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Multiple-*Rusophycus* assemblage from the Parnaíba Basin (NE Brazil) reflects trilobites as tracemakers and molting behavior

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Trilobites inhabited all environments of Paleozoic seas, ranging from estuaries to continental slopes, and were globally distributed. Although their functional morphology and phylogenetic relations are established by well-preserved body fossils, the behavior of trilobites has received less attention. Three well-known trace fossils are interpreted to be produced by trilobitiforms when preserved in Paleozoic rocks, *Rusophycus* (a resting trace), *Cruziana* (a furrowing trace), and *Diplichnites* (a locomotion trace). Those trace fossils unveil some aspects of trilobite behavior, but they were not investigated to test paleoecologic strategies based on morphometric parameters. This study uses *Rusophycus* to access the paleoecologic strategies of trilobites in storm-dominated shallow marine deposits of the Pimenteira and Cabeças formations (Middle to Upper Devonian, Parnaíba Basin, Brazil). It was conducted a detailed analysis of the *Rusophycus* specimens in a section that represents the transition between the Pimenteira and Cabeças formations (Parnaíba Basin). The width and length of the *Rusophycus* were measured, and statistical analyses were performed to understand the population characteristics. Relatively small-sized *Rusophycus* are dominant in such deposits, suggesting the dominance of young tracemakers and inferred r-strategist populations. The here reported multiple-*Rusophycus* assemblage reveals paleoecologic strategies of the population, and tiers relationship (cross-cutting epistratal and shallow-tier trace fossils such as *Bergaueria*, *Palaeophycus*, and *Protopaleodictyon*) indicate deep *Rusophycus*. The main reason for those burrowing activities deep in the substrate might be protection during ecdysis. Thus, the random distribution, lack of hunting evidence, and depth of *Rusophycus* suggest molting activity as the trigger for their production in storm-influenced beds of the Pimenteira Formation, probably by calmoniids or homalonotids.

KEYWORDS

pimenteira formation, cabeças formation, canindé group, molting, trilobites

1. Introduction

Trilobites are among the most prominent Paleozoic tracemakers that inhabited worldwide almost all marine settings, from estuaries to the continental slope (Fortey, 2014; Mángano et al., 2021). Their well-preserved fossils have helped to establish their functional morphology and phylogenetic relations. However, ethological studies based on trilobite trace fossils have received little attention (Seilacher, 2007), although trilobites are among the taxa with the greatest behavior representation in the fossil record (Hsieh and Plotnick, 2020). Three classical ichnogenera are assumed to be produced by trilobites when preserved in lower Paleozoic rocks, *Rusophycus* (a resting trace), *Cruziana* (a furrowing trace), and *Diplichnites* (a locomotion trace). The latter is rarely preserved because depositional processes, such as waves and currents, easily obliterate or remove the trackways. *Cruziana* and *Rusophycus*, otherwise, are preserved as they represent burrows produced in response to a combination of feeding, locomotion, and resting habits (Crimes and Herdman, 1970; Goldring, 1985; Brandt, 2007; Seilacher, 2007). In some cases, *Cruziana* and *Rusophycus* may occur as connected or representing a continuous, making it challenging to distinct between the ichnogenera (Keighley and Pickerill, 1996). Pickerill (1995) suggested that a length/width ratio lower than 2:1 could be applied to identify *Rusophycus* and a ratio over 2:1 to identify *Cruziana*.

Rusophycus specimens can occur isolated or form multiple-*Rusophycus* assemblages (Brandt, 2007). In multiple-*Rusophycus* assemblages, *Rusophycus* may intergrade with *Cruziana*, suggesting a feeding strategy of a single individual that possibly alternates detritus-feeding (*Cruziana*) with forays (*Rusophycus*) for prey (Brandt, 2007). However, multiple-*Rusophycus* assemblages might be produced by different individuals randomly or nonrandomly distributed. Brandt (2007) stated that random distribution occurs in resource-rich, low-energy environments. Non-randomly distributed multiple traces were interpreted as reflecting a rheotactic behavior, in which trilobites oriented themselves against the current to passively capture organic matter (Crimes and Herdman, 1970; Pickerill, 1995), or a circling behavior reflecting a mode of sediment feeding (Neto de Carvalho, 2006).

Trilobites have been reported in Devonian strata of the Parnaíba Basin (Kegel, 1953; Castro, 1968; Carvalho et al., 1997; Meira et al., 2016); however, there has been a lack of ethological studies based on their trace fossils. Considering that *Rusophycus* dimensions might evidence ontogenetic phases and paleoecologic strategies of trilobites (Levi-Setti, 1995), this study aims to (i) discuss the preservational bias represented by multiple-*Rusophycus* assemblages in a storm-dominated setting, and (ii) infer the paleoecological strategies of trilobites in this context.

2. Geological setting

The study area is located on the eastern border of the Parnaíba Basin, in Picos Municipality (Figure 1). The intracratonic Parnaíba Basin covers an area of approximately 600,000 km², reaching ~3,500 m thick in the depocenter (Góes and Feijó, 1994; Milani and ZalAn, 1999). Vaz et al. (2007) divided the stratigraphic record of the basin into five supersequences. The deposits studied herein belong to the Devonian–Mississippian Supersequence, comprising siliciclastic

deposits of the lithostratigraphic Canindé Group. This unit is represented by storm-influenced shelf, deltaic, and glacial deposits, recording deposition in shallow marine environments (Barbosa et al., 2015).

Lithostratigraphically, the Canindé Group is divided into four units, from base to top: Itaim, Pimenteira, Cabeças, and Longá formations (Góes and Feijó, 1994; Vaz et al., 2007). Grahn et al. (2008) dated the transition between the Pimenteira and Cabeças formations, where the *Rusophycus* specimens studied here are preserved, as Givetian and lower Frasnian. The Pimenteira Formation comprises dark gray to black shales interbedded with thin beds of very fine-grained sandstone (Góes and Feijó, 1994; Young, 2003). In contrast, the Cabeças Formation is dominated by sandstones representing storm-influenced and glacial beds (Vaz et al., 2007; Vettorazzi, 2012; Barbosa et al., 2015).

