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Review

Stromatolites and Their "Kin" as Living Microbialites in Contemporary Settings Linked to a Long Fossil Record

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Abstract: Organo-sedimentary deposits that result from fine-grained sediment trapping, binding, and likely precipitation (of carbonate) by microbes in flat-mat, branching, and dome-shaped constructions are termed microbialites. They were first identified as stromatolites by paleontologists well before the discovery of cyanobacteria that build the same kinds of structures in contemporary settings around the world. Earth's earliest life forms were prokaryotes (bacteria and bacteria-like forms) that reproduced under anaerobic conditions and later produced increasingly aerobic conditions. Stromatolites persisted through later Archean and Proterozoic times through the subsequent Phanerozoic to the present. At the start of the Cambrian Period 538 million years ago, stromatolites continued alongside rapidly diversifying plant and animal phyla during the Cambrian explosion of eukaryotic life, which have complex cells with internal structures and tissue-grade organization in multicellular taxa. The type locality exhibiting clear examples of stromatolite structures is conserved at Lester Park near Saratoga Springs in northeastern New York State. Paleontologist James Hall (1811–1898) was the first in 1884 to assign a Latin binomen (*Cryptozoon proliferum*) to stromatolite fossils from Lester Park. Thereafter, reports on formally named stromatolites proliferated, as did examples from virtually all subsequent geological time intervals including the Pleistocene Epoch. However, recognition that living cyanobacteria formed stromatolites identified as *Cryptozoon* took place much later in 1961 with the announcement by geologist Brian W. Logan (1933–2008) who described modern constructions in Hamlin Pool, Shark Bay, Western Australia. Initially, Shark Bay was regarded as a one-of-a-kind sanctuary for stromatolites living under restricted conditions with elevated levels of salinity that prohibited competition or grazing by eukaryotes. Most notably, among other settings with living stromatolites discovered and described since then are the Bahamas, East African rift lakes, Mexico's Baja California, and saline lakes in Argentina. This report reviews the history of discoveries of modern-day stromatolites, more commonly called microbialites by biologists. All are predicated on the ground-breaking efforts of geologists and paleontologists who first described fossil stromatolites but were unaware of their living counterparts. The Lester Park locality is highlighted together with a master list of other North American localities that feature purported Cryptozoons.

Keywords: prokaryotes; eukaryotes; cyanobacteria; organo-sedimentary structures; oligotrophs; extremophiles

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1. Introduction and Perspective

Dominant groups of larger organisms preserved as fossils are used to name popular divisions of geological time even though those groups have much earlier or later occurrences in the rock record. Thus, an "Age of Dinosaurs" is a casual term for the Mesozoic Era ca. 251–66 Ma (where Ma is "million years ago"), even though dinosaurs have a late, ca. 233 Ma, oldest occurrence and their feathered cousins (birds) persisted through the subsequent "Age of Mammals". Earlier still, an "Age of Invertebrates" characterizes the Paleozoic Era (ca. 538–251 Ma) though marine invertebrates persist to the present and had a somewhat earlier first appearance. Similarly, the record of bioconstructed rocks at a macro-scale could be termed the “Age of Stromatolites”, with macroscopic planar, domal, and columnar build-ups formed by microbial microorganisms appearing at ca. 3.45 Ga (where Ga is “billion years ago”), which contributed to the photosynthetic production and accumulation of oxygen [1,2]. There is no convenient upper bracket to this fundamentally important “Age of Stromatolites” as stromatolites persisted through the origin and diversification of the Cambrian Evolutionary Radiation at ca. 538 Ma [3] and, as reviewed herein, occur in modern aqueous environments.

Humans perceive the living world to be dominated by relatively large (macroscopic) organisms referable to three biological kingdoms: multicellular higher plants and animals, with a passing awareness of fungi. These groups are eukaryotes with complex cell structures characterized by a nucleus and other organelles enclosed by intracellular membranes and capable of asexual cell division by mitosis and production of sexual cells (gametes) by meiosis. Organisms classified in these kingdoms thrive under aerobic conditions and multiply by sexual reproduction but also by asexual reproduction in certain cases. Biologists recognize five kingdoms, which include unicellular protoctists (commonly termed “protists”) as a fourth kingdom that share the same cellular and reproductive characteristics as animals and plants [4].

Unseen by the human eye, the fifth kingdom is yet more diverse and divided between two types of bacteria: the eubacteria (commonly termed “bacteria”) and the archaea. They are exclusively unicellular with a prokaryotic organization lacking a separately enclosed nucleus and with cell reproduction reliant on binary fission. During the first four billion years of Earth’s development, the two groups reigned supreme with the archaea living under anaerobic conditions before sufficient oxygen became available by the activity of photosynthetic eubacteria [5]. Both kinds of prokaryotes continued to exist with the other four kingdoms that exploded in diversity at the beginning of the Phanerozoic (or “visible life”) Eon at 538 Ma, coincident with the start of the Cambrian Period. Exactly when the earliest prokaryotes appeared during the Archean Eon remains under debate, but evidence from the 3.4 Ga Strelley Pool Chert in Western Australia supports multiple physical settings in which the archaea proliferated in zones interpreted as peritidal, rocky-shore, and reef-like environments [6]. The term “stromatolite” is applied to these early forms in a general way to emphasize a shared organization based on laminate structures.

Meaning “layered rock”, the word “stromatolith”, anglicized to “stromatolite”, was introduced to the scientific literature in 1908 [7] by the German geologist Ernst L. Kalkowsky (1851–1938) to define laminar structures previously described in the literature as having possible non-biologic and biologic origins, including animal relationships. Shortly after, the role of microbes in sediment trapping, binding, and perhaps cementation in producing late Proterozoic stromatolites was proposed [8,9]. Confirmation of fossilized microbes associated with stromatolites was first recognized in 1965 on the basis of evidence from the two-billion-year-old Gunflint Chert of Ontario, Canada [10]. Subsequently, additional evidence of fossil microbes from stromatolites preserved in Precambrian rocks in Australia and Siberia became widely publicized [11].

Fossilized microbes from the Cambrian of northwestern China’s Tarim Basin as well as He’nan Province are also well documented [12,13]. Fossil and present-day microbialites are comparable in having filaments that encase a string of individual bacterial cells within a larger network of layered films or mats. Cell damage by ultraviolet light in shallow water is limited in living stromatolites by filaments coated with mucus. Strands with a thickness of only 10 µm elongate as neighboring cells encased within multiply through binary fission. The exposed surface of mat-forming and domed structures is thus able to fix and bind fine sediment from the water column until a new layer of microbial growth is added above. Oxygenated water in this environment provides for aerobic respiration of bacterial cells, but archaea colonies may thrive below the surface where anaerobic conditions prevail within a given stromatolite structure. Thus, modern stromatolites and their functional biology can be linked to analogs by a shared design based on fossilized microbes that persisted as procaryotes from the remote geologic past.

The goals of this review are two-fold: (1) to summarize the history of ongoing discoveries on the life properties and environments of modern stromatolites in varied settings around the world and (2) to review the history of discoveries made by paleontologists that outline the success and persistence of stromatolites through geologic time. A particular emphasis is given to the recognition and conservation of the site at Lester Park in eastern New York, which is relevant to ancient stromatolites in terms of what may be regarded as the "type locality" for stromatolites. Additional background material is provided to illustrate how the descriptive terminology has advanced by a growing knowledge of the complexities in stromatolite morphology. Examples of stromatolites as recognized in Cambrian strata are reviewed to show the current status of studies, particularly in North America.

2. Background Geography and Geological Oceanography

On the basis of the original definition [4], stromatolites and their past and present kinship are almost exclusively aqueous in habitat, although rare exceptions are recognized with the production of layered (i.e., stromatolitic) structures by lichens in the formation of caliche in subaerial (albeit wet) environments [14]. Examples from the geologic record include common occurrences of stromatolites in shallow marine (i.e., well-illuminated) conditions during intervals characterized by globally high sea levels and extensive shallow marine shelves. The type reference locality for fossil stromatolites is at Lester Park in northeastern New York State on a Late Cambrian (Furongian Epoch, ca. 490 Ma) tropical marine shelf marginal to ancient (i.e., 1.0 + Ga, Mesoproterozoic) basement rock of the Adirondack massif on the Laurentia ("ancestral North America") paleocontinent (Figure 1, dot 1). The ancestral North American continent was in a different position during that time and the Adirondacks and its surrounding marine shelf were located at ca. 35° S in the southern hemisphere in a fully tropical setting [15].

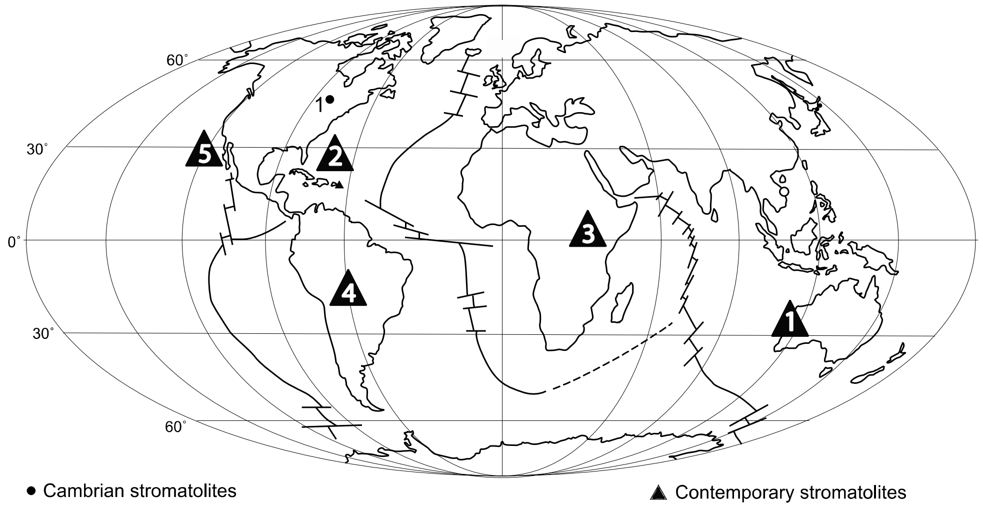

Figure 1. Global representation of today's continents and oceans on a Mollweide projection showing major ocean spreading zones. Numerals on black triangles denote the locations of oligotrophic stromatolites living today in (1) Shark Bay, Western Australia; (2) Bahamas; (3) Lake Tanganyika, Africa; (4) saline lakes in northwestern Argentina; and (5) saline ponds in Mexico's Baja California. The numbered black dot marks the location of fossil stromatolites from present-day Upper New York State (1).

In the context of paleoceanography and paleoclimatology, stromatolites and kin are disproportionately reported from carbonate platform successions, and thus are primarily tropical to subtropical in ancient and modern occurrences. However, siliciclastic stromatolites are known in mixed carbonate and siliciclastic facies, and this suggests that early cementation by carbonate mineral (calcite and aragonite) cementation in mats was prominent in lending rigidity to the form of stromatolites and kin [16]. Locally, rhodochrosite (manganese carbonate) and typical carbonate stromatolites occur in high temperate latitude Middle Cambrian deposits in Maritime Canada and North Wales on the Avalonia paleocontinent. These Avalonian stromatolites mantle depositional early Middle Cambrian depositional sequence unconformities where their development as the first deposits during epeirogenic onlaps may reflect a sort of sedimentary condensation with restriction of siliciclastic sediments to adjacent on-shore facies [17,18]. A middle latitude occurrence at 43° N is shown by calcareous thrombolites (discussed in Section 3.2) and large (baseball-size) spherical microbialites at Green Lake State Park near Syracuse, New York [19]. Thrombolites were defined for the first time by Aitken in 1967 [20] as distinctly non-laminated bodies characterized by a clotted fabric.

