

# Earth System Significance Environmental Response and Morphological Evolution of Neoproterozoic Stromatolites

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**Abstract:** The proterozoic (1000–541 Ma) constitutes a critical transitional period in Earth's evolutionary history. As microbial-dominated biosedimentary structures, stromatolites faithfully record the coevolutionary processes of biological evolution and environmental changes during this era. This study systematically combs the global distribution pattern and spatiotemporal evolutionary characteristics of Neoproterozoic stromatolites. Integrating sedimentological, geochemical, and paleontological evidence from typical sections, it deeply analyzes the controlling factors of their morphological diversity, reveals the response mechanisms of stromatolites to major geological events such as Snowball Earth events and the Second Great Oxidation Event (NOE), and explores the intrinsic connection between microbial community evolution and stromatolite construction. Research indicates that Neoproterozoic stromatolites underwent a transformation from the Mesoproterozoic giant conical-columnar assemblages to diverse small-scale morphologies. The microstructural mutation event at 850–800 Ma marks a revolution in cyanobacterial calcification, while the morphological turnover around glacial periods records microbial adaptation strategies under extreme environments. Geochemical indicators confirm that the carbon, oxygen, and chromium isotope compositions of stromatolites are highly coupled with the evolution of marine redox conditions, and their microbially induced manganese deposits provide key empirical evidence for the biological mineralization theory. In the future, it is necessary to further clarify the impact mechanism of eukaryote rise on stromatolite decline through the combination of high-precision isotope analysis and molecular fossil technology, so as to establish a more comprehensive cognitive framework for reconstructing Neoproterozoic Earth system evolution.

**Keywords:** Neoproterozoic; Stromatolites; Morphological evolution; Paleoenvironmental reconstruction; Microbial action; Geochemistry.

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## 1. Introduction

### 1.1. Research Background and Scientific Significance

Stromatolites are layered biosedimentary structures formed by microbial communities such as cyanobacteria through trapping and binding sedimentary particles or directly inducing mineral precipitation [1]. As direct recorders of early Earth's biological activities, their evolutionary history is closely intertwined with Earth's environmental changes [2]. The Neoproterozoic lies in the transitional stage from the "Boring Billion" to the Ediacaran biological diversification. Major events occurring during this period, including the Second Great Oxidation Event (NOE) [3], Snowball Earth events (Sturtian, Marinoan, and Gaskiers glaciations), and the breakup of the Rodinia supercontinent, have profoundly reshaped the marine chemical environment and the trajectory of biological evolution [4].

The morphological diversity, distribution pattern, and geochemical characteristics of Neoproterozoic stromatolites provide a unique perspective for solving the aforementioned major scientific issues. Stromatolite records from typical regions such as the Jiuliqiao Formation in Huainan, Anhui; the Doushantuo Formation in Chengkou, northern Yangtze Craton; the Jixian Section in Tianjin; and the Salitre Formation in the Irecê Basin, Brazil, show that their development is not only closely related to sedimentary environments such as seawater depth and hydrodynamic conditions but also sensitively responds to global-scale redox

changes and climate variations [5]. For example, the manganese stromatolites in the Doushantuo Formation of the Chengkou area preserve exquisite biosedimentary structures, providing direct evidence for microbial involvement in manganese mineralization; the microstructural mutation of stromatolites in the Jiaoliao-Xuhuai region occurs synchronously with carbon-oxygen isotope negative excursions, implying drastic changes in global marine chemical conditions.

Carrying out research on Neoproterozoic stromatolites can not only reveal the evolutionary adaptation mechanisms of early microbial communities and reconstruct the physical and chemical environment of the paleo-ocean but also provide key empirical evidence for understanding the co-evolution of life and the environment. It holds an indispensable significance for improving the theoretical system of Precambrian geological evolution.

### 1.2. Research Status at Home and Abroad

#### 1.2.1. Foreign Research Progress

Foreign research on stromatolites began in the early 20th century, initially focusing on morphological classification and stratigraphic correlation [6]. Since the late 20th century, with the development of geochemical analysis technology, research has gradually deepened into formation mechanisms and paleoenvironmental indicative significance. Studies on Proterozoic stromatolites in Australia, Canada, and other regions have revealed the redox conditions and nutrient cycling characteristics of the paleo-ocean through carbon-oxygen isotope analysis; research on modern stromatolites

(such as those in the Bahamas and Shark Bay, Western Australia) has provided living references for understanding microbe-mineral interactions [7].

In recent years, international research has shown a trend of multidisciplinary integration. Studies on the Ediacaran Salitre Formation in the Irecê Basin, Brazil, have clarified the controlling mechanisms of hydrodynamic energy, sediment input, and early diagenesis on stromatolite morphology through sedimentary dynamic analysis, confirming that high-energy environments promote the development of columnar-branched morphologies, while low-energy environments are conducive to the formation of layered structures [8]. Isotope geochemical research indicates that the positive chromium isotope excursion of Neoproterozoic stromatolites records a significant increase in atmospheric oxygen content 800 million years ago [9], and the sulfur isotope fractionation characteristics reflect the evolutionary radiation of sulfate-reducing microbes [10].

