

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 spongin 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 spongin 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; Noffke 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, Stromatoporoidea; Hartman et al., 1980; Senowbari-Daryan and Rigby, 2011) and silica (e.g., Lithistida, Hexactinellida; Hooper and Van Soest, 2002; Reischwig, 2002), to spongin (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 spongin of keratosaurs, 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 (Flügel 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 spongin 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

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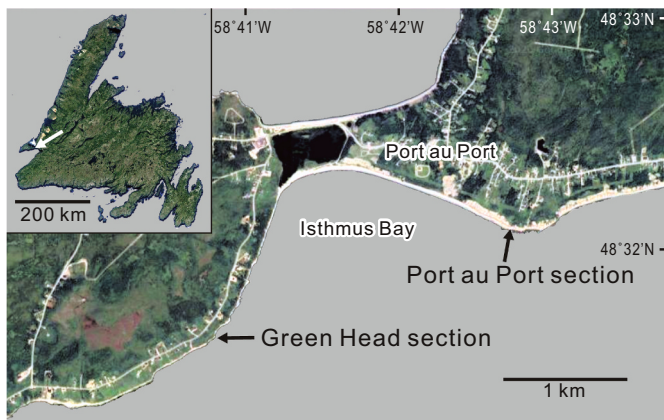


Fig. 1. Location of the study area in western Newfoundland. The Port au Port (48°33'05.8"N 58°42'15.9"W) and Green Head (48°32'36.8"N 58°44'12.5"W) sections are located on the eastern and western sides of Isthmus Bay, respectively. Modified from Google (2020).

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 keratosaurs – could have originated in the Neoproterozoic (Wörheide 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; Lavoie et al., 2012; Lavoie, 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; Scorer et al., 2019, fig. 2). On the

