



# New Species of Macroalgae from Tamengo Formation, Ediacaran, Brazil

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The Tamengo Formation (Corumbá Group) is an important Ediacaran stratigraphic unit in South America due to the presence of metazoan fossils and geochemistry data of carbonate rocks, with excellent geochronological delimitation (between 555–541 Ma) obtained by U–Pb dating on volcanic zircons. The present work shows three new species of macroalgae found as carbonaceous compressions and studied for their morphology and taxonomy. All new taxa are characterized as centric macroalgae; *Tamengophyton espinosa* sp. nov. is a fan-shaped alga with striated thalli, dichotomous branches, trichomes with perpendicular growth, and a connecting membrane. *Ladariella hidria* sp. nov. is formed by a set of striated and branched thalli in a cylindrical form with almond-shaped structures in the top. *Ladariophyton veinosa* sp. nov. is characterized by the main growth thallus and an enlarged longitudinal structure at the center. These new occurrences of macroalgae add to the largest life assemblages in the Neoproterozoic of South America, which contributes to documentation of the evolutionary history of macroalgae and the paleoecological settings of the Late Ediacaran.

**Keywords:** Macroalgae, taxonomy, Ediacaran, Tamengo, Brazil

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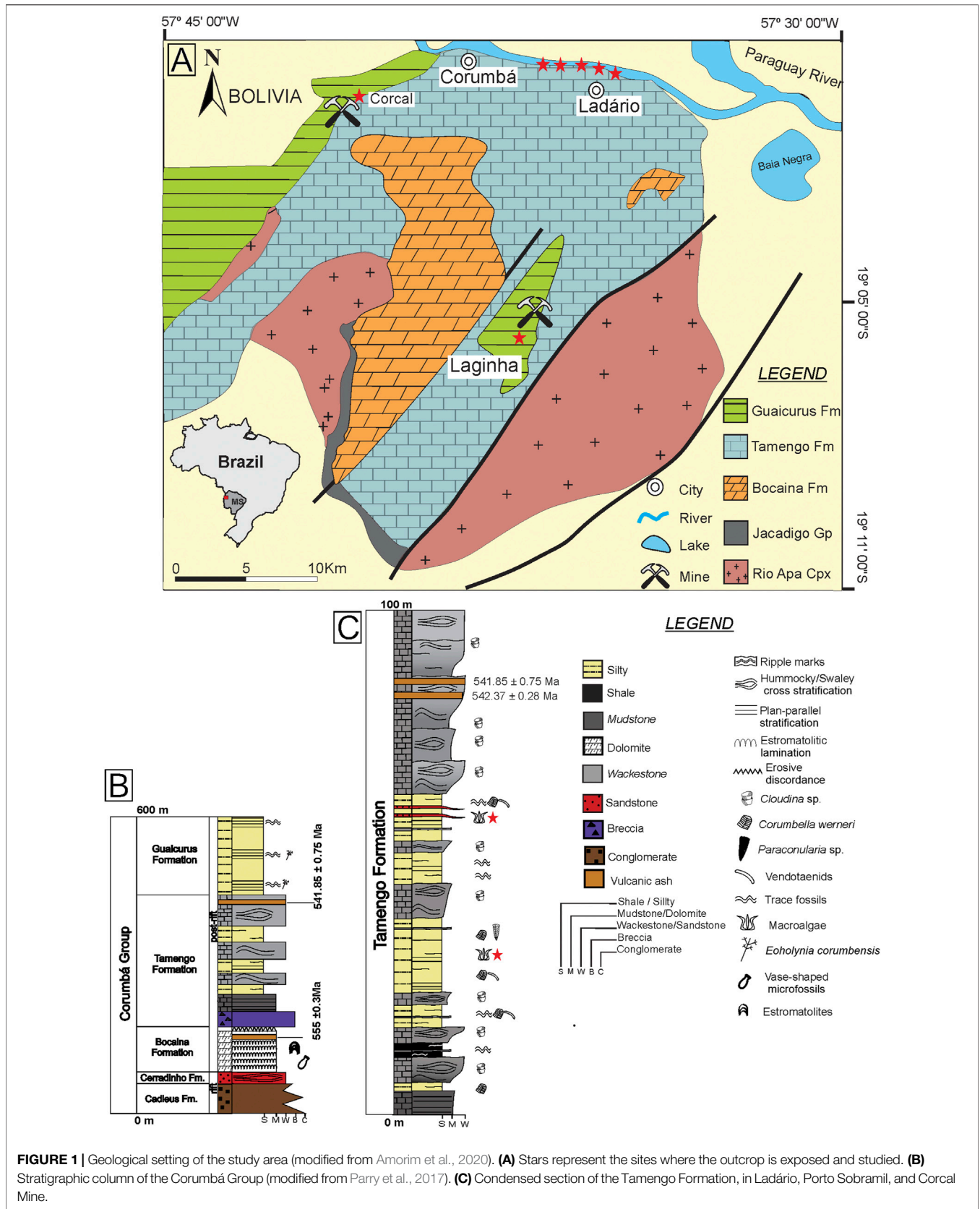
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## INTRODUCTION

The evolution of eukaryotic organisms changed the dynamic of the Earth. Even though the timing of their appearance is debated, through the paleontological data and molecular clock analysis, we have an estimative age for the last eukaryotic ancestor appearance between 1.8 and 2.3 Ga in the Paleoproterozoic Era (Hedges et al., 2004; Knoll et al., 2006; Parfrey et al., 2011). These evolutions brought new cellular behaviors, which were capable of sensing and reacting to environmental change (Cohen and McDonald, 2015; Wan and Jekély, 2021). Reaching a higher level of multicellular organization, they could expand and differentiate the cells to adapt to new opportunities.

