

# Evolutionary, paleoecological, and biostratigraphic implications of the Ediacaran-Cambrian interval in West Gondwana

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## ABSTRACT

**The Ediacaran-Cambrian transition interval is described for the west part of the Gondwana Supercontinent. This key interval in Earth's history is recorded in the upper and lower part of the Tagatiya Guazú and Cerro Curuzu formations, Itapucumi Group, Paraguay, encompassing a sedimentary succession deposited in a tidally influenced mixed carbonate-siliciclastic ramp. The remarkable presence of cosmopolitan Ediacaran shelly fossils and treptichnids, which are recorded in carbonate and siliciclastic deposits, respectively, suggests their differential preservation according to lithology. Their distribution is conditioned by substrate changes that are related to cyclic sedimentation. The associated positive steady trend of the  $\delta^{13}\text{C}$  values in the carbonate facies indicates that the Tagatiya Guazú succession is correlated to the late Ediacaran positive carbon isotope plateau. Sensitive high-resolution ion microprobe U-Pb ages of volcanic zircons from an ash bed ~30 m above the fossil-bearing interval in the Cerro Curuzu Formation indicate an Early Cambrian (Fortunian) depositional age of  $535.7 \pm 5.2$  Ma. As in other coeval sedimentary successions worldwide, the co-occurrence of typical Ediacaran skeletal taxa and relatively complex trace fossils in the studied strata highlights the global nature of key evolutionary innovations.**

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## INTRODUCTION

The transition from late Ediacaran to Early Cambrian is recognized in a number of successions worldwide mainly based on the sudden appearance of complex trace fossils produced by bilaterian metazoans (Brasier et al., 1994). Despite its rare co-occurrence with remains of skeletal metazoans and datable ash beds (Nelson et al., 2022; Bowyer et al., 2022), the *Trepichnus (T.) pedum* Assemblage Zone has been considered as evidence for ecologic innovations in the dawn of the Phanerozoic Eon (Narbonne et al., 1987; Jensen, 2003; Buatois, 2018). The fact that small shelly fossils tend to be present in carbonate deposits and *T. pedum* occurs in siliciclastic rocks has complicated global correlations of the Ediacaran-Cambrian boundary (Shahkarami et al., 2020; Bowyer et al., 2022). While treptichnids are recorded in late Ediacaran rocks (Jensen et al., 2000), the first appearance datum (FAD) of *T. pedum* appears to post-date the last appearance datum (LAD) of *in situ* *Cloudina* and *Namacalathus* in all environments with high-resolution  $\delta^{13}\text{C}_{\text{carb}}$  data (Bowyer et al., 2022; Nelson et al., 2022).

In recent years, there have been several reports of claudinids from basal Cambrian strata and Cambrian-style shelly fossils from terminal Ediacaran strata (Yang et al., 2016; Cai et al., 2019; Álvaro et al., 2020; Zhu et al., 2017). Also, evidence of Cambrian-style sediment bulldozers has been documented in terminal Ediacaran strata (Buatois et al., 2018; Darroch et al., 2021). These reports provide

evidence for evolutionary continuity across the Ediacaran-Cambrian boundary, indicating that key biologic innovations arose in the terminal Ediacaran and expanded in the Cambrian. From a stratigraphic perspective, these findings help to better characterize the poorly constrained range of the Terminal Ediacaran Biozone (*sensu* Muscente et al., 2019) and expand the temporal extent of the previously proposed *Cloudina-Namacalathus-Sinotubulites* Assemblage Zone (545–540 Ma, Zhu et al., 2017). Despite this, the paucity of reliable geochronologic data makes it difficult to precisely define the temporal range of the terminal Ediacaran interval or biozone (Muscente et al., 2019) and its relationship with the *T. pedum*-bearing interval (Nelson et al., 2022). Among the exceptions are mixed carbonate-siliciclastic successions in Mexico and Namibia, where volcanic zircon grains indicate maximum and minimum ages of  $539.4 \pm 0.23$  Ma (maximum age, Hodgin et al., 2021) and  $538.8 \pm 538.6$  Ma (Linnemann et al., 2019), and  $538.3 \pm 0.14$  Ma (minimum age, Nelson et al., 2022) for the Ediacaran-Cambrian interval. These radiometric ages are consistent with those recently available for the global Ediacaran-Cambrian age model and the FAD of *T. pedum* that suggests a ca. 538.8 Ma age for this boundary (see Nelson et al., 2022 for further discussion). However, the sedimentary successions of SW Gondwana, which hosts skeletal assemblages of *Cloudina*, *Namacalathus*, and *Corumbella* (see Cortijo et al., 2010; Warren et al., 2011, 2017; Adorno et al., 2017), remain poorly constrained due to the scarcity of high-resolution

geochronologic and  $\delta^{13}\text{C}_{\text{carb}}$  data. Aiming to fill this gap in the terminal Ediacaran record from the southwest part of that supercontinent, we carried out a comprehensive stratigraphic, paleontologic, and geochronologic study of the late Ediacaran Tagatiya Guazú Formation and the Early Cambrian Cerro Curuzu Formation, both included in the Itapucumi Group, Paraguay. A relatively diverse fossil assemblage and a sensitive high-resolution ion microprobe (SHRIMP) zircon U-Pb age from a tuffaceous layer help us to precisely constrain the Ediacaran-Cambrian interval in this sedimentary succession. Based on these new data, we can now better address key questions on the temporal and spatial dynamics of Ediacaran skeletal fossils.

## GEOLOGY OF TAGATIYA GUAZÚ AND CERRO CURUZU FORMATIONS

The Itapucumi Group crops out in the northern part of Paraguay, comprising a ~400-m-thick siliciclastic and carbonate succession (Warren et al., 2019a). In its western area, the unit is deformed and metamorphosed in greenschist facies (chlorite zone), whereas in the eastern part it constitutes an extensive undeformed cover directly deposited over the Paleoproterozoic terrains of the Rio Apa Craton (Warren et al., 2011). In the western domain, coarse- to fine-grained arkose and volcanic rocks from the Vallemi Formation constitute the basal succession lying unconformably above rocks of the Paleoproterozoic basement. Carbonate rocks from the Camba Jhopo and Tagatiya Guazú formations overlie the Vallemi Formation, culminating in fine- and very fine-grained sandstone, siltstone, marl, and grainstone of the Cerro Curuzu Formation.

