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The 'classic stromatolite' *Cryptozoön* is a keratose sponge-microbial consortium

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Abstract

Animal evolution transformed microbial mat development. Canonically inferred negative effects include grazing, disturbance and competition for space. In contrast, ancient examples of cooperation between microbial mats and invertebrates have rarely been reported. Late Cambrian (~485 million years) *Cryptozoön* is widely regarded as the first stromatolite to have received a taxonomic name and has been compared with present-day examples at Shark Bay, Australia. Here, we show that *Cryptozoön* is an interlayered consortium of keratose ('horny') sponge and microbial carbonate in roughly equal proportions. *Cryptozoön's* well-defined layering reflects repeated alternation of sponge and microbial mat. Its distinctive lateral growth is due to the ability of keratosans to colonize steep and overhanging surfaces. Contrary to the perception of Phanerozoic stromatolites as anachronistic survivors in a eukaryotic world, *Cryptozoön* suggests mutualistic behaviour in which sponges and microbial mats co-operated to gain support, stability and relief, while sharing substrates, bacteria and metabolites. Keratosan-microbial consortia may have been mistaken for stromatolites throughout the record of the past 500 million years, and possibly longer.

KEYWORDS

Cambrian, keratose sponge, microbial carbonate, mutualism, stromatolite

1 | INTRODUCTION

Microbial carbonates, such as stromatolites, provide the longest fossil record of life on Earth, from at least 3.4 Gyr ago (Allwood et al., 2006; Hofmann, 2000; Lowe, 1980) to the present day (Black, 1933; Logan, 1961). Yet they guard their secrets well and continue to pose persistent research challenges, especially regarding the organisms and processes involved in their formation (Javaux, 2019). These key questions are not restricted to Precambrian examples. Here, we show that late Cambrian *Cryptozoön* (Hall, 1883), the first stromatolite to receive a formal name (Burne & Moore, 1993) and the focus of an early life controversy (Schopf, 2000), is composed of an intimate association of keratose sponge and microbial carbonate. It has long been suggested that the rise of animals in the late Proterozoic and early Palaeozoic significantly impacted stromatolite development (Awramik, 1971; Grotzinger & Knoll, 1999; Riding, 2006) and restricted their abundance (Garrett, 1970). Recognition of *Cryptozoön* as a sponge-microbial consortium highlights a very different, mutualistic, relationship between animals and stromatolites. This flies in the face of conventional wisdom that animals outcompeted stromatolites and demonstrates that, in some cases at least, animals and microbial mats developed mutually beneficial associations. In addition to prompting reassessment of exactly how and why stromatolites have changed through time, this raises the intriguing possibility that many supposed stromatolites of the past 500 or more million years may not be what they seem.

2 | GEOLOGICAL SETTING

Late Cambrian and early Ordovician shallow water platform carbonates of the Beekmantown Group were deposited on a passive margin south-east of the Proterozoic Adirondack massif (Landing, 2012). Within this succession, the uppermost Cambrian Little Falls Formation is unconformably overlain by the Lower Ordovician Tribes Hill Formation (Landing et al., 2003). The Little Falls Formation (~40 m thick according to core from Pallette Quarry; Mazzullo et al., 1978) is largely dolomitic, but has limestones at it base (Hoyt Limestone) and top (Ritchie Limestone), both of which are latest Cambrian (Furongian, ~485 Ma) in age based on conodonts (Landing et al., 2011) (Figure 1). The Hoyt was deposited in a shallow, tidally influenced, restricted but normal marine, inner-shelf environment (Mazzullo et al., 1978).

3 | METHODS

Vertically orientated slabs and corresponding thin sections (7.6 × 5.2 cm size) were prepared from each sample. Polished slabs were scanned using a flatbed scanner. Thin sections were observed and photographed with a binocular microscope coupled with a digital camera. Dimensions of samples were measured using ImageJ.

3.1 | *Cryptozoön*

Cryptozoön was described and named by Hall (1883) from the upper Cambrian Hoyt Limestone near Saratoga Springs, NY, USA, ~300 km north of New York City (Figure 1). Goldring (1938) recognized at least four thin (≤1 m) layers containing innumerable closely packed *Cryptozoön*, within and immediately above the Hoyt Limestone, each layer being associated with oolite and quartz sand and dominated by a particular species: *C. proliferum*, *C. ruedemanni* and *C. undulatum*. Friedman (2000) interpreted *Cryptozoön* to have formed in a lagoon in the '*lee of an oolite shoal*' within a shallowing peritidal sequence. Present-day exposures include Petrified Sea Gardens, a 20th-century tourist attraction 5 km west of central Saratoga Springs, and Lester Park together with Hoyt Quarry, 1 km north of Petrified Sea Gardens (Friedman, 2000) (Figure 1).