During the Ediacaran, such new life forms were mainly represented by macroalgae (Bykova et al., 2020). They still are defined as eukaryotic multicellular organisms capable of doing photosynthesis, megascopic with a size larger than 1 mm, and possible to see with the naked eye, whose oldest fossil record dates to the Neoproterozoic (Xiao and Dong, 2006; Tang et al., 2020). Their complexity and diversity have records in China (Xiao et al., 1998), India (Srivastava, 2012), the United States (Rowland and Rodriguez, 2014), Russia (Nagovitsin et al., 2015), Mongolia (Dornbos et al., 2016), and Canada (Maloney et al., 2021). Interacting with other organisms of their time, the macroalgae form biotas, which serve as protection sites or creating oxygen niches (Xiao et al., 2002; Zhao et al., 2004). Here, we present three new species of macroalgae from Mato Grosso do Sul Brazil and discuss their significance to the Ediacaran assemblage from Tamengo Formation and the influence of the depositional process from the Corumbá Group in their preservation.



**FIGURE 1** | Geological setting of the study area (modified from Amorim et al., 2020). **(A)** Stars represent the sites where the outcrop is exposed and studied. **(B)** Stratigraphic column of the Corumbá Group (modified from Parry et al., 2017). **(C)** Condensed section of the Tamengo Formation, in Ladário, Porto Sobramil, and Corcal Mine.

## GEOLOGICAL CONTEXT

The Corumbá Group exposes in Serra da Bodoquena and Corumbá region (**Figure 1A**) (Mato Grosso do Sul State, SW Brazil), close at Urucum Massif. The fossiliferous sites are located in the cities of Corumbá, Ladário, in mines and at the margin of the Paraguay River, in the Pantanal plain. The lowest units in the Corumbá Group (**Figure 1B**) are the Cadieus and Cerradinho formations representing a terrigenous sedimentation. Follow-up by the Bocaina Formation containing stromatolitic dolomites and a volcanic ash at the top dating  $555.18 \pm 0.30$  Ma. The Tamengo Formation is the best-known unit from the Corumbá Group, around 200 m thick, characterized by black limestones, grainstones, organic siltstones, where the macroalgae occur, and shales. Follow-up by the the Guaicurus Formation containing laminated siltstones and macroalgae named *Eoholynia corumbensis*-up (Boggiani, 1998; Boggiani et al., 2010; Parry et al., 2017).

The Tamengo Formation (**Figure 1C**) is marked at the base by carbonatic breccia, overlain by carbonate facies of grainstones and mudstones with sedimentary structures, such as hummocky cross-stratification and wave marks with a volcanic ash at the top, in which zircons are dated at  $541.85 \pm 0.75$  Ma. Packages of shales, siltstones, and fine sandstones with parallel plane lamination are interspersed with the carbonate facies (Boggiani et al., 2010; Parry et al., 2017; Amorim et al., 2020).

The Ediacaran Tamengo Formation exhibits paleontological remains with metazoan fossils such as *Corumbella weneri* (Pacheco et al., 2015; Walde et al., 2019), *Cloudina* sp. (Adorno et al., 2017; Becker-Kerber et al., 2017), *Paraconularia* sp. (Van Iten et al., 2014), and trace fossils such as *Multina minima* (Parry et al., 2017). Based on geological and paleontological evidence, the Tamengo Formation represents a carbonatic ramp in a marine environment, between the fair-weather wave base level and storm wave base level during a transgression phase. The facies characterized by siliciclastic rocks, metazoans, trace fossils, and plane parallel structures suggest an environment of low energy, associated with the offshore zone. The facies with limestone, hummocky cross-stratification, wave ripples, and *Cloudina* sp., is associated with the shoreface zone (Boggiani et al., 2010; Oliveira et al., 2019; Amorim et al., 2020).

## MATERIALS AND METHODS

The fossils described here were collected in the siltstones of Tamengo Formation near Ladário city from Mato Grosso do Sul state. Each species has one specimen deposited in the Geoscience Institution, University of São Paulo. The samples were analyzed and photographed under a Zeiss stereomicroscope, and the fossil measurement data from each specimen were made with digital images using software Zen™ (ZEISS), where we catalog and measure the entire dimension containing their morphological features.

The samples were subjected to analysis in a scanning electron microscopy (SEM) to observe main morphological features in

high resolution and energy dispersive spectroscopy (EDS) to make elemental mapping, allowing for the characterization of the chemical composition of the macroalgae.

## SYSTEMATIC PALEONTOLOGY

Usually, the morphological features of the fossils are fundamental to the taxonomy, since other characteristics such as biochemistry or the cellular structure is more difficult and rarely. The use of morphological characters to propose a new taxon needs to be approached with caution because the convergent evolution process does not make it a conclusive tool to identify phylogenetic affinity (Xiao and Dong, 2006). Also, the morphological features can be altered or lost through taphonomic processes, which strongly affects fossil algae. Their soft bodies are often recorded as broken, flattened, or distorted, and their most fragile structures can be dissolved and lost. But despite taphonomic processes, information can also be interpreted based on the fossil record.

The systematics of the fossils presented here is based only on their morphology, taking into account the taphonomic bias. The characteristics and description of the structures are based on Xiao et al. (2002) and Ye et al. (2019) who proposed the distinction of each genus considering the general morphology, branching pattern, the width of the thallus, the change in width along the length, the internode length flexibility, and the presence of microstructures. The phylogenetic affinities of the macroalgae are still uncertain because it needs a cellular information that the fossil record cannot provide. The systematic description is based on the genus and species levels. The descriptions of the new taxa follow the international code for plant, fungi, and algae nomenclature (IAPT global).

Genus *Tamengophyton* C.Q.C. Diniz & J.M. Leme sp. nov.