In the studied section it was recognized eight sedimentary facies (Table 1; Figure 2), from proximal (ME1) to distal (ME6) marine environments: (M1) Facies Sh and Sl are represented by stratified (horizontal stratification or low angle cross-stratification), very fine- to medium-grained sandstone, generally low bioturbated, deposited in shoreface settings; (ME2) facies Sw, represented by very fine- to fine-grained sandstone with wave cross-lamination locally with asymmetric ripples, rarely bioturbated, deposited in shoreface settings; (ME3) facies St and Sp characterized by fine- to medium-grained sandstone bearing trough or planar cross-stratification, with low bioturbation, representing deposition in shoreface settings; (ME4) facies Shcs characterized by interbedded, very fine-grained sandstone with hummocky cross-stratification and siltstone, locally highly bioturbated, reflecting a mix of suspension and tractive processes and indicating transitional offshore settings; (ME5) facies F characterized by moderately bioturbated heterolithic deposits alternating siltstone and fine-grained sandstone showing parallel lamination and locally lenticular to wavy bedding, rich in plant debris, reflecting deposition in upper offshore settings close to storm-wave base; and (ME6) facies M represented by parallel-laminated siltstone with low to locally high bioturbation, locally with plant debris, reflecting deposition in relatively quiet environments in offshore settings.

3. Materials and methods

The studied section is in Picos Municipality, Piauí State, Brazil (7°04'36.3" S, 41°29'00.9" W; Figure 1) and represents the transition between the Pimenteira and Cabeças formations (see Figure 2A). Trace fossil characterization used the ichnotaxobases approach (Bromley, 1996). We measured the length and width of all *Rusophycus* specimens preserved in very fine- to fine-grained sandstone available in the study area ($n = 70$; see Supplementary Table S1). All *Rusophycus* specimens used for statistical analysis came from the same bed. For facies analysis, we considered texture, general composition, primary sedimentary structures, trace fossils, geometry, and fossils.

In order to investigate the trends of colonization, five different tests were performed on the data: (i) modality, to verify the existence of more than one mode; (ii) normality, to observe whether the inferred population follows a normal Gaussian distribution; (iii) a skewness test, to verify trends toward a larger number of individuals in a certain size; (iv) density estimates of multi-distribution of length using Gaussian mixture models, and (v) linear regression to observe the

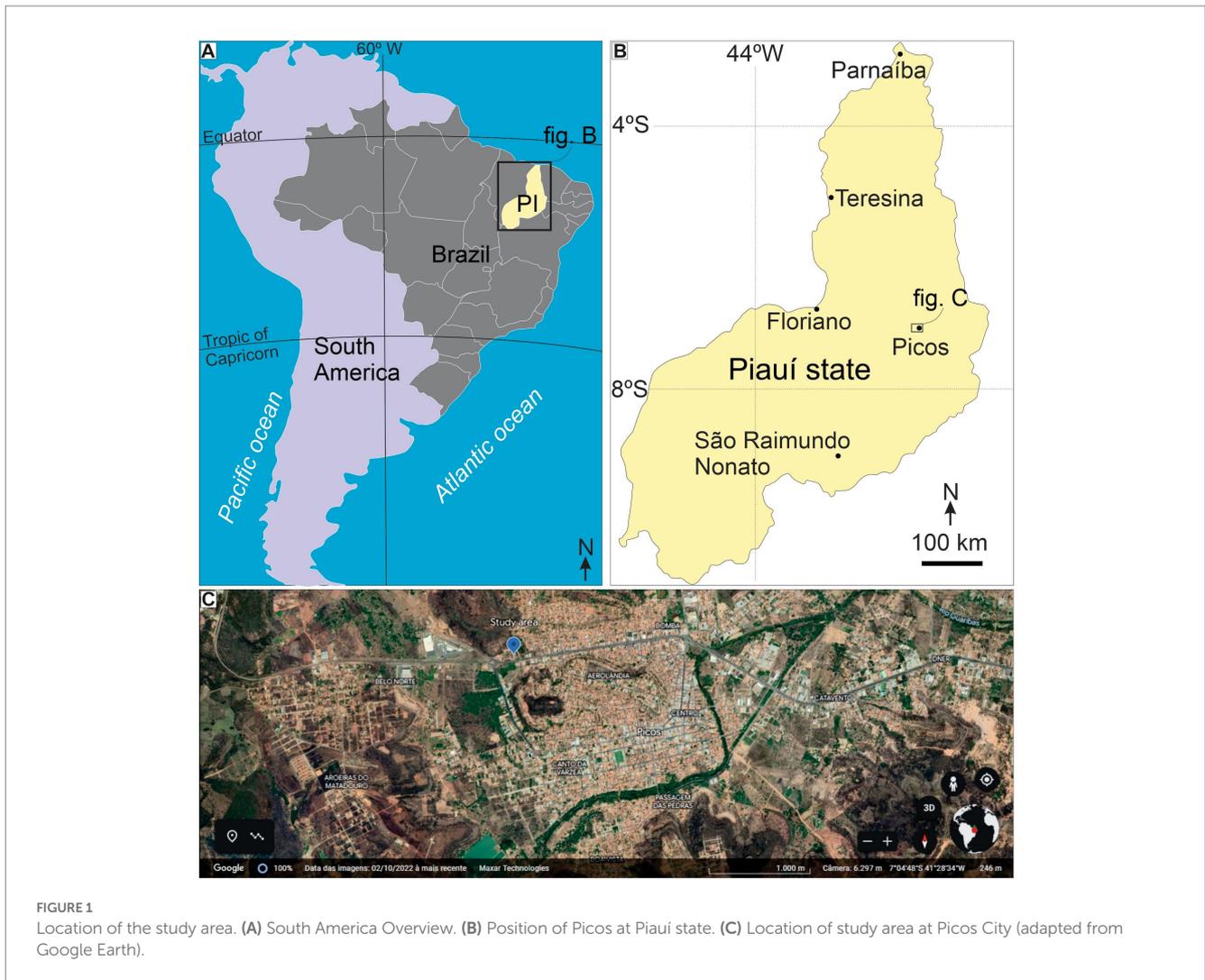


TABLE 1 Sedimentary facies and inferred processes from studied sections.