Steele (1825) described distinctive layered domes in the Hoyt Limestone as 'calcareous concretions', but Hall (1847) recognized them to be organic and suggested they were 'sea plants'. Much later, however, from thin sections, Hall (1883) noted laminae traversed by '*numerous, minute, irregular canaliculi which branch and anastomose without regularity*', which also contained '*extraneous and inorganic substances between the concentric laminae*'. He named these large concentrically layered deposits *Cryptozoön* and contrasted them with stromatoporoids (now considered hypercalcified sponges, but at that time often likened to hydrozoans). Hall (1883) realized that although *Cryptozoön* and stromatoporoids both have '*concentric structure*', they differ in significant detail. Macroscopically, stromatoporoids grow convex-up '*from a broad base which is covered by an epitheca*', whereas *Cryptozoön* expands '*from a point below*' with the convex surface '*on the lower side*' and is '*made up of irregular, concentric laminae of greater or less density and of very unequal thickness*' (Hall, 1883). Microscopically, *Cryptozoön* has '*irregular canaliculi*' and lacks '*the regular succession of layers of tubuli characteristic of*' stromatoporoids (Hall, 1883). Goldring (1938, figs. 15, 18c) also noted '*branching tubes in dense ground mass*'. However, Walcott (1914) compared '*Cryptozoön*-like species' with calcified cyanobacteria in present-day freshwater lakes. After this, Hall's perceptive comparisons with stromatoporoids and other animals were set-aside, and *Cryptozoön* came to be regarded as algal/cyanobacterial in origin (Goldring, 1938): a stromatolite (Burne & Moore, 1993; Friedman, 2000; Logan, 1961).

Glaciated bedding surfaces at Lester Park and Petrified Sea Gardens display thousands of closely spaced layered 'cabbage-like' domes, typically < 1 m wide, that form a very thin (<1 m) *Cryptozoön proliferum* biostrome (Friedman, 2000; Goldring, 1938)

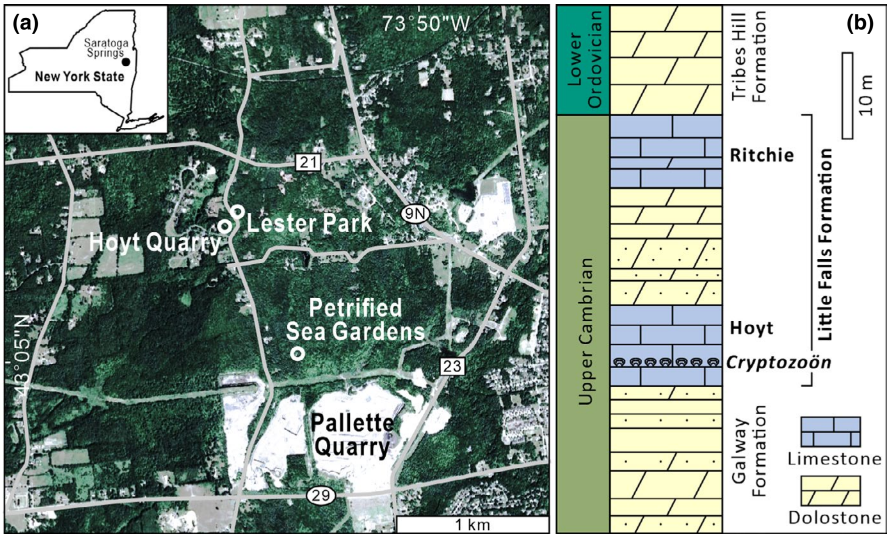

FIGURE 1 Locations and geological setting. (a) *Cryptozoön* is currently exposed in the Hoyt Limestone at localities north-west of Saratoga Springs, New York State, USA: Petrified Sea Gardens (43°05'02"N 73°50'36"W), Lester Park (43°05'32"N 73°50'52"W) and adjacent Hoyt Quarry (43°05'29"N 73°50'55"W). (b) Stratigraphy of the upper Cambrian–lower Ordovician succession near Saratoga Springs (after Landing, 2012; Mazzullo et al., 1978)

FIGURE 2 Vertical section of *Cryptozoön*, Petrified Sea Gardens, Saratoga Springs, New York State, USA (see Figure 1a for location). Overhanging laminae (e.g. lower left) contribute to *Cryptozoön's* distinctive bulbous to oblate morphology. Coin scale is 25 mm in diameter [Colour figure can be viewed at wileyonlinelibrary.com]

