The missing mats: MISS diversity and influence on life preservation in the late Ediacaran of the Tandilia System, Argentina

María Julia Arrouy[1]* , Lucas Veríssimo Warren[2] , Fernanda Quaglio[3] , Lucía Gómez-Peral[4] , Lucas Inglez[2] , Victoria Penzo[4] , Marcello Guimarães Simões[5] , Daniel Gustavo Poiré[4]

Abstract

The terminal Ediacaran fossil record includes microbial mats and body fossils characterized by simple morphologies, which represents a challenge to understand several aspects related to the paleoecology of the emerging complex life. The marine siliciclastic deposits of the Cerro Negro Formation (~560–550 Ma) contain evidence of different styles of microbially induced sedimentary structures (MISS) and discoidal forms associated with them. Different types of MISS, such as *Kinneyia* and wrinkle structures, elephant skin, and *Arumberia*, are reported and related to shallow marine depositional environments. These morphologies are commonly associated with the high quality of preservation of body fossils in Ediacaran deposits. The preservation of *Aspidella* discoidal holdfast is related to biotic and abiotic processes involving substrate sealing by microbial mats, fluidization, and probably organic matter decay. Both abiotic factors (tidal currents and waves, added to liquefaction and sand injection) and biotic factors (substrate biostabilization by microbial mats favoring sediment cohesion) are considered the main ones responsible for the preservation style in the Cerro Negro Formation. This formation constitutes a remarkable example in SW-Gondwana of how preservation dynamics took place on a seabed sealed by microbial mats and is an important deposit conserving diverse Ediacaran forms of life in South America.

KEYWORDS: microbial mats; taphonomy; preservational styles; marine siliciclastic settings; Clymene Ocean; South West Gondwana.

INTRODUCTION

Microbially induced sedimentary structures (MISS, *sensu* Noffke *et al*. 1996) are sedimentary structures that arise from the interaction of benthic microbiota with physical sediment dynamics in siliciclastic deposits (Noffke *et al*. 2006). They leave particular features in the form of mats that grow at the sediment-water interface. The presence of MISS in the fossil record assists us to reconstruct the paleoenvironmental distributions and understand the paleoecological aspects involved in the existence of discoidal organisms during the late

[1]Instituto de Hidrología de Llanuras "Dr. Eduardo Jorge Usunoff" – Buenos Aires, Argentina. E-mail: jarrouy@ihlla.org.ar

[2]Universidade Estadual Paulista "Júlio de Mesquita Filho", Instituto de Geociências e Ciências Exatas, Departamento de Geologia – Rio Claro (SP), Brazil. E-mail: lucas.warren@unesp.br

[3]Universidade Federal de São Paulo, Departamento de Ecologia e Biologia Evolutiva – Diadema (SP), Brazil. E-mail: quaglio@usp.br

[4]Centro de Investigaciones Geológicas – La Plata, Argentina. E-mails: lperal@cig.museo.unlp.edu.ar, vpenzo@cig.museo.unlp.edu.ar, poire@cig.museo.unlp.edu.ar

[5]Universidade Estadual Paulista "Júlio de Mesquita Filho", Instituto de Biociências, Departamento de Zoologia – Botucatu (SP), Brazil. E-mail: btsimoes@ibb.unesp.br

*Corresponding author.

Ediacaran. In fact, in the Precambrian era, microbial mats colonized most surfaces where environmental conditions allowed their growth. This explains the relatively common record of the MISS (Noffke *et al*. 1996) during this time interval (Schieber 1986, Hagadorn and Bottjer 1997, Bottjer *et al*. 2000, Gehling and Droser 2009).