The Tagatiya Guazú Formation comprises an extensive unmetamorphosed, undeformed cratonic sedimentary cover constituted by ~60-m-thick carbonate succession of thrombolite, oncolite, and cross-stratified, graded, and laminated grainstone, locally presenting mudstone drapes (Warren et al., 2019a). Breccia deposits associated with tepee structures and salt pseudomorphs are also locally observed (Warren et al., 2011). Previous paleontologic studies of the Tagatiya Guazú Formation revealed an association of Nama-style skeletal remains of *Cloudina*, *Corumbella*, and *Namacalathus*, as well as simple trace fossils (Warren et al., 2011, 2017). The facies association consisting of low-energy shallow-water facies with rare subaerial exposure is indicative of deposition in an inner ramp environment, rimmed by a coastal oolitic belt (Warren et al., 2011, 2017, 2019a). The Tagatiya Guazú Formation lies unconformably over igneous and metamorphic rocks of the base-

ment and is laterally equivalent to the Camba Jhopo Formation in the western domain of the Itapucumi Group (Warren et al., 2011, 2019a).

The mixed siliciclastic-carbonate Cerro Curuzu Formation occurs stratigraphically above the Tagatiya Guazú and Camba Jhopo formations and is mainly characterized by mudstone and thin-bedded grainstone that grade to heterolithic facies, siltstone, grainstone, and wave-rippled fine-grained sandstone (Warren et al., 2019a). The ~80-m-thick succession is representative of deposition in deep- to shallow-water environments of an outer ramp setting. The unit is barren of fossils except for possible organic (carbonaceous?) remains that are not taxonomically identifiable. The Itapucumi Group is interpreted to have been deposited in a gently sloping mixed carbonate-siliciclastic ramp opened to the Clemene Ocean to the west (Warren et al., 2019a).

In both the carbonate (Tagatiya Guazú Formation) and the mixed carbonate-siliciclastic succession (Cerro Curuzu Formation),  $\delta^{13}\text{C}_{\text{carb}}$  values are consistently positive (mean value of +1.93‰) and the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios range from 0.7084 to 0.7089 (see data in Warren et al., 2019a). These values are consistent with che-  
mostratigraphic data from other terminal Ediacaran and Early Cambrian successions around the world (Halverson et al., 2010; Bowyer et al., 2022).

## EDIACARAN-CAMBRIAN SEDIMENTARY SUCCESSION OF THE ITAPUCUMI GROUP

Laterally continuous metric-scale carbonate cycles constituted by trough-cross bedded grainstone grading to thin laminated microbialite or heterolithic beds marked by the alternation of thrombolite and marl characterize the sedimentary succession of the upper part of the Tagatiya Guazú Formation (Fig. 1C). Intraformational breccia, coarse-grained bioclastic concentrations, wackestone, and oncolite are also common. This interval is interpreted to have been deposited in very shallow water in a tidally influenced setting. In this context, the trough-cross bedded grainstone represents deposits of shallow subtidal channels that migrated laterally during high-energy events over microbialite and heterolithic sediment deposited in back-shoal settings, rarely affected by subaerial exposure (Warren et al., 2011, 2019a). The cyclic repetition of this facies association is indicative of peritidal shallowing upward cycles, suggesting marked allogenic controls on deposition (Spence and Tucker, 2007).

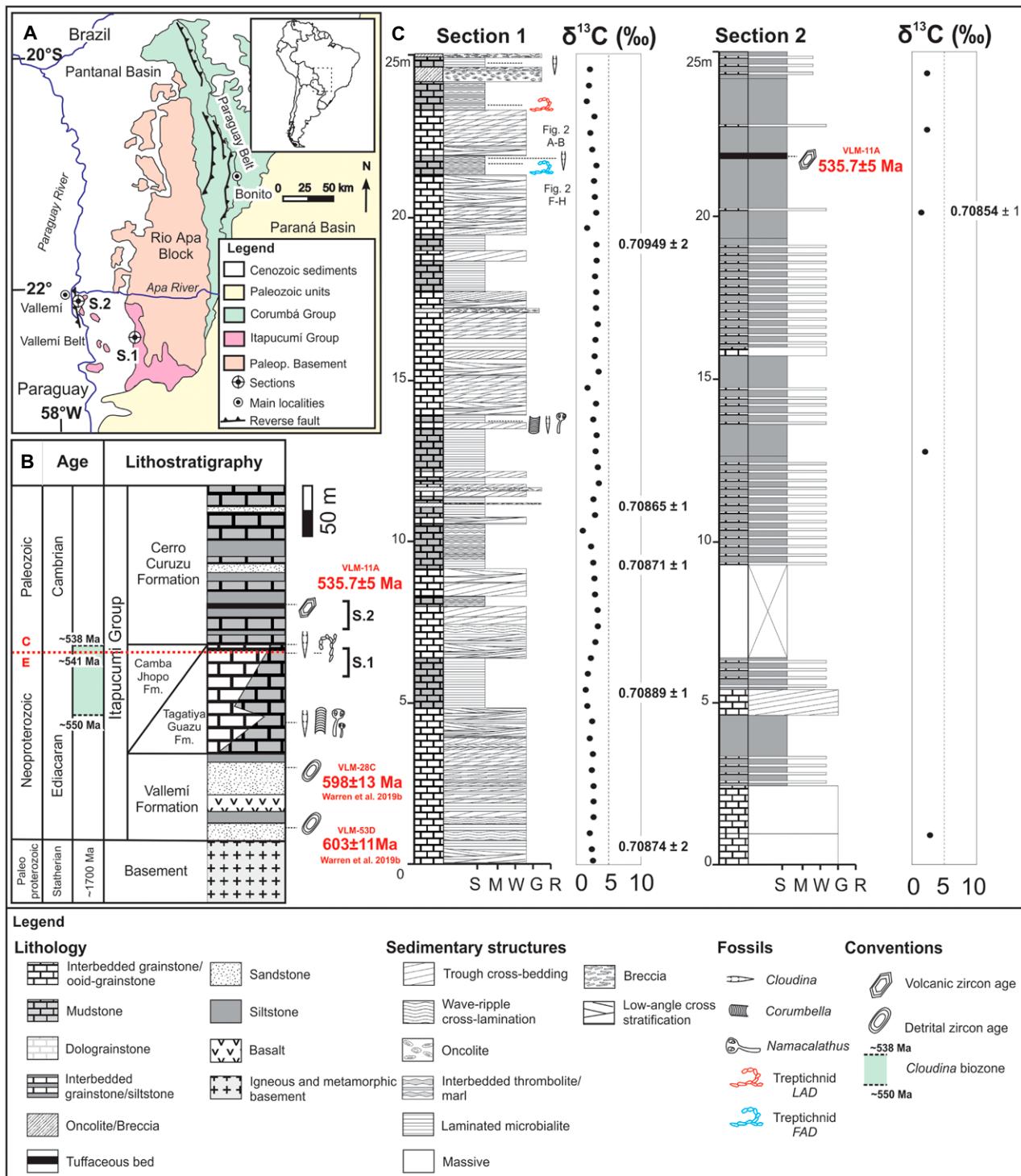
The skeletal organisms recorded at this stratigraphic interval are abundant specimens of

