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The discovery and description of an extremophile microcosmos in a Cretaceous paleogeothermal field

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We report a new Fossil-Lagerstätte at the Cretaceous hydrothermal field of Sanagasta, La Rioja, northwestern Argentina, which opens a window into the paleobiology of an exceptionally preserved fossil ecosystem. Active geothermal systems harbor a diverse microbial life that thrive in high temperature, unique mineral composition and fluctuating pH. These environments are dominated by a meso- and hyperthermophilic community, including bacteria and archaea, that proliferate around the hot springs and geysers. In these environments, fossilization occurred rapidly by abiotic factors and through biomineralization—chiefly biosilicification. This process is mediated by thermophilic microorganisms, mainly cyanobacteria, allowing for the exceptional preservation of the biota. Here, we describe an ~80 million-year-old fossil extremophile biocoenosis encrusted within microbialites from the Sanagasta paleohydrothermal field. The core of the microbialites was explored using petrography, Scanning Electron Microscopy (SEM) and Energy-Dispersive Spectroscopy (EDS) analyses in SEM. These microbialites exhibit remarkable three-dimensional preservation of microorganisms through extensive biosilicification, directly mediated by the extremophile communities. The taxonomic range of the sinterized assemblage encompasses the three domains: a noteworthy array of thermophilic 'prokaryotes' (chiefly bacteria and archaea), along with a rich diversity of eukaryotic 'protists' microorganisms (i.e., amoebozoans, myxomicetes, red algae, diatoms, and alveolates), green algae, plant remains, fungi and a variety of arthropod remains, all preserved in notable microanatomical details. The Sanagasta GeoPark contains one of the most diverse and exquisitely preserved records of microfossils known to date, illuminating a complex inland ecosystem within the first documented Cretaceous terrestrial hydrothermal environment.

KEYWORDS

extremophiles, hydrothermalism, La Rioja, lagerstätten, late Cretaceous, Sanagasta, silicification

1 Introduction

Rothschild and Mancinelli stated that there is life wherever there is liquid water on Earth regardless of environmental conditions (Rothschild and Mancinelli, 2001). Modern hydrothermal environments in active geothermal fields foster a considerable diversity of extremophile communities and other microorganisms that thrive in harsh conditions in high temperatures, mineral compositions, and extreme pH (Brock, 1985; Reysenbach and Cady, 2001; Rothschild and Mancinelli, 2001; Benning et al., 2005; Renaut and Jones, 2003, 2011; Power et al., 2018; Colman et al., 2019; Rasmussen et al., 2023). These unique ecosystems, where extremophiles flourish, have shed light on early life on Earth, the search for life beyond it and even the possibility of panspermia (Stetter, 1996; Farmer, 2000; Reysenbach and Cady, 2001; Rothschild and Mancinelli, 2001; Kázmierczak and Kremer, 2002; Pinti et al., 2009; Brasier et al., 2015; Dodd et al., 2017; Des Marais and Walter, 2019). Hot springs and geysers are “end members” of the final surface expression in complex terrestrial hydrothermal fields. Hot springs discharge and preserve micro and macro-structures in areas on the Earth’s surface that are under the influence of geothermalism through an intricate underground plumbing network (Renaut and Jones, 2003, 2011; Jones and Renaut, 2011). These extreme environments were key in the origin and evolution of life on early Earth (Rothschild and Mancinelli, 2001; Pirajno and Van Kranendonk, 2005; Pinti et al., 2009; Brasier et al., 2015; Dodd et al., 2017; Des Marais and Walter, 2019). Current evidence strongly suggests that the Last Universal Common Ancestor (LUCA) was a thermophile and, therefore, it is no coincidence that the most basal groups of Bacteria and Archaea are thermophiles -i.e. Thermotogales, Aquificales, Pyrodictiales, Thermoproteales, and so forth- (Stetter, 1996; Reysenbach and Cady, 2001; Di Giulio, 2003; Colman et al., 2016; Gogarten and Deamer, 2016; Hug et al., 2016; Weiss et al., 2016, Weiss et al., 2018; Morales and Delaye, 2020; Moody et al., 2024).

Hydrothermal ecosystems support a vast biological diversity that consists chiefly of microbial organisms (Stetter, 1996; Reysenbach and Cady, 2001; Rothschild and Mancinelli, 2001). These environments are dominated by a substantial and diverse community of meso- and hyperthermophiles: chemo- and photoautotroph archaea and cyanobacteria, proliferate around and close by hot springs and geysers, often forming conspicuous photosynthetic microbial mats and biofilms (Rothschild and Mancinelli, 2001; Stetter, 2006; Colman et al., 2019; Rasmussen et al., 2023; Sriaporn et al., 2023). Moreover, these environments support a great diversity of basal eukaryotes (e.g. protozoan), photosynthetic stramenopiles members of the SAR supergroup (e.g. diatoms, golden and brown algae), photoautotrophic archaeplastids (e.g. green algae and some plants), coupled with a notable microscopic assortment of fungi and animals (Reysenbach and Cady, 2001; Rothschild and Mancinelli, 2001; López-García et al., 2003; Brown and Fritz, 2019; Silva et al., 2021; Pop et al., 2023; Rappaport and Oliverio, 2023).

Hot springs and geysers are found presently on every continent, including mainland Antarctica (Jones and Renaut, 2011; Renaut and Jones, 2011; Noell et al., 2025). The most iconic and best-known modern geothermal fields are the Yellowstone National Park (USA), El Tatio in the Andes in Chile, the Taupo Volcanic Zone in New Zealand, the Kronotski National Park in Kamchatka (Russia), Tengchong in China, and the Haukadulur Valley in Iceland (Renaut and Jones, 2003, 2011; Pirajno and Van Kranendonk, 2005; Cowan et al., 2012; Jones, 2021; Gong et al., 2022). In these environments, fossilization of the biological community results from a combination of abiotic components: occur rapidly, influenced by water mineral concentration –i.e., saturation of SiO_2–, pH, and temperature; however, it also occurs by biotic factors through biomineralization –i.e., biosilicification– which produces a rapid and exceptional preservation of the living biota (Cady and Farmer, 1996; Farmer, 2000; Reysenbach and Cady, 2001; Yee et al., 2003; Benning et al., 2005; Channing et al., 2005; Campbell et al., 2015a; Iniesto et al., 2016; Liesegang and Gee, 2020; Jones and Renaut, 2021; Rasmussen et al., 2023). Although biosilicification is a common biological process used by many organisms (e.g., for skeletons and shells), it is particularly prevalent in hydrothermal environments. In such environments, biosilicification is mediated by thermophilic microorganisms—mainly cyanobacteria—and this process has been extensively studied for decades (Ferris et al., 1986; Jones et al., 1997, 1998, 2003, 2004b, 2005; Phoenix et al., 1999, 2000, 2001, 2002, 2003; Toporski et al., 2002; Guidry and Chafetz, 2003; Jones and Renaut, 1996, 2003, 2021; Konhauser et al., 2003, 2004, 2008; Yee et al., 2003; Benning et al., 2004, 2005; Lalonde et al., 2005; Phoenix and Konhauser, 2008; Doi and Fujino, 2013;

Campbell et al., 2015b; Ikeda, 2021; Jones, 2021). As these previous studies have shown, it is important to note that silicification in hot spring settings occurs incredibly rapidly, even while the microbes are still alive (Guidry and Chafetz, 2003). Thus, silicification in hydrothermal environments has proven to be an extraordinary process for preserving micro- and nanostructural features in fossils and soft tissues, in addition to highlighting the diagenetic resilience of silica (Rasmussen et al., 2023, 2024). Nevertheless, reports of fossil preservation on continental hydrothermal paleoenvironments remain seldom, aside from a few world-famous fields of Archean, Devonian, Jurassic, and Miocene ages, as well as several near-modern Quaternary records (Rice et al., 2002; Channing et al., 2007; Guido et al., 2010; Campbell et al., 2015b, 2019; Djokic et al., 2017; Des Marais and Walter, 2019; Garwood et al., 2019).

Among the paleohydrothermal sites documented worldwide, the Sanagasta GeoPark (SGP) in La Rioja Province, northwestern Argentina, is the only one dated to the Cretaceous period (Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012). This site (Figure 1) constitutes the first fossil evidence of coeval geothermal activity and Cretaceous dinosaur nesting behavior, as indicated by the discovery of more than 90 titanosaur egg clutches associated with fossilized hot springs and geysers (Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012; Grellet-Tinner et al., 2012; Hechenleitner et al., 2015; Leuzinger et al., 2021). Several investigations focused on paleobiological aspects of the titanosaur eggs and nesting behavior, such as the gas conductance or the adaptations of eggs and eggshells to the harsh thermal environment (Grellet-Tinner et al., 2012; Fiorelli et al., 2013; Hechenleitner et al., 2016a, Hechenleitner et al., 2018a; Leuzinger et al., 2021). However, no study has addressed yet the extremophilic fossil microbiological community of this Cretaceous paleohydrothermal field.

Here we describe an exceptional Late Cretaceous (*ca.* 80-my-old) fossil microbial community encrusted in microbialites from paleogeysers and hot-springs at SGP (Figure 1). The microorganisms in this paleoenvironment underwent a phenomenal silicification, yielding some of the most exceptionally well-preserved and diverse micro and nanofossils known worldwide to date. Microorganisms show an exquisite preservation in three dimensions within siliceous cast sinter deposits by abiotic SiO_2

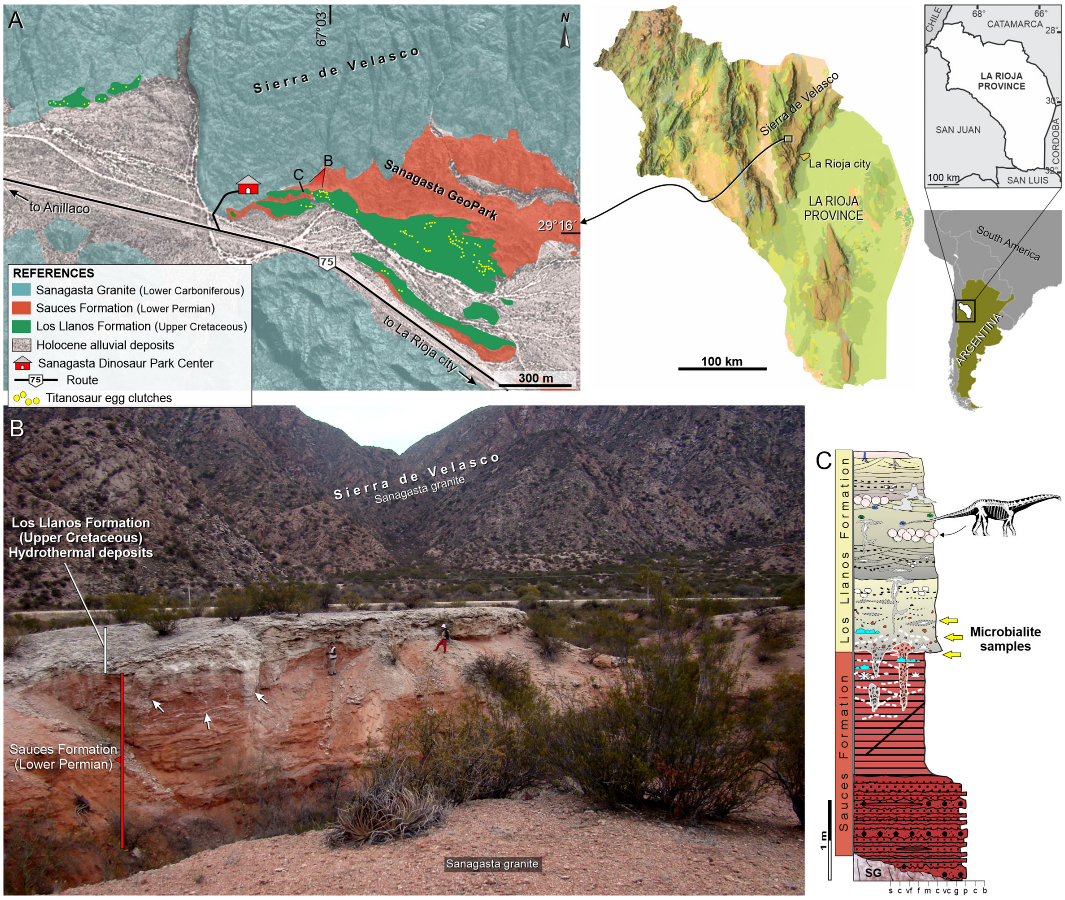

FIGURE 1
Sanagasta GeoPark, La Rioja, Northwestern Argentina. **(A)** Geographical and geological maps of SGP in La Rioja province with the distribution of titanosaur egg clutches -yellow dots- (modified from Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012) showing the panoramic photo in **(B)** and profile in **(B, C)** Panoramic overview of SGP with the white Cretaceous Los Llanos Formation above the red Permian Sauces Formation; some hydrothermal alteration macrostructures can be observed -white arrows-. **(C)** Stratigraphic profile of the Cretaceous Los Llanos Formation in the SGP showing the levels of the microbialite samples -yellow arrows-.

precipitations (poikilotopic silica) and biotic-induced silicification mediated by extremophiles. The microfossils show exceptional diversity, encompassing prokaryote-like forms and eukaryotic groups such as 'protists', algae, fungi, plants, and arthropods. Exceptional preservation includes fine anatomical details and nanostructures, offering a unique window into the biological diversity and paleoecology of the first known Cretaceous hydrothermal terrestrial environment. The site is indeed a *Konzentrat* and *Konservat-Lagerstätten* revealing a complex Late Cretaceous microecosystem.

1.1 Institutional abbreviations

CRILAR-MNP: Micro and Nanopaleontology Collection, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja, Anillaco, La Rioja Province, Argentina.

2 Materials and methods

2.1 Fieldwork and samples collection

All analyzed samples are microbialitic rocks and were collected in the Sanagasta Geological Park at the main nesting site during several fieldtrips. Unexposed deep samples were collected from outcrops near the park tourist center (site A; Figure 1) (Fiorelli et al., 2012). Specimens were taken in the Permian-Cretaceous strata contact conduits and proximal hot-spring vent facies from the Cretaceous egg-bearing level (Figure 2) (Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012; see Geological Setting and Supplementary file for more information). The samples were processed and mechanically broken in the laboratory. Small (<1 cm) internal fragments were used for the SEM analyses (Figure 3) while larger pieces (~5 cm) for petrographic thin sections (Figure 4).

2.2 Rock and paleontological samples repository

All microfossil specimens (Bacteria, Archaea, and Eukarya) described in this study are preserved within samples of hydrothermal microbialites (Figures 2, 3). These rock samples with fossils and primary thin sections are housed in the Petro Laboratory and Micro- and Nanopaleontology Collection at CRILAR (Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja, Anillaco, La Rioja Province, Argentina), under the acronyms CRILAR-MNP 001 and CRILAR-MNP 002.

CRILAR-MNP 001 corresponds to brecciated silica sinter from the boundary between the Permian Los Sauces Formation and Cretaceous levels of Los Llanos Formation (Supplementary Figure S4). CRILAR-MNP 002 corresponds to brecciated calc- and silica sinter containing botryoidal geyserite veins from the lower levels of the Cretaceous Los Llanos Formation (Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012) (Supplementary Figure S4). Both samples were subdivided into smaller fragments identified with subnumbers (e.g., CRILAR-MNP 001/1, CRILAR-MNP 001/2, etc. Supplementary Figure S3), which were analyzed using SEM and EDS techniques. See the Supplementary Data Sheet 1 for more details.

2.3 Petrographic thin sections

Microbialite thin sections were made at the CRILAR Petrographic Laboratory using the following protocol: specimens were washed with distilled water and cut with PetroThin, dried at 42°C in an oven during 24 hours, and subsequently glued with compound glue (Araldit CY 248 and hardening HY 956) on glass slides of 1.8 mm. All thin sections are housed in the paleontological and geological collection of the CRILAR. Thin section observations were made with a stereoscopic microscope (Leica MZ12), Leica DM LB light, and petrographic DM2500P microscopes.

2.4 Scanning electron microscopy and energy dispersive spectrometry

The scanning electron microscopic (SEM) analysis and preparation of the rock samples following the standard methods. Microbialite samples were mechanically broken and tiny fresh fragments were immediately used for the analyses. Each specimen was mounted on an aluminum stub and coated immediately with gold using a Quorum Q150R Plus Series Coaters. The metallized samples were instantly introduced into the electron microscope. The SEM analyses were carried out with a field emission electron microscopic (FE-SEM) Zeiss Sigma 560 VP at the CRILAR Advanced Microscopy Laboratory, Anillaco, La Rioja, Argentina. For the SEM control was used the SmartSEM software, work in high vacuum, with a standard aperture size (Ap) at 30 μm for images, and determinate working distances (WD) between 8 and 12 mm. The analyses were conducted at variable keVs (for SEM images at 3 to 7 keV and EDS at 15 to 20 keV). We use inLens, secondary electron (SE) and backscatter (BSD) detectors. The images were taken with scan speed ±7 and store resolution of 4096x3072 pixels. Elemental analyses were carried out with an energy-dispersive X-ray spectrometry detector UltimMax40 (by Oxford Instruments) and the AZtec software to process the data.

2.5 Image and graphics design

CorelDRAW Graphics Suite 2020 and Adobe Photoshop CC14 were used for storage and processing of the images, and final design of the figures. All photos and drawings were taken and drawn by the authors.

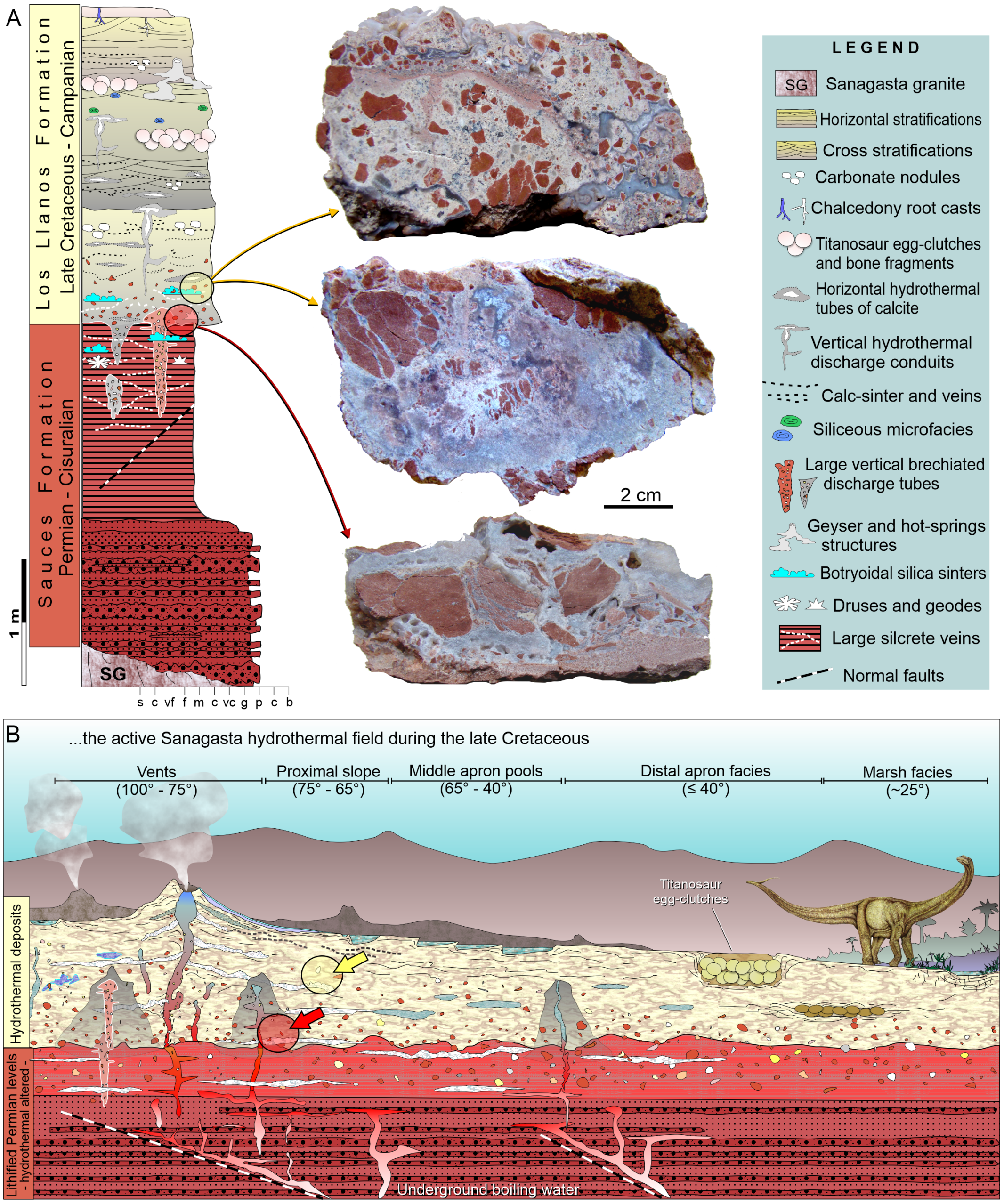

FIGURE 2
Stratigraphy, samples and paleoenvironment model of the SGP. **(A)** Detailed stratigraphic profile of the SGP showing the levels of the three microbialite samples: one from the Permian–Cretaceous boundary (CRILAR-MNP 001) and two from the lower levels of the Cretaceous Los Llanos Formation (CRILAR-MNP 002). **(B)** Simplified stratigraphic model of the active Sanagasta hydrothermal field during the Late Cretaceous, highlighting lateral gradients that indicate the proximal facies from which the samples originated (based on Fiorelli et al., 2012, Campbell et al., 2015b).