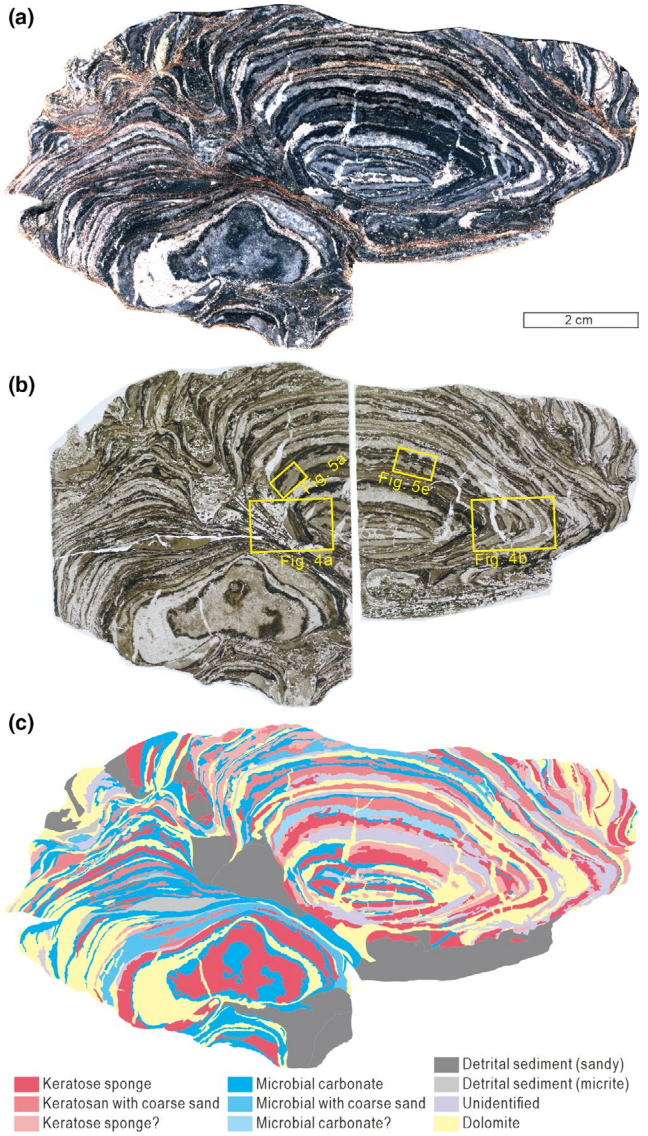

FIGURE 3 (a) Vertical slab of *Cryptozoön*, (b) thin section, (c) map of main components

(Figures S1-S3). In plan view, the domes are distinctly layered, closely juxtaposed masses with smoothly rounded external surfaces. Vertical sections in 1–2 m deep narrow karst fissures at Petrified Sea Gardens show individual masses of *Cryptozoön* originating as small oblate domes, 10–20 cm wide, with steep to overhanging sides (Figures 2 and 3, Figure S1). These domes often expand upward, but tend to accrete laterally more than vertically, producing branched bulbous masses typically up to ~60 cm thick and often slightly wider than high (Figure 2). The basal parts can show horizontal and vertical internal fractures that emphasize, but do not appear to have created, their oblate morphology (Figure 3). *Cryptozoön* margins are locally eroded, suggesting syndepositional scour (Figure 4a, d). Internally, *Cryptozoön* consists of millimetric layers of relatively even thickness, amalgamated into pale to dark grey bands, that are generally laterally persistent and locally enveloping (Figures 2–4, Figures S2 and S3). *Cryptozoön's* well-defined layering and oblate to bulbous form, with overhangs and lateral expansion, are distinctive features. At Shark Bay, Australia, Logan (1961) regarded individual club-shaped stromatolites as *Cryptozoön* and likened confluent heads to Mesoproterozoic *Collenia willisii* in Montana (Fenton & Fenton, 1931). Noting *Cryptozoön's* tendency for lateral expansion, Burne and Moore (1993) compared its surface appearance to the tops of present-day thrombolite domes at Lake Clifton, Australia, and to 'flat-topped mounds' in the Great Salt Lake, Utah, attributed to the cyanobacterium *Aphanothece* (Carozzi, 1962). They suggested that *Cryptozoön proliferum* '*grew laterally without any restriction other than that provided by neighbouring structures*' and are '*depositional forms in which upward growth was restricted*' (Burne & Moore, 1993).

Cryptozoön has three main primary components, keratose sponge, microbial carbonate and allochthonous sediment, together with secondary dolomite (Figures 3–5). Thin-section mapping indicates the following proportions: 24.8% keratose sponge (plus 6.5% uncertain keratosan), 19.8% microbial carbonate (plus 4.3% uncertain microbial carbonate), 14.4% detrital sediment, 22.6% dolomite, with 7.6% of fabric unidentified (Figure 6). The keratose sponge and microbial carbonate layers alternate with one another and are approximately similar in abundance. Both types—but especially the sponge layers—incorporate allochthonous sediment and often extend across the full width of domes, enveloping previous layers (Figure 7). Although superficially similar, these layers differ macroscopically and microscopically. The sponge layers are up to ~3 mm thick, commonly with regular bases and uneven tops. They tend to be thicker than microbial layers, especially on steep and overhanging margins (Figure 8). The sponges consist of distinctive '*vermiform*' fabric: a pervasive meshwork of narrow anastomosing light-coloured, microspar-filled, tubules of varied diameter, ~20–50 μm wide (Figure 5a–d). The tubules are separated by irregular areas of micrite ~50–150 μm across, locally peloidal or clotted, that may reflect bacterial degradation of