*Cloudina* sp., *Corumbella wernerii*, and more rarely *Namacalathus* sp. (Figs. 2A–2D). These are mainly preserved as complete or fragmented skeletal remains in intertidal microbialite facies not affected by subaerial exposure (Warren et al., 2012, 2013, 2017). Locally, centimeter-thick packed shell beds constituted by parautochthonous fragments of *Cloudina* shells and other indeterminate tubular taxa occur at the top of trough cross-bedded grainstone, characterizing subtidal lags made of remains reworked by short-term currents and deposited close to where the skeletal organisms lived. In the upper part of the Tagatiya Guazú Formation, peritidal stratiform microbialites and thrombolites are interbedded with red-colored mudstone and marl, indicating a notable increase in siliciclastic input to the basin.

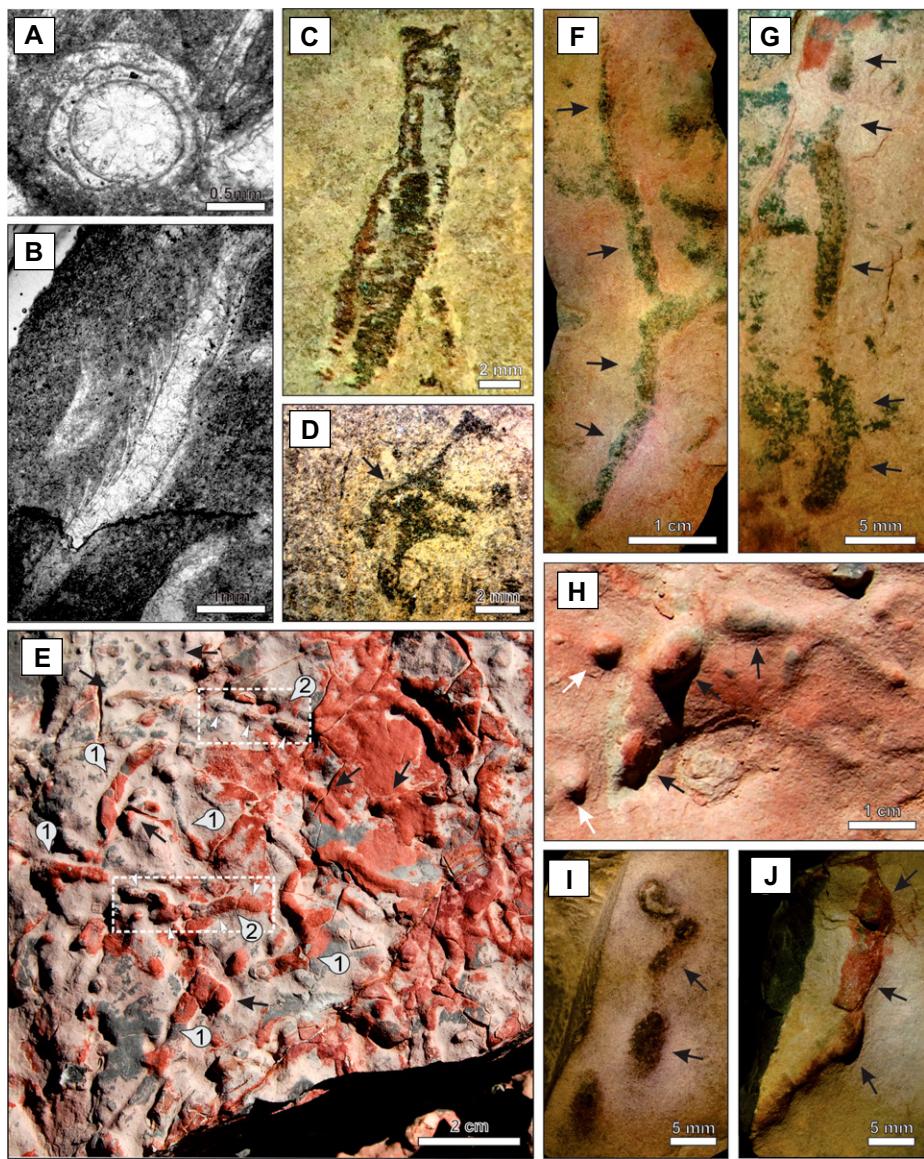
Monotonous intercalation of dark-colored mudstone interbedded with cm- to dm-thick beds of very fine grainstone characterizes the basal part of the Cerro Curuzu Formation (Fig. 1C). This interval also show the presence of a tuffaceous bed interlayered with mudstone facies (Fig. 1C, but see Warren et al., 2019b). The Cerro Curuzu Formation is interpreted to have been deposited in a mixed siliciclastic-carbonate outer ramp formed in response to a regional sea-level rise (Warren et al., 2019a).

## TRACE FOSSILS FROM THE TAGATIYA GUAZÚ FORMATION

At the top of the last two shallowing-upward cycles in the upper part of the Tagatiya Guazú Formation (Section 1, Fig. 1C), abundant trace fossils are observed (Fig. 2E). They are commonly preserved at the bottom of cm- to dm-thick impure calcareous mudstone beds (1–8% bedding plane disruption, bioturbation index 2, *sensu* Miller and Smail, 1997), at the junction with marl and limestone rich in siliciclastic components (Fig. 3B). Trace fossils are typically preserved as positive hyporelief, but are locally observed as full-relief structures either at the top or bottom of beds. They consist of horizontal to slightly inclined, straight to loosely meandering burrows, in some cases showing regular to irregularly spaced constrictions (Figs. 2E and 2F). They are infilled with dark-colored calcareous mudstone, which is distinguishable from the material in adjacent mudstone-microbialite beds (Figs. 2E–2G), and the constrictions may indicate actively infilled burrows produced by deposit-feeding organisms, revealing affinities with *Planolites* and *Torrowangea*. When preserved, burrow margins are commonly marked by a well-defined red-colored surface, which occurs independently of other morphologic features (Fig. 2E).