3 Geological setting and paleoenvironment of the Sanagasta GeoPark

The Sanagasta paleohydrothermal field is located in the SGP, La Rioja Province, Northwestern Argentina (Figure 1), where a large titanosaur colonial nesting site was first discovered (Grellet-Tinner and Fiorelli, 2010). The SGP is confined to the Los Llanos Formation (LLF), an Upper Cretaceous unit exposed with several outcrops (2–20 km^2) in the central-east region of La Rioja province, Western Argentina (Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012; Basilici et al., 2017) (Supplementary Data Sheet 1, Supplementary Figure S1). The LLF usually rests unconformably on different Permian units of the Paganzo Basin and is characterized mostly by a succession of cumulative paleosol profiles with a typical Gondwanan vertebrate fauna (Fiorelli et al., 2012, 2016; Hechenleitner et al., 2016b, 2018b; Basilici et al., 2017) (Supplementary Data Sheet 1). However, at SGP, the LLF is featured by a few meters thick of entirely paleohydrothermal deposits (Supplementary Data Sheet 1) with numerous titanosaur egg-clutches (Figure 1) (Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012). Here the unit is characterized by a complex depositional system, dominated by large sedimentary structures and microfacies typical of a geothermal environment (Figure 2B, Supplementary Figure S2): brecciated network of conduits and pipes cutting the horizontal beds, long horizontal calcite veins, calcite and silica sinters such as pseudotravertines and geyserites (Fiorelli et al., 2012). The microfossils described here are embedded in poikilotopic silica formed by silicon dioxide-rich fluids that filled the rock cavities during the active life of the thermal system (Figures 2, 3).

The brecciated microbialitic samples (Figure 2) were collected from the interior of the main outcrop of the SGP to avoid potential modern contamination. It is important to emphasize that these samples represent proximal facies of the paleohydrothermal environment and correspond to the same stratigraphic level as the titanosaur egg clutches (Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012), which were discovered from distal facies (Figure 2B). Nevertheless, some differences between these locations are expected due to the temporal and spatial variability of the paleohydrothermal system. The concept of *stratigraphic overlap of facies* (Walther's Law of Facies) plays a key role in this context (see Middleton, 1973; Miall, 1997).

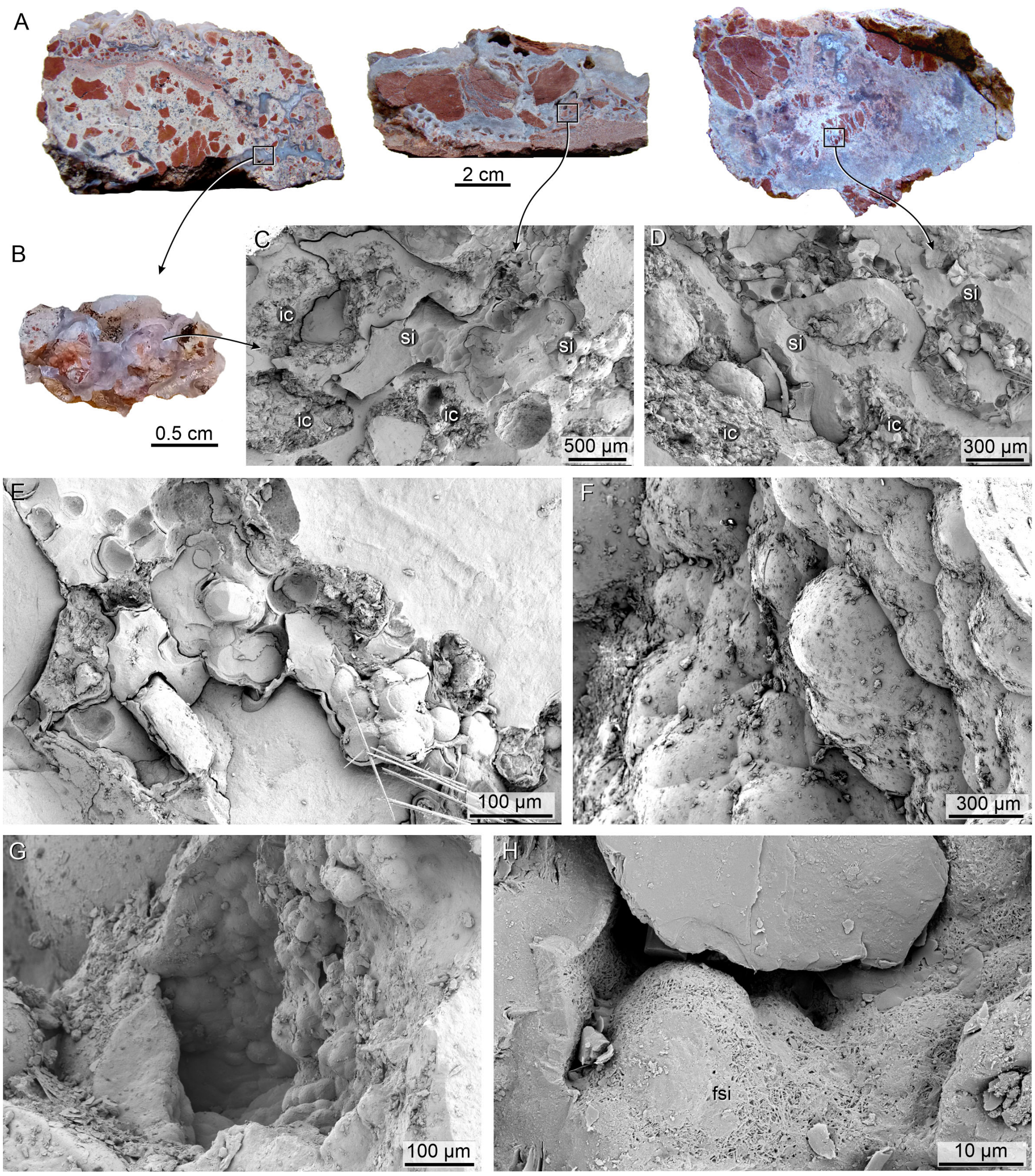

FIGURE 3
Microbialite samples from SGP. **(A)** The three hand-size samples from the P-K boundary and lower Cretaceous levels with silica cements -poikilotopic-. **(B)** One of the small broken brecciated pieces with microbotryoid facies used for SEM and EDS analyses. **(C-H)** Poikilotopic and botryoidal silica microfacies and microcavities encompassing the full diversity of recorded fossil microorganisms. fsi, nano-fibrous silica. ic, intraclasts. si, silica.

According to this principle, the vertical superposition of facies observed in the Sanagasta sedimentary column (Figure 2) reflects the lateral succession of depositional environments. This process has been documented in modern hydrothermal settings (e.g., Fouke et al., 2000; Campbell et al., 2015b). In the Sanagasta paleohydrothermal field, lateral migrations of facies produced spatial arrangements in which eggs and clutches occur at the same stratigraphic level as the sampled microbialites. However, the egg clutches are restricted to the distal facies of the system (see Figures 2B). Dinosaurs that nested at Sanagasta laid their eggs in facies where temperatures were suitable for incubation (between 35 and 40°C; see Hechenleitner et al., 2015; Leuzinger et al., 2021), namely the distal facies. Thus, Sanagasta dinosaur avoided oviposition in intermediate and proximal facies, where higher temperatures would have rendered nesting biologically unviable (Figure 2B).

The Late Cretaceous hydrothermal fluids, related to the regional Gondwanic extensional cycle, partially altered the Carboniferous Sanagasta granite and the upper levels of the pre-existing lower red Permian strata of the Sauces Formation (Figure 2) (Fiorelli et al., 2012). The earliest Cretaceous thermal sediments were deposited over the Permian host rock. They are characterized by prominent vertical and horizontal calcitic conduits and siliceous sinters (Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012) (Figures 2, 3, Supplementary Figure S2). On the surface, conspicuous large domed paleogeysers and hot spring structures, terraced mounds, fossil ponds and pools, apron and discharge channel facies, mini-dams, and fossil mud drainages and runoffs are readily visible and conspicuous (Supplementary Data Sheet 1, Supplementary Figure S2) (Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012, 2013). All these structures display distinctive hydrothermal mineral facies and fabric crystallizations (e.g., “dogtooth” crystals, stromatolite-like

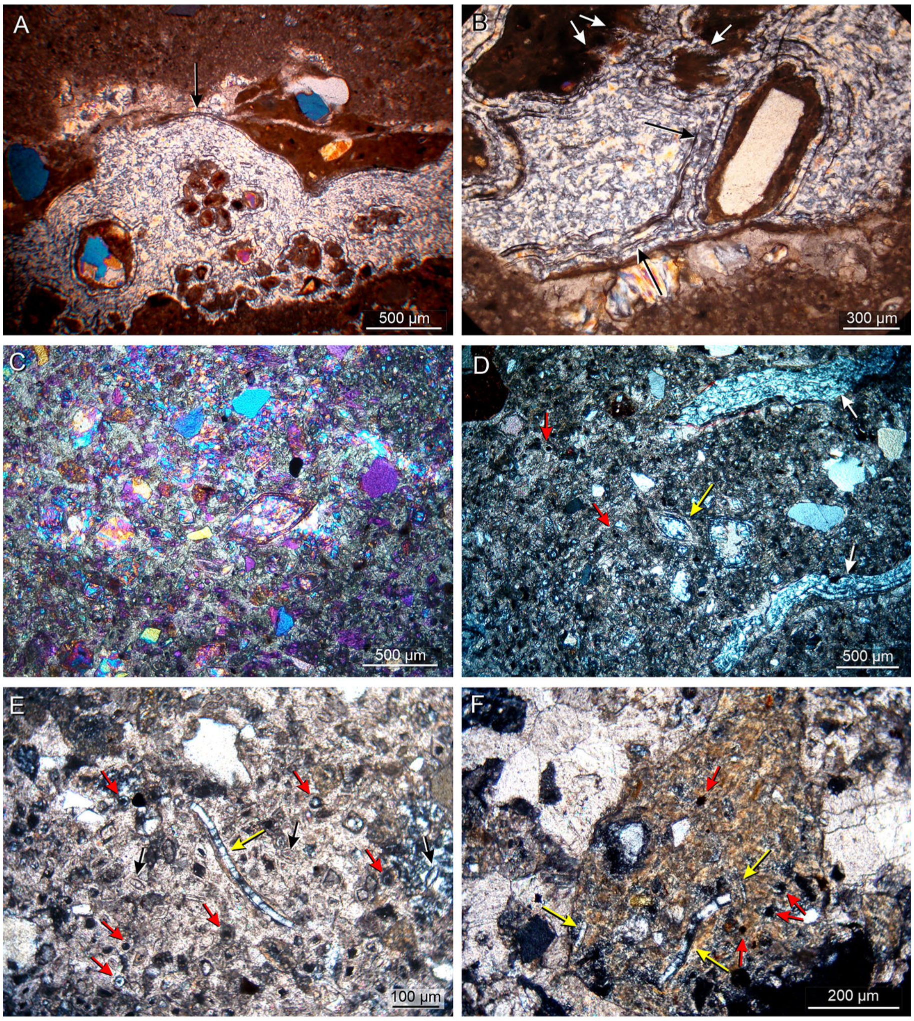

FIGURE 4
Photomicrographs of microbialite samples thin sections from SGP bearing some microfossils. **(A, B)** Thin section from the P-K boundaries showing poikilotopic and botryoidal silica microfacies with pseud-stromatolitic laminations -black arrows- and cavities -white arrows- in which microorganisms are preserved. **(C, D)** Thin sections of the hydrothermal sediments with micritic and silica matrix containing numerous silicified microfossils, such us laminated pseud-stromatolites -white arrows-, dense clustering of pennate diatoms -yellow arrows- (diatomaceous matrix) and filamentous microbes in cross section -red arrows-. **(E, F)** The same sample with large and silicified filamentous microbes (cyanobacteria)? -yellow arrows- between microbes in cross section -red arrows- and some pennate diatoms -black arrows-. Modified from Fiorelli et al., 2012.

structures, tuffed, palisade in terracetes, and pseudotravertines) (see Fiorelli et al., 2012). Some structures exhibit microbialite facies dominated by brecciated carbonate microfacies, sinterized microbotryoids and cavities filled by poikilotopic silica (Supplementary Figures S2-S4). Other microsections of the rock display a microbially induced sedimentary structure (MISS, according to Noffke et al., 2001; Stal, 2012). Thin sections of proximal slope microfacies and microbial framestones exhibit silicified, layered, and laminated, crust-like microstromatolites, along with filamentous microorganisms—such as cyanobacteria—embedded in a diatomaceous matrix composed of pennate diatoms (Figure 4; Supplementary Figures S5-S7) (Fiorelli et al., 2012). These brecciated, microbotryoidal and silicified microbialites display all the sampled microfossils below-described (Figure 3).

The Late Cretaceous age for the LLF and the SGP outcrops is based on the discovery of several reptile fossil remains typical of other Cretaceous Gondwanan associations, including different species of titanosaur nesting sites –both in the type locality of Tama and SGP–, titanosaur and theropod bone remains, turtle bones fragments, the abelisaurid *Vitosaura* and the notosuchian *Llanosuchus* (Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2016; Hechenleitner et al., 2016b, 2018b; Jiménez Velandia et al., 2025). More precisely, an association of microfossils in palustrine muddy facies of the Tama pedotype at the type locality (see Basilici et al., 2017), including charophytes and several freshwater ostracodes (Carignano et al., 2013; De Sosa Tomas et al., 2017), strongly suggest a Campanian age for the Los Llanos Formation. Instead, at the SGP locality, the Late Cretaceous age is substantiated not only by the exceptional and indisputable titanosaur nesting site—comprising over 90 egg clutches, some of them with up to 30 complete eggs—(Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012), but also by the hydrothermal event temporally associated with the Gondwanan extensional tectonic active cycle during the Cretaceous in the central-west region of Argentina (Rapela and Llambías, 1999; Mutti et al., 2005; Fiorelli et al., 2012). This extensional phase gave rise to hydrothermal fluid circulation characterized by distinctive mineralogical assemblages and unique geochemical signatures, which have been documented at SGP and is temporally coeval with the late Cretaceous dinosaur nesting activity (Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012; Leuzinger et al., 2021). A comprehensive and detailed geological description of the SGP and LLF has been already published in previous contributions (Fiorelli et al., 2012, 2013, 2016; Hechenleitner et al., 2016b, 2018b; Basilici et al., 2017; Jiménez Velandia et al., 2025). See the Supplementary Data Sheet 1 for more details on geology, rock petrography, taphonomy, and EDS analyses.

4 Results

4.1 Fossil microbiota assemblage of the SGP - generalities

Environmental niches in geysers and hot springs are temporally limited and spatially variable, furthermore the magnitude, duration, temperature, chemistry and pH of heated water vary and control the distribution of the microenvironmental niches and foster a complex biota (Rothschild and Mancinelli, 2001; Campbell et al., 2019). Spring systems in modern hydrothermal environments display a diverse biota including photosynthetic and chemosynthetic bacteria, heterotrophic bacteria, archaea, protozoa, algae, mosses and vascular plants, fungi, arthropods and vertebrates (Rothschild and Mancinelli, 2001; Jones, 2021). Therefore, and depending on the geological age and biological evolution over time, a similar diversity of taxonomic groups should be expected in fossil hydrothermal environments. As such, the fossil hydrothermal assemblage in the Sanagasta microbialites shows morphotypes with similarities to organisms belonging to the three domains: Bacteria, Archaea and Eukarya (Figures 4–13). The microbialites exhibit a great diversity of bacterial morphotypes, eukaryotic microorganisms ('protists') and microscopic remains of the large groups (plants, fungi and animals). Most microfossils are encrusted in sinterized microbialites (Figures 3, 4) and extraordinarily preserved in 3D with their original parts. Some specimens are interpreted as fossil agglutinations, organic precipitated cores and/or pellets. Furthermore, ubiquitous indeterminate microorganisms of intermediate size between bacteria and 'protists' are represented at the samples. Fossil microbial communities were observed incrusted into the interstices and microcavities of the host rock within poikilotopic silica, in between microbotryoids (Figures 3, 4).

