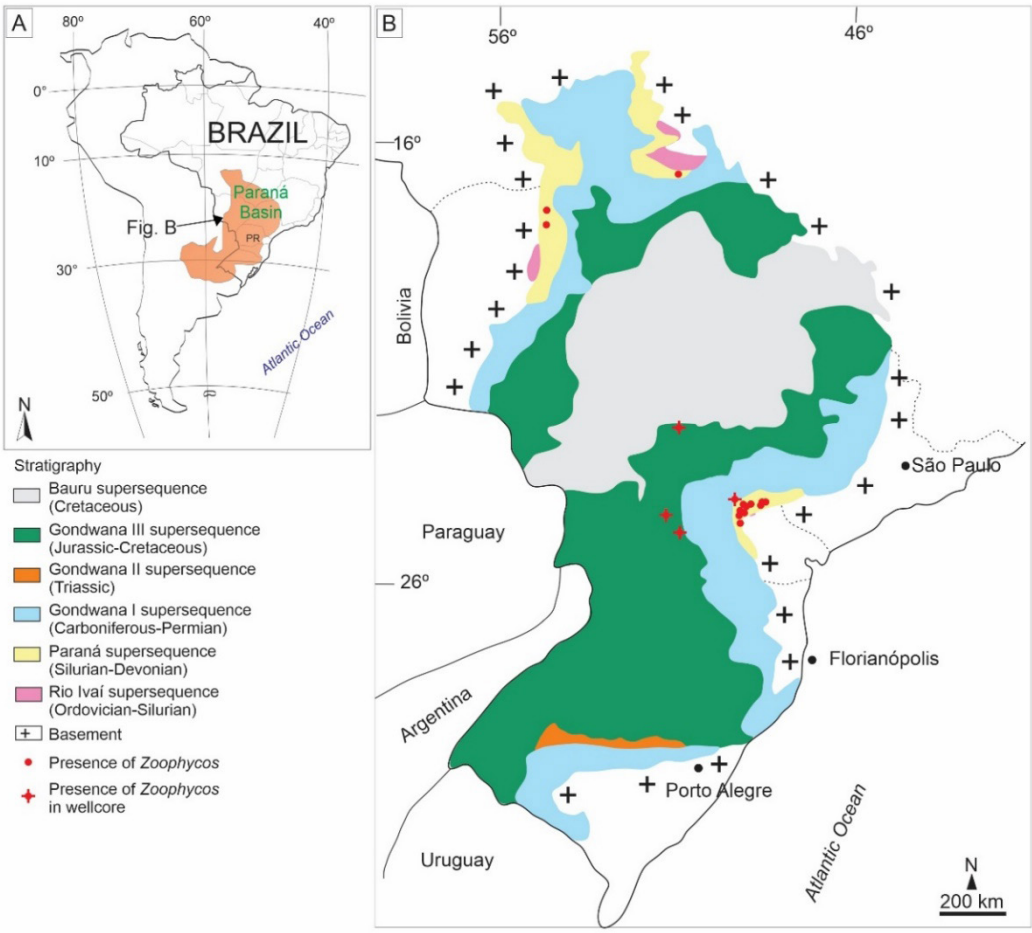
MATERIAL AND METHODS

Extensive bibliographic research aimed to group studies that report trace fossils in the Paraná State and *Zoophycos* for Paraná Basin. The distribution of *Zoophycos* in the Paraná Basin was summarized to identify the geographic and stratigraphic position, represented in the map modified from Milani et al. (2007, Fig. 1). Each point in the map considered the *Zoophycos* occurrence (Fig. 1B), but density was not considered. The works reporting *Spirophyton* (Carvalho & Pinto, 1938 apud Fernandes, 1996; Caputo, 1984 apud Fernandes, 1996) were excluded from this analysis due to the impossibility to access the specimens and lack of illustrations.