Facies code	Lithology and Texture	Sedimentary structures	Geometry	Sedimentary process	Suites
Sh	Fine to medium-grained sandstone	Horizontal lamination	Lenticular	High energetic flows above fair-weather wave-base	Absent
Sl	Very fine to medium-grained sandstone	Low angle cross-stratification	Lenticular	High energetic flows above fair-weather wave-base	A, B
Sw	Very fine- to fine-grained sandstone	Wave cross-lamination locally with asymmetric ripple	Lenticular	Oscillatory flows generated above fair-weather wave-base, locally influenced by combined unidirectional flows	A
St	Fine- to medium-grained sandstone	Trough cross-stratification	Lenticular	Unidirectional flows above fair-weather wave base	A, B
Sp	Fine- to medium-grained sandstone	Planar cross-stratification	Lenticular	Unidirectional flows above fair-weather wave base	Absent
Shcs	Very fine- to fine-grained sandstone	Hummocky cross-stratification	Lenticular	Oscillatory flows storm-generated, between storm and fair-weather wave-base	A
F	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	A, B
M	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	C

trend between lengths vs. width in the ichnospecimens. The Gaussian mixture model was adapted based on the method developed for trilobite (*Triarthrus eatoni*) analysis by Pauly and Holmes (2022).

The statistical analysis was produced in the R (R Core Team, 2013; v. 4.2.0) programming language, using the integrated development environment RStudio (RStudio Team, 2022; v. 2022.02.2). The “readxl”

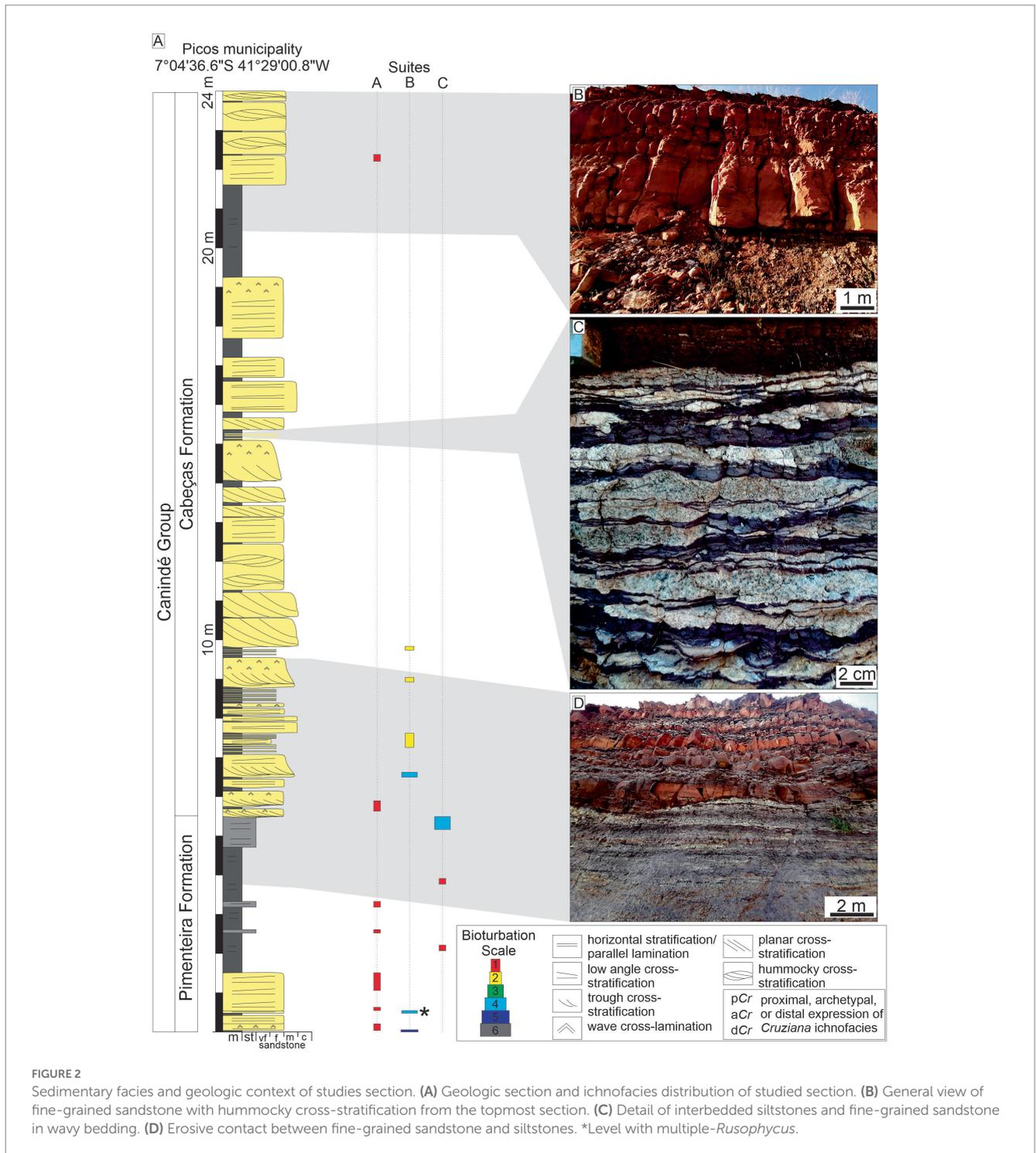


FIGURE 2

Sedimentary facies and geologic context of studies section. (A) Geologic section and ichnofacies distribution of studied section. (B) General view of fine-grained sandstone with hummocky cross-stratification from the topmost section. (C) Detail of interbedded siltstones and fine-grained sandstone in wavy bedding. (D) Erosive contact between fine-grained sandstone and siltstones. *Level with multiple-*Rusophycus*.