Living stromatolites and related microbial build-ups from Hamlin Pool in Shark Bay occur in an intertidal to shallow subtidal setting in Western Australia on the Indian Ocean (Figure 1, triangle 1). Somewhat deeper habitats for microbial build-ups also appear off the Exuma Cays in the Bahamas in the eastern Atlantic Ocean (Figure 1, triangle 2). In contrast, large domal microbial build-ups are found in lakes in the East African Rift System, including Lake Tanganyika (Figure 1, triangle 3), as well as in interior western Argentina in South America (Figure 1, triangle 4). Finally, mat-forming stromatolites are restricted to high-salinity coastal and island lagoons along Mexico’s Gulf of California (Figure 1, triangle 5). All represent contemporary settings that entail elevated salinity with the exception of the Exuma Cays in the Bahamas. In effect, the geographical spread of known living stromatolites is reliant on settings where competing eukaryotic life is limited or excluded.

3. Definitions and Review Methods

3.1. Growth of Stromatolites and Kin

Studies on the morphogenesis of living and fossil stromatolites that followed after the first introduction of the term “stromatolite” [4] typically focus on intrinsic or internal biological factors that affect the growth of an organo-sedimentary structure as opposed to competing extrinsic or environmental factors [9]. Internal factors entail the production of extra-cellular polymeric secretions (EPSs) that make mucus coatings on the filaments housing microbial cells but also the biomineralization that cements laminae.

3.2. Types of Microbialites

Additional terms that differentiate several types of microbialites from densely laminated stromatolites are important in the discussion of these ancient and modern build-ups and are reviewed in [2,17]. Although the terminology for microbialite build-ups is sometimes vague and contradictory [2], the consistent confusion of stromatolites with “thrombolites” should be corrected [16]. As first described in 1967 by Aitken [20], thrombolites differ significantly from stromatolites due to reticulopodial protists that disrupt the lamination of these marine and freshwater microbialites and create voids [21]. What this means is that stromatolites are the earliest appearing microbialite build-ups, while thrombolites appear only later in the Neoproterozoic, seemingly with the appearance of eumetazoans, as the earliest indication of the Cambrian Evolutionary Radiation. Technically, it should not be said that a thrombolite is a specific sub-category of a generalized stromatolite. Along with stromatolites and thrombolites, three additional types of late Proterozoic–modern microbialite build-ups are part of the lexicon, as shown in [2,16]. Dendrolites feature columnar build-ups that are shrub-like but lack laminae. Leiolites, commonly called mud mounds, are internally structureless, very fine-grained, and commonly dome-like, but include irregularly formed shapes sometimes at a different scale. Finally, MISS (microbially induced sedimentary structures) are typically siliciclastic, laminated structures that can often be shown to be cohesive and relatively “plastic” during formation.

3.3. Macroscopic Form of Stromatolites and Kin

Extrinsic factors affecting stromatolite morphology include the nature of suspended sediment in the water column, water salinity, relative availability of nutrients, sunlight intensity, and wave or current activity that may abrade build-ups or focus growth and are responsible for the shape of the build-up. The combination of these factors is responsive to simulations based on a stochastic model to illustrate different structural shapes that range from flat mats to simple domes and to branching forms with variable morphology described as stubby, tuberous, divergent branches, or ragged columns [22].

Yet another consideration relates to the more formal naming of stromatolites based on the Linnean binomial system of nomenclature. Now outmoded and essentially of historical interest in the opinion of many workers, this has meant that genera and species names have been proposed in the literature based primarily on the morphological shape of a stromatolite build-up and other structural details (e.g., presence/absence of columnar build-ups and their shapes). A Linnean nomenclature has primarily been the practice in Precambrian build-ups where the detailed morphology is thought to be useful in biostratigraphic correlations. Modern microbialite build-ups occur worldwide (Figure 1), and can be compared with fossil examples based on the authors' experience.

4. Results

4.1. Review of Contemporary Regions with Stromatolites and Kin

In this section, five regions widely spread around the globe with living stromatolites (Figure 1) are described as a sample of key localities based on published materials and from personal experience in two of those locations.

4.1.1. Hamelin Pool, Shark Bay, Western Australia

The Western Australia coast along the Indian Ocean (Figure 2a) includes the Shark Bay World Heritage conservation area that was designated in 1991 by the United Nations Educational, Scientific and Cultural Organization (UNESCO). Located at the inner southeast corner of Shark Bay within the World Heritage zone, (Figure 2b), an over-lapping conservation zone is maintained by the Western Australia Department of Parks and Wildlife. This zone is designated as the Hamelin Pool Marine Nature Reserve. Hamelin Pool is famous for its living stromatolites (Figure 1, triangle 1). It is protected within an adjoining land and marine district covering 127,000 hectares that includes a nature center and boardwalk, allowing visitors to explore the intertidal to shallow subtidal zone without damaging wildlife. A scientific paper from 1961 by geologist Brian W. Logan [23] described the stromatolites at Hamelin Pool, which at that time was the only place in the world where living stromatolites were recognized. The average salinity of marine water at Hamelin Pool is 65 parts per thousand, which is nearly twice the salinity of normal seawater. Few eukaryotic organisms are able to tolerate such a high salinity and it is argued that the lack of competition, as discussed below, by encrusting eukaryotes or by eukaryote grazing with disruption of the microbial mats is the principal reason why the stromatolites are able to thrive there. The Latin binomen *Cryptozoon proliferum*, meaning proliferating hidden animal (with the frequently coalesced domes suggesting the tubers of the common onion, *Alium proliferum*), was initially assigned to the Australian stromatolites, following the usage first applied to fossil stromatolites in New York State, USA, by paleontologist James Hall in 1884 [24]. In this section, the Hamelin Pool microbialites are loosely designated "stromatolites", though their structure has long been known to be transitional into thrombolites [25], with intertidal forms in nearby Lake Clinton dominantly thrombolites and stromatolites restricted to the upper intertidal zone [26].

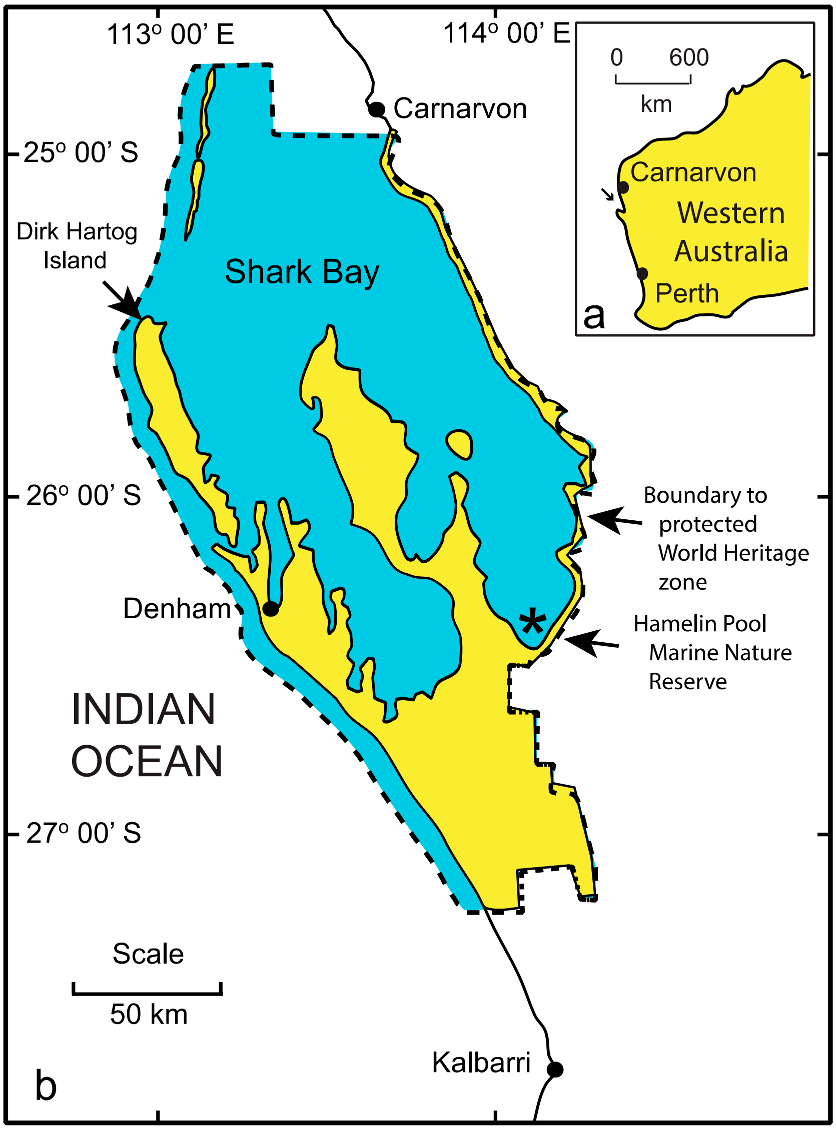

Figure 2. Maps showing the coast of Western Australia on the Indian Ocean: (**a**) Western Australia with a small arrow pointing to Shark Bay; and (**b**) enlargement showing the location of the Hamelin Pool Marine Nature Reserve (asterisk) within the UNESCO World Heritage zone protecting the greater Shark Bay.

Variations in stromatolite morphology are readily observable at Hamelin Pool [27]. The dominant forms are represented by thin club-shaped or stockier stool-shaped stromatolites that rise from intertidal to very shallow subtidal waters to a height of 50 cm or more. The visitor to the Hamelin Pool Marine Nature Reserve will observe that stromatolites exposed along the inner shore during low tide are stony hard. These are not living stromatolites but the semi-fossilized remains of stromatolites that lived during the recent past before the coastal zone underwent exposure due to epeirogenic rise 1000 years ago [28]. Exposure to subaerial conditions at the shore over time caused the surface layers with delicate microbial films to dry out. A distinctly local variation in morphology is discernable among the stony stromatolites close to shore. These are markedly loaf-shaped or elongated stromatolites oriented with the long axis perpendicular to the shore. Structures that are individually 12 to 15 cm high, 9 to 15 cm wide, and 40 to 50 cm long are fully exposed at low tide (Figure 3a). They are barely covered by water during the returning tide (Figure 3b). These stromatolites are oriented in a uniform direction with roughly 10 to 20 cm of open space in between each "bread loaf". The logical explanation for this shape is due to the influence of tidal currents washing back and forth along the shore. The shapes are well preserved in three dimensions, with all surfaces being stony hard. The upper surfaces are smooth to the touch and exhibit patches of iron-brown discoloration, which is likely due to oxidation. Clearly, there was a failure of extra-cellular polymeric secretions (EPSs) necessary to keep exposed surfaces sticky with mucus.

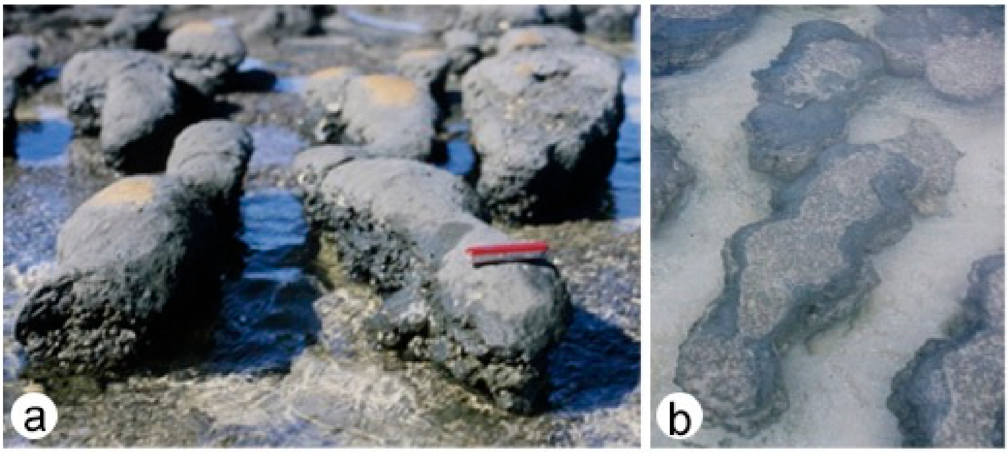

Figure 3. Examples of stromatolites shaped like large bread loaves oriented perpendicular to the shore at the Hamelin Pool Marine Nature Reserve, Shark Bay: (**a**) stromatolites exposed during low tide (pocket knife 9 cm long for scale); (**b**) stromatolites barely awash at high tide with narrow, open galleries from 10 to 20 cm wide.