GEOLOGICAL SETTING

The intracratonic Paraná Basin extends from Brazil to Argentina, Paraguay, and Uruguay (Fig. 1A). Its sedimentary filling comprises six supersequences - Rio Ivaí, Paraná, Gondwana I, Gondwana II, Gondwana III, and Bauru (Milani et al., 2007). These supersequences were generated in response to tectonic-eustatic cycles associated with the evolution of the Western Gondwana, deposited from Late Ordovician to Late Cretaceous in several depositional settings mostly controlled by eustatic and subsidence cycles during Silurian to Devonian (see Assine, 1996; Bergamaschi, 1999; Cândido & Rostirola, 2007; Sedorko, Netto & Savrda, 2018b; Vargas et al., 2020, for a stratigraphic framework of Paraná Supersequence). Trace fossils are well-distributed along the whole Paraná Supersequence (Sedorko, Netto & Horodyski, 2019), but *Zoophycos* is only preserved in Pragian to Eifelian strata (Sedorko, Netto & Horodyski, 2018c). Regarding lithostratigraphy, this cycle is composed of Furnas and Ponta Grossa formations (sensu Lange & Petri, 1967; other lithostratigraphic nomenclature is proposed in Grahn, Mendelowicz Mauller, Bergamaschi & Bosetti, 2013). Assine (1999), based on lithological and stratigraphic aspects, divided the Furnas Formation into three units, naming them as lower, middle, and upper units. The Furnas Formation presents expressions of proximal *Cruziana* and *Skolithos* ichnofacies (Sedorko et al., 2017). The Ponta Grossa Formation is traditionally divided into Jaguariaíva, Tibagi, and São Domingos members (Lange & Petri, 1967) and presents the dominance of archetypal to distal expressions of Cruziana ichnofacies (Sedorko *et al.*, 2019). The *Zoophycos* distribution in Ponta Grossa Formation was discussed in Sedorko, Netto & Horodyski (2018c, 2019), and Sedorko et al. (2021).

Figure 1: Location map of Paraná Group (Paraná Supersequence) and *Zoophycos* occurrences in Paraná Basin.



Source: Modified from Milani et al. (2007).

RESULTS AND DISCUSSION

Furnas Formation

Sedorko, Netto and Bosetti (2013) presented an overview of trace fossils studies for Paraná Group, demonstrating two main phases: an ichnotaxonomic approach up to the 1990s; and an applied ichnologic approach after the 1990s (mainly as indicators of depositional settings). Under the second approach view, Borghi (1993; 1994) reported trace fossils expressing *Skolithos* and *Cruziana* ichnofacies for Furnas Formation, corroborated by later studies attesting a shallow marine depositional setting for the trace-fossils bearing levels (Fernandes, 1996; Assine, 1996, 1999). After 2013, Netto et al. (2014) identified the occurrence of dense colonization of *Rosselia* ichnofabrics in the "Transition Layers" of the Furnas Formation, previously recorded mainly in Cenozoic strata, signalizing the ecological strategies in storm events and a tolerant behavior to stress conditions. Then, Sedorko et al.

(2017) characterized the ranges with trace fossils with ichnostratigraphic value for Furnas Formation, such as *Arthrophycus alleghaniensis, A. brongniartii,* and *Cruziana acacensis* in the lower and middle units. It was possible to insert these strata as Lower Silurian and not Lower Devonian as classically positioned through these ichnotaxa. The upper Furnas unit is inserted in the Lower Devonian by evidence of palynomorphs and macrofossils of vascular plants (Dino & Rodrigues, 1995; Mussa et al., 1996; Grahn et al., 2013).

Thus, the trace fossils identified for the lower unit are *Arenicolites* isp., *Cruziana* isp., *Cylindrichnus* isp., *Didymaulichnus lyelli, Diplocraterion* isp., *Planolites* isp., *Palaeophycus* isp., *Palaeophycus tubularis*, *Rusophycus* isp., *Rusophycus acacensis*, *Skolithos* isp., and *Thalassinoides* isp. (Assine, 1996; 1999; Bergamaschi, 1999; Assine & Góis, 1996; Ciguel, 1996; Fernandes, 1996; Tognoli, Assine & Netto, 2002; Netto, Tognoli & Gandini, 2012; Netto et al., 2014; Sedorko et al., 2017). For the middle unit, the trace fossils identified are *Arenicolites* isp., *Arthrophycus alleghaniensis*, *A. brongniartii*, *Cruziana* isp., *Cruziana acacensis*, *Didymaulichnus lyelli*, *Didymaulyponomos rowei*, *Heimdallia chatwini*, *Lockeia siliquaria*, *Psammichnites implexus*, *Rhizocorallium commune*, *Rusophycus* isp., *Rusophycus acacensis*, *Skolithos* isp., and *Thalassinoides* isp. (Assine, 1996; 1999; Assine & Góis, 1996; Ciguel, 1996; Fernandes, 1996; Tognolli, Assine & Netto, 2002; Netto, Tognoli & Gandini, 2012; 2014; Sedorko et al., 2017). Finally, the strata comprising the upper unit present *Cylindrichnus* isp., *Lockeia* isp., *Monocraterion* isp., *Palaeophycus* isp., *Planolites* isp., *Rhizocorallium* isp., *Rosselia socialis*, *Skolithos* isp., *Thalassinoides* isp., and *Teichichnus* isp. (Fernandes, 1996; Bergamaschi, 1999; Tognoli, Assine & Netto, 2002; Netto et al., 2014; Sedorko et al., 2017).