4.2 'Prokaryotes' from SGP—bacteria and archaea

The hydrothermal rocks at SGP reveal a huge diversity 1–2 micron microbe morphotypes (Figures 5–7; Supplementary Figures S10-17), which coincide with the sizes and shapes of current prokaryotes. Fossil bacteria and archaea do not permit genetic comparisons for taxonomic assignment. However, the exceptional 3D preservation of the Sanagasta microfossils enables micromorphological comparisons with previously described forms and thermophilic bacteria and archaea inhabiting modern continental hot springs (e.g., Stetter, 1996; Reysenbach and Cady, 2001; Silva et al., 2021; Sriaporn et al., 2023). The fossil microbes recorded at Sanagasta exhibit high morphological diversity in shape, size, and organization, occurring as single cells, complex biofilms, or extensive microbial mats composed of multiple morphospecies and their silicified extracellular polymeric substances (EPS) (Figure 5; Supplementary Figures S10-S16; see EDS analyses). Microbial mats prominently develop on the surface of geyserite botryoids within microbialites. These botryoids are characterized by an intricate network of silica nanofibers interwoven with bacteria and microbial mats, which induced biosilicification (Figures 3H, 4C, D, G, 6B). The most abundant microbes are ~1-2 µm long, kidney-shaped bacterial morphotype, such as vibrio and bacillus (Figures 5–7; Supplementary Figures S11-S17). They number in the thousands per square millimeter, generally encapsulated and surrounded by a sheath-like envelope (Figures 5F, 7A). Cocci, diplococci (even encapsulated), staphylococci, and streptococci

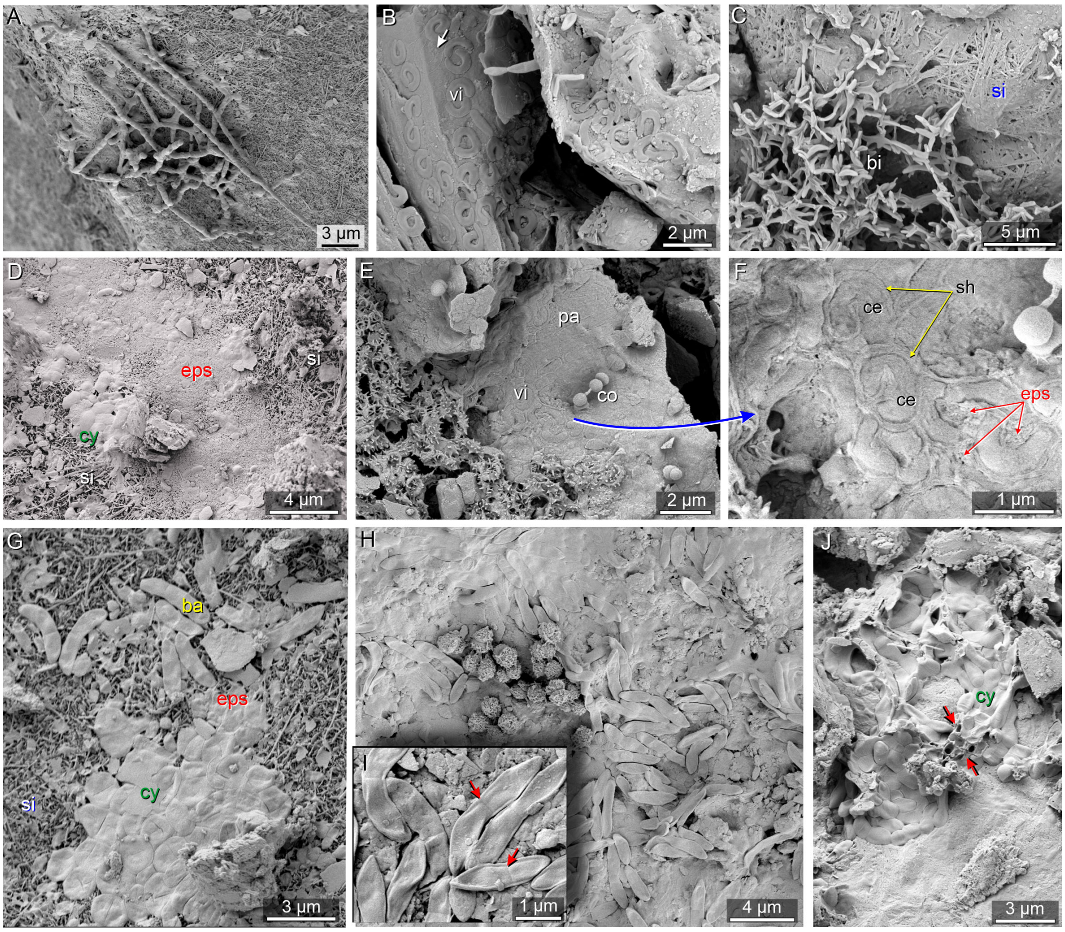

FIGURE 5
Fossil prokaryotes from the SGP. **(A)** *Phromidium*-like filamoentous cyanobacteria over amorphous fibrous silica matrix. **(B)** Accumulation of vibrios-together with some isolated actinomycetes-like forms; arrows indicate fully encrusted vibrios (magnify the image). **(C)** Dense colonies of tiny actinomycetes-like bifidobacteria over the fibrous botryoidal silica. **(D)** A diversity of several kind of prokariotes (including many cyanobacteria) on a silicified microbial mat. **(E)** Colony of bacteria growing on the encrusted remains of an arthropod's exoskeleton. **(F)** Magnification of E with encrusted vibrios-like bacteria showing encapsulated cells and cocci. **(G)** Silicified clusters of bacilli, diplobacilli and cyanobacteria over the fibrous silica of a botryoid. **(H)** A community of small, rounded cocci-like microbes, living on a high density of bacilli and diplobacilli partially encrusted on silica. **(I)** Cluster of partially entombed diplobacilli displaying extraordinary details of the cell wall and cytoplasmatic membrane; note the medial division between both bacilli -red arrows-. **(J)** Silicified community of cyanobacteria; some broken cells with their interior empty can be seen -red arrows-. ba, bacillus; bi, bifidobacteria; ce, cells; co, cocci and streptococci; cy, cyanobacteria; eps, silicified extracellular polymeric substances; pa, palisade; sh, sheath; si, silica; vi, vibrios.

are abundant in some microbiofacies of these microbialites; in some microfacies the cellular type with sarcinal morphology predominates. A similar pattern is observed with the bacillus group, presenting themselves individually, diplobacilli, streptobacilli, palisades-like configurations and complex nets of bacillus mats. Streptobacilli and filamentous bacteria occur mostly associated with fungi coating and other structures or fossil remains (e.g. over arthropods) (Figures 5E, F, 7C, Supplementary Figures). Some filamentous microbes which display broken transverse sections and show an open lumen of ~2 µm (Figures 5A, 6D), resemble to *Phormidium* and *Chloroflexus* (Jones et al., 2004a). Other micromorphologies are similar to *Bifidobacterium*, displaying typical branching features characterized by a Y-shaped morphology and hyphae-like structures (Figures 5C, 6A). As such, we noted very dense colonies of minute bacteria with an extensive type of mycelium present similar features to the Actinomycetota (the actinomycetes) or Myxococcota phylum (Figures 5B-C; Supplementary Figures S16d-S18c). Coccobacillus, ovate-shaped bacteria (e.g., cyanobacteria-like), characterized by binary division are superabundant and conspicuous in the MISS; *Cyanobacterium*-, *Gloeothece*-, *Cyanobium*-, *Synechococcus*-, *Cyanothece*-, and *Synechocystis*-like bacteria, and hydrogenothermaceae-like cells are abundant (Figures 5–7; Supplementary Figures S10-16). Many of these cyanobacteria form cell clusters in platelike colonies and display cell division with perpendicular binary fission -pinching-like- and someone slightly keritomized or markedly lengthwise-striated cell walls (Figure 6F; Supplementary Figure S16c). The striated cell walls of living cyanobacteria result from the parallel position of photosynthetically active thylakoid membranes that are surrounding the cytoplasm (Komárek, 2003). Some morphotypes, chiefly vibrios and cocci, encapsulated in silica, presenting cells with a polysaccharide-like capsule or sheath and an external biofilm-like

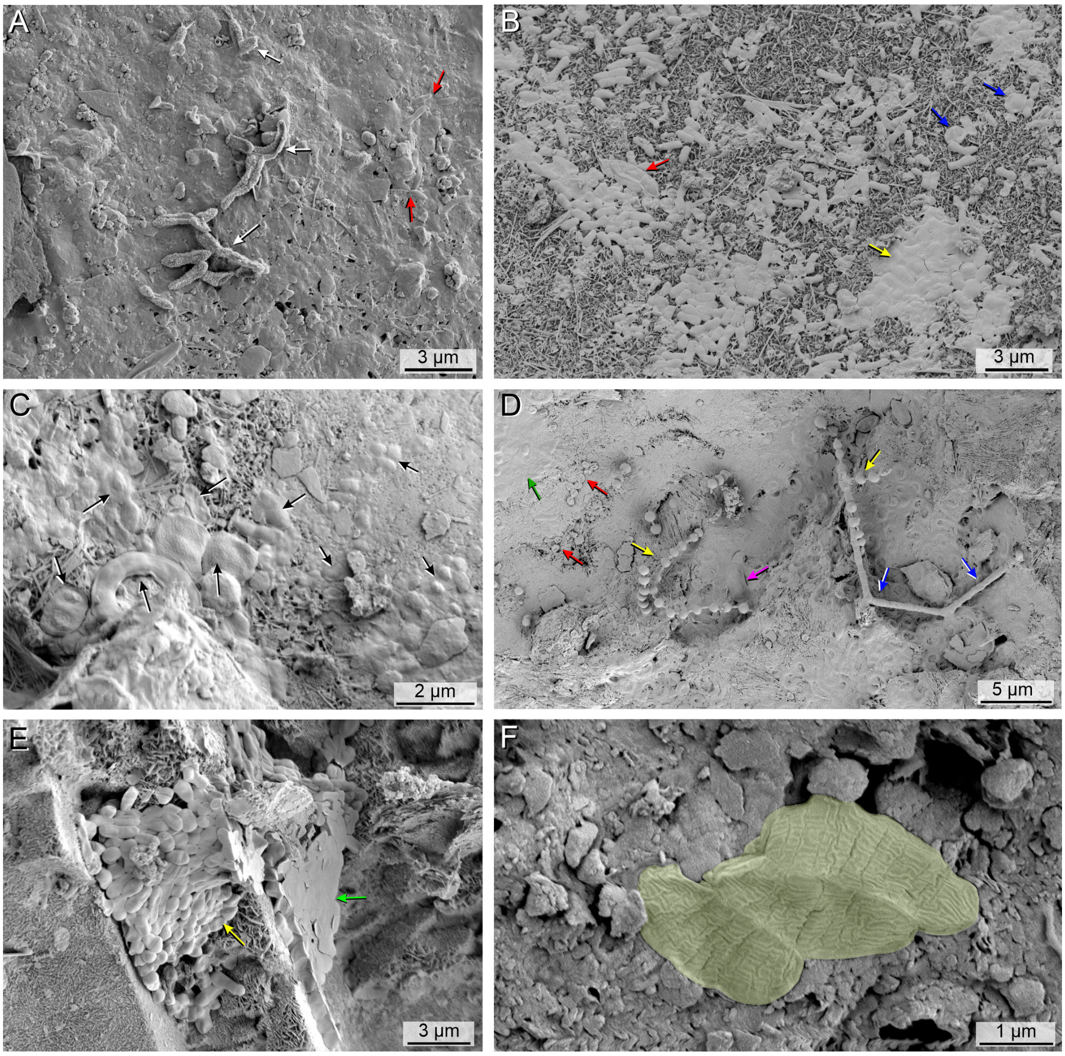

FIGURE 6
More prokaryotes from the SGP. **(A)** A tiny partially encrusted colony of actinomycetes-like bifidobacteria -white arrows- and some isolated diplobacilli -red arrows- (magnify the image). **(B)** Some isolated differentiated bacteria morphotypes -arrows- in association with a dense colony of diplobacilli over the amorphous fibrous silica. **(C)** High diversity of bacteria -arrows- over the fibrous silica. **(D)** Diversity of prokaryotes -arrows- over a community of vibrios-like bacteria on fibrous silica; note the chains of streptococci -yellow arrows-, *Pseudanabaena*-like filamentous bacteria -blue arrows-, large cyanobacteria -magenta arrow-, archaea-like forms -red arrows- and a dense microbial mat -green arrow-. **(E)** Silicified cyanobacteria microbial mats - yellow and green arrows- in a botryoid cavity; observe in the broken section -green arrow- the deep silicification with amorphous silica replacing completely the cells and their inner cytoplasm. **(F)** Artificial colored group of three large cyanobacteria with striated cell walls—keritomization.

matrix similar to the EPS (Stal, 2012). Comparable configurations of microbes and EPS have been described in modern hot spring sediments (Jones et al., 2003; Jones and Renaut, 2017; Jones, 2021; Sriaporn et al., 2023). Most fossil bacterial cells are smooth, however, there are few indeterminate microbial mats of bifidobacteria-like and biofilms with rough cells, as well as cells with distinct transversal and longitudinal ornamentation (Supplementary Figure S16c). The wall or capsule of some of the cells shows a dot and dimple ornamentation, while exhibiting a micronodular and granular/tuberculate sculpture (Figure 6A, Supplementary Figure S12). This appearance could be due to the deposition of opal nanospherules but also to nanostructures on the cytoplasmic membrane (e.g., pili, macromolecules, or bacteriophages). Partially silicified encrusted coccoidal morphologies form abundant thread-like or knobbed appendages joining cells in chains—putative F-pilus—suggesting bacterial conjugations (Figures 5E, I, 6D; Supplementary Figures S14-S16) (Patkowski et al., 2023). The conjugation is the transmission of plasmids that occur in bacteria and archaea (Catchpole et al., 2023). In addition to cyanobacteria, many microbes have the shapes and morphologies similar to the basal phyla Thermotogota and Aquificota, as well as with some basal archaea groups (e.g., *Pyrodictium* and *Thermoproteus*) typical from active geysers and modern hot spring environments (Figures 5H, 7F; Supplementary Figures S11, S16) (Stetter, 1996; Lalonde et al., 2005; Kysela et al., 2016). Some microbial mats show similarities with round flat and

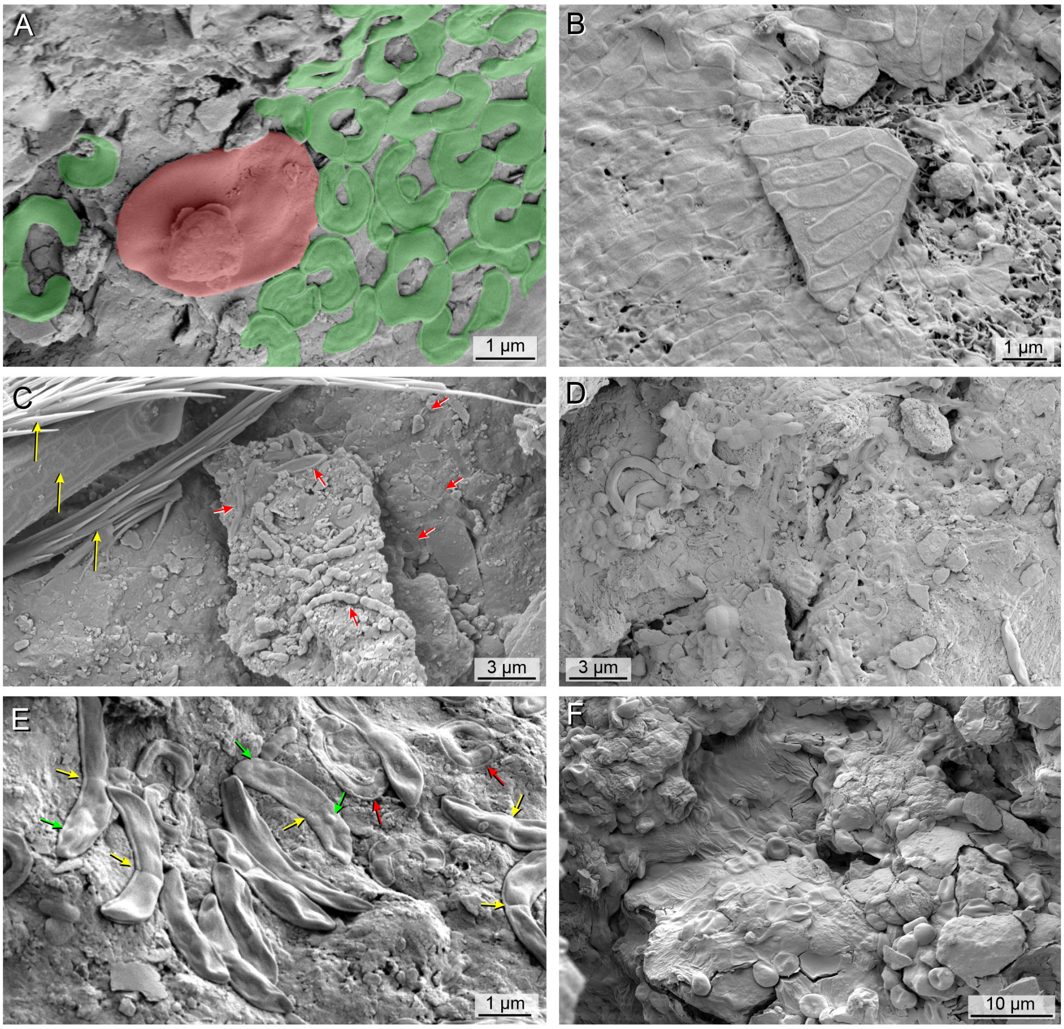

FIGURE 7
Association of prokaryotes from the SGP. **(A)** Some vibrios-like bacteria -green- showing encapsulated sheath cells associated with a large cell -in red- of a suggested red alga; artificial colored. **(B)** Dense monotypic community of bacteria in a palisade configuration over the fibrous silica. **(C)** Different types of bacteria -red arrows- near the remains of a partially encrusted mite -yellow arrows-. **(D)** Remarkable diversity of hundreds silicified bacteria with more than eight different morphotypes in almost 20 µm^2. **(E)** Some vibrios and diplobacilli with an extraordinary preservation; observe de sheath -red arrows-, cell division -yellow arrows-, and surface marks of possible internal organelles -green arrows-. **(F)** Dense microbial mats of alleged rounded monotypic archaea.

long palisades archaea (i.e., Sulfolobales, Desulfurococcales, Thermoproteales. Supplementary Figures S15, S16). The remarkable preservation of fossil alleged prokaryotes at the SGP renders the site globally unique, exhibiting an extensive and distinctive diversity of 3D cellular morphologies.

4.3 Eukaryotic microorganisms ('protists')

The origin, evolution and systematics of eukaryotes is extremely complex and a topic of scientific debates in recent years (Butterfield, 2015; Adl et al., 2019; Burki et al., 2020; Eme et al., 2023; Vosseberg et al., 2024; Kay et al., 2025; Porter et al., 2025; Williamson et al., 2025). Microbial eukaryotes are ubiquitous in many environments, yet their diversity in hot springs has not been comprehensively addressed (Oliverio et al., 2018; Rappaport and Oliverio, 2023, 2024). Only recently, the diversity and ecology of 'protists' have been summarized for extreme environments such as hot springs (Rappaport and Oliverio, 2023). Despite the vast diversity of prokaryotes, the eukaryotic microorganisms are also extremely abundant and diverse in some sections of the samples from the Sanagasta hydrothermal field (Figure 8, Supplementary Figure S18). There are some remarkable specimens associated with microremains of algae, arthropods, and prokaryotes that looks like lobosea amoeba of 5 to 10 µm (*Tubulinea*- or *Discosea*-like forms), sharing similar size, shape and structures (i.e., organelles, pseudopods) (Figure 8A). Indeterminate flat and circular non-ciliated 'protists' of approximately 25 µm in diameter, display structures similar to internal organelles; these microorganisms are also comparable to amoebas. Abundant remains of myxogastroid mold (Supplementary Figure S18D) were silicified and also recorded, covering large surfaces of some microbotryoids. These

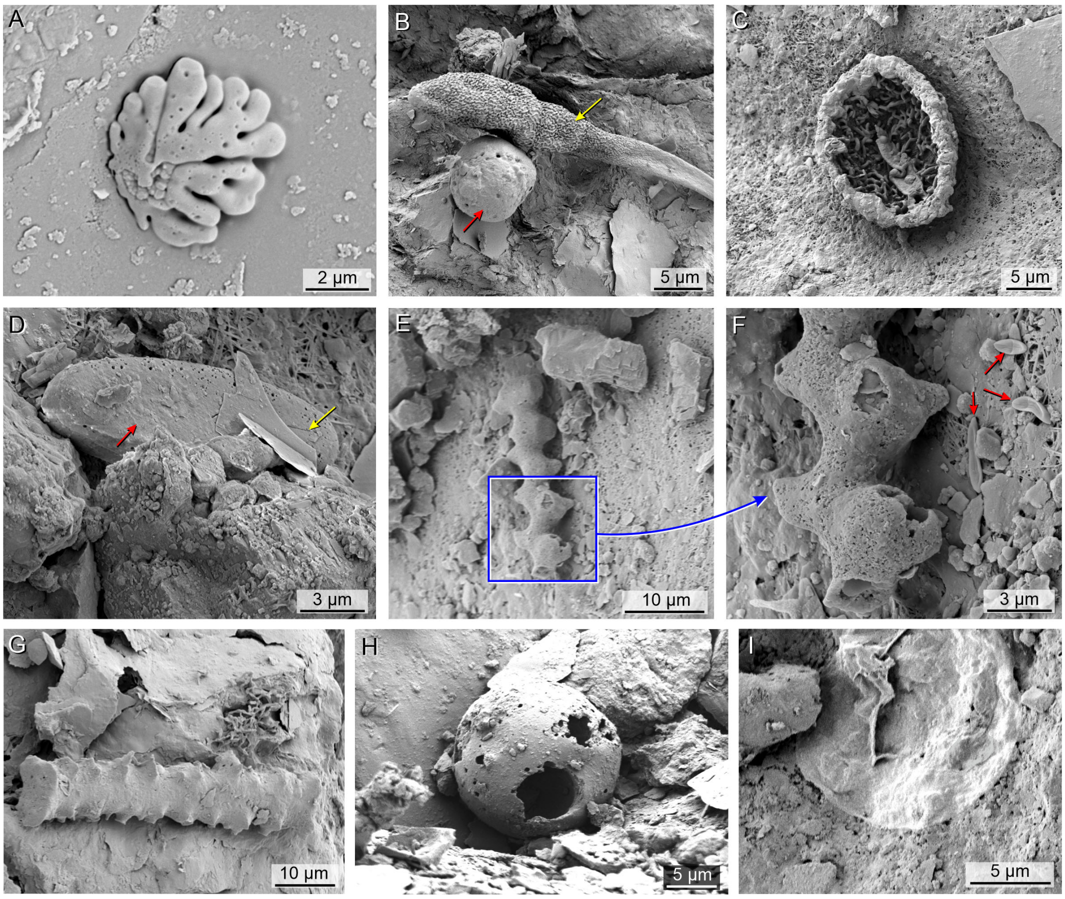

FIGURE 8
Fossil 'protists' from the SGP. **(A)** Silicified amoeba-like microbe. **(B)** Indeterminate eucaryotic parasite-like microbe -yellow arrow- and microcyst -red arrow-. **(C)** Indeterminate tiny microbe. **(D)** Extraordinary preserved raphid -yellow arrow- pennate diatom partially covered by silica -red arrow-. **(E-G)** Filamentous microthallos corresponding to silicified colonial-like chrysophytes; red arrows: bacteria. **(H)** Rounded stomatocysts -endogenous silicified cysts- of possible chrysophyte. **(I)** Rounded cell of cyanidial red algae or a myxoamoeba-like form.

specific microfacies exhibit various stages of the vegetative and reproductive cycle of myxomycetes, including minute myxoamoebozoan forms, protoplasmodia, plasmodia with pseudopodia, developing stipitate sporangia, and possibly mature sporangia containing spores and capillitia.

