Keratolite–stromatolite consortia mimic domical and branched columnar stromatolites

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ABSTRACT

The term keratolite is proposed for keratosan sponge carbonate dominated by vermiform fabric that preserves the outlines of the original spongion skeleton. Thinly (~<2 cm) interlayered keratosan–microbial carbonate consortia in peritidal sediments near the Cambrian–Ordovician boundary in Newfoundland, Canada, are macroscopically indistinguishable from stromatolites. These carbonate domes and columns consist of approximately equal proportions of keratolite and stromatolite. The keratolite is characterized by pervasive microscopic vermiform fabric, which reflects the original spongion framework. The stromatolite is characterized by fine-grained carbonate with cross-cutting laminae, which primarily formed by sediment trapping. The intimate association of keratolite and stromatolite in these deposits indicates that the sponges and microbes involved shared similar environmental tolerances and requirements. Synchronicity of sponge colonization, followed by stromatolite regrowth, across adjacent columns suggests coordinated responses by both sponges and microbes to local ecophysiological stimuli. Due to their macroscopic similarity, keratolite and fine-grained stromatolite may commonly have been confused with one-another throughout the Phanerozoic, and possibly longer.

1. Introduction

Recognition and definition are recurring themes in microbial carbonate research (Semikhatov et al., 1979; Burne and Moore, 1987; Riding, 1999, 2011; Nofke and Awramik, 2013; Grey and Awramik, 2020; Shapiro and Wilmeth, 2020). Early studies struggled with the question of biogenicity (Kalkowsky, 1908; Seward, 1931; Schopf, 2000) and the challenge of distinguishing stromatolites (defined here as laminated benthic microbial deposits; Riding, 1999) from simple animals, such as prokaryotes and sponges (Dawson, 1876, 1896; Walcott, 1895; Wieland, 1914). Progress mainly resulted from comparative studies of present day microbial mat sediments in non-marine and marine environments such as Canandaigua Lake (Walcott, 1914), Andros Island (Black, 1933), and Shark Bay (Logan, 1961). In addition to assisting recognition of ancient examples, these advances stimulated research into microbial communities and the associated processes that localize and precipitate carbonate sediment (Walter, 1976; Monty, 1981; Bertrand-Sarfati and Monty, 1994; Riding and Awramik, 2000; Konhauser, 2006; Reitner et al., 2011).

In this context, the realization that keratosan sponges can mimic stromatolites in macroscopic appearance (Luo and Reitner, 2016) is a discomfiting development. The composition of the skeletal framework of sponges ranges from CaCO3 (e.g., Archaeocyatha, Calcarea, Scleractinia; Hartman et al., 1980; Senowbari-Daryan and Rigby, 2011) and silica (e.g., Lithistida, Hexactinellida; Hooper and Van Soest, 2002; Reiswig, 2002), to spongion (e.g., Keratosa; Erpenbeck et al., 2012; Reitner and Keupp, 1991; Vacelet, 1991). The original siliceous spicules of hexactinellids and lithistids, as well as the spongion of keratosans, are commonly replaced by CaCO3 (Warnke, 1995; Luo and Reitner, 2014). Much of the fossil record of these groups resides in carbonate sediments, and it is often possible to distinguish the distinctive outlines and spicular elements of hexactinellids and lithistids in reefal and microbial carbonates (Fiugel and Reinhardt, 1989; Leinfelder et al., 1996; Lee et al., 2016a). In contrast, keratosan demosponges preserved in carbonate can be macroscopically indistinguishable from microbial carbonate (Luo and Reitner, 2016).

Here we propose the term keratolite for sediment dominated by the calcified – typically vermiform – remains of keratosan spongion skeleton, and describe examples of intimately interlayered keratolite–stromatolite associations from peritidal carbonates near the Cambrian–Ordovician (485 Myr) boundary in western Newfoundland, Canada. In the field, these sponge–microbial consortia closely resemble branched and
Domical stromatolites, casting doubt on the ability of meso-macroscopic (e.g., field-based) studies, on their own, to confidently recognize fine-grained stromatolites (Reitner et al., 1995). This supports the troubling realization that – even though bona fide Phanerozoic stromatolites are well-documented – keratosan-microbial consortia could have been mistaken for stromatolites throughout the Phanerozoic (Luo and Reitner, 2016), and possibly also in the late Proterozoic, since it is widely thought that sponges – including keratosans – could have originated in the Neoproterozoic (Worheide et al., 2012; Sperling and Stockey, 2018). On a more positive note, keratosan–microbial consortia demonstrate that metazoan-mat relationships were not exclusively competitive, and that these groups could cooperate in building calcified benthic communities (Luo and Reitner, 2016; Lee and Riding, 2021).