Those trace fossils are expressions of Cruziana and Skolithos ichnofacies, indicating a shallow marine depositional system (Assine, 1996; Sedorko et al., 2017). The relative age assignment for the basal and intermediate intervals as Lower Silurian were only possible using trace fossils with ichnostratigraphic value.

Ponta Grossa Formation

The Ponta Grossa Formation is characterized as a predominantly shale unit representing marine paleoenvironment, as attested by their rich paleofauna included in the context of the Malvinokaffric Realm (Richter, 1941). When compared to Furnas Formation, trace fossils from these deposits were mostly studied after 2000 (Tognoli et al., 2002; Netto, Tognoli & Gandini, 2012; Netto et al., 2014; Sedorko, Bosetti & Netto, 2018a; Sedorko, Netto & Savrda, 2018b; Sedorko, Netto & Horodyski, 2018c; 2019; Sedorko et al., 2021; Bosetti et al., 2021), although early studies had been conducted before 2000 (Campanha, 1985; Fernandes, 1996). Recent updates to the Devonian strata of the Paraná State have identified expressions of *Glossifungites*, *Skolithos*, and *Cruziana* ichnofacies (Sedorko, Bosetti & Netto, 2018a).

The ichnotaxa identified for the Ponta Grossa Formation are *Arenicolites* isp., *Asterosoma* isp., *Bergaueria* isp., *Bifungites* isp., *Bifungites paranaensis*, *B. cruciformis*, *Chondrites* isp., *Cylindrichnus* isp., *Diplichnites* isp., *Diplocraterion* isp., *Heimdallia* isp., *Helminthopsis* isp., *Helichodromites* isp., *Laevicyclus* isp., *Lingulichnus* isp., *Lockeia* isp., *Palaeophycus* isp., *Phycosiphon* isp., *Planolites* isp., Psammichnites isp., *Rhizocorallium commune*, *Rosselia* isp.,

Rosselia socialis, *Rusophycus* isp., *Schaubcylindrichnus* isp., *Skolithos* isp., *Taenidium* isp., and *Zoophycos* isp. (Campanha, 1985; Fernandes & Melo, 1985; Fernandes, 1996; Tognoli, Assine & Netto, 2002; Bosetti & Silva, 2009; Carelli & Borghi, 2011; Netto, Tognoli & Gandini, 2012; Bosetti, Borghi, Sedorko & Myszynski Jr, 2017; Bosetti et al., 2021; Sedorko, Bosetti & Netto, 2018a; Sedorko, Netto & Savrda, 2018b; Sedorko, Netto & Horodyski, 2018c).

Recently, Sedorko, Bosetti and Netto (2018a) demonstrated that accurate paleoenvironmental interpretations could be derived through integrated approaches between ichnology, sedimentology, and taphonomy. Analyzing the paleoenvironmental context of a section of the Ponta Grossa Formation, they observed that sets of taphofacies associated with certain ichnofabrics showed variations in paleofauna control, triggered by energy conditions and oxygenation levels due to sea-level changes. In another study, Sedorko, Netto and Savrda (2018b) refined stratigraphic frameworks applying trace fossils data. In the same year, Sedorko et al. (2018d) analyzed a regressive section of the Lower Devonian from the northwest Paraná Basin, demonstrating the dominance of shallower environments compared to the southern part of the Paraná Basin. Later, Sedorko, Netto & Horodyski (2019) used trace fossils to propose a paleobathymetric curve for the Silurian–Devonian strata of the Paraná Basin. Finally, Sedorko et al. (2021) applied ichnology as a relative proxy to understand the impact of the main paleobiological events that led to the decline of the Malvinokaffric Realm in the Paraná Basin. Thus, compared to Furnas Formation, most applied studies on ichnology for Ponta Grossa were conducted after 2000, especially after 2017.