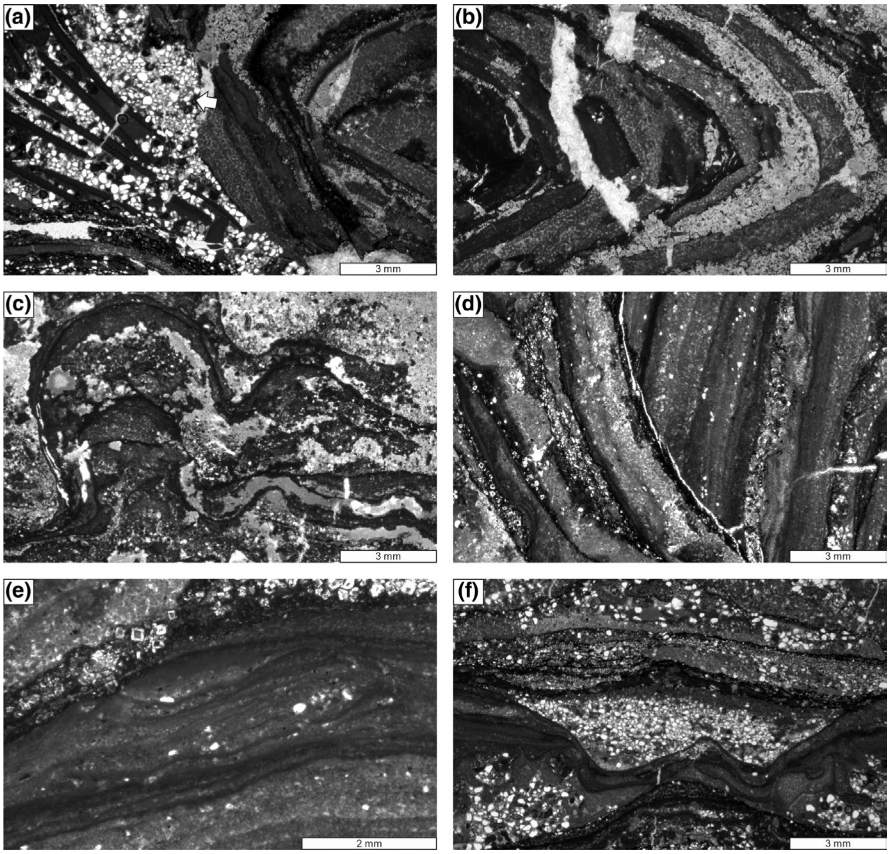

FIGURE 4 Photomicrographs of *Cryptozoön*. (a) Eroded margin of dome (arrow) juxtaposed with micrite flakes, quartz sand and occasional ooids. (b) Fractured oblate margin of dome. (c) Rare ministromatolites within a dome. (d) Eroded overhanging dome margin (erosion surface enhanced by stylolitization), recolonized on left by microbial and sponge layers. (e) Thinly laminated microbial layers with occasional sand grains. (f) Small grain-filled depression (centre) between sponge and microbial layers that also incorporate sand grains

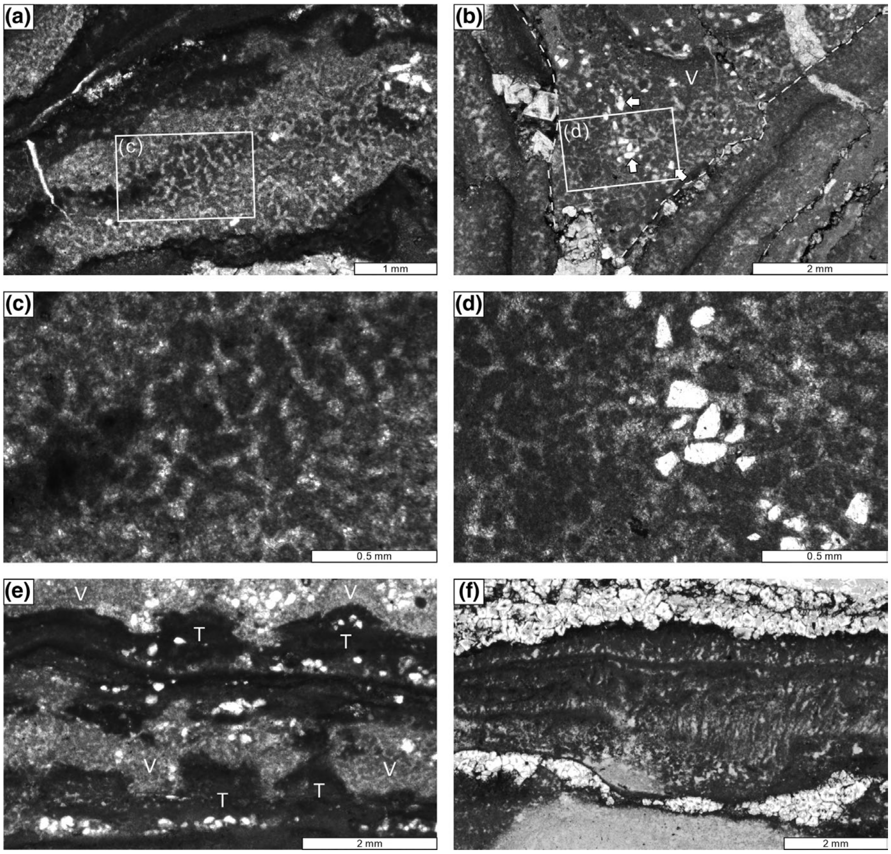

FIGURE 5 Photomicrographs of *Cryptozoön*. (a) Vermiform keratose sponge fabric showing narrow anastomosing microspar-filled tubules in micritic matrix. Dark grey, micritic microbial carbonate occurs above and below the vermiform fabric. (b) Vermiform fabric (V) between two *Cryptozoön* domes (contacts indicated by dotted lines). Quartz sand (arrows) is incorporated within the vermiform fabric. (c) Detail of (a), showing vermiform fabric. (d) Detail of (b), showing quartz sand embedded within vermiform fabric. (e) Alternation of light-coloured vermiform fabric (V) and dark-coloured dense 'tufted' microbial carbonate (T). (f) Vertically oriented filamentous microbial carbonate between dolomitized layers

sponge tissue (see Reitner, 1993). Sponge fabric also occurs attached to the walls of sediment pockets and rarely within bivalve shells.