2. Geological setting

Upper Cambrian–Lower Ordovician shallow marine carbonates are common along the eastern margin of Laurentia (Kennard and James, 1986; Pratt and James, 1986; James et al., 1989; Kennard et al., 1989; de Freitas and Mayr, 1995; Stouge et al., 2001; Lavioie et al., 2012; Lavioie, 2019, fig. 6). In western Newfoundland, this succession is well exposed in coastal sections on the south-eastern side of the Port au Port Peninsula and immediately to the east along the shores of Isthmus Bay, ~10 km west of Stephenville (Williams et al., 1985). The upper Cambrian (Stage 10, Furongian) and lowermost Ordovician Berry Head Formation, at the top of the Port au Port Group, is overlain by the Lower Ordovician (Tremadocian) Watts Bight Formation, at the base of the St George Group (Knight et al., 2008, fig. 2; Scorrer et al., 2019, fig. 2). On the
eastern side of Isthmus Bay, conodont studies locate the Cambrian–Ordovician boundary at a conformable contact ~16 m below the base of the Watts Bight Formation (Scorrer et al., 2019, fig. 8). The Cambrian–Ordovician succession in this area corresponds to a major unconformity further west (Lavoie et al., 2012; Lavoie, 2019). Berry Head–Watts Bight sediments are dominated by fine-grained, often burrowed, peritidal carbonates with intraclastic sand and rudstone horizons (Knight et al., 2008). Thrombolites and putative stromatolites are common (Kennard and James, 1986; Pruss and Knoll, 2017) and locally form Lower Ordovician mounds in association with sponges (Archaeoscyphia, Pulchrilamina), sponge-like organisms (Calathium) and Amsasia (Pratt and James, 1982, 1989a; Knight and James, 1987; Knight et al., 2008; Elias et al., 2021).

3. Field descriptions

We collected putative stromatolites (which we now recognize as keratolite–stromatolite consortia) from the uppermost Cambrian (Berry Head Formation) and lowermost Ordovician (Watts Bight Formation; ~485 Ma) successions in coastal exposures on the eastern and western sides of Isthmus Bay (Fig. 1). These localities were respectively named Port au Port and Green Head by Ji and Barnes (1994).

3.1. Locality 1, Port au Port (uppermost Cambrian, Berry Head Fm.)

A ca. 200 m thick northward-younging Cambrian–Ordovician boundary succession is exposed along the eastern shore of Isthmus Bay, south and southeast of Port au Port (Fig. 1). This section has also been referred to as East Isthmus Bay (Scorrer et al., 2019, fig. 1). Our sample horizon is ~30–33 m below the top of Berry Head Formation, and ~14–17 m below the Cambrian–Ordovician boundary, corresponding to thickness level 133–130 m of Scorrer et al. (2019, fig. 3).

We sampled branched columns that form broad low domes, up to ~1 m thick and a few meters wide, overlying thin bedded lime mudstone (Fig. 2A) and laterally surrounded by intraclastic rudstone. The rudstones contain subrounded pebbles that include reworked columns, 1–3 cm in size, indicating synsedimentary lithification of the columns (Fig. 2E). The columns in the domes are 1–2 cm wide, short (~2–4 cm high), erect, closely spaced, and irregularly branched, with margins that can be smooth but are more commonly irregular. Their convex-up laminae indicate relatively low primary relief. Adjacent columns occur in subhorizontal horizons 5–10 cm thick, separated by thin (~1 cm) layers of medium to coarse intraclastic packstone-grainstone (Fig. 2B–D). Similar sediment occupies intercolumn spaces. The columns often widen upward, and locally show bridging. Their margins are commonly ornamented by irregular lateral projections and protrusions (Fig. 2C). Branching ranges from parallel to slightly divergent (see Walter, 1972, fig. 3), primarily in response to influx of carbonate sediment. In overall appearance, these branched columns broadly resemble stromatolites that were widespread in the Neoproterozoic, ~800 Ma (e.g., Walter, 1972; Grey and Blake, 1999, fig. 6; Grey and Awramik, 2020, fig. 94a, d). The immediately associated sequence includes small steep-sided putative stromatolite domes with up to 15 cm of primary relief, thrombolite domes, and carbonates ranging from locally bioturbated thinly bedded micrite to coarse intraclastic rudstone (Scorrer et al., 2019, fig. 3) and flat pebble conglomerate. These deposits suggest shallow water environments in which sediments were commonly reworked by waves and currents. Skeletal fossils are scarce in the sampled horizon, but brachiopods, trilobites and conodonts in the associated succession (Scorrer et al., 2019) indicate normal marine salinity.

3.2. Locality 2, Green Head (lowermost Ordovician, Watts Bight Fm.)

This northward-younging Cambrian–Ordovician boundary succession is exposed in coastal cliffs along the western side of Isthmus Bay, southwest of Port au Port (Fig. 1). It comprises sections termed Green Head (Pratt and James, 1982, fig. 2 and p. 558; Ji and Barnes, 1994, fig. 1) and Isthmus Bay (Pratt and James, 1986, fig. 2; Knight et al., 2008, fig. 3), as well as the Watts Bight and Boat Harbour reference sections of Knight and James (1987, fig. 3d). Our samples are early Tremadocian in age. They overlie thrombolite mounds with abundant chert nodules, ~5 m above the base of the Watts Bight Formation (Knight et al., 2008, fig. 4 column B).