(Wickham and Bryan, 2017) package was used to support the import of Excel files (“.xlsx”) into R. Graphics were produced using the “ggplot2” (Wickham, 2016) and “ggpubr” (Kassambara, 2020) packages, while data organization and manipulation were performed with the “dplyr” (Wickham et al., 2022) package. The “multimode” (Ameijeiras-Alonso et al., 2021) package was used for the HH (Hartigan and Hartigan) test to determine the number of modes, “stats” (R Core Team, 2013) to do the Shapiro–Wilks and fitting of linear models, and “moments” (Komsta and Novomestky, 2022) package was employed for the skewness test. Finally, “mclust” (Scrucca et al., 2016) package was used to fit Gaussian mixture

models to investigate multi-distribution patterns. R Script can be found in [Supplementary data 2](#).

4. Results

The trace fossil content of the section can be subdivided into three suites. Suite A is characterized by low bioturbated beds with *Arenicolites*, *Asterosoma*, *Palaeophycus*, *Rosselia*, *Rhizocorallium*, *Skolithos*, and *Thalassinoides* (Figures 3A–D). Suite B, the focus of

this study, is represented by *Arenicolites*, *Bergaueria*, *Cruziana*, *Diplichnites*, *Diplocraterion*, *Helminthopsis*, *Lockeia*, *Palaeophycus*, *Protopaleodyction*, *Rusophycus*, and *Skolithos* (Figures 3E–H, 4), showing moderate to high bioturbation in the bedding plane. *Rusophycus* and *Protopaleodyction* dominate suite B. Suite C comprise *Chondrites*, *Phycosiphon*, and *Planolites* (Figure 3I), with low to locally moderate bioturbation.

The *Rusophycus* specimens are preserved in positive hyporelief (*sensu* Seilacher, 1970) in the sandy beds interbedded to the fine-grained facies (mudstones to siltstones). They are bilobed ovate traces presenting a central groove that separates two symmetrical lobes ornamented by scratches (Figures 4B–E). Their widths range from 14 to 87 mm, and lengths from 21 to 155 mm (Supplementary Table S1; Figure 5). Considering that most of the investigated specimens were found in moved blocks (*ex situ*), their azimuthal orientation was not measured. However, no preferential orientation is evident in blocks showing more than 10 specimens. Multiple-*Rusophycus* assemblages occur with several specimens preserved. *Rusophycus* can locally intersect or overlap *Protopaleodyction* and *Palaeophycus* (Figure 4) or be associated with *Bergaueria* (Figures 4D,D'), all in the same stratigraphic level. It also occurs forming continuous traces with *Cruziana* (Figures 4H,H').

The width and length of the specimens (Figures 5A,B) do not follow a normal distribution (Shapiro–Wilk; $W=0.868$, $p=2.51e-6$ for width, $W=0.802$, $p=2.68e-8$ for length), indicating only one mode (Hartigan and Hartigan; $Dip=0.043$, $p=0.44$ for width, $Dip=0.035$, $p=0.81$ for length). These data have a positive skewness (D'Agostino; $skew=1.411$, $p=2.92e-5$ for width, $skew=1.850$, $p=5.75e-7$ for length), showing a trend toward a population with more individuals of small width and a predominance of short lengths.

This trend toward a population with more small individuals is also evident in the multi-distribution analysis and the scatter-plot regression (Figures 5A,D). We used a density estimate of the Gaussian mixture model to observe the multi-distribution in the length of the ichnospecimens, and the analysis suggested three main components (ml1–3) with means of 34.70 mm (ml1), 62.43 mm (ml2), and 147.75 mm (ml3).

The length/width ratio was also examined to determine if it could be used to distinguish between different animal groups producing the same ichnogenus (Figure 5D). According to the results, the data follow a normal distribution ($W=0.971$, $p=0.104$). There is a small peak related to specimens with a greater length/width ratio (Figure 5D), but there is no statistical basis for attesting that there is more than one mode in the data ($Dip=0.036$, $p=0.76$), and no skewness was observed ($skew=0.198$, $p=0.465$). The normality, unimodality, lack of skewness, and the prevalence of a 1.5:1 length/width ratio ($\mu=1.52\pm 0.22$) in the majority of *Rusophycus* specimens suggest that these traces were most likely produced by the same trilobite species, representing a population. A strong linear correlation was found between the length and width of the specimens ($R^2=0.8988$, $p=2.2e-16$).

5. Discussion

The three trace fossil suites registered in the study area, A, B, and C, represent different expressions of the *Cruziana* ichnofacies. Suite A is considered a proximal expression of *Cruziana* ichnofacies because it presents a mix of shallow-tier, suspension-feeding, or domicile trace fossils (e.g., *Arenicolites*, *Palaeophycus*, *Skolithos*, and *Thalassinoides*) and shallow- to middle-tiers, detritus-feeding trace fossils (e.g.,