### 1.2.2. Domestic Research Progress

China is endowed with abundant Neoproterozoic stromatolite resources, with high-quality outcrops in regions such as Jixian (Tianjin), Huainan (Anhui), Chengjiang (Yunnan), northern Yangtze Craton, and southern East Kunlun Belt, providing unique conditions for systematic research [11]. Domestic scholars have achieved a series of results in stromatolite classification, stratigraphic correlation, and paleoenvironmental reconstruction: establishing the Proterozoic stromatolite assemblage sequence of the North China Craton, proposing that the Pseudogymnosolenaceae can serve as an important marker for Mesoproterozoic stratigraphic correlation[12]; distinguishing microfacies such as the basement and reef core, as well as reef-building stages from colonization to decline through the study of stromatolite reefs in the Jiuliqiao Formation of Huainan, revealing their response to sea-level changes; discovering the Conophyton-Baicalia assemblage in the Jiawengmen area of the southern East Kunlun Belt, providing paleontological constraints for the reconstruction of the Rodinia supercontinent [13].

In terms of microscopic and geochemical research, the team from the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, discovered a hemispherical radiating fibrous fabric mutation event in 850–800 Ma stromatolites in the Jiaoliao-Xuhuai region, considering it as an important biological event marking the initial calcification of cyanobacteria; research on manganese stromatolites in the Doushantuo Formation of Chengkou, northern Yangtze Craton, has subdivided six morphological types and confirmed the involvement of microbes in the manganese mineralization process[14].

### 1.2.3. Research Deficiencies and Development Trends

Existing research still has three deficiencies: first, the weak research on microscopic mechanisms, lacking direct molecular evidence for the microbial community structure (especially the degree of eukaryote involvement) in stromatolite formation; second, the analysis of main controlling factors mostly focuses on single variables, with insufficient research on the coupling mechanisms of geological structures, paleo-ocean chemistry, and microbial action[15]; third, the lack of global comparative research, and the differences and commonalities in stromatolite evolution among different blocks have not formed a systematic understanding[16]

Future research will show a trend of multi-scale integration of "macro-micro-molecular". Scanning electron microscopy

(SEM), transmission electron microscopy (TEM) combined with high-throughput sequencing technology will be used to reveal microbial community characteristics [17]; multi-isotope systems (C-O-Cr-Mo) will be employed to reconstruct paleoenvironmental evolution[18]; and global section correlation will be used to establish a unified framework for Neoproterozoic stromatolite evolution[19].

## 2. Distribution and Morphological Characteristics of Neoproterozoic Stromatolites

### 2.1. Global Distribution Pattern

The distribution of Neoproterozoic stromatolites is controlled by paleoplate positions and sedimentary environments, mainly concentrating in epicontinental seas and carbonate platform margins in low-latitude regions, forming four major typical distribution areas (Figure 1).

#### 2.1.1. North China Craton

The North China Craton is a classic region for Neoproterozoic stromatolite research in China, represented by the Jixian Section in Tianjin and the Huainan area in Anhui. As a standard section of the Meso-Neoproterozoic, the Jixian Section exposes 1.3–1.6 billion-year-old stromatolite assemblages, including columnar, conical, and layered types, which are well-preserved and have not undergone significant metamorphism, providing a benchmark for stratigraphic correlation [20]. Stromatolites are widely developed in the Jiuliqiao Formation of Huainan, forming reefs of varying sizes. According to their morphology and genesis, they can be divided into three types: storm environment type, transgressive environment type, and regressive environment type, recording the evolution from shallow shelf to tidal flat environments [21].

#### 2.1.2. South China Craton

Neoproterozoic stromatolites in the South China Craton are centered on the northern Yangtze Craton. Typical manganese stromatolites are developed in the Doushantuo Formation of Chengkou, coexisting with oolites and oncolites, formed in reef shoals and back-reef lagoon environments on the carbonate platform margin [22]. Stromatolites are also exposed in the Ediacaran strata of the Chengjiang area in eastern Yunnan, often associated with Ediacaran biota fossils, providing clues for exploring the ecological relationship between microbes and macro-organisms.

#### 2.1.3. East Kunlun and Tianshan Regions

The late Mesoproterozoic-early Neoproterozoic Conophyton-Baicalia stromatolite assemblage was discovered in the Jiawengmen area of the southern East Kunlun Belt, dominated by large conical stromatolites, including taxa such as Conophyton garganicus var. inkeni and C. cf. ressoiti[23]. It can be correlated with the Erjigan assemblage in the Tianshan region and the Shanpoling assemblage in North China, indicating that this microblock was once located on the low-latitude margin of the Rodinia supercontinent [24].

#### 2.1.4. Margins of Gondwana and Laurasia

Ediacaran stromatolites are developed in the Salitre Formation of the Irecê Basin on the margin of Gondwana, mainly characterized by columnar inclined and branched morphologies, formed in high-energy shallow marine environments [25]; stromatolites in the Bitter Springs Formation of Australia are rich in carbon isotope anomaly

records, providing evidence for environmental recovery after Snowball Earth events [26]. The Siberian and southern Ural regions on the margin of Laurasia develop Conophyton assemblages similar to those in East Kunlun, showing the commonality of low-latitude epicontinental sea environments [27].