*Type species: Tamengophyton espinosa* C.Q.C. Diniz & J.M. Leme sp. nov.

*Material:* One specimen preserved.

*Diagnosis:* As for type species, by monotype.

*Etymology:* Tamengo Formation, where it was found.

*Type locality:* Ladário city located in the west of Mato Grosso do Sul state, Brazil.

*Type horizon and stratigraphy:* Ediacaran, Tamengo Formation, Brazil.

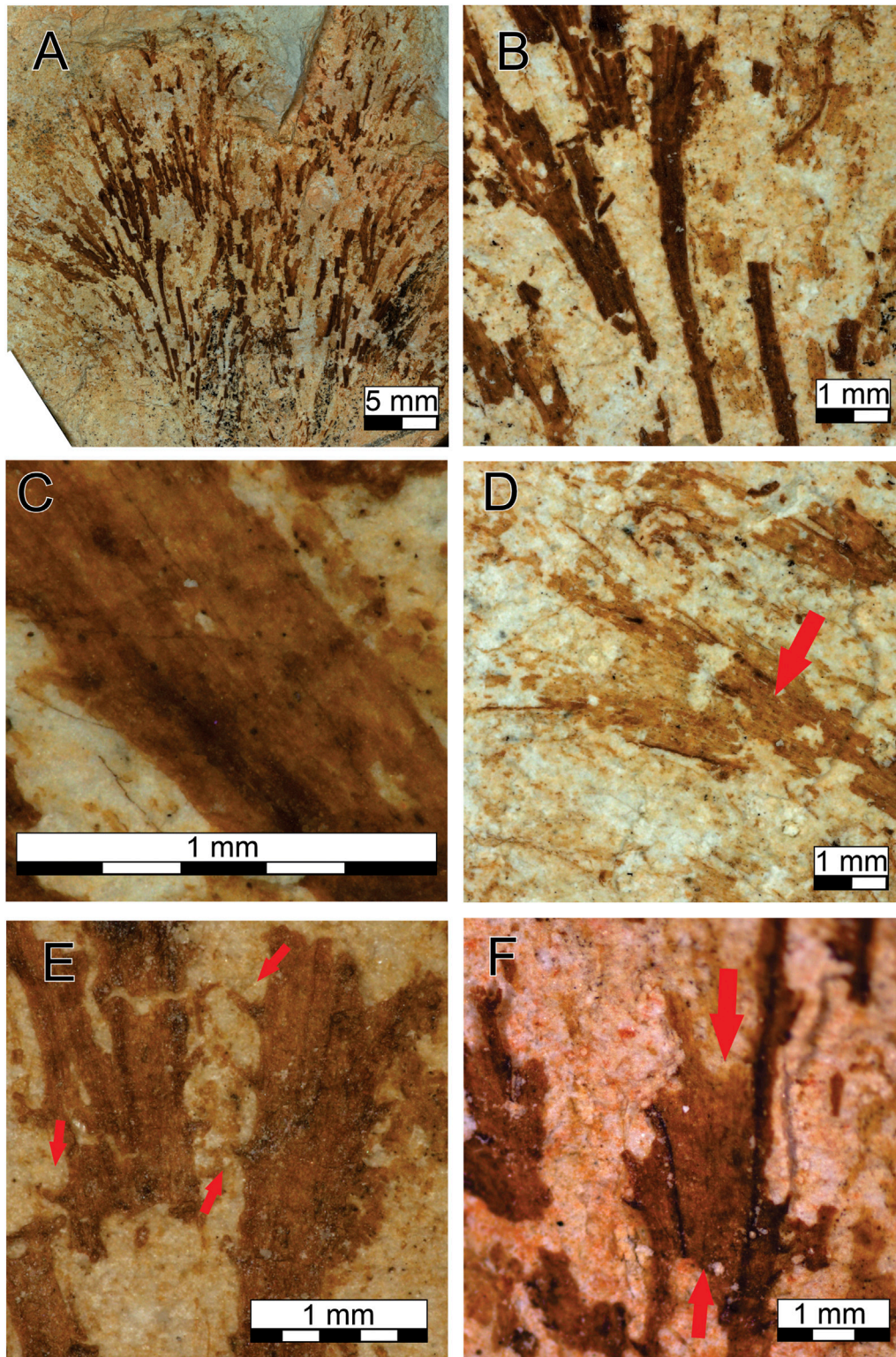
*Tamengophyton espinosa* C.Q.C. Diniz & J.M. Leme sp. nov.

*Holotype:* GP/1E - 10,990 (**Figure 2**), from the Tamengo Formation, Ediacaran, Corumbá Group, Ladário, Brazil (Repository: IGc-USP).

*Diagnosis:* A centimeter-scale fan-shaped macroalgal fossil. Possess thalli with heterogeneous thickness (**Figure 2B**), striated, and with dichotomous ramifications (**Figures 2C,D**). Along the thalli, microstructures projects in the edges (**Figure 2E**). In the apical part, a membrane is preserved that connects the stems (**Figure 2F**).

*Description:* The sample preserved in two-dimensional carbonaceous compression, with a size of 2.9 cm and a minimum width of 0.5 cm at base and a maximum width of 3.5 cm, formed by a set of approximately 27 striated thalli that branch per segment,





**FIGURE 2** | *Tamengophyton espinosa*. **(A)** Complete fossil. **(B)** Widening in width through the length of thalli. **(C)** Details of the striation. **(D)** branching (arrow). **(E)** Details of the trichomes (arrows). **(F)** Details of the membrane (between the arrows).

widening at the top. The thalli do not overlap each other and are arranged in a straight pattern. The thickness of each thallus varies from 0.2 mm to 0.8 mm along the fossil species, with the base thinner than the top; this heterogeneity is repeated along the entire fossil. Parts preceding the branches tend to be thicker, appearing from the base through the top but can be observed only once per thallus. The preserved striation pattern follows the same longitudinal direction of the thalli. Microstructures are projecting throughout the thalli; there is no pattern for their positioning, and some are quadrilateral grouped, while others are arranged horizontally or vertically. They are preserved in different sizes, their length varies from 0.1 to 0.25 mm, and their width varies from 0.06 to 0.09 mm. The membrane is present in the distal part of the fossil, where a connection between the thalli is visible, and has the same composition as the thallus but is not striated.

