Possible poriferan body fossils in early Neoproterozoic microbial reefs

Molecular phylogeny indicates that metazoans (animals) emerged early in the Neoproterozoic era, but physical evidence is lacking. The search for animal fossils from the Proterozoic eon is hampered by uncertainty about what physical characteristics to expect. Sponges are the most basic known animal type, and are assumed to have been produced or influenced by in vivo and/or post-mortem biogeochemical activity, and to formalize the ‘taxonomy’ of their morphology and microstructure.

The existence of metazoans by the Ediacaran period (the last period of the Neoproterozoic) is indicated by bilaterian ‘body’ and trace fossils, and geochemical evidence (biomarkers) provides disputed indirect evidence for Cryogenian poriferans. The search for definitive physical evidence of pre-Cryogenian metazoans is confounded by uncertainty about what physical evidence should be small, subtle and possibly altogether unfamiliar. Given that sponges are the most basic of known animals, physical evidence of Neoproterozoic sponges could be sought, but effort focused on the characteristics of mineralized sponge skeletons (siliceous or calcareous spicules) and on the aspects of their morphology and microstructure that eventually become passively filled with sparry calcite cement. Although questioned, the association between vermiform microstructure and sponges has been confirmed in undisputed body fossils of Phanerozoic sponges. Three-dimensional reconstruction of vermiform microstructure has shown that tubule shape and branching configuration are too consistent and complex to be abiogenic (for example, compacted pellets), and that they resemble the branching style of other possible organism types (microbial or fungal) and are identical to the spongion meshworks of keratose sponges.

Recent work has shown that vermiform microstructure—an unusual microscopic feature in Phanerozoic reefs and stromatolites, that was initially interpreted as being related to algae or protozoans—is instead a keratose sponge body fossil comprising complexly anastomosing cement-filled microtubules enclosed in carbonate microspar. It is produced taphonomically in nonspicular keratose demosponges through the calcification of soft tissue to produce carbonate microspar (auto-micrite), which surrounds the tough spongin fibres of the ‘skeleton’ of the sponge. Decay of the spongin then produces a network of complexly anastomosing tubular moulds that eventually become passively filled with sparry calcite cement. The calcification of decaying sponge soft tissue has been documented in modern sponges and produces sponge ‘mummies’ as well as a range of subtle carbonate sedimentary textures (such as peloid clusters) in living and Phanerozoic fossil sponges. Taphonomic sediment textures (polymuds) that may be poriferan-related have previously been identified in the reefs that are the subject of this Article.

Background
This petrographic study presents possible evidence of sponge body fossils in thin sections (30-μm thick rock slices, viewed microscopically in...
transmitted light) from the approximately 890-million-year-old (Ma) Little Dal reefs (Stone Knife Formation, northwestern Canada) (Fig. 1a, b). These large (about 500 m in thickness, and kilometres in diameter) microbial reefs33–36 were built mainly by variously preserved calcimicrobes that have been interpreted as filamentous cyanobacteria (photosynthesizers)33,35,36, and developed palaeotopographic relief of up to about 100 m above the surrounding subphotic, level-bottom carbonate-mud seafloor. Reef framework, which is generally not discernible in natural exposures, was documented from slabbed hand samples and thin sections35.

The reefs grew in five stages (Fig. 1c), each with different microbialite morphologies: anastomosing millimetre-to-centimetre-scale masses with no consistent shape (stages I–II); centimetre-scale anastomosing columns and digits (stages II, III and V); and steep sheet-like masses at a millimetre-to-metre-scale (stages II and III). Void-filling vermiform microstructure of reef stages II and III. Void-filling vermiform microstructure of microfacies i and ii either underlies (Fig. 2f) or overlies (Fig. 2e) isopachous void-filling marine cement.