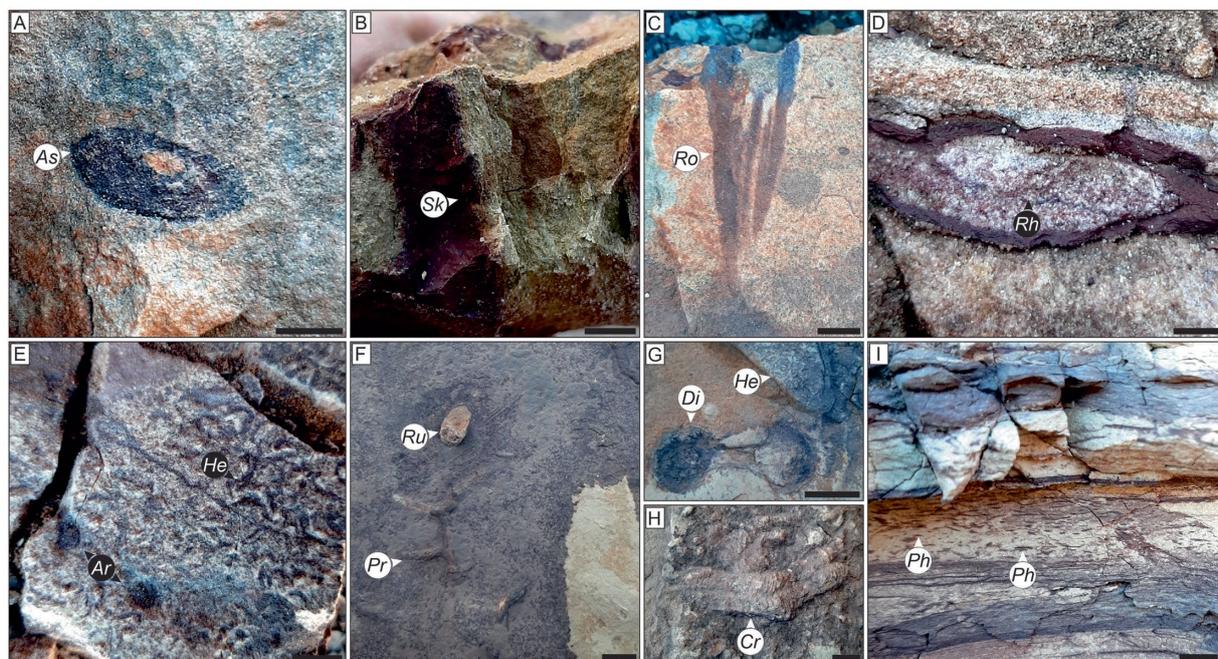


FIGURE 3

Trace fossil suites from studied section. (A–D) Suite A with *Asterosoma* (As), *Skolithos* (Sk), *Rosselia* (Ro), and *Rhizocorallium* (Rh). (E–H) Trace fossils from suite B, focus of this study, with *Arenicolites* (Ar), *Helminthopsis* (He), *Rusophycus* (Ru), *Protopaleodyction* (Pr), *Diplocraterion* (Di), and *Cruziana* (Cr). (I) Suite C represented by *Phycosiphon* (Ph). Scale bar=1 cm.