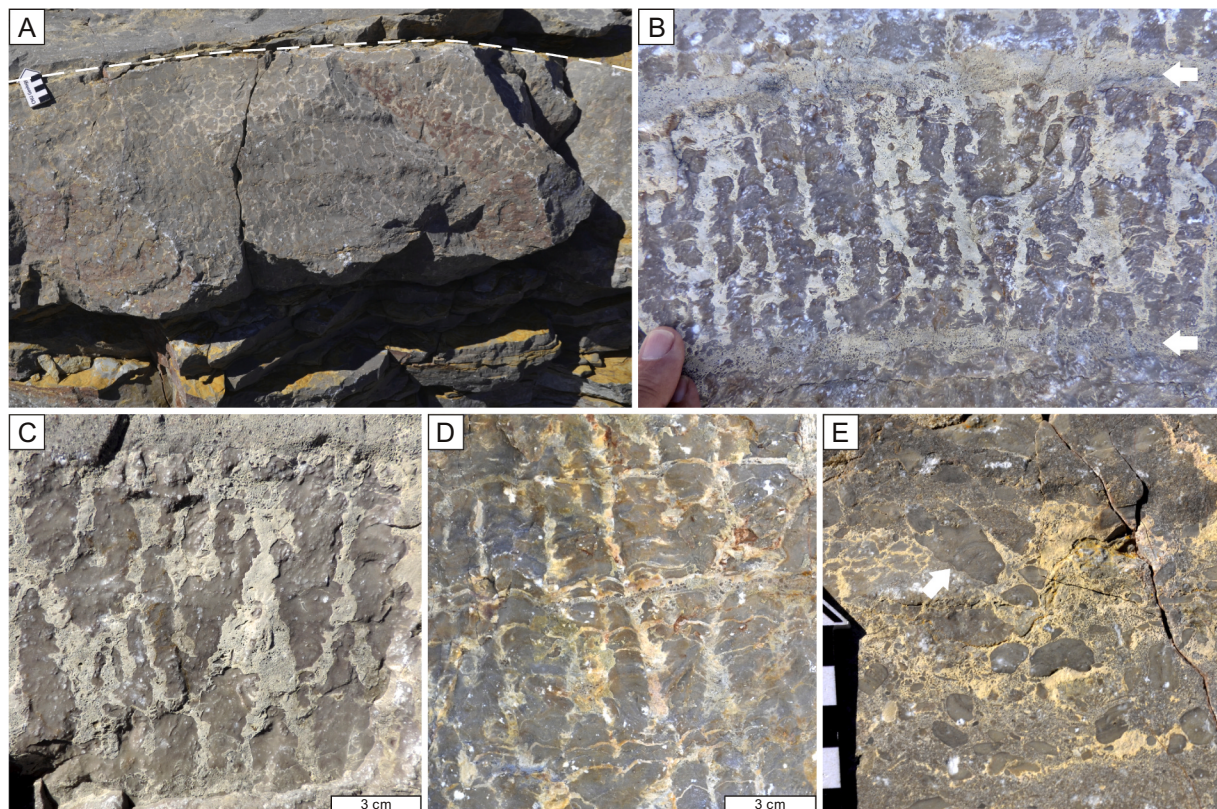


Fig. 2. Branching keratolite-stromatolite columns; uppermost Cambrian (Berry Head Formation), Port au Port section. Location, see Fig. 1. (A) Numerous columns form a broad low dome, 2–3 m wide and 60–70 cm thick, underlain by thin-bedded lime mudstone and overlain by rudstone which also occurs lateral to the dome. Cm scale. (B) Erect columns surrounded by light-gray coarse dolomitic matrix, which also forms layers above and below the columns (arrows). (C) Divergent, upward-widening columns with coarse sediment layers at base and top. (D) Densely packed columns with thin layers of coarse sediment that cross the columns. (E) Broken column fragments (large example arrowed) in adjacent rudstone. Cm scale.

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 syngedimentary 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 Awwam, 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

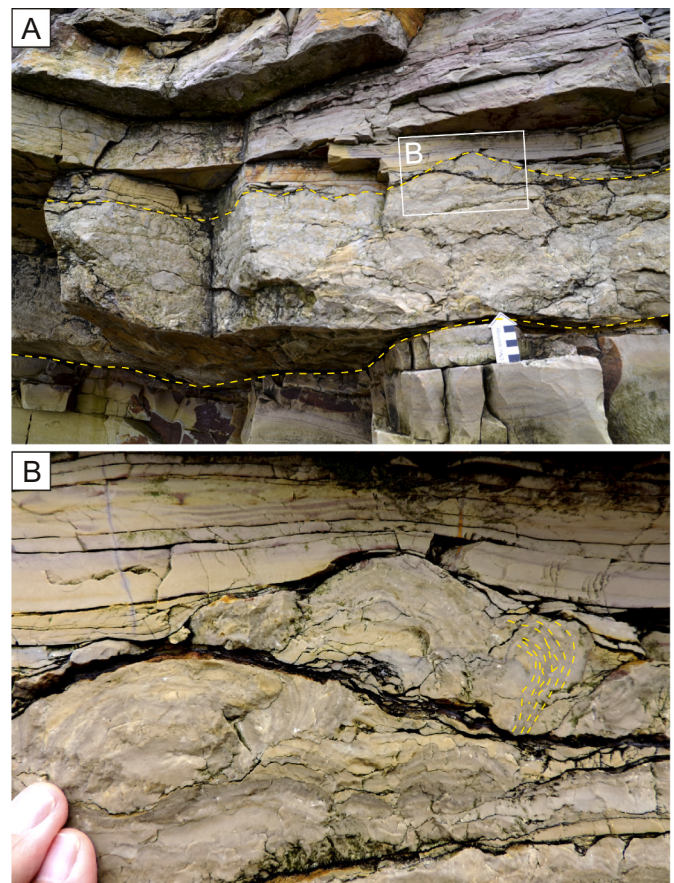


Fig. 3. Domical keratolite–stromatolite, lowermost Ordovician (Watts Bight Formation), Green Head section. Location, see Fig. 1. (A) Biostrome (dashed outline) of small keratolite–stromatolite domes, underlain and overlain by fine-grained tan colored carbonate. Cm scale. (B) Detail of (A) showing domes with steep to over-hanging margins (dotted lines).