The complex interaction of environmental parameters between benthic microbial communities and the animals that lived and proliferated on the ocean floor can affect the probability of preservation. Several records are not clearly phylogenetically related to modern crown groups (Xiao and Laflamme 2009, Droser and Gehling 2015, Howard *et al*. 2022). This hinders the correct identification of the Ediacaran fossils, as the use of uniformitarianism from the ecological and taxonomical points of view becomes more difficult (Dodd and Stanton 1990, Romano 2015). Despite that, it is globally accepted that microbial mats have played a vital role in the preservation of Ediacaran fossils. The death mask hypothesis (Gehling 1999, Liu 2016, Liu *et al*. 2019) and the disappearance of Ediacaran fossils at the Ediacaran-Cambrian boundary might be related to the waning of microbial mats after the evolution of metazoans. An alternative proposal was that microbial mats on shallow marine seafloors might generate an oxygenated oasis that might have stimulated the diversification of metazoans (Ding *et al*. 2019, Xiao *et al*. 2020, Gingras *et al*. 2011). In addition, Darroch *et al*. (2015) suggested that the first mass extinction of complex life may have been largely biologically mediated
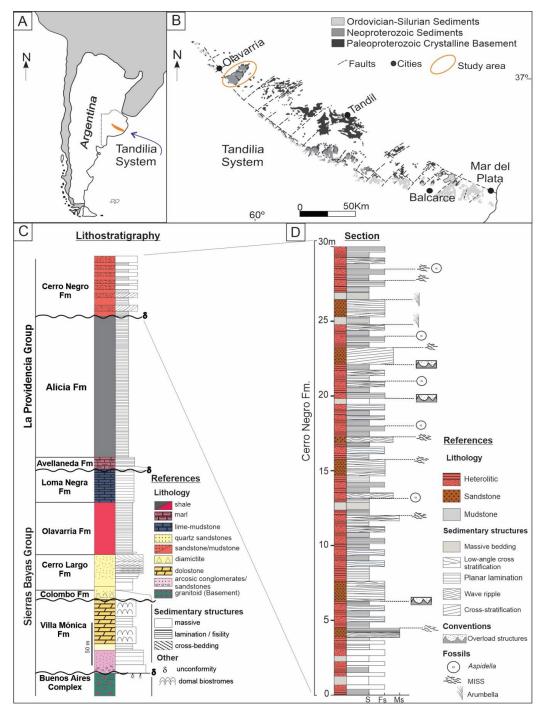
and caused by a combination of evolutionary innovation, ecosystem engineering, and biological interactions.

In the Río de la Plata Craton, the terminal Ediacaran Cerro Negro Formation is the only unit in Argentina that could testify to the presence of abundant and different types of MISS and Ediacaran discoidal organisms. In this sense, the deposit comprises a testimony to particular environmental conditions that record distinct structures of biogenic origins at the end of Precambrian times in South America.

This study analyzes the record of lifestyles in the Cerro Negro Formation in order to: report and describe distinct types of MISS in siliciclastic sediment; discuss the paleoecological aspects involved in the coexistence of discoidal organisms and different kinds of MISS; and explore the intrinsic relationship between microbial mats and preservation of body fossils.

GEOLOGICAL SETTING

The unique Ediacaran succession in the Argentinean territory is included in the Tandilia System, an ancient orographic belt located in the central part of the Buenos Aires Province (Fig. 1A). This unit is mainly composed of igneous

Fm: formation; S: siltstone; Fs: fine sand; Ms: medium sand.
Source: figure based on Arrouy *et al.* (2016).
Figure 1. (A) Location of Tandilia System in eastern Argentina. (B) Simplified geologic map of the NW portion of the Tandilia System. (C) Lithostratigraphic column of the Sierras Bayas and La Providencia groups in Olavarría area (modified from Arrouy *et al.* 2021). (D) Columnar section of the lower part of the Cerro Negro Formation, highlighting the association of MISS and members of the discoidal Ediacaran biota.

and metamorphic rocks of the Paleoproterozoic basement covered by Neoproterozoic to Lower Paleozoic sedimentary successions.

In Olavarría district (Fig. 1B), the Neoproterozoic record is represented by a ~455-m-thick succession (Fig. 1C) encompassing the Sierras Bayas Group, with Villa Mónica, Colombo, Cerro Largo, Olavarría, and Loma Negra formations (Iñiguez Rodríguez 1999, Poiré and Spalletti 2005, Poiré and Gaucher 2009, Gómez-Peral *et al.* 2014, 2018, 2019, Arrouy *et al.* 2021) and the La Providencia Group, encompassing the Avellaneda, Alicia, and Cerro Negro formations (Arrouy *et al.* 2015, Arrouy and Goméz-Peral 2021). The Sierras Bayas Group is separated from the overlain La Providencia Group by an erosional unconformity related to eustatic sea-level fall (Barrio *et al.* 1991, Poiré *et al.* 2007). Since the age of the Sierras Bayas Group is poorly constrained, the precise time encompassed by this hiatus is unknown. In the study area, the Cerro Negro Formation is a 30 m thick siliciclastic succession (Fig. 1D) deposited above the regional unconformity of the upper part of Alicia Formation. This unit is composed of centimeter-to-decimeter tabular and lenticular beds of terrigenous rocks, arranged as cyclic intercalation of massive and trough cross-bedding fine-grained sandstones, massive red mudstones, and heterolithic facies. The scarcity of mud cracks and other sedimentary structures indicative of subaerial exposure (as raindrop marks) allowed us to interpret the deposition of the Cerro Negro Formation as inter- to subtidal setting as was suggested previously (Arrouy *et al.* 2015).