Living stromatolites occur offshore, where club-shaped and dome-shaped structures are prevalent in the subtidal. Samples on display from this zone in the nature center are cut vertically to exhibit interior layering typical of the club-shaped or stubby morphotype [27] and have an internal fabric indicative of thrombolites.

During a 1968 visit by the junior author to Carbla Point on the mainland a short distance north of Hamelin Pool, the opportunity arose to swim into subtidal waters where stromatolites the size of large footstools rise from the seafloor (Figure 4). Structures roughly 50 cm high with an upper-surface diameter of 50 cm to 100 cm are closely spaced with narrow open passages in between. These were found to be living stromatolites. A forefinger could be poked through the surface to a depth of 5 cm to feel mucus characteristic of extra-cellular polymeric secretions (EPSs). Below that depth, the structure was dense and hard. Presumably, the inner core of these structures is stony and dead. A more nuanced overview of eight different morphotypes around the margins of the Hamelin Pool Marine Nature Reserve provides further insight into the spatial relationship of different stromatolite morphotypes through the mapping of bathymetrical zones. These zones separate stromatolites with an elongated loaf shape from those with a club shape or footstool shape, and those characterized by a massively tabular structure from the merger of multiple columnar heads [27].

4.1.2. Exuma Cays in the Bahamas of the Western Atlantic Ocean

Following the growing interest in living stromatolites in Western Australia's Shark Bay, the next major discovery was in the Bahamas in the western Atlantic Ocean (Figure 1, triangle 2). Columnar stromatolites up to 2 m in height were found to be growing at depths as much as 8 m in current-swept channels off the Exuma Cays on the eastern bank of the Bahamas [28,29]. The stromatolites occur in rows. The laminae in the columns are produced by microbes that trap carbonate sand, including ooids and pelletal material stirred up by waves and currents into the water column. The adjacent Exuma Sound marks a precipitous drop-off into deeper water open to the Atlantic Ocean. Seawater carried by the tides onto the bank is within the range of normal salinity (37 to 38 parts per thousand). However, water salinity increases during ebb tide to reach as much as 40 parts per thousand [29].

Tidal flow rates between 60 and 100 cm s^{-1} were concluded to be the primary reason why the stromatolites remain free from disturbance by potential grazers. Thereafter, expanded research on stromatolite distribution in the Bahamas revealed that localities within the Exuma Cays are far more extensive, amounting to more than a dozen sites that exhibit tabular, ridge-forming, and columnar examples in waters mostly between 2 and 3 m in depth but as much as 10 m deep [30]. The upshot of this research was the pronouncement that Bahamian stromatolites are "uncommonly common".

Figure 4. A field of living stromatolites in permanently subtidal seawater offshore Carbla Point near Hamelin Pool in Shark Bay. Junior author for scale.

4.1.3. Lake Tanganyika in the East African Rift System

Living and fossil stromatolites are known from a freshwater setting in Lake Tanganyika (Figure 1, triangle 3), which occupies a branch of the great East African Rift System [31]. Occupying a series of structural grabens, the lake is the largest of the African rift lakes. It has a maximum depth of 1470 m and is considered the second-deepest lake in the world after Russia's Lake Baikal. As a result of investigations by SCUBA divers in 1997, at least 22 stromatolite-bearing localities are known mostly along the eastern side of the 800 km-long lake [31]. The depth of water in which the freshwater stromatolites were found to thrive ranges between 4 and 46 m, with 46 m being only the limit that the divers were able to reach.

The stromatolites occur in isolated patches, taking the form of biohermal accumulations with a diameter of tens of meters with the intergrowth of domes and columns. Variations in shape include stratiform encrustations that cover boulders to vertical walls, dome-shaped structures, and branching columns. The saturation of lake water by carbonates including calcium and magnesium is elevated, more so during the dry season. Microbes are described as responsible for producing fine-scale laminations that fit with the traditional description of stromatolites as opposed to thrombolites. The principal fauna associated with the stromatolites is dominated by the freshwater gastropod *Paramelania imperialis*, which is unusually large and thickly shelled; these characteristics are perhaps coincidental with the lake's uniquely calcium-rich water chemistry [32]. The gastropods are equipped with mouth parts that function for rasping algae, but the stromatolites apparently are not overgrazed. In turn, the gastropods are preyed on by crabs.

4.1.4. Saline Lakes of Northwestern Argentina

Preliminary information indicates giant stromatolites in hypersaline pools surrounded by salt flats on the arid plateau in the Puna de Atacama district of northwestern Argentina in the Salta Province [33,34]. Geologist Brian Hynek from the University of Colorado at Boulder and microbiologist Maria Farías from a consulting firm in Argentina first identified a region with a system of salt lagoons by satellite imagery in April 2022 and subsequently visited the remote region bordered by northern Chile (Figure 1, triangle 4). Not easily accessed, a dozen salt lagoons are spread over an area of 10 hectares located 1880 km northwest of Buenos Aires. The coalescing stromatolites in the Argentinian salt lagoons are dome-shaped, up to 4.5 m in diameter, and a meter in height. Extremely dry and at an elevation of 3650 m above sea level, the salt flats are essentially devoid of plant and animal life. This represents one of the most exciting recent discoveries related to living stromatolites. Details on the microbial biology of the Argentine stromatolites have yet to be published but will be of much interest.

4.1.5. Hypersaline Pools from Islands in Mexico's Gulf of California

Stromatolites living in a sheltered lagoon on the Pacific shores of Mexico's Baja California peninsula were first reported in 1975 [35]. Their discovery was fortuitous, much as in the case of the sighting by geologist B.W. Logan of living stromatolites fourteen years earlier in Western Australia's Hamelin Pool [23]. Geologists who landed on Isla Ángel de la Guarda in Mexico's Gulf of California made the unexpected discovery of living stromatolites in hypersaline pools on that island [36]. The junior author (of this review) was part of the 2007 expedition. Strategically located 32 km east of Bahía de los Angeles on the peninsular mainland (Figure 5a), the island was named Guardian Angel because the settlement is sheltered from major storms in the lee of the large island. With an area of 936 km^2, it is the second-largest island in the Gulf of California (Figure 5b). The island is uninhabited except for populations of large lizards (*Sauromalus hispildus*) and the endemic rattlesnake (*Crotalus angelencis*). Local fishermen generally avoid the island's east-facing windward side due to highly changeable weather conditions. The 2007 expedition went to the south end of the island with the goal of mapping a small paleoisland that rises above the coastal plain as a volcano previously spotted by aerial reconnaissance (Figure 5b).

The paleoisland on Isla Ángel de la Guarda (Figure 5b) was first investigated in 2007. In carrying out that project, however, living stromatolites were discovered on the shores of two hypersaline lagoons (Figure 5c) [36]. The small lagoon (Figure 5c) is 375 m long and covers an area of approximately 2250 m^2, whereas the big lagoon extends for a distance of 1250 m and covers an area of approximately 125,000 m^2. Thrombolites having the shape of small cauliflower heads (Figure 6a) occur around the shores of the small lagoon. Regular stromatolites with thinly matted layers of black, mucus-rich matter occur in a wide band around the shores of the big lagoon, where the surface mud is encrusted with lime and deeply cut by desiccation cracks (Figure 6b).

For the team on Isla Ángel de la Guarda in 2007, the objective was quickly prioritized to consider how the lagoons formed in the first place. It is theorized that each pond began as an embayment open to seawater with normal salinity in the Gulf of California. Through time, cobbles and boulders transported across the opening by strong longshore currents during episodic storms closed off the bays, turning them into isolated ponds. Once fully cut off from the open gulf, intense evaporation of seawater isolated in the ponds resulted in hypersaline conditions. Salinity was measured at 148 parts per thousand, more than four times the salinity of normal seawater [36]. Erosional features that scar the outer berms enclosing the ponds show that spill-over by storm waves adds normal seawater from time to time and thereby modulates lagoonal salinity. Subsequent exploration farther north on both sides of Isla Ángel de la Guarda confirmed that living stromatolite mats also occur in other closed lagoons [37]. Moreover, Isla Ángel de la Guarda is not the only island in the Gulf of California with closed lagoons where stromatolites thrive under conditions of high salinity that qualify the inhabitants as extremophiles. The geographical range of microbialites in the region raises unanswered questions about how they are seeded from one island to another.

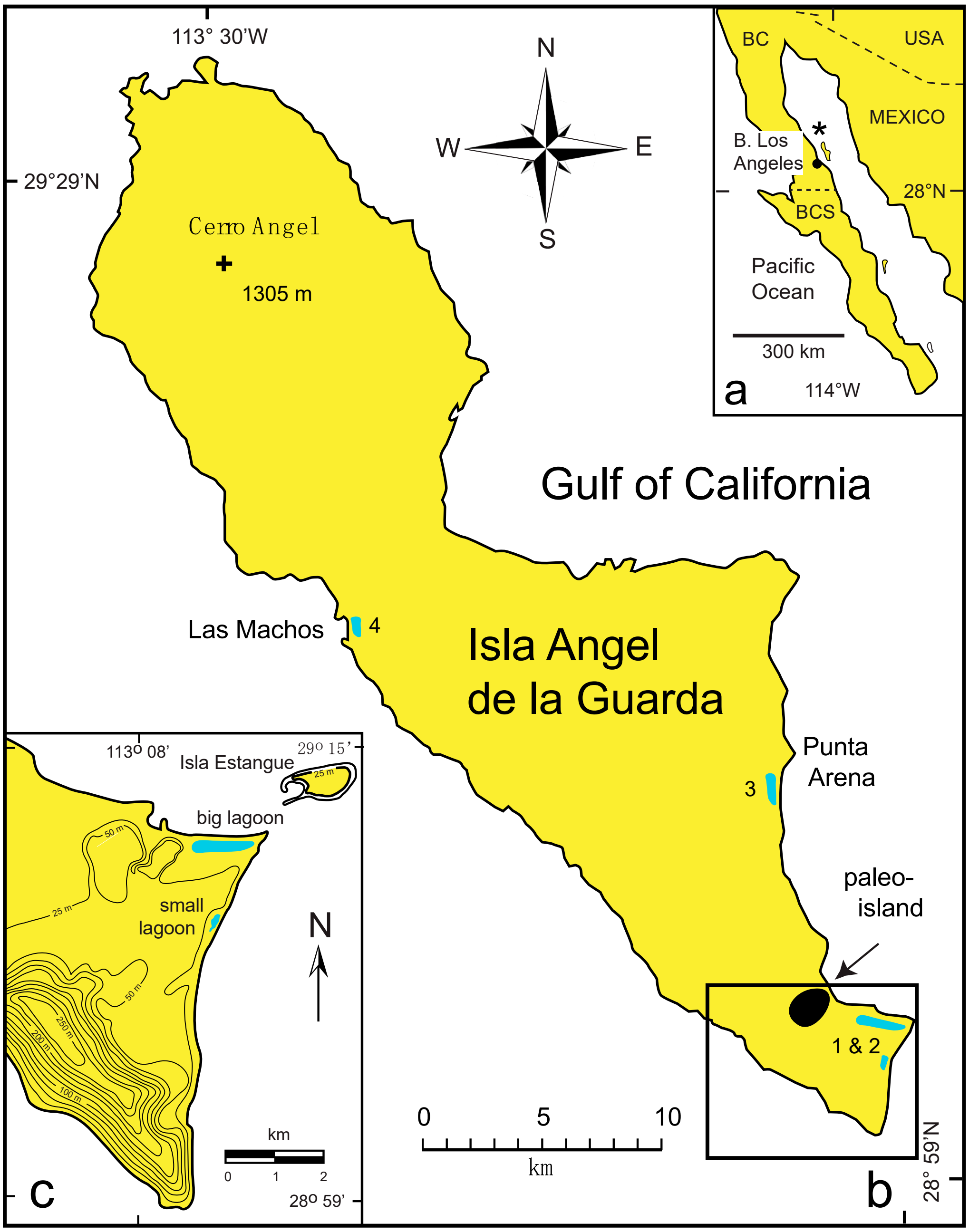

Figure 5. Maps showing Mexico's Isla Ángel de la Guarda in relation to the Baja California peninsula: (**a**) the full peninsula adjacent to the Gulf of California off the Mexican mainland with the island's location (asterisk) near the head of the gulf; (**b**) map of Isla Ángel de la Guarda marking the four localities (blue) where stromatolites occur in closed lagoons; and (**c**) topographic map enlarged from box in (**b**) showing the island's southeast end, where thrombolites and mat-forming stromatolites were discovered in 2007.