**Figure 1. Geology and stratigraphy of the studied area. (A)** Simplified geologic map of the southern part of Paraguay (Brazil) and Vallemi fold belts (Paraguay), highlighting the studied sections. **(B)** Simplified lithostratigraphic framework of the Itapucumi Group and sensitive high-resolution ion microprobe U-Pb ages obtained from detrital (VLM-28C and VLM-53D) and volcanic zircons (VLM-11A). The stratigraphic section corresponds to the upper part of the Tagatiya Guazú Formation in which the Ediacaran-Cambrian boundary is positioned. **(C)** Stratigraphic columns and carbonate carbon isotope data from the upper Tagatiya Guazú (S.1) and lower Cerro Curuzu (S.2) formations. Note the presence of *Cloudina* above the bed containing abundant treptichnids. Modified from Campanha et al. (2010) and Warren et al. (2019a). Fm.—Formation; Paleop.—Paleoproterozoic; S—shale; M—mudstone; W—wackestone; G—grainstone; R—rudstone; S.1—Section 1; S.2—Section 2; Treptichnid FAD—local first appearance datum of treptichnid; Treptichnid LAD—local last appearance datum of treptichnid. The  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios, C and O isotopic values of sections 1 and 2 from Warren et al. (2019a).



**Figure 2. Fossil assemblage from the Tagatiya Guazú Formation, northern Paraguay, peritidal facies association.** (A and B) *Cloudina hartmannae* from the bed located immediately above the treptichnid occurrences (see Figs. 1C and 3B for precise stratigraphic position). (C) *Corumbella wernerii*. (D) *Namacalathus hermanastes* with possible clonal budding reproduction feature (black arrow). (E) High density of trace fossils preserved at the bottom of bed consisting of potentially active infilled burrows marked by regular constrictions (1) and rudimentary probing burrow systems of treptichnids (2). Other putative structures are indicated by black arrows. (F) Horizontal burrow with regularly spaced constrictions (black arrows). (G and H) Disconnected aligned burrows (black arrows) forming rectilinear (G) or curved patterns (H), indicating either vertical oscillatory movements or rudimentary probing burrows of treptichnids. (I and J) Partially disconnected burrows in approximate zig-zag (I) and imbricated patterns (J). A and B are thin-section photomicrographs, and C–J are reflected light photographs. F–H correspond to trace fossils in positive hyporelief (lower bedding view) (white arrow). I–J correspond to positive relief burrows with uncertain orientation. For the precise stratigraphic position of trace fossils, see Figure 1C (local first appearance datum of treptichnids) and Figure 3B.

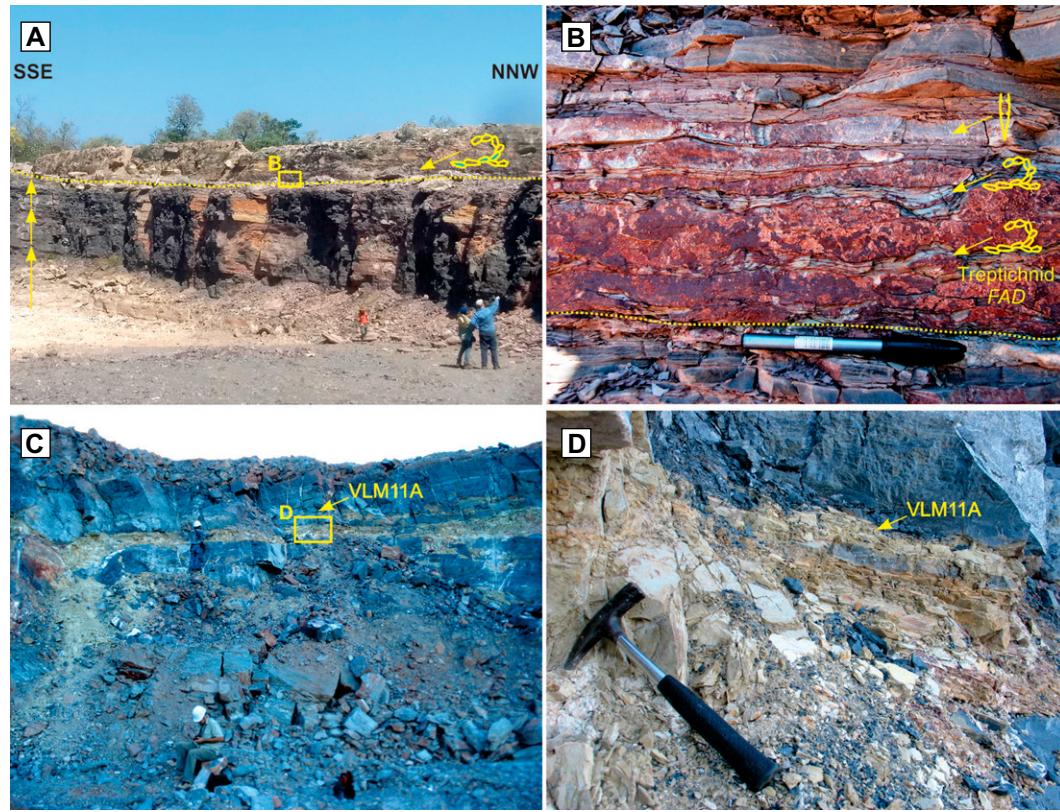
Several specimens grade to or are entirely marked by discontinuous aligned or imbricated segments which seem to follow approximately straight, curved, or slightly zig-zag trajectories (Figs. 2G–J). The simple alignment of discontinuous burrows as seen in some specimens

(Figs. 2E, 2G, and 2H) may indicate occasional vertical excursions of the trace maker, regularly crossing the horizontal bedding plane. This probing behavior is similar to that inferred from preservational variants of treptichnids from late Ediacaran of Namibia (Jensen et al., 2000). Similar patterns may reflect changes in trajectory as the animal searched for resources at different levels within the substrate and at the water-sediment interface (Xiao et al., 2019). A few centimeters (~10 cm) above the trace fossil-bearing bed, there occur at least three cm-thick intervals with abundant fragments of *Cloudina* (Figs. 2A, 2B, and 3B). This pattern of fossil distribution, with cloudiniids stratigraphically above treptichnids is similar to what is described in the Spitskop Member of the Ursus Formation in southern Namibia (Linnemann et al., 2019).

#### DATING THE EDIACARAN-CAMBRIAN INTERVAL IN WESTERN GONDWANA

The dm-thick volcanic tuffaceous bed located at the top of geologic section S.2 of the Cerro Curuzu Formation (Figs. 1C, 3C, and 3D) is composed of intensely weathered, light yellow amorphous material containing euhedral zircon grains (Fig. 4B). The contact between the Tagatiya Guazú and Cerro Curuzu formations is not well exposed in the study area, but the detailed stratigraphic correlation between the western and eastern sections (Figs. 1A–1C) allows us to infer that the top of S.1 is located a few meters below the base of S.2. Thus, the dated tuffaceous bed at the basal part of the Cerro Curuzu Formation (Figs. 1B, 1C, 3A, and 3B) is stratigraphically placed ~30 m above the top of S.1.