The precise depositional age of the Cerro Negro Formation and its relation to the underlying units of the Sierras Bayas Group have been controversial so far. The igneous and metamorphic basement indicates ages around 2.62 ± 80 Ga, whereas detrital zircons from siliciclastic rocks embedded in this unit indicate maximum depositional ages of 2.7 Ga (Rapela *et al.* 2007). Indirect dating based on the carbon-isotope curve suggests the depositional age of the upper part of the Sierras Bayas Group (Loma Negra Formation) is around 580 Ma (Gómez-Peral *et al.* 2007, 2018). Gaucher *et al.* (2005) also described putative individuals of *Cloudina riemkeae* in micritic limestones of the underlying Loma Negra Formation, enabling the assignment of this unit to an Upper Ediacaran age. However, the presence of this guide fossil in the Loma Negra Formation is considered controversial and inconsistent with the paleontological findings in the La Providencia Group (Arrouy *et al.* 2016, 2019, 2021). Well-preserved discoidal structures assigned to the *Aspidella* plexus were previously reported in the Cerro Negro Formation (Arrouy *et al.* 2016). This occurrence can be tentatively correlated with the Ediacaran White Sea assemblage described in Australia and Russia and would suggest a depositional age around 560–550 Ma for the lower part of the unit (Waggoner 2003, Cracknell *et al.* 2021). The Ediacaran age is consistent (Xiao and Laflamme 2009) with the acritarch assemblage composed of *Synsphaeridium* sp., *Trachysphaeridium* sp., and *Leiosphaeridia* sp. (see Gaucher *et al.* 2005, Gaucher and Poiré 2009, Arrouy *et al.* 2015, 2019).

MATERIALS AND METHODS

All the numerous meter-sized slab samples were extracted from "La Cabañita" quarry located in the vicinity of Olavarría town, Argentina (Figs. 2A and 2B). The fossil-bearing samples collected from the Cerro Negro Formation were also stratigraphically oriented following the protocol of Chen *et al.* (2013) (⊤ for top bedding surface view, ⊥ for bottom bedding surface view, and ↑ the stratigraphic top). The samples suspected to bear MISS were sectioned and polished using a standard diamond saw. More than 15 slab samples were polished using a polishing machine, Minitech 233, with different types of sandpaper discs and observed under a stereomicroscope Olympus coupled with a digital camera LC 2.0 MP in the Department of Applied Geology, Universidade Estadual Paulista "Júlio de Mesquita Filho" (UNESP), Brazil. The thin sections prepared from the selected rock slabs were analyzed under a petrographic microscope Nikon Eclipse E200, coupled with a digital camera Leica, to characterize and recognize microscopic features. The SEM analyses were made using a scanning electron microscopy JEOL model JSM-6010 LA, equipped with an energy dispersive spectrometer (EDS) device. All micro- and ultrastructural analyses were carried out in the Department of Petrology and Metallogeny of the Universidade Estadual Paulista "Júlio de Mesquita Filho" (UNESP), Brazil.

The pictures and images were prepared using the CorelDraw X7 software. The studied material was originally collected by M.J. Arrouy, L.V. Warren, D.G. Poiré and F. Quaglio during a field campaign in 2015, 2016, and 2022. The material is housed in the Instituto de Hidrología de Llanura "Dr Eduardo Usunoff" (IHLLA-CONICET), Azul, Buenos Aires, Argentina, and the Institute of Geosciences and Exact Sciences of Universidade Estadual Paulista "Júlio de Mesquita Filho (UNESP), Rio Claro, Brazil.

RESULTS

MISS were recorded in the sedimentary succession of the Cerro Negro Formation, being much more common in the lower to intermediate part of this unit (Fig. 1D). The section of the succession rich in MISS is commonly recognized in outcrops in both quarry walls and the subsurface (Figs. 2A and 2B). This is characterized by red- and gray-colored siliciclastic massive sandstone (Sm facies, Fig. 2C), laminated mudstone (Ml facies, Fig. 2C), wavy heterolithic sandstone/claystone bedding (Ht facies, Figure 2D), and wave-rippled fine-grained sandstone (Sr facies, Figs. 2C and 2E). In addition, this section of the unit presents flute marks and gutter casts in the base of some sandstone beds (Fig. 2E) and longitudinal grooves in the top of other beds (Fig. 2G). MISS structures are particularly common on the top of the fine sandstone beds and are associated with ripple marks (Fig. 2F).