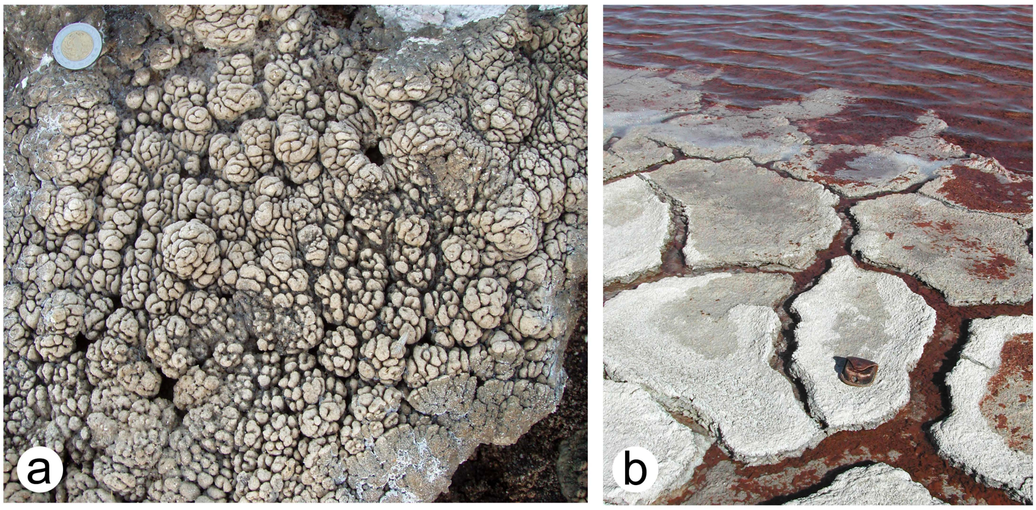

Figure 6. Photos showing living stromatolites from closed lagoons on the shores of southeast Isla Ángel de la Guarda (see Figure 5c for location): (**a**) thrombolite assemblage of branched forms the size of small cauliflower heads from the small lagoon (coin 2.4 cm in diameter for scale); (**b**) matted microbialites dissected by desiccation polygons along the shore of the big lagoon (compass case 10 cm across for scale).

4.2. Stromatolites from the Archean–Phanerozoic Eons

Comprehensive reviews of the temporal distribution of stromatolites and thrombolites [2,16] show their persistence in aqueous environments from their earliest known occurrence in the earlier part of the Archean (4.0–2.5 Ga) through to the present. Whether or not the oldest known (ca. 3.45 Ga) coniform build-ups with continuous laminae and calcite spar fabrics from the Pilbara craton, Western Australia, are stromatolites [38] was resolved with the recognition of microbial fossils in the build-ups and analysis that showed the presence of organic molecules [39]. Stromatolites are relatively rare in the Archean but abruptly appear as giant, elongate, decameter domes on the terminal Archean (2.55 Ga) carbonate platform in South Africa [40] and show mm- to cm-sized areas of calcareous cement [41], which may suggest the fabric of thrombolites.

Stromatolites show limited morphologic diversity in the earlier part of the Proterozoic Eon (2.5 Ga to 438 Ma). A purported abrupt increase in morphologic diversity characterizes the onset of the Mesoproterozoic (1.6–1.0 Ga) with diversity then falling progressively through the later Mesoproterozoic and reaching its lowest relative values at the end of the Proterozoic [16,42]. A significant development includes the appearance of calcified cyanobacteria at ca. 1.2 Ga [43], which led to the development of thrombolites by at least ca. 775 Ma [44]. A fall in pCO_2, and consequently higher marine pH and lower carbonate solubility, has been proposed as the environmental control that allowed calcification [45].

This 1.2 Ga change in oceanic geochemistry is, however, at odds with an interpretation that a purported fall in later Meso- and Neoproterozoic stromatolite morphologic diversity records the opposite change in oceanic geochemistry, i.e., a fall in carbonate saturation [16,45]. However, there does not seem to be a consistently defined trend in stromatolite diversity from the later Proterozoic into the early Phanerozoic in Western (i.e., English language) and Russian reports. As opposed to Western workers who emphasized verbal descriptions and comparisons of stromatolite morphology, the tradition of stromatolite workers in the USSR and Russia has been the use of a binomial nomenclature to distinguish stromatolites in the Riphean (ca. 1650–600 Ma, roughly equivalent to the Mesoproterozoic and most of the Neoproterozoic) and Vendian (ca. 600 Ma to base of Cambrian, roughly equivalent to the Ediacaran), e.g., [46]. Based on work on carbonate platform successions largely in Siberia, long-ranging "groups" (i.e., form genera largely based on the morphology of stromatolite columns) sequentially appeared and persisted through the Riphean, with a fall in diversity only in the Vendian and Cambrian, which show the origin of new "groups" [47].

An interesting development in some Proterozoic stromatolites is an alternation of calcite spar and micritic layers [16,48] that form dark–light layers interpreted as alternations of microbial mat and abiogenic crust and are also seen in the Late Cambrian *Cryptozoon proliferum* (discussed below). Spar-filled tubes that form a vermiform microstructure in the dark layers of *C. proliferum* were reported as first appearing in the Ediacaran [49] but are known in far older Proterozoic stromatolites [2].

The Phanerozoic featured a transient, abrupt increase in stromatolite morphologic diversity and high abundance of thrombolites in the Late Cambrian and Early Ordovician, while the younger Phanerozoic features a generalized stromatolite decline [16,43,50]. We are unaware of any explanation(s) of the efflorescence of Late Cambrian–Early Ordovician stromatolites. Indeed, no single factor may be involved. Their abundance may not reflect perturbations in pCO_2 (discussed above) but may be, in part, essentially an artifact of very high sea levels in this time interval [51]. Thus, very high eustatic levels would mean broad submergence of the large paleocontinents in this time interval. This would have led to extensive shallow shelf facies and widespread microbialite build-ups on large paleocontinents that were largely tropical [52] and in which carbonate supersaturation in shallow tropical seas would have promoted microbial and abiotic cementation of stromatolites and thrombolites. This explanation as a diversity sample area artifact may explain high Cambrian and Ordovician stromatolite and thrombolite diversity and abundance. However, the gradual diminishment of these litho/biofacies in the later Phanerozoic with resurgences in the Silurian, late Devonian–early Mississippian, early Triassic, and locally (in China) in the Jurassic and Miocene (Spain) is problematic [53].

A common explanation of this later Phanerozoic decrease and the common limitation of modern stromatolites to highly saline or freshwater environments (see modern localities, above) features the origin and diversification of animal metazoans, particularly mollusks. These animals would graze and destroy microbial films and, thus, preclude the onset and growth of microbialites; however, this interpretation is countered [54] by the presence of microbialite build-ups, as those noted above, in areas of normal marine salinity in tidal channels in the Bahamas. Examples such as the classic Late Cambrian stromatolite *Cryptozoon proliferum* and higher giant thrombolites at Lester Park, eastern New York (Figure 7), are also in unrestricted marine facies [15]. However, this association does not contribute to understanding the later Paleozoic decrease in stromatolite and thrombolite abundance because possible grazing metazoans (gastropods and polyplacophorans) are known from very rare fossil remains both locally and elsewhere. More importantly, encrusting metazoans are abundant after the Late Cambrian [55,56].

Thus, an alternative explanation of the decline in stromatolites, as well as thrombolites, after the Early Ordovician is metazoan competition and apparent changes in carbonate saturation in marine waters [55]. The origin and diversification of colonial reef-building corals, bryozoans, and other groups [57] and increased abundance of calcareous algae led to microbialite build-ups being out-competed for habitat space in shallow marine areas through the later Phanerozoic. After the Early Ordovician, a generalized long-term fall in pCO_2 took place [57], which should have promoted calcareous microbialite growth with higher pH and increasing marine carbonate saturation. However, for the resurgences listed above, higher stromatolite and thrombolite abundances in marine facies with increased carbonate saturation are not recorded. This further emphasizes that long-term eumetazoan competition for habitat area limits their abundance and occurrences generally to inhospitable (at least to grazing eumetazoans) habitats of highly saline water and freshwater. The alternative explanation of resurgences in microbialite abundance resurgences in the Phanerozoic may simply be the same as that suggested above for that in the Late Cambrian–Early Ordovician. The middle Paleozoic and Mesozoic resurgences appear to track eustatic levels and reflect increased habitat areas during times of highest sea levels but may also entail recovery from post-biological crises.

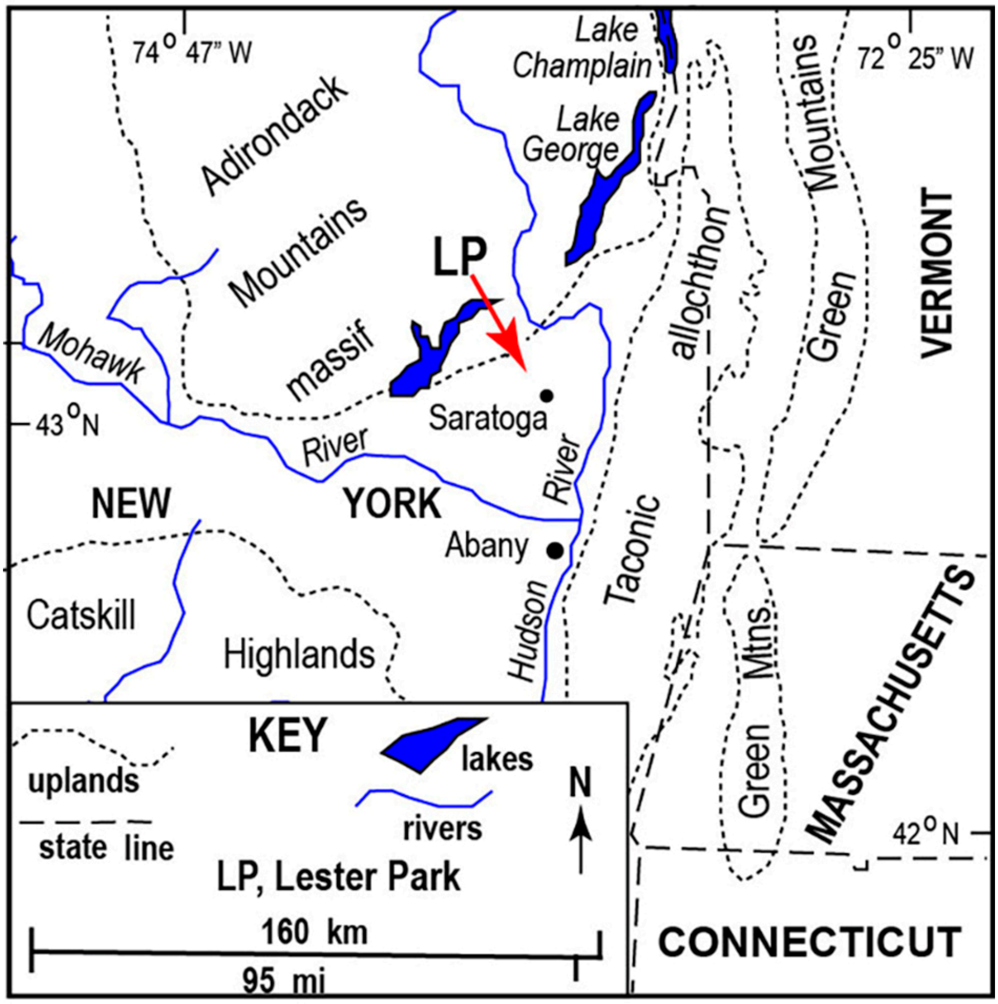

Figure 7. Location of Lester Park in the Upper Cambrian–Upper Ordovician lowlands southeast of the Mesoproterozoic Adirondack Mountains massif, northeast of the upper Middle Devonian Catskill Highlands, and west from the terminal Ediacaran–lower Upper Ordovician Taconic Allochthon.