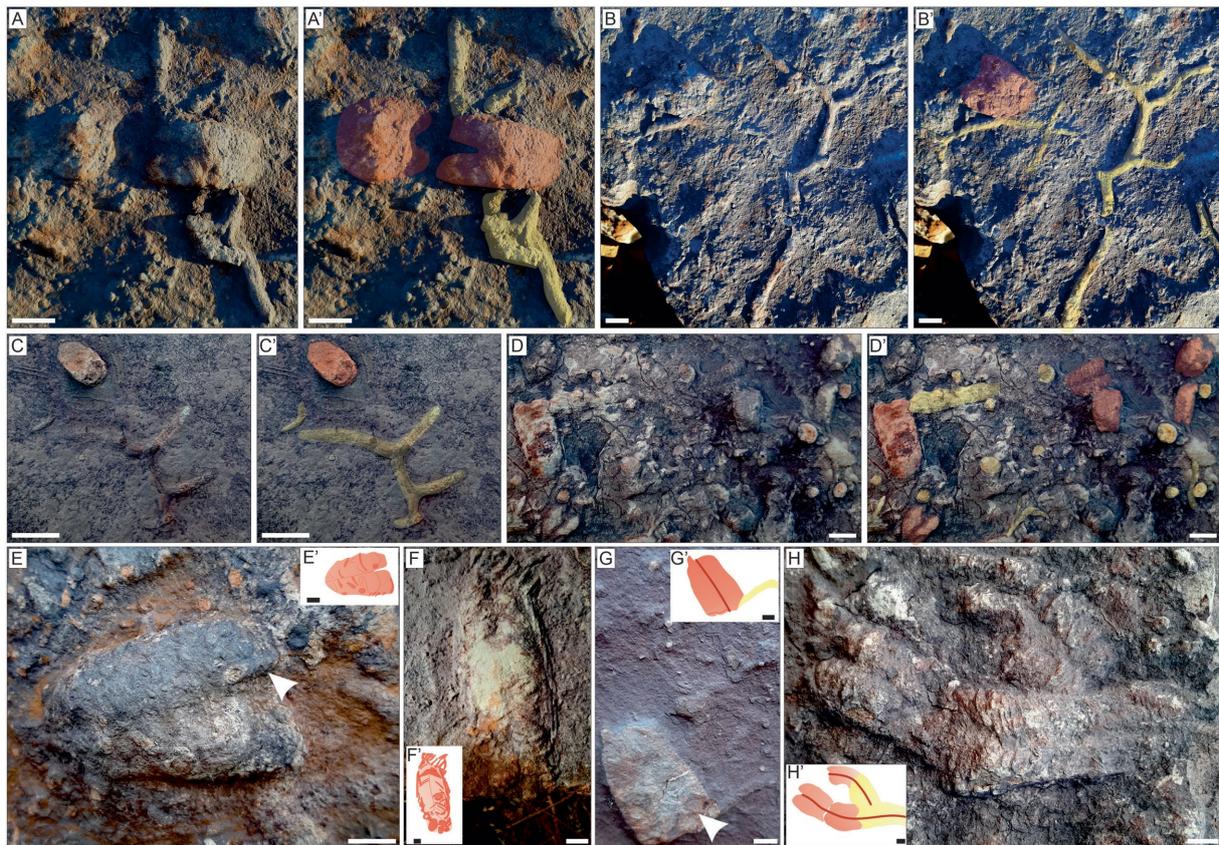


FIGURE 4

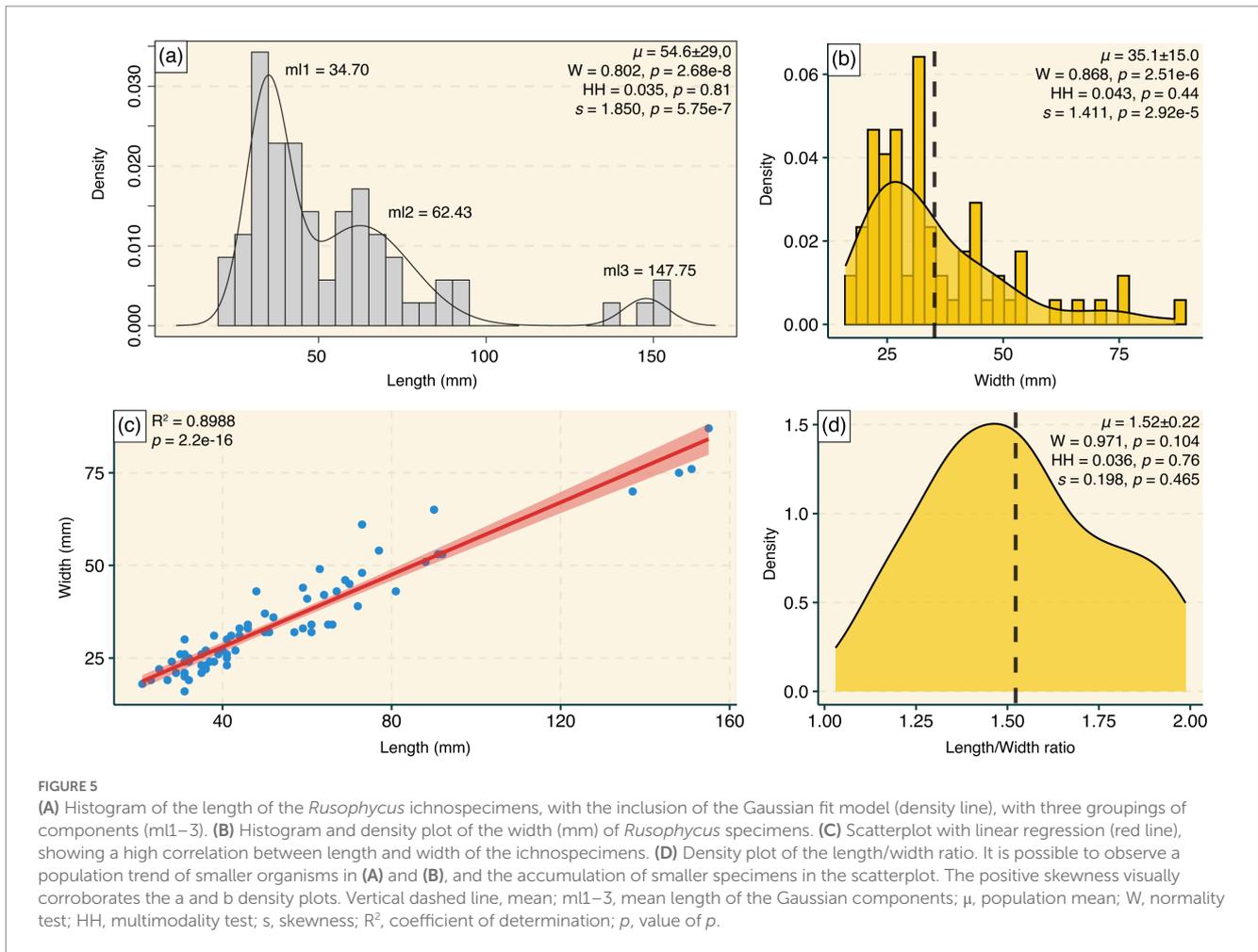
Details of *Rusophycus* from the studied section. (A–C, A'–C') *Rusophycus* (highlighted in red) in association with *Protopaleodyction* (highlighted in yellow). (D, D') *Rusophycus* (highlighted in red) in association with *Bergaueria* and *Palaeophycus* (highlighted in yellow). (E–G, E'–G') Detail of the morphology of *Rusophycus*. *Rusophycus* also overlaps *Palaeophycus* (white arrow) in (E, G). (H, H') *Rusophycus* (highlighted in red) in association with *Cruziana* (highlighted in yellow). Scale bars=2 cm.

Asterosoma, *Rosselia*; MacEachern et al., 2007; Sedorko et al., 2018c), suggesting colonization dominantly in lower shoreface settings. Suite B is interpreted as archetypal *Cruziana* ichnofacies due to the higher ichnodiversity and variation on preserved behaviors, such as resting traces (*Bergaueria*, *Lockeia*, and *Rusophycus*), locomotion (*Cruziana* and *Diplichnites*), grazing activity (*Helminthopsis* and *Protopaleodyction*), dwelling or suspension-feeding (*Arenicolites*, *Palaeophycus*, and *Skolithos*), and equilibrium (*Diplocraterion*); they present moderate to high bioturbation degree and were produced in fine-grained substrates, but often cast by overlying sandy strata, suggesting colonization in a transitional offshore zone (MacEachern et al., 2007; Sedorko et al., 2018a). Lastly, Suite C represents low-energy settings, with deposit-feeding habits (e.g., *Chondrites*, *Phycosiphon*, and *Planolites*) in offshore settings (MacEachern et al., 2007; Sedorko et al., 2018b). Thus, in the transition between the Pimenteiras and Cabeças formations, the *Cruziana* ichnofacies dominate in a lower shoreface to offshore setting, and the trilobites had their trace fossils preferentially preserved in an offshore transition zone.

Rusophycus has been recorded in the Lower Paleozoic beds of the Parnaíba Basin, particularly in the Pimenteiras Formation. However, none of the known ichnospecies shows the same morphological features that characterize the analyzed specimens. *Rusophycus polonica*

(Seilacher (1970) shows a deep oval central area and thicker ridges (Correa et al., 2004). *Rusophycus dispar* Linnarsson, 1869 is characterized by a heart shape and scratches in several directions (Gracioso, 2011). *Rusophycus biloba* Vanuxem, 1842 presents thick bifid transverse scratches and united posterior and anterior margins (Silva et al., 2012). *Rusophycus piauiensis* Agostinho et al. (2004) described in the Longá Formation, shows a smaller length/width ratio and thicker striae when present (Muniz, 1982). Considering that not all observed *Rusophycus* in this study bear a clear pattern of scratches, we treat them at the ichnogenetic level.