We sampled a horizon of small, pale tan colored, planar to laterally linked low domes, in beds up to ~20 cm thick. Individual domes, ~5 cm wide with ~2–3 cm of primary synoptic relief, are underlain and overlain by bedded micrites (Fig. 3A). Samples were collected from the uppermost part of the bed, where thinly bedded micrite onlaps the domes (Fig. 3B). The immediately associated sequence includes laminated lime
mudstones and bioturbated dolostones with abundant thrombolite mounds (Knight et al., 2008). A horizon of microbial domes with chert linings, slightly lower in the sequence, marks the base of the Watts Bight Formation (Knight et al., 2008). The “Green Head Mound Complex”, with thrombolite and Amsassia (Pratt and James, 1982; Elias et al., 2021), occurs ~20 m above the sampled horizon. The overall depositional environment of the Watts Bight Formation has been interpreted as peritidal (Pratt and James, 1986). Macrofossils are generally scarce (Knight et al., 2008).

4. Slab and thin section descriptions

4.1. Port au Port branched columns

The keratolite–stromatolite columns either maintain their width vertically or, more commonly, slowly expand upward. They are generally closely spaced, and typically equal or exceed the volume of intercolumn sediment (Fig. 4). Each column consists of regular to irregular alternations of keratolite sponge and microbial carbonate (Figs. 4, 5). The overall ratio of keratolite to microbial carbonate is 38% to 62% (Fig. 4C). Branching appears unrelated to whether the column is dominated by keratolite or microbial carbonate at the point of branching, and bridges that connect the columns can be formed by keratolite and/or microbial carbonate (Fig. 5C). Intercolumn matrix is dominated by subrounded-angular fine to coarse intraclast packstone-grainstone (Fig. 5A–C), locally with small column fragments, and is commonly dolomitized (Fig. 4A, B).

The keratolite layers can be exceedingly thin, and typically range ~1–10 mm in thickness. They are characterized by pervasive “vermiform” fabric: microscopic sparry networks that traverse micritic groundmass (Fig. 5A–D; see Section 5.3. Vermiform fabric, below). Keratolite layers generally maintain their millimetric thickness across the column width, which is typically ~1–4 cm, and can often be traced at the same level from column to column across entire hand samples (~10 cm; Figs. 2B–D, 4). These layers tend to have relatively even, well-defined bases, with slightly to moderately irregular – often less well-defined – tops (Fig. 5A, B). Correspondingly, microbial carbonate layers have slightly to moderately irregular bases, and relatively even tops. Small scale lateral interfingering occurs locally between sponge and microbial carbonate (Fig. 5A, B).

Preservation is generally good in both microbial and keratolite fabrics, consistent with synsedimentary lithification, and the columns are only slightly dolomitized. In shape and size, the outlines of these Port au Port keratosan sponges closely resemble those of some present-day examples (e.g., Luo and Reitner, 2016, fig. 6F). Microbial fabrics show both even and cross-cutting fabrics (Fig. 5E) and locally incorporate carbonate silt-sand grains (e.g., lower part of Fig. 5A), suggesting agglutination of allochthonous sediment. Nonetheless, adjacent reworked keratolite–stromatolite clasts (Fig. 2E) also indicate synsedimentary lithification.

4.2. Green head domes

These small, laterally linked (see Logan et al., 1964) and well-laminated keratosan-stromatolite domes, with locally steeply angled margins, occur within sand-poor, very fine-grained, carbonate
mudstones (Fig. 3B). The keratolite–microbial carbonate ratio within the mapped domes is equal (50:50; Fig. 6C), and overall layer thicknesses, as well as the internal structures of both the keratosan sponges and the microbial carbonates, are similar to those of Port au Port columns (Fig. 7). The fine-grained micritic microbial carbonate is dominated by well-defined uneven laminae that commonly show cross-cutting (Fig. 7). Allomicrite layers are commonly intercalated with sponge/microbial carbonate layers (Figs. 6, 7B). The keratolite layers range from very thin to 5 mm thick. They have smooth bases, but the tops can be even more irregular (Figs. 6, 7A) than those of the Port au Port columns, and small, isolated growths surrounded by allomicrite occur locally (Fig. 7B).

4.3. Comparisons

The branched columns (Port au Port) and small domes (Green Head) are both macroscopically laminated. Microscopically they consist of interlayered keratose sponge (keratolite) and microbial carbonate (stromatolite). Each of these components tends to form discrete laterally persistent bands that alternate with one-another on mm–cm scales. The matrix is coarse in the Port au Port samples, and fine in the Green Head samples. Nonetheless, these domes and branches both contain roughly similar proportions of keratolite and stromatolite. In both cases, the keratolite is dominated by vermiform microfabric and the stromatolite is typically finely layered micrite with thin, cross-cutting laminae that
likely resulted from trapping and binding (Tosti and Riding, 2017). Reworked columns at Port au Port indicate synsedimentary lithification. In nearly all the cases observed, sponge bases are relatively smooth and sponge tops tend to be irregular. Thus, despite differences in immediately associated carbonate sediment (coarse at Port au Port vs. fine at Green Head), morphology (branched vs. domical), and age (Late Cambrian vs. Early Ordovician), in many respects the keratolite and stromatolite components are similar at the two localities.