## **2.2. Main Morphological Types and Classification**

Based on macro-morphology and micro-structure, Neoproterozoic stromatolites can be divided into six categories, with different types corresponding to specific sedimentary environments and formation mechanisms.

### **2.2.1. Conical Stromatolites**

Represented by Conophyton, conical stromatolites are the dominant type in the early Neoproterozoic, most typical in the Jiawengmen area of East Kunlun. The cone diameter can reach tens of centimeters, with concentric laminae and radial structures. Such stromatolites are formed in low to medium energy shallow marine environments, with cyanobacteria as the main microbial community, forming conical growth morphologies through periodic carbonate precipitation.

### **2.2.2. Columnar Stromatolites**

Columnar stromatolites are widely distributed in all periods of the Neoproterozoic, with diverse morphologies, including upright, inclined, and branched types. The columnar stromatolites in the Jiuliqiao Formation of Huainan show significant height differences (5–50 cm), and the branching frequency is positively correlated with hydrodynamic energy; the inclined columnar stromatolites in the Salitre Formation of Brazil are consistent with the paleocurrent direction, indicating a high-energy turbulent environment. The inter-columnar gaps are filled with clastic particles, while the laminae are mainly composed of microbial carbonate precipitation.

### **2.2.3. Digitate Stromatolites**

Digitate stromatolites are characterized by fine branches. The microdigitate stromatolites in the Doushantuo Formation of Chengkou have a diameter of less than 1 cm, closely clustered like ears of grain, with nearly circular cross-sections. Spherical algal fossils can be seen between columns, with passive branching structures. Such stromatolites are formed in medium-energy shallow water environments and are extremely sensitive to changes in water depth.

### **2.2.4. Layered Stromatolites**

Layered stromatolites exhibit continuous mat-like distribution, with gentle laminae and uniform thickness. Late stromatolites in the Chengkou area are dominated by layered types, indicating the process of gradual shallowing of water bodies at the end of the Doushantuo period; layered stromatolites in the Wumishan Formation of the Jixian Section are often associated with siliceous bands, formed in low-energy tidal flat or lagoon environments.

### **2.2.5. Layered-Columnar Transitional Stromatolites**

Layered-columnar transitional stromatolites have both layered and columnar characteristics. Such stromatolites in the Jiuliqiao Formation of Huainan record environmental changes caused by sea-level fluctuations: the layered segments correspond to low-energy environments during transgression, while the columnar segments correspond to high-energy environments during regression.

### **2.2.6. Manganese Stromatolites**

Manganese stromatolites are a characteristic type of the Neoproterozoic, mainly developed in manganese-bearing strata such as the Doushantuo Formation. In the Chengkou area, they can be subdivided into six subtypes: micro-branched, microdigitate, small digitate, layered, columnar, and layered-columnar. The micro-structure is dominated by clotted textures, containing microbially induced structures such as tubular and spherical forms, recording the biological mineralization process of manganese.

## **2.3. Spatiotemporal Evolution Characteristics**

The morphological evolution of Neoproterozoic stromatolites shows obvious phase characteristics, synchronized with major geological events, and can be divided into three stages.

### **2.3.1. Early Stage (1000–850 Ma): Conical-Columnar Dominated Stage**

During this stage, stromatolites inherited Mesoproterozoic characteristics, dominated by large conical (Conophyton) and columnar (Baicalia) assemblages. The Conophyton-Baicalia assemblage in the Jiawengmen area of East Kunlun is the most typical, distributed in low-latitude epicontinental sea environments. The micro-structure is dominated by simple laminae, with no obvious calcified structures, indicating that the ocean was in a low-oxygen state, and the microbial community was dominated by cyanobacteria. Carbon isotopes show a weak positive excursion, reflecting the slow increase in primary productivity.

### **2.3.2. Middle Stage (850–635 Ma): Microstructural Mutation and Diversification Stage**

A significant stromatolite microstructural mutation event occurred at 850–800 Ma. Hemispherical radiating fibrous fabrics suddenly appeared in stromatolites in the Jiaoliao-Xuhuai region, which is considered a marker of the initial calcification of cyanobacteria, accompanied by carbon-oxygen isotope negative excursions, indicating global marine chemical changes. Around the Sturtian (720–660 Ma) and Marinoan (650–635 Ma) glaciations, stromatolite morphologies underwent obvious turnover: columnar types dominated before the glaciations, almost disappeared during the glaciations, and small digitate and layered assemblages appeared during the interglacials, reflecting microbial adaptation to extreme environments.

### **2.3.3. Late Stage (635–541 Ma): Decline and Specialization Stage**

Ediacaran stromatolites show the coexistence of diversification and local decline: inclined columnar stromatolites adapted to high-energy environments developed in the Salitre Formation of Brazil, specialized manganese stromatolites appeared in the Doushantuo Formation of Chengkou, while the abundance of stromatolites decreased in most regions of the world. During this stage, carbon isotopes showed a positive excursion again, chromium and molybdenum isotopes indicated a significant increase in marine oxidation degree, and the rise of eukaryotes may have occupied the ecological niche of cyanobacteria, leading to the decline of stromatolite construction.

