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The Sirius Passet Lagerstätte of North Greenland: a remote window on the Cambrian Explosion

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Abstract: The lower Cambrian Lagerstätte of Sirius Passet, Peary Land, North Greenland, is one of the oldest of the Phanerozoic exceptionally preserved biotas. The Lagerstätte evidences the escalation of numbers of new body plans and life modes that formed the basis for a modern, functionally tiered ecosystem. The fauna is dominated by predators, infaunal, benthic and pelagic, and the presence of abundant nekton, including large sweep-net feeders, suggests an ecosystem rich in nutrients. Recent discoveries have helped reconstruct digestive systems and their contents, muscle fibres, and visual and nervous systems for a number of taxa. New collections have confirmed the complex combination of taphonomic pathways associated with the biota and its potentially substantial biodiversity. These complex animal-based communities within the Buen Formation were associated with microbial matgrounds, now preserved in black mudstones deposited below storm wave base that provide insight into the shift from late Neoproterozoic (Ediacaran) to Cambrian substrates and communities. Moreover, the encasing sediment holds important data on the palaeoenvironment and the water-column chemistry, suggesting that these animal-based communities developed in conditions with very low oxygen concentrations.

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The Sirius Passet fossil biota is the most remote, one of the least well-known and, to date, one of the least diverse of the major Cambrian Lagerstätten. Following its serendipitous discovery in 1984 (Conway Morris *et al.* 1987; see Conway Morris 1998 and Peel & Ineson 2011, for detailed accounts of the discovery and early exploration), the locality in the Buen Formation of North Greenland has been visited by only nine collecting expeditions in the 35 years since the discovery, most recently in 2009 and 2011 by multidisciplinary and multinational groups led by the Natural History Museum of Denmark, University of Copenhagen and, in 2016, 2017 and 2018, by the Korea Polar Research Institute–University of Bristol–Copenhagen group. The Sirius Passet Lagerstätte occurs in black mudstones deposited at the shelf–slope break on the Laurentian margin. Although deformed and metamorphosed by a Devonian tectonic event, the Ellesmerian Orogeny, the locality preserves the original depositional relationships to a large degree and allows a detailed interpretation of the environmental setting of this early Cambrian ecosystem, and thus assists in understanding the ecological and environmental constraints on the Cambrian Explosion (Babcock 2005). The fossiliferous site is located beside J. P. Koch Fjord, Peary Land, North Greenland, at 82° 47.59' N, 42° 13.54' W (Fig. 1) and an altitude of 420 m. This remote locality can be reached only by short take-off and landing aircraft that can use a rough, 200 m strip in the valley 2 km to the west of the fossiliferous site (Fig. 2).

Geological context

During the early Cambrian, Sirius Passet lay on the northern margin of Laurentia, at a palaeolatitude of around 15° S (Fig. 1a) (Cocks & Torsvik 2011). This segment of the Greenland–Canada margin is commonly referred to as the Franklinian Basin (Higgins *et al.* 1991; Trettin *et al.* 1991); it accommodates a succession of Ediacaran–Devonian age extending from Kronprins Christian Land in eastern North Greenland, westwards to Ellesmere Island and the Arctic islands of Nunavut, Canada (Fig. 1b) (Higgins *et al.* 1991; Trettin *et al.* 1991; Blom 1999). Despite tectonic deformation (Soper & Higgins 1987, 1990), the early Paleozoic margin of Greenland is notable for preserving an intact transition between shelf, slope and deep-water basin, and its changing position and character through time has been documented in detail (Higgins *et al.* 1991).

The Buen Formation overlies a carbonate unit, the Portfjeld Formation (Figs 1c and 2), which crops out extensively across North Greenland and is the lateral correlative of the Ella Bay Formation on Ellesmere Island (Long 1989; Dewing *et al.* 2004). In the southern part of North Greenland, the Portfjeld Formation is subdivided by a