4.4. Environment

These keratolite–stromatolite consortia formed in shallow water peritidal environments generally poor in shelly fossils (Pratt and James, 1986; Knight et al., 2008; Pruss and Knoll, 2017). Globally, the Late Cambrian–Early Ordovician was the prelude to an interval of major transition in marine biotas (Sepkoski Jr., 1981, fig. 5; Webby et al., 2004; Servais et al., 2016; Lee and Riding, 2018; Muscente et al., 2018; Stigall et al., 2019). The boundary interval was itself part of a significant peak in stromatolite development in North America (Peters et al., 2017, fig. 2), particularly along the margins of Laurentia (Aitken, 1967; Ahl, 1971; Chafetz, 1973; Campbell, 1976; Kennard and James, 1986; Knight and James, 1987; de Freitas and Mayr, 1995; Hersi et al., 2002; Miller et al., 2012). At the same time, metazoans were increasing in reefs (Fagerstrom, 1987; Wood, 1999), often in close association with microbial carbonates (Webby, 2002; Lee et al., 2015, 2019; Lee and Riding, 2018).

In the Boat Harbour Formation, ~100 m higher in the succession than our Green Head samples, Pruss and Knoll (2017) found that animal trace fossils and microbialite only rarely co-occur, supporting an antagonistic relationship, whereas skeletons of benthic invertebrates commonly co-vary positively with thrombolites, suggesting facilitation between microbial bioherms and at least some animals, which is also inferred in the “Green Head Mound Complex” (Pratt and James, 1982). In these dynamic peritidal environments, it is possible that keratosans, in consortium with stromatolites, occupied transient habitats unsuitable for other sessile metazoans. The Port au Port branched columns are arranged in broad low domes, and abundant relatively coarse sediment separates the columns (Fig. 2A). In contrast, small steep-sided domes at Green Head are surrounded by fine-grained carbonate (Fig. 3A). We infer that influx and movement of coarse sediment at Port au Port engendered and maintained branching, whereas small domes at Green Head developed relatively rapidly during intervals of slower sedimentation in less dynamic muddy environments. Irrespective of associated sediment, however, the stromatolite and keratolite fabrics in both situations are generally fine-grained. At Port au Port, sponge growth/colonization across adjacent closely spaced columns suggests a locally coordinated response to environmental and/or biotic triggers.

These interlayered sponges and mats, at Port au Port and Green Head, evidently shared similar environmental preferences and tolerances. Light could have promoted photosynthesis in both mat bacteria and sponge photo-endosymbionts, water movement would have brought food for sponges and nutrients for microbial mats, and current scour may have hindered burial by sediment. Microbial mats and sponges often tolerate fluctuations in temperature (although sponges are more sensitive to elevated temperature; Webster et al., 2008), and low oxygen levels could have favored both sponges (Mills et al., 2014) and mats (Des Marais, 1990; Gutiérrez-Preciado et al., 2016). Mats and sponges alike require stable substrates and sufficient relief to avoid over-burial by sediment. These requirements, together with ability to occupy similar environments, are typical of reef consortia in general (Riding, 2002).

5. Discussion

5.1. Keratosan sponges

Keratosa (“horny sponges”) constitute a subclass of demosponge
traversed by delicate tubules that represent the original supportive elements and framework (Keupp, 1991). The notable exception is the hypercalcified Triassic–present day keratose Vaceletia (Reitner, 1992; Reitner et al., 1997), which has superficial similarities with archaeocyaths (Wörheide, 2008; Germer et al., 2015). Instead, most keratosans are very effectively supported by a network of proteinaceous spongin fibers (Erpenbeck et al., 2012; Ehrlich et al., 2018; Jesionowski et al., 2018), as in the economically important “bath sponge”, Spongia officinalis. Present-day keratosans commonly contain photosynthetic symbionts, such as cyanobacteria (Wilkinson and Cheshire, 1990; Konstantinou et al., 2018), and typically occupy relatively shallow water habitats (Maldonado and Young, 1998). The absence of a rigid mineral skeleton in most keratosans hinders their present-day classification as well as their preservation and recognition as fossils. Molecular studies suggest links between Keratosa (Dictyoceratida, Dendroceratida) and a sister-group Myxospongiae (Verongida, Halisarcida, Chondrosida; Borchiellini et al., 2001; Erpenbeck et al., 2012, 2020). We follow Luo and Reitner (2014) in using Keratosa in a broad sense to include all with a fibrous spongin network and lacking spicules (Minchin, 1900), since fossil material often does not preserve the additional taxonomically important features required to confidently distinguish these groups.

5.2. Synsedimentary calcification

Under suitable conditions, initially uncalcified sponges can become synsedimentarily calcified. This occurs widely in lithistid demosponges and hexactinellids, where calcification of the primary siliceous skeleton appears to be generated by microbial decomposition that ultimately preserves the sponge body as fine-grained carbonate fabrics, typically traversed by delicate tubules that represent the original supportive elements and framework (Keupp et al., 1993; Reitner, 1993; Reitner et al., 1995; Warnke, 1995). The resulting fossils have long been recognized in Phanerozoic reefs, particularly from poorly oxygenated environments (Brunton and Dixon, 1994), often in association with microbial carbonates where they create what we here term Sponge–Microbial Consortia (see Section 5.4. Terminology), as in the Cambrian–Early Ordovician (Adachi et al., 2011; Lee et al., 2016a), Mississippian (Webb, 1987; Shen and Webb, 2005; Yao et al., 2020), Late Permian–Early Triassic (Weidlich, 2002; Brayard et al., 2011), and Mid–Late Jurassic (Leinfelder et al., 1996; Leinfelder, 2001; Aurell and Badenas, 2015; Tomás et al., 2019).