SHRIMP U-Pb age determinations revealed that the tuffaceous bed at the base of the Cerro Curuzu Formation (sample VLM-11A, Figs. 3C and 3D) is dominated by a population of Neoproterozoic xenolith zircon grains (Fig. 4A), covering 75% of the 40 zircon grains analyzed. The Ediacaran zircons represent 52.5% of the grains analyzed, and the yielded ages are between 542 Ma to 627 Ma. Cryogenian and Tonian grains compose a subordinate population, with ages of 648–649 Ma (7.5% of grains analyzed) and 783–821 Ma (12.5% of grains analyzed). The precise origin of the Neoproterozoic zircon grains is unknown but they may have been inherited from local granitic intrusions, such as the Urucum Granite and Rodinian magmatic rocks of the Amazon Craton (Hasui and Almeida, 1970; Manoel et al., 2021). Three older grains are also documented, with ages of 1116 Ma (Stenian, 2.5% of grains analyzed), 2084 Ma (Rhyacian, 2.5% of grains analyzed), and 2908 Ma (Archean, 2.5% of grains analyzed). These three zircon grains were likely



**Figure 3.** Key sections of the Ediacaran-Cambrian interval in the Itapucumi Group, northern Paraguay. (A) Ediacaran-Cambrian interval corresponding to the upper part of the Tagatiya Gauzu Formation, Itapucumi Group. (B) Stratigraphic position of treptichnids in the section. Detail of the *T. cf. pedum* FAD in A. Treptichnid-rich interval is overlain by a thrombolite bed with *Cloudina* specimens. (C) Early Cambrian ash bed from outer ramp facies association of the Cerro Curuzu Formation. (D) Detail of the whitish ash bed in C. The pen in B is 11 cm long and the hammer in D is 28 cm long. Yellow arrows in A mark carbonate cycles. Treptichnid FAD—Treptichnid first appearance datum.

inherited from basement units of the Rio Apa Craton, such as the Apa Basal Complex, Alumíador, and Centurión suites (Cordani et al., 2010).

Cambrian zircon grains account for 20% of the grains analyzed and have ages of 496 Ma (Furongian, one grain), 500 Ma (Miaolingian, one grain), and 528–539 Ma (Terreneuvian, seven grains). These zircon grains are small (<100  $\mu$ m) euhedral prisms showing discrete oscillatory zoning (Fig. 4B), and they are interpreted as igneous in origin. Late Ediacaran to Early Cambrian magmatism and volcanism between  $548 \pm 6$  Ma (Sonora Granite) and  $518 \pm 4$  Ma (São Vicente Granite) is widely reported in the southern part of the Paraguay Belt and is the best candidate for the volcanic source of the analyzed zircon grains (Godoy et al., 2007; McGee et al., 2012).

Previous U-Pb depositional age analysis of the same tuffaceous bed (Warren et al., 2019b), using 12 volcanic zircon grains with ages varying between  $537 \pm 10$  Ma and  $565 \pm 10$  Ma, provided a “concordia” age of  $545 \pm 4.5$  Ma, placing the upper part of the Itapucumi Group close to the Ediacaran-Cambrian boundary. However, if we consider only the Cambrian volcanic zircon grains in the depositional age analysis, this stratigraphic interval would be even closer to the Ediacaran-Cambrian boundary, yielding a “concordia” age of  $540 \pm 4.2$  Ma. Based on the three

youngest igneous zircon grains (Coutts et al., 2019) from the tuffaceous bed ( $496 \pm 19$  Ma;  $500 \pm 43$  Ma and  $634 \pm 9$  Ma, see Fig. 4A and Supplemental Materials 1 and 2<sup>1</sup>), a depositional age of  $535.7 \pm 5.2$  Ma (Fortunian) can be inferred. This age fits well with the youngest peak identified in the kernel density estimate diagram (Fig. 4A), confirming an Early Cambrian depositional age for the lower Cerro Curuzu Formation.

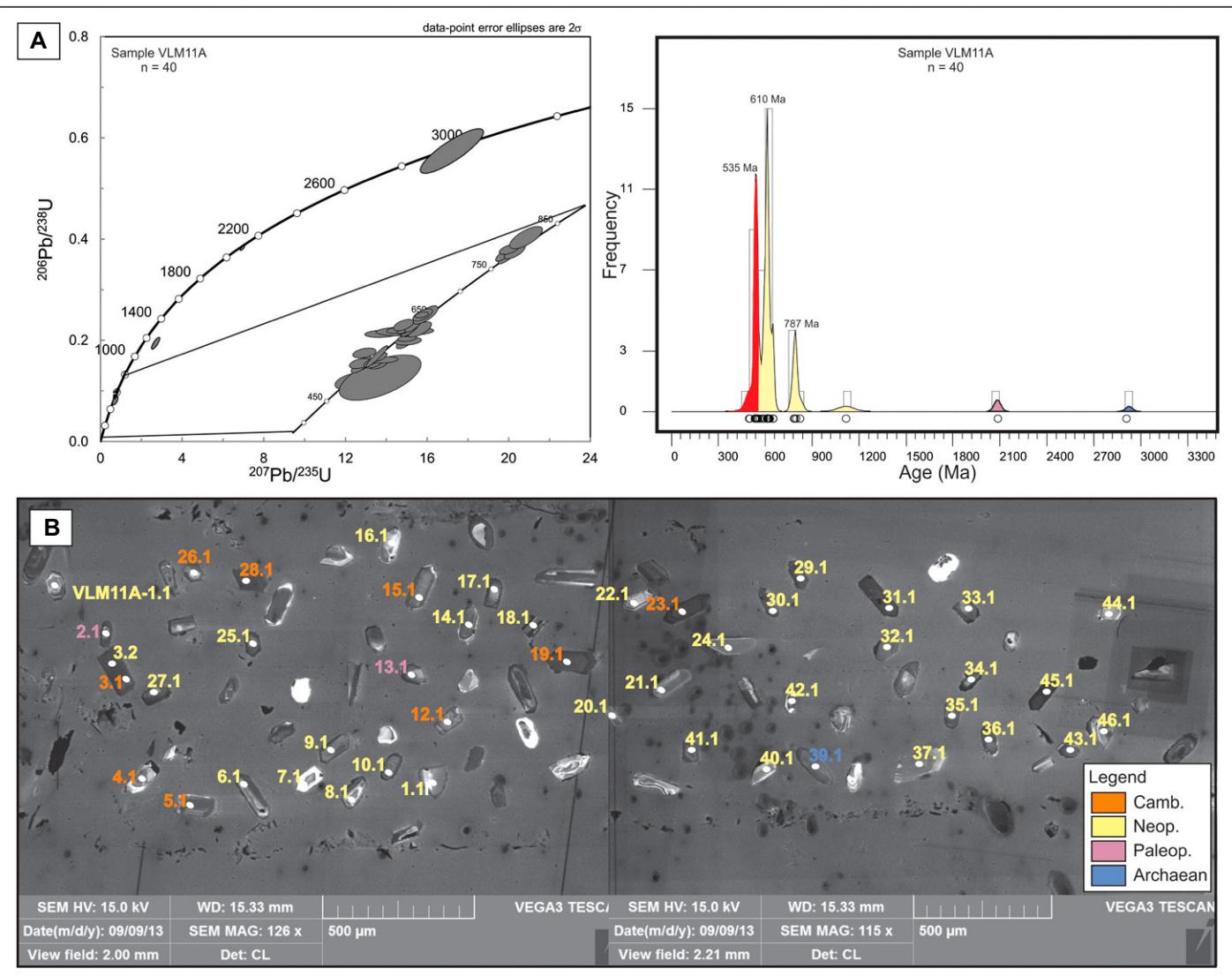
## PALEOENVIRONMENTAL AND EVOLUTIONARY IMPLICATIONS