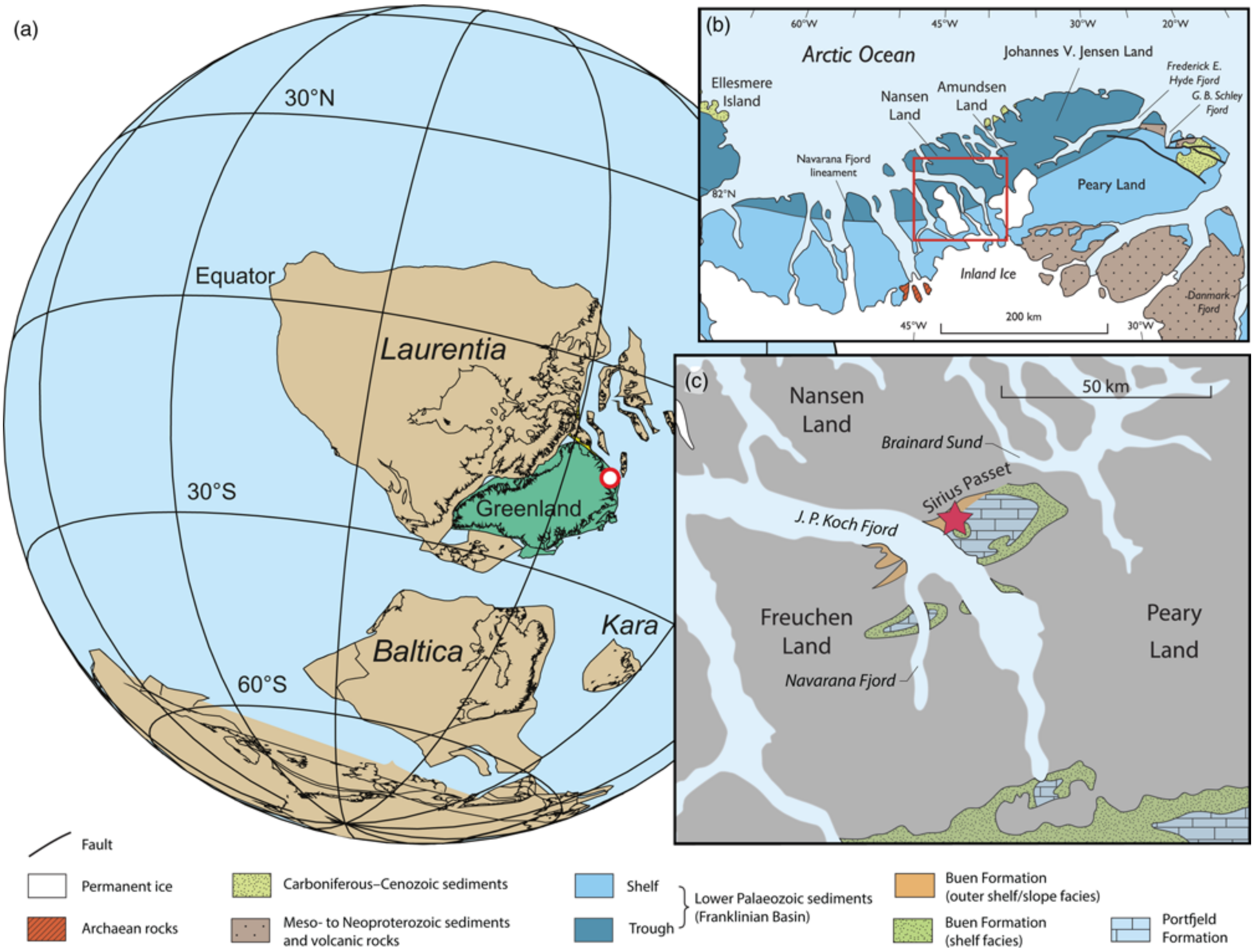

Fig. 1. Maps of the palaeogeographical and geographical setting of the Sirius Passet Lagerstätte. (**a**) Location of North Greenland in the early Cambrian at *c.* 520 Ma constructed in Bugplates (Torsvik 2009). Circle indicates location of the Sirius Passet Lagerstätte. (**b**) The eastern Franklinian Basin (modified from Ineson & Peel 2011). Red box indicates position of (c). (**c**) The Sirius Passet locality at 82° 47.59’ N, 42° 13.54’ W, east of J. P. Koch Fjord, is marked with a red star (modified from Le Boudec *et al.* 2014).

regionally developed karst surface into a lower (180 m thick) unit of storm-dominated dolostones and an upper 100 m thick, mixed carbonate–clastic succession of fluvial and shallow marine sediments (Higgins *et al.* 1991; Ineson & Peel 2011).

The Portfjeld Formation thickens northwards towards the continental margin, where it is 400–700 m thick, and passes into its deep-water equivalent, the Paradisfjeld Group, which is made up of dark siliciclastic and carbonate mudstones interbedded with carbonate turbidites and debris-flow deposits, some of which contain large olistoliths (Surlyk & Ineson 1987; Higgins *et al.* 1991; Ineson & Peel 2011). The presence of large-scale debris flows and olistoliths led Surlyk & Ineson (1987) to infer the exposure of an escarpment bounding the Portfjeld Formation to the north, and an intact example of the escarpment with abutting debris flows was documented by Ineson & Peel (2011), 2 km NE of the Sirius Passet locality.

The age of the Portfjeld Formation–Paradisfjeld Group has been the subject of some debate. Dewing *et al.* (2004) considered the Portfjeld Formation to be of Ediacaran age on the basis of regional correlations, but Peel (1988) described cyanobacteria he considered to be of early Cambrian age and Peel & Higgins (1980) documented the coeloscleritophoran *Chancelloria* and nonarticulated brachiopods from the upper part of the Paradisfjeld Group. The presence of a disconformity within the formation suggests that both ages are correct, the unit comprising an older Ediacaran component and a younger early Cambrian part. The latter stratigraphic unit suggests that the younger part of this phase of basin development is no older than Cambrian Stage 2.

The Portfjeld Formation is overlain unconformably by sandstones and mudstones of the Buen Formation. The boundary is well exposed adjacent to the Sirius Passet locality, where the upper part of the carbonates is deeply fretted by karstic erosion, with deep grykes, vadose fissures and accompanying shallow phreatic tubes, all of which are infilled by millet-seed quartz arenite. This lithology is also seen as a thin sheet overlying the Portfjeld Formation regionally and passing upwards into black mudstones and siltstones of the basal Buen Formation (Fig. 2). In the deep-water succession the uppermost limestone conglomerate bed of the Paradisfjeld Group has a distinctive quartz sand matrix (Higgins *et al.* 1991), which is partly correlative with the erosion surface.

The Buen Formation and its correlatives crop out extensively across North Greenland. The most inboard development, in southern Peary Land, is up to 500 m thick and dominated by sandstones deposited on a tide- and storm-influenced shelf that pass northwards to a more mudstone- and siltstone-dominated shelf to the north, where the unit is up to 700 m thick (Higgins *et al.* 1991). Transgressive surfaces bound three coarsening-upward sequences across the shelf that show an overall deepening trend (Davis & Higgins 1987; Ineson & Peel 2011). Northwards, the shelf sediments pass into the deep-water succession of the Polkorridoren Group, where the turbidites and deep-water mudstones of units 3, 4 and 5 of Davis & Higgins (1987) are correlatives