Zoophycos distribution in Paraná Basin

The most common morphology in the Ponta Grossa Formation is a planar U-shaped, multiple whorl *spreiten* burrow; however, helical and lobed forms are also preserved, with a maximum of two whorls. *Spreite* thickness varies from 0.5 to 3.2 cm, and the width of *spreite* oscillates can reach 50 cm. These morphologies were discussed in Sedorko, Netto and Horodyski (2018c). The first study to apply *Zoophycos* for paleonvironmental inferences in the Paraná Basin was elaborated by Campanha (1985), interpreting the strata of Ponta Grossa Formation with *Zoophycos* deposited in offshore settings (Table 1). In the same year, Diniz (1985) reported *Zoophycos* for several well-cores that sampled Ponta Grossa Formation (Table 1). Castro (1988) also registered *Zoophycos* in this unit. Fernandes (1996) described different *Zoophycos* morphologies and expanded the geographic distribution of *Zoophycos* in Goiás State, besides describing this ichnogenus in Paraná State. Simões et al. (2000) inferred that *Zoophycos* was responsible for the reorientation of some conularids, and Bosetti, Horodyski, Matsumura and Myszynski Jr. (2013) used *Zoophycos* to correlate stratigraphic successions in Ponta Grossa city. The stratigraphic control of *Zoophycos* was presented in Sedorko, Netto & Horodyski (2018c), demonstrating that this ichnogenus is absent in post-Eifelian beds of the Ponta Grossa Formation. After extensive bibliographic research, only one study reported *Zoophycos* for non-Devonian strata of the Paraná Basin (Oliveira, 2019). The author analyzed the facies of the Itararé Group, but the illustrated

specimen referred to as *Zoophycos* seems to be a *Taenidium* (Fig. 26 of Oliveira, 2019) by the lack of evident *spreite*. Thus, *Zoophycos* occurs exclusively in the Lower-Middle Devonian in Paraná Basin due to environmental control.

Table 1: Studies that described *Zoophycos* in Paraná Basin.

Locality	Period	Lithostratigraphic unit	Referred ichnotaxa	Reference
Ponta Grossa (PR)	Devonian	Ponta Grossa Formation	*Zoophycos*	Campanha (1985)
Cuiabá Paulista (SP) well-core 3-CB-2-SP	Devonian	Ponta Grossa Formation	*Zoophycos*	Diniz (1985)
Chapéu do Sol (PR) well-core 1-CS-2-PR	Devonian	Ponta Grossa Formation	*Zoophycos*	Diniz (1985)
Roncador (PR) well-core 1-RO-1-PR	Devonian	Ponta Grossa Formation	*Zoophycos*	Diniz (1985)
Ponta Grossa (PR)	Devonian	Ponta Grossa Formation	*Zoophycos*	Castro (1988)
Amorinópolis (GO)	Devonian	Ponta Grossa Formation	*Zoophycos* ichnosp. 1	Fernandes (1996)
Ponta Grossa (PR)	Devonian	Ponta Grossa Formation	*Zoophycos* ichnosp. indet	Fernandes (1996)
Ponta Grossa (PR)	Devonian	Ponta Grossa Formation	*Zoophycos* ichnosp. 2	Fernandes (1996)
Jaguariaíva (PR)	Devonian	Ponta Grossa Formation	*Zoophycos* ichnosp. indet	Fernandes (1996)
Jaguariaíva	Lower Devonian	Ponta Grossa Formation	*Zoophycos* ichnosp. indet	Simões et al. (2000)
Ponta Grossa (PR)	Devonian	Ponta Grossa Formation	*Zoophycos*	Abelha Borghi & Fernandes (2007)
Ponta Grossa (PR)	Devonian	Ponta Grossa Formation	*Zoophycos*	Netto, Tognoli & Gandini (2012)
Ponta Grossa (PR)	Lower Devonian	Ponta Grossa Formation	*Zoophycos* isp.	Bosetti et al. (2013)
Tibagi (PR)	Lower Devonian	Ponta Grossa Formation	*Zoophycos* isp.	Sedorko, Bosetti & Netto, (2018a)
Tibagi (PR)	Lower-Middle Devonian	Ponta Grossa Formation	*Zoophycos* isp.	Sedorko, Netto & Savrda (2018b)
Arapoti (PR)	Lower Devonian	Ponta Grossa Formation	*Zoophycos* isp.	Sedorko, Netto & Savrda (2018b)
Tibagi (PR)	Lower-Middle Devonian	Ponta Grossa Formation	*Zoophycos* isp.	Sedorko, Netto & Horodyski (2018c)
Rio Negro (MS)	Lower Devonian	Ponta Grossa Formation	*Zoophycos* isp.	Sedorko et al. (2018d)
Tibagi (PR)	Lower-Middle Devonian	Ponta Grossa Formation	*Zoophycos* isp.	Sedorko, Netto & Horodyski (2019)
Tibagi (PR)	Lower-Middle Devonian	Ponta Grossa Formation	*Zoophycos* isp.	Sedorko et al. (2021)