Peritidal sedimentary facies deposited in a rimmed mixed-carbonate ramp facing the Clymene Ocean characterize the upper part of the Tagatiya Guazú Formation (Warren et al., 2019a). With a regional transgression, moderately deep-water conditions were established, enabling deposition of fine-grained sediments by settling and preservation of the interbedded tuffaceous material at the base of the Cerro Curuzu Formation (Fig. 1C). The Fortunian

( $535.7 \pm 5.2$  Ma) depositional age indicates that the tuffaceous material is possibly related to the Early Cambrian magmatism (Godoy et al., 2007) and associated volcanism (Trivelli et al., 2017) in the southern part of the Paraguay Belt.

The entire Tagatiya Guazú and basal Cerro Curuzu formations are characterized by consistently positive  $\delta^{13}\text{C}_{\text{carb}}$  values of nearly +1.9‰. In the *Cloudina* and trace fossil-bearing interval, which corresponds to the upper part of the Tagatiya Guazú Formation (Fig. 1C), the average value is +2.96‰. This  $\delta^{13}\text{C}_{\text{carb}}$  chemostratigraphic pattern is consistent with the positive plateau described in other coeval *Cloudina*-bearing successions worldwide (Boggiani et al., 2010; Cui et al., 2016; Smith et al., 2016; Linnemann et al., 2019; Xiao and Narbonne, 2020; Bowyer et al., 2022). Thus, considering the co-occurrence of cloudinids and treptichnids within the upper part of the Tagatiya Guazú Formation, we hypothesize that both this unit and the basal part of the Cerro Curuzu Formation may correspond to the late Ediacaran positive  $\delta^{13}\text{C}_{\text{carb}}$  plateau (Zhou and Xiao, 2007; Smith et al., 2016; Zhu et al., 2017). This supports a marine connection between the rimmed carbonate ramp in the Itapucumi basin and the Ediacaran-Cambrian Clymene Ocean (Warren et al., 2019a). Similar to Ediacaran-Cambrian successions in the Spitskop Member, Nama Group (Linnemann et al.,

<sup>1</sup>Supplemental Material. Supplemental Material 1: Sampling and analytical procedures. Supplemental Material 2: U-Pb SHRIMP data. Please visit <https://doi.org/10.1130/GSAB.S.21681614> to access the supplemental material, and contact [editing@geosociety.org](mailto:editing@geosociety.org) with any questions.



**Figure 4.** (A) Concordia diagram (left) and Kernel density plots (right) of sensitive high-resolution ion microprobe (SHRIMP) U-Pb ages obtained from a tuffaceous bed in the Cerro Curuzu Formation, Industria Nacional del Cemento quarry, Vallemi town, northern Paraguay. (B) Scanning electron microscope (SEM) image of the 40 zircons analyzed. See Supplemental Materials 1 and 2 (see text footnote 1) for analytic procedures and U-Pb SHRIMP data, respectively. Camb—Cambrian; Neop.—Neoproterozoic; Paleop.—Paleoproterozoic; MAG—magnification; HV—high accelerating voltage; WD—working distance; Det: CL—cathodoluminescence.

2019), Villarta Formation, Ibor Group (Álvaro et al., 2020), and the Bambú Group (Uhlein et al., 2019), the Paraguayan succession does not preserve the basal Cambrian negative carbon isotope excursion (i.e., BACE, Zhu et al., 2006; Zhu et al., 2017). Thus, it is possible that there are either sedimentary breaks in these Ediacaran-Cambrian successions in Gondwana, or that the BACE onset may not represent a global event (Zhu et al., 2017). However, considering that treptichnids have been reported from terminal Ediacaran strata (Jensen et al., 2000), it is also possible that the Ediacaran-Cambrian boundary is farther up-section in the Cerro Curuzu Forma-

tion and the BACE is not captured in our study either because of low stratigraphic resolution or inappropriate lithologies (Fig. 1C).

Oxic, shallow-water deposits with cosmopolitan skeletal organisms of the terminal Ediacaran Nama Assemblage characterize the Ediacaran-Cambrian interval in the Tagatiya Guazú Formation (Warren et al., 2011). In this setting, skeletal animals, such as *Cloudina*, *Corumbella*, and *Namacalathus*, were the major ecosystem engineers, interacting with microbial bioherms, and providing bioclastic grains to the seafloor for the first time in the Earth's history (Warren et al., 2013). The increase in detrital sediment input