Well-preserved discoidal forms (Fig. 3) occur in association with MISS. In the studied section, these structures appear as hundreds to more than a thousand (Figs. 3A and B). The largest discs comprise convex forms (negative epirelief) with diameters varying from 65 to 100 mm; they commonly show an
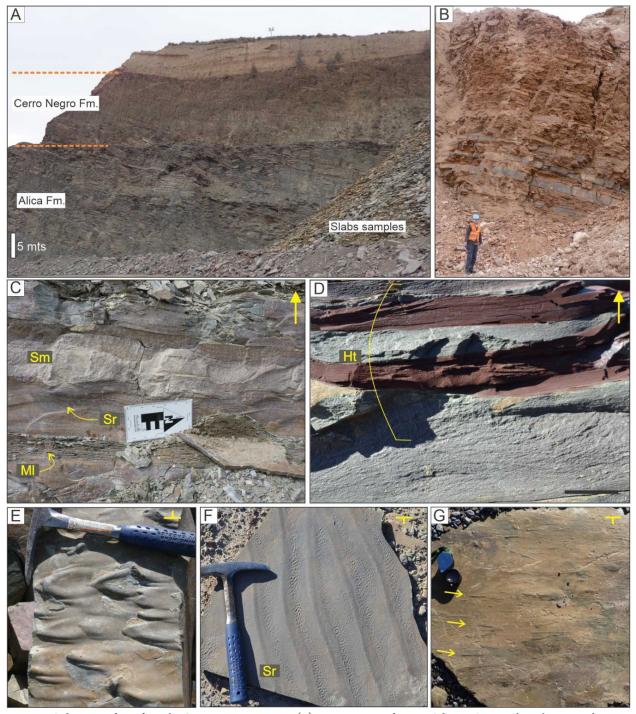
Figure 2. Sedimentary facies from the Cerro Negro Formation. (A) Panoramic view from La Cabañita Quarry. Show the contact between the Alicia Formation and the Cerro Negro Formation and the slab samples. (B) Details of an outcrop of the Cerro Negro Formation at La Cabañita Quarry, showing the sandstone facies interbedded with mudstone facies. (C) Detail view of massive sandstone facies (Sm), sandstones with current ripple facies (Sr), and laminate mudstone facies (Ml). (D) Interbedded red claystone and fine-grained sandstone with heterolithic lamination (Ht; Adapted from Arrouy *et al.* 2019), scale bar in black is 1 cm. (E) Symmetrical ripples showing MISS in the trough between the rectilinear ridges. F. Detail of flute casts at the base of a sandstone bed. (G) Erosional structures with a longitudinal groove. The flow is to the right (yellow arrows). The hammer in E and F is 33 cm long. ⊤ for top bedding surface view, ⊥ for the bottom bedding surface view, and ↑ the stratigraphic top.

invaginated center, creases, and strong radial grooves extending from the center to the margin of the disc (Figs. 3C and 3D).

The most common MISS resembles a small crinkle and is characterized by mm-scale discontinuous elongate and bifurcated forms with flat-topped crests separated by irregular and parallel depressions (Figs. 4A and 4B). This structure is characterized by interconnected crests and grooves, which

are always facing in one direction and commonly crinkled. It is also found on fine- to medium-grained rippled sands, where microbial activity has protected ripples from erosion (Fig. 2E). Another type of arrangement is honeycomb-like features that are very rare and occasionally occur in the troughs of ripple marks, with clear lateral gradation to structures with parallel ridges (*Kinneyia* marks, Fig. 4C). On the contrary, the
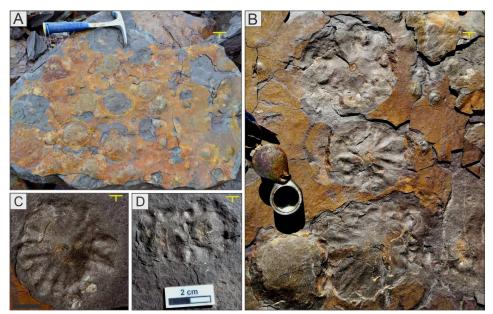
Figure 3. Discoidal structures assigned to the *Aspidella* plexus. (A) A general view of several specimens with variable diameters. (B) Three discoidal specimens preserved in negative epirelief and showing radial groves. (C) Detail of the specimen with a very well-preserved small boss in the center of the disc. (D) Detail of two specimens deforming each other. The hammer in A is 33 cm long. ⊤ for top bedding surface view, ⊥ for bottom bedding surface view, and ↑ for stratigraphic top.
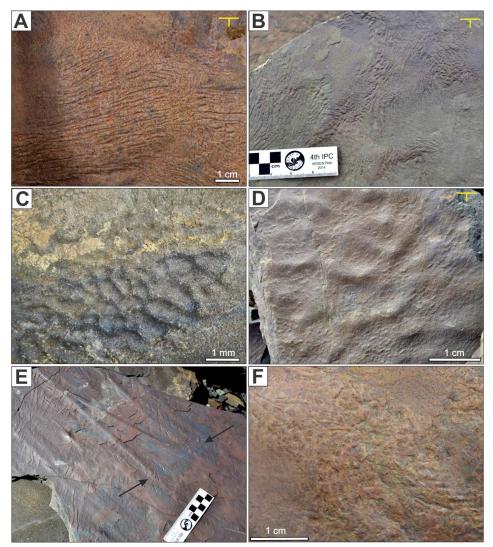