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

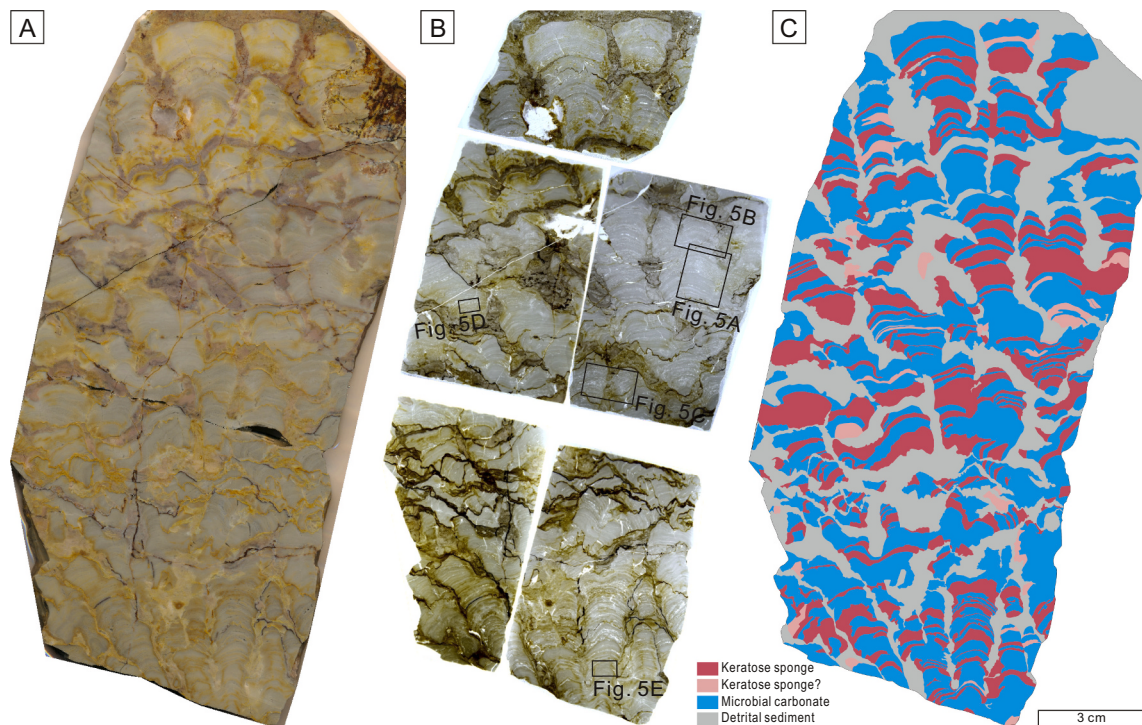


Fig. 4. Columnar branching keratolite–stromatolite; Port au Port section. (A) Vertical slab. (B) Thin-sections of the slab, showing positions of the photomicrographs shown in Fig. 5. (C) Map showing keratolite and microbial carbonate (stromatolite). Both form relatively even alternating layers, mostly up to ~2 cm thick, that tend to persist laterally across adjacent columns.

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 inter-column sediment (Fig. 4). Each column consists of regular to irregular alternations of keratolite 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 symsedimentary lithification, and the columns are only slightly dolomitized. In shape and size, the outlines of these Port au Port keratolite 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 symsedimentary lithification.

4.2. Green head domes

These small, laterally linked (see Logan et al., 1964) and well-laminated keratolite–stromatolite domes, with locally steeply angled margins, occur within sand-poor, very fine-grained, carbonate