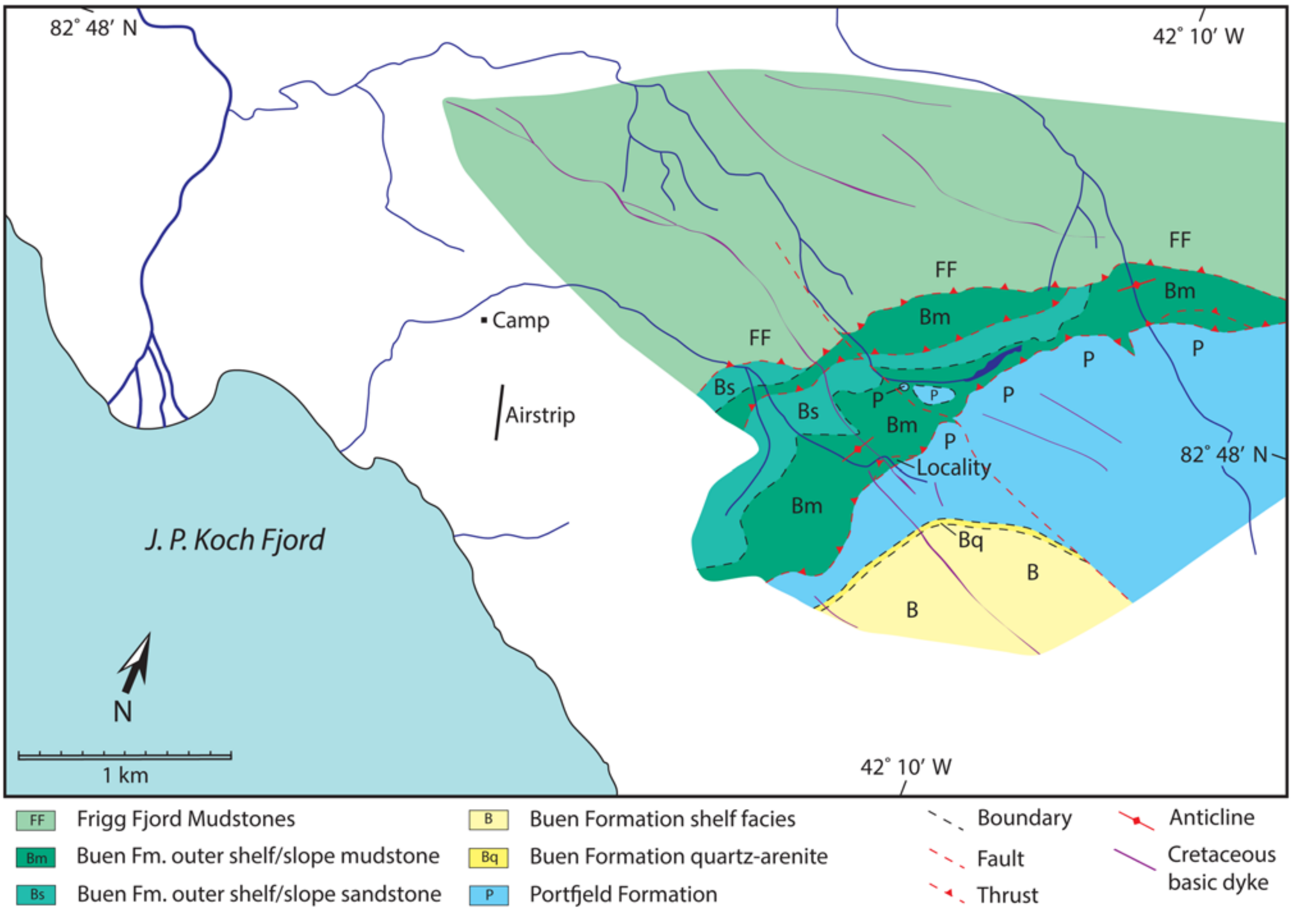

Fig. 2. Geological map of the Sirius Passet Lagerstätte and surrounding area in Peary Land, North Greenland. The outer shelf–slope mudstone and sandstone units of the Buen Formation are equivalent to the 'Transitional Buen Formation' of Ineson & Peel (2011).

of the three coarsening-upwards sequences of the Buen Formation (Davis & Higgins 1987). The lower units of the Polkorridoren Group (units 1 and 2 of Davis & Higgins 1987) are probably correlative with the erosion surface at the top of the Portfjeld Formation together with the uppermost part of the Paradisfjeld Group.

The identification of carbonate debris flows in depositional contact with the Portfjeld Formation escarpment, and the location of the Sirius Passet Lagerstätte adjacent to a vertical boundary with Portfjeld Formation dolostones, led Ineson & Peel (2011) to infer a depositional model in which mudstones of the lower Buen Formation lie at the foot of a relict escarpment of eroded Portfjeld Formation, analogous to some hypotheses for the depositional location of the Burgess Shale Lagerstätte (Fletcher & Collins 1998). However, regional mapping during the 2009 and 2011 field seasons (Figs 2 and 3a) suggests that the relationship is more complex (see below).

Although Ineson & Peel (2011) noted that the trilobites at the Sirius Passet locality are typically inverted (lying ventral up) they considered the section to be the right way up. However, detailed logging in 2011 showed that 93% ($n = 737$) of the trilobites and much of the soft-bodied fauna is also inverted, and thin graded beds and cross-laminations were also seen to be inverted in thin section. The strata containing the Sirius Passet Lagerstätte are thus inverted, but directly adjacent to near-horizontal and right way up Portfjeld Formation (Fig. 3). The Lagerstätte is thus interpreted here as being located within a thin, inverted horse of Buen Formation bounded on both sides by faults that are part of a duplex beneath the Buen Thrust (Soper & Higgins 1987, 1990), the position of which is locally determined by the Portfjeld escarpment. At the time of deposition, the Sirius Passet Lagerstätte did not sit at the foot of the escarpment; instead, local mapping (Figs 2 and 3a) suggests that it was positioned at the outer edge of the relict platform, at the contemporary shelf–slope break.

The late Paleozoic Ellesmerian orogenic activity that generated the fold-and-thrust belt also led to regional metamorphism. Platy chloritoid porphyroblasts, up to 5 mm in size, are distributed throughout the muddier intervals of the Sirius Passet Lagerstätte and are typically randomly oriented relative to laminations (Strang *et al.* 2016*b*, fig. 3F). They are accompanied by abundant Al-rich chlorite–mica aggregates up to 10–20 µm in diameter (Strang *et al.* 2016*b*). Together, these are taken to represent low greenschist-facies metamorphism, which has influenced the presentation of the taphonomic detail.

Age of the Sirius Passet Lagerstätte

The most reliable indicator for the age of the Sirius Passet fauna is the very abundant nevadiid trilobite *Buenellus higginsi* Blaker, 1988. Its range is correlated with the *Nevadella* trilobite biozone (Palmer & Repina 1993; Blaker & Peel 1997), and this age interpretation is supported by the distribution of other olenelline trilobites in the Buen Formation (Blaker & Peel 1997). Acritarch samples from the basal part of the Buen Formation are either barren or contain a sparse non-age diagnostic flora (Vidal & Peel 1993). The Lagerstätte is thus correlated with the middle to upper Montezuman Stage in Laurentian terms, as it contains a trilobite species (and is therefore younger than the pre-trilobite series) and lies below strata that contain early Dyeran trilobites (Palmer & Repina 1993; Blaker & Peel 1997; Babcock & Peel 2007). The