**Etymology:** The fossil species name is determined by the presence of the microstructures that resemble thorns.

**Remarks:** *Tamengophyton* gen. nov. is characterized by the overall fan shape caused by the spreading of the stalks due the branching at the top; the straight thallus indicates little flexibility, the micro-triangle-shaped structures that grow perpendicularly throughout the thalli here is known as trichomes. No cellular structure has been preserved, but the presence of longitudinal striations implies a more complex internal structure resembling a pseudoparenchyma.

*T. spinosa* is similar to other species of macroalgae from Ediacaran around the world. The phylogeny of higher grades is uncertain, but the specimen fits into the family of Eoholyneacea (Hoffman 1994) and could be attributed to macroalgae of the Neoproterozoic due to the presence of branching. In addition, similar morphological features such as compressed cylindrical bifurcated thalli and a width < than 2 mm can also be observed with the morphogroup denominated delicately dichotomously branched, as proposed by LoDuca et al. (2017) for specimens of early Paleozoic seaweeds.

*T. spinosa* can be compared with genera of *Doushantuophyton* (Steiner, 1994), *Konglingiphyton* (Chen and Xiao, 1992) emend. Xiao et al. (2002) and *Maxiphyton* Ye et al. (2019) because it presents similar characteristics such as straight and rigid branches, regular dichotomy, and the capacity to widen the thallus toward the distal part. But their size does not combine; *Doushantuophyton* is 0.04–0.2 mm wide per thallus and *Konglingiphyton* can reach 1.4 mm, while the size of *T. spinosa* stays between the two genera. However, the principal diagnosis for distinguishing them is that the other taxa have smooth branches, while *T. spinosa* possesses the trichome projections and the connecting membrane to assign a new genus and new species.

Genus *Ladariella* C.Q.C. Diniz & J.M. Leme gen. nov.

**Type species:** *Ladariella hidria* C.Q.C. Diniz & J.M. Leme sp. nov.

**Material:** One specimen preserved.

**Diagnosis:** As for type species, by monotype.

**Etymology:** After the city of Ladário, located close to the type section where the fossil genus was found.

**Type locality:** Ladário city located in the west of Mato Grosso do Sul state, Brazil.

**Type horizon and stratigraphy:** Ediacaran, Tamengo Formation.

*Ladariella hidria* C.Q.C. Diniz & J.M. Leme sp. nov.

**Holotype:** GP/1E - 10,989 (Figure 3), from the Tamengo Formation, Ediacaran, Corumbá Group, Ladário, Brazil (Repository: IGc-USP).

**Diagnosis:** Centimeter-sized fossil preserved as a set of irregular curved thalli (Figures 3A,B). Presents rhizoidal holdfasts (Figure 3C) with a central axis and secondary elements at the base of the specimens. Possesses dichotomous striated branches (Figures 3D,E) and almond-shaped structures formed at the top (Figures 3F,G).

**Description:** The sample consists of a two-dimensional carbonaceous compression. With an elongate rhizoidal holdfast structure that grows perpendicular from the base of the thallus with 0.13 to 0.20 mm in width. It has a set of 20 thalli, with 1.5 cm maximum length. Each thallus is arranged obliquely and overlap each other from varied angles and difficult to measure their length, but the overall size varies from 5 to 15 mm. The width also varies between 0.15 and 0.9 mm, getting thinner in the top. The branching occurs once per thallus, and the striation follows the same longitudinal direction. The almond-shaped structures at the end ranges in size from 0.08 to 0.2 mm and are positioned obliquely with no apparent direction.

**Etymology:** Reference to the Greek mythological creature named hydra based on the similarity of the structure of the thalli arranged as one set and the multiple heads of the hydra in mythology.

**Remarks:** In the basal part, one structure at each side grows a central axis perpendicular to the thallus, most likely attributed to rhizoidal holdfasts. The branching of the thallus only occurs in the basal part of the fossil so the thickness in that area can be caused due to the enlargement of the branching process. The curvature state of the thalli indicates a flexibility that could help in a better response to hydrodynamics, and the almond-shaped structures has more accumulation of organic matter.

The phylogeny of higher grades remains uncertain, and the specimen fits into the Eoholyneacea family proposed by Hoffman (1994) because of the presence of branching and also shares the same features of *T. spinosa*, such as compressed cylindrical bifurcated thalli and a width < 2 mm that fits in the morphogroup proposed by LoDuca et al. (2017) based on delicately dichotomously branches.

*L. hidria* and *Miaohephyton* (Xiao et al. 1998) share a characteristic of a possible apical meristem. Nevertheless, considering the entire morphology, branching pattern, the heterogeneity, and especially the flexibility of the thallus as well as the almond structures, a new genus needs to be established.

Genus *Ladariophyton* C.Q.C. Diniz & J.M. Leme gen. nov.