Similar stromatolite-associated fabrics have been reported in late Proterozoic (e.g. *Borlogella* Vologdin, 1962) and early Cambrian (e.g. *Ilicta* Sidorov, 1960) 'stromatolites'. Walter (1972) recognized this fabric in Cambrian *Madiganites mawsoni* and named it '*vermiform microstructure*': '*narrow, sinuous areas of sparry carbonate surrounded by darker, usually finer-grained, carbonate*'. He attributed it to '*small filamentous red and green algae*' and suggested that these '*first participated in stromatolite formation on a large scale during the Vendian*' (Walter, 1972). He also noted that vermiform fabric is '*strongly developed in some Cambrian stromatolites such as Cryptozoön proliferum Hall*' (Walter, 1972). We infer that '*vermiform*' fabric (Walter, 1972), '*irregular canaliculi*' (Hall, 1883) and '*branching tubes*' (Goldring, 1938), all refer to the remains of the proteinaceous spongin skeleton of keratosan demosponges (including Dictyoceratida, Dendroceratida and Verongida sensu Minchin (1900) as in Luo and Reitner (2014)), exemplified by the present-day 'bath sponge' *Spongia*. Vermiform fabric closely resembles the distinctive sponge microstructure (Worheide et al., 2012) first observed by Hooke (1665).

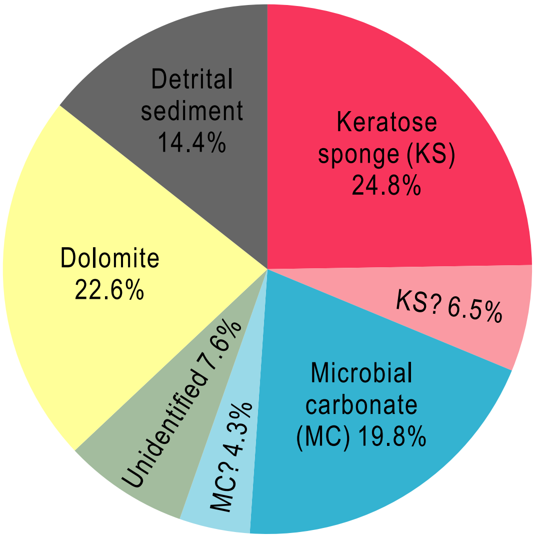

FIGURE 6 Pie chart based on Figure 3c showing the relative proportions of *Cryptozoön* components

The structure of vermiform fabric is distinctly different from the skeletons of lithistid sponges, which are also common in the Cambrian–Ordovician (Lee et al., 2015). Anthaspidellids, the only family of lithistids known from the Cambrian, are characterized by regular ladderlike spicule networks that consist of dendroclones (lithistid-type spicules) and trabs (fused dendroclones) (Lee et al., 2016) (Figure 9a, b). Although poorly preserved anthaspidellid fabrics may somewhat resemble vermiform fabric, even these are often sufficiently ladderlike to be confidently recognized (Hong et al., 2016, Figure 4). Nonetheless, in addition to being overlooked or confused with algal filaments (Walter, 1972), it appears that keratosans have also been misidentified as lithistids. Upper Cambrian specimens from