The rock samples display some between ~20 µm long parasite-like microbes showing an ornate, rough surface and a smooth apical end (Figure 8B); these tiny organisms are similar to some apicomplexan-like alveolates. There are other indeterminate ~15 µm in size, ribbon-like microorganisms (Supplementary Figure S22b) with a micro-reticulated sculpture on a smooth surface mixed with pellets and precipitated nucleus—many agglutinated microfossils. Some indeterminate prokaryote of ~5 µm in size possess an ornate external cell membrane with reticulated or nodose-globular surfaces. Many other microorganisms in the microbialite samples are currently undetermined and could be classified as basal eukaryotes (i.e., 'protists' grade) but they lack key features to assign them to a definite clade, Cryptophyte-, euglenid-, eustigmatophyceae- or alveolate-like microbes (Figures 8B, C; Supplementary Figures S18E, F). It is well established that high-temperature springs harbor substantial protist diversity (Oliverio et al., 2018; Adl et al., 2019; Rappaport and Oliverio, 2023), and the Cretaceous Sanagasta hydrothermal field appears to be no exception. This site reveals a remarkable variety of protists and may represent one of the most significant paleontological locations for the exceptional preservation of fossilized microeukaryotes. However, the observed diversity may be incomplete due to potential taphonomic and sampling biases, as well as the specific locations from which samples were collected. In particular, the documented microeukaryotic diversity at Sanagasta may be influenced by sampling limited to the proximal slope facies, despite the fact that geysers and hot springs are known to support distinct and diverse protistan communities (Rappaport and Oliverio, 2023).

4.4 Stramenopiles

4.4.1 Diatomista (Bacillariophyceae)

Diatoms are unicellular eukaryotic organisms, that live as solitary cells or in colonies, with unique external walls–frustule highly patterned consisting of two parts and composed of

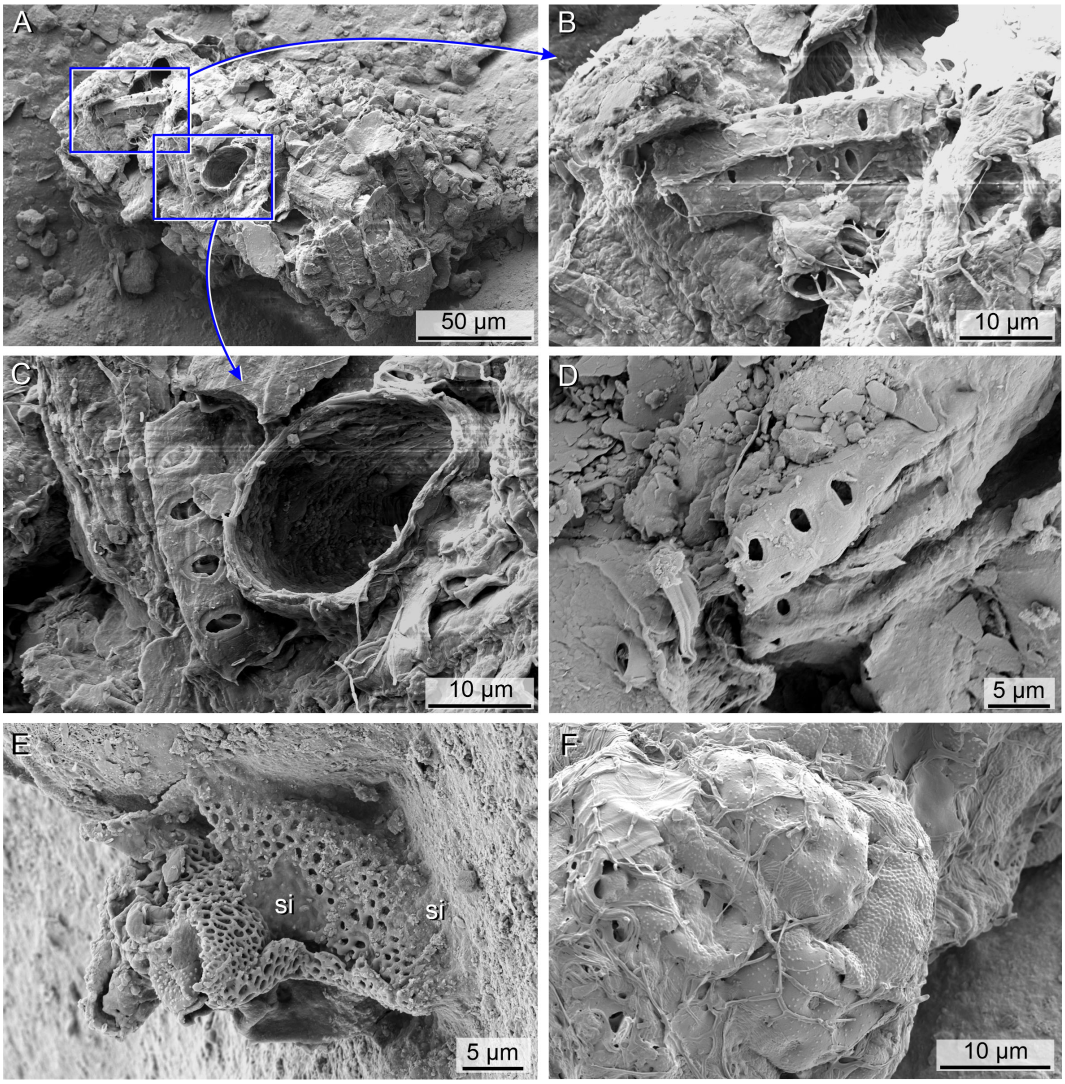

FIGURE 9
Some fossil plant remains from the SGP. **(A-D)** Several gymnosperm tracheids with characteristic areolated pits -secondary xylem elements- embedded in a pellet. **(E, F)** Angiosperm pollen grains encrusted in silica -si- displaying a fragmentary pollen grain with semitectate, columellate, microreticulate exine **(E)** and a periporate pollen grain with tectate and granulate exine **(F)**. Note the different hyphae and conindia that cover some tracheids and pollen surfaces.

amorphous silica [$(SiO2)n(H2O)$] (Brinkmann et al., 2011). They are photosynthetic, species-rich algae found in fresh and marine waters worldwide, and similarly in damp terrestrial habitats (Mann et al., 2017), and markedly diverse in continental hydrothermal environments (Owen et al., 2008; Brown et al., 2019). With enormous biases in the fossil record, diatoms first appeared in the Jurassic, diversified in the Early Cretaceous, and became abundant in the Cenozoic (Sims et al., 2006; Medlin, 2016; Mann et al., 2017; Westacott et al., 2021; Bryłka et al., 2023, 2024), while raphid diatoms emerged in the Paleocene (Medlin, 2016; Mann et al., 2017). However, in line with some Maastrichtian pennate diatoms from India (Singh et al., 2006), some authors suggest an earlier origin for these derived Bacillariophyta (Medlin, 2016; Bryłka et al., 2023, 2024). More interesting, Late Cretaceous -Maastrichtian- pennate diatoms from non-marine chert deposits from Mexico were reported (Beraldi-Campesi et al., 2015). Although showing large inconsistencies, molecular clocks suggest that diatoms originated near the Triassic–Jurassic boundary (Nakov et al., 2018; Bryłka et al., 2023). According to a recent pivotal study, the evolutionary history of diatoms may have been more complex than previously understood: pennate diatoms originated in the middle Jurassic, whereas raphid diatoms were already present by the middle Cretaceous (Alverson et al., 2025). Putative pennate diatoms at SGP were previously mentioned as diatomaceous matrix in thin sections (Fiorelli et al., 2012), but unverified with conclusive fossils (Figures 4C, D). Now we confirm here the presence of several species with remarkable exceptional preservation and the unequivocally oldest Late Cretaceous raphid diatoms record worldwide (Figure 8D; Supplementary Figures S18A, S19).

Overall, there are several broken fragments of diatoms partially entombed in the botryoidal silica, such as rod shape kind of

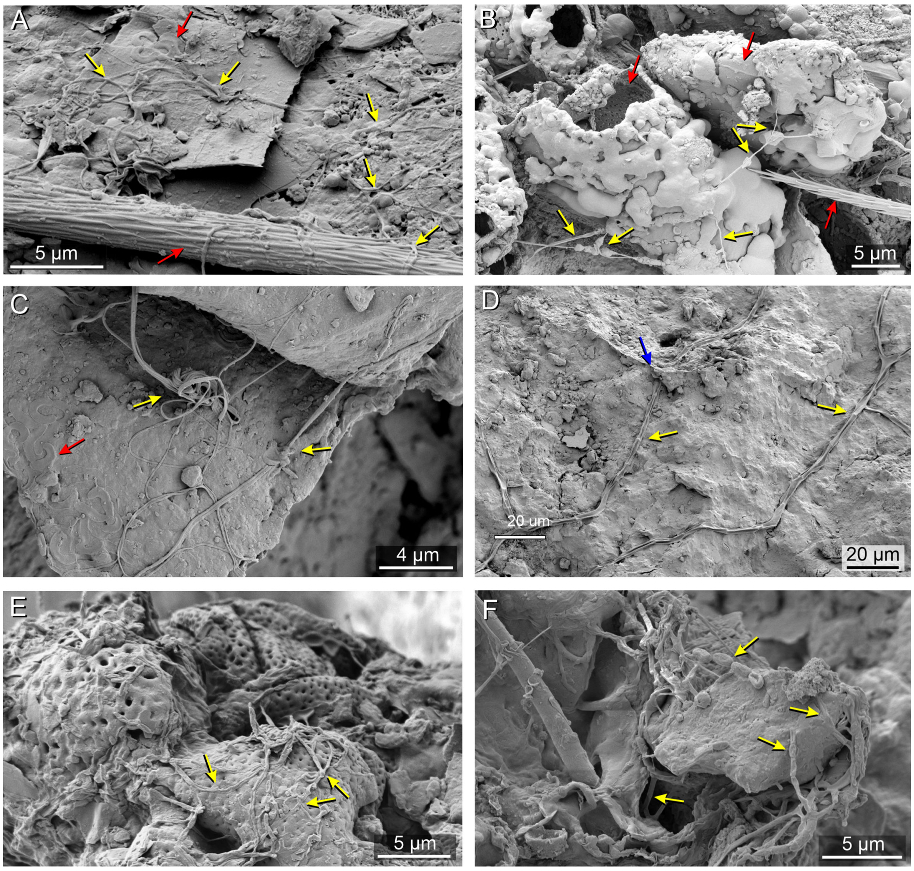

FIGURE 10
Fossil fungi from the SGP. **(A-C)** Very fine coenocytic hyphae with sparse branching -yellow arrows- belonging to Mucoromycotina clade that cover decomposing remains of arthropods and bacteria -red arrows-; note the fine partially encrusted hyphae -yellow arrows- and arthropod remains -red arrows- with fluorite (CaF_2) in **(B, D)** Large branched and septate hyphae -yellow arrows- partially cover by rock matrix -blue arrow-. **(E, F)** Larger and regularly septate hyphae of ascomycete fungi display branching as well as structures such as arthrospores and conidia -arrows-; these kinds of hyphae grow mainly on plant debris (pollens and tracheids).

rhizosoleniineae or raphid diatoms and also other associated araphid pennate fragments encrusted or agglutinated in pellets and precipitated cores. However, some nearly complete specimens display similar features to raphid pennate rhopalodiaceae and cymbellaceae diatoms with a typical areolae ornamentation. Most preserved diatom specimens are partially embedded in amorphous silica and measure between 5-10 µm, but some can reach up to 40 µm. The more diverse are generic diatom specimens with a raphe system medially placed quite similar to some genera of Naviculales such as *Pinnularia* and *Navicula* (Figure 8D), while others suggest a resemblance to *Planothidium*, *Craticula* or *Gomphonema*. Other specimens display a raphe laterally located that resemble *Nitzschia*. There are some elongated fragments that resembling *Aulacoseira* (Supplementary Figure S19). Besides, some remains display two lunate valves with an eccentric raphe, and a visible canal, positioned along the ventral margin and each branch is arched toward the dorsal margin, characteristic of rhopalodiaceae diatoms (Supplementary Figure S18A). Some of these specimens show both thecas and the cingulum well-preserved with their epitheca overlapping the hypotheca. Internally, in broken specimens, the epitheca displays large, transapical costae or fibulae and the internal raphe opens into a porate canal with circular holes. Several silicified bacteria can be observed encrusted in the frustule surfaces of various species. The sampled diatoms in SGP are not abundant but show considerable diversity, which may be biased by lateral variations in the paleohydrothermal microfacies. However, they show some resemblance to the diversity of diatoms in modern hydrothermal environments (Owen et al., 2008; Brown et al., 2019; Roy et al., 2020). The occurrence of these pennate diatoms in ~80 My old hydrothermal sediments has tremendous implications for the evolutionary history of Bacillariophyceae, which will be discussed later.

4.4.2 Chrysophyta algae

Hot springs discharge groundwater on the surface and form very diverse microhabitats in which many algal communities develop. Chrysophyceae are one of the most common groups of microalgae in freshwaters, including lakes, wetlands, streams, rivers and hot springs (Nicholls and Wujek, 2015; Kristiansen and Škaloud, 2017). Overall, the fossil record of chrysophytes is still quite incomplete and poorly understood; their evolutionary origin and diversification are mostly based on molecular clock calculations

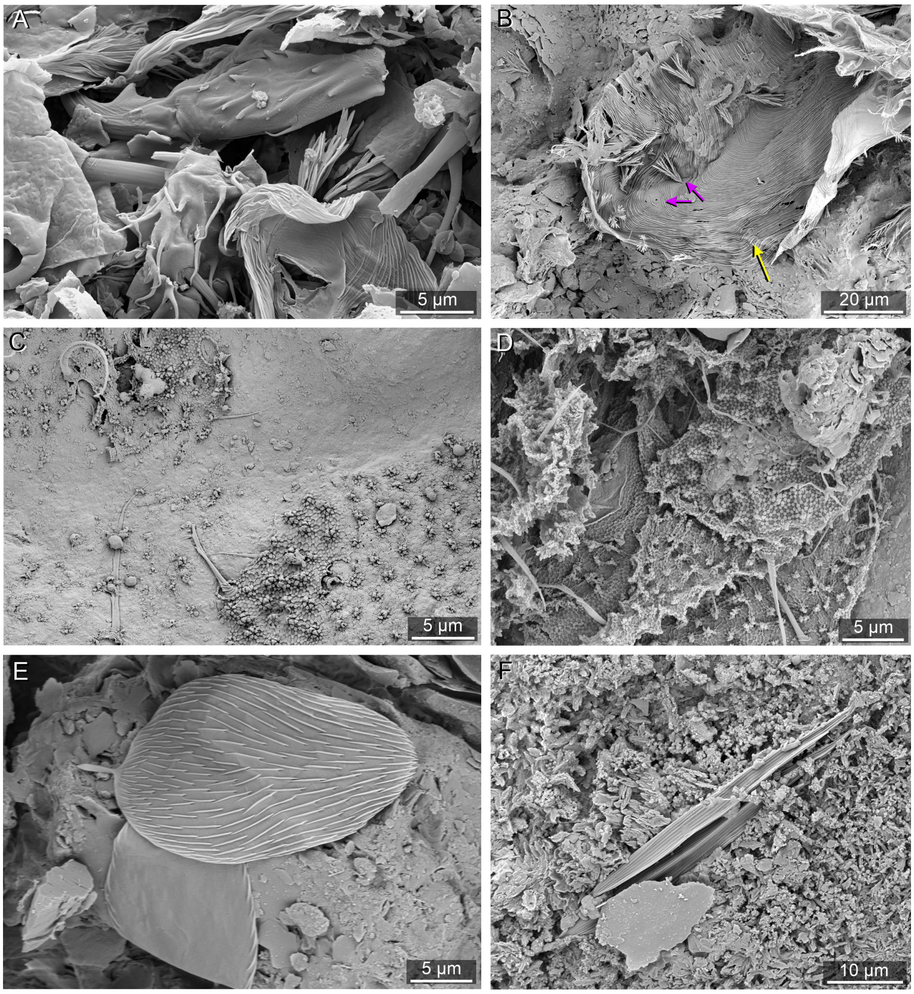

FIGURE 11
Fossil arthropods in 3D from the SGP. **(A)** Broken remains of an alleged mite. **(B)** Partially entombed broken exoskeleton of a mite, with the characteristic dorsal cuticle -yellow arrow-; note the plumose setae and pits -magenta arrows-. **(C)** Exoskeleton of a springtail heavily encrusted in silica displaying several articular setae over its particular hexagonal and superhydrophobic cuticular pattern. **(D)** Other section of the same springtail with their exoskeleton exposed and exhibiting exceptional preservation. **(E)** Two perfectly preserved springtail scales (next to the springtail in D). **(F)** Double setae of an indeterminate arthropod partially encrusted in carbonate and silica.

(Kristiansen and Škaloud, 2017). Although there is a record of fossil chrysophytes from the Paleogene inland environments, stomatocysts are known from lower Cretaceous marine sediments (Kristiansen and Škaloud, 2017; Channing and Wujek, 2010). Despite limited samples, several fragmentary algal remains have been recorded in the Sanagasta microbialite that most seemingly belong to the group of yellow-brown pigmented golden algae (Figures 8E-G; Supplementary Figure S18B). There are some fragmentary silicified colonial-like chrysophytes, such as encrusted filamentous microthalli that fits well with the colonial -*lorica*- protective forms, analogous in size and morphology with Dinobryaceae or Phaeothamniales (Nicholls and Wujek, 2015). These specimens resemble rarer *Epipyxis* or *Dinobryon*-like chrysophytes and display 10 to 15 μm-in-diameter thalli with an alternating structure, where single cells in cup-like shells were inserted. The sample also exhibits some rounded and isolated stomatocysts—endogenous silicified cysts with an average diameter of 20 μm. Cyst formation involves autogamic processes (fusion of nuclei formed by mitosis) or gametic fusion of cells of chrysophyte loricate colonies (Kristiansen and Škaloud, 2017). Other microremains of indeterminate calcareous algae are observed, even putatively desmidials and sphaeropleals green algae fragments agglutinated between pellets and precipitated cores. Like diatoms, these chrysophyte remains from the Sanagasta hydrothermal field shed light on the evolution and adaptation of the group to inland environments.