**Type species:** *Ladariophyton veinosa* C.Q.C. Diniz & J.M. Leme sp. nov.

**Material:** One specimen preserved.

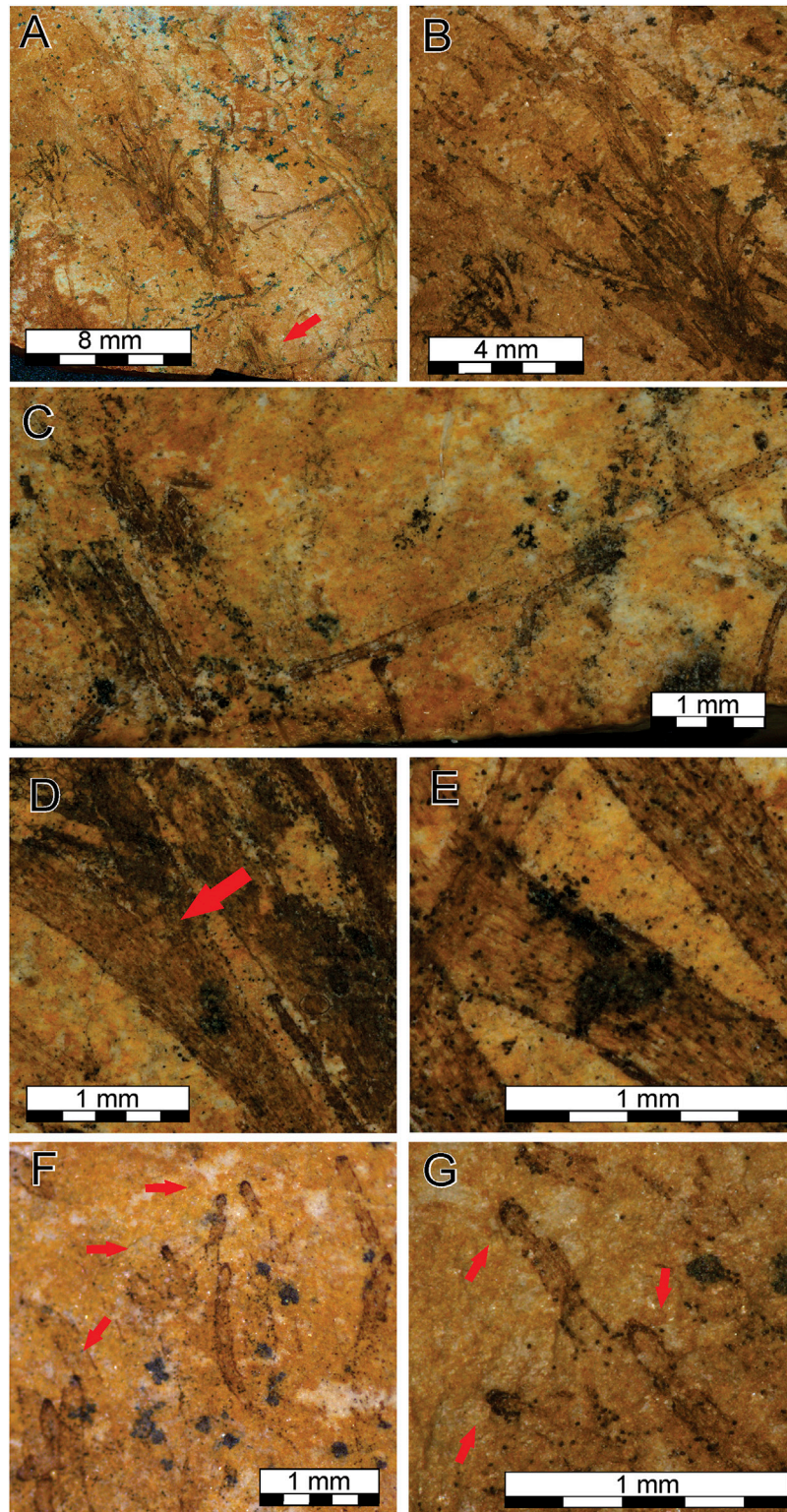
**Diagnosis:** As for type species, by monotype.