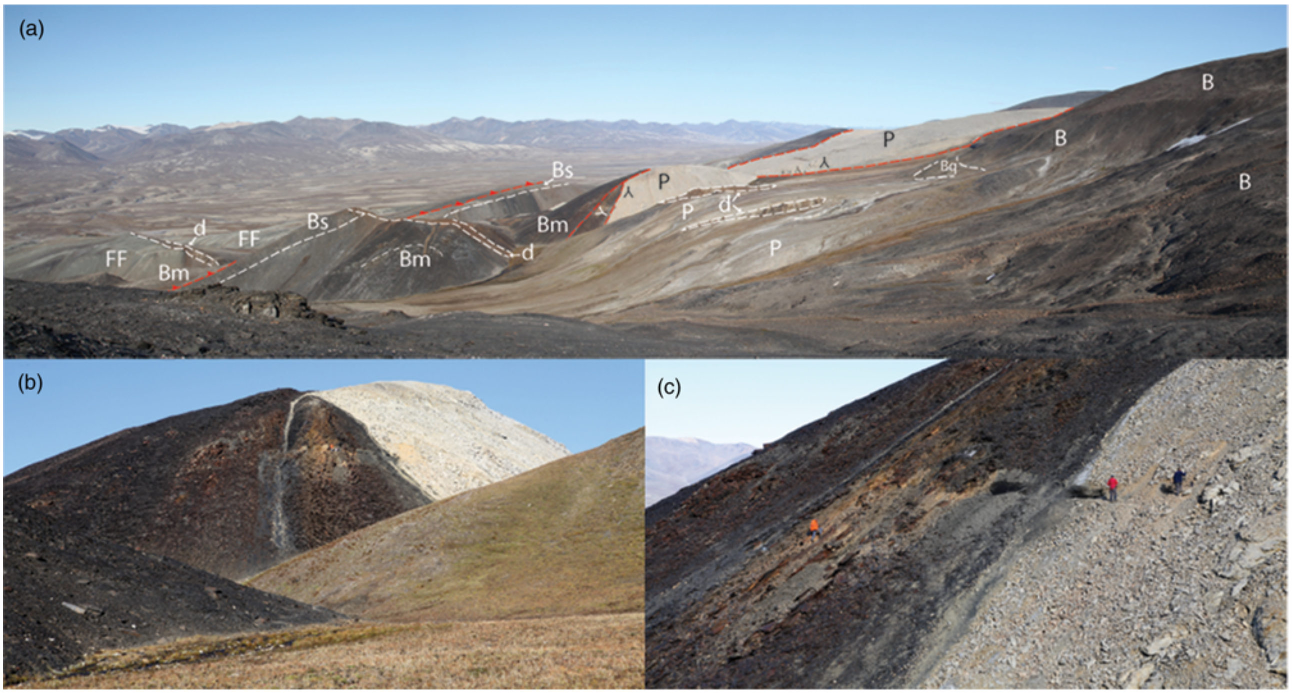

Fig. 3. (**a**) Panoramic view of the Sirius Passet locality, looking towards the NE, showing the geological relationships at the shelf–slope boundary. The locality is indicated by the inverted white, younging symbol. B, sandstone-dominated shelf Buen Formation; Bm, mudstone-dominated Buen Formation of the shelf–slope transition (= 'Transitional Buen Formation' mudstone of Ineson & Peel 2011); Bq, basal quartz-arenites of the Buen Formation; Bs, sandstone-dominated Buen Formation of the shelf–slope transition (= 'Transitional Buen Formation' sandstone of Ineson & Peel 2011); d, Cretaceous basic dykes; FF, Frigg Fjord Mudstones of the Polkorridoren Group; P, Portfjeld Formation. Unit boundaries are indicated by heavier white dashed lines, bedding traces by lighter weight dashed lines; faults are shown as red dashed lines. (**b**) The Sirius Passet Lagerstätte locality viewed from the west, showing the dark silty mudstones of the Buen Formation in faulted contact with the white carbonate rocks of the Portfjeld Formation. (**c**) Close-up of the Sirius Passet locality showing the quarry opened up on the 2011 expedition; people for scale.

recently described *Buenellus chilhoweensis* Webster & Hageman, 2018 from the Murray Shale of Tennessee is very similar to the Greenland species and is assumed to be of a broadly similar age. In international terms, the *Nevadella* zone age of the Sirius Passet Lagerstätte corresponds to middle to upper Cambrian Stage 3 (Atdabanian; 515–518 Ma) (Ogg *et al.* 2016). The fauna is thus of closely similar age to the more fully explored Chengjiang fauna of southern China (Zhang *et al.* 2008; Yang *et al.* 2018), and with the available biostratigraphic resolution is of indistinguishable age.

In sequence stratigraphic terms, the Buen Formation corresponds to the base of the Sauk 1 supersequence (Sloss 1963; Palmer & Peel 1981; Golonka & Kiessling 2002), which is recognizable across Laurentia as a major marine flooding and continental inundation event (Morgan 2012; Peters & Gaines 2012). Farther to the south, along the Laurentian margin in NE Greenland, the base of Sauk 1 is marked by the base of the Kap Holbæk, Slottet and Kløftelv formations of the autochthon and allochthon (Smith *et al.* 2004; Smith & Rasmussen 2008), in NW Scotland by the Eriboll Formation (Higgins *et al.* 2001; Raine & Smith 2012) and in Newfoundland by the Bradore Formation (Lavoie *et al.* 2012).

The base of Sauk I is often marked across Laurentia by unfossiliferous quartz arenitic sandstones and granulestones and, in consequence, the age of the flooding event is poorly constrained in many places. The *Nevadella* Zone Sirius Passet fauna at the base of the Buen Formation represents one of the few accurate temporal constraints on this event in northern Laurentia (Fig. 1).

Sedimentology and depositional setting

In the distal Buen Formation of the central J. P. Koch Fjord area, Davis & Higgins (1987) recognized a basal unit of mature quartz arenites up to 40 m thick. This unit, as noted above, also penetrates the karstic erosion surface on top of the Portfjeld Formation. In the vicinity of the Sirius Passet locality, the quartz arenite thins from a few metres to the south of the locality to being present only as infills in the Portfjeld Formation palaeokarst adjacent to the locality. This basal sandstone unit is overlain by two coarsening-upwards sequences of mudstone and siltstone capped by sandstone, which equate to the 'Transitional Buen Formation' of Ineson & Peel (2011); the lower sequence is 50 m thick and the upper is 80 m (Davis & Higgins 1987). These two sequences may be correlated for over 200 km along-strike from northern Nyeboe Land in the west to Peary Land in the east. The lowest part of each of the sequences contains black mudstones and siltstones, which Davis & Higgins (1987) noted had a 'varved', finely interlaminated appearance. The Sirius Passet Lagerstätte is located within the lower of these two mudstone units, and the geological context together with the high proportion of mudstone relative to siltstone indicate that it lies toward the base.

The Lagerstätte section has been excavated to a thickness of 12 m and is covered by extensive talus at both ends; it is also terminated by a small fault at the stratigraphic base. The sediments range from laminated mudstones to muddy siltstones and siltstones that have been metamorphosed to pelites and semi-pelites; protolith terminology, relating to the original sedimentary rock types, is used for the following description. Four lithofacies were recognized and represent progressively higher proportions of silt-grade material relative to mud from (1) finely laminated mudstones to (2) silty mudstones with 3–10 mm lamination, (3) flaggy muddy siltstones and (4) massive siltstones (Fig. 4).

The silty mudstones and muddy siltstones are dark grey and have a more widely spaced parting, ranging from 3 mm up to 10 cm. Bioturbation, with occasional preserved burrow forms, is present from 0 to 3 m and from 9 to 12 m in the measured section, and in the coarser siltstone beds from 3 to 9 m, but is conspicuously absent from the thinly laminated mudstones containing the exceptional