Figure 4. MISS from the Cerro Negro Formation. (A and B) Parallel linear wrinkles are slightly curved and associated with current lineation. (B) Detail of elephant skin structure, with a slightly reticulate arrangement of pinnacles and bulges. (C) Honeycomb-like feature. (D) Detail of interference ripples in fine sandstones showing discontinuous elephant-skin texture. (E) Lineation currents associated with wrinkle structures. The arrows point to fold-over biomat-covered bottoms. (F) External molds of elephant skin texture in fine to medium-coarse sandstone.

microbial textures are eventually deformed in the Cerro Negro Formation (Figs. 4D–4F).

An additional microbial texture is also relatively common in the formation. They are characterized by mm- to cm-scale irregularity (Figs. 4D and 4F) formed by coalescent nodules and asymmetrical polygons. These features occur on top of fine sandstones or ripple marks and small bedforms, which partially preserve the depositional surface relief. Another particular feature is the millimetric recurrence of microbial mats (related to elephant skin structures) associated with quartz, sericite, and muscovite flakes (Figs. 5A and 5B). The intercalation of thin organic layers and phyllosilicate grains is reinforced by SEM analyses that reveal significant C (carbon) concentrations between siliciclastic mixed layers that show equidimensional anhedral laths with irregular borders in crystals with less than 3 µm, which offer a dominance of Si (silicon), Al (aluminum), K (potassium), and occasionally Ca (calcium) (Figs. 6A and 6B).

Other features possibly originated by the influence of microbial activity are hundreds of discoidal structures preserved as positive relief in very fine micaceous sandstone facies (Figs. 7A and 7B). The densely distributed small pustular or blister-like discs have diameters varying from 1 to 7 mm and are characterized by the presence of a pronounced depression in their central part. Despite their very simple morphology and low size variation, the discoidal forms are invariably connected with oriented and elongated positive relief features conforming to current lineations (Fig. 7B).

Enigmatic sedimentary surfaces assigned to *Arumberia* (Figs. 7C–7F) are also reported in the same stratigraphic interval, marked by the frequent occurrence of elephant skin and *Kinneyia* structures. *Arumberia* is found in fine sandstone facies apparently covering the original flat surface in positive epirelief (Figs. 7C–7F) and is characterized by near parallel, slightly curved, thin ridges and groves (0.5–2 cm width and less than 1 mm depth). The non-bifurcated ribbons locally present branches constituted of irregular and continuous wrinkles that radiate from diverse points along the subparallel ridges (Figs. 7C and 7D). In some samples, the grooves are crisscrossed, forming different shapes like leaves, oblate, and lobate. A long leaf shape is also observed, with a point marked at the beginning of the structure (Figs. 7E and 7F).
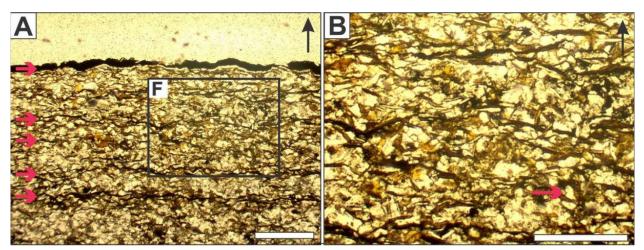

Figure 5. (A) Thin-section micrograph of the MISS showing the intercalation of several irregular dark organic layers (red arrows), 50×, parallel polarizers. (B) Detail of A showing muscovite and sericite flakes (orange/ocher objects) adhered to the organic irregular layers. The scale bar is 10 cm in A, 1 cm in B, 200 µm in A, and 500 µm in B.
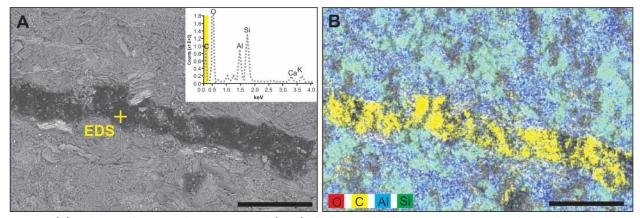