**Etymology:** Named after the city of Ladário, in where it was found.

**Type locality:** Ladário city located in the west of Mato Grosso do Sul state, Brazil.

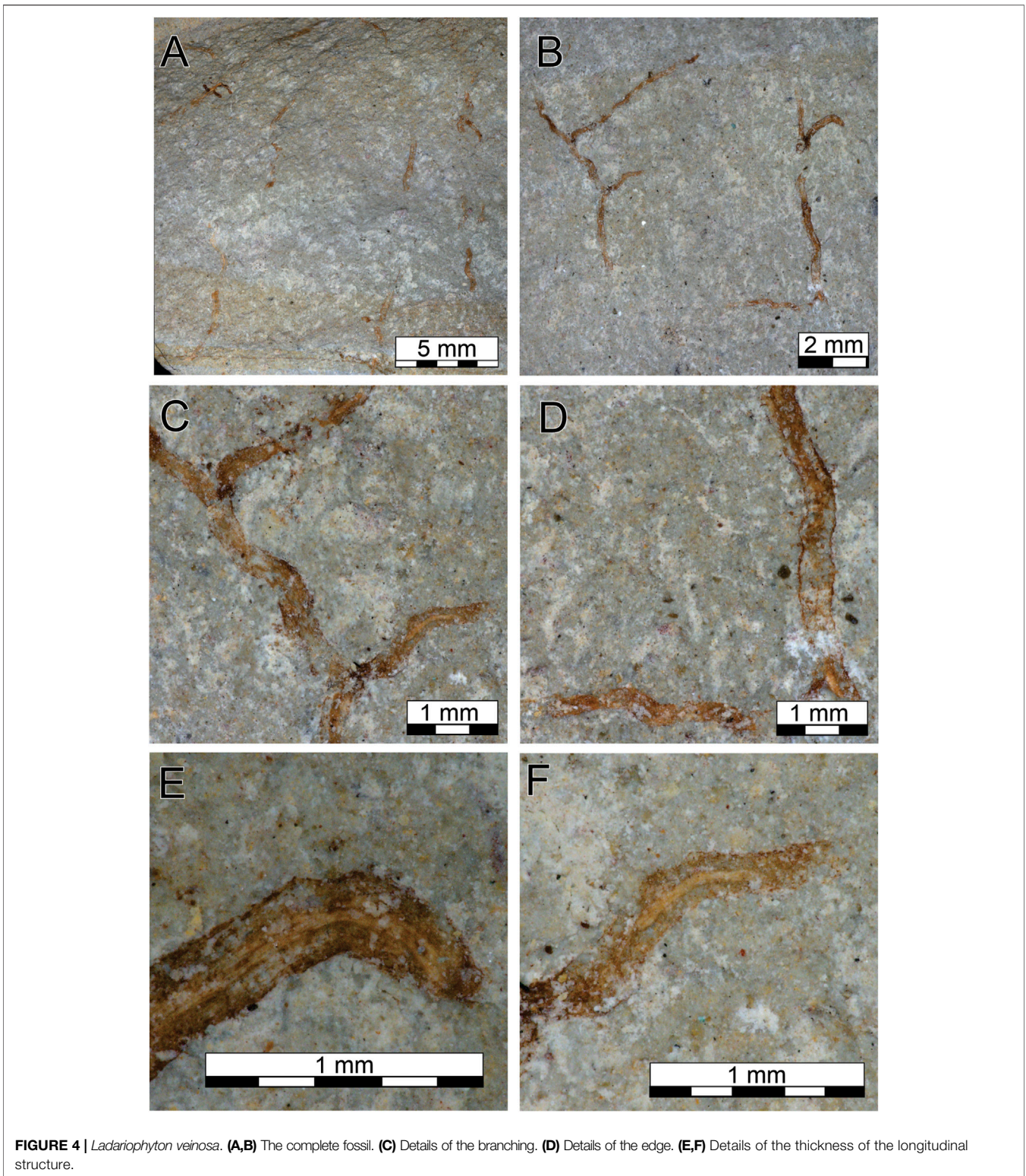
**Type horizon and stratigraphy:** Ediacaran, Tamengo Formation, Brazil.





**FIGURE 3** | *Ladariella hidria*. **(A,B)** Complete fossil with the arrow pointed out to the rhizoidal holdfasts in **(A)**. **(C)** Details of the rhizoidal holdfasts. **(D)** Branching (arrow). **(E)** Details of the striation in the thalli. **(F,G)** Details of the almond structure (arrows).



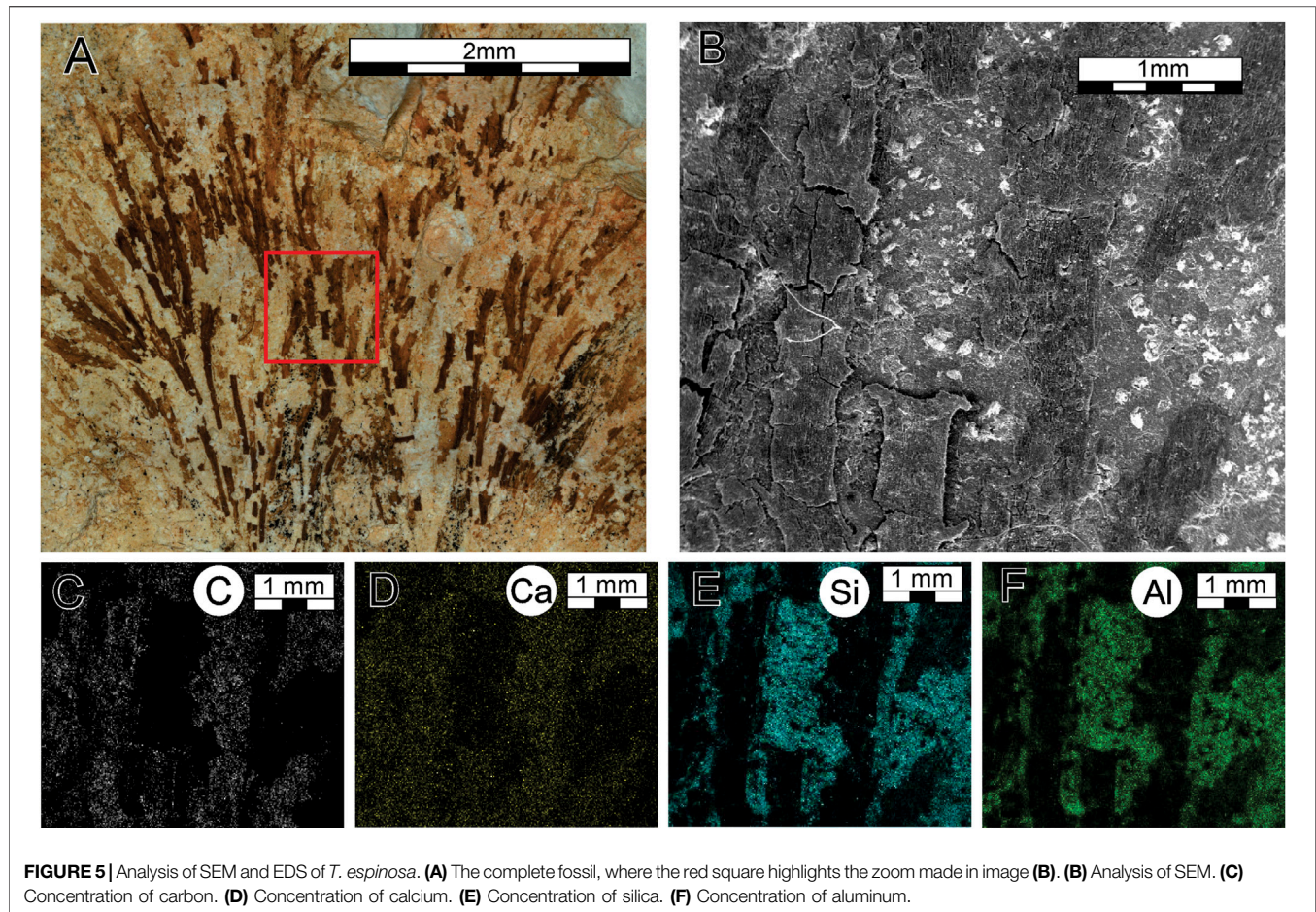


*Ladariophyton veinosa* C.Q.C. Diniz & J.M. Leme sp. nov.