The statistical analysis of the studied specimens revealed three components (grouping) of sizes (Figure 5A), indicating different ontogenetic stages of burrowing trilobites. In the early ontogenetic phases (protaspis and meraspis), trilobites were extremely small (less than 1 or 2 mm), hampering a prominent ichnologic record. This situation changes when they reach the holaspis phase and assume a burrowing behavior (Seilacher, 2007). Smaller tracemakers dominate the analyzed suite (Suite B), suggesting a typical form for r-strategists' populations (Bromley, 1996; Ruppert et al., 2005). The dominance of small organisms in storm-influenced strata points to the prevalence of opportunistic strategies in a stressful substrate, possibly due to high hydrodynamic levels and short colonization windows (*sensu* Pollard



et al., 1993). The high depositional frequency is also corroborated by the occurrence of *Diplocraterion*, both protrusive and retrusive in the same bed, suggesting frequent vertical replacement of the infauna (Buatois and Mángano, 2011).

The growth pattern observed in trilobite species in the fossil record is relatively continuous (e.g., Kim et al., 2002; Crónier, 2003; Park and Choi, 2009; Shen et al., 2014; Hou et al., 2017; Pauly and Holmes, 2022; Dai et al., 2023), and this trend is also evident in the size patterns of *Rusophycus* from the studied section (see Figure 5C, $R^2 = 0.8988$). The *Rusophycus* ichnospecimens show a pattern of greater prolongation in length than the width (Figure 5C), possibly due to the accumulation of new segments in post-protaspis trilobites (Hughes, 2003; Hughes et al., 2006), leading to slightly greater growth in length than in width.

The population trend of smaller organisms is a common phenomenon in trilobite species, as observed in previous studies (Sheldon, 1988; Kim et al., 2002; Crónier, 2003; Park and Choi, 2009; Shen et al., 2014; Hou et al., 2017; Pauly and Holmes, 2022; Dai et al., 2023). This trend is characterized by a higher number of smaller individuals, and as the size increases, the number of individuals decreases continuously, which is a typical trait of r-strategist species (Pianka, 1970) and type III survivorship curves (Demetrius, 1978).

In this work, the analysis of *Rusophycus* reveals a similar pattern of size abundance as that observed in trilobite species (see Figure 5 and positive skewness). This is consistent with the survival pattern of trilobites, where many die in the process of protaspis and small meraspis stages, with few reaching the larger holaspis stage (Cisne, 1973; Brezinski, 1986; Sheldon, 1988; Shen et al., 2014; Hou et al., 2017; Pauly and Holmes, 2022; Dai et al., 2023). This is similar to a type III survivorship curve (Demetrius, 1978). Our analysis also revealed three different groups of components in the length of the *Rusophycus* specimens (Figure 5A). This pattern of “pulses” of size has been observed in trilobite species (see Cisne, 1973), and reevaluation of the data by Brezinski (1986) and Pauly and Holmes (2022) could be related to different instars in trilobite tracemakers (Hunt and Chapman, 2001) resulting in *Rusophycus* of different sizes.

Trilobites are generally considered marine organisms, although some trace fossils attributed to trilobites were found in estuarine settings (Mángano et al., 2021). In the studied area, the *Rusophycus* occur at the bottom of a storm-influenced bed but were generated in the fine-grained deposits of facies F and M, characterizing pre-depositional colonization.

The dominance of *Rusophycus* in an ichnoassemblage, as observed in Suite B, has been interpreted as a hunting strategy, in which trilobites hide in shallow burrows to catch detritus or hunt for

soft-bodied prey, as reported in other Paleozoic units (e.g., Whittington, 1980; Seilacher, 1985; Jensen, 1990; Brandt et al., 1995; Pickerill and Blissett, 1999; Rydell et al., 2001; Brandt, 2007). However, the close association of *Rusophycus* with *Protopaleodyction* in these beds and their overlapping by *Palaeophycus* (Figures 4A,B,G) indicate that they were relatively deep burrows. Although a carnivorous habit cannot be discharged, in study area there is no record of *Rusophycus* overlapping a trace fossil that would be produced by some worm-like organism. In addition, there is no record of carnivorous trilobites in the Brazilian sedimentary basins (Carvalho and Ponciano, 2015; Carbonaro et al., 2018).

The depth of the *Rusophycus* specimens, the random distribution against the currents, the concentration in a single bed, and the presence of different component groups of length (Figure 5A) with positive skewness, allow interpreting the studied *Rusophycus* as result of a resting behavior related to molting burrow for ecdysis. The trilobites probably excavated deeper in a previously bioturbated substrate for protection during the molting process, as proposed for some burrows attributed to trilobites (Seilacher, 2007). The preservation of *Rusophycus* in palimpsest preservation with other burrows (as represented in Figure 6) further supports this interpretation.

The dominance of traces produced by smaller organisms in the Suite B assemblage suggests that trilobites had an opportunistic behavior in offshore transition settings. The prevalence of an r-strategist population in stable environments such as the offshore transition zone indicates punctual ecologically stressing conditions, probably due to salinity fluctuations resulting from episodic continental inputs, as suggested by the presence of combined flow ripples and abundant phytodebris (Ponciano and Della Fávera, 2009). However, the spawning behavior of trilobites naturally implies a high

number of small and fewer mature adults in the population, since the option of a reproductive strategy with simultaneous spawning reduces the possibility of individuals within the same cluster being consumed by predators (Hegna et al., 2017). According to Cisne (1973) and the reevaluation of Pauly and Holmes (2022), the spawning of trilobites was seasonal (once a year), resulting in populations of high rates of small organisms compared to holaspis individuals. Although the spawning behavior of trilobites could explain the record of a population with a higher number of young adults compared with the mature ones, there is no evidence of seasonal events in the studied deposits. The erosive nature of the sandy beds that preserved the trilobite burrows suggests episodic storm events. The presence of sedimentary structures that suggest continental input, allied with plant debris, reinforces the hypothesis of sporadic salinity stress as the most parsimonious cause of stress for the studied section.