4.2.1. Cambrian Stromatolites from Lester Park in New York State

The earliest named stromatolite received the binomial designation of *Cryptozoon proliferum* Hall, 1881 [24]. Almost all reports incorrectly report an 1883 naming of the species [2,58–66], as do such on-line international taxonomic databases as AlgaeBase and others [67,68]. The proposal for the genus and species is in the 1883 Thirty-sixth Annual Report of the State Museum of Natural History and was written in 1882. However, the report was printed and released with an 1884 cover. Hall's report [24] built on Steele's early description [69] of hundreds of domal structures that he regarded as inorganic concretions on a bedding surface in the Town of Greenfield just NE of Saratoga Springs, eastern New York. This extensive surface (ca. 500 m^2) immediately east of Lester Park Road (43°05′32.14″ N, 73°50′5342″) was part of the old Hoyt family farm and is now part of Lester Park Scientific Reservation (Figure 7). Lester Park was deeded to the New York State Museum in 1915 in honor of Willard Lester, Esq. [15,16,70]. The bedding surface extends ca. 1.0 km south to the Petrified Sea Gardens, a now-closed tourist attraction owned by the Pompa Bros. stone company, with this long exposure traditionally termed the "*Cryptozoon* ledge" [71].

The Lester Park surface (Figure 8a) is a ca. 490 Ma exposure of the Late Cambrian Laurentian (ancestral North America) shallow tropical platform [16,72]. The gently west-dipping (ca. 5°) surface is low in the Hoyt Member of the Little Falls Formation (here ca. 11.35 m exposed) and underlies the thrombolite-bearing strata in the Hoyt quarry ca. 75 m west (Figure 8b). Minor hydrothermal calcite and dolomite veins (Figure 9) that cut the stromatolite domes and surrounding limestone matrix were likely produced during the Taconic orogeny (ca. 460 Ma). The recovery of thermally blackened euconodont elements (color alteration index of 4.0) in the Lester Park area is consistent with burial temperatures in excess of 200 °C [73] and a ca. 7.5 km burial depth [74].

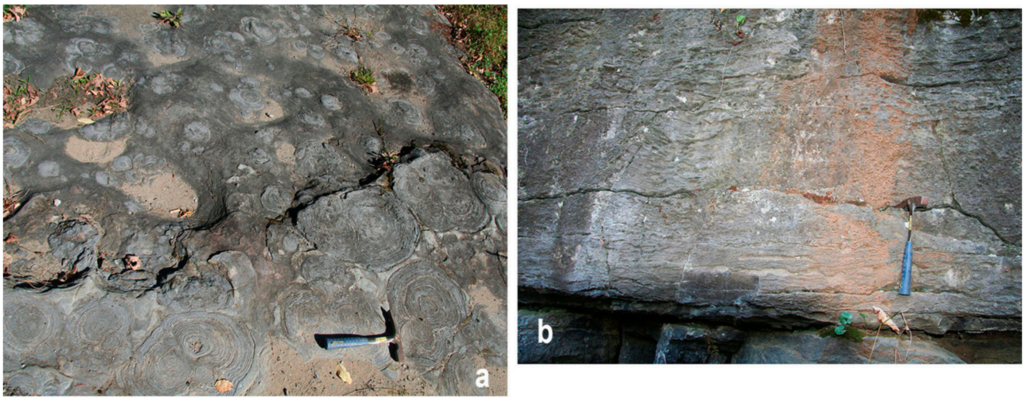

Figure 8. Coalesced topotype specimens of the first-named stromatolite *Cryptozoon proliferum* Hall, 1884, at Lester Park, Saratoga County, eastern New York: (**a**) View of the top of a shoaling cycle abraded and truncated to show growth laminae by the movement of coarse quartz sand that weathers brownish; narrower, lower parts of domes (upper part of the figure) were exposed by glacial (Pleistocene) plucking of the upper part of domes. (**b**) Detail of clotted thrombolite structure surrounded by bedded limestone from Hoyt quarry, ca. 5 m above the *C. proliferum* surface at Lester Park. Hammer (30 cm) for scale in both pictures.

Figure 9. *Cryptozoon proliferum* from older Galway Formation (lower Upper Cambrian *Elvina* Zone) NE of Lester Park shows two generations of fracturing: (1) brownish carbonate mud-filled cracks in the lower part of the specimen that separate and also run transverse to growth laminae are syndepositional fractures (ca. 490 Ma) and reflect continued extension of the rifted margin of NE Laurentia; (2) thin white calcite veins parallel to growth laminae produced during the Taconic orogeny (ca. 460 Ma) [74]. Hypotype NYSM 19512 from the middle of the Galway Formation railroad cut above U.S. Route 9 just N of the intersection of U.S. Route 9 with Daniels Road [74], with a USD 25 cent coin (23 mm) for scale.

The northern end of the bedding surface at Lester Park shows broad, coalesced, light grey weathering (i.e., limestone) *Cryptozoon* build-ups that have been truncated and show fine growth laminae (Figure 8a, lower part). The bedding surface underwent glacial plucking in the Pleistocene, which removed the tops of the build-ups and exposed the lower parts of the build-ups in the southern part of the Lester Park surface. The bases are embedded in buff weathering (i.e., dolomitic) fossiliferous ooid–fossil hash limestone and show a roughly E–W arrangement (Figure 8a, upper part of photograph). The upper parts of the domes were not truncated by glacial activity, as repeatedly reported [25,58–63], but were beveled during a shoaling cycle and are overlain by a brownish-weathering, coarse-grained sandstone (0–10 cm thick) [15,72].

An alternative explanation for the flat tops of the *Cryptozoon proliferum* build-ups at Lester Park is that they are analogous to modern, flat-topped thrombolites in hypersaline facies in Lake Clifton in Western Australia. These thrombolites can grow only as high as high tide levels and then expand laterally [26]. However, the specimen figured by Burne and Moore [26] as a “microatoll” shows erosional truncation of its top and lateral margins and is buried in a calcareous sandstone with clasts of *C. proliferum* (Figure 10).

Figure 10. Small *Crytozoon proliferum* dome at the north end of the Lester Park surface. This specimen was termed a “microatoll” [26], but it has an erosion-truncated top and lateral margins and is surrounded by a coarse-grained sandstone with light grey-colored *C. proliferum* clasts (yellow arrows).

Hall initially accepted Steele’s interpretation of the build-ups as non-biologic [75], but later, without explanation, followed Mather [76] who regarded them as “organic” and later referred to them as “sea plants” [77,78]. Hall’s [24,79] next taxonomic assignment shifted to some sort of marine animal (*Cryptozoon*, i.e., “hidden animal”). He regarded the form as similar to the much younger *Stromatopora* as understood then (now regarded as either a sponge or a hydrozoan). However, *Cryptozoon* differed, based on Hall’s quite early use of thin sections, by lacking tabulae and by having build-up shapes that did not have a broad base as in *Stromatopora* but, rather, broadened upward.

Steele [69] reported that the Lester Park concretions had “compact” dark blue or black laminae and a lighter-colored “stalactical” or “granular” layer. He did not note any of the fenestrae associated with thrombolites. Similarly, Hall [78] also distinguished two types of lamellae, light and dark, noting that “the substance between the concentric lines [i.e., the dense laminae] is traversed by numerous, minute, irregular canaliculi which branch and anastomose without regularity”. In terms of more recent petrographic work on fossil stromatolites, these correspond, respectively, to spongiostromate and porostromate textures [80]. The essential difference is that dense laminations are typical of spongiostrommate development and Goldring [57] specifically states that calcite-filled tubes in the porostromate texture are “vesicular” in assigning *Cryptozoon proliferum* to the red algae.

4.2.2. Distribution of Cryptozoon

Hall's publications set a standard for late nineteenth-century paleontology, and *Cryptozoon* was quickly recognized across North America as a readily recognizable build-up characterized by domal shapes that could coalesce and, with thin section analysis, distinctive alternations of light laminae and dark laminae having a vesicular microfabric of carbonate-filled, straight to curving tubes. Subsequent reports suggest that build-ups attributed to *Cryptozoon proliferum* or which are likely synonyms of the type material of the "*Cryptozoon* ledge" are confidently limited to Upper Cambrian–Lower Ordovician tropical successions in Laurentia. The uniform morphology (macro and micro) and apparent limited stratigraphic range (discussed below) suggest the form is more than a form taxon and is a biological taxon. In the following review of *Cryptozoon* occurrences, an incorrect 1883 date for *C. proliferum* is regularly cited.

Midwestern United States occurrences include two form species of *Cryptozoon*-like build-ups that were named from the Shakopee Formation in Minnesota (Lower Ordovician, middle Tremadocian, Stairsian Stage [81]). Winchell [82] distinguished the broadly domal *C. minnesotense* from the type material of the Upper Cambrian *C. proliferum* (he did not include a publication year for *Cryptozoon*) based on its growth up and outward from a flat base. The flat base of a series of *C. minnesotense* build-ups is figured in outcrop drawings by Chaney [83], who proposed a nomen nudum (*C. giganteum*) for specimens larger than 40 cm in diameter. Winchell [82] also named *C. minnesotense libertis* for fragments of an elongate, cylindrical build-up that are up to ca. 9 cm in diameter. These are likely fragments of closely packed columns that Stauffer [84] named *C. rosemontensis*. Other than fine, mm-scale growth lamination illustrated from broken or slabbed specimens [82,84], little is known about the microhistology of the laminae, and these form species might be questionably attributed to *Cryptozoon*.

Eastern North American occurrences include the Upper Cambrian report of the genus in western Vermont [85] from their Beekmantown Division B, which is the Little Falls Formation [72]. The genus was early reported in the Upper Cambrian of eastern Pennsylvania [9,86]. The quality of the topotype Upper Cambrian Lester Park material led to early redescriptions by Walcott [87] and as part of Rothpletz's review of Proterozoic and Cambrian Cryptozoons [88].