Zoophycos in Ponta Grossa Formation is a common component of *Cruziana* ichnofacies in Pragian–Eifelian deposits (Table 2) but can express archetypal or distal conditions within this ichnofacies. When representing archetypal conditions, *Zoophycos* is mostly associated with *Asterosoma, Teichichnus, Planolites, Palaeophycus, Schaubcylindrichnus, Rosselia, Cylindrichnus, Chondrites, and Phycosiphon*. *Zoophycos* expressing distal conditions occurs associated with *Chondrithes, Phycosiphon,* and, less common, *Helichodromites*. The *Zoophycos* ichnofacies is restrict to post-Mesozoic deposits (Zhang, Fan & Gong, 2015), not occurring in Paraná Basin.

Table 2: List of *Zoophycos* occurrences in Ponta Grossa Formation.

Age	Locality (coordinates)	Ichnofacies	Reference
Pragian	Tibagi - PR, portal da cidade (-24.52766964493291, -50.39955964002155)	Archetypal *Cruziana*	Sedorko, Netto & Savrda (2018b)
Pragian-Emsian	Tibagi - PR, Arroio São Domingos (-24.51186960834, -50.42229237066247)	Archetypal *Cruziana*	Sedorko, Netto & Savrda (2018b)
Pragian-Emsian	Tibagi - PR, acima arroio São Domingos (-24.51429274382312, -50.428404618755074)	Archetypal *Cruziana*	Sedorko, Netto & Savrda (2018b)
Pragian-Emsian	Arapoti - PR, PR 092, entrada CEEP (-24.168075299799053, -49.80142437022979)	Archetypal *Cruziana*	This study
Pragian-Emsian	Arapoti - PR, CEEP (-24.193704213996508, -49.78393796069782)	Archetypal *Cruziana*	Sedorko, Netto & Savrda (2018b)
Pragian-Emsian	Jaguariaíva - PR, trilho (-24.241278747041477, -49.71778874523683)	Archetypal *Cruziana*	Simões et al. (2000)
Pragian-Emsian	Rio Negro - MS, estrada ponte nova (-19.43705405108732, -55.00280606955078)	Archetypal *Cruziana*	Sedorko et al. (2018d)
Emsian	Tibagi - PR, entrada da cidade (-24.55672958704829, -50.45546641393211)	Archetypal *Cruziana*	Sedorko, Netto & Savrda (2018b)
Emsian	Tibagi - PR, BR 153, km 211 (-24.56454774785814, -50.45431255274105)	Archetypal *Cruziana*	Sedorko, Bosetti & Netto (2018a), Sedorko, Netto & Savrda (2018b)
Emsian	Tibagi - PR, BR 153, km 211 (-24.56454774785814, -50.45431255274105)	Distal *Cruziana*	Sedorko, Bosetti, & Netto (2018a), Sedorko, Netto & Savrda (2018b)
Emsian	Piraí do Sul - PR, Rio Guaricanga (-24.3588600872764, -50.09816506919163)	Archetypal *Cruziana*	This study
Emsian	Piraí do Sul - PR, Fazenda Mutuca (-24.28871509229243, -50.088358999162374)	Archetypal *Cruziana*	This study
Emsian	Ponta Grossa - PR, Curva 1 (-25.063786583020153, -50.132983806921615)	Archetypal *Cruziana*	Bosetti et al. (2013)
Emsian	Ponta Grossa - PR, UEPG (-25.0897755824982, -50.108767653642765)	Archetypal *Cruziana*	This study
Emsian	Ponta Grossa - PR, Volsul (-25.0507682638905, -50.17527589768459)	Archetypal *Cruziana*	This study
Emsian-Eifelian	Tibagi - PR, BR 153, km 214 (-24.58497860474662, -50.43713745137998)	Archetypal *Cruziana*	Sedorko, Netto & Savrda (2018b), Sedorko, Netto & Horodyski (2018c)
Emsian-Eifelian	Palmeira - PR, Rio Caniú (-25.309387530212355, -50.091613307979074)	Archetypal *Cruziana*	Ng (2013)
Emsian-Eifelian	Rio Verde do Mato Grosso - MS, MS 29 (-18.926181318927952, -54.83969733553473)	Archetypal *Cruziana*	Scheffler, Silva & Sedorko (2020); Sedorko et al. (2021)
Emsian-Eifelian	Coxim, Taquari river (-18.36351069876289, -54.61197543995809)	Archetypal *Cruziana*	This study