During molting, arthropods are more vulnerable to potential predators, so burrowing becomes a useful protection strategy for the tracemaker (e.g., Bromley, 1996; Seilacher, 2007). The presence of three different groups of sizes (Figure 5A) reinforces the interpretation of this strategy of burrow during molting (Hunt and Chapman, 2001). Body fossils of homalonotid and calmoniid trilobites have been recorded in the Brazilian Devonian beds (e.g., Simões et al., 2009; Carvalho and Ponciano, 2015), and in some cases there is a record of trilobites (*Burmeisteria notica* and *Metacryphaeus cf. australis* = *M. meloi*) with *Rusophycus* (Leme et al., 2013). According to Simões et al. (2009), homalonotids occur associated with shallow, sandy subaquatic deposits accumulated just in and/or above the fair-weather wave base zone and calmoniids are more common in muddy facies (flooding surfaces) generated below the storm wave base zone. Therefore, considering this paleoenvironmental distribution, calmoniids might be considered

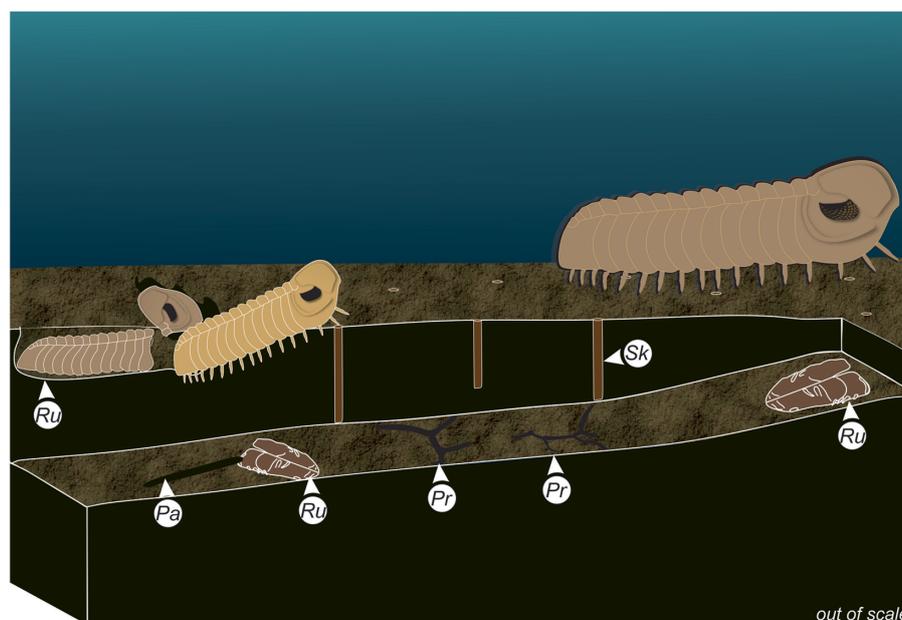


FIGURE 6

Reconstitution of the molting strategy of trilobites while producing *Rusophycus*, and tier relation of commonly associated trace fossils. Pr, *Protopaleodyction*; Ru, *Rusophycus*; Sk, *Skolithos*.

as the main potential tracemaker of the studied *Rusophycus* specimens, mostly during the molting phase.

However, the Parnaíba Basin has a limited record of trilobites, with only few species from the Calmonidae and Homalonotidae families (Ghilardi and Simões, 2007; Meira, 2014; Carbonaro et al., 2018). The most common genus within Calmonidae is *Metacryphaeus*, with three species recorded: *M. tuberculatus*, *M. meloi*, and *M. kegei* (Carvalho et al., 1997; Leme et al., 2013; Meira, 2014; Meira et al., 2016; Carbonaro et al., 2018), along with a record of *Eldredgeia cf. venusta* (Carvalho and Ponciano, 2015). In the Homalonotidae family, only *Burmeisteria notica* has been identified (Leme et al., 2013; Meira, 2014), with a width range of 22–40 mm (Leme et al., 2013), similar to the mean width of the *Rusophycus* specimens studied here (~35 mm). The sizes of the *Metacryphaeus* species differ, with *M. kegei* being the smallest, ranging widthwise from ~7 to 23 mm (Carvalho et al., 1997), *M. meloi* ranging in width from ~17 to 31 mm (Carvalho et al., 1997; Leme et al., 2013), and *M. tuberculatus* ranging in width from approximately from 30 to 108 mm, with some complete specimens ranging lengthwise from 75 to 176 mm (Carvalho et al., 1997; Meira et al., 2016). Therefore, it is possible that both calmoniids and homalonotids have produced the *Rusophycus* traces reported in this study.

6. Final remarks

The trace fossil suites in the studied section are an expression of proximal, archetypal, and distal Cruziana ichnofacies in lower shoreface to offshore settings. The suite with multiple *Rusophycus* can be interpreted as a pre-depositional suite, generated in the underlying muddy beds, and cast by the sandy sediments carried by storm-generated and combined current flows in transitional offshore to offshore settings. Most *Rusophycus* can be attributed to a tracemaker in meraspis and few holaspis stages. This distribution suggests an r-strategist population. The random distribution in low energy depositional setting, absence of hunt evidence, and high deep of *Rusophycus* allowed the assumption that a molting activity is the triggered behavior to the production of *Rusophycus* in those storm-influenced beds from Pimenteira Formation, while *Cruziana* represents detritus-feeding strategy.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary material](#), further inquiries can be directed to the corresponding author.

Author contributions

DS: conceptualization, methodology, formal analysis, investigation, validation, visualization, data curation, writing—original draft, review and editing, and project administration. GB: methodology, software, formal analysis, data curation, writing—original draft, review and editing, and visualization. RN: conceptualization, formal analysis, investigation, validation,

writing—original draft, and review and editing. RG: formal analysis, validation, writing—original draft, review and editing, and project administration. SA: methodology, validation, and review and editing. KR: methodology, formal analysis, validation, visualization, and writing—original draft. EFN: methodology, visualization, and writing—original draft. CM: visualization and writing—original draft. LB: methodology, validation, writing—original draft, and review and editing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2023.1117947/full#supplementary-material>

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