4.5 Archaeplastida

4.5.1 Rhodophyta—Cyanidiophyceae

Hot springs and acidic environments around the world are successfully inhabited by mixed communities of Cyanidiophyceae, a unique unicellular group of extremophilic rhodophyte red algae (Yoon et al., 2006; Hirooka et al., 2022; Cho et al., 2023; Rappaport and Oliverio, 2024). These photosynthetic eukaryotes are exclusive

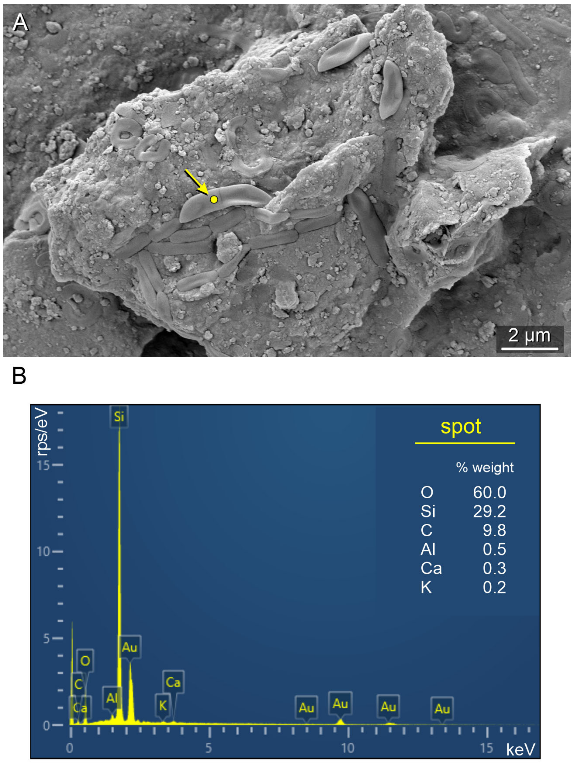

FIGURE 12
EDS analysis of the SGP microbialite. **(A)** The EDS analysis carried out on an encrusted bacterial community in the microbialite taken from the lower Cretaceous levels; the yellow arrow indicates the analyzed spot over a large diplobacilli. **(B)** Analysis result of the spot in A; despite the extraordinary preservation, observe the deep silicification of the microbes. See the Supplementary Data Sheet 1 for further EDS analysis on the Sanagasta samples.

to hot springs and capable of thriving in extreme pH conditions and high temperature (Cho et al., 2023; Van Etten et al., 2023). Furthermore, these extremophiles form biofilms in association with other extremophilic prokaryotes in the springs and can establish endolithic populations within the surrounding rocks (Van Etten et al., 2023).

Highly silicified microfacies of the SGP contain numerous fossilized unicellular microorganisms that bear a striking resemblance to Cyanidiophyceae red algae (Figures 7A, 8I; Supplementary Figures S18C, S20). In general, these fossil remains are associated with silicified biofilms of vibrios and bacilli and exhibit rounded cells with average diameters of 4 to 5 μm. Certain putative cyanidial cells on the silica nanofibers show ornamentations and notorious structures that may represent internal organelles of the cytoplasm, such as vacuoles, vesicles, nuclei, and/or mitochondria (Supplementary Figure S20). Other well-preserved cells display a rounded edge, a structure suggestive of the characteristic arrangement of internal single plastids and thylakoids in cyanidials. While there are several fossil records of red algae, including some representing the oldest known eukaryotes (Bengtson et al., 2017a), no fossilized cyanidials have been documented to date. These fossils from the Sanagasta hydrothermal field could thus represent the first and only fossil evidence of this distinctive group of extremophilic unicellular red algae.

4.5.2 Spermatophytes—plant remains

Although macroscopic plant specimens are common in modern hot spring environments due to a rapid silicification process (Channing and Edwards, 2009, ChanningEdwards, 2013), no macroscopic silicified plants are presently recorded at SGP (see Discussion) (Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012). However, few microfragmentary plant remains are now visible partially encrusted in amorphous silica or in pellets and organic precipitated cores; these plant remains consist essentially of two fossil types (Figures 9A-D; Supplementary Figures S21, S22, S25): isolated woody tracheary elements and pollen grains. Tracheids are observed singly or in pairs, and possess areolated pits, characteristic of secondary xylem elements of gymnosperms (Philippe, 1995; Boura et al., 2021) (Figures 9A-D; Supplementary Figure S21). Observed pits are uniseriate, circular to slightly flattened, and spaced (i.e., abietinean). A single fragment preserves contiguous flattened pits (i.e., araucarian), also showing a biseriate alternate disposition, which probably represents a different taxonomic group. Although fragmentary, the tracheid remains are well preserved also in 3D.

Fragmentary angiosperm pollen grains were also identified as part of pellet-like structures or partially encrusted in silica. They exhibit semitectate, columellate, and microreticulate exine, psilate muri and irregular to subcircular/subpolygonal lumina. One type of pollen grain, represented by several fragments, presents homobrochate reticulum and muri having widths similar or narrower than lumina (Figures 9E, F; Supplementary Figures S21, S22). Another morphotype, represented by a single fragment, presents a heterobrochate reticulum, with a lumina decreasing in size towards the periphery of the preserved element, and muri having widths typically wider than lumina (Figure 9E). In both types, the structure of the wall allows to recognize them as angiosperms, but their fragmentary preservation and the absence of apertures are challenging to formulate a more specific identification.

Other abundant angiosperm remains consist of periporate pollen grains with tectate, columellate, and granulate exine, with more than 20 pores circular or nearly (1-2 μm in diameter), regularly distributed over the whole surface, and having sculptured pore membranes (Figure 9F; Supplementary Figures S21A, B, S22). These pollen grains can be attributed to the genus *Chenopodipollis*, a taxon commonly interpreted as a representative of the Chenopodioidea of the Amaranthaceae, a plant clade typically present in dry, saline or disturbed habitats of both hemispheres (Kadereita et al., 2005). Chenopodioidea are recorded from the Upper Cretaceous strata (Nichols, 2002; Yoshino et al., 2017).

4.6 Opisthokont

4.6.1 Holomycota—fossil fungi

The fungal fossil record is meager compared to other major organism groups, making their evolutionary history challenging to

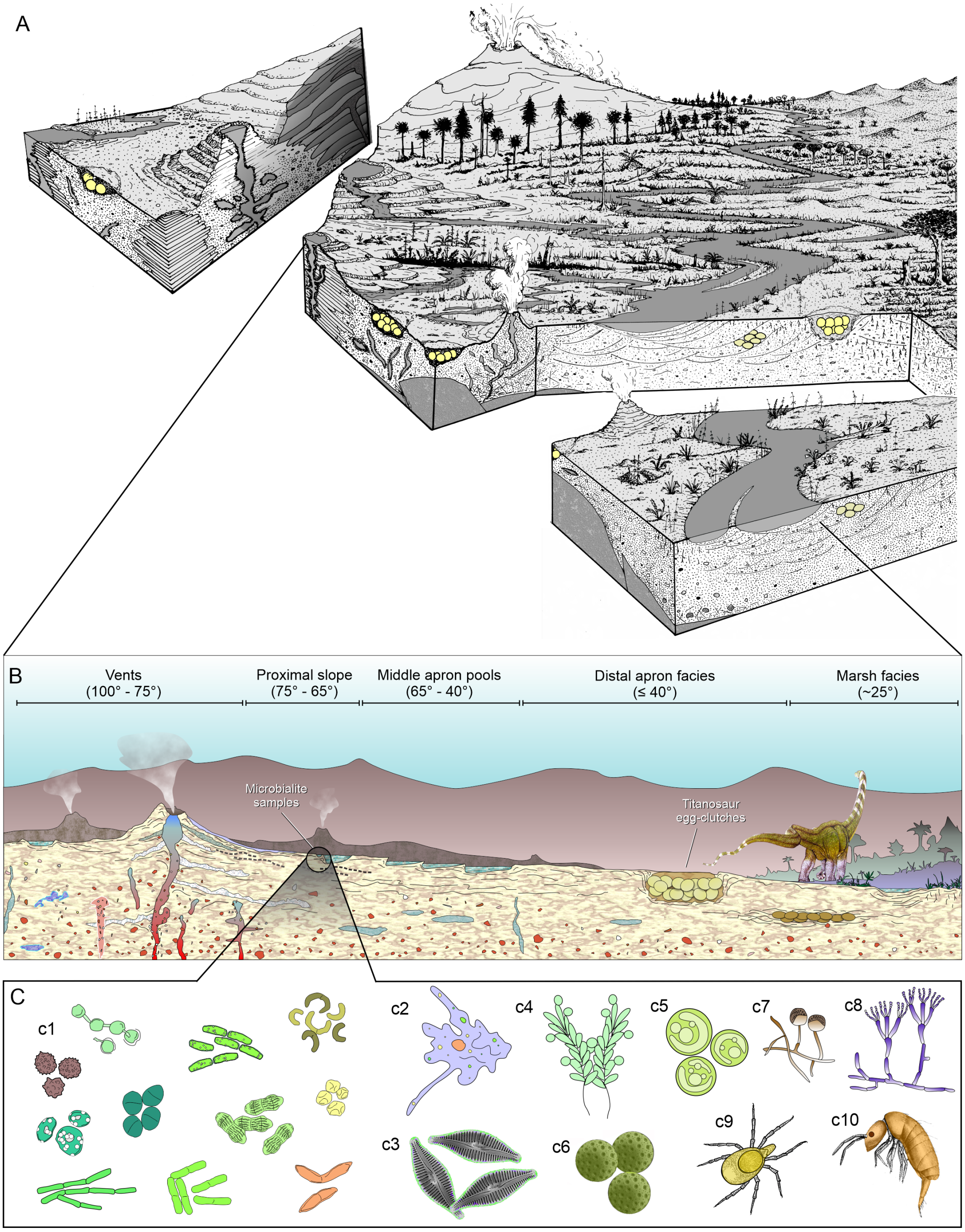

FIGURE 13
Schematic reconstruction of the fossil-*Lagerstätte* of Sanagasta and the titanosaur nesting site in the first Cretaceous inland geothermal field. **(A)** Detail of different nesting environments and nesting strategies of titanosaurs (modified from Hechenleitner et al., 2015). **(B)** Schematic cross-section reconstruction of the Sanagasta hot spring deposits showing different facies and localization of microbialites at proximal facies and titanosaur egg-clutches at distal facies (based on Campbell et al., 2015b). **(C)** Overview of the microcosmos recovery from the microbialite sample of the Sanagasta GeoPark, showing a high diversity of prokaryotes and a variety of eukaryotes: c1, some morphotypes of bacteria and archaea; c2, amoeba and myxamoeba; c3, diatoms; c4 and c5, golden and red algae; c6, plant remains; c7, mucoromycotine fungi; c8, dikaryan fungi; c9, mites; c10, springtails. Image not in scale.

reconstruct (Bengtson et al., 2017b; Loron et al., 2019; Gan et al., 2021). Fossil fungi from hydrothermal environments are even scarcer, documented only in the classic Devonian Rhynie Chert, known for its high diversity (Krings et al., 2017; Garwood et al., 2019; Strullu-Derrien et al., 2023), and the Late Jurassic Deseado Massif hot spring (Channing et al., 2007; García Massini et al., 2012; Campbell et al., 2015b). However, the SGP preserves numerous fungal specimens and hyphae of uncertain affinity (Figures 9, 10; Supplementary Figure S21). The hyphae occur over the microbotryoid surfaces between the interstices of the rock covering other decayed organic remains, on pellets, and are associated mostly with plants and arthropod exoskeletons. Two predominant hyphal morphotypes are observed: *i*) fine coenocytic hyphae (0.2 µm wide) with sparse branching, which could belong to the mucoromycotine clade because of their morphological characters and their putative saprophytic habit (Figures 10A-C); *ii*) another common morphotype in the specimens fits well with the morphological characters of ascomycete fungi (Figures 9, 10D-F): hyphae with regular septa (~0.5 µm wide), with abundant branching, resistance and dispersal structures such as arthrospores and asexual reproductive structures such as conidiophores and conidia (Figure 10F). The growth pattern of the fungal mycelia denotes their saprophytic habit on woody tracheids, pollen grains and arthropods (Supplementary Figure S21). Some of these fungi, in particular the mucoromycotines, could be entomopathogenic (Araújo and Hughes, 2016). It is important to mention that some species of hydrothermal mesophilic fungi can grow near pH 0 (Rothschild and Mancinelli, 2001).

4.6.2 Holozoa—extremophilic arthropods

Hydrothermal environments could represent an ecological refuge for plants and animals. Hot springs also preserve elements of the local ecosystem, chiefly arthropods that are usually abundant in mesophile hydrothermal environments such as insects that could tolerate temperatures up to 50°C and pH 2.5 (Pritchard, 1991; Williams, 1991; Rothschild and Mancinelli, 2001; Jones, 2021; Santos et al., 2022). Similarly, the SGP microbialitic samples display several arthropods partially encrusted in the siliceous matrix (Figures 10A-B, 11; Supplementary Figures S23, S24). In soil environments, the most abundant microarthropods groups are springtails (Hexapoda) and mites (Chelicerata: Arachnida) (Görres and Amador, 2021). Overall, the fossil mites and springtails are collapsed yet display a fine preservation with microscopic life-like cuticle structures (Figure 11). Mite specimens consist chiefly of parts of the main body exoskeleton (with the characteristic micromorphology of the dorsal cuticle composed of annuli having a whorl of microtubercles along them, typical of some mites) and partial fragments of articulated limb (tarsi and claw) (Supplementary Figure S23A). Cuticles unusually exhibit plumose setae and trichobothria (Figures 11A, B). With respect to springtails, we observe several encrusted integuments with a typical geometric pentagonal or hexagonal interconnect ridges pattern in addition to several cuticular outgrowth structures (i.e. setae and scales) (Figures 11C-E). This characteristic hexagonal cuticular pattern is exclusive of some hydrophobic exoskeleton of springtails (Hopkin, 1997; Gundersen et al., 2014) (Figures 11C, D; Supplementary Figure S23C). Isolated setae and hairs are also very commonly encrusted in the silica or covered by amorphous fluorite (Figure 10B; see Supplementary Data Sheet 1, Supplementary Figure S30). In wetland environments, like hot springs, mites primarily feed on fungi and plant debris, but may also consume small arthropods and nematodes. In contrast, springtails are omnivorous, feeding mainly on bacteria, fungi, nematodes, algae, and decaying plant material (Walter and Proctor, 2013; Görres and Amador, 2021).

4.6.3 Vertebrate—dinosaurs

The Sanagasta nesting site has yielded to date over 90 titanosaur egg clutches, some with up to 30 complete eggs, associated with hydrothermal structures at the geothermal field (Figure 2; Supplementary Figures S2, S5) (Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012, 2013). The nesting and reproduction of the Sanagasta titanosaur were well adapted to this particular hydrothermal paleoenvironment, by their egg, eggshell anatomy, pore system morphology, and the water vapor conductance (Grellet-Tinner et al., 2012; Hechenleitner et al., 2015, 2016a, 2018a; Leuzinger et al., 2021) Indeed, the eggshell displays several synchronous hydrothermal alterations, recrystallization of calcite and more notably silicification into opal (Fiorelli et al., 2012, 2013). The calcite recrystallization was produced by acidic hot spring solutions, while silicification is ubiquitous, recrystallizations indicate alterations under exceptional conditions mediated by cyanobacteria (Benning et al., 2005; Fiorelli et al., 2013). A few indeterminate bony fragments have been discovered at the main nesting site, unlike the numerous, partially articulated remains of several large dinosaurs found in other localities of the Los Llanos Formation (Hechenleitner et al., 2018b). These fossils seem to belong to a small, few meters long vertebrate, possibly a juvenile titanosaur dinosaur.

4.7 Pellets/precipitated cores

Fecal micropellets among other specimens are preserved in the microbialite (Figure 9A; Supplementary Figures S22, S25) partially encrusted in a silicate or carbonate matrix but always associated with fungal hyphae and bacterial biofilms. They were produced by micropredators and phytophagous–e.g. mites and springtails. These micropellets and other fossil organic remains form partially encrusted precipitated cores over the bothryoids of silica from the small cavities of the rock, as in hydrothermal settings, opal-A rapidly precipitates over organic remains, thus commonly produces well-preserved silicified biota (Jones, 2021).

5 Discussion

5.1 Sanagasta paleohydrothermal field: a *Fossil-Lagerstätte*

The discovery of titanosaur egg clutches in Sanagasta 20 years ago (Grellet-Tinner and Fiorelli, 2010) highlighted a monospecific, communal nesting site of paramount paleobiological interest. Subsequent studies suggest that these titanosaurs repeatedly utilized the Cretaceous Sanagasta hydrothermal site, where geothermal activity likely facilitated egg incubation, demonstrating a species specific adaptation and abaptation

(Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012, 2013; Grellet-Tinner et al., 2012; Hechenleitner et al., 2015, 2016a, 2018a; Leuzinger et al., 2021). Modern dinosaurs, like the megapode birds, nest in active geothermal environments and incubate their eggs by thermodynamics (Grellet-Tinner and Fiorelli, 2010; Hechenleitner et al., 2015). The Mesozoic dinosaurs at Sanagasta, like their modern counterparts (i.e., the endemic Polynesian megapode, *Megapodius pritchardii*, Göth and Vogel, 1997), chose specific nesting sites for ovideposition. Sanagasta titanosaurs used geothermalism to incubate their eggs through a low enthalpy geothermal system of tectonic origin without magmatic influence (Grellet-Tinner and Fiorelli, 2010; Hechenleitner et al., 2015; Leuzinger et al., 2021). Therefore, the appropriate selection of a nesting site becomes a critical factor for the species' reproduction and survival (Hechenleitner et al., 2015). That discovery represents the first confirmed symbiotic/commensalism relationship between Mesozoic dinosaur nesting behaviors and a geothermal field (Grellet-Tinner and Fiorelli, 2010; Fiorelli et al., 2012).

Terrestrial hot spring systems can support a highly diverse microbiota with potential exquisite taphononic and diagenetic preservations (Cady and Farmer, 1996; Rothschild and Mancinelli, 2001; Renaut and Jones, 2003; Yee et al., 2003; Benning et al., 2005; Des Marais and Walter, 2019; Jones and Renaut, 2021; Rasmussen et al., 2024). The biota in thermal ecosystems is fossilized in sinters and has been documented in the geological record in rocks dating back to 3.5 Ga (Pinti et al., 2009; Brasier et al., 2015; Djokic et al., 2017; Dodd et al., 2017; Des Marais and Walter, 2019). However, occurrences of paleo-hydrothermal geyserite settings preserving fossils are rare prior to the Cenozoic (Campbell et al., 2015b; Des Marais and Walter, 2019). A few exceptions are the Devonian Drummond Basin (Australia), the renowned Devonian Rhynie Cherts (Scotland), and the Late Jurassic Deseado Massif (Patagonia, Argentina) (Rice et al., 2002; Channing et al., 2007; Guido et al., 2010; Campbell et al., 2015b; Garwood et al., 2019). The Sanagasta GeoPark (La Rioja, NW Argentina) is therefore the first and only known Cretaceous hydrothermal inland environment to preserve a vast range of fossils with exceptional anatomical detail, confirmed by several microanalytic analyses (Figure 12; Supplementary Figures S26-30). This paleogeothermal field provides paramount information on fossil biota and the evolution of life in these ecosystems during the Mesozoic. In general, the hot springs are described as a 'tropical rainforest' of the fossil microbial world (Des Marais and Walter, 2019). Therefore, Sanagasta hydrothermal field provides a unique fossil record with one of the best-preserved micro- and nannofossils. Furthermore, the site harbors a microdiversity encompassing the three domains of life (Bacteria, Archaea, and Eukarya), preserving fossils of microbes, plants, and a diverse range of micro- and macroscopic fauna (Figure 12). Cretaceous hydrothermal paleofluids percolated into the interstices and microcavities of the host rock—in between microbotryoids, where these fossil microbial communities flourished.