Figure 6. (A) Backscattered scanning electron micrograph (SEM) of a thin microbial layer. SEM-EDS spectra evidencing the main presence of carbon (yellow) and oxygen in the middle portion of the sample. (B) Microfluorescence map of the MISS layer shown in A confirming its organic composition. The scale bar is 50 µm in A and B.
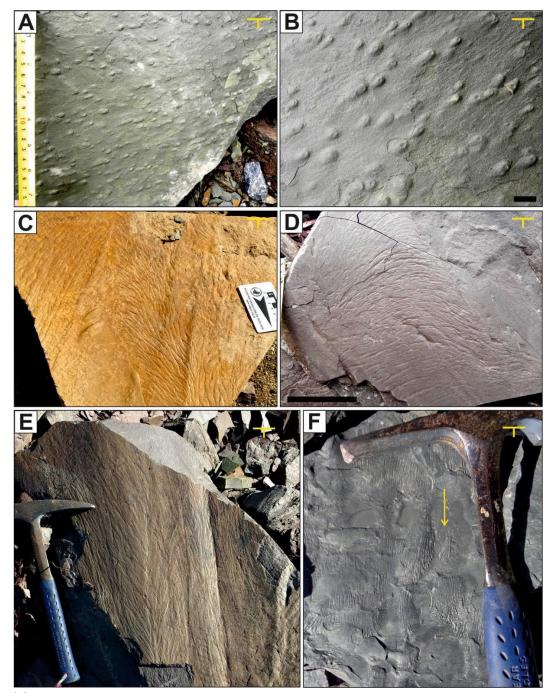
Figure 7. (A) Rock slab showing centimeter discoidal forms interpreted as *Intrites*-like structures. Note that all small discs are oriented in a preferential direction. (B) Detail of simple, slightly deformed discoidal impressions showing a central depression. *Arumberia banksi*-type from the Cerro Negro Formation. (C) *Arumberia*-type structure composed of bunches of near parallel and curved ridges. (D and E) *Arumberia*-type showing multidirectional grooves on a rippled sandstone surface. (F) View of the flute-cast surface of very fine sandstone showing the development of *Arumberia banksi*; the yellow arrow shows the paleocurrent direction. The scale bar in B is 5 cm. ⊤ for top bedding surface view, ⊥ for bottom bedding surface view, and ↑ for the stratigraphic top.

DISCUSSION

MISS diversity and sedimentary environments

The Cerro Negro Formation stands out from other Ediacaran units in South America due to the frequent presence of different types of discoidal structures, acritarchs (Gaucher *et al.* 2005, Arrouy *et al.* 2016, 2019), and abundant and diverse MISS. The occurrence of these structures in fine-grained sandstone facies indicates that the substrate was continuously bounded and colonized by microbial mats. As pointed out by Arrouy *et al.* (2016), the association between *Aspidella-like* discs and MISS suggests that the substrate was continuously protected by biomats (Figs. 8A and 8B), which probably led to the preservation of numerous discs (see also Gehling and Droser 2013, for an analogous situation).

Kinneyia structures were historically interpreted as a biotic or abiotic feature (Hagadorn and Bottjer 1997, 1999), mainly produced by small-scale ripples, raindrop impacts, sediment loading, or dewatering processes (Noffke *et al.* 2002, Porada
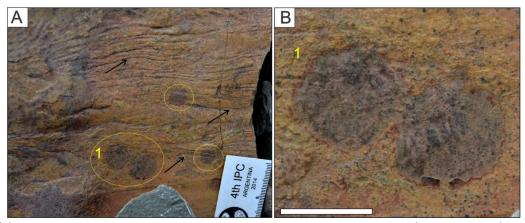
Figure 8. (A) Discoidal structures assigned to the *Aspidella* plexus are preserved in negative hyporelief (yellow dashed line) associated with microbial mats (black arrows) on the Cerro Negro sandstone bedding surface. (B) Detail of discoidal structure (yellow dashed line with number 1). The scale bar in B is 1 cm.

and Bouougri 2007). Despite the abiotic interpretation of *Kinneyia* as a capillary adhesion structure (Hagadorn and Bottjer 1999), there is a consensus that *Kinneyia* is produced by gas buildup or trapping of gases due to biomat degradation (Porada and Bouougri 2007). Thus, the *Kinneyia*-type wrinkle structures probably do not represent the microbial mat or biofilm itself but a structure formed beneath the buried organic layer. On the contrary, Seilacher (2007) interpreted elephant skin structures as small load casts formed below the biofilm or microbial mat. However, the above-described structures found in the fine sandstone facies of the Cerro Negro Formation suggest that the velvety-like, irregular texture observed at the surface probably reflects the original mat surface.