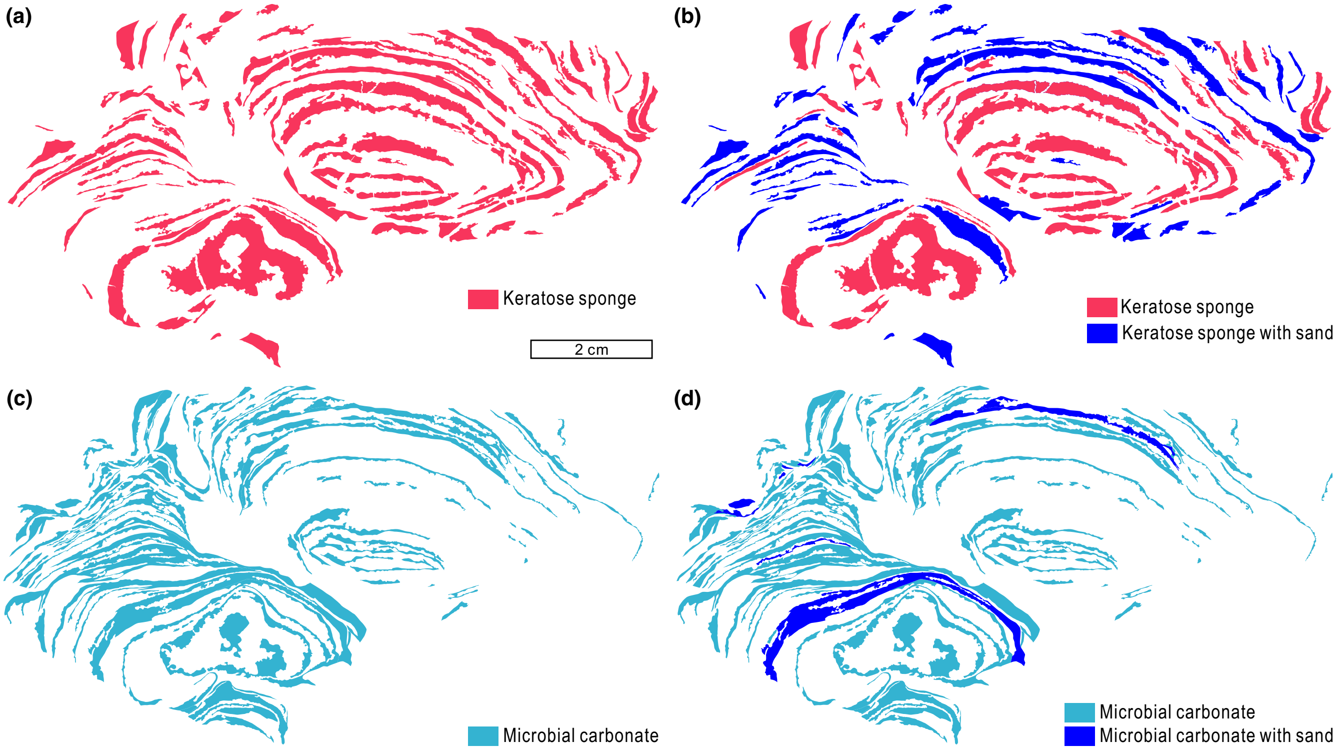

FIGURE 7 Dissection of the *Cryptozoön* components mapped in Figure 3c, showing comparative thickness and arrangement of sponge and microbial layers, together with sand incorporation. (a) Keratose sponge. (b) Keratose sponge with and without sand. (c) Microbial carbonate. (d) Microbial carbonate with and without sand. Note that sponge layers incorporate more sand and are generally thicker and shorter than microbial layers (Figure 8). Only confidently identified layers are shown

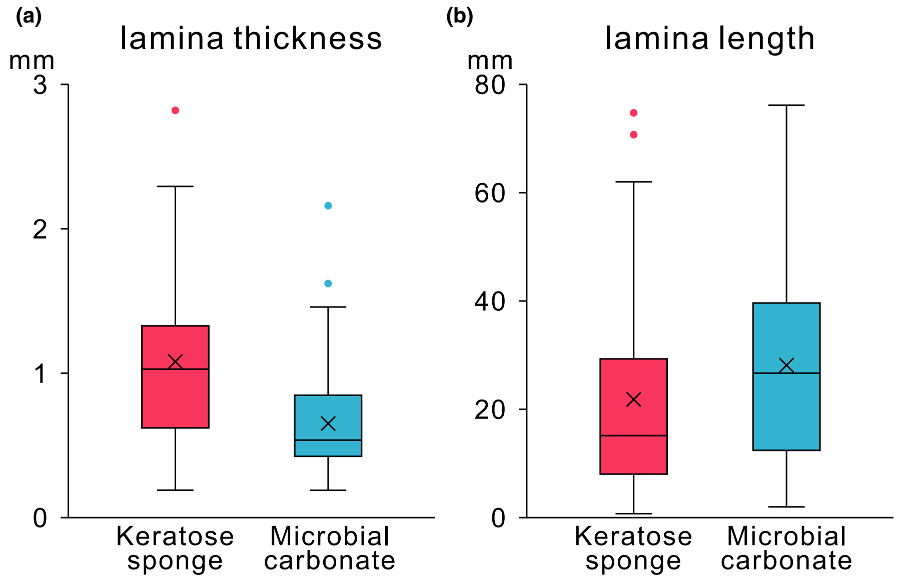

FIGURE 8 Box plots of *Cryptozoön* lamina thickness and length. Sponge layers average 1.07 mm thick and 21.85 mm long ($n = 47$). Microbial layers average 0.64 mm thick and 28.15 mm long ($n = 69$). X indicates median values. One-sided t tests [$P(T <= t)$] show that these sponge and microbial laminae differ significantly in length, and especially in thickness

the Hellnmaria Member of the Notch Peak Formation in south-western Utah were described as lithistid sponge spicule networks within 'sponge-microbial "stromatolites"' (Coulson & Brand, 2016). However, these sponges lack lithistid spicules, and the 'weakly fused spicule networks' cited as evidence of lithistid affinity by Coulson and Brand (2016) are transverse sections of adjoining vermiform tubules, typical of keratosans. Apart from one example of disarticulated siliceous sponge spicules (Coulson & Brand, 2016, fig. 7g), all the sponges illustrated by Coulson and Brand (2016, figs. 6–8) appear to be keratosans, as shown by their characteristic vermiform fabric. Keratosan sponges also occur in Furongian sponge-microbial reefs in Shandong, China, but were originally described as siliceous sponges (Lee et al., 2014) (Figure 9c). It therefore appears that keratosan-microbial consortia similar in age to *Cryptozoön* also occur in Shandong and Utah.

Microbial layers are up to ~2 mm thick. They can be delicately laminated, and their bases and tops are relatively even in comparison with those of the sponge layers (Figure 3). In thin section, they consist of thin (~0.5 mm) dark layers that are generally sub-parallel to underlying layers (Figure 4e), or form tufts (Figure 5e) resembling calcified biofilm (Riding, 2002a) and, rarely, smooth steep-sided millimetric domes (Figure 4c). They are dominated by dark grey clotted micritic fabrics with occasional areas containing closely spaced irregular subvertical micritic filaments 0.5–1.5 mm long (Figure 5f).