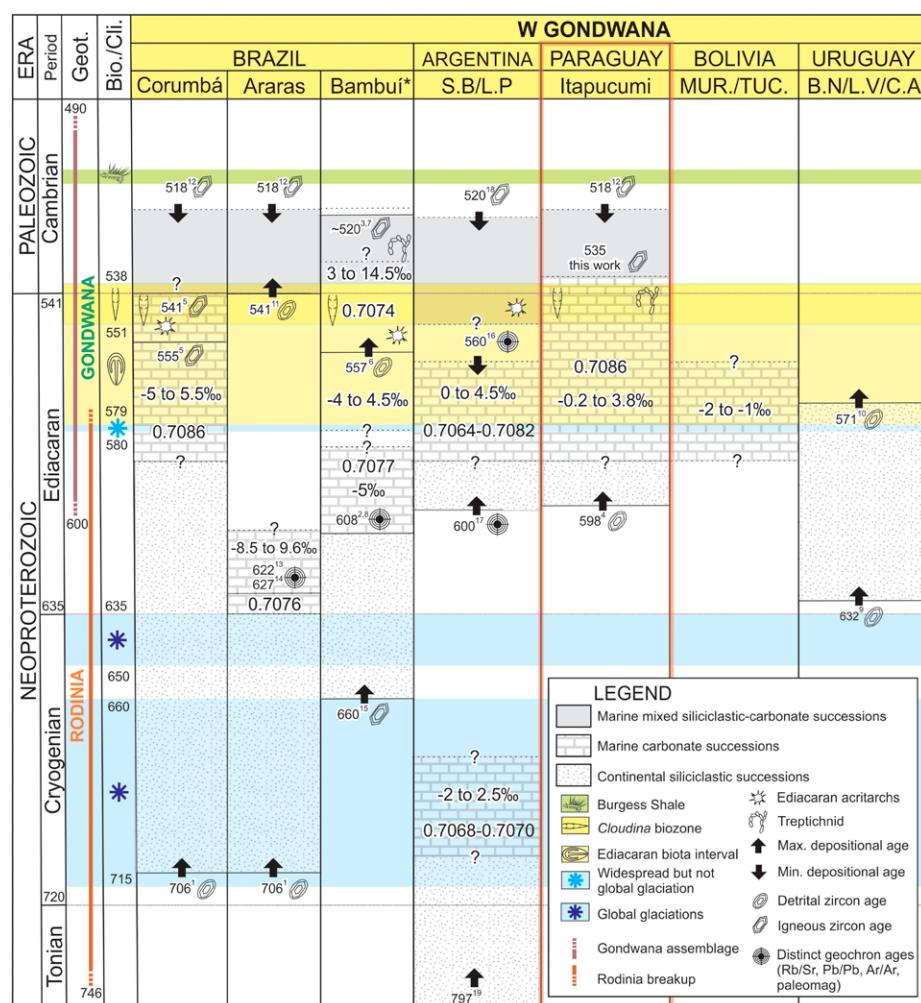
into the basin was related to local fluctuations in sea level and was a key factor controlling the faunal turnover in the upper Tagatiya Guazú Formation, represented by the sudden appearance of marl beds with treptichnids. Consequently, deposition of fine-grained detrital sediment and establishment of a nutrient-rich soft substrate may have been crucial for the formation and preservation of trace fossils produced by benthic detritus- and/or deposit-feeders (Buatois et al., 2018). With the subsequent decrease in detrital sediment input, the return of carbonate sedimentation established suitable environmental conditions for skeletal organisms to recolonize the

substrate. As observed in almost all Ediacaran successions, early skeletal animals mainly occur in carbonate facies, indicating that specific environmental controls (i.e., shallow and non-turbid waters saturated with carbonate) allow sessile benthic skeletal animals to colonize early lithified substrates (Wood et al., 2017). Thus, local environmental conditions (e.g., composition, type, and stability of substrate) seem to explain the alternation of preserved Ediacaran-type skeletonized animals and burrows produced by early bilaterians at the Ediacaran-Cambrian interval.

The presence of skeletonized animals in strata interbedded with treptichnid-bearing deposits indicates that typical Ediacaran shelly fossils probably extend above the Ediacaran-Cambrian boundary in the Itapucumi Group, as is also observed in Namibia (Linnemann et al., 2019; Bowyer et al., 2022) and China (Yang et al., 2016). Thus, there is no evidence that skeletal organisms perished instantly by an abrupt global extinction event at the Ediacaran-Cambrian transition (Laflamme et al., 2013). At least in the Ediacaran-Cambrian interval of the Itapucumi Group, it is suggested that the faunal replacement is a protracted process (see also Park et al., 2021 and Bowyer et al., 2022). That is, in this part of Gondwana, faunal turnover across the Ediacaran-Cambrian interval fits the double wedge model (Muscente et al., 2018; Linnemann et al., 2019), in which older, predominantly sessile Ediacaran lineages were progressively replaced by mobile, burrowing bilaterians (Darbonch et al., 2015, 2018).

## PALEOGEOGRAPHY AND CORRELATION: DECIPIERING THE ARCHIVES OF EDIACARAN-CAMBRIAN TRANSITION IN WEST GONDWANA

Extensive carbonate platforms facing the Clymene Ocean characterize the late Ediacaran and Early Cambrian in the western part of Gondwana (Warren et al., 2019a). In this context, the Itapucumi (Paraguay) and Corumbá (Brazil) groups are considered correlative successions with similar fossil content and stratigraphic architecture, although deposited in distinct paleoenvironmental contexts (Warren et al., 2019a; Amorim et al., 2020). To the north, the Araras Group comprises a carbonate platform formed in the southeastern border of the Amazon Craton during the early Ediacaran (Romero et al., 2013) and is thought to be older than the Itapucumi and Corumbá groups (Fig. 5). In this locality and in other sections of northwest Gondwana, the interval comprising the Ediacaran-Cambrian transition is apparently not recorded, either not deposited or having been eroded (Nogueira et al., 2019). This



**Figure 5. Geochronologic constraints and litho-, chemo-, and biostratigraphic correlation among representative Ediacaran successions of Gondwana.** Geochronologic, paleontologic, and lithostratigraphic data compiled from: 1—Babinski et al. (2013); 2—Babinski et al. (2007); 3—Tavares et al. (2020); 4—Warren et al. (2019b); 5—Parry et al. (2017); 6—Paula-Santos et al. (2015); 7—Moreira et al. (2020); 8—Caxito et al. (2018); 9—Demarco et al. (2019); 10—Hartmann et al. (2002); 11—Bandeira et al. (2012); 12—McGee et al. (2012); 13—Romero et al. (2013); 14—Babinski et al. (2006); 15—Pedrosa-Soares et al. (2011); 16—Gómez-Peral et al. (2018); 17—Rapalini et al. (2013); 18—Tohver et al. (2012); 19—Cingolani and Bonhomme (1988). Geochemical data from: Sial et al. (2010, 2016); Gómez-Peral et al. (2017, 2018); Warren et al. (2019a, 2019b). S.B/L.P.—Sierras Bayas/La Providencia; MUR./TUC.—Murciélagos/Tucavaca; B.N/L.V/C.A.—Barriga Negra/Las Ventanas/Cerro de Aguirre; Geot.—Geotectonic Events; Bio./Cli.—bioevolutive and climatic events; Bambuí\*—including Una, Ubajara, Rio Preto, and Miaba groups. Geochronologic data references used for this figure: Cingolani and Bonhomme (1988); Hartmann et al. (2002); Babinski et al. (2006, 2007, 2013); Pedrosa-Soares et al. (2011); McGee et al. (2012); Romero et al. (2012); Tohver et al. (2012); Rapalini et al. (2013); Paula-Santos et al. (2015); Parry et al. (2017); Caxito et al. (2018); Gómez-Peral et al. (2018); Demarco et al. (2019); Warren et al. (2019b); Moreira et al. (2020); Tavares et al. (2020). Geochemical data references used for this figure: Sial et al. (2010); Gómez-Peral et al. (2017, 2018); Warren et al. (2019a). The lower limit of the Ediacaran Biota Interval (ca. 579 Ma) is defined by the age of oldest macroscopic organism described in the Lantan Formation, South China (Yuan et al., 2011).