The *Kinneyia* wrinkle marks are common in the studied section of the Cerro Negro Formation (Fig. 4A), which appears to be related to inter- to subtidal facies associations that evidence shallow and oxic tidal plain conditions (Arrouy *et al.* 2015, 2016). The presence of parting lineation and primary current lineation clearly deforming the biofilm (Fig. 4E) indicates that these features are probably produced by the shear currents and waves in shallow water conditions, enhanced by the confined higher flux in the channel-like depressions caused by the previously formed flute marks. In the same sense, erosional structures with parallel ridges and furrows at the basis of the sandstone beds are related to flute casts, longitudinal grooves, and gutter casts (see Figs. 2F and 2G). These massive and fine-grained beds with scour structures are interpreted as a product of high-energy, episodic flows generated by storms (i.e., tempestites).

Indeed, elephant skin (Gehling 1999, Gehling and Droser 2009, Bottjer and Hagadorn 2007) is currently explained as being formed by the growth of linear aggregations of bacterial filaments over a depositional surface (Hagadorn and Bottjer 1999). Therefore, these structures may correspond to microbial growth structures on mat surfaces (Porada and Bouougri 2007); lithified microbially covered depositional surfaces (Noffke *et al.* 2001); or the microbial mat itself (Noffke 2000, Noffke *et al.* 2022). Petrographic and compositional evidence suggests the preservation of repeated organic layers associated with these structures, which leads us to consider the third

hypothesis as the most reliable for our study case (Figs. 5A and 5B). Thin organic layers with significant C concentrations intercalated with siliciclastic grains probably represent the continuous colonization of the substrate by microbial mats and the presence of trapped detrital grains (phyllosilicate and small-size quartz grains, among others) adhered to an original EPS-biofilm (Porada and Bouougri 2007).

As occurred with the *Kinneyia* structure in the recent past, the biogenicity of *Arumberia* was also questioned, being compared to flutes with radial ridges produced in flume experiments (Dzulynski and Walton 1965) or aligned sedimentary structures generated by unidirectional currents (McIlroy and Walter 1997). Indeed, there is a complete absence of preserved body fossils in the microbial community of *Arumberia* structures of the Cerro Negro Formation as well as in other Ediacaran occurrences (Mapstone and McIlroy 2006, Kumar and Pandey 2008). Nevertheless, petrographic studies show features typical of microbial mats, such as the laminar dark anisotropy and crenulations. Also, its delicate and complex morphology with evidence of plastic deformation attests to the biogenicity of these structures (Kumar and Pandey 2008, Kolesnikov *et al.* 2012). As such, *Arumberia* has been explained in several mutually exclusive ways, mainly being interpreted as a complex (organized?) microbial community. Moreover, it represents an example of an ancient type of microbial mat (Kolesnikov *et al.* 2012) and, on the other hand, a physical sedimentary structure formed with or without a microbial mat covering (Brasier 1979, McIlroy and Walter 1997, Allen and Leather 2006, Seilacher 2007, Sharma and Mathur 2014, Becker-Kerber *et al.* 2020). Historically, it is interpreted as restricted to the Ediacaran and lower Cambrian (Bland 1984), considering that the significant majority of *Arumberia* occurrences worldwide are recorded from rocks dated to 520–560 Ma in age (McMahon *et al.* 2021). However, Kolesnikov *et al.* (2012) described new occurrences of *Arumberia*-type structure in the Central and South Urales in Upper Vendian non-marine sediments, which proved that *Arumberia* occur in a broad temporal range. All known fossil specimens were found in siliciclastic rocks deposited in a shallow and disturbed substrate, occasionally subjected to periodic subaerial exposure (Glaessner and Walter 1975, Kumar

and Pandey 2008, Kolesnikov *et al.* 2012). This suggests that *Arumberia* was relatively common in tidal flats and shallow coastal settings, where a complex microbial community (Kolesnikov *et al.* 2012) adapted to the physical processes that are inherent to these environments (i.e., high-frequency tidal oscillation, intermittent desiccation, incidence of waves and currents, insolation, and even evaporitic conditions). In this way, *Arumberia* (like other types of MISS) figures as a crucial actor in the biostabilization of the shallow water substrates (Kolesnikov *et al.* 2012). In the Cerro Negro Formation, *Arumberia* is closely associated with sole marks at the base of event beds, suggesting that the genesis of this structure may be related to episodic and energetic bottom currents. As observed in Figs. 7C–7E, the *Arumberia* seems to have been deformed by the flows responsible for producing the groove casts. In any case, the samples described for the Cerro Negro Formation help to support the hypothesis that *Arumberia* may represent a complex microbial community, possibly deformed under the action of currents or waves in a shallow marine environment (Glaessner and Walter 1975, McMahon *et al.* 2021).