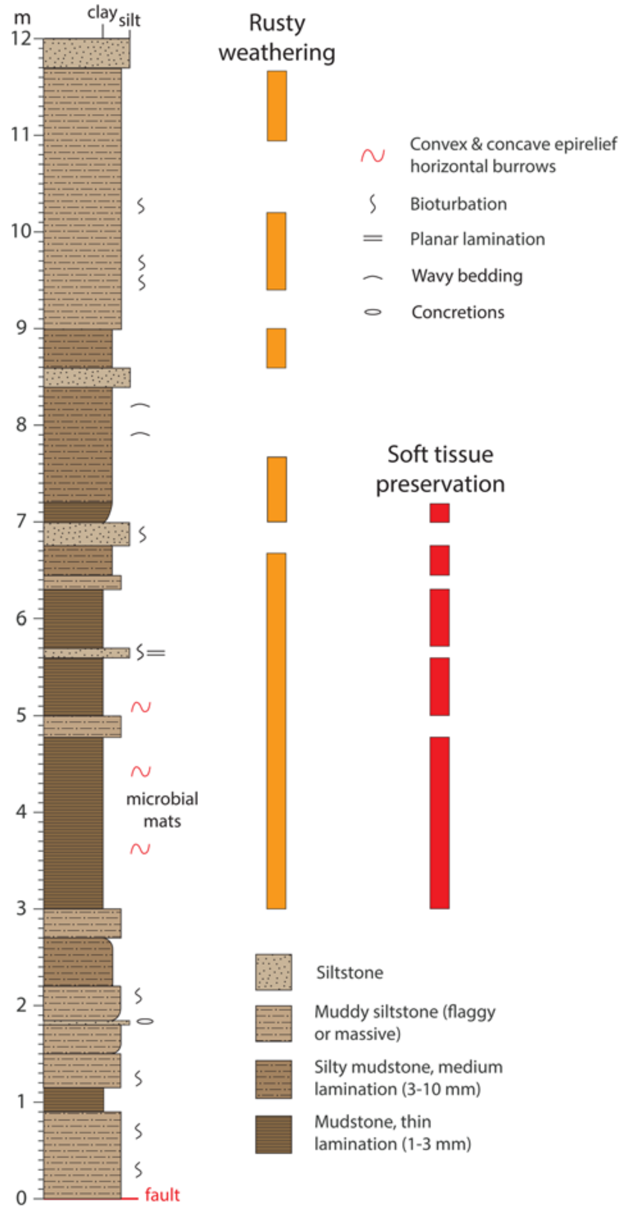

Fig. 4. Sedimentary log of the Sirius Passet Lagerstätte, Peary Land, North Greenland. Orange bars indicate the presence of particulate iron oxides and films on bedding surfaces, and red bars indicate the incidence of exceptionally preserved soft tissues. The event beds that make up the bulk of the sediment are of millimetre scale.

preservation (Fig. 4). The coarsest intervals in the section are mid- to dark grey siltstones that are typically massive or bioturbated, but contain occasional planar lamination (Fig. 4).

In thin section, silty layers are typically interlaminated with mudstone on a millimetre scale, but occasionally display planar lamination and ripple cross-lamination; sharp-based graded beds are also present on a millimetre scale (Strang *et al*. 2016*b*, fig. 3A, D, E, G, H). Silt laminae are often discontinuous on a millimetre to centimetre scale and may be no thicker than a single grain. Although the sharp-based graded and laminated beds are on a millimetre scale, coarsening-upwards packages from mudstone to siltstone can also be recognized on a decimetre to metre scale (Fig. 4).

The finest-grained sediments are thinly laminated, very dark grey to black mudstones with minor silt and a 1–3 mm parting. It is this interval, from 3 to 6 m, that contains the exceptional preservation of the Sirius Passet Lagerstätte (Fig. 4), and the conspicuously smooth bedding surfaces exhibit abundant, meandering, bedding-parallel burrows preserved in convex and concave epirelief (Fig. 4). The burrow systems are concentrated around body fossils, particularly those of the large euarthropod *Arthroaspis* (Mángano *et al.* 2012). Bedding surfaces are frequently covered by yellow to orange iron oxide–hydroxide films and powder; the latter the result of weathering.

Mángano *et al.* (2012) considered the morphology of the burrow systems in this interval to have clear commonalities with the feeding strategies of under-mat miners (Seilacher 1999). From this lithofacies, Strang *et al*. (2016*b*, fig. 2C–F) also documented the presence of crinkly, occasionally anastomosing, carbonaceous laminae, sometimes silicified, that are interlaminated with mudstone and siltstone. The carbonaceous laminae have markedly different cathodoluminescence properties from the non-organic laminae (Strang *et al*. 2016*b*, fig. 4C). Together, this evidence supports the presence of microbial mats that overgrew the sediment surface, and the cadavers of arthropods, and that exhibit many of the diagnostic characters of microbial mats on muddy substrates (Schieber 2007). Intraclasts interpreted as fragments of early silicified microbial mat occur infrequently in both finer and coarser lithofacies (Strang *et al.* 2016*b*, fig. 3C). Evidence for these matgrounds is found only in the interval with exceptional preservation (Fig. 4).

In contrast, the presence in the Sirius Passet succession of grading, planar lamination and cross-lamination is consistent with deposition from low-density sediment gravity flows at or just below storm wave base. These gravity flows periodically covered the microbial mats and their fauna. The high proportion of mud and the presence of very thin, millimetre-scale fining-upwards packages suggests that the depositional site lay below storm wave base, and that sediment was transported from further inboard by dilute density currents. A depositional site below storm wave base, and probably the photic zone, in turn might suggest that the mats were chemoautotrophic. Dense mats do occur in low light conditions (Haas *et al.* 2018) below the photic zone in the modern ocean (Karl *et al.* 1988; Emerson & Moyer 2002; Levin 2003), which are also associated with specific low-oxygen niches that are presumed to have been more common in the past (Glazer & Rouxel 2009).

The combination of sedimentological observations and the geological context indicates that the depositional site of the Sirius Passet Lagerstätte was situated below storm wave base at the shelf–slope break in the Franklinian Basin (Fig. 5). Microbial mats in this location would have been periodically obruted by distal, dilute gravity flows transporting mud and silt. Given the low gradient of the outer shelf, these gravity flows were probably generated by storms. In most of the section, the sediment deposited from gravity flows was subject to bioturbation but in the interval containing exceptional preservation this did not occur.

The Sirius Passet fauna

The Sirius Passet fauna has some similarities to that of the Burgess Shale, although it is of lower diversity, currently comprising approximately 45 species (see Box 1), including trilobites, sponges, worms, halkieriids, lobopods and non-trilobite bivalved euarthropods. The faunal list is provided in Table 1; a number of additional taxa are under investigation and more await description following the 2009, 2011, 2016, 2017 and 2018 field seasons.

The depositional context of microbial mats with a periodic influx of dilute sediment gravity flows is also reflected in the Sirius Passet biota, which may be divided into (1) a guild of mat dwellers and (2) allochthonous components. The mat-dwelling guild includes suspension feeders (sponge species), mat grazers (for example, *Halkieria*) and probable deposit feeders or omnivores (the trilobite *Buenellus* and possibly the euarthropod *Arthroaspis*). The mat-dwelling guild is predominantly found at bed partings, corresponding to the bases of event beds where they were obruted, whereas the