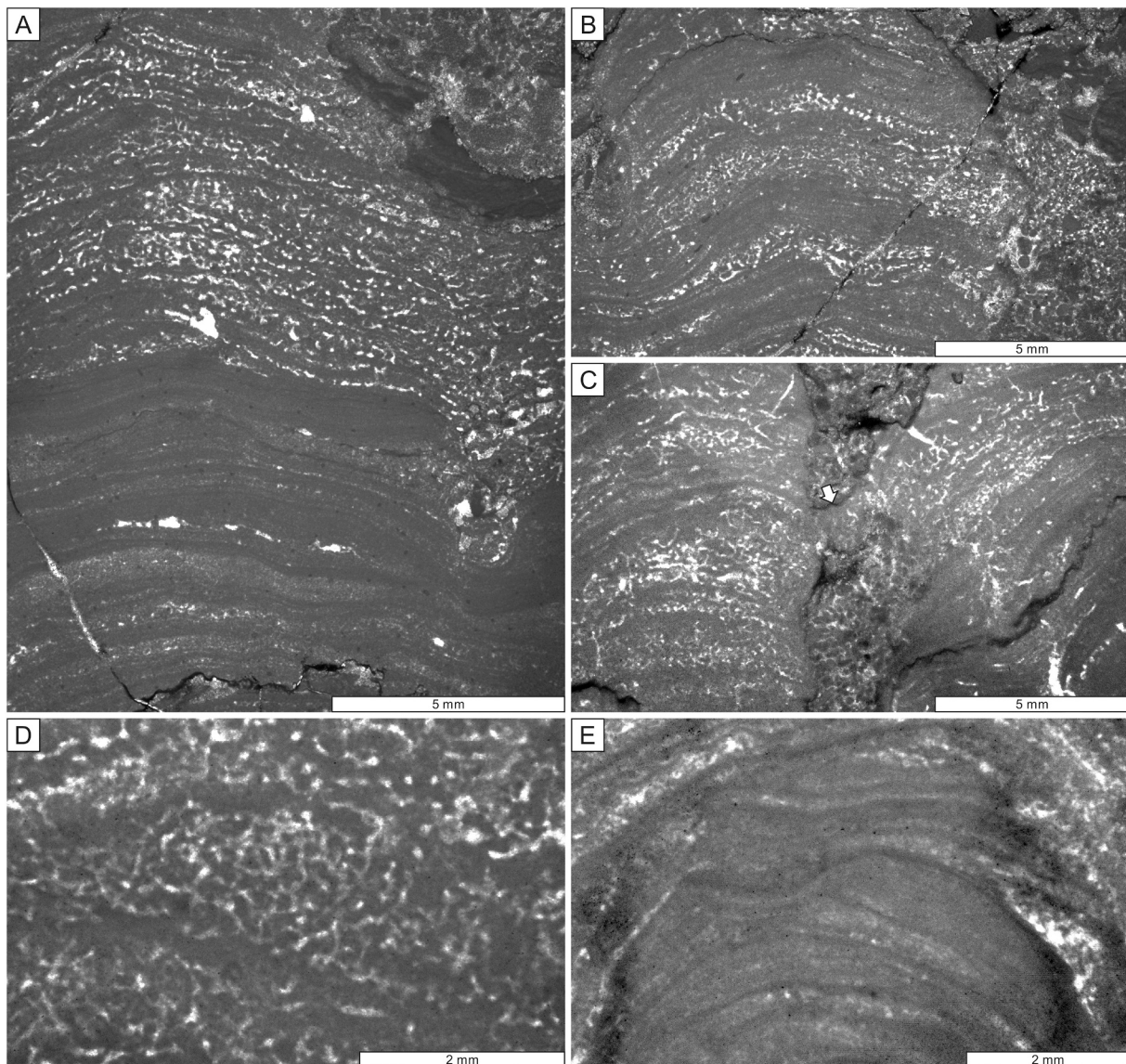


Fig. 5. Photomicrographs of columnar keratolite–stromatolite; Port au Port section. See positions of thin-sections in Fig. 4B. (A) Stromatolite (lower part) overlain by vermiform keratose sponge (keratolite; upper part). Both show lamination, which is more delicate in the stromatolite. (B) Thinly interlayered keratolite–stromatolite column. (C) Adjacent columns separated by intraclastic grainstone but connected by a sponge (keratolite) bridge (arrow). (D) Detail of keratose sponge (keratolite) showing characteristic vermiform fabric produced by the original spongin fiber network. (E) Detail of stromatolite column, showing cross-cutting laminae suggestive of sediment trapping associated with current transport. Keratose sponge (vermiform fabric; keratolite) occurs at the sides and top.

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 keratose 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

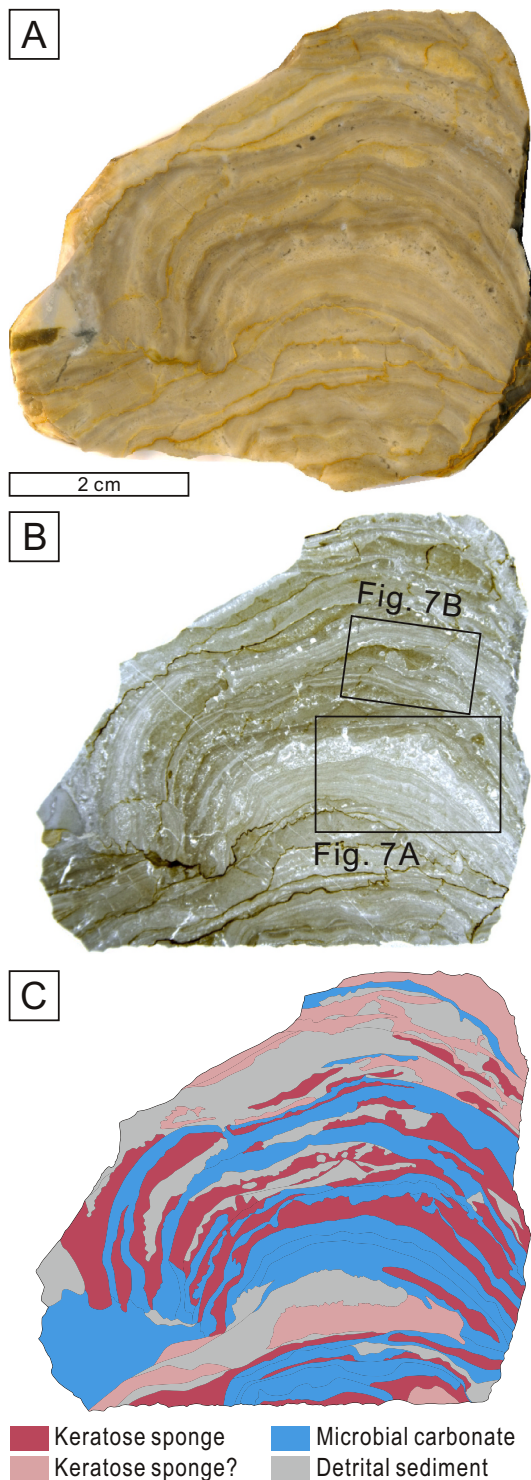


Fig. 6. Domical keratolite–stromatolite with steep margins; Green Head section. (A) Vertical slab. (B) Thin-section of the slab, showing positions of the photomicrographs in Fig. 7. (C) Map showing keratolite and microbial carbonate (stromatolite). Both components form irregular alternating layers up to ~1 cm thick that tend to persist laterally. Keratolite layers often have smooth bases and more irregular tops. Layers of mostly fine-grained detrital carbonate may locally have terminated sponge growth.