Dawson [89] redescribed the topotype *Cryptozoon proliferum* and extended the range of the genus into the Proterozoic and Late Ordovician. However, his figure of *Cryptozoon boreale* from the Upper Ordovician of Quebec is a branching *Cyathophyllum*-like coral. He [89] also named the then-oldest *Cryptozoon* as *C. occidentale*, whose spartan description (i.e., both build-up shape or size are undescribed) and locality information seemingly brought *Cryptozoon* into "strata which may be regarded as Pre-cambrian" in the Grand Canyon, Arizona, succession. However, his description and supposed illustration of "ragged cells, giving off on all sides numerous small tortuous and branching canals" are not distinguishable in Figure 3, which shows euhedral calcite (?) crystals in a black field. In short, *C. occidentale* should be regarded simply as a rounded stromatolite. The youngest apparent *C. proliferum* in Laurentia is *C. saxiroseum*, which Seely [90] described from domal build-ups with spongiostromate and porostromate laminae from the middle Lower Ordovician (Floian) "Division D" (i.e., Fort Cassin Formation) at Shoreham, Vermont.

An exceptionally early *Cryptozoon* was reported in the middle Mesoproterozoic Belt Supergroup of Montana by Walcott and others [8,91,92]. These reports illustrate and differentiate *Cryptozoon* from taxa but do not provide useful thin sections of the laminae, and thus do not establish whether *Cryptozoon* is actually present in the Mesoproterozoic. Rezak [92] recognized Dawson's [89] problematic *C. occidentale* (discussed above) in the Belt Supergroup but his description and illustration of a thin section are also inadequate in resolving lamellae microstructure. Even older reports of purported *Cryptozoon* include Rothpletz's [88] proposal of *Cryptozoon walcotti* from the Steep Rock Lake area of northwestern Ontario. This taxon from the lowest Neoarchaen (ca. 2.8 Ga) Mosher carbonate platform would seemingly be the oldest occurrence of *Cryptozoon*, [93]. Fralick and Riding [94] detailed the stromatolite-rich interval in the Hogarth Member that yielded *C. walcotti*. Although many of the Hogarth's small, coalesced columnar build-ups are similar to lower Phanerozoic *Cryptozoon*, their microfabric is essentially undocumented. Rothpletz [88], pl. 2, his Figure 6), showed a chaotic (tectonized?) fabric of alternating coarser carbonate and darker, fine-grained carbonate that lacks the filaments and threads of the porostromate layers diagnostic of *C. proliferum*. Thus, the several reports of purported lowest Neoarchaen and Mesoproterozoic *Cryptozoon* do not establish a Precambrian record of *Cryptozoon* s.s. with its characteristic spongiostromate and porostromate laminae.

The geologically youngest reports of purported *Cryptozoon* in North American successions are from the Carboniferous and Permian. Two species were proposed by J.H. Johnson [95] of *Cryptozoon* from the upper Carboniferous (*C. kansasensis*) and Permian (*C. wrefordensis*) of Kansas. They are described as small domal build-ups but their shapes are unillustrated. Neither species can be assigned to the form genus. *Cryptozoon kansasensis* seems to be poorly laminated and consists of a dense fabric of anastomosing, carbonate-filled, *Girvanella*-like threads while *C. wrefordensis* is completely composed of stacked, very lenticular laminae with finer calcite-filled threads.

We are unaware of younger reports of *Cryptozoon* except for the early reports of the genus from modern environments at Shark Bay, Western Australia, e.g., [23]. However, these build-ups are not stromatolites and should not be attributed to *Cryptozoon*. Even if coarsely laminated, they show the small to large voids of thrombolites [25,26]. The designation of "stromatolites" for the Western Australian and other modern domal build-ups is, unfortunately, incorrectly embedded in the literature, e.g., [96]. The fundamental biological difference by which reticulopodial protists are associated with the production of thrombolite porosity in marine to lacustrine habitats [21] should be recognized in the distinction of stromatolites from thrombolites [16].

5. Discussion of Modern *Cryptozoon* Research

A remaining question about *Cryptozoon* and *C. proliferum* is whether these terms are appropriate only to form taxa that reflect environmental factors or are actually biological entities as claimed for many Precambrian stromatolites. The definitive criteria of Hall's [24] diagnosis of the taxon are not only a domal build-up form but the alternation of stromatostromate and porostromate laminae as determinable by thin/polished section analysis. The absence of this information on many purported occurrences of *Cryptozoon*, which have emphasized only a laminated domal/coalescing build-up form, has created a number of binomial/Linnean taxa that are distinct from the genus. The demonstration of spongiostromate and porostromate microstructure, perhaps reflecting a consortium of sediment grain-binding and carbonate-secreting organisms, limits the demonstrated occurrence of *Cryptozoon* to lower Paleozoic reports.

At the very least, the application of a new non-traditional Linnean taxonomy to Phanerozoic build-ups [97], even if used to compare build-ups that are characterized/distinguished by overall morphology in an individual study, would simplify literature searches and make them more efficient and thorough. There is undoubtedly any number of Phanerozoic or older *Cryptozoon*-like build-ups with the distinctive lamellae microsculpture of the type "species", but they are hidden under informal morphological descriptions used in individual reports.

The first-named "classic" stromatolite, *Cryptozoon proliferum*, is biologically enigmatic. Does the alternation of spongiostromate and porostromate laminae reflect the possibly environmentally controlled activity of a microbial consortium or the alternation of the activities of much different organisms? These laminae in topotype *C. proliferum* from Lester Park are detailed by Lee and Riding [63,64] and Neuweiler et al. [66], who reach contrary interpretations, respectively, that the porostromate texture shows that the "classic stromatolite" is formed by alternations of keratose (non-spiculate) demosponges and cyanobacteria [63,64] or that the porostromate layer is merely an accumulation of diagenetically altered micrite [66]. The problems in assigning the porostromate microtexture to keratose sponges or interpreting it as microbially mediated micrite are reviewed by Kershaw et al. [65], who conclude that current techniques are inadequate to provide a conclusive interpretation for each and every porostromate texture. In yet another interpretation by Neuweiler et al. [98], the porostromate laminae reflect the effects of deep burial metamorphism and hydrothermal activity of the Lester Park area, i.e., [75].

This ambiguity in the interpretation of porostromate textures makes the proposal of "keratolite" [63,64] for the "classic stromatolite" *Cryptozoon* and other stromatolites very problematic. "Keratolite" is doubly problematic as it concludes formation by a taxonomic group, which is at least uncertain or questioned, i.e., [65,66], and also creates a synonymous new designation (keratolite) for build-ups that have long been termed "stromatolites". Furthermore, "keratolite" leads to ambiguity as to whether stromatolites such as *Cryptozoon* are ecologically a metazoan–microbial (cyanobacterial) or simply a microbial consortium. This has consequences for understanding the early occurrence of eumetazoans (i.e., keratose sponges) in the Cambrian Evolutionary Radiation.

Indeed, porostromate-like fabrics have been proclaimed as evidence for early sponges in the early Neoproterozoic (ca. 890 Ma) by Turner [99] and are relevant to understanding the origin of metazoans. However, this interpreted early existence drives the origin of simple metazoans and sponges into an interval well before the Cambrian Evolutionary Radiation as traditionally documented in the Ediacaran–Cambrian transition. Alternatively, porostromate laminae might show the persistence of a non-spiculose sponge–microbial (cyanobacterial) consortium for ca. 400 Ma into the early Paleozoic as recorded by *Cryptozoon*. However, associations of tangled calcareous filaments may have any number of origins, such as microbial or diagenetic alterations in micrite. Indeed, the presence of filamentous fabric in the Mesoproterozoic (e.g., [100], their Figure 3e), and well before most estimated earliest origins of sponges may be only a taphonomic artifact that does not support the participation of keratose sponges in the construction of *Cryptozoon*-like build-ups in the Precambrian.

6. Conclusions

The "Age of Stromatolites" persists into the present with the occurrence of such charismatic build-ups as stromatolites and thrombolites in a variety of habitats. Examples of such modern habitats described in this report include normal marine (Exuma Cays, Bahamas) and high-salinity marine facies (Hamlin Pool, Shark Bay, Western Australia, with enclosed lagoons in the Gulf of California) more indicative of extremophiles. In addition, microbialite build-ups occur in freshwater (Lake Tanganyika; Green Lakes State Park, central New York), hypersaline lacustrine environments (saline lakes in Argentina), and waterlogged subaerial habitats where a type of caliche is formed.

In many of these modern habitats, a large domal microbial build-up has come to be casually, and incorrectly, termed a stromatolite [100]. However, ancient and modern microbial build-ups with mm- to cm-sized voids should be termed a "thrombolite". This is a significant difference, not merely a terminological distinction, as colonization by reticulopodial protists controls the development of voids in lacustrine and marine microbialites. In short, although the shape of the columnar build-ups in lateral profile in Shark Bay is that of *Cryptozoon*, i.e., [101], and many studies report "stromatolites" from Shark Bay, Western Australia, repeated studies over several decades of the diverse fabrics of the Hamlin Pool build-ups show that they are best regarded as thrombolites, commonly with fenestrae, e.g., [102]. As they lack the diagnostic spongiostromate and porostromate laminae of *C. proliferum*, there is no modern record of *Cryptozoon.*

The abundance and morphologic diversity of stromatolites and their "kin" beginning in the Archean into the present reflects both global changes in the environment and the evolution of eumetazoans. Thus, stromatolite diversity and abundance, after reaching a maximum, fall through much of the Precambrian. This change tracks an apparent fall in pCO_2 associated with a rise in pO_2 and burial of carbon, due at least in part to photosynthesis by microbialite communities. After a second rise in diversity and abundance in the

Late Cambrian–Early Ordovician, stromatolites and thrombolites again become rare, with resurgences in the Silurian, Devonian, and Carboniferous. This suppression and their abundance in some high-salinity and freshwater habitats have frequently been explained by the origin and diversification of eumetazoan grazers that would have restricted the origination and growth of microbialites. Alternatively, a combination of substrate competition with the origin and diversification of encrusting eumetazoan plants and animals, along with a generalized trend to lower pCO_2 levels in the Phanerozoic, would have the effect of limiting their occurrence and abundance. Ultimately, however, abundance resurgences in the later Phanerozoic, at times with long-established grazing and competition for habitat space, may simply reflect protracted high eustatic levels and greater areas of shallow marine habitats.

The earliest named and, thus, "classic stromatolite" is *Cryptozoon proliferum*, which has a range bracketed to the Late Cambrian–Early Ordovician based on reports that illustrate not only a build-up shape but the presence of alternating spongiostromate and porostromate growth laminae. Recent work on topotype *C. proliferum* shows that this early named fossil remains the subject of controversy, with its alternating laminae variably seen as alternations in microbial communities, simple diagenetic changes in microbial mud, the presence of keratose sponges in a microbial–sponge consortium, or the result of alteration with deep burial.