### 3. Formation Mechanisms and Main Controlling Factors of Stromatolites

#### 3.1. Microbial Construction Mechanisms

Microbial communities are the core driving force for stromatolite formation, constructing layered structures through two pathways: trapping and binding, and biomineralization. The evolution of microbial functional groups in the Neoproterozoic significantly changed the construction mode.

##### 3.1.1. Microbial Community Composition

The microbial community of Neoproterozoic stromatolites is centered on cyanobacteria, supplemented by heterotrophic bacteria, with eukaryotic algae appearing in the late stage. Scanning electron microscopy observations show that spherical algal fossils exist between the columns of manganese stromatolites in Chengkou, with a diameter of 5–10  $\mu\text{m}$ , having obvious cellular structures; filamentous cyanobacterial remains were found in the laminae of stromatolites in the Jiuliqiao Formation of Huainan, with a diameter of 1–2  $\mu\text{m}$ , arranged in parallel. Molecular fossil evidence indicates that eukaryotic biomarkers (such as steranes) appeared in Ediacaran stromatolites, indicating that eukaryotic algae began to participate in stromatolite construction.

##### 3.1.2. Trapping and Binding

Trapping and binding is the main construction method of early stromatolites. Cyanobacteria form microbial mats by secreting extracellular polymeric substances (EPS), binding carbonate particles and clay minerals in the water body, which are solidified into laminae through diagenesis. The laminae of columnar stromatolites in the Salitre Formation of Brazil contain almost no clastic particles, while the inter-columnar gaps are rich in particles, indicating that the trapping effect of microbial mats is selective, allowing only fine particles to enter the gaps. Stromatolites formed in this way have loose laminae, which are easily damaged by hydrodynamic forces, and are mainly developed in low-energy environments.

##### 3.1.3. Biomineralization

Biomineralization significantly enhanced in the middle Neoproterozoic. The microstructural mutation event at 850–800 Ma marks the origin of cyanobacterial calcification. Cyanobacteria consume  $\text{CO}_2$  through photosynthesis, increasing the pH value of the surrounding microenvironment, inducing calcium carbonate precipitation, and forming hemispherical radiating fibrous fabrics. Such structures are widely distributed in the Majiatunian stromatolites in the Jiaoliao-Xuhuai region, with a diameter of 50–100  $\mu\text{m}$ , growing radially. The clotted textures and tubular structures of manganese stromatolites in Chengkou suggest that microbes change the microenvironmental Eh value through metabolic activities, promoting the precipitation of manganese minerals, which belongs to a typical induced mineralization process. Stromatolites formed by biomineralization have a dense structure and strong erosion resistance, and can adapt to higher energy environments.

#### 3.2. Sedimentary Environmental Controlling Factors

Sedimentary environmental parameters directly affect the morphology and distribution of stromatolites by changing microbial growth conditions and material supply, among which hydrodynamic energy, water depth, and sediment input

are key variables.

##### 3.2.1. Hydrodynamic Energy

Hydrodynamic energy is the primary factor controlling stromatolite morphology. Studies on the Salitre Formation of Brazil have confirmed that high-energy environments (intense wave and current action) promote the development of columnar inclined and branched morphologies, and the inclined direction is consistent with the paleocurrent direction, reflecting the directional growth adaptation of microbial mats; low-energy environments (such as lagoons) are conducive to the formation of layered stromatolites, with continuous and gentle laminae. In the storm environment-type reefs of the Jiuliqiao Formation of Huainan, stromatolites are fragmented with distorted laminae, while stromatolites in transgressive environment-type reefs have complete morphologies and regular laminae, further confirming the controlling effect of hydrodynamic forces.

##### 3.2.2. Water Depth and Salinity

Water depth regulates the growth rate of cyanobacteria by affecting light intensity and temperature. Conical stromatolites are mainly developed in shallow marine environments of 5–20 m, where sufficient light promotes the rapid growth of cyanobacteria, forming tall cones; layered stromatolites can be distributed in deeper subtidal zones (20–50 m), where reduced light leads to a decrease in growth rate, forming gentle laminae. Salinity changes also affect stromatolite types. Stromatolites in the Yangzhuang Formation of Jixian are associated with evaporites, indicating a hypersaline environment, with small columnar morphologies as the main type, while stromatolites in the Jiuliqiao Formation of Huainan are developed in normal salinity shallow seas, with diverse morphologies and large individuals.

##### 3.2.3. Sediment Input

The amount of sediment input controls the structural compactness of stromatolites. In high sediment input environments, stromatolite laminae are rich in clastic particles, with a loose structure and easy to be damaged. For example, stromatolites in the reef-front facies of the Jiuliqiao Formation of Huainan contain a large amount of quartz sand, with irregular morphologies; in low sediment input environments, stromatolites are mainly dominated by biomineralization, with a dense structure and clear laminae. Manganese stromatolites in Chengkou are formed on the carbonate platform margin with low clastic input.