Keratosan sponges appear to be preserved by synsedimentary calcification processes similar to those that affect siliceous sponges (Luo and Reitner, 2014): the skeletal scaffolding remains more-or-less intact, the associated soft-tissue is permineralized to CaCO$_3$, most likely during microbial degradation, and the skeletal network (spongin in keratosans) is either replaced or infilled by microspar (Bracht, 1991; Reitner, 1993; Reitner et al., 1995; Warnke, 1995). Nonetheless, keratosans are generally macroscopically much less conspicuous as fossils than similarly calcified siliceous sponges. This is probably due to the delicate nature of keratosan spongin network in comparison to siliceous spicules, and to the commonly less distinctive overall morphology of keratosans. Recent studies have drawn attention to keratosans in Cambrian microbial carbonates (Lee et al., 2014) and show that keratose sponges can be significant components of structures long thought to be purely microbial in origin, such as Cryptozoön (Lee and Riding, 2021). In significant contributions, Luo and Reitner (2014, 2016) identified “vermiform” microfabric as keratosan spong network and demonstrated that keratosans likely have been widely overlooked in Phanerozoic shallow marine fine-grained carbonates generally (Table 1). The interlayered association with microbial carbonates characteristic of our Newfoundland examples is not unique to keratosans. Some lithistids and archaeocyaths, for example, also form relatively thin layers within and between microbial carbonate (Kruse and Reitner, 2014; Debrenne et al., 2015).

5.3. Vermiform fabric

The internal organic fibrous meshwork that supports keratose sponges (Erpenbeck et al., 2012) can be preserved in carbonates as “vermiform” fabric, a delicate microscopic sparry filamentous pattern created by the outlines of the original proteinaceous spong network within fine-grained carbonate matrix (Luo and Reitner, 2014). Vermiform fabric is characterized by straight to slightly curved bifurcating filaments of moderately even thickness that create a somewhat irregular anastomosing network of curvilinear Y-shaped tubules (Figs. 5D, 8). In contrast, in siliceous spicular frameworks silica is deposited on proteinaceous filaments, forming regular spicules with distinctive shapes (Reiswig and Mackie, 1983; Weaver et al., 2007). For example,
Table 1
Reports of Phanerozoic fossils and fabrics regarded here as keratolite. Bold text indicates occurrences originally attributed to non-keratosan sponges. Bold underlined text indicates references in which keratosans can be discerned in illustrations but were not mentioned by the original author(s). All other occurrences were originally identified as keratosans.