view is reinforced by the presence of the Ediacaran Complex Acanthomorph Palynoflora at the upper Araras Group, which extends between

580 and 570 Ma (Grey, 2005; Rudnitski et al., 2016), and a typically lower Cambrian trace fossil assemblage reported from the unconformably

overlying Raizama Formation (Santos et al., 2017; Mángano and Buatois, 2020).

Prior to the evolution of the Clymene Ocean between 540 and 490 Ma, sedimentation in the central part of West Gondwana was marked by the incursion of marine waters from the eastern Adamastor Ocean (585–540 Ma) to intracontinental areas (Caxito et al., 2021). During this period of oceanic connection, enhanced oxygen circulation and input of nutrients into the intracratonic Bambuí Basin allowed for the local development of an Ediacaran marine ecosystem in the basin (Warren et al., 2014). With the subsequent closure of the Clymene Ocean (540–490 Ma, Fig. 5), the rise of large mountain belts led to the formation of a restricted basin where oceanic anoxia and eutrophication developed (Caxito et al., 2021). This event potentially precluded the continuing development of metazoan communities in this intracratonic basin (Caxito et al., 2021), perhaps explaining the scarcity of marine macrofossils in the upper part of the Bambuí Group. During this period of basin restriction, carbonates deposited in the Bambuí Basin are characterized by unusual isotopic and geochemical signatures influenced by weathering fluxes from surrounding mountains (Cui et al., 2020; Fig. 5). For instance, strongly positive values of  $\delta^{13}\text{C} > 10\text{‰}$  and high  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios in the middle-upper Bambuí Group decoupled from the global marine signatures may imply a disconnection between the Bambuí Basin and global ocean waters (Cui et al., 2020; Okubo et al., 2022).

Following this geodynamic model, the deformation of the Itapucumi Group basin is related to the closure of the Clymene Ocean between 540 and 490 Ma (Warren et al., 2019a) that took place after 535.7 Ma, certainly extending into the Cambrian. Recent discoveries of late Ediacaran and Early Cambrian volcanic and detrital zircons from the upper Bambuí (Moreira et al., 2020) and Itapucumi groups (Warren et al., 2019b; this contribution) further indicate deposition coeval to active volcanism during the last pulses of crustal accretion and the final amalgamation of Gondwana (Tohver et al., 2012).

## CONCLUSIONS

The Ediacaran-Cambrian transition in the West Gondwana is identified in the Itapucumi Group, Paraguay, close to the contact between the Tagatiya Guazú and Cerro Curuzu formations. The corresponding stratigraphic interval is marked by the co-occurrence of *Cloudina* and treptichnids, similar to other Ediacaran-Cambrian successions such as the Nama Group in Namibia. A SHRIMP zircon U-Pb depositional age of  $535.7 \pm 5.2$  Ma from the basal Cerro

Curuzu Formation, a few meters above the first appearance of treptichnids in the upper Tagatiya Guazú Formation is similar to other terminal Ediacaran successions and indicate a terminal Ediacaran age for the uppermost part of this unit.

Integrated biostratigraphic and sedimentologic analyses show that the distribution of in situ *Cloudina* and bioturbation structures in the Tagatiya Guazú Formation might have responded to broad lithologic contrasts. This, in turn, could have been determined by parameters such as substrate consistency and composition, bathymetry, and water turbidity, because excess of suspended particles might have had a detrimental effect on filter-feeding strategies (that have been hypothesized for many of the epibenthic tube-dwelling organisms of terminal Ediacaran skeletal communities). At the local scale, it seems that being jelly or shelly depended largely on the environmental factors driven by water turbidity, substrate composition and stability, and nutrient availability.  $\delta^{13}\text{C}$  data from the Tagatiya Guazú and Cerro Curuzu formations also show that, like the terminal Ediacaran Spitskop Formation in Namibia, the Itapucumi Group does not capture the negative  $\delta^{13}\text{C}$  excursion the BACE at the Ediacaran-Cambrian interval, possibly because the BACE was masked by a cryptic unconformity or unsuitable lithology, or perhaps the BACE may not represent a global event.

Our data reinforce the notion that Ediacaran skeletonized organisms possibly survived into the Early Cambrian. Finally, the Ediacaran-Cambrian interval in this part of the world not only inaugurates the eon of complex multicellular life, but also marks the birth of Gondwana, the largest known austral supercontinent in Earth's history.

## ACKNOWLEDGMENTS

The authors would like to thank Paulo Boggiani and the Industria Nacional del Cemento (Paraguay) for all logistic and operational support during the field activities. We are especially grateful to Eric Tohver who performed the U-Pb sensitive high-resolution ion microprobe analysis presented in this piece. The authors would like to thank Associate Editor Brian Pratt, the first anonymous reviewer, and Fred Bowyer for their valuable comments and suggestions on this paper. This research was sponsored by Fundação de Amparo à Pesquisa do Estado de São Paulo (grants 2010/19584-4 and 2018/26230-6). LVW and MGS are fellows of the Conselho Nacional de Desenvolvimento Científico e Tecnológico de Brazil. Additional financial support was provided by the Natural Sciences and Engineering Research Council of the Government of Canada Discovery Grants 311727-15/20, and 311726-13, and 422931-20 awarded to MGM and LAB, respectively. MGM also thanks funding by the George J. McLeod Enhancement Chair in Geology, University of Saskatchewan, Saskatoon, Canada. SX acknowledge support from the National Science Foundation Frontier Research in Earth Sciences program (EAR-2021207).

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SCIENCE EDITOR: BRAD SINGER  
ASSOCIATE EDITOR: BRIAN PRATT

MANUSCRIPT RECEIVED 19 AUGUST 2022  
REVISED MANUSCRIPT RECEIVED 18 OCTOBER 2022  
MANUSCRIPT ACCEPTED 29 NOVEMBER 2022

Printed in the USA