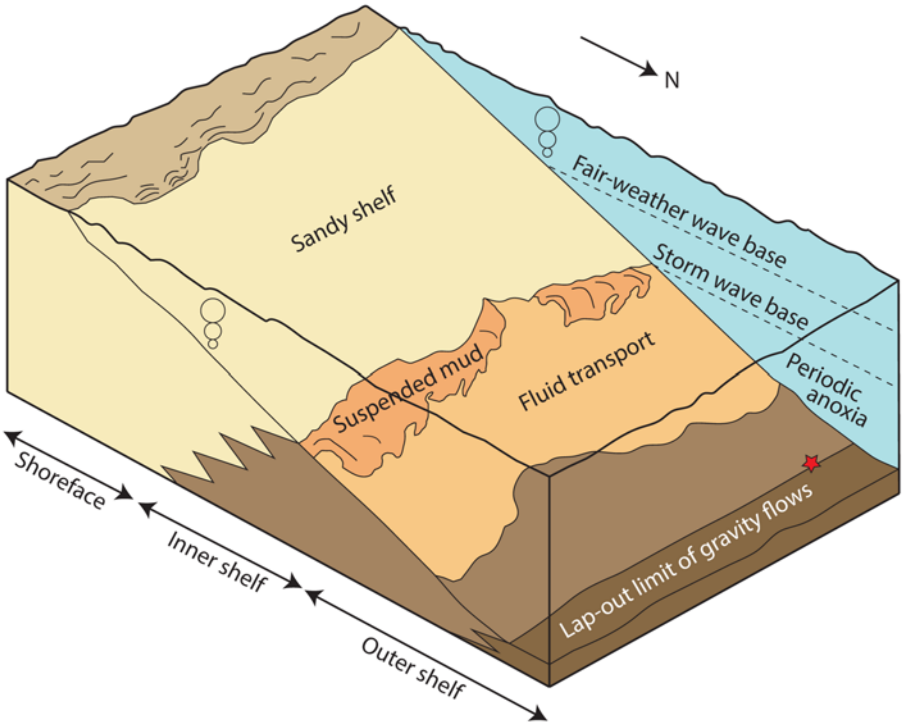

Fig. 5. Schematic block diagram illustrating the depositional environment of the Sirius Passet Lagerstätte and the Buen Formation of the Franklinian shelf during the early Cambrian (Stage 3). The depositional location of the Sirius Passet Lagerstätte is indicated by a red star. Vertical scale greatly exaggerated. Modified after Strang *et al.* (2016*b*).

allochthonous components are preferentially encased as Burgess Shale-type films within the event beds.

Penetrative, vertical or subvertical burrows are absent in the mudstone intervals with microbial mats. The allochthonous components are more diverse and include infaunal burrowers (e.g. priapulids, palaeoscolecids and possibly loriciferans) and components of the nekton (*Isoxys*, gilled lobopodians including *Kerygmachela* and the radiodontan *Tamisiocaris*, together with vetulicolians) (see Box 2 for detail on the ecology of the biota).

Preservation and taphonomy

The Sirius Passet Lagerstätte predates the Burgess Shale (*c.* 510 Ma) and is comparable in age with the Chengjiang biotas (*c.* 518 Ma; Yang *et al.* 2018); it is therefore one of the earliest examples of high-fidelity, soft-tissue preservation in the Phanerozoic record. The taphonomic pathways of the Sirius Passet Lagerstätte are yet to be fully understood, but preservation has been interpreted to be a result of fluctuating oxygen conditions on the seafloor (Budd 1995; Ineson & Peel 2011; Peel & Ineson 2011), strong redox gradients and hampered diffusion aided by the carcasses themselves (Mángano *et al.* 2012) or even deposition under a veneer of wind-blown dust (Le Boudec *et al.* 2014). Despite these uncertainties, the Sirius Passet Lagerstätte has been considered to lie within the spectrum of Burgess Shale-type (BST) preservation (Budd 2011; Topper *et al.* 2018). Preservation through the deposit is, however, variable. Trilobites are preserved as complete moulds showing a veneer of authigenic silica (Strang *et al.* 2016*b*) and other mineralized forms such as hyolithids and halkieriids also preserve much of their relief (Conway Morris & Peel 1995; Peel 2010*a*). Less biomineralized taxa, such as *Campanamuta* and *Arthroaspis*, are preserved in slight relief, replicated by silica and clay minerals (Budd 2011), and some taxa are preserved as 2D kerogenous compressions (Vinther *et al.* 2011*a*, *b*; Topper *et al.* 2018) with some degree of fidelity (Park *et al.* 2018). Digestive tracts are commonly phosphatized and preserved in three dimensions (Peel 2017*c*) and some taxa (e.g. *Campanamuta mantonae* Budd, 2011 and *Pambdelurion whittingtoni* Budd, 1998*a*) preserve silicified 3D muscle fibres (Budd 2011; Peel 2017*c*; Young & Vinther 2017).

Although the presence of 2D kerogenous films and some phosphatized digestive tracts in the Sirius Passet Lagerstätte is comparable with preservational modes seen in BST deposits, there are a number of distinct taphonomic differences. The authigenic silica veneer documented from trilobite specimens (Strang *et al.* 2016*b*) is more reminiscent of preservation seen in some Ediacaran deposits (Tarhan *et al.* 2016) than of preservation in conventional BST deposits (Gaines 2014). In fact, the large majority of documented organisms from the Sirius Passet Lagerstätte have an element of 3D preservation (e.g. Budd 1993, 1999, 2011; Conway Morris & Peel 1995; Stein *et al.* 2010), which is dissimilar to the BST deposits where organisms have experienced a complete loss of cellular detail and are predominantly preserved in two dimensions (Butterfield 1990, 1995, 2003; Gaines *et al.* 2008; Gaines 2014; Briggs 2015). Hyoliths, for example, in the Sirius Passet Lagerstätte are generally preserved as moulds in three dimensions (Peel 2010*a*), contrasting with specimens from the Burgess Shale Lagerstätte that are preserved as kerogenous compressions (Moysiuk *et al.* 2017). However, an easier comparison can be drawn with hyoliths documented from the Chengjiang Lagerstätte that are also preserved as moulds with slight topographic relief (Hou *et al.* 2017). Indeed, quite a few taxa in the Chengjiang biota retain a level of three dimensionality, as elegantly exhibited by Zhai *et al.* (2019). Fossils from the Burgess Shale Lagerstätte also typically show tissue-specific variation in the elemental composition of phyllosilicate templates (Orr *et al.* 1998; Page *et al.* 2008). The kerogenous films in the Sirius Passet do not generally show any specific tissue-related mineral variation and are instead homogeneous, most probably as a result of exposure to higher temperatures during metamorphism (Topper *et al.* 2018). Nevertheless, there is some high-fidelity preservation; most notably, the brain, nervous system and eyes of *Kerygmachela* (Park *et al.* 2018). The preservation of muscles in three dimensions is rare in Cambrian Lagerstätten, having been documented only in *Campanamuta* and *Pambdelurion* in the Sirius Passet fauna; muscles have been also identified in specimens of *Myoscolex* from the Emu Bay Shale in South Australia (Briggs & Nedin 1997), a site, like Sirius Passet, not currently considered to be BST (Jago *et al.* 2012; Paterson *et al.* 2016) owing to the effects of early and/or late diagenetic mineralization (Gaines 2014).