In rare microfacies iii (Fig. 2g–k, Extended Data Fig. 4), vermiform microstructure encrusts non-calcimicrobial microbialite columns and mingles with irregular muddy microbialite microstructure of reef stages II and III. Vermiform microstructure is sub-millimetrically interlayered with stage-V non-calcimicrobial stromatolites where it locally passes laterally to geopetal peloidal accumulations in lenticular voids.

Discussion

The shape, size, branching style and polygonal meshworks of the Little Dal vermiform tubules closely resemble both spongin fibre networks of modern keratosan sponges2,3 (Fig. 2a–c) and vermiform microstructure either demonstrated or interpreted to be sponge-derived in diverse Phanerozoic microbial, reefal and non-reefal carbonate rocks8,9,10,24,32,37,38. The compositional and textural homogeneity of the mesoporous groundmass supports an origin through permineralization of a pre-existing biological substance, rather than incremental accumulation of detrital sediment or microbial carbonate that passively incorporated complexly anastomosing tubular microfossils. Vermiform microstructure or association with geopetal peloidal accumulations are familiar aspects of Phanerozoic sponge taphonomy35,39,40. In previous work, detailed comparison of the three-dimensional characteristics of vermiform microstructure with branching cylindrical organism types yielded no convincing alternative to the sponge interpretation6.

Vermiform microstructure for environments that were not inhabited by photosynthetic calcimicrobes (reef flanks, depressions on active reef growth surface, and framework and shelter voids), versus its absence from filamentous calcimicrobial reef-framework components, suggests that (1) illumination may not have been a requirement and (2) the organism may have been unable to compete with reef-building photosynthesizers that grew and/or calcified rapidly. The interlaying of vermiform microstructure with calcimicrobe-free microbialite (microfacies iiiib) in the high-energy, well-illuminated reef surfaces of reef stage V supports the
Mingled with microbialite at base of inter-column sediment

Vermiform microstructure (deinite possible)
Microbialite-dominated
Intermicrobialite space (detrital carbonate mudstone)
Marine cement

Adheres to microbialite margin
Intercalated with sediment

Fig. 2 | Characteristics and distribution of Little Dal vermiform microstructure in stratigraphically oriented 30-μm-thick thin sections. 

a, Well-preserved vermiform microstructure exhibits a polygonal meshwork of anastomosing, slightly curved, approximately 30-μm-diameter tubules embedded in calcite microspar (KEC25). Scale bar, 500 μm. 
b, Enlarged rectangle from a, showing branching tubules forming three-dimensional polygons intersected at various angles by the thin section; clear calcite crystals, about 10–20 μm in width, fill tubules in groundmass of more finely crystalline calcite (dark grey). Scale bar, 50 μm. 
c, Three-dimensional fragment of sponge skeleton from a modern keratosan sponge, illustrating its branching and anastomosing network of fibres (incident light). Scale bars, 100 μm (main panel), 20 μm (inset). 
d, Vermiform microstructure in debris that includes calcimicrobialite and other reef-derived clasts (C) flanking reef stage III (MV63). Scale bars, 1 mm (main panel), 100 μm (inset). 
e, Vermiform microstructure in shelter pore beneath microbialite clast, in detrital sediment occupying a reef-top depression; pore is thinly lined with marine calcite cement (MC) (indicated with an arrow), and partly filled with geopetal carbonate sediment (GCS) (KEC25; stage-III reef core). Rectangle is enlarged in a. Scale bar, 1 mm. 
f, Vermiform microstructure in a microbialite (M) framework void is overlain by pore-occluding marine calcite cement; circled area indicates moderately well-preserved tube meshwork (DL32a; reef stage II; detailed characteristics depicted in Extended Data Fig. 1). Scale bar, 1 mm. 
g, Patches of vermiform microstructure in various relationships with micritic microbialite masses (white dashed outline) and detrital carbonate sediment (CS) (KES23; resedimented stage-II reef clast). Rectangles are enlarged in i–k. Scale bar, 1 mm. 
h, Simplified depiction of relationships among vermiform microstructure, microbialite masses and detrital carbonate sediment in g. Scale bar, 1 mm. 
i, Vermiform microstructure mingled with microbialite within a microbialite digit (enlarged from g). Scale bar, 500 μm. 
j, Vermiform-microstructured mass within sediment between microbialite digits; also contains diagenetic dolomite patches (D) (enlarged from g). Scale bar, 500 μm. 
k, Vermiform-microstructured mass adhering to the margin of microbialite digit (enlarged from g). Scale bar, 500 μm. 
All images except c are in plane-polarized transmitted light. Samples from resedimented reef debris are depicted in depositional orientation based on geopetal structures. Reef locations and abbreviations (such as KEC) are described in a previous publication35. Larger versions of vermiform microstructure photomicrographs are provided in Extended Data Figs. 1–5.
The organism lived (i) on poorly illuminated to non-illuminated carbonate mud surfaces in depressions on the reef surface and on debris aprons mantling reef flanks; (ii) in voids produced by the growth of the complex microbial framework of the reef; and (iii) interlayered with non-calcimicrobial microbialites (cement-rich and muddy-laminated stromatolites in high-energy reef-capping phase V), irregularly muddy-laminated to clotted microbialites in moderate-energy environments of reef stages II and III. Scale bars, 5 mm.