| Age                  | Locality                            | Lithology                                      | Name given in paper                  | Reference                                      |
|----------------------|-------------------------------------|------------------------------------------------|---------------------------------------|------------------------------------------------|
| Middle Miocene       | Spain                               | Deep fore-reef mud mound                       | Keratose sponge                      | Luo (2015)                                     |
| Late Cretaceous      | Spain                               | Between shallow-waterstromatolites             | Keratose sponge                      | Rodríguez-Martínez et al. (2012)               |
| (Turonian)           |                                     |                                                 |                                      |                                                 |
| Early Cretaceous     | Spain                               | Unknown                                        | Keratose sponge                      | Luo (2015)                                     |
| (late Albian)        | Germany                             | Oyster patch reef                              | Keratose sponge                      | Luo (2015)                                     |
| Late Jurassic        | Germany                             | Crinoid reef                                    | Keratose sponge                      | Luo (2015)                                     |
| (early Kimmeridgian) |                                     |                                                |                                      |                                                 |
| Middle Triassic      | Germany                             | Flacopus-s-tromatolite                          | Keratose sponge                      | Luo and Reitner (2016)                         |
| Middle Triassic      | Germany                             | Flacopus                                        | Keratose sponge                      | Luo (2015)                                     |
| (Ladinian)           |                                     |                                                |                                      |                                                 |
| Middle Triassic      | Poland                              | Stromatolite                                    | Keratose sponge                      | Luo and Reitner (2014)                         |
| Middle Triassic      | Utah, USA                           | Sponge-serpulid-microbial reef                  | Lyssacine hexactinellids            | Brayard et al. (2011, supp. fig. 2)            |
| Early Triassic       | Griesbachian                        | Thrombolite                                     | Keratose sponge                      | Heindel et al. (2018)                         |
| (Griesbachian)       |                                     |                                                |                                      |                                                 |
| Early Triassic       | Griesbachian                        | Thrombolite                                     | Keratose sponge                      | Heindel et al. (2018)                         |
| Early Triassic       | Griesbachian                        | Aragonia                                        | Keratose sponge                      | Friesenbichler et al. (2018)                  |
| (Griesbachian)       |                                     |                                                |                                      |                                                 |
| Earliest Triassic    | Hubei, China                        | Stromatolite                                    | Micrite with meshlike sponge texture | Adachi et al. (2017, fig. 8D)                  |
| Mississippian        | Iran                                | Ostracod wackestone                            | Keratose sponge                      | Luo (2015)                                     |
| (Visean)             |                                     |                                                |                                      |                                                 |
| Late Devonian        | United Kingdom                      | Stromatolite                                    | Keratose sponge                      | Luo and Reitner (2016)                         |
| (Famennian)          |                                     |                                                |                                      |                                                 |
| Late Devonian        | Utah, USA                           | Stromatolite                                    | Keratose sponge                      | Stock and Sandberg (2019)                      |
| (Famennian)          |                                     |                                                |                                      |                                                 |
| Late Devonian        | Germany                             | Mud mound with Renalcis and hexactinellids     | Keratose sponge                      | Ahlbrecht (1997), identified by Luo (2015)    |
| (Famennian)          |                                     |                                                |                                      |                                                 |
| Early Triassic       | Iran                                | Stromatolite                                    | Non-lithistid demospoange            | Zhou and Pratt (2019)                          |
| (Griesbachian)       |                                     |                                                |                                      |                                                 |
| Early Triassic       | Turkey                              | Stromatolite                                    | Vermiform microstructure             | Pratt et al. (1982, fig. 15A, B)               |
| (Griesbachian)       |                                     |                                                |                                      |                                                 |
| Middle Devonian      | France                              | Bryozoan reef                                   | Keratose sponge                      | Reitner et al. (2007), Luo and Reimer (2014)  |
| (Givetian)           |                                     |                                                |                                      |                                                 |
| Middle Devonian      | Morocco                             | Holland mud mound                               | Keratose sponge                      | Luo (2015)                                     |
| (Eifelian–Givetian)  |                                     |                                                |                                      |                                                 |
| Late Ordovician      | Jiangxi, China                      | Tetriad-sponge reef, micritic limestone, intraoskeletal crypt | Siliceous sponge (Kwon et al., 2012), non-lithistid demospoange (Park et al., 2015, 2017) | Kwon et al. (2012); Park et al. (2015, 2017)   |
| (Katian)             |                                     |                                                |                                      |                                                 |
| Late Ordovician      | Quebec, Canada                      | Unknown                                         | Vermiform microstructure             | Larmagnat and Neuweiler (2015)                |
| (Katian)             |                                     |                                                |                                      |                                                 |
| Middle–Late Ordovician| Shaanxi, China                      | Bivalve-sponge-microbial reef                   | Siliceous sponge                     | Lee et al. (2016b)                            |
| (Sandbian?)          | Vermont, USA                        | Stromatoporoid-Solenopora-tabulateline-thristo-bryozaan mound | Vermiform fabric                      | Desmoulin and James (1987, fig. 70)           |
| Middle Ordovician    | Quebec, Canada                      | Lithistid-bryozaan-tabulate-Solenopora bioherm  | Vermiform fabric                      | Hong et al. (2018)                            |
| (Darrinwillian)      |                                     |                                                |                                      |                                                 |
| Middle Ordovician    | Korea                               | Stromatoporoid-bryozaan-reed                    | Siliceous sponge                     | Hong et al. (2018)                            |
| (Darrinwillian)      |                                     |                                                |                                      |                                                 |
| Middle Ordovician    | Korea                               | Brachiopod wackestone, Stromatoporoid reef     | Spiculate sponge                     | Park et al. (2015, fig. 8B); Hong et al. (2017) |
| (Darrinwillian)      |                                     |                                                |                                      |                                                 |
| Middle Ordovician    | Tarim, China                        | Calathium-demospoange reef                      | Keratose sponge                      | Li et al. (2017a, b); Shen and Neuweiler (2018) |
| (Darrinwillian)      |                                     |                                                |                                      |                                                 |
| Middle Ordovician    | Nevada, USA                         | Meiklejohn mud mound                            | Meshwork of uncertain origin or peloid (=) texture (Ross et al., 1975); vermiform microstructure (Pratt, 1982) | Ross et al. (1975, figs. 23, 25); Pratt (1982, fig. 15C, D7) |
| (Darrinwillian)      |                                     |                                                |                                      |                                                 |
| Middle Ordovician    | St. Petersburg, Russia              | Hekker-type mud mound                           | Keratose sponge                      | J.-H. Lee (personal observation)               |
| Early Ordovician     | Guizhou, China                      | Lithistid-Calathium reef                        | Keratose sponge                      | Li et al. (2017a)                             |
| (Floian)             |                                     |                                                |                                      |                                                 |
| Early Ordovician     | Hubei, China                        | Lithistid-microbial reef                        | Keratose sponge                      | Liu et al. (1997, fig. 4A, E)                  |
| (Tremadocian–Floian) |                                     |                                                |                                      |                                                 |
| Early Ordovician     | Anhui, China                        | Lithistid-microbial reef                        | Not recognized                       | Adachi et al. (2009), fig. 5D                 |
| (Tremadocian–Floian) |                                     |                                                |                                      |                                                 |
| Early Ordovician     | Oklahoma, USA                       | Stromatolite                                    | Clotted microstructure (vermiform)    | Li et al. (2015, fig. SC)                      |
| (Tremadocian)        |                                     |                                                | Lithistid sponge                     | Headl (2004)                                   |
| Early Ordovician     | Malaysia                            | Sponge-bearing thrombolites andstromatolites   | Probable keratose sponge             | Li et al. (2019a)                              |
| (Tremadocian)        |                                     |                                                |                                      |                                                 |
| Early Ordovician     | Korea                               | Lithistid-microbial reef                        | Spiculate sponge                     | Hong et al. (2014, 2015)                      |
| (Tremadocian)        |                                     |                                                |                                      |                                                 |
| Early Ordovician     | Korea                               | Stromatolite and thrombolite                    | Keratose sponge                      | Pham and Lee (2020)                           |
| (Tremadocian)        |                                     |                                                |                                      |                                                 |
| Early Ordovician     | Newfoundland, Canada                | Thrombolite                                     | Vermiform fabric                     | Pratt (1982, fig. 13C); Pratt and James (1989b, fig. 7) |
| (Tremadocian)        |                                     |                                                |                                      |                                                 |
| Earliest Ordovician  | Newfoundland, Canada                | Stromatolite                                    | Keratose sponge                      | This study                                     |
| (Tremadocian)        |                                     |                                                |                                      |                                                 |
| Latest Cambrian      | Newfoundland, Canada                | Stromatolite                                    | Keratose sponge                      | This study                                     |
| (Stage 10)           |                                     |                                                |                                      |                                                 |
| Late Cambrian        | Korea                               | Ribbon rock                                     | Keratose sponge                      | Lee et al. (2018)                             |
| (Stage 10)           | Nevada, USA                         | Lithistid-microbial reef                        | Keratose-like sponge                 | Lee et al. (2019)                             |