likely resulted from trapping and binding (Tosti and Riding, 2017). Reworked columns at Port au Port indicate syndimentary 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; Ahr, 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 keratolites, 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., 2018). 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. Keratolite sponges

Keratolite (“horny sponges”) constitute a subclass of demosponge

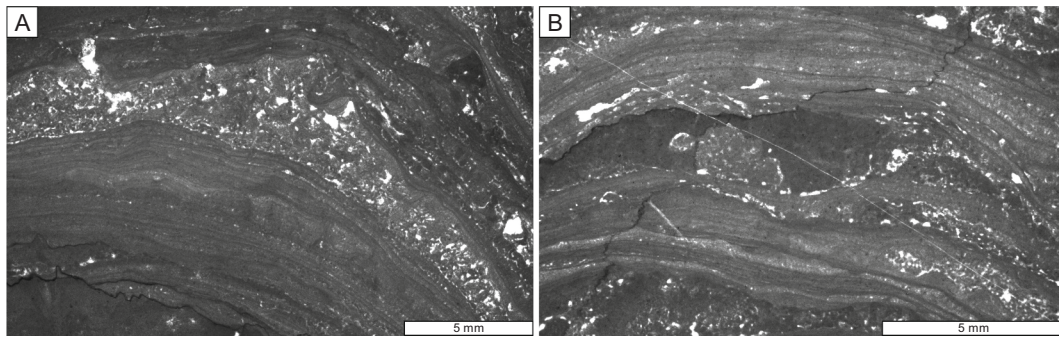


Fig. 7. Thin-section photomicrographs of domical keratolite–stromatolite; Green Head section. See positions of thin-sections in Fig. 6B. (A) Delicately laminated stromatolite overlain by keratolite with a relatively flat-base and more irregular top. (B) Intricately interlayered keratolite and stromatolite. Note isolated keratolite mass (left-center) surrounded by micrite.

(Wörheide et al., 2012). Unlike most sponges with a fossil record, keratosans do not produce either siliceous spicules (e.g., as in demosponges, hexactinellids) or heavily calcified skeletons (e.g., as in archaeocyaths, chaetetes, sphinctozoans, stromatoporoids; Wood, 1990; Reitner and Keupp, 1991). The notable exception is the hypercalcified Triassic–present day keratosan *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; Borchellini 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. Syndimentary calcification

Under suitable conditions, initially uncalcified sponges can become syndimentarily 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 Bádenas, 2015; Tomás et al., 2019).

Keratosan sponges appear to be preserved by syndimentary 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 (Brachert, 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 spongin 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 spongin 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 keratosaurs can be discerned in illustrations but were not mentioned by the original author(s). All other occurrences were originally identified as keratosaurs.