The obligatory spatial association of vermiform microstructure with reefs built by oxygen-producing cyanobacteria may indirectly support a metazoan interpretation. Prior to the Neoproterozoic oxygenation event, marine dissolved oxygen was probably low except perhaps in the vicinity of photosynthesizing microbial communities; the metabolic requirements of metazoans may have limited early animals to localized, comparatively well-oxygenated (for the time) environments (oxygen ‘oases’). Given the approximately 590-Ma depositional age, the vermiform-structured Little Dal organism may be tolerant of ‘low’ oxygen (that is, relative to modern levels), which is a characteristic of some modern and fossil sponges.

If the vermiform-structured masses in the Little Dal reefs are accepted as early sponge body fossils, their approximately 590-Ma age would imply that (1) the evolutionary emergence of metazoans was decoupled from the Neoproterozoic oxygenation event and (2) early animal life was not catastrophically affected by the Neoproterozoic glacial episodes. If the Little Dal objects are truly sponge body fossils, they are older than the next-youngest undisputed sponge body fossils (Cambrian) by approximately 350 million years.

It would not be surprising to find that the earliest sponges were reef-dwellers; the history of Phanerozoic reefs is rich with reef-building and reef-dwelling sponges. The masses of vermiform microstructure in the Little Dal reefs were to be accepted as an early Neoproterozoic expression of sponge tissue preservation, their age and proposed identity would be compatible with (1) evidence that the opisthokont (animal + fungus) clade was already established by the time of the Mesoproterozoic–Neoproterozoic transition (2) possible evidence of 1-billion-year-old multicellular holozoans, (3) molecular clock estimates for the emergence of the Porifera in the early Neoproterozoic and (4) a revised taxonomy of nonspiculate keratose sponges showing that they are a sister group to other demosponges. The Little Dal vermiform microstructure is perhaps exactly what should be expected of the earliest metazoan body fossils: preservation through post-mortem calcification of sponge-grade soft tissue in the decaying bodies of small, shapeless, sessile, epibenthic and cryptic animals most closely affiliated with keratose sponges.
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Field work was done on foot from two-person, backpacking-style camps placed at sites that are accessible only by helicopter. Samples were collected at various times between 1992 and 2018, under all required permits. Recording sample locations using GPS is not possible for most sites owing to the extreme topography of the exposures’ cliffs, pinnacles and canyons, and so sample location was documented using photographs and sketches. Several samples are from a mineral-exploration drill-core stored on-site in the field. Owing to the homogeneous grey weathering of reef surfaces, lithofacies cannot be identified in the field. Instead, hand samples were collected and later slabbed and thin-sectioned. Vermiform microstructure was identified in a small proportion of the samples collected. Repeat visits focused primarily on resampling the rare areas in which vermiform microstructure had been identified.