Relationship between Ediacaran microbial communities and discoidal structures

The fossil assemblage of the Cerro Negro Formation is mainly characterized by the presence of more than a hundred discoidal structures preserved in positive epirelief associated with the *Aspidella*-like and *Intrites*-like discs, several types of MISS, and microfossils. Despite the intrinsic preservational characteristics of discoidal structures, their close association with the MISS (Fig. 8) is remarkable.

In terms of the problematic nature of the discoidal structures, it is worth mentioning that three taphonomic styles are recognized for the preservation of discoidal Ediacaran fossils: a *Conception Style*, where the soft-bodied specimens would be molded with underlying sediments after early cementation of their upper surfaces covered by volcanic ashes (Seilacher 1992, Narbonne 2005, MacGabhann 2007); a *Gravity Cast Style*, where the organism's lower surface would be molded by the infilling of sediments coming from above after an episodic burial event (MacGabhann 2007, Tarhan *et al.* 2010, 2015); and a *Death Mask Style*, characterized by the infilling of organic tissues with underlying sediments during compaction due to early cementation of their upper surfaces associated with mat decay on a microbially bounded substrate (Gehling 1999). Considering the evidence of the preservation style reported for the *Aspidella*-like specimens from the Cerro Negro Formation (Arrouy *et al.* 2016), it is typical of previous authors' "death mask" specimens being compatible with the hyporelief morph types (Figs. 8A and 8B).

However, it is not excluded that part of the discoidal structures, in the basal part of the Cerro Negro Formation, can be constituted by very simple *Intrites*-like structures with similar size (Figs. 7A and 7B). The presence of the discs preserved in positive epirelief on the top of the sandstone beds suggests that these structures were probably formed at the water-sediment interface. In this case, they resulted from the interaction of biotic and abiotic processes, possibly generated by a unique and synchronous event, after fluidization and fluid escape

under a microbial mat sealing the substrate (Menon *et al.* 2015, 2016). In this regard, Inglez *et al.* (2021) proposed an alternative origin for some of the discoidal forms of the basal section of the Cerro Negro Formation as the possible result of fluid injection beneath microbial mats.

The sealing of the sediment by the reconstruction of a microbial mat on top of the bed may have been essential in isolating the pore waters from the oxic water column above, controlling the availability of sulfate ions, and maintaining anoxic pore waters in even porous sediments (Gehling *et al.* 2005, Callow and Brasier 2009). The biostabilization by microbial communities is responsible for the considerable increase in sediment cohesion, which permits the development of plastic deformation in sandy deposits (including microbial textures). Furthermore, biostabilization protects the substrate against erosional processes that would otherwise destroy delicate primary structures. Such a taphonomic scenario (extensively discussed by Gehling 1999, Seilacher 1999, Tarhan *et al.* 2015, Inglez *et al.* 2021, among others) can also explain the preservation of at least part of the hundreds to thousands of *Aspidella*-like structures observed in the studied section of the Cerro Negro Formation (Fig. 3). The abundance of those otherwise rare features (either representatives of a plexus of Ediacaran macroorganisms or some poorly understood abiotic structures) is here interpreted as a strong argument in favor of microbially influenced preservation.

FINAL REMARKS

The terminal Ediacaran siliciclastic deposits of the Cerro Negro Formation hold a significant fossil assemblage, mainly constituted by discoidal forms in close association with microbial mats. Several lines of evidence suggest that the high preservation of *Aspidella* and *Intrites*-like structures is tied to biotic and abiotic processes involving substrate sealing by microbial mats, fluidization, sand injection, and probably organic matter decay. In this way, different MISS preserved in the shallow marine bottom, such as *Kinneyia* and wrinkle structures, elephant skin, and *Arumberia*, are associated with the occurrence of soft-bodied fossils. Thus, the joint action of abiotic (tidal currents and waves inducing liquefaction and sand injection) and biotic factors (substrate biostabilization by microbial communities necessary for the increase in sediment cohesion) is the main one responsible for the preservation of body fossil style in the Cerro Negro Formation. Like other coeval units recorded in the SW Gondwana, the Later Ediacaran Cerro Negro Formation configures a remarkable example of how the preservation dynamics took place on a seabed sealed by microbial mats in the Clymene Ocean context.

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