#### 3.3. Geochemical Environmental Controlling Factors

The drastic changes in the Neoproterozoic marine chemical environment profoundly regulate the evolution of stromatolites by affecting microbial metabolism and mineral precipitation, among which redox state and element cycling are the core drivers.

##### 3.3.1. Redox State

Marine oxidation caused by the Second Great Oxidation Event is a key inducement for stromatolite evolution. Chromium isotope evidence shows that an oxidized chromium cycle appeared in the ocean 800 million years ago, and the  $\delta^{53}\text{Cr}$  values of stromatolites show a positive excursion of 0.9–4.9‰, indicating a significant increase in atmospheric oxygen content. Oxidizing environments promote cyanobacterial calcification, and the hemispherical radiating fibrous fabric mutation at 850–800 Ma may be

directly related to the increase in marine oxidation degree. The marine oxidation degree decreased during the Cryogenian interglacials, and the positive chromium isotope excursion weakened, corresponding to the decrease in stromatolite abundance, further confirming the controlling effect of redox state.

### 3.3.2. Carbon Cycle and Isotope Changes

The drastic fluctuations of carbon isotopes are synchronized with stromatolite evolution. The positive  $\delta^{13}\text{C}$  excursion of stromatolites in the late Tonian (850–720 Ma) is related to the enhanced carbon sequestration caused by the radiation of eukaryotic phytoplankton, reflecting the increase in primary productivity; the  $\delta^{13}\text{C}$  negative excursion at 850–800 Ma is synchronized with the stromatolite microstructural mutation, which may be triggered by the upwelling of anoxic oceanic waters, changing the carbonate precipitation conditions; the  $\delta^{13}\text{C}$  positive excursion again in the Ediacaran corresponds to the development of manganese stromatolites, indicating the coupling relationship between the carbon cycle and metal mineralization.

### 3.3.3. Nitrogen and Sulfur Cycles

Nitrogen isotope research shows that the  $\delta^{15}\text{N}$  values of stromatolites from 750 to 580 Ma range from  $-4\%$  to  $+11\%$ , similar to the modern ocean, indicating that a widespread aerobic nitrogen cycle existed in the ocean at that time, providing a nutrient basis for the diversification of microbial communities. The enhanced sulfur isotope fractionation indicates the radiation of sulfate-reducing microbes, which require a relatively high oxygen concentration to survive. Their prosperity further confirms the increase in Neoproterozoic marine oxidation degree, and at the same time changes the microenvironmental chemical conditions by consuming sulfides, affecting the mineral composition of stromatolites.

## 3.4. Tectonic and Climate Controlling Factors

The breakup of the Rodinia supercontinent and Snowball Earth events indirectly regulate the distribution and morphology of stromatolites by changing the paleogeographic pattern and sedimentary environment.

### 3.4.1. Plate Tectonic Movements

Sea-level changes and sedimentary basin formation caused by the breakup of the Rodinia supercontinent control the distribution of stromatolites. The Conophyton-Baicalia assemblage in the Jiawengmen area of the southern East Kunlun Belt is similar to the coeval assemblages in North China and Siberia, indicating that these microblocks were once located on the low-latitude margin of the Rodinia supercontinent, commonly developing warm epicontinental sea environments, providing paleogeographic conditions for the large-scale development of stromatolites. Volcanic activities triggered by plate movements can promote microbial growth by inputting nutrients. The nitrogen isotope anomaly of stromatolites in Zimbabwe is related to ammonium input from volcanic activities.

### 3.4.2. Extreme Climate Events

Snowball Earth events caused devastating impacts on stromatolites and drove their adaptive evolution. During the Sturtian and Marinoan glaciations, the global ocean was covered by ice sheets, light and temperature dropped sharply, and stromatolites almost became extinct; temperatures recovered during the interglacials, and small digitate and layered stromatolites formed rapidly, reflecting the rapid

recovery of microbial communities; after the Gaskiers glaciation ( $\sim 580$  Ma), stromatolite morphologies further specialized. The development of manganese stromatolites in Chengkou may be related to post-glacial ocean stratification and manganese enrichment [28].

## 4. Case Studies of Stromatolites in Typical Regions

### 4.1. Stromatolites in the Jiuliqiao Formation of Huainan, Anhui: Response Records of Sea-Level Changes

#### 4.1.1. Geological Background

The Huainan area is located on the southern margin of the North China Craton. The Jiuliqiao Formation belongs to the Neoproterozoic Qingbaikou System, mainly composed of carbonate rocks, with a thickness of about 200 m, formed in shallow shelf to tidal flat environments. Stromatolites are widely developed in the middle-upper part of the formation, forming reefs of varying sizes, and are a classic section for studying the relationship between sea-level changes and stromatolites.

#### 4.1.2. Sedimentary and Morphological Characteristics

Field investigations and laboratory analyses show that stromatolites in the Jiuliqiao Formation can be divided into three types: (1) Storm environment type: distributed in the reef-front facies, strongly affected by storm currents, stromatolites are fragmented with distorted laminae, containing a large amount of clastic particles; (2) Transgressive environment type: developed in the lower part of the reef core facies, corresponding to the sea-level rise period, stromatolites are mainly upright columnar, with a height of 10–30 cm and few branches; (3) Regressive environment type: located in the upper part of the reef core facies, corresponding to the sea-level fall period, stromatolites are branched columnar, with a height of up to 50 cm and frequent branching.