Standard 30-μm-thick thin sections were examined in plane-polarized transmitted light using a Nikon C-Pol binocular microscope fitted with digital camera and Luminera Infinity Analyze software (for lower-magnification images) and an Olympus BX-51 petrographic microscope equipped with Q-Imaging digital capture system (for higher-magnification images).

**Reporting summary**

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

**Data availability**

All relevant data are contained with the Article and its Supplementary Information, or are available from the author upon reasonable request.

**Acknowledgements**

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**Author contributions**

E.C.T. conducted all aspects of the study.

**Competing interests**

The author declares no competing interests.

**Additional information**

**Supplementary information** The online version contains supplementary material available at https://doi.org/10.1038/s41586-021-03773-z.

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Extended Data Fig. 1 | Vermiform microstructure of microfacies 1.

Elaboration of Fig. 2d. **a**, Vermiform microstructure is intercalated with detrital sediment (lower 1/3 of image) that includes calcimicrobialite clasts. **b**, Three-dimensional meshwork of vermiform microstructure transected by the plane of the 30-μm-thick thin section shows anastomosing tubule system; enlarged from **a**. **c**, Anastomosing tubules occluded by clear blocky calcite enclosed by cloudy calcite groundmass of slightly smaller crystals; enlarged from **b**. The tubules have no constructional walls and are defined by the dark enclosing groundmass. Oriented sample MV63 in plane-polarized transmitted light.
Extended Data Fig. 2 | Vermiform microstructure of microfacies i. Elaboration of Fig. 2e. a, Vermiform microstructure in a shelter void beneath an irregular microbialite clast and floored by angular reef clasts in carbonate mud, from a reef-top depression. Fibrous isopachous marine calcite cement lined the pore before its occupation by the vermiform mass. b, Three-dimensional meshwork of vermiform microstructure transected by the plane of the 30-μm-thick thin section shows anastomosing tubule system; enlarged from a. c, Anastomosing tubules occluded by clear blocky calcite enclosed by cloudy calcite groundmass of slightly smaller crystals; enlarged from b. The tubules have no constructional walls and are defined by the dark enclosing groundmass. Oriented sample KEC25 in plane-polarized transmitted light.
See next page for caption.
Extended Data Fig. 3 | Spatial–temporal relationships among vermiform microstructure, geopetal detrital sediment and marine cement that collectively fill reef framework voids of microfacies ii. Elaboration of Fig. 2f. a, Reef framework void among non-calcimicrobial stromatolites of reef stage II. Detrital sediment (DS) occupies lowest part of the void. Much of the void is occupied by vermiform microstructure (V); uppermost parts of the void are occupied by marine cement (MC) and local burial cement (BC). b, Detrital sediment accumulation, which includes quartz silt (transparent white particles); enlarged from a. c, Upper part of void is lined by isopachous cloudy marine calcite cement (arrow) (MC) and the remaining porosity occluded by burial calcite cement (pale) (BC); enlarged from a. d, Enlargement from c to demonstrate cloudy, isopachous, fibrous nature of the marine calcite cement, versus more transparent, equant, blocky shape of burial cement that occupies the small amount of pore space remaining after accumulation of geopetal sediment, growth of vermiform microstructure and precipitation of marine cement. e, Moderately preserved vermiform microstructure; enlarged from a. Oriented sample DL32a from reef stage II, in plane-polarized transmitted light.
Extended Data Fig. 4 | Associations of vermiform microstructure, micritic microbialite columns and detrital sediment in microfacies i and iii.