Age	Locality	Lithology	Name given in paper	Reference
Middle Miocene	Spain	Deep fore-reef mud mound	Keratose sponge	Luo (2015)
Late Cretaceous (Turonian)	Spain	Between shallow-water stromatolites	Keratose sponge	Rodríguez-Martínez et al. (2012)
Early Cretaceous (late Albian)	Spain	Unknown	Keratose sponge	Luo (2015)
Late Jurassic (early Kimmeridgian)	Germany	Oyster patch reef	Keratose sponge	Luo (2015)
Middle Triassic	Germany	Crinoid reef	Keratose sponge	Luo (2015)
Middle Triassic (Ladinian)	Germany	<i>Placunopsis</i> -stromatolite reef	Keratose sponge	Luo and Reitner (2016)
Middle Triassic	Germany	<i>Placunopsis</i> reef	Keratose sponge	Luo (2015)
Middle Triassic (Anisian)	Poland	Stromatolite	Keratose sponge	Luo and Reitner (2014)
Early Triassic (Smithian)	Utah, USA	Sponge-serpulid-microbial reef	Lyssacine hexactinellids	Brayard et al. (2011, supp. fig. 2)
Early Triassic (Griesbachian)	Iran	Thrombolite	Keratose sponge	Heindel et al. (2018)
Early Triassic (Griesbachian)	Turkey	Thrombolite	Keratose sponge	Heindel et al. (2018)
Early Triassic (Griesbachian)	Armenia	Stromatolite	Keratose sponge	Friesenbichler et al. (2018)
<u>Earliest Triassic</u>	<u>Hubei, China</u>	<u>Stromatolite</u>	<u>Micrite with meshlike spongy texture</u>	<u>Adachi et al. (2017, fig. 8D)</u>
Earliest Triassic	Iran	Ostracod wackestone	Keratose sponge	Luo (2015)
<u>Mississippian (Visean)</u>	<u>Belgium</u>	<u>Spongostroma mæandrinum</u>	<u>Canal system</u>	<u>Gürich (1906)</u>
Mississippian (Visean)	United Kingdom	Stromatolite	Keratose sponge	Luo and Reitner (2016)
Late Devonian (Famennian)	Utah, USA	Stromatolite	Keratose sponge	Stock and Sandberg (2019)
Late Devonian (Frasnian)	Germany	Mud mound with <i>Renalcis</i> and hexactinellids	Keratose sponge	Ahlbrecht (1997), identified by Luo (2015)
<u>Late Devonian (Frasnian)</u>	<u>Alberta, Canada</u>	<u>Stromatactis mud mound</u>	<u>Non-lithistid demosponge</u>	<u>Zhou and Pratt (2019)</u>
<u>Late Devonian</u>	<u>Belgium</u>	<u>Unknown</u>	<u>Vermiform microstructure</u>	<u>Pratt (1982, fig. 15A, B)</u>
Middle Devonian (Givetian)	France	Rugose- <i>Rothpletzella</i> -sponge reef	Keratose sponge	Reitner et al. (2001); Luo and Reitner (2014)
Middle Devonian (Eifelian–Givetian)	Morocco	Hollard mud mound	Keratose sponge	Luo (2015)
<u>Late Ordovician (Katian)</u>	<u>Jiangxi, China</u>	<u>Tetradiid-sponge reef, micritic limestone, intraskeletal crypt</u>	<u>Siliceous sponge (Kwon et al., 2012), non-lithistid demosponge (Park et al., 2015, 2017)</u>	<u>Kwon et al. (2012); Park et al. (2015, 2017)</u>
Late Ordovician (Katian)	Québec, Canada	Bryozoan reef	Microtubules of keratose sponges or fungi	Larmagnat and Neuweiler (2015)
<u>Middle–Late Ordovician (Sandbian?)</u>	<u>Shaanxi, China</u>	<u>Bivalve-sponge-microbial reef</u>	<u>Siliceous sponge</u>	<u>Lee et al. (2016b)</u>
<u>Middle Ordovician (Darriwilian)</u>	<u>Vermont, USA</u>	<u>Stromatoporoid-Solenopora-tabulate-lithistid-bryozoan mound</u>	<u>Algal crust</u>	<u>Kapp (1975, fig. 3); J.-H. Lee (personal observation)</u>
<u>Middle Ordovician (Darriwilian)</u>	<u>Québec, Canada</u>	<u>Lithistid-bryozoan-tabulate-Solenopora bioherm</u>	<u>Vermiform fabric</u>	<u>Desrochers and James (1989, fig. 7f)</u>
Middle Ordovician (Darriwilian)	Korea	Stromatoporoid-bryozoan reef	Siliceous sponge	Hong et al. (2018)
Middle Ordovician (Darriwilian)	Korea	Brachiopod wackestone, Stromatoporoid reef	Spiculate sponge	Park et al. (2015, fig. 8B); Hong et al. (2017)
Middle Ordovician (Darriwilian)	Tarim, China	Calathiid-demosponge reef	Keratase sponge (Shen and Neuweiler, 2018), lithistid sponge (Li et al., 2017b)	Li et al. (2017b); Shen and Neuweiler (2018)
<u>Middle Ordovician</u>	<u>Nevada, USA</u>	<u>Meiklejohn mud mound</u>	<u>Meshwork of uncertain origin or pelletoid(?) texture (Ross et al., 1975); vermiform microstructure (Pratt, 1982)</u>	<u>Ross et al. (1975, figs. 23, 25); Pratt (1982, fig. 15C, D)</u>
Middle Ordovician	St. Petersburg, Russia	Hekker-type mud mound	Keratase sponge	J.-H. Lee (personal observation)
Early Ordovician (Floian)	Guizhou, China	Lithistid- <i>Calathium</i> reef	Keratase sponge	Li et al. (2017a)
<u>Early Ordovician (Tremadocian–Floian)</u>	<u>Hubei, China</u>	<u>Lithistid-microbial reef</u>	<u>Not recognized</u>	<u>Liu et al. (1997, fig. 6.1–6.3)</u>
Early Ordovician (Tremadocian–Floian)	Anhui, China	Lithistid-microbial reef	Not recognized (Adachi et al., 2009), sponge remains (Li et al., 2015)	Adachi et al. (2009, fig. 5D); Li et al. (2015, fig. 5C)
<u>Early Ordovician</u>	<u>Oklahoma, USA</u>	<u>Stromatolite</u>	<u>Clotted microstructure (vermiform)</u>	<u>Headd (2004)</u>
Early Ordovician	Malaysia	Sponge-bearing thrombolites and stromatolites	Lithistid sponge	Li et al. (2019a)
Early Ordovician (Tremadocian)	Thailand	“Stromatolite” of sponge-microbial association	Probable keratase sponge	Li et al. (2019b)
Early Ordovician (Tremadocian)	Korea	Lithistid-microbial reef	Spiculate sponge	Hong et al. (2014, 2015)
Early Ordovician (Tremadocian)	Korea	Stromatolite and thrombolite	Keratase sponge	Pham and Lee (2020)
<u>Early Ordovician (Tremadocian)</u>	<u>Newfoundland, Canada</u>	<u>Thrombolite</u>	<u>Vermiform fabric</u>	<u>Pratt (1982, fig. 13C); Pratt and James (1989b, fig. 7)</u>
Earliest Ordovician (Tremadocian)	Newfoundland, Canada	Stromatolite	Keratase sponge	This study
Latest Cambrian (Stage 10)	Newfoundland, Canada	Stromatolite	Keratase sponge	This study
Late Cambrian (Stage 10)	Korea	Ribbon rock	Keratase sponge	Lee et al. (2018)
Late Cambrian (Stage 10)	Nevada, USA	Lithistid-microbial reef	Keratase-like sponge	Lee et al. (2019)