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Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Heard, A.W.; Bekker, A.; Kovalick, A.; Evans, H.; Ireland, T.; Dauphas, N. Oxygen production and rapid iron oxidation in stromatolites immediately preceding the Great Oxidation Event. *Earth Planet. Sci. Lett.* **2022**, *282*, 117416. [CrossRef]
2. Grey, K.; Awramik, S.M. *Handbook for the Study and Description of Microbialites*; Geological Survey of Western Australia, Bulletin No. 147; Geological Survey, Western Australia: Perth, WA, Australia, 2020; 278p.
3. Landing, E.; Geyer, G.; Brasier, M.D.; Bowring, S.A. Cambrian Evolutionary Radiation: Context, correlations, and chronostratigraphy—Overcoming deficiencies of the first appearance datum (FAD) concept. *Earth-Sci. Rev.* **2013**, *123*, 133–177. [CrossRef]
4. Margulis, L.; Schwartz, K.V. *Five Kingdoms—An Illustrated Guide to the Phyla of Life on Earth*, 2nd ed.; W.H. Freeman & Co.: New York, NY, USA, 1982; 375p.
5. Margulis, L.; Sagan, D. *Microcosmos—Four Billion Years of Microbial Evolution*; Allen & Unwin: Boston, MA, USA, 1987; 301p.
6. Allwood, A.C.; Walter, M.R.; Kamber, B.S.; Marshall, C.P.; Burch, I.W. Stromatolite reef from the Early Archaean era of Australia. *Nature* **2006**, *441*, 04764. [CrossRef] [PubMed]
7. Kalkowsky, E. Oölith und Stromatolith im norddeutchen Bundsandstein. *Z. Deutshen Geol. Ges.* **1908**, *60*, 68–125.
8. Walcott, C.D. Cambrian geology and paleontology. III. No. 2.—Pre-Cambrian Algonkian algal flora. *Smithson. Misc. Collect.* **1914**, *65*, 79–156.
9. Wieland, G.R. Further notes on Ozarkian seaweeds and oolites. *Bull. Am. Mus. Nat. Hist.* **1914**, *33*, 237–260.
10. Barghoorn, E.S.; Stanley, A.T. Microorganisms from the Gunflint Chert. *Science* **1965**, *147*, 563–577. [CrossRef]
11. Schopf, J.W. *Cradle of Life—The Discovery of Earth's Earliest Fossils*; Princeton University Press: Princeton, NJ, USA, 1999; 367p.
12. You, X.L.; Sun, S.; Zhu, J.Q. Significance of fossilized microbes from the Cambrian stromatolites in the Tarim Basin, Northwest China. *Sci. China Earth Sci.* **2014**, *57*, 2901–2913. [CrossRef]
13. Chang, Y.; Bai, W.; Qi, Y.; Sun, F.; Wang, M. Microfossil assemblage and its sedimentary environment in Cambrian stromatolites, western He'nan. *Adv. Earth Sci.* **2014**, *29*, 456–463. (In Chinese with English Summary)

14. Klappa, C.F. Lichen stromatolites: Criterion for subaerial exposure and a mechanism for formation of lamellar calcretes (caliche). *J. Sediment. Petrol.* **1979**, *49*, 387–410.
15. Landing, E. Tropical seas and volcanic fire in eastern New York. *Nat. Hist.* **2022**, *130*, 36–41.
16. Riding, R. Microbialites, stromatolites, and thrombolites. In *Encyclopedia of Geobiology*; Reiter, J., Thiel, V., Eds.; Springer: Dordrecht, The Netherlands, 2011; pp. 635–654.
17. Landing, E.; Westrop, S.R. Upper Lower Cambrian depositional sequence in Avalonian New Brunswick. *Can. J. Earth Sci.* **1996**, *33*, 404–417. [CrossRef]
18. Landing, E.; Westrop, S.R.; Geyer, G. Trans-Avalonian green–black boundary (early Middle Cambrian): Transform fault-driven epeirogeny and onset of 26 m.y. of shallow-marine, black mudstone in Avalonia (Rhode Island–Belgium) and Baltica. *Can. J. Earth Sci.* **2023**, *60*, 133–171. [CrossRef]
19. Vanuxem, L. *Geology of New York. Part III*; Survey of the Third Geological District of New York: Albany, NY, USA, 1842; 306p.
20. Aitken, J.D. Classification and environmental significance of cryptalgal limestones and dolomites with illustrations from the Cambrian and Ordovician of southwest Alberta. *J. Sediment. Petrol.* **1967**, *37*, 1163–1178. [CrossRef]
21. Bernhard, J.M.; Fisher, L.A.; Murphy, Q.; Sen, L.; Yeh, H.D.; Louyakis, A.; Gomaa, F.; Reilly, M.; Batta-Lona, P.G.; Bucklin, A.; et al. Transition from stromatolite to thrombolite fabric: Potential role for reticulopodial protists in lake microbialites of a Proterozoic ecosystem analog. *Front. Microbiol.* **2023**, *14*, 1210781. [CrossRef]
22. Dupraz, C.; Pattisina, R.; Verrecchia, E.P. Translation of energy into morphology: Simulation of stromatolite morphospace using a stochastic model. *Sediment. Geol.* **2006**, *185*, 185–203. [CrossRef]
23. Logan, B.W. *Cryptozoon* and associated stromatolites from the Recent, Shark Bay, Western Australia. *J. Geol.* **1961**, *69*, 517–533. [CrossRef]
24. Hall, J. *Cryptozoön*, n.g., *Cryptozoön proliferum*. n.sp. In *Thirty-Sixth Annual Report of the Trustees of the State Museum of Natural History to the Legislature 1883. Transmitted January 10, 1883. New York State Senate Paper 53*; Pierson, H.R., Ed.; (Two covers, same material, inner printed January 10, 1883, and outer January 10, 1884), unnumbered end page and Pl. 6 with caption; Weed, Parsons & Company: Albany, NY, USA, 1884. [CrossRef]
25. Playford, P.E.; Cockbain, A.E. Modern algal stromatolites at Hamelin Pool, a hypersaline basin in Shark Bay, Western Australia. In *Developments in Sedimentology, 20, Stromatolites*; Walter, M.R., Ed.; Elsevier: Amsterdam, The Netherlands; Oxford, UK; New York, NY, USA, 1976; pp. 389–411.
26. Burne, R.V.; Moore, L.S. Microatoll microbialites of Lake Clifton, Western Australia: Morphological analogues of *Cryptozoon proliferum*, the first formally named stromatolite. *Facies* **1993**, *29*, 149–178. [CrossRef]
27. Suosaari, E.P.; Reid, R.P.; Playford, P.E.; Foster, J.S.; Stolz, J.F.; Casaburi, G.; Hagan, P.D.; Chirayath, V.; Macintyre, I.G.; Planavsky, N.J.; et al. New multi-scale perspectives on the stromatolites of Shark Bay, Western Australia. *Sci. Rep.* **2016**, *1*, 20557. [CrossRef]
28. Dravis, J.J. Hardened subtidal stromatolites Bahamas. *Science* **1983**, *219*, 385–386. [CrossRef]
29. Dill, R.F.; Shinn, E.A.; Jones, A.T.; Kelly, K.; Steinen, R.P. Giant subtidal stromatolites forming in normal salinity waters. *Nature* **1986**, *324*, 57–58. [CrossRef]
30. Reid, R.P.; Macintyre, I.G.; Browne, K.M.; Steneck, R.S.; Miller, T. Modern marine stromatolites in the Exuma Cays, Bahamas: Uncommonly common. *Facies* **1995**, *33*, 1–17. [CrossRef]
31. Cohen, A.S.; Talbot, M.R.; Awramik, S.M.; Dettman, D.L.; Abell, P. Lake level and paleoenvironmental history of Lake Tanganyika, Africa, as inferred from late Holocene and modern stromatolites. *Geol. Soc. Am. Bull.* **1997**, *109*, 444–460. [CrossRef]
32. West, K.; Cohen, A. Morphology and behavior of crabs and gastropods from Lake Tanganyika, Africa: Implications for lacustrine predator-prey coevolution. *Evolution* **1991**, *45*, 589–607.
33. Argentinian Stromatolites. Available online: https://www.cnn.com/2023/12/16/americas/stromatolites-argentina-discovery-lagoons-ecosystem-scn/index.html (accessed on 14 November 2024).
34. CU Boulder Today. Available online: https://www.colorado.edu/today/2023/12/06/deep-within-inhospitable-desert-window-first-life-earth (accessed on 14 November 2024).
35. Horodyski, R.J.; Vonder Haar, S.P. Recent calcareous stromatolites from Laguna Mormona (Baja California) Mexico. *J. Sed. Petrol.* **1975**, *45*, 894–906.
36. Johnson, M.E.; Ledesma-Vázquez, J.; Backus, D.H.; González, M.R. Lagoon microbialites on Isla Angel de la Guarda and associated peninsular shores, Gulf of California (Mexico). *Sediment. Geol.* **2012**, *263–264*, 76–84. [CrossRef]
37. Bowen, T. *On Desert Shores—Archaeology & History of the Western Midriff Islands in the Gulf of California*; University of Utah Press: Salt Lake City, UT, USA, 2022; 313p.
38. Baumgartner, R.J.; Van Kranendonk, M.J.; Wacey, D.; Fiorentini, M.L.; Saunders, M.; Caruso, S.; Pages, A.; Homann, M.; Guagliardo, P. Nano-porous pyrite and OM in 3.5-billion-year-old stromatolites record primordial life. *Geology* **2019**, *47*, 1039–1043. [CrossRef]
39. Hickman-Lewis, K.; Cavalazzi, B.; Giannoukos, K.; D'Amico, L.; Vrbaski, S.; Saccomano, G.; Dreossi, D.; Tromba, G.; Foucher, F.; Brownscombe, W.; et al. Advanced two- and three-dimensional insights into Earth's oldest stromatolites (ca. 3.5 Ga): Prospects for life on Mars. *Geology* **2022**, *51*, 33–38. [CrossRef]