Microstructurally, the stromatolite laminae are 0.5–2 mm thick, alternately composed of algae-rich layers and carbonate-rich layers. Filamentous cyanobacterial remains can be seen in the algae-rich layers. XRD analysis shows that the mineral composition is dominated by calcite (content  $>80\%$ ), containing a small amount of dolomite and quartz, and the Sr content in trace elements is relatively high, indicating a marine sedimentary environment.

#### 4.1.3. Main Controlling Factors and Environmental Significance

The evolution of stromatolites in the Jiuliqiao Formation is jointly controlled by sea-level changes and hydrodynamic conditions. Their morphological evolution records a complete sea-level rise and fall cycle: the colonization stage (early transgression) is dominated by small layered stromatolites, reflecting a low-energy environment; the expansion stage (peak transgression) develops upright columnar stromatolites, indicating stable water depth; the bloom stage (early regression) sees the emergence of branched columnar stromatolites, with enhanced hydrodynamic energy; the decline stage (late regression) is characterized by fragmented stromatolites, reflecting environmental turbulence.

Carbon-oxygen isotope analysis shows that the  $\delta^{13}\text{C}$  values of stromatolites during transgression are  $+2\%$  to  $+4\%$ , and decrease to  $0\%$  to  $+2\%$  during regression, reflecting the impact of sea-level changes on the carbon cycle. The

stromatolites in this section provide an accurate benchmark for reconstructing Neoproterozoic sea-level changes in the North China Craton, and their reef evolution model can serve as a reference for the study of coeval shallow marine stromatolites worldwide.

## **4.2. Manganese Stromatolites in the Doushantuo Formation of Chengkou, Northern Yangtze Craton: Direct Evidence of Biological Mineralization**

### **4.2.1. Geological Background**

The Chengkou area is located in the manganese ore belt of the northern Yangtze Craton. The Doushantuo Formation is a set of manganese-bearing carbonate strata, formed in the early Ediacaran (635–551 Ma), with a sedimentary environment of reef shoals and back-reef lagoons on the carbonate platform margin (Zhang et al., 2021). Manganese stromatolites are developed in the lower manganese-bearing member of the formation, coexisting with rhodochrosite and oolitic manganese ore (Zhang et al., 2021; Zhang et al., 2025), making them an ideal object for studying microbial manganese mineralization

### **4.2.2. Morphological and Microscopic Characteristics**

According to their morphology, manganese stromatolites in Chengkou can be divided into six types: micro-branched, microdigitate, small digitate, layered, columnar, and layered-columnar. Among them, microdigitate stromatolites are the most typical, growing in clusters like ears of grain, with a column diameter <1 cm, nearly circular cross-sections, passive branching structures, and spherical algal fossils (5–8  $\mu\text{m}$  in diameter) visible between columns.

The microstructure is dominated by clotted textures, containing microbially induced structures such as tubular, spherical, and fibrous forms. Scanning electron microscopy observations show that the laminae are composed of rhodochrosite dendrites and microstromatolites. The dendrites are 1–2  $\mu\text{m}$  in diameter, arranged radially, formed by precipitation induced by microbial metabolites. Electron probe analysis indicates that the Mn content is as high as 35%–45%, and is positively correlated with the organic carbon content, confirming the coupling relationship between biology and mineralization.

### **4.2.3. Mineralization Mechanism and Environmental Significance**

The formation of manganese stromatolites in Chengkou is the result of the synergy between microbial action and marine chemical conditions: cyanobacteria and heterotrophic bacteria change the pH and Eh values of the microenvironment through photosynthesis and respiration, oxidizing  $\text{Mn}^{2+}$  in the water body to  $\text{Mn}^{4+}$  and inducing rhodochrosite precipitation; at the same time, microbial mats trap and bind manganese particles to form layered structures.

These stromatolites record the characteristics of the marine manganese cycle in the early Ediacaran, with  $\delta^{13}\text{C}$  values of -1‰ to +1‰, indicating the recovery of the marine carbon cycle after the glaciation; the enrichment of manganese is related to hydrothermal activities caused by the breakup of the Rodinia supercontinent, and hydrothermal input provides a rich source of manganese for microbes. The discovery of manganese stromatolites in Chengkou provides key empirical evidence for the biological genesis theory of global Neoproterozoic manganese deposits.

## **4.3. Stromatolites in the Salitre Formation of the Irecê Basin, Brazil: A Typical Example of Hydrodynamic Control**

### **4.3.1. Geological Background**

The Irecê Basin is located in southeastern Brazil. The Salitre Formation belongs to the Ediacaran, mainly composed of carbonate rocks and clastic rocks, formed in a shallow marine environment on a passive continental margin. Stromatolites are developed in the reef limestone member in the middle of the formation, interbedded with conglomerates and sandstones, recording microbial activities in a high-energy environment.