The Phanerozoic distribution of *Zoophycos* is hypothesized to have been mostly controlled by the distribution of food resources. The "first bloom" of *Zoophycos* occurred during Lower Devonian, linked to the plant diversification that might have increased the availability of organic matter in shallow seas (Zhang, Fan & Gong, 2015). Coincidentally, in the Paraná Basin, the most basal *Zoophycos* occurs few meters above the first land plants found in the basin (*Cooksonia* sp.), corroborating this control. The *Zoophycos* is a stenohaline trace fossil, being preserved in fully marine facies since the Cambrian (Zhang, Fan & Gong, 2015). Considering that unequivocal *Zoophycos* are preserved only in the Lower-Middle

Devonian of the Paraná Basin, this ichnogenus can be regarded as a biomarker of optimum marine settings for the Paraná Basin. The absence of *Zoophycos* in Ordovician–Silurian marine deposits (*i.e.*, Alto Garças, Iapó, Vila Maria, and Furnas formations) might be related to low productivity rates, considering that the distribution of *Zoophycos* throughout Phanerozoic was controlled by the disposition of food within substrates (Kotake, 2014; Zhang, Fan & Gong, 2015; Sedorko, Netto & Horodyski, 2018c). The worldwide bloom of *Zoophycos* during the Devonian is well documented in the Paraná Basin (Ponta Grossa Formation). However, its occurrence decreases until disappearance after the plant diversification in Middle Devonian, suggesting changes in the basin configuration (Vargas et al., 2020; Sedorko et al., 2021). *Zoophycos* is virtually absent in post-Eifelian strata, reflecting impacted, and later, absence of marine conditions represented in upper units. This distribution follows paleogeographic reconstructions that assume the Paraná Basin as a gulf opened to the Panthalassa Sea during the Devonian (Milani et al., 2007).

SUMMARY

After earlier reports from the beginning of the last century, trace fossil studies had an exclusively ichnotaxonomic approach, with most studies focusing on Furnas Formation up to the 1990s. Trace fossils were decisive in better understanding the depositional settings represented by the Furnas Formation deposits and determining a Lower Silurian age for its lower and middle units. Nowadays, most ichnologic studies have been focused on the Ponta Grossa Formation ichnofauna, using trace fossils as indicators of depositional settings and for paleobiological, paleoecological, and taphonomic interpretations. Only Ponta Grossa Formation preserves unequivocal *Zoophycos* in the whole Paraná Basin. This ichnogenus is restricted to marine facies since Cambrian; thus, this distribution highlights the optimal marine conditions represented during Devonian in the Paraná Basin.

ACKNOWLEDGMENTS

D. Sedorko thanks to the Brazilian Scientific and Technological Research Council – CNPq for the post-doc fellowship (proc. 159548/2018-7). The authors thanks Renata G. Netto for discussions and language revision.

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Data de submissão: 21/jul./2021

Data de aceite: 30/ago./2021