Elaboration of Fig. 2g–k. 

a, Low-magnification image of two irregular microbialite columns and inter-column sediment (outlined by white dashed line). 
b, Vermiform microstructure is intermingled with muddy microbialite in column interior; enlarged from a. 

c, Vermiform microstructure intercalated with inter-column sediment; enlarged from a. 
d, Vermiform microstructure encrusting the margin of a microbialite column; enlarged from a. Sample KES23, from reef stage II, in plane-polarized transmitted light; sample is from a resedimented reef clast and is oriented on the basis of geopetal structures out of the field of view.
Extended Data Fig. 5 | Spatial and textural association of vermiform microstructure and geopetal peloids in microfacies iib. This association suggests that geopetal peloid accumulations are a taphonomic product derived through poor preservation of vermiform microstructure. a, Poorly preserved vermiform microstructure (arrowed; inset c) adjacent to laminar to lenticular voids containing geopetal peloid accumulations (arrowed; inset b) in cement-rich non-calcimicrobial stromatolites of reef stage V. Oriented IR drillcore sample RT A19-495.4′ in plane-polarized transmitted light.
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Software and code

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Data collection Photomicrographs were imaged using Luminera Infinity Analyze v.6.5 and Qcapture 2.98.0.

Data analysis No software was used for data analysis.

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**Study description**
Describes petrographic evidence of possible body fossils of sponges that are approximately 890 million years old.

**Research sample**
Thin sections (30-micon-thick rock slices) from fossil reef rock in the Stone Knife Formation (“Little Dal reefs”) in Northwest Territories, Canada.

**Sampling strategy**
Over a thousand approximately fist-sized rock samples were separated from natural rock exposures using a rock hammer. The samples were later slabbed and thin-sectioned. Initially, samples had been collected for an unrelated purpose (documenting reef microbialites in a separate, published study); sample distribution was randomly dispersed throughout all exposed parts of selected reefs in an attempt capture spatial variability in microbialites, which are not discernible on natural rock exposures. Sample field locations were documented using photographs and diagrams; obtaining accurate GPS points for sample locations is not possible given the extreme topography (limits satellite access) and the small size of the samples relative to GPS error. Areas where the thin sections contained vermiform microstructure were later revisited and resampled. Sample size is considerably larger than the masses of vermiform microstructure. Sample distribution in the reefs is dense enough and reef facies well enough understood (previously published study) for the reefal subenvironments in which vermiform microstructure is preserved to be characterised.

**Data collection**
Rock samples were separated from natural rock exposures using a rock hammer. Samples were shipped to the lab, sawed, polished, and thin-sectioned using standard petrographic preparation.

**Timing and spatial scale**
Rock samples were collected during field work between 1992 and 2018. Sample size is considerably larger than the masses of vermiform microstructure that are the subject of the study.

**Data exclusions**
No data were excluded.

**Reproducibility**
Reproducibility depends on locating the exact field locations and places on exposure surfaces from which samples containing vermiform microstructure were collected. Field locations of rock samples were recorded in detail using photographs and diagrams. Revisiting and resampling these locations in the years following the initial collection successfully yielded more material containing vermiform microstructure in thin section.

**Randomization**
This was not an experimental study.

**Blinding**
This was not an experimental study.

Did the study involve field work?  
☐ Yes  ☐ No

Field work, collection and transport

**Field conditions**
Remote alpine-subarctic locations in the Mackenzie Mountains, Northwest Territories, Canada, that are accessible only by helicopter. Field work is possible only in the summer months when snow cover is minimal (mid-June to mid-August).

**Location**
Numerous locations between 64°47’N / 129°35’W and 64°59’N / 130°55’W.

**Access and import/export**
Field work was conducted under science licencing from the Aurora Research Institute (2016 Licence #15888; 2017, 2018 Licence #15993), and associated permissions from land use, water board, renewable resource, community, land claim, band council, and hunting-trapping organisations.

**Disturbance**
No temporary nor long-term disturbances were introduced.

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### Methods

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| Specimen deposition           | Field data, rock samples, and thin sections are archived in the author’s collection at Laurentian University. |
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