Current challenges in the interpretation of microbial fossils arise from the dynamic nature of knowledge in taxonomy, phylogenetics, and genomics. Advances in genetic analyses and emerging technologies have substantially reshaped the classification of bacteria, archaea and basal eukaryotes, refined phylogenetic frameworks and expanded our understanding of their evolutionary histories (e.g., Hug et al., 2016; Castelle and Banfield, 2018; Weiss et al., 2018; Burki et al., 2020; Eme et al., 2023; Moody et al., 2024; Vosseberg et al., 2024; Kay et al., 2025; Porter et al., 2025; Williamson et al., 2025). The SGP demonstrates the highest documented morphodiversity of prokaryotes within an inland fossil deposit to date, with over 25 distinct and identified morphotypes in a single paleothermal microfacies (Supplementary Figure S17). Moreover, the site displays the best-preserved and most diverse fossil prokaryotes worldwide and many of these morphotypes show similarities to modern extremophile bacteria and archaea. The microbes, even the microalgae, preserve minute cell details, plasma membrane ornamentation, cell division, silicified EPS and biofilm with microbial mats, and possible cytoplasm's internal nanostructures, such as probable thylakoid membranes, vacuoles, and organelles. Thus, the micro-details of "prokaryotes" and "protists", microalgae (i.e., diatoms exquisitely preserved, alveolates, and cyanidials), plants, fungi and arthropods (with unique cuticle features) make Sanagasta GeoPark an exceptional site to understand their paleoecology. The fossilization features of this complex Late Cretaceous microecosystem, exclusive for a Phanerozoic deposit, bolster the previous hypothesis (Fiorelli et al., 2013) that the Sanagasta paleohydrothermal field represents an instance of *Konzentrat* and *Konservat Fossil-Lagerstätte* (according to the definition given by Kimmig and Schiffbauer, 2024). Fossil lagerstätten are among the most important windows into ancient ecosystems, representing deposits of exceptional preservation that provide both high quantity (*Konzentrat*) and high quality (*Konservat*) paleontological information (Seilacher et al., 1985; Allison, 1988; Shields, 1998; Muscente et al., 2017; Kimmig and Schiffbauer, 2024). Although in most Lagerstätten bacterial degradation works against exceptional preservation—particularly of soft tissues—(Allison and Briggs, 1993), in Sanagasta, bacteria actually promoted exceptional preservation through biosilicification (Fiorelli et al., 2013).

5.2 Processes and exceptional preservation in Sanagasta

Microbial activity can also lead to excellent preservation (Grellet-Tinner, 2005), provided that the rate of mineralization or stabilization exceeds that of tissue decomposition. In general, the Sanagasta microremains exhibit extensive silicification, which has replaced all microorganisms and even filled the interiors of their cells with amorphous silica (Figures 6A, 11). Cyanobacteria, a key group of phototrophic prokaryotes, play a pivotal role in silica polymerization, deposition, and sinter formation in geothermal environments (Jones et al., 2003; Phoenix et al., 1999, 2000, 2001; Toporski et al., 2002; Guidry and Chafetz, 2003; Jones and Renaut, 2021; Konhauser et al., 2003, 2004, 2008; Yee et al., 2003; Benning et al., 2004, 2005; Lalonde et al., 2005; Phoenix and Konhauser, 2008; Doi and Fujino, 2013; Ikeda, 2021; Jones, 2021). Silicification of sheathed cyanobacteria occurs as silica colloids accumulate on their impermeable sheath surfaces (Benning et al., 2004). This process is very rapid and begins during biofilm viability but progresses to cell death, lysis, and promotes immediate fossilization (Renaut et al., 1998; Phoenix et al., 2000). It incorporates microorganisms into the sintered structure as fossil microbial colonies and encrusts everything as the process progresses (Benning et al., 2004, 2005; Konhauser et al., 2004; Jones, 2021; Rasmussen et al., 2023, 2024). Notably, silica nanocolloids can preserve fine microfeatures, including cell wall pores and macromolecules (Benning et al., 2005; Rasmussen et al., 2023). As in SGP, active, lithified yet living microbial communities in modern hot springs are primarily composed of cyanobacteria, heterotrophic bacteria, and fungi (Rasmussen et al., 2024). Different microbial communities successively construct and inhabit silicified biofabrics over time and evolve throughout the lithification process and burial (Rasmussen et al., 2024). Similar geobiological processes observed in modern hot springs (Rothschild and Mancinelli, 2001; Benning et al., 2005; Konhauser et al., 2004; Jones, 2021; Rasmussen et al., 2023, 2024) likely contributed to siliceous sinter formation and microbial fossilization in the SGP (Figure 12) (see Fiorelli et al., 2012).

The conservation potential at Sanagasta is interesting, preserving remains mainly in SiO_2, but also $CaCO_3$ and CaF_2 casts are observed, generating encrustation on their surfaces and permineralization of tissues (Figure 12; Supplementary Figures S26-S30). Although flora is easily and rapidly silicified and preserved in hot springs environments, such as Yellowstone (Channing et al., 2007; Channing and Edwards, 2009), plant remains are scarce and very fragmentary—mostly in micropellets—at SGP. Several factors control the preservation of organisms in a hydrothermal environment, such as taphonomic biases or facies in the geothermal gradient—e.g. proximal slope, middle apron, etc (Channing et al., 2007; Fouke, 2011; Campbell et al., 2019; Jones, 2021). However, the paleoenvironment is key to understanding biases and particular preservations in SGP. During the Cretaceous, Sanagasta was under the influence of a semiarid climate regime (Basilici et al., 2017) and its ~80 My landscape was similar to the El Tatio hot springs in current days (Glennon and Pfaff, 2003; Ruff and Farmer, 2016) at the Atacama Desert in the high Andes, with poor Puna-type xerophytic low vegetation (Supplementary Figure S31). Independently, the presence of *Chenopodipollis* bolster this hypothesis of dry and disturbed habitats.

Our study provides insights into key aspects of continental evolutionary biology and their ecosystems. Certain groups dominate modern freshwater environments but have a scarce or absent fossil record prior to the Cretaceous, such as some basal eukaryotes or pennate diatoms (Sims et al., 2006; Medlin, 2016; Bryłka et al., 2024; Rappaport and Oliverio, 2024). However, the ~80-million-year-old Cretaceous hot springs at the SGP preserve several prokaryotic morphotypes and paleobiological features that have never been documented in the fossil record (e.g., vibrios, cellular nanostructures, etc.). Furthermore, there is a scarce fossil record of amoebas, myxomycetes and other protists, especially those preserved in 3D. Therefore, Sanagasta offers a valuable opportunity to further study these microorganisms, including the origin and diversification of certain groups. For instance, the Sanagasta hydrothermal field preserve the world's oldest known raphid pennate diatoms, thereby providing invaluable evidence regarding the evolutionary trajectory of this group (Medlin, 2016). The occurrence of pennate diatom remains from the Cretaceous of Sanagasta is unequivocal. Although well preserved, these remains are partially fragmented—owing to both sample preparation and diagenetic processes—and are embedded within amorphous silica and calcite and overlain by silicified bacteria. These inherent characteristics, in conjunction with the geological context, the synchronicity with paleohydrothermal activity, and the assemblage of associated microfossils and macrofossils—i.e., dinosaur eggs, substantiate their late Cretaceous age. The evolutionary history of pennate diatoms is far from resolved, currently facing intense debate with numerous gaps and ghost lineages (Sims et al., 2006; Brinkmann et al., 2011; Medlin, 2016; Mann et al., 2017; Westacott et al., 2021; Bryłka et al., 2024). According to some authors, pennate diatoms first appeared in the fossil record during the late Cretaceous—Maastrichtian about 70 million years ago (Sims et al., 2006; Beraldi-Campesi et al., 2015), although others estimated their appearance much earlier (Alverson et al., 2025). Subsequently, raphid diatoms have emerged, leading to their significant diversification into freshwater environments (Brinkmann et al., 2011). Some researchers suggest that the apparent abundance of diatoms in the late Cretaceous sedimentary record might be influenced by variations in preservation potential, as well as the availability and recycling of silica (Westacott et al., 2021). Nevertheless, the discovery of world's oldest raphid pennate diatoms in this late Cretaceous hot spring implies reconsidering the evolution, diversification and the conquest of inland aquatic ecosystems by the Bacillariophyceae. As such, thermal environments could have been key in the rise of derived raphid diatoms.

The chrysophyte cysts are resistant siliceous structures present in older sediments and common in geological deposits (Kristiansen and Škaloud, 2017). However, and alike to diatoms, the oldest chrysophytes fossils are stomatocysts from lower Cretaceous marine sediments (Harwood and Gersonde, 1990; Kristiansen and Škaloud, 2017). Therefore, the chrysophyte remains from the Sanagasta hydrothermal field are the world's oldest record from inland environments, hence this site played a key and transcendent role in their early continental evolution and adaptation. Despite Sanagasta remains, the fossil record of chrysophytes is very incomplete and poorly understood. Likewise, the putative cyanidiophycea reported here could represent the only fossils of this peculiar group of extremophilic unicellular red algae (Hirooka et al., 2022).

Although sparse, the plant remains from Sanagasta are well-preserved (e.g., tracheids and pollen) and have significant paleoecological and evolutionary implications. For example, the oldest records to date of pollen grains of Chenopodioidea are typically Maastrichtian (Kadereita et al., 2005), although reported from slightly older assemblages (Philippe, 1995). Thus, the pollen grains of *Chenopodipollis* from SGP represent the world's oldest unequivocal record of Chenopodioidea. Regarding Holomycota, and similar to the Rhynie Chert (Krings et al., 2017; Garwood et al., 2019; Strullu-Derrien et al., 2023), SGP preserves abundant silicified fungal hyphae remains; however, at Sanagasta, the fossils are preserved in 3D inside botryoidal microcavities. This exceptional preservation of fungal hyphae, including all their flawlessly recognizable structures—from the stipe to the conidia, is highly significant for paleobiological and evolutionary studies of Fungi. The SGP arthropods are particularly remarkable, by featuring abundant fossil remains of mites and springtails. Interestingly, fossil mites have also been documented in the Rhynie paleohydrothermal environment (Garwood et al., 2019), in several amber deposits (Sidorchuk, 2018; Klimov et al., 2021; Arillo et al., 2022), and are known to inhabit modern hot springs—i.e., Thermacaridae (Heron and Sheffield, 2016). Instead, there is a single documented occurrence of springtails in hydrothermal environments, where their distinctive exoskeletons were initially misinterpreted as those of mites or insects (Bonny and Jones, 2008). Fossil specimens are mostly known from amber (Robin et al., 2019). Therefore, the springtails from the Devonian Rhynie Chert and the SGP represent the only known fossil records of hydrothermal springtails worldwide to date.

6 Conclusion

The dinosaur nesting site of Sanagasta (Grellet-Tinner and Fiorelli, 2010) has provided a unique glimpse into a novel Cretaceous hydrothermal terrestrial ecosystem (Figure 13). Featuring partially preserved thermal paleostructures and in-between titanosaur egg clutches, the Sanagasta GeoPark exposes sinterized microfacies that are highly conducive to the preservation of fossil life in an extreme paleoenvironment. As a result, it harbors some of the most exceptionally well-preserved and taxonomically diverse microfossils known worldwide, including numerous bacteria, archaea, and a wide array of eukaryotes. Instead of assigning definitive taxonomic labels, our study highlights the immense potential of organic diversity to challenge and refine our understanding of the history of life and its evolutionary pathways. The Sanagasta GeoPark bridges a gap in the record of Phanerozoic geothermal fields, playing a key role in understanding the evolution of extremophile communities. Advancements in microscopic observations and technologies along with future explorations promise more interesting discoveries in this extremophile paleosite. In line with Margulis's concept of a symbiotic planet (Margulis, 1998), Sanagasta exhibits a symbiotic structure of micro- and macrobiology rooted in the past and their interaction between the biosphere and geosphere (Fiorelli et al., 2012). Its complex and intricate fossilized ecosystem embodies an *autopoietic* unity (Maturana, 1975)—a hallmark of life's capacity for self-organization and self-sustainment. A comprehensive paleoecosystemic approach is crucial to understanding the geo-biological interactions and survival strategies of this paleoecosystem within this challenging Cretaceous environment. This perspective encourages further exploration of fossil microbial life and extremophiles at geothermal sites, with implications extending beyond Earth.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

LF: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Validation, Writing – original draft. CW: Formal analysis, Investigation, Methodology, Validation, Writing – original draft. JT: Formal analysis, Investigation, Methodology, Validation, Writing – original draft. IA: Formal analysis, Investigation, Methodology, Validation, Writing – original draft. CR: Formal analysis, Investigation, Methodology, Validation, Writing – original draft. MS: Formal analysis, Investigation, Methodology, Writing – original draft. VP: Formal analysis, Investigation, Methodology, Validation, Writing – original draft. EV: Formal analysis, Investigation, Methodology, Validation, Writing – original draft. JC: Formal analysis, Investigation, Methodology, Writing – original draft. EH: Data curation, Investigation, Methodology, Validation, Writing – original draft. GG-T: Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Validation, Writing – original draft.

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Conflict of interest

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References

Adl, S. M., Bass, D., Lane, C. E., Lukeš, J., Schoch, C. L., Smirnov, A., et al. (2019). Revisions to the classification, nomenclature, and diversity of Eukaryotes. *J. Eukaryot. Microbiol.* 66, 4–119. doi: 10.1111/jeu.12691

Allison, P. A. (1988). Konservat-lagerstätten: cause and classification. *Paleobiology* 14, 331–344. doi: 10.1017/S0094837300012082

Allison, P. A., and Briggs, D. E. G. (1993). Exceptional fossil record: distribution of soft-tissue preservation through the Phanerozoic. *Geology* 21, 527–530. doi: 10.1130/0091-7613(1993)021%3C0527:EFRDOS%3E2.3.CO;2

Alverson, A. J., Roberts, W. R., Ruck, E. C., Nakov, T., Ashworth, M. P., Bryłka, K., et al. (2025). Phylogenomics reveals the slow-burning fuse of diatom evolution. *Proc. Natl. Acad. Sci. U.S.A.* 18, e2500153122. doi: 10.1073/pnas.2500153122

Araújo, J. P. M., and Hughes, D. P. (2016). "Chapter One - Diversity of entomopathogenic fungi: which groups conquered the insect body?," in *Advances in genetics volume 94: genetics and molecular biology of entomopathogenic fungi*. Eds. B. Lovett and R. J. Leger (Amsterdam, Netherlands: Elsevier Inc), 1–39. doi: 10.1016/bs.adgen.2016.01.001

Arillo, A., Subías, L. S., and Álvarez-Parra, S. (2022). First fossil record of the oribatid family Liacaridae (Acariformes: Gustavioidea) from the lower Albian amber-bearing site of Ariño (eastern Spain). *Cret. Res.* 131, 105087. doi: 10.1016/j.cretres.2021.105087

Basilici, G., Hechenleitner, E. M., Fiorelli, L. E., Dal Bó, P. F., and Mountney, N. P. (2017). Preservation of titanosaur egg clutches in Upper Cretaceous cumulative paleosols (Los Llanos Formation, La Rioja, Argentina). *Paleogeogr. Paleoclimatol. Paleoecol.* 482, 83–102. doi: 10.1016/j.paleo.2017.05.034

Bengtson, S., Rasmussen, B., Ivarsson, M., Muhling, J., Broman, C., Marone, F., et al. (2017b). Fungus-like mycelial fossils in 2.4-billion-year-old vesicular basalt. *Nat. Ecol. Evol.* 1, 141. doi: 10.1038/s41559-017-0141

Bengtson, S., Sallstedt, T., Belivanova, V., and Whitehouseal, M. (2017a). Three-dimensional preservation of cellular and subcellular structures suggests 1.6 billion-year-old crown-group red algae. *PloS Biol.* 15, e2000735. doi: 10.1371/journal.pbio.2000735

Benning, L. G., Phoenix, V., and Mountain, B. W. (2005). "Biosilicification: the role of cyanobacteria in silica sinter deposition," in *Micro-organisms and earth systems - advances in Geomicrobiology*. Ed. G. M. Gadd (Cambridge University Press, UK), 131–150. doi: 10.1017/CBO9780511754852.008

Benning, L. G., Phoenix, V. R., Yee, N., and Konhauser, K. O. (2004). The dynamics of cyanobacterial silicification: an infrared micro-spectroscopic investigation. *Geochim. Cosmochim. Ac.* 68, 743–757. doi: 10.1016/S0016-7037(03)00488-5

Beraldi-Campesi, H., Mann, D. G., and Cevallos-Ferriz, S. R. S. (2015). Life cycle of 70 Ma-old non-marine pennate diatoms. *Cret. Res.* 56, 662–672. doi: 10.1016/j.cretres.2015.07.004

Bonny, S. M., and Jones, B. (2008). Petrography and textural development of inorganic and biogenic lithotypes in a relict barite tufa deposit at Flybye Springs, NT, Canada. *Sedimentology* 55, 275–303. doi: 10.1111/j.1365-3091.2007.00899.x

Boura, A., Bamford, M., and Philippe, M. (2021). Promoting a standardized description of fossil tracheidoxyls. *Rev. Paleobot. Palynol.* 295, 104525. doi: 10.1016/j.revpalbo.2021.104525

Brasier, M. D., Antcliffe, J., Saunders, M., and Wacey, D. (2015). Changing the picture of Earth's earliest fossils (3.5–1.9Ga) with new approaches and new discoveries. *Proc. Natl. Acad. Sci. U.S.A.* 112, 4859–4864. doi: 10.1073/pnas.1405338111

Brinkmann, N., Friedl, T., and Mohr, K. I. (2011). "Diatoms," in *Encyclopedia of geobiology*. Eds. J. Reitner and V. Thiel (Springer, Dordrecht), 326–330. doi: 10.1007/978-1-4020-9212-1_74

Brock, T. D. (1985). Life at high temperatures. *Science* 230, 132–138. doi: 10.1126/science.230.4722.132

Brown, S. R., and Fritz, S. C. (2019). Eukaryotic organisms of continental hydrothermal systems. *Extremophiles* 23, 367–376. doi: 10.1007/s00792-019-01101-y

Brown, S. R., Fritz, S. C., Morgan, L. A., and Shanks, I. I. I. (2019). Fossilized diatoms of siliceous hydrothermal deposits in Yellowstone National Park, USA. *Diatom Res.* 34, 193–204. doi: 10.1080/0269249X.2019.1698466

Bryłka, K., Alverson, A. J., Pickering, R. A., Richoz, S., and Conley, D. J. (2023). Uncertainties surrounding the oldest fossil record of diatoms. *Sci. Rep.* 13, 8047. doi: 10.1038/s41598-023-35078-8

Bryłka, K., Richoz, S., Alverson, A. J., and Conley, D. J. (2024). Looking for the oldest diatoms. *Mar. Micropaleontol.* 190, 102371. doi: 10.1016/j.marmicro.2024.102371

Burki, F., Roger, A. J., Brown, M. W., and Simpson, A. G. B. (2020). The new tree of Eukaryotes. *Trends Ecol. Evol.* 35, 43–55. doi: 10.1016/j.tree.2019.08.008

Butterfield, N. J. (2015). Early evolution of the eukaryota. *Paleontology* 58, 5–17. doi: 10.1111/pala.12139

Cady, S. L., and Farmer, J. D. (1996). "Fossilization processes in siliceous thermal springs: trends in preservation along thermal gradients," in *Evolution of hydrothermal systems on Earth (and Mars)?*Eds. G. R. Bock and J. A. Goode (West Sussex, England: Chichester Wiley), 150–153.

Campbell, K. A., Guido, D. M., Gautret, P., Foucher, F., Ramboz, C., and Westall, F. (2015b). Geyserite in hot-spring siliceous sinter: Window on Earth's hottest terrestrial (paleo)environment and its extreme life. *Earth-Sci. Rev.* 148, 44–64. doi: 10.1016/j.earscirev.2015.05.009

Campbell, K. A., Guido, D. M., John, D. A., Vikre, P. G., Rhys, D., and Hamilton, A. (2019). The Miocene Atastra Creek sinter (Bodie Hills volcanic field, California and

Nevada): 4D evolution of a geomorphically intact siliceous hot spring deposit. *J. Volcanol. Geoth. Res.* 370, 65–81. doi: 10.1016/j.jvolgeores.2018.12.006

Campbell, K. A., Lynne, B. Y., Handley, K. M., Jordan, S., Farmer, J. D., Guido, D. M., et al. (2015a). Tracing biosignature preservation of geothermally silicified microbial textures into the geological record. *Astrobiology* 15, 858–882. doi: 10.1089/ast.2015.1307

Castelle, C. J., and Banfield, J. F. (2018). Major new microbial groups expand diversity and alter our understanding of the Tree of Life. *Cell* 172, 1181–1197. doi: 10.1016/j.cell.2018.02.016

Catchpole, R. J., Barbe, V., Magdelenat, G., Marguet, E., Terns, M., Oberto, J., et al. (2023). A self-transmissible plasmid from a hyperthermophile that facilitates genetic modification of diverse Archaea. *Nat. Microbiol.* 8, 1339–1347. doi: 10.1038/s41564-023-01387-x

Carignano, A. P., Hechenleitner, E. M., and Fiorelli, L. E. (2013). Hallazgo de ostrácodos (Crustacea) Cretácicos continentales en laFormación Los Llanos, localidad de Tama, La Rioja. *Ameghiniana* 50(Supl.), R39.