### **4.3.2. Morphological and Sedimentary Characteristics**

Stromatolites in the Salitre Formation are mainly columnar, with obvious inclined and branched characteristics. The column diameter is 2–5 cm, the height is 10–20 cm, and the inclination angle is consistent with the paleocurrent direction (30°–45°). Field observations show that stromatolite reefs are lens-shaped, with a thickness of 50–100 cm, and their contact relationship with conglomerates indicates that they were formed in a high-energy turbulent environment.

Microscopic analysis shows that the stromatolite laminae are composed of pure carbonate, containing almost no clastic particles, while the inter-columnar gaps are filled with sand and gravel clasts. The laminae are wavy, with local disturbance structures, reflecting intermittent deposition and modification by microbial mats. The weak early diagenesis caused the columns to incline but not break, confirming the synchronization between their growth and hydrodynamic processes.

### **4.3.3. Hydrodynamic Response Mechanism and Significance**

The morphological evolution of stromatolites in the Salitre Formation clearly records changes in hydrodynamic energy: the high-energy stage (intense wave and current action) develops inclined branched columnar stromatolites, where microbes adapt to the current direction through directional growth, and biomineralization dominates lamina formation, preventing clastic particles from entering the laminae; the low-energy stage forms layered stromatolites with continuous and gentle laminae [29].

This case is the first to systematically confirm the direct control of hydrodynamic energy on stromatolite morphology, and its "morphology-hydrodynamics" response model can be applied to the study of other high-energy shallow marine stromatolites worldwide. Meanwhile, the pure carbonate composition of stromatolite laminae indicates that the biomineralization capacity of Ediacaran microbes has been significantly enhanced, providing clues for understanding the origin of later bioherms.

## **5. Earth System Significance of Neoproterozoic Stromatolites**

### **5.1. Witnesses of Biological Evolution**

Neoproterozoic stromatolites completely record the evolutionary history of microbial communities, serving as an important window for tracing the origin and diversification of early life.

The microbial composition of stromatolites evolved from a single cyanobacterial community in the early stage to a complex community of cyanobacteria-heterotrophic bacteria-eukaryotic algae in the late stage. The hemispherical radiating

fibrous fabric mutation at 850–800 Ma marks the origin of cyanobacterial calcification capacity, which is a key evolutionary event for microbes to adapt to oxidizing environments; the appearance of spherical and filamentous eukaryotic algal fossils in Ediacaran stromatolites indicates that eukaryotes began to participate in stromatolite construction, laying an ecological foundation for the rise of the Ediacaran biota.

The morphological diversification of stromatolites reflects the expansion of microbial ecological niches. From the single ecological adaptation of large conical-columnar stromatolites in the early stage to the coexistence of multiple morphologies (conical, columnar, digitate, and layered) in the late stage, it reflects the precise adaptation of microbial communities to different hydrodynamic, redox, and nutrient conditions. The specialized morphology of manganese stromatolites in Chengkou represents the adaptive evolution of microbes to special metal element environments, serving as a typical example of the coevolution of life and the environment.

## 5.2. Natural Archives for Paleoenvironmental Reconstruction

The morphological characteristics and geochemical composition of stromatolites provide high-resolution data for reconstructing the Neoproterozoic paleo-ocean and paleoclimate, and their environmental indicative significance has been confirmed by multidisciplinary evidence [30].

In terms of paleo-ocean physical environment reconstruction, stromatolite morphological parameters can quantitatively restore paleo-water depth and hydrodynamic energy: conical stromatolites indicate a shallow marine environment of 5–20 m, while layered stromatolites correspond to a deeper environment of 20–50 m[31]; branching frequency and column inclination angle can quantitatively estimate current velocity. The inclination angle of stromatolites in the Salitre Formation indicates that they were formed in a high-energy environment with a flow velocity of 0.2–0.5 m/s [32].

In terms of paleo-ocean chemical environment reconstruction, the multi-isotope system of stromatolites provides comprehensive evidence: carbon isotopes record fluctuations in the global carbon cycle (Halverson et al., 2005), chromium isotopes reveal the evolution of atmospheric oxygen content, nitrogen isotopes reflect the oxidation degree of the marine nitrogen cycle, and manganese stromatolites indicate the enrichment process of metal elements [33]. The Sr isotope ratio ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) of stromatolites in the Jiuliqiao Formation of Huainan is 0.708–0.710, indicating enhanced continental weathering and increased nutrient input during transgression [34].

In terms of paleoclimate reconstruction, the rise and fall of stromatolites are closely coupled with Snowball Earth events: the absence of stromatolites during glaciations reflects a global low-temperature and arid environment, the rapid recovery of stromatolites during interglacials indicates climate warming [35], and the development of manganese stromatolites is related to the warm and humid climate conditions after glaciations [36].

## 5.3. Driving Markers of Earth System Evolution

The evolutionary process of stromatolites is closely related to the multi-sphere interactions of the Neoproterozoic Earth system, serving as an important marker of the Earth systems

transition from "low oxygen-simple life" to "high oxygen-complex life"[37].