40. Beukes, N.J. Facies relations, depositional environments and diagenesis in a major early Proterozoic stromatolitic carbonate platform to basinal sequence, Campbellrand Subgroup, Transvaal Supergroup, Southern Africa. *Sediment. Geol.* **1987**, *54*, 1–46. [CrossRef]
41. Sumner, D.Y.; Grotzinger, J.P. Implications for Neoarchaean ocean chemistry from primary carbonate mineralogy of the Campbellrand-Malmani platform, South Africa. *Sedimentology* **2004**, *51*, 1273–1299. [CrossRef]
42. Awramik, S.M.; Sprinkle, J. Proterozoic stromatolites: The first marine evolutionary biota. *Hist. Biol.* **1999**, *13*, 241–253. [CrossRef]
43. Kah, L.C.; Riding, R. Mesoproterozoic carbon dioxide levels inferred from calcified cyanobacteria. *Geology* **2007**, *35*, 799–802. [CrossRef]
44. Aitken, J.D.; Narbonne, G.M. Two occurrences of Precambrian thrombolites from the Mackenzie Mountains, northwestern Canada. *Palaios* **1989**, *4*, 384–388. [CrossRef]
45. Riding, R. Cyanobacterial calcification, carbon dioxide concentrating mechanisms, and Proterozoic-Cambrian changes in atmospheric composition. *Geobiology* **2006**, *4*, 299–316. [CrossRef]
46. Grotzinger, J.P. Geochemical model for Proterozoic stromatolite decline. *Am. J. Sci.* **1990**, *290-A*, 80–103.
47. Chumakov, N.M.; Semikhatov, M.A. Riphean and Vendian of the USSR. *Precambrian Res.* **1981**, *15*, 229–253. [CrossRef]
48. Sami, T.T.; James, N.P. Synsedimentary cements as Paleoproterozoic platform building blocks, Pethei Group, northwestern Canada. *J. Sediment. Res.* **1996**, *66*, 209–222.
49. Riding, R. Abiogenic, microbial and hybrid authigenic carbonate crusts: Components of Precambrian stromatolites. *Geol. Croat.* **2008**, *61*, 73–103. [CrossRef]
50. Walter, M.R. Stromatolites and the biostratigraphy of the Australian Precambrian and Cambrian. *Spec. Pap. Palaeontol.* **1972**, *11*, 190.
51. Landing, E. Time-specific black mudstones and global hyperwarming on the Cambrian-Ordovician slope and shelf of the Laurentia palaeocontinent. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2012**, *367–368*, 256–272. [CrossRef]
52. Landing, E.; Keppie, J.D.; Keppie, F.D.; Geyer, G.; Westrop, S.R. Greater Avalonia—Latest Ediacaran–Ordovician "peribaltic" terrane bounded by continental margin prisms ("Ganderia," Harlech Dome, Meguma): Review, tectonic implications, and paleogeography. *Earth-Sci. Rev.* **2022**, *255*, 103863. [CrossRef]
53. Kiessling, W. Secular variations in the Phanerozoic reef ecosystem. In *Phanerozoic Reef Patterns*; Kiessling, W., Flügel, E., Golonka, J., Eds.; Society of Economic Paleontologists and Mineralogists—SEPM Special Publication; SEPM: Tulsa, OK, USA, 2002; Volume 72, pp. 625–690.
54. Pratt, B.R. Stromatolite decline—A reconsideration. *Geology* **1982**, *10*, 512–515. [CrossRef]
55. Fischer, A.G. Fossils, early life, and atmospheric history. *Proc. Natl. Acad. Sci. USA* **1965**, *53*, 1205–1215. [CrossRef]
56. Landing, E.; Antcliffe, J.B.; Geyer, G.; Kouchinsky, A.; Bowser, S.S.; Andreas, A. Early evolution of colonial animals (Ediacaran Evolutionary Revolution-Cambrian Evolutionary Radiation-Great Ordovician Diversification Interval). *Earth-Sci. Rev.* **2018**, *178*, 105–135. [CrossRef]
57. Foster, G.; Royer, D.; Lunt, D. Future climate forcing potentially without precedent in the last 420 million years. *Nat. Commun.* **2017**, *8*, 14845. [CrossRef]
58. Goldring, W. Algal barrier reefs in the Lower Ozarkian of New York with a chapter on the importance of coralline algae as reef builders through the ages. *N. Y. State Mus. Bull.* **1938**, *315*, 5–75. [CrossRef]
59. Friedman, G.M. Hoyt Limestone of Late Cambrian, eastern New York State: Spectacular domed stromatolites as Lester Park and Petrified Sea Gardens. *Northeast. Geol. Environ. Sci.* **2000**, *22*, 336–349.
60. Lindemann, R.H. The historic significance of a petrified cabbage patch at Greenfield, New York. *Northeast. Geol. Environ. Sci.* **2006**, *28*, 101–109.
61. Friedman, G.M. Late Cambrian cabbage-head stromatolites from Saratoga Springs, New York, USA. *Carbonates Evaporites* **2012**, *15*, 37–44. [CrossRef]
62. Lee, J.-H. Stromatolite. In *Encyclopedia of Geology*, 2nd ed.; Alderton, D., Elias, S.A., Eds.; Elsevier: Rotterdam, The Netherlands, 2019; pp. 75–388.
63. Lee, J.-H.; Riding, R. The 'classic stromatolite' *Cryptozoon* is a keratose sponge-microbial consortium. *Geobiology* **2021**, *9*, 189–198. [CrossRef]
64. Lee, J.-H.; Riding, R. Keratolite–stromatolite consortia mimic domical and branched columnar stromatolites. Palaeogeography, Palaeoclimatology. *Palaeoecology* **2021**, *571*, 110288. [CrossRef]
65. Kershaw, S.; Li, Q.; Li, Y. Phanerozoic carbonate facies conundrum—Sponges or clotted fabric? Evidence form Early Silurian reefs. *Stratigr. Rec.* **2021**, *19*, 3–10.
66. Neuweiler, F.; Kershaw, S.; Boulva, F.; Matysik, M.; Sendino, C.; McMenamin, M.; Munnecke, A. Keratose sponges in ancient carbonates—A problem of interpretation. *Sedimentology* **2023**, *70*, 927–969. [CrossRef]
67. Guiry, M.D.; Guiry, G.M. AlgaeBase. World-Wide Electronic Publication. National University of Ireland, Galway. Available online: https://algaebase.org (accessed on 1 October 2024).
68. World Register of Marine Species. Available online: https://www.marinespecies.org/ (accessed on 19 November 2024).
69. Steele, J.H. A description of the oolite formation lately described in the County of Saratoga and in the State of New York. *Am. J. Sci.* **1825**, *9*, 16.

70. Flick, A.C. Suggestions of a state policy relating to historic and scientific reservations. Twenty-third Report of the Director of the Division of Science and the State Museum. *N. Y. State Mus. Bull.* **1929**, *284*, 68–71.
71. Cushing, H.P.; Ruedemann, R. Geology of Saratoga Springs and vicinity. *N. Y. State Mus. Bull.* **1914**, *169*, 177.
72. Landing, E. Ediacaran–Ordovician of east Laurentia—geologic setting and controls on deposition along the New York Promontory. In *Ediacaran–Ordovician of East Laurentia—S. W. Ford Memorial Volume. New York State Museum Bulletin 510*; Landing, E., Ed.; The NewYork State Education Department: Albany, NY, USA, 2007; pp. 5–24.
73. Landing, E.; Westrop, S.R.; Kröger, B.; English, A.M. Left behind—Extinction and a relict trilobite fauna in the Cambrian–Ordovician boundary succession, (northeast Laurentian platform, New York). *Geol. Mag.* **2010**, *148*, 529–557. [CrossRef]
74. Friedman, G.M.; Sanders, J.E. Time-temperature-burial significance of Devonian anthracite implies former great (~6.5 km) depth of burial of Catskill Mountains, New York. *Geology* **1982**, *10*, 93–96. [CrossRef]
75. Landing, E.; Webster, M.; Bowser, S.S. Terminal Ediacaran–Late Ordovician of the NE Laurentia palaeocontinent: Rift-drift–onset of Taconic orogeny, sea-level change, and "Hawke Bay" onlap (not offlap). In *Supercontinents, Orogenesis, and Magmatism*; Nance, R.D., Strachan, R.A., Quesada, Q., Lin, S., Eds.; Geological Society of London, Special Publication; Geological Society Publications: London, UK, 2023; Volume 542. [CrossRef]
76. Hall, J. *Natural History of New York. Geology of New-York. Part 4—Comprising the Geology of the Fourth Geological District*; Carroll and Cook: Albany, NY, USA, 1843; 683p.
77. Mather, W.W. *Geology of the First Geologic District of New York*; Carroll and Cook: Albany, NY, USA, 1843; 832p.
78. Hall, J. *Palaeontology of New York. 1. Organic Remains of the New York System*; C. van Benthuysen: Albany, NY, USA, 1847; 338p.
79. Hall, J. Report of the Director. Albany December 23, 1882, p. 1–17. In *Thirty-Sixth Annual Report of the Trustees of the State Museum of Natural History to the Legislature. Transmitted January 10, 1883: New York State Senate Paper, 53*; Pierson, H.R., Ed.; Weed, Parsons & Company: Albany, NY, USA, 1884; printed 10 January 1884.
80. Monty, C. Spongiostromate vs. porostromate stromatolites and oncolites. In *Phanerozoic Stromatolites. Case Histories 1–4*; Monty, C., Ed.; Springer: Berlin/Heidelberg, Germany, 1981.
81. Smith, G.L.; Clark, D.L. Conodonts of the Lower Ordovician Prairie du Chien Group of Wisconsin and Minnesota. *Micropaleontology* **1996**, *42*, 363–373. [CrossRef]
82. Winchell, N.H. VII New species of fossils. In *The Fourteenth Annual Report for the Year 1885. Geological and Natural Historical Survey of Minnesota*; Winchell, N.H., Ed.; Minnesota Geological Survey; Pioneer Press Company: St. Paul, MN, USA, 1886; pp. 313–318.
83. Chaney, L.W., Jr. *Cryptozoon minnesotense* in the Shakopee Limestone at Northfield, Minnesota. *Minn. Acad. Nat. Sci. Bull.* **1889**, *3*, 280–284.
84. Stauffer, C.R. Cryptozoons of the Shakopee Dolomite. *J. Paleontol.* **1945**, *19*, 376–379.
85. Brainerd, E.; Seely, H.M. The Calciferous Formation in the Champlain valley. *Geol. Soc. Am. Bull.* **1890**, *1*, 501–516. [CrossRef]
86. Bassler, R.S. Systematic paleontology of the Cambrian and Ordovician deposits of Maryland. In *The Cambrian and Ordovician deposits of Maryland*; Bassler, R.S., Ed.; Maryland Geological Survey Report; The Johns Hopkins Press: Baltimore, MD, USA, 1919; pp. 184–373.
87. Walcott, C.D. Cambrian geology and paleontology II No. 9. New York Potsdam–Hoyt fauna. *Smithson. Misc. Collect.* **1912**, *57*, 251–304.
88. Rothpletz, A. Über die systematische Deutung und die stratigraphishe Stellung der ältesten Versteinerungen Europas und Nordamerika mit besonderer Berücksichtigung der *Cryptozoon* und Oolithe. Teil II: Über *Cryptozoon*, *Eozoon* und *Artikokania*. *Abh. Könglich Bayer. Akad. Wiss. Matimatische-Phys. Kl.* **1916**, *28*, 91.
89. Dawson, J.W. Notes on *Cryptozoon* and other ancient fossils. *Can. Rec. Sci.* **1896**, *7*, 203–209.
90. Seely, H.M. Beekmantown and Chazy formations in the Champlain Valley. Contribution to their geology and paleontology. In *Fifth Report of the Vermont State Geologist*; Vermont Department of Environmental Conservation: Montpelier, VT, USA, 1906; pp. 115–145.
91. Fenton, C.L.; Fenton, M.A. Algae and algal beds in the Belt Series of Glacier National Park. *J. Geol.* **1931**, *39*, 670–688. [CrossRef]
92. Rezak, R. Stromatolites of the Belt Series in Glacier National Park, Montana. *U. S. Geol. Surv. Prof. Pap.* **1957**, *294*, 127–150.
93. Wilks, M.E.; Nisbet, E.G. Archaean stromatolites from the Steep Rock Group, northwestern Ontario, Canada. *Can. J. Earth Sci.* **1985**, *22*, 792–797. [CrossRef]
94. Fralick, P.; Riding, R. Steep Rock Lake: Sedimentology and geochemistry of an Archean carbonate platform. *Earth-Sci. Rev.* **2015**, *151*, 132–175. [CrossRef]
95. Johnson, J.H. Lime-secreting algae from the Pennsylvanian and Permian of Kansas. *Geol. Soc. Am. Bull.* **1946**, *57*, 1087–1120. [CrossRef]
96. Vahrenkamp, V.; Chandra, V.; Garuglieri, E.; Marasco, R.; Hachmann, K.; Khanna, P.; Daffonchio, D.; Petrovic, D. Discovery of modern living intertidal stromatolites on Sheybarah Island, Red Sea, Saudi Arabia. *Geology* **2024**, *52*, 347–351. [CrossRef]
97. Shapiro, R.S. Stromatolites: A 3.5 billion year ichnologic record. In *Trace Fossils: Concepts, Problems, Prospects*; Ajello, M., Brotton, S.J., Eds.; Elsevier: Amsterdam, The Netherlands, 2007; pp. 381–389.
98. Neuweiler, F.; Mueller, M.; Walter, B.; Landing, E.; Beranoaguirre, A.; Sendino, C.; Amati, L.; Kershaw, S. Fossil record misconstrued: Sponge-like fabric reflect incipient carbonate metamorphism. *Res. Sq.* **2024**. [CrossRef]
99. Turner, E.C. Possible poriferan body fossils in early Neoproterozoic microbial reefs. *Nature* **2021**, *596*, 87–91. [CrossRef] [PubMed]

100. Grotzinger, J.P.; Knoll, A.H. Stromatolites in Precambrian carbonates: Evolutionary mileposts or environmental dipsticks? *Annu. Rev. Earth Planet. Sci.* **1999**, *27*, 313–358. [CrossRef]
101. Hoffman, H.J. Stromatoid morphometrics. In *Stromatolites. Developments in Sedimentology 20*; Walter, M.R., Ed.; Elsevier: Amsterdam, The Netherlands, 1976; pp. 45–54.
102. Reid, P.R.; James, N.P.; Macintyre, I.G.; Dupraz, C.P.; Burne, R.V. Shark Bay stromatolites: Microfabrics and reinterpretation of origins. *Facies* **2013**, *49*, 299–324. [CrossRef]
103. Landing, E.; Geyer, G.; Schmitz, M.D.; Wotte, T.; Kouchinsky, A. (Re)proposal of three Cambrian Subsystems and their geochronology. *Episodes* **2021**, *44*, 273–283. [CrossRef]