*Holotype*: GP/1E - 11,187 (**Figure 4**), from the Tamengo Formation, Ediacaran, Corumbá Group, Ladário, Brazil (Repository: IGc-USP).

*Diagnosis*: Fossil organism of centimeter-scale with pseudomonopodial irregular branches (**Figure 4B**). It presents a defined border and has an enlarged





**FIGURE 5** | Analysis of SEM and EDS of *T. espinosa*. **(A)** The complete fossil, where the red square highlights the zoom made in image **(B)**. **(B)** Analysis of SEM. **(C)** Concentration of carbon. **(D)** Concentration of calcium. **(E)** Concentration of silica. **(F)** Concentration of aluminum.

longitudinal structure on the center of each thallus (**Figure 4D–F**).

**Description:** The sample has a set of thalli, which are arranged in a specific direction without overlapping each other. They vary in length, with the longer thallus being 1.1 cm. This does not represent the full length of the organism because none of the thallus is complete without a basal and an apical part. The thalli are homogeneous in width, measuring between 0.2 and 0.35 mm. Branching can be observed more than once, but one thallus represents the principal growth of the alga where the branching always occurs. The fossil has well-demarcated edges with a corrugated shape. The characteristic, which differentiates and defines this fossil, is a thickening in the longitudinal structure present at the center of the thalli of approximately 0.1 mm.

**Etymology:** Reference for veins, based on the central structure along the thalli.

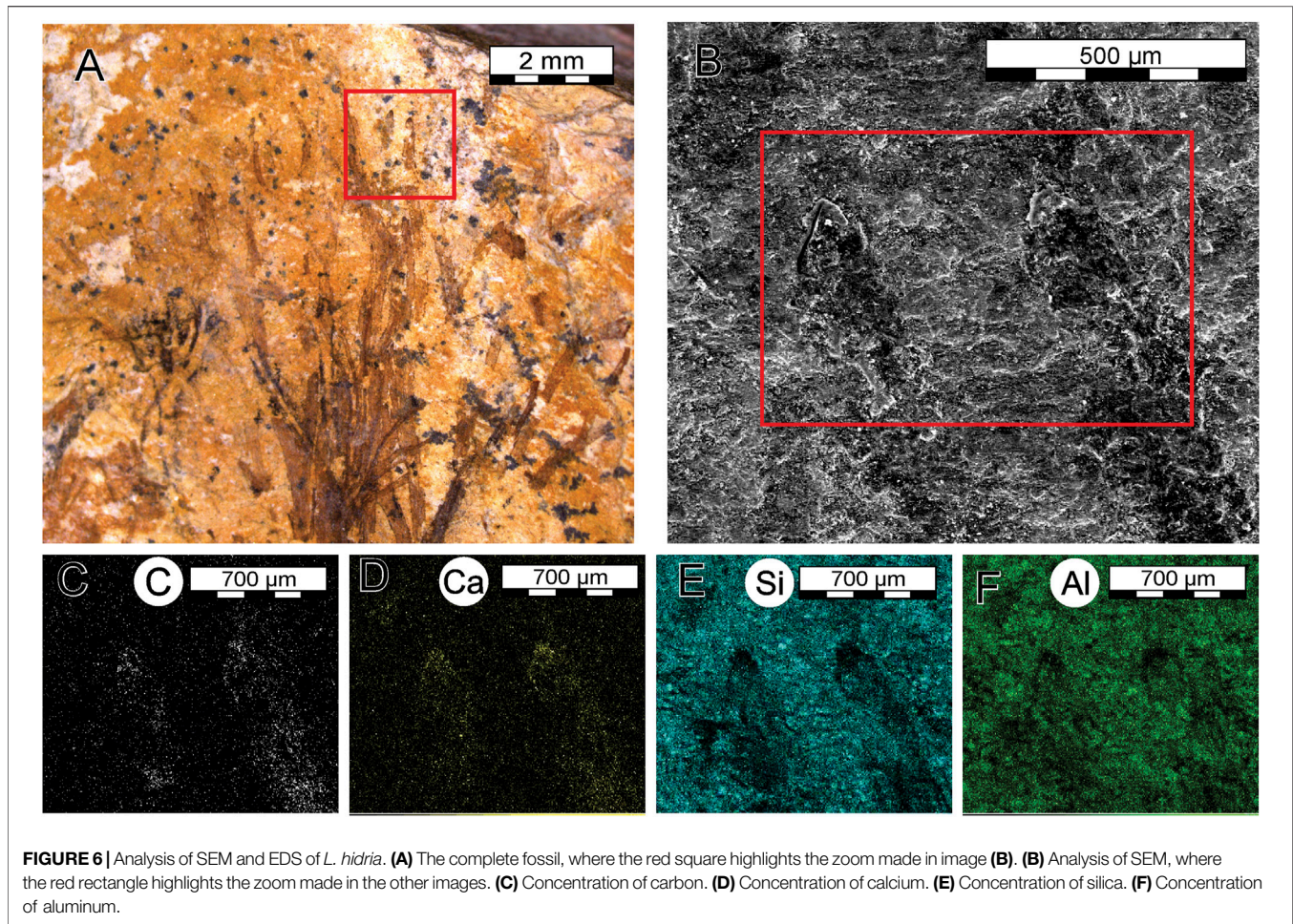
**Remarks:** This specimen fits into the Eoholyniaceae family proposed by Hoffman (1994) for macroalgae of the Neoproterozoic because of the presence of branches and the presence of characteristics of the morphogroup of delicately dichotomous branches as proposed by LoDuca et al. (2017) for specimens of early Paleozoic seaweeds.