Table 1. *The Sirius Passet fauna*

Aaveqaspis inesoni	Peel & Stein, 2009	Euarthropoda
Arthroaspis bergstroemi	Stein *et al.*, 2013	Euarthropoda
Buenaspis forteyi	Budd, 1999	Euarthropoda
Buenellus higginsi	Blaker, 1988	Euarthropoda
Campanamuta mantoni	Budd, 2011	Euarthropoda
Isoxys volucris	Williams *et al.*, 1996; Stein *et al.* 2010; Nielsen *et al.* 2017	Euarthropoda
Isoxys sp.	Williams *et al.* 1996	Euarthropoda
Kiisortoqia soperi	Stein, 2010	Euarthropoda
Kleptothule rasmusseni	Budd, 1995	Euarthropoda
Molaria steini	Peel, 2017*a*	Euarthropoda
Pauloterminus spinodorsalis	Taylor, 2002	Euarthropoda
Sidneyia sp.	Peel 2017*b*	Euarthropoda
Siriocaris trollae	Lagebro *et al.*, 2009	Euarthropoda
Hadranax augustus	Budd & Peel, 1998	Lobopodia
Kerygmachela kierkegaardi	Budd, 1993, 1999; Park *et al.* 2018	Lobopodia
Pambdelurion whittingtoni	Budd, 1998*a*; Vinther *et al.* 2016	Lobopodia
Tamisiocaris borealis	Daley & Peel, 2010; Vinther *et al.* 2014	Radiodonta
Chalazoscolex pharkus	Conway Morris & Peel, 2010	Palaeoscolecida
Xystoscolex boreogyrus	Conway Morris & Peel, 2010	Palaeoscolecida
Singuuriqia simony	Peel, 2017*a*	Priapulida
Phragmochaeta canicularis	Conway Morris & Peel, 2008	Annelida
Pygocirrus butyricampum	Vinther *et al.*, 2011*a*	Annelida
Halkieria evangelista	Conway Morris & Peel, 1990, 1995; Vinther & Nielsen 2005	Mollusca
Hyolithus cf. *tenuis*	Peel 2010*a*	Hyolitha
Hyolithid sp.	Peel 2010*a*	Hyolitha
Orthothecid sp.	Peel 2010*a*	Hyolitha
Trapezovitus sp.	Peel 2010*a*	Hyolitha
Sirilorica carlsbergi	Peel, 2010*b*; Peel *et al.* 2013	Loricifera
Sirilorica pustulosa	Peel, 2010*b*; Peel *et al.* 2013	Loricifera
Ooedigera peeli	Vinther *et al.*, 2011*b*	Vetulicolia
Genus and species indeterminate A	Vinther *et al.* 2011*b*	Vetulicolia
Archaeocyatha spp.	Peel 2010*a*	Porifera
Choia cf. *carteri*	Botting & Peel 2016	Porifera
Constellatispongia canismajorii	Botting & Peel, 2016	Porifera
Crassicoactum cucumis	Botting & Peel, 2016	Porifera
Demospongiae indet.	Botting *et al.* 2015	Porifera
Fieldospongia bellineata	Botting & Peel 2016	Porifera
Hamptonia limatula	Botting & Peel, 2016	Porifera
Lenica cf. *unica*	Botting & Peel 2016	Porifera
Lenica hindei	Botting & Peel 2016	Porifera
Lenica perverse	Botting & Peel 2016	Porifera
Saetaspongia cf. *densa*	Botting & Peel 2016	Porifera
Saetaspongia procera	Botting & Peel, 2016	Porifera
Salactiniella cf. *plumata*	Botting & Peel 2016	Porifera
Stephanella? sp.	Botting & Peel 2016	Porifera

Moreover, the remarkable preservation of guts in *Campanamuta* (Strang *et al.* 2016*a*) and midgut glands in the lobopodian *Pambdelurion* indicates the evolution of carnivory and macrophagy within the trajectory of arthropod evolution (Vannier *et al.* 2014).

These different preservation modes in the Sirius Passet biota may reflect differences in the general composition of the original tissues of the organism, and their variable susceptibility to decay (Topper *et al.* 2018), but also potentially to fluctuations in ocean chemistry and the presence or absence of microbial mats at the time. Trilobites and other three-dimensionally preserved taxa, for example, are preserved in association with the microbial mats, whereas the compressed kerogenous films are more typically preserved within gravity flows with no direct association with the microbial mats. The understanding of the preservational processes in the Sirius Passet Lagerstätte is currently less advanced than that for the Burgess Shale and Chengjiang Lagerstätten and new investigations may provide further clarification of these preservational modes. However, the clear presence of matgrounds and trace fossils in close association with fossils is fairly unusual for Cambrian Lagerstätten preserving soft parts (Buatois *et al.* 2014) and, in combination with the complex set of taphonomic modes present, shows that the Sirius Passet represents a rather unusual Cambrian Lagerstätte.

Water column chemistry

Our high-resolution geochemical exploration of palaeoenvironmental conditions in the Sirius Passet Lagerstätte has involved, to date, the analysis of 144 samples through 12 m of the Buen Formation (Hammarlund *et al.* 2019; Fig. 10). The geochemical trends displayed through the succession are subtle but appear to be mutually correlated, especially at the transitions into and out of the interval with thinly laminated mudstones that, also, contain the highest fossil abundance (2.8–7.7 m) (Fig. 10). At these two transitions, both the content of total organic carbon (TOC) (*c.* 1 wt %) and ratios of highly reactive iron to total iron (Fe_{HR}/Fe_T) increase (Fig. 10). Occasionally, high Fe_{HR}/Fe_T values (maximum 0.69) indicate intervals of water column anoxia but, generally, Fe_{HR}/Fe_T

Box 1. Rarefaction analysis

How diverse was the Sirius Passet fauna?

The remote location, inability to transport large sample collections and the relatively short field seasons populated by small groups of researchers have led to relatively small-scale investigations of the site to date. The extensive sampling programmes led by the Geological Survey of Greenland, with the universities of Cambridge and Uppsala, relied almost entirely on specimens from the richly fossiliferous scree slopes. Collections were accumulated and courtesy of Dr Martin Stein, who curated the collections in Uppsala University, data were made available for rarefaction analysis (Hammer *et al.* 2001). Based on a sample size of some 8000 specimens, species diversity appeared to level off at around 25 species, suggesting that no further collecting would increase the diversity of the fauna (Fig. 6a). The scree-slope fauna appears, however, to have limited ability to capture or predict the possible diversity of the entire fauna, presumably owing to the more weathered scree specimens being more challenging to identify. During the 2011 field season, the section was sampled bed-by-bed and despite the uncertainties of field identification, the *c.* 6000 specimens suggest a diversity in excess of 45 species with a curve that has yet to level off (Fig. 6b). There is thus much more to be gleaned from the exposures regarding the diversity of the Sirius Passet fauna together with its composition, structure and taphonomy.