Externally, *Cryptozoön* masses are surrounded by bedded sediments of quartz sand, ooids, peloids, bioclasts (e.g. trilobites, bivalves) (Figure 2, Figures S2 and S3) and micritic flakes up to ~ 1 cm long and 0.3 mm ~ thick (Figures 3b and 4a). Thin elongate layers and lenses, as well as pockets, of similar coarse sediment and minor allomicrite occur locally within domes, and fill depressions between branches (Figure 4f). Allochthonous sediment is also common within both the sponge and microbial fabrics, as noted by Hall (1883). Conspicuous local concentrations of sand in the sponge fabric appear to have been irregularly trapped or incorporated as pockets within spongocoels, or between spongin fibres as isolated grains (Figure 5b, d). Sand particles are less abundant in the microbial fabrics, often occurring as very thin layers (sometimes single-grain thickness) (Figures 4e and 5e). Sediment incorporation may be more common in the upper parts of the domes (Figures 3 and 7b, d) and has not been observed in 'overhanging' layers, in either microbial or sponge fabric.

Secondary dolomite typically constitutes about one-fifth of *Cryptozoön* (Figure 6), affecting both sponge and microbial fabrics and enhancing the layering in hand specimen and outcrop (Figure 3). It mainly consists of 100–200 μm euhedral (idiotopic) crystals (Figure 5b, f). Sponge and microbial layers both laterally grade into dolomite, suggesting that dolomitization has not significantly affected the relative proportions of the primary constituents.

3.2 | Sponge-microbe mutualism

Present-day microbial mats and keratosans can both colonize and accumulate allochthonous sediment, and it is estimated that 10% of sponges, particularly Demospongiae and Hexactinellida, are well-adapted to life with and within allochthonous sediment (Hoffmann et al., 2007; Strehlow et al., 2017). Despite the risk of clogging and burial, sediment incorporation in sponges can deter predation, reduce the need for spicule formation, provide strength, stability and protection (Schönberg, 2016), and increase competitiveness (Biggerstaff et al., 2017). Coarse sediment increases stability (Cerrano et al., 2004), and some sponges selectively discriminate between silica and carbonate grains (Bavestrello et al., 1998). Laminar keratosans cope better with high sediment levels than cup- and hat-shaped forms (Bell et al., 2015; Schönberg, 2016). Our *Cryptozoön* measurements show that keratosan laminae are shorter and thicker than the microbial carbonate laminae (Figure 8). We performed one-sided t tests [$P(T <= t)$] to assess these differences. The derived p-value for length (.038) is less than the standard significance level of .05, indicating that sponge and microbial lamina lengths are statistically significantly different. The difference in thickness is even larger, with $p = .00000072, << .05$.

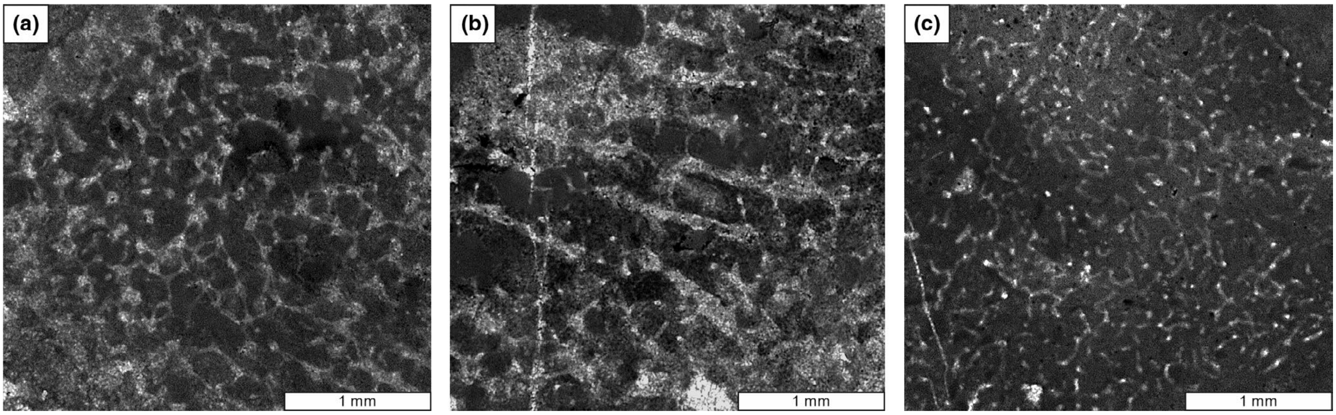

FIGURE 9 Comparison of Cambrian lithistid and keratosan sponge microfabrics. (a, b) The lithistid anthaspidellid sponge *Rankenella zhangxianensis* Lee et al. (2016), Miaolingian, Shandong, China. (c) Keratosan vermiform fabric, Furongian, Shandong, China (Lee et al., 2014). In lithistids, the primary silica spicules have been secondarily replaced by Ca-carbonate. Anthaspidellids are characterized by regular spicule networks that consist of thin dendroclones and thick trabs (fused dendroclones). The resulting structure is polygonal in transverse section (a) and ladderlike in longitudinal section (b). In keratosans, original spongin protein network has been secondarily replaced by Ca-carbonate and is preserved as vermiform fabric

In *Cryptozoön*, agglutinated sand-size sediment is more common in keratose sponge layers than in microbial carbonate (Figure 7b, d). This, together with faster innate sponge growth, could account for generally greater thickness of the keratosan layers.