*L. veinosa* sp. nov. is a very simple macroalga difficult to attribute a major group, can be compared to *Chingiskhaania bifurcata* (Dornbos et al. 2016) due to its a thin filament with an average width of 0.45 mm, does not densely assemble and without distal tapering in width, but lacks a longitudinal striation. Macroalgae from Dolores Creeks Formation, Canada (Maloney et al., 2021), presents a longitudinal division but have septa along the fossil, structure that our specimen does not have; the aspects differentiating *L. veinosa* are the corrugated edges and the thick longitudinal structure in the center of the thallus.

## DISCUSSION

The different records of Ediacaran fossils have various modes of exceptional preservation, such as phosphatization (e.g., Xiao et al., 2004), permineralization (e.g., Zhang et al., 1998), pyritization (e.g., Cai et al., 2010), and silicification (e.g., Liu, 2016). Analysis using energy-dispersive X-ray spectroscopy (EDS) of two samples was performed (**Figures 5, 6**), which indicated a high carbon and a low aluminum and silica content in the fossil in relation to the matrix.





The macroalgal fossils are preserved as carbonaceous compressions in pelite, from the information provided by SEM and EDS, which can be compared to Cambrian Burgess Shale-type preservation (Butterfield, 1995; Xiao et al., 2002; Butterfield, 2005). In addition, the preservation occurred because of a transformation of the non-mineralized soft tissues (organic matter) to a stable kerogen is a process named kerogenization (Cai et al., 2012).

Amorim et al. (2020) propose a facies association in the deposits from the Tamengo Fm. where the macroalgae were found. The silty shale facies have a parallel lamination with wide paleodiversity, such as fossils of *Corumbella weneri*, *Paraconularia* sp., and vendotaenids. It is intercalated with carbonated facies such as massive to poorly laminated calcimudstone, laminated wackestone, and hummocky/swaley cross-stratified packstone. The alternation between fossiliferous pelites with tempestites (carbonates) suggested the preservation of the fragile macroalgae during the interval of the storms, during the suspension fallout of fine sediments (Labaj and Pratt, 2016; Amorim et al., 2020).

The absence of hard structures in the macroalgae makes these fossils difficult to be preserved, especially their delicate characteristics as presented in the two samples (*T. espinosa* and *L. hidria*). The fossil *T. espinosa* have a basal part

incomplete, where the distal part is more preserved, which has been difficult to measure the full length of individual thallus. The absence of structures such as trichomes and membranes at the base of the fossil could be explained by an influence of taphonomic processes shaping the preserved morphology of the algae. The flattening of the fossil is visible, creating a two-dimensional form, affecting the trichomes forming small circles, and causing rupture in the thalli.

In *Ladariella hidria*, taphonomic processes influenced the preservation and shape of the fossil organism, including flattening throughout the structure. Better preservation occurs in the almond structures, where a thicker and darker layer was reported due to a larger accumulation of organic matter. This might indicate an apical meristem, where greater cell division for algae growth is expected.

In the case of *Ladariophyton veinosa*, a connection between the thalli is missing, together to an indication of a basal and top parts. Therefore, it is hard to acknowledge the total length of the fossil. The corrugated shape of the edges could also have been formed by a taphonomic influence; when body parts start to lose humidity, they tend to wrinkle.

Even though the macroalgae are not preserved in life position, a fossil of higher fragility could not be transported over long

distances or remain in the active high-energy zone for a long period of time without significant destruction. So, the presence of the macroalgae could indicate a depth when they would receive enough sunlight to enable photosynthesis and with energy sufficient to partially destroy their body.

Other fossils of metazoan are preserved in the same stratigraphic level such as *Corumbella weneri*; they also miss the basal part but present an overall well-preserved level in their carapace (Amorim et al., 2020). *Corumbella weneri* possess a thin organic and delicate wall (Pacheco et al., 2015; Walde et al., 2019), so the well-preserved fossil associated with the silty shale facies can indicate a minimal transportation or rework at a low-energy environment (Warren et al., 2012; Amorim et al., 2020).

The preservation of macroalgae together with carapaces of metazoan in the siltstone bed in the Tamengo Formation can be explained by environmental variations in higher sedimentation rates, probably a sedimentary deposit under offshore condition in a depth below storm wave base, with a low-energy environment representing an outer to distal mid-ramp.

## CONCLUSION

Three specimens of macroalgae are described for the Brazilian Ediacaran, Tamengo Formation in Mato Grosso do Sul, representing new taxonomic species and genera. The new descriptions contribute to the local paleobiodiversity along with metazoans, ichnofossils, and microfossils previously documented in this formation. This further reinforces the contribution of Brazil to the knowledge of the Ediacaran fossils. These three genera and species add new evidence to evolutionary issues of macroalgae during the Ediacaran, especially *T. spinosa* with its more complex features such as differentiated trichome and an interconnecting membrane. This also emphasizes more complex organisms already existed before

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the Cambrian but remain extremely rare in the fossil record due to their fragile structures.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary materials; further inquiries can be directed to the corresponding author.

## AUTHOR CONTRIBUTIONS

CD, JL, and PB collected the fossils. CD performed laboratory work and morphological taxon identifications. JL assisted with the interpretation. PB collaborated with hypothesis in the discussion. All authors contributed to the article and approved the submitted version.

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