(continued on next page)

Table 1 (continued)

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

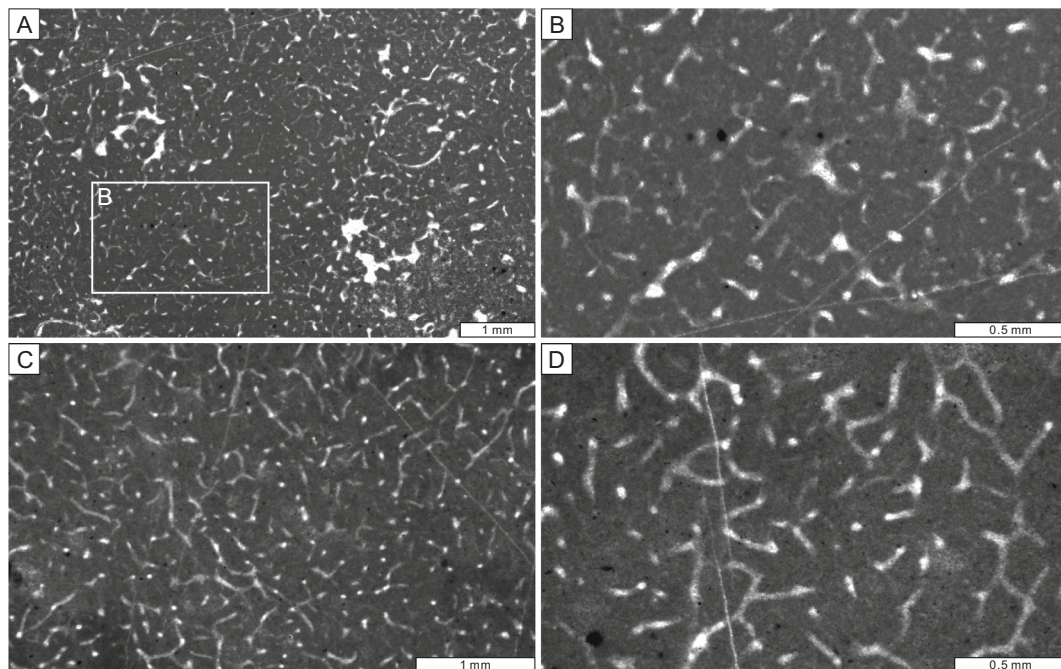


Fig. 8. Other examples of keratosan vermiform fabric. (A, B) Middle–Late Ordovician, Shaanxi Province, China (see [Lee et al., 2016b](#)). (C, D) Late Ordovician (Katian), Jiangxi Province, China (see [Park et al., 2015](#)).