(continued on next page)
hexactinellid sponges have six-pointed spicules (hexactines) with square or rectangular cross-sections (e.g., Brachert, 1991, fig. 3A–C), whereas demosponges contain spicules of various shapes (e.g., monaxons, tetraxons), but never contain triaxons (Hooper and Van Soest, 2002).

In fossils, keratosan spongin "vermiform" fabric has been confused with protozoans, filamentous algae, cyanobacteria and fungi. In Late Cambrian Cryptozoön, Hall (1883) described "numerous, minute, irregular canaliculi which branch and anastomose without regularity". Gürich (1906, p. 44) described "des canaux coloniaux curvilignes et vermiiformes" (curvilinear and vermiciform colonial canals) in Mississippian Spongiostruma, which he (p. 32) provisionally interpreted as protozoans due to their structural irregularity. Referring to Cryptozoön, Walter (1972) described similar fabric in Cambrian Madiganites mawsoni, termed it "vermiform", and interpreted it as the remains of algal filaments. Bertrand-Sarfati (1976, p. 255) was uncertain of the origin of vermiform fabric, but noted that it occurred sporadically in the late Proterozoic. Kennard (1994, p. 459) interpreted Middle to Late Cambrian vermiform microstructure as molds of "sheaths and tri- chomes". Reitner (1994, p. 405) initially compared vermiform fabric with fungal mycelia. Subsequently, Reitner et al. (2001) suggested that vermiform fabric represents the remains of keratose sponges, and 3-D fabric reconstruction by serial grinding tomography confirmed its morphologic similarity to the fibrous spongin network of keratose demosponges (Luo and Reitner, 2014). As comprehensively pointed out by Luo (2015), vermiform fabric has often been mistaken for the spicular framework of siliceous sponges, including lithistids, or simply overlooked (Table 1).

### Table 1 (continued)

| Age                | Locality          | Lithology                  | Name given in paper          | Reference                     |
|--------------------|-------------------|----------------------------|-------------------------------|-------------------------------|
| Late Cambrian      | New York, USA     | Cryptozoön proliferum     | Keratose sponge               | Lee and Riding (2021)         |
| (Jiangshanian–Stage 10?) |                  | Maceriate reef, stromatolite | Lithistid sponge              | Coulson and Brand (2016)      |
| Late Cambrian      | Utah, USA         | Stromatolite               | Siliceous sponge              | Chen et al. (2014)            |
| (Jiangshanian–Stage 10) |                | Maceriate reef             | Siliceous sponge              | Chen et al. (2014); Lee et al. (2014) |
| Late Cambrian      | Shandong and Beijing, China | Stromatolite          | Keratose sponge               | J.-H. Lee (personal observation) |
| (Jiangshanian)     | New York, USA     | Stromatolite               | Unidentified siliceous sponge | Chen et al. (2014); Lee et al. (2014) |
| Late Cambrian (Paibian?) |                  |                            |                              |                               |
| Middle–Late Cambrian | Amadeus Basin, Australia | Madiganites mawsoni     | Vermiform fabric              | Walter (1972); Kennard (1994); Park et al. (2015, fig. 8A) |
| Middle Cambrian    | Shandong, China   | Ribbon rock                | Non-lithistid demosponge      | Lee et al. (2016c)            |
| (Guzhangian)       | Inner Mongolia, China | Maceriate reef             | Siliceous sponge              | Lee et al. (2016c)            |
| Middle Cambrian    | Korea             | Thrombolite-sponge boundstone | Siliceous sponge              | Hong et al. (2012, 2016)      |
| (Drumian)          | Shandong, China   | Epiphyton microbialite     | Sponge-like fabric            | Adachi et al. (2015); Lee et al. (2016a) |
| Middle Cambrian    | South Australia   | Acaciella angepena         | Algal boring                  | Preiss (1971, pl. 5b)         |
| (Tommotian)        | Siberia, Russia   |                          | Keratose sponge               | Luo (2015)                    |