Channing, A., and Edwards, D. (2009). Silicification of higher plants in geothermally influenced wetlands: Yellowstone as a Lower Devonian Rhynie analog. *Palaios* 24, 505–521. doi: 10.2110/palo.2008.p08-131r

Channing, A., and Edwards, D. (2013). Wetland megabias: ecological and ecophysiological filtering dominates the fossil record of hot spring floras. *Paleontology* 56, 523–556. doi: 10.1111/pala.12043

Channing, A., Schweitzer, M. H., Horner, J. R., and McEneaney, T. (2005). A silicified bird from Quaternary hot spring deposits. *Proc. R. Soc B* 272, 905–911. doi: 10.1098/rspb.2004.2989

Channing, A., and Wujek, D. E. (2010). Preservation of protists within decaying plants from geothermally influenced wetlands of Yellowstone National Park, Wyoming, United States. *Palaios* 25, 347–355. doi: 10.2110/palo.2009.p09-057r

Channing, A., Zamuner, A. B., and Zúñiga, A. (2007). A new Middle–Late Jurassic flora and hot spring chert deposit from the Deseado Massif, Santa Cruz province, Argentina. *Geol. Mag.* 144, 401–411. doi: 10.1017/S0016756807003263

Cho, C. H., Park, S. I., Huang, T. Y., Lee, Y., Ciniglia, C., Yadavalli, H. C., et al. (2023). Genome-wide signatures of adaptation to extreme environments in red algae. *Nat. Commun.* 14, 10. doi: 10.1038/s41467-022-35566-x

Colman, D. R., Jay, Z. J., Inskeep, W. P., Jennings, R. deM., Maas, K. R., Rusch, D. B., et al. (2016). Novel, deep-branching heterotrophic bacterial populations recovered from thermal spring metagenomes. *Front. Microbiol.* 7, 304. doi: 10.3389/fmicb.2016.00304

Colman, D. R., Lindsay, M. R., Amenabar, M. J., and Boyd, E. S. (2019). The intersection of geology, geochemistry, and microbiology in continental hydrothermal systems. *Astrobiology* 19, 1–18. doi: 10.1089/ast.2018.2016

Cowan, D., Tuffin, M., Mulako, I., and Cass, J. (2012). "Terrestrial hydrothermal environments," in *Life at extremes: environments, organisms and strategies for survival*, vol. 12 . Ed. E. M. Bell(Cabi, England: Cabi Digital Library), 219–241.

De Sosa Tomas, A., Carignano, A. P., Fiorelli, L. E., and Hechenleitner, E. M. (2017). Carófitas del Cretácico Tardío de laFormación Los Llanos, La Rioja. Reporte preliminar. *V Jornadas de Las Ciencias de La Tierra Dr. Eduardo Musacchio*, 34–36.

Des Marais, D., and Walter, M. R. (2019). Terrestrial hot spring systems: Introduction. *Astrobiology* 19, 1419–1432. doi: 10.1089/ast.2018.1976

Di Giulio, M. (2003). The universal ancestor and the ancestor of bacteria were hyperthermophiles. *J. Mol. Evol.* 57, 721–730. doi: 10.1007/s00239-003-2522-6

Djokic, T., Van Kranendonk, M., Campbell, K., Walter, M. R., and Ward, C. R. (2017). Earliest signs of life on land preserved in ca. 3.5 Ga hot spring deposits. *Nat. Commun.* 8, 15263. doi: 10.1038/ncomms15263

Dodd, M. S., Papineau, D., Grenne, T., Slack, J. F., Rittner, M., Pirajno, F., et al. (2017). Evidence for early life in Earth's oldest hydrothermal vent precipitates. *Nature* 543, 60–64. doi: 10.1038/nature21377

Doi, K., and Fujino, Y. (2013). "Biomineralization in geothermal environments," in *Thermophilic microbes in environmental and industrial biotechnology: biotechnology of thermophiles*. Eds. T. Satyanarayana, J. Littlechild and Y. Kawarabayasi (Springer, Dordrecht), 233–247. doi: 10.1007/978-94-007-5899-5_8

Eme, L., Tamarit, D., Caceres, E. F., Staris, C. E., De Anda, V., Schön, M. E., et al. (2023). Inference and reconstruction of the heimdallarchaeial ancestry of eukaryotes. *Nature* 618, 992–999. doi: 10.1038/s41586-023-06186-2

Farmer, J. D. (2000). Hydrothermal systems: doorways to early biosphere evolution. *GSA Today* 10, 1–9.

Ferris, F. G., Beveridge, T. J., and Fyfe, W. S. (1986). Iron-silica crystallite nucleation by bacteria in a geothermal sediment. *Nature* 320, 609–611. doi: 10.1038/320609a0

Fiorelli, L. E., Grellet-Tinner, G., Alasino, P. H., and Argañaraz, E. (2012). The geology and paleoecology of the newly discovered Cretaceous neosauropod hydrothermal nesting site in Sanagasta (Los Llanos Formation), La Rioja, northwest Argentina. *Cret. Res.* 35, 94–117. doi: 10.1016/j.cretres.2011.12.002

Fiorelli, L. E., Grellet-Tinner, G., Argañaraz, E., and Salgado, L. (2013). Taphonomy of the neosauropod nesting site from Sanagasta (La Rioja, Argentina): exceptional preservation in a Cretaceous hydrothermal paleoenvironment. *Ameghiniana* 50, 389–406. doi: 10.5710/AMGH.15.11.2012.523

Fiorelli, L. E., Leardi, J. M., Hechenleitner, E. M., Pol, D., Basilici, G., and Grellet-Tinner, G. (2016). A new Late Cretaceous crocodyliform from the western margin of Gondwana (La Rioja Province, Argentina). *Cret. Res.* 60, 194–209. doi: 10.1016/j.cretres.2015.12.003

Fouke, B. W. (2011). Hot-spring Systems Geobiology: abiotic and biotic influences on travertine formation at Mammoth Hot Springs, Yellowstone National Park, USA. *Sedimentology* 58, 170–219. doi: 10.1111/j.1365-3091.2010.01209.x

Fouke, B. W., Farmer, J. D., Des Marais, D. J., Pratt, L., Sturchio, N. C., Burns, P. C., et al. (2000). Depositional facies and aqueous–solid geochemistry of travertine depositing hot springs (Angel Terrace, Mammoth Hot Springs, Yellowstone National Park, U.S.A.). *J. Sediment. Res.* 70, 565–585. doi: 10.1306/2DC40929-0E47-11D7-8643000102C1865D

Gan, T., Luo, T., Pang, K., Zhou, C., Zhou, G., Wan, B., et al. (2021). Cryptic terrestrial fungus-like fossils of the early Ediacaran Period. *Nat. Commun.* 120, 641. doi: 10.1038/s41467-021-20975-1

García Massini, J. F., Channing, A., Guido, D. M., and Zamuner, A. B. (2012). First report of fungi and fungus-like organisms from Mesozoic hot springs. *Palaios* 27, 55–62. doi: 10.2110/palo.2011.p11-076r

Garwood, R. J., Oliver, H., and Spencer, A. R. T. (2019). An introduction to the Rhynie chert. *Geol. Mag.* 157, 47–64. doi: 10.1017/S0016756819000670

Glennon, J. A., and Pfaff, R. M. (2003). The extraordinary thermal activity of El Tatio Geyser Field, Antofagasta Region, Chile. *GOSA Trans.* 8, 31–78.

Gogarten, J., and Deamer, D. (2016). Is LUCA a thermophilic progenote? *Nat. Microbiol.* 1, 16229. doi: 10.1038/nmicrobiol.2016.229

Gong, J., Munoz-Saez, C., Wilmeth, D. T., Myers, K. D., Homann, M., Arp, G., et al. (2022). Morphogenesis of digitate structures in hot spring silica sinters of the El Tatio geothermal field, Chile. *Geobiology* 20, 137–155. doi: 10.1111/gbi.12471

Görres, J. H., and Amador, J. A. (2021). "The soil fauna," in *Principles and applications of soil microbiology*. Eds. T. J. Gentry, J. F. J. Fuhrmann and D. A. Zuberer (Amsterdam, Netherlands: Elsevier), 191–212.

Göth, A., and Vogel, U. (1997). Egg laying and incubation of the Polynesian Megapode. *Annu. Rev. World Pheasant Assoc.*, 43–54.

Grellet-Tinner, G. (2005). The membrana testacea of titanosaurid dinosaur eggs from Auca Mahuevo (Argentina): implications for the exceptional preservation of soft tissue in Lagerstätten. *J. Vert. Paleontol.* 25, 99–106. doi: 10.1671/0272-4634(2005)025[0099:MTOTDE]2.0.CO;2

Grellet-Tinner, G., and Fiorelli, L. E. (2010). A new Argentinean nesting site showing neosauropod dinosaur reproduction in a Cretaceous hydrothermal environment. *Nat. Commun.* 1, 32. doi: 10.1038/ncomms1031

Grellet-Tinner, G., Fiorelli, L. E., and Salvador, R. B. (2012). Water vapor conductance of the Lower Cretaceous dinosaurian eggs from Sanagasta, La Rioja, Argentina: paleobiological and paleoecological implications for South American faveoloolithid and megaloolithid eggs. *Palaios* 27, 35–47. doi: 10.2110/palo.2011.p11-061r

Guido, D. M., Channing, A., Kampbell, K. A., and Zamuner, A. (2010). Jurassic geothermal landscapes and fossil ecosystems at San Agustín, Patagonia, Argentina. *J. Geol. Soc Lon.* 167, 11–20. doi: 10.1144/0016-76492009-109

Guidry, S. A., and Chafetz, H. S. (2003). Anatomy of siliceous hot springs: examples from Yellowstone National Park, Wyoming, USA. *Sediment. Geol.* 157, 71–106. doi: 10.1016/S0037-0738(02)00195-1

Gundersen, H., Leinaas, H. P., and Thaulow, C. (2014). Surface structure and wetting characteristics of collembola cuticles. *PloS One* 9, e86783. doi: 10.1371/journal.pone.0086783

Harwood, D. M., and Gersonde, R. (1990). Lower Cretaceous diatoms from ODP Leg 113, Site 693 (Weddell Sea). Part 2: Resting spores, chrysophycean cysts, endoskeletal dinoflagellates, and notes on the origin of diatoms. *Proc. Ocean Drill. Progr. Sci. Res.* 113, 403–426.

Hechenleitner, E. M., Fiorelli, L. E., Grellet-Tinner, G., Leuzinger, L., Basilici, G., Taborda, J. R. A., et al. (2016b). A new Upper Cretaceous titanosaur nesting site from La Rioja (NW Argentina), with implications for titanosaur nesting strategies. *Paleontology* 59, 433–446. doi: 10.1111/pala.12234

Hechenleitner, E. M., Fiorelli, L. E., Martinelli, A. G., and Grellet-Tinner, G. (2018b). Titanosaur dinosaurs from the Upper Cretaceous of La Rioja province, NW Argentina. *Cret. Res.* 85, 42–59. doi: 10.1016/j.cretres.2018.01.006

Hechenleitner, E. M., Grellet-Tinner, G., and Fiorelli, L. E. (2015). What do giant titanosaur dinosaurs and modern Australasian megapodes have in common? *PeerJ* 3, e1341. doi: 10.7717/peerj.1341

Hechenleitner, E. M., Grellet-Tinner, G., Foley, M., Fiorelli, L. E., and Thompson, M. B. (2016a). Micro-CT scan reveals an unexpected high-volume and interconnected pore network in a Cretaceous Sanagasta dinosaur eggshell. *J. R. Soc Interface* 13, 20160008. doi: 10.1098/rsif.2016.0008

Hechenleitner, E. M., Taborda, J. R. A., Fiorelli, L. E., Grellet-Tinner, G., and Nuñez Campero, S. R. (2018a). Biomechanical evidence suggests extensive eggshell thinning during incubation in the Sanagasta titanosaur dinosaurs. *PeerJ* 6, e4971. doi: 10.7717/peerj.4971

Heron, J., and Sheffield, C. (2016). First Canadian record of the water mite Thermacarus nevadensis Marshall 1928 (Arachnida: Acariformes: Hydrachnidiae:

Thermacaridae) from hot springs in British Columbia.*Biodiv. Data J.* 4, e9550. doi: 10.3897/BDJ.4.e9550

Hirooka, S., Itabashi, T., Ichinose, T. M., Onuma, R., Fujiwara, T., Yamashita, S., et al. (2022). Life cycle and functional genomics of the unicellular red alga Galdieria for elucidating algal and plant evolution and industrial use. *Proc. Natl. Acad. Sci. U.S.A.* 119, e2210665119. doi: 10.1073/pnas.2210665119

Hopkin, S. P. (1997). *Biology of springtails (Insecta: collembola)* (New York: Oxford University Press), 340.

Hug, L. A., Baker, B. J., Anantharaman, K., Brown, C. T., Probst, A. J., Castelle, C. J., et al. (2016). A new view of the tree of life. *Nat. Microbiol.* 1, 16048. doi: 10.1038/nmicrobiol.2016.48

Ikeda, T. (2021). Bacterial biosilicification: a new insight into the global silicon cycle. *Biosci. Biotech. Bioch.* 85, 1324–1331. doi: 10.1093/bbb/zbab069

Iniesto, M., Buscalioni, A. D., Guerrero, M. C., Benzerara, K., Moreira, D., and López-Archilla, A. I. (2016). Involvement of microbial mats in early fossilization by decay delay and formation of impressions and replicas of vertebrates and invertebrates. *Sci. Rep.* 6, 25716. doi: 10.1038/srep25716

Jiménez Velandia, H., Ezcurra, M. E., Hechenleitner, E. M., Basilici, G., Martinelli, A. G., and Fiorelli, L. E. (2025). A new Late Cretaceous abelisauroid species from La Rioja province, Northwestern Argentina. *Ameghiniana* 62, 1–23. doi: 10.5710/AMGH.24.09.2025.3653

Jones, B. (2021). Siliceous sinters in thermal spring systems: review of their mineralogy, diagenesis, and fabrics. *Sediment. Geol.* 413, 105820. doi: 10.1016/j.sedgeo.2020.105820

Jones, B., Konhauser, K. O., Renaut, R. W., and Wheeler, R. (2004a). Microbial silicification in Iodine Pool, Waimangu Geothermal area, North Island, New Zealand: implications for recognition and identification of ancient silicified microbes. *J. Geol. Soc Lon.* 161, 983–993. doi: 10.1144/0016-764903-172

Jones, B., and Renaut, R. W. (1996). Influence of thermophilic bacteria on calcite and silica precipitation in hot springs with water temperatures above 90°C: evidence from Kenya and New Zealand. *Can. J. Earth Sci.* 33, 72–83. doi: 10.1139/e96-008

Jones, B., and Renaut, R. W. (2003). Hot spring and geyser sinters: the integrated product of precipitation, replacement, and deposition. *Can. J. Earth Sci.* 40, 1549–1569. doi: 10.1139/e03-078

Jones, B., and Renaut, R. W. (2011). "Hot springs and geysers," in *Encyclopedia of geobiology*. Eds. J. Reitner and V. Thiel (Springer, Dordrecht), 447–479. doi: 10.1007/978-1-4020-9212-1_103

Jones, B., and Renaut, R. W. (2017). Modern travertine precipitation at Lýsuhóll hot springs, Snæfellnes, Iceland: implications for calcite crystal growth. *J. Sediment. Res.* 87, 1121–1114. doi: 10.2110/jsr.2017.61

Jones, B., and Renaut, R. W. (2021). Multifaceted incremental growth of a geyser discharge apron – Evidence from Geysir, Haukadalur, Iceland. *Sediment. Geol.* 419, 105905. doi: 10.1016/j.sedgeo.2021.105905

Jones, B., Renaut, R. W., and Konhauser, K. O. (2005). Genesis of large siliceous stromatolites at Frying Pan Lake, Waimangu geothermal field, North Island, New Zealand. *Sedimentology* 52, 1229–1252. doi: 10.1111/j.1365-3091.2005.00739.x

Jones, B., Renaut, R. W., and Rosen, M. R. (1997). Biogenicity of silica precipitation around geysers and hot-spring vents, North Island, New Zealand. *J. Sediment. Res.* 67, 88–104. doi: 10.1306/D42684FF-2B26-11D7-8648000102C1865D

Jones, B., Renaut, R. W., and Rosen, M. R. (1998). Microbial biofacies in hot-spring sinters: a model based on Ohaaki Pool, North Island, New Zealand. *J. Sediment. Res.* 68, 413–434. doi: 10.2110/jsr.68.413

Jones, B., Renaut, R. W., and Rosen, M. R. (2003). Silicified microbes in a geyser mound: the enigma of low-temperature cyanobacteria in a high-temperature setting. *Palaios* 18, 87–109. doi: 10.1669/0883-1351(2003)18<87:SMIAGM>2.0.CO;2

Jones, B., Renaut, R. W., and Rosen, M. R. (2004b). Taxonomic fidelity of silicified microbes from hot spring systems in the Taupo Volcanic Zone, North Island, New Zealand. *Earth Env. Sci. T. R. Soc* 94, 475–483. doi: 10.1017/S0263593300000821

Kadereita, G., Gotzek, D., Jacobs, S., and Freitag, H. (2005). Origin and age of Australian chenopodiaceae. *Org. Div. Evol.* 5, 59–80. doi: 10.1016/j.ode.2004.07.002

Kay, C. J., Spang, A., Szöllősi, G. J., Pasini, D., Williams, T. A., and Donoghue, P. C. J. (2025). Dated gene duplications elucidate the evolutionary assembly of eukaryotes. *Nature*, 1–12. doi: 10.1038/s41586-025-09808-z

Kázmierczak, J., and Kremer, B. (2002). Thermal alteration of the Earth's oldest fossils. *Nature* 420, 477–478. doi: 10.1038/420477b

Kimmig, J., and Schiffbauer, J. D. (2024). A modern definition of Fossil-Lagerstätten. *Trends Ecol. Evol.* 39, 621–624. doi: 10.1016/j.tree.2024.04.004

Klimov, P. V., Vorontsov, D. D., Azar, D., Sidorchuk, E. A., Braig, H. R., Khaustov, A. A., et al. (2021). A transitional fossil mite (Astigmata: Levantoglyphidae fam. n.) from the early Cretaceous suggests gradual evolution of phoresy-related metamorphosis. *Sci. Rep.* 11, 15113. doi: 10.1038/s41598-021-94367-2

Komárek, J. (2003). "Coccoid and colonial cyanobacteria," in *Freshwater algae of north america*. Eds. R. G. Sheath and J. D. Wehr (Elsevier, Amsterdam), 59–116. doi: 10.1016/B978-012741550-5/50004-0

Konhauser, K. O., Jones, B., Phoenix, V. R., Ferris, F. G., and Renaut, R. W. (2004). The microbial role in hot spring silicification. *Ambio* 33, 552–558. doi: 10.1579/0044-7447-33.8.552

Konhauser, K. O., Jones, B., Reysenbach, A. L., and Renaut, R. W. (2003). Hot Spring sinters: keys to understanding Earth's earliest life forms. *Can. J. Earth Sci.* 40, 1713–1724. doi: 10.1139/e03-059

Konhauser, K. O., Lalonde, S. V., and Phoenix, V. R. (2008). Bacterial biomineralization: Where to from here? *Geobiology* 6, 298–302. doi: 10.1111/j.1472-4669.2008.00151.x

Krings, M., Harper, C. J., and Taylor, E. L. (2017). Fungi and fungal interactions in the Rhynie chert: a review of the evidence, with the description of *Perexiflasca tayloriana* gen. et sp. nov. *Phil. Trans. R. Soc Lond.* 373, 20160500. doi: 10.1098/rstb.2016.0500

Kristiansen, J., and Škaloud, P. (2017). "Chrysophyta," in *Handbook of the protists*. Eds. J. M. Archibald, A. G. B. Simpson and C. H. Slamovits (Springer, Cham), 331–366. doi: 10.1007/978-3-319-28149-0_43

Kysela, D. T., Randich, A. M., Caccamo, P. D., and Brun, Y. V. (2016). Diversity takes shape: understanding the mechanistic and adaptive basis of bacterial morphology. *PloS Biol.* 14, e1002565. doi: 10.1371/journal.pbio.1002565

Lalonde, S. V., Konhauser, K. O., Reysenbach, A. L., and Ferris, F. (2005). The experimental silicification of Aquificales and their role in hot spring sinter formation. *Geobiology* 3, 41–52. doi: 10.1111/j.1472-4669.2005.00042.x

Leuzinger, L., Bernasconi, S. M., Vennemann, T., Luz, Z., Vonlanthen, P., Ulianov, A., et al. (2021). Life and reproduction of titanosaurians: Isotopic hallmark of mid-paleolatitude eggshells and its significance for body temperature, diet, and nesting. *Chem. Geol.* 583, 120452. doi: 10.1016/j.chemgeo.2021.120452

Liesegang, M., and Gee, C. T. (2020). Silica entry and accumulation in standing trees in a hot-spring environment: cellular pathways, rapid pace and fossilization potential. *Paleontology* 63, 651–660. doi: 10.1111/pala.12480

López-García, P., Philippe, H., Gail, F., and Moreira, D. (2003). Autochthonous eukaryotic diversity in hydrothermal sediment and experimental microcolonizers at the Mid-Atlantic Ridge. *Proc. Nat. Ac. Sci. U.S.A.* 100, 697–702. doi: 10.1073/pnas.0235779100

Loron, C. C., François, C., Rainbird, R. H., Turner, E. C., Borensztajn, S., and Javaux, E. J. (2019). Early fungi from the Proterozoic era in Arctic Canada. *Nature* 570, 232–235. doi: 10.1038/s41586-019-1217-0

Mann, D. G., Crawford, R. M., and Round, F. E. (2017). "Bacillariophyta," in *Handbook of the protists*. Eds. J. Archibald, A. Simpson and C. Slamovits (Springer, Cham), 205–266. doi: 10.1007/978-3-319-28149-0_29

Margulis, L. (1998). *Symbiotic planet: A new look at evolution* (New York: Basic Books), 176.