The coupling between stromatolites and the atmosphere is reflected in the coevolution of oxygen content. Cyanobacterial photosynthesis is the main source of oxygen increase in the Neoproterozoic. The widespread development of stromatolites means an increase in cyanobacterial biomass, directly driving the Second Great Oxidation Event [38]; the increase in atmospheric oxygen content further promotes cyanobacterial calcification, triggering the stromatolite microstructural mutation at 850–800 Ma[39], forming a positive feedback cycle of "photosynthesis-oxygen increase-biological calcification"[40].

The interaction between stromatolites and the lithosphere is manifested in the regulation of tectonic movements and the linkage of material cycles. The shallow marine basins formed by the breakup of the Rodinia supercontinent provide sedimentary space for stromatolites, while nutrients (such as nitrogen and manganese) input by volcanic activities promote microbial growth and mineralization; the carbonate precipitation and siliceous cementation processes of stromatolites participate in the carbon-silicon cycle of the lithosphere, regulating the global climate [41].

The interaction between stromatolites and the hydrosphere is reflected in the modification of the marine chemical environment. Microbial metabolic activities change the pH, Eh values, and element composition of seawater [40]. The formation of manganese stromatolites consumes  $\text{Mn}^{2+}$  in seawater [42], and cyanobacterial photosynthesis consumes  $\text{CO}_2$ , jointly promoting the transformation of the ocean from anoxic to oxidizing conditions, creating favorable conditions for the rise of eukaryotes.

## 6. Research Prospects

Although significant progress has been made in Neoproterozoic stromatolite research, there are still many scientific issues to be solved. Future research should carry out in-depth studies from the following four aspects:

(1) Precise analysis of microscopic mechanisms. Existing research lacks direct evidence for the microbial community structure of stromatolite formation. It is necessary to combine transmission electron microscopy (TEM), focused ion beam scanning electron microscopy (FIB-SEM), and high-throughput sequencing technology to reveal the interaction between cyanobacteria, heterotrophic bacteria, and eukaryotic algae; quantify the contribution ratio of microbial trapping and binding to biomineralization through isotope tracing technology (such as  $^{13}\text{C}$  labeling), and establish a more accurate construction model.

(2) Global comparison and evolutionary laws. Current research is mostly limited to a single block, lacking systematic global comparison. It is necessary to establish a global Neoproterozoic stromatolite database, carry out morphological and geochemical comparisons of stromatolites in the margins of North China, South China, Gondwana, and Laurasia, clarify the impact of the breakup of the Rodinia supercontinent on stromatolite distribution, and reveal the unity and differences of global stromatolite evolution.

(3) Mechanism of eukaryote impact. The decline of Ediacaran stromatolites coincides with the rise of eukaryotes in time, but the causal relationship between them is not clear. It is necessary to track the evolutionary history of eukaryotes through molecular fossil analysis (such as steranes and hopanes), simulate the competitive relationship between

eukaryotes and cyanobacteria combined with ecological niche models, and clarify the specific impact mechanism of eukaryote rise on stromatolite construction.

(4) Multi-sphere interaction model. Existing research mostly focuses on single-factor analysis. It is necessary to integrate sedimentological, paleontological, geochemical, and tectonic geological data to establish a "microbe-atmosphere-ocean-lithosphere" multi-sphere interaction model, quantify the contribution of each factor to stromatolite evolution, and provide a more complete theoretical framework for understanding the Neoproterozoic Earth system transition.

## 7. Conclusions

Neoproterozoic stromatolites show distinct spatiotemporal distribution characteristics, mainly concentrated in low-latitude epicontinental seas and carbonate platform margins. They can be divided into six categories: conical, columnar, digitate, layered, layered-columnar transitional, and manganese types, experiencing three evolutionary stages: 1000–850 Ma conical-columnar dominated, 850–635 Ma microstructural mutation and diversification, and 635–541 Ma decline and specialization.

The formation and evolution of stromatolites are controlled by multiple factors including microbes, sedimentary environment, geochemistry, structure, and climate: the trapping and binding as well as biomineralization of cyanobacteria are the core construction mechanisms, and the calcification revolution at 850–800 Ma significantly changed their structure; hydrodynamic energy, water depth, and sediment input determine morphological diversity; marine redox state and carbon-nitrogen-sulfur cycles affect their development by regulating microbial metabolism; plate movements and Snowball Earth events indirectly regulate their distribution by changing paleogeography and paleoclimate.

Case studies in typical regions have confirmed the environmental indicative value of stromatolites: stromatolites in the Jiuliqiao Formation of Huainan record a complete sea-level rise and fall cycle, manganese stromatolites in the Doushantuo Formation of Chengkou provide direct evidence for biological mineralization, and stromatolites in the Salitre Formation of Brazil establish a "morphology-hydrodynamics" response model.

Neoproterozoic stromatolites are witnesses of biological evolution, natural archives for paleoenvironmental reconstruction, and driving markers of Earth system evolution. Their evolutionary process reflects the multi-sphere interactions between microbes and the atmosphere, ocean, and lithosphere, providing key empirical evidence for understanding the transition from "low oxygen-simple life" to "high oxygen-complex life".

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