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 *Cryptozoon*, [Hall \(1883\)](#) described “numerous, minute, irregular canaliculi which branch and anastomose without regularity”. [Gürlich \(1906, p. 44\)](#) described “des canaux coloniaux curvilignes et vermiformes” (curvilinear and vermiform colonial canals) in Mississippian *Spongiostroma*, which he (p. 32) provisionally interpreted as protozoans due to their structural irregularity. Referring to *Cryptozoon*, [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 trichomes”. [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). Late Cambrian *Cryptozoon* was long regarded as a “classic” stromatolite ([Logan, 1961](#)), even though the “canaliculi”

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 syndementarily 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 vermiform 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 spiculate skeletons, have variously been termed tuberoïd, tuberculolith (Fritz, 1958), spongiolith (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 spongiolite should be restricted to refer to syndementarily calcified *siliceous* sponges. In this usage, keratolite (syndementarily calcified *proteinaceous* sponge) and spongiolite are varieties of syndementarily 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 keratosaurs 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 (Antcliffe 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). Seafloors 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 (Schönberg, 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; Antcliffe et al., 2014;

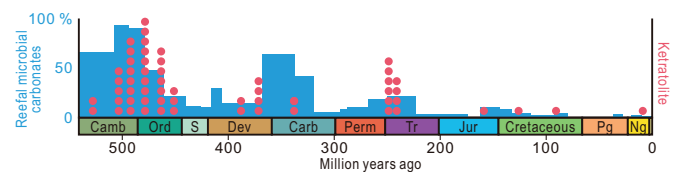


Fig. 9. Stratigraphic distribution of examples of keratolite in Phanerozoic marine limestones shown by red dots (data in Table 1) superimposed on abundance of reefal microbial carbonates (after Kiessling, 2002; Riding et al., 2019).

Droser and Gehling, 2015; Wood and Penny, 2018). Fabrics resembling keratolite occur in the late Proterozoic (Vologdin, 1962, pl. 61; Bertrand-Sarfati, 1976, p. 255; Luo, 2015, fig. 6.3).

Sponge calcification can involve microbial activity (Reitner, 1993; Reitner et al., 1995), and the conditions necessary for syndementary calcification to preserve keratosaurs were likely enhanced at times when microbial calcification in general was widespread. The secular distribution of keratolite compiled here (Table 1) broadly coincides with intervals when reefal microbial carbonates were generally abundant: Cambrian–Ordovician, Late Devonian–Mississippian, Early–Middle Triassic, and Late Jurassic–Cretaceous (Riding, 2006, fig. 6; Fig. 9). However, it is also possible that calcifying endosymbiotic bacteria might be involved in keratosan calcification, as in some present-day siliceous demosponges (Uribe et al., 2012; Garate et al., 2017).

The presence of fossil keratosaurs in carbonate sediment is only clearly revealed by recognition of vermiform fabric in thin-section (e.g., Lee et al., 2010, 2014; Luo and Reitner, 2014). Current understanding suggests that, despite their local volumetric abundance (Hong et al., 2016), keratosaurs do not create morphotypes readily distinguishable from those of stromatolites, and their overall form probably broadly reflects environmental controls. This underscores the likelihood that keratosaurs–microbial associations have often gone unnoticed and may have been widely mistaken as purely stromatolitic (i.e., microbial) in origin. Many putative “stromatolites” of the past 500 or more million years may harbor substantial volumes of previously unrecognized keratolite.

6. Conclusions

1. Keratolite (new term) is defined as keratosan sponge carbonate dominated by vermiform fabric that preserves the outlines of the original spongin skeleton.
2. Branched columnar and domical morphotypes formed by keratolite–stromatolite consortia in the Late Cambrian–Early Ordovician of Newfoundland are macroscopically indistinguishable from similar morphotypes that are entirely stromatolite.
3. In these deposits, keratolite is intimately interlayered with stromatolite fabric and forms layers that can be traced across domes, and from column to column in branched forms. The keratosan sponge layers typically display smooth bases and irregular tops. They constitute ~38–50% of the combined keratolite–stromatolite volume.
4. Microscopically, keratolite is distinguished by pervasive vermiform fabric. This distinctive delicate, sparry, anastomosing filamentous network results from syndementary calcification of the supportive keratosan spongin framework within fine-grained carbonate. In contrast, associated fine-grained stromatolites in our samples lack vermiform fabric and often display evenly layered and also cross-cutting laminae that likely resulted from agglutination of allochthonous sediment. Keratolite and stromatolite both experienced syndementary lithification, as shown by reworked fragments.
5. We suggest that spongiolite (originally *siliceous* sponge), and keratolite (originally *proteinaceous* sponge) are both varieties of

syndimentarily calcified sponge that, in close association with microbial carbonates, create Sponge–Microbial Consortia.

6. The macroscopic similarities of keratolite and stromatolite, together with the long geological range of keratolites, make it likely that keratolite 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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