Cryptozoön shows a tendency for lateral expansion on steep and overhanging surfaces (see Goldring, 1938, fig. 8). Burne and Moore (1993) attributed *Cryptozoön's* limited upward growth to restricted water depth. Sponge fabric is prominent in these marginal downward accreting, 'overhanging', layers that help to create *Cryptozoön's* oblate basal morphology (Figures 2, 3 and 4a, b). This likely reflects the ability of keratosans to encrust steep and overhanging surfaces, as in present-day *Aplysilla*, *Dysidea* and *Spongia* (Manconi et al., 2013; Wiedenmayer, 1977).

Microbial and keratosan layers repeatedly, and relatively thinly, alternate in *Cryptozoön* (Figure 3). This is unlikely to be fortuitous. In addition to having similar environmental preferences and behaviours, the microbial mats and keratosans that constructed *Cryptozoön* could have been mutualistic in providing substrates, bacteria and organic matter. Keratosan larvae preferentially settle on biofilm, and microbial mats would therefore offer attractive and stable substrates for sponge colonization (Whalan & Webster, 2014). In addition, sponges acquire bacterial symbionts from the surrounding environment (Tout et al., 2017), including bacterial mats (Cleary et al., 2019). On the other hand, dead sponges would have provided organic-rich substrates for microbial mat colonization. Keratosans are prone to mortality events (Di Camillo & Cerrano, 2015) due to factors such as bacterial competition (Rützler, 1988), phytoplankton blooms (Stevely et al., 2010), disease (Easson et al., 2013) and temperature stress (Webster et al., 2008) which is associated with loss of endosymbionts (Cebrian et al., 2011). Stress due to elevated temperature and salinity may have been common in the shallow water environments occupied by *Cryptozoön* during late Cambrian 'greenhouse' conditions (Lee & Riding, 2018). We suggest that frequent alternation of microbial mat and sponge layers reflects cooperation in *Cryptozoön* construction as follows:

1. Mats/biofilm surfaces provided sponges with favourable substrates for larval settlement and possibly contributed bacterial symbionts.
2. Keratosans relatively rapidly created extensive enveloping layers but were prone to mortality events that tended to be dome-wide.
3. Microbial mats colonized dead keratosan surfaces, benefited nutritionally from tissue decay and recreated a substrate suitable for sponge larval settlement.

Repetition of this cycle created *Cryptozoön's* distinctive alternating and laterally extensive layering. At the same time, key macromorphic features of *Cryptozoön*, such as oblate basal growth, lateral expansion and overhanging margins, reflect the ability of keratosans to encrust steep and overhanging surfaces. *Cryptozoön* is a sponge-microbial consortium and can therefore be considered an early example of inter-laminated reef construction by differing organisms. Its overall organization broadly resembles that of laminar stromatoporoid and bryozoan consortia in the Middle Ordovician (Hong et al., 2018, fig. 5). A simpler example might be the Early Ordovician sponge *Pulchrilamina*, which typically is interlayered with fine-grained sediment (Toomey & Ham, 1967, p. 987 and pl. 128). From this perspective, *Cryptozoön* can be considered a forerunner of the laminar intergrowth that was a key strategy of reef formation in the Mid–Late Ordovician (Fagerstrom, 1987, p. 344; Kröger et al., 2017, p. 597) and continues to the present day (Riding, 2002b).

3.3 | Recognizing keratosan-microbial consortia

It is likely that sponges widely cooperated with microbial mats in the construction of layered calcified sediments since the Cambrian or even earlier. Stable potentially mutualistic relationships between animals and microbial mats, such as those present in *Cryptozoön*, probably arose in the late Proterozoic (Alegado & King, 2014) on poorly oxygenated seafloors that were dominated by bacteria (Gingras et al., 2011). Many putative 'stromatolites' since then may harbour substantial volumes of previously unrecognized keratosan sponge fabric (Luo & Reitner, 2014, 2016). In contrast to the stereotype of Phanerozoic stromatolites as victims of animal competition, *Cryptozoön* provides persuasive evidence of mutualistic behaviour by which bacterial mats and sponges both benefited. Cooperation was favoured by convergent environmental requirements and tolerances (Lee & Riding, 2018), as well as by similar abilities to incorporate sediment (Schönberg, 2016), that allowed sponges and mats to share substrates, possibly nutrients and bacteria, thereby both gaining relief, stability and support.

Cryptozoön is evidently a sponge-microbial consortium. Paradoxically, therefore, this 'earliest named stromatolite' is only partly stromatolitic. The ability of keratosans to create laminar morphology and incorporate sand grains, together with the superficial similarity of spongin network to algal and cyanobacterial filaments, and its resemblance—when calcified—to clotted peloidal fabric, have made it easy to confuse encrusting keratosans with microbial carbonate, as pointed out by Luo and Reitner (2016). Fossil keratosans have also been mistaken for other sponges such as lithistids. Nonetheless, calcified keratosans are distinguished by their distinctive vermiform fabric and may also leave macroscopic clues to their presence, as in *Cryptozoön's* oblate morphology and overhanging lateral expansion. It is likely that keratosan-microbial consortia are widespread in seafloor carbonate accumulations hitherto regarded as essentially microbial (Friesenbichler et al., 2018; Lee et al., 2014; Luo & Reitner, 2016) and do not all necessarily resemble *Cryptozoön*. This can be tested by scrutiny of well-preserved putative microbial carbonates of all ages. A search for keratosans could be particularly rewarding in the late Proterozoic where the suspected origins of sponges have long defied unambiguous confirmation (Botting & Nettersheim, 2018) and where vermiform-like fabrics have been observed (Vologdin, 1962).

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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