Maturana, H. R. (1975). The organization of the living: a theory of the living organization. *Int. J. Man-mach. Stu.* 7, 313–332. doi: 10.1016/S0020-7373(75)80015-0

Medlin, L. K. (2016). Evolution of the diatoms: major steps in their evolution and a review of the supporting molecular and morphological evidence. *Phycologia* 55, 79–103. doi: 10.2216/15-105.1

Miall, A. D. (1997). *The geology of stratigraphic sequences* (Berlin Heidelberg: Springer Verlag), 433.

Middleton, G. V. (1973). Johannes walther's law of the correlation of facies. *Geol. Soc America Bull.* 84, 979–988. doi: 10.1130/0016-7606(1973)84<979:JWLOTC>2.0.CO;2

Moody, E. R. R., Álvarez-Carretero, S., Mahendrarajah, T. A., Clark, J. W., Betts, H. C., Dombrowski, N., et al. (2024). The nature of the last universal common ancestor and its impact on the early Earth system. *Nat. Ecol. Evol.* 8, 1654–1666. doi: 10.1038/s41559-024-02461-1

Morales, G. P., and Delaye, L. (2020). "Was LUCA a hyperthermophilic prokaryote? The impact-bottleneck hypothesis revisited," in *Astrobiology and Cuatro Ciénegas Basin as an analog of early Earth*. Eds. V. Souza, A. Segura and J. Foster (Springer, Cham). doi: 10.1007/978-3-030-46087-7_3

Muscente, A. D., Schiffbauer, J. D., Broce, J., Laflamme, M., O'Donnell, K., Boag, T. H., et al. (2017). Exceptionally preserved fossil assemblages through geologic time and space. *Gondwana Res.* 48, 164–188. doi: 10.1016/j.gr.2017.04.020

Mutti, D., Tourn, S., Caccaglio, O., Herrmann, C., Geuna, S., Di Marco, A., et al. (2005). Evolución metalogenética de las Sierras Pampeanas de Córdoba y sur de Santiago del Estero: ciclos famatiniano, gondwánico y ándico. *Rev. Asoc. Geol. Arg.* 60, 467–485.

Nakov, T., Beaulieu, J. M., and Alverson, A. J. (2018). Accelerated diversification is related to life history and locomotion in a hyperdiverse lineage of microbial eukaryotes (Diatoms, Bacillariophyta). *New Phytol.* 219, 462–473. doi: 10.1111/nph.15137

Nicholls, K. H., and Wujek, D. E. (2015). "Chrysophyceae and phaeothamniophycea," in *Freshwater algae of north america*. Eds. J. D. Wehr, R. D. Sheath and J. P. Kociolek (Amsterdam, Netherlands: Elsevier Inc), 537–586. doi: 10.1016/B978-0-12-385876-4.00012-8

Nichols, D. J. (2002). Palynology and palynostratigraphy of the Hell Creek Formation in North Dakota: A microfossil record of plants at the end of Cretaceous time. *Geol. Soc Am. Sp. Pap.* 361, 393–456. doi: 10.1130/0-8137-2361-2.393

Noell, S. E., Abbaszadeh, J., Richards, H., Saint Vincent, M. L., Lee, C. K., Herbold, C. W., et al. (2025). Antarctic geothermal soils exhibit an absence of regional habitat generalist microorganisms. *Environ. Microbiol.* 27, e70032. doi: 10.1111/1462-2920.70032

Noffke, N., Gerdes, G., Klenke, T., and Krumbein, W. E. (2001). Microbially induced sedimentary structures–a new category within the classification of primary sedimentary structures. *J. Sedim. Res.* 71, 649–665. doi: 10.1306/2DC4095D-0E47-11D7-8643000102C1865D

Oliverio, A. M., Power, J. F., Washburne, A., Cary, S. C., Stott, M. B., and Fierer, N. (2018). The ecology and diversity of microbial eukaryotes in geothermal springs. *ISME J.* 12, 1918–1928. doi: 10.1038/s41396-018-0104-2

Owen, R. B., Renaut, R. W., and Jones, B. (2008). Geothermal diatoms: a comparative study of floras in hot spring systems of Iceland, New Zealand, and Kenya. *Hydrobiologia* 610, 175–192. doi: 10.1007/s10750-008-9432-y

Patkowski, J. B., Dahlberg, T., Amin, H., Gahlot, D. K., Vijayrajratnam, S., Vogel, J. P., et al. (2023). The F-pilus biomechanical adaptability accelerates conjugative dissemination of antimicrobial resistance and biofilm formation. *Nat. Commun.* 14, 1879. doi: 10.1038/s41467-023-37600-y

Philippe, M. (1995). Bois fossiles du Jurassique de Franche-Comté (nord-est de la France): systématique et biogéographie. *Paleont. Abt. B* 236, 45–103.

Phoenix, V. R., Adams, D. G., and Konhauser, K. O. (2000). Cyanobacterial viability during hydrothermal biomineralisation. *Chem. Geol.* 169, 329–338. doi: 10.1016/S0009-2541(00)00212-6

Phoenix, V. R., and Konhauser, K. O. (2008). Benefits of bacterial biomineralization. *Geobiology* 6, 303–308. doi: 10.1111/j.1472-4669.2008.00147.x

Phoenix, V. R., Konhauser, K. O., and Adams, D. G. (1999). "Photosynthetic controls on the silicification of cyanobacteria," in *Geochemistry of the earth's surface*. Ed. H. Armannsson (Balkema, Rotterdam, The Netherlands), 275–278.

Phoenix, V., Konhauser, K. O., Adams, D. G., and Bottrell, S. H. (2001). Role of biomineralization as an ultraviolet shield: implications for Archean life. *Geology* 29, 823–826. doi: 10.1130/0091-7613(2001)029<0823:ROBAAU>2.0.CO;2

Phoenix, V. R., Konhauser, K. O., and Ferris, F. G. (2003). Experimental study of iron and silica immobilization by bacteria in mixed Fe-Si systems: Implications for microbial silicification in hot-springs. *Can. J. Earth Sci.* 40, 1669–1678. doi: 10.1139/e03-044

Phoenix, V. R., Martinez, R. E., Konhauser, K. O., and Ferris, F. G. (2002). Characterization and implications of the cell surface reactivity of calothrix sp. Strain KC97. *Ap. Environ. Microbiol.* 68, 4827–4834. doi: 10.1128/AEM.68.10.4827-4834.2002

Pinti, D. L., Mineau, R., and Clement, V. (2009). Hydrothermal alteration and microfossil artefacts of the 3,465-million-year-old Apex chert. *Nat. Geosci.* 2, 640–643. doi: 10.1038/ngeo601

Pirajno, F., and Van Kranendonk, M. J. (2005). Review of hydrothermal processes and systems on Earth and implications for Martian analogues. *Aust. J. Earth Sci.* 52, 329–351. doi: 10.1080/08120090500134571

Pop, M. M., Di Lorenzo, T., and Iepure, S. (2023). Living on the edge – An overview of invertebrates from groundwater habitats prone to extreme environmental conditions. *Front. Ecol. Evol.* 10. doi: 10.3389/fevo.2022.1054841

Porter, S. M., Riedman, L. A., Woltz, C. R., Gold, D. A., and Kellogg, J. B. (2025). Early eukaryote diversity: a review and a reinterpretation. *Paleobiology* 51, 132–149. doi: 10.1017/pab.2024.33

Power, J. F., Carere, C. R., Lee, C. K., Wakerley, G. L. J., Evans, D. W., Button, M., et al. (2018). Microbial biogeography of 925 geothermal springs in New Zealand. *Nat. Commun.* 9, 2876. doi: 10.1038/s41467-018-05020-y

Pritchard, G. (1991). Insects in thermal springs. *Mem. Entomol. Soc Can.* 123, 89–106. doi: 10.4039/entm123155089-1

Rapela, C. W., and Llambías, E. J. (1999). El magmatismo Gondwánico y los ciclos Fanerozoicos. In: Caminos R. ed. *Geología Argentina SEGEMAR Anales* 29, 373–376.

Rappaport, H. B., and Oliverio, A. M. (2023). Extreme environments offer an unprecedented opportunity to understand microbial eukaryotic ecology, evolution, and genome biology. *Nat. Commun.* 14, 4959. doi: 10.1038/s41467-023-40657-4

Rappaport, H. B., and Oliverio, A. M. (2024). Lessons from extremophiles: functional adaptations and genomic innovations across the eukaryotic tree of life. *Gen. Biol. Evol.* 16, evae160. doi: 10.1093/gbe/evae160

Rasmussen, K. L., Stamps, B. W., Vanzin, G. F., Ulrich, S. M., and Spear, J. R. (2023). Spatial and temporal dynamics at an actively silicifying hydrothermal system. *Front. Microbiol.* 14. doi: 10.3389/fmicb.2023.1172798

Rasmussen, K. L., Thieringer, P. H., Nevadomski, S., Martinez, A. M., Dawson, K. S., Corsetti, F. A., et al. (2024). Living to lithified: construction and preservation of silicified biomarkers. *Geobiology* 22, e12620. doi: 10.1111/gbi.12620

Renaut, R. W., and Jones, B. (2003). Sedimentology of hot spring systems. *Can. J. Earth Sci.* 40, 1439–1442. doi: 10.1139/e03-085

Renaut, R. W., and Jones, B. (2011). "Hydrothermal environments, terrestrial," in *Encyclopedia of geobiology*. Eds. J. Reitner and V. Thiel (Dordrecht, Netherlands: Springer Dordrecht), 467–479. doi: 10.1007/978-1-4020-9212-1_114

Renaut, R. W., Jones, B., and Tiercelin, J. J. (1998). Rapid in *situ* silicification of microbes at Loburu hot springs, Lake Bogoria, Kenya Rift Valley. *Sedimentology* 45, 1083–1103. doi: 10.1046/j.1365-3091.1998.00194.x

Reysenbach, A. L., and Cady, S. L. (2001). Microbiology of ancient and modern hydrothermal systems. *Trends Microbiol.* 9, 79–86. doi: 10.1016/S0966-842X(00)01921-1

Rice, C. M., Trewin, N. H., and Anderson, L. I. (2002). Geological setting of the Early Devonian Rhynie Cherts, Aberdeenshire, Scotland: an early terrestrial hot spring system. *J. Geol. Soc Lon.* 159, 203–214. doi: 10.1144/0016-764900-181

Robin, N., D'Haese, C., and Barden, P. (2019). Fossil amber reveals springtails' longstanding dispersal by social insects. *BMC Evol. Biol.* 19, 213. doi: 10.1186/s12862-019-1529-6

Rothschild, L. J., and Mancinelli, R. L. (2001). Life in extreme environments. *Nature* 409, 1092–1101. doi: 10.1038/35059215

Roy, C., Rameez, M. J., Haldar, P. K., Peketi, A., Mondal, N., Bakshi, U., et al. (2020). Microbiome and ecology of a hot spring-microbialite system on the Trans-Himalayan Plateau. *Sci. Rep.* 10, 5917. doi: 10.1038/s41598-020-62797-z

Ruff, S. W., and Farmer, J. D. (2016). Silica deposits on Mars with features resembling hot spring biosignatures at El Tatio in Chile. *Nat. Commun.* 7, 13554. doi: 10.1038/ncomms13554

Santos, A. A., Nel, A., Rodríguez-Barreiro, I., Sender, L. M., Wappler, T., Diez, J. B., et al. (2022). Insect and plant diversity in hot-spring ecosystems during the Jurassic-Cretaceous boundary from Spain (Aguilar Fm., Palencia). *Biology* 11, 273. doi: 10.3390/biology11020273

Seilacher, A., Reif, W.-E., and Westphal, F. (1985). Sedimentological, ecological and temporal patterns of fossil Lagerstätten. *Philos. Trans. R. Soc B* 311, 5–23. doi: 10.1098/rstb.1985.0134

Shields, G. (1998). What are lagerstätten. *Lethaia* 31, 124. doi: 10.1111/j.1502-3931.1998.tb00498.x

Sidorchuk, E. A. (2018). Mites as fossils: forever small? *Int. J. Acarol.* 44, 349–359. doi: 10.1080/01647954.2018.1497085

Silva, B., Antunes, C., Andrade, F., da Silva, E. F., Grande, J. A., and Luís, A. T. (2021). Prokaryotic and eukaryotic diversity in hydrothermal continental systems. *Arch. Microbiol.* 203, 3751–3766. doi: 10.1007/s00203-021-02416-1

Sims, P. A., Mann, D. G., and Medlin, L. K. (2006). Evolution of the diatoms: insights from fossil, biological and molecular data. *Phycologia* 45, 361–402. doi: 10.2216/05-22.1

Singh, R. S., Stoermer, E. F., and Kar, R. (2006). Earliest freshwater diatoms from Deccan intertrappean (Maastrichtian) sediments. *Micropaleontol.* 52, 545–551. doi: 10.2113/gsmicropal.52.6.545

Sriaporn, C., Campbell, K. A., Van Kranendonk, M. J., and Handley, K. M. (2023). Bacteria and archaeal community distributions and cosmopolitanism across physicochemically diverse hot springs. *ISME Commun.* 3, 80. doi: 10.1038/s43705-023-00291-z

Stal, L. J. (2012). "Cyanobacterial mats and stromatolites," in *Ecology of cyanobacteria II*. Ed. B. A. Whitton (Springer, Dordrecht), 65–125. doi: 10.1007/978-94-007-3855-3_4

Stetter, K. O. (1996). Hyperthermophilic procaryotes. *FEMS Microbiol. Rev.* 18, 149–158. doi: 10.1016/0168-6445(96)00008-3

Stetter, K. O. (2006). History of discovery of the first hyperthermophiles. *Extremophiles* 10, 357–362. doi: 10.1007/s00792-006-0012-7

Strullu-Derrien, C., Goral, T., Spencer, A. R. T., Kenrick, P., Aime, M. C., Gaya, E., et al. (2023). A fungal plant pathogen discovered in the Devonian Rhynie Chert. *Nat. Commun.* 14, 7932. doi: 10.1038/s41467-023-43276-1

Toporski, J. K. W., Steele, A., Westall, F., Thomas-Keprta, K. L., and McKay, D. S. (2002). The simulated silicification of bacteria—New clues to the modes and timing of bacterial preservation and implications for the search for extraterrestrial microfossils. *Astrobiology* 2, 1–26. doi: 10.1089/153110702753621312

Van Etten, J., Cho, C. H., Yoon, H. S., and Bhattacharya, D. (2023). Extremophilic red algae as models for understanding adaptation to hostile environments and the evolution of eukaryotic life on the early earth. *Sem. Cell Dev. Biol.* 134, 4–13. doi: 10.1016/j.semcdb.2022.03.007

Vosseberg, J., van Hooff, J. J. E., Köstlbacher, S., Panagiotou, K., Tamarit, D., Ettema, T. J. G., et al. (2024). The emerging view on the origin and early evolution of eukaryotic cells. *Nature* 633, 295–305. doi: 10.1038/s41586-024-07677-6

Walter, D. E., and Proctor, H. C. (2013). *Mites: ecology, evolution and behaviour* (Dordrecht: Springer), 494.

Weiss, M. C., Preiner, M., Xavier, J. C., Zimorski, V., and Martin, W. F. (2018). The last universal common ancestor between ancient Earth chemistry and the onset of genetics. *PloS Gen.* 14, e1007518. doi: 10.1371/journal.pgen.1007518

Weiss, M. C., Sousa, F., Mrnjavac, N., Neukirchen, S., Roettger, M., Nelson-Sathi, S., et al. (2016). The physiology and habitat of the last universal common ancestor. *Nat. Microbiol.* 1, 16116. doi: 10.1038/nmicrobiol.2016.116

Westacott, S., Planavskya, N. J., Zhao, M. Y., and Hull, P. M. (2021). Revisiting the sedimentary record of the rise of diatoms. *Proc. Nat. Ac. Sci. U.S.A.* 118, e2103517118. doi: 10.1073/pnas.2103517118

Williams, D. D. (1991). Life history traits of aquatic arthropods in springs. *Mem. Entomol. Soc Can.* 123, 63–87. doi: 10.4039/entm123155063-1

Williamson, K., Eme, L., Baños, H., McCarthy, C. G. P., Susko, E., Kamikawa, R., et al. (2025). A robustly rooted tree of eukaryotes reveals their excavate ancestry. *Nature* 640, 974–981. doi: 10.1038/s41586-025-08709-5

Yee, N., Phoenix, V. R., Konhauser, K. O., Benning, L. G., and Ferris, F. G. (2003). The effect of cyanobacteria on silica precipitation at neutral pH: implications for bacterial silicification in geothermal hot springs. *Chem. Geol.* 199, 83–90. doi: 10.1016/S0009-2541(03)00120-7

Yoon, H. S., Ciniglia, C., Wu, M., Comeron, J. M., Pinto, G., Pollio, A., et al. (2006). Establishment of endolithic populations of extremophilic Cyanidiales (Rhodophyta). *BMC Evol. Biol.* 6, 78. doi: 10.1186/1471-2148-6-78

Yoshino, K., Wan, X. Q., Xi, D. P., Li, W., and Matsuoka, A. (2017). Campanian–Maastrichtian palynomorph from the Sifangtai and Mingshui formations, Songliao Basin, Northeast China: Biostratigraphy and paleoflora. *Paleoworld* 26, 352–368. doi: 10.1016/j.palwor.2016.10.001