![Fig. 8](image_url) Other examples of keratosan vermiform fabric. (A, B) Middle–Late Ordovician, Shaanxi Province, China (see Lee et al., 2016b). (C, D) Late Ordovician (Katian), Jiangxi Province, China (see Park et al., 2015).
recognized in it by Hall (1883) reflect the presence of keratosan sponges (Lee and Riding, 2021).

5.4. Terminology

We propose the term keratolite for carbonate that preserves the vermiform outlines (e.g., Figs. 5D, 8) of the originally spongin keratosan skeleton. Keratolite characteristically consists of dense fine-grained millimetric to centimetric layers that represent synsedimentarily calcified organic tissue initially supported by a network of anastomosing spongin fibers. Internally, keratolite fabric can range from irregularly (Fig. 7A) to sub-millimetrically layered (Fig. 5A, B). Locally, it can incorporate fine sand grains (Lee and Riding, 2021). Keratolite can be closely associated with stromatolite (laminated microbial carbonate), as in our Newfoundland examples, as well as with diverse metazoan and other microbial reef fabrics (Table 1). In addition to vermiciform fabric, cylindrical outlines and central cavities (spongocoel) typical of filter-feeding organisms can occasionally be recognized (Lee et al., 2014, fig. 7A–C).

In contrast to keratosan sponges, which have commonly been overlooked (Luo and Reitner, 2016), rock-forming associations between siliceous sponges and microbial carbonates are well-documented in the Phanerozoic (Brunton and Dixon, 1994). In Jurassic reefs, lithified siliceous sponges, typically lithistids and hexactinellids with distinctive spicular skeletons, have variously been termed tuberoid, tuberolith (Fritz, 1958), spongolith (Geyer, 1962) and spongiolite (Keupp et al., 1993, 1996; also spelt spongolite, e.g., Gammon, 2000; Gammon et al., 2000; Gammon and James, 2003). To standardize terminology, we suggest that spongolith should be restricted to refer to synsedimentarily calcified siliceous sponges. In this usage, keratolite (synsedimentarily calcified proteinaceous sponge) and spongolith are varieties of synsedimentarily calcified sponge that, in close combination with microbial carbonates, create Sponge–Microbial Consortia. These likely originated in the late Proterozoic (Seilacher, 1999).

5.5. Keratolite distribution and recognition

Porifera are widely regarded as the oldest metazoan group (Feuda et al., 2017; Simion et al., 2017). The earliest currently confirmed sponge fossils are earliest Cambrian (Fortunian) in age (Chang et al., 2017, 2019), and keratosans are preserved in Early (Luo et al., 2020) and Middle Cambrian Burgess Shale-type biotas (Botting et al., 2013; Ehrlich et al., 2013; Yang et al., 2017). Although many uncertainties remain (Antcliff et al., 2014; Botting and Muir, 2018; Nettersheim et al., 2019), biomarker (Love et al., 2009; Sperling and Stockey, 2018) and phylogenetic (Wörheide et al., 2012) studies suggest the likelihood that sponges were extant in the Neoproterozoic.

Present-day sponges harbor diverse inter- and intracellular symbiotic microbes (Rützler, 1990, 2012; Reitner, 1993; Rodriguez-Marconi et al., 2015) that can constitute a significant proportion of body mass (Hentschel et al., 2006), in some cases up to 40% (Taylor et al., 2007). These bacteria participate in key functional roles that facilitate nutrition, and provide metabolic pathways not otherwise available (Taylor et al., 2007; Richardson et al., 2012; Pita et al., 2018). Secondary metabolites can also be effective in defense (Taylor et al., 2007), and biofilms can assist sponge larval settlement (Whalan and Webster, 2014). Seafoils in the late Proterozoic are generally thought to have been poorly oxygenated and dominated by bacteria (Gingras et al., 2011; Evans et al., 2019). Bacteria and sponges likely became intimately associated as soon as sponges evolved (Li et al., 1998; Pick et al., 2010; Yin et al., 2015). Sponges, in addition to having low oxygen requirements (Mills and Canfield, 2014) and interacting intensely with microbes, can accumulate and colonize allochthonous sediment (Schniberg, 2016), similar to microbial mats. Thus, it would not be surprising if sponges, from very early in their history, were intimately associated with stromatolites and thrombolites (Seilacher, 1999; Hadfield, 2011; Antcliff et al., 2014;...
6. The macroscopicsimilarities of keratite and stromatolite, together with the long geological range of keratosans, make it likely that keratite has been mistaken for stromatolite throughout the Phanerozoic, and possibly in the late Proterozoic too.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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