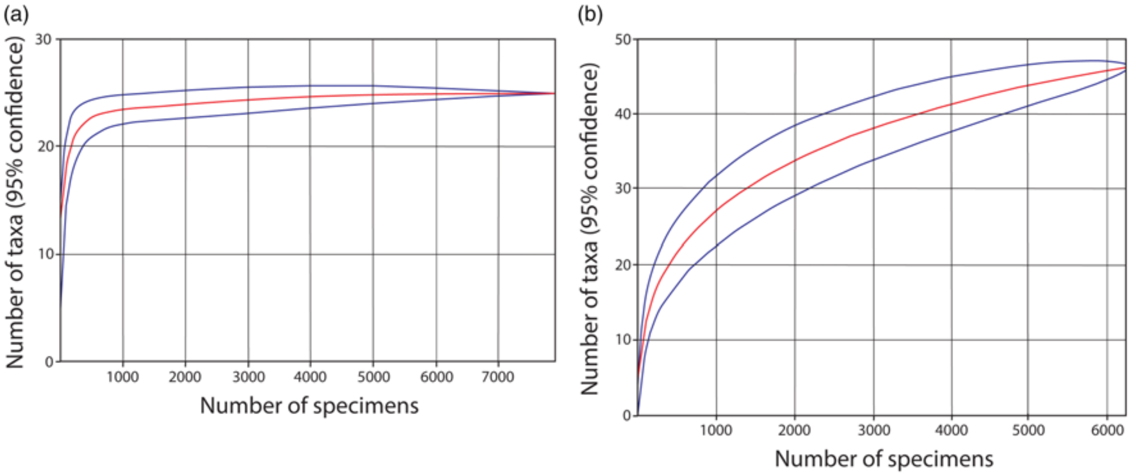

Fig. 6. Rarefaction curves: (**a**) based on data from the scree collections, kindly provided by M. Stein; (**b**) based on data from the intensive bed-by-bed sampling during the 2011 expedition.

values remain below the threshold of 0.38 that is conventionally used to define anoxic settings (Poulton & Canfield 2011). In low-grade metamorphic rocks like those at Sirius Passet, highly reactive iron may have become unavailable for extraction and, thus, compromise the proxy and underestimate the presence of water column anoxia (Poulton & Canfield 2011). However, the Sirius Passet Lagerstätte also contains trace fossils of a meiofauna (Mángano *et al.* 2012). This indicates that the water column was probably not persistently anoxic, suggesting that the iron-based proxy has not been dramatically altered in favour of lower values. Therefore, the Fe_{HR}/Fe_T values in the interval of thinly laminated mudstones and highest fossil abundance (0.23 ± 0.11) are accepted as realistic and can be considered 'intermediate'. These Fe_{HR}/Fe_T values fall within the range of intermediate Fe_{HR}/Fe_T values (above 0.14 but below 0.38) observed in low-oxygen depositional settings, both modern and ancient (Raiswell & Canfield 1996; Farrell *et al.*

Box 2. Composition and ecology of the fauna

Some 45 species of animals are currently known from the Sirius Passet fauna (see Table 1) representing at least eight major clades. The fauna is unique, showing a high level of endemism and sharing only a few taxa with other Cambrian Lagerstätten (Holmes *et al.* 2018). Taxon counts are summarized in Figure 7 for diversity and abundance. The specimens illustrated are reposited in the Natural History Museum of Denmark, University of Copenhagen (prefix MGUH). They indicate the diversity and preservation of the abundant euarthropods (Fig. 8), evidencing the presence of key stem groups (Budd 1998*a*,*b*) and other key elements of the fauna (Fig. 9). In terms of taxa, species numbers are dominated by euarthropods and sponges (Fig. 7a) and bed-by-bed identifications of specimens during the 2011 field season indicate that, numerically, euarthropods are significantly the most dominant (Fig. 7b). Ecologically, the biota comprises a mat-dwelling fauna, including a grazing and omnivorous mobile benthos (e.g. the mollusc *Halkieria*, the trilobite *Buenellus*; Fig. 8a, and the euarthropods *Buenaspis* and *Kleptothule*; Fig. 8d and e) and fixed suspension-feeders (e.g. sponges; Fig. 8j; and hyoliths). The infauna included a range of worms with carnivorous life styles, including palaeoscolecides (Fig. 8i) and polychaetes (Fig. 9c), but these taxa are not interpreted to be preserved *in situ*. Nektobenthos and nekton included a range of predators, including various euarthropods (e.g. *Campanamuta* and *Kiisortoqia*; Fig. 8c and g), *Isoxys* (Fig. 8f), which probably formed shoals, together with a diverse fauna of lobopodians (e.g. *Hadranax*, *Pambdelurion* and *Kerymachela*; Fig. 9e and f) and the sweep-net feeder *Tamisiocaris* (Fig. 9a).

This is also an emerging pattern in other early Cambrian Lagerstätten, where detritus and suspension-feeders are much less common than during the subsequent Phanerozoic (Bush & Bambach 2011). Nevertheless, the presence of large sweep-net feeders such as *Tamisiocaris* indicates already a sufficiency of pelagic prey in the early Cambrian oceans (Vinther *et al.* 2014). New discoveries from the Sirius Passet Lagerstätte have not only increased the diversity of early Cambrian faunas, but the excellence of preservation, despite some metamorphism and tectonism, has presented new information on the gut contents of a number of euarthropods and lobopods, supporting predatory and/or scavenging life modes (Strang *et al.* 2016*a*; Peel 2017*c*), as well as on their visual and nervous systems (Park *et al.* 2018) together with muscle fibres (Budd 2011; Peel 2017*c*). This distinctive ecosystem structure emphasizes the contrast between the Cambrian and Paleozoic evolutionary faunas, the latter dominated by a suspension-feeding benthos generated during the Great Ordovician Biodiversification Event (Harper 2006; Servais *et al.* 2010; Servais & Harper 2018). The early Cambrian assemblages display a high degree of endemism (Meert & Lieberman 2008; Peng *et al.* 2012) that changed only later in the Cambrian with the more widespread distribution of nonarticulate brachiopods (Bassett *et al.* 2002) and more complex and diverse distributional patterns in the trilobites (Álvaro *et al.* 2013).

2013; Scholz *et al.* 2014; Hammarlund *et al.* 2017) and are higher than the average Fe_{HR}/Fe_T ratio (0.14 ± 0.11) determined for Cambrian sediments deposited below an oxic water column (Poulton & Raiswell 2002). An intermediate setting is also consistent with the occurrence of sparse trace fossils. On one hand, the finely laminated mudstones suggest that the setting was uninhabitable for bioturbating organisms that would have vertically disrupted and mixed the sediment. On the other hand, the presence of the meiofauna that left a network of fine calibre burrows (Mángano *et al.* 2012) excludes a persistently anoxic water column. Thus, trace fossils and Fe_{HR}/Fe_T data collectively suggest a low-oxygen, but not anoxic, water column. The co-enrichment of trace metals (V/Al and Mo/Al) is also consistent with a depositional setting below a water column with very low concentrations of oxygen (Piper & Dean 2002; Brumsack 2006). Taken together, Fe_{HR}/Fe_T, TOC, V/Al and Mo/Al data are consistent with intervals of very low water-column oxygen concentrations during deposition of the Sirius Passet succession. What drove the development of these conditions remains unclear, but changes in sea-level or primary production, or both, are options consistent with these observations.

The highest diversity of animal species recorded in the interval between 3.0 and 7.7 m in the Sirius Passet succession corresponds to an interval where the water column appears to have contained very low concentrations of dissolved oxygen (Fig. 10); there is a significant positive correlation ($P = 5.3 \times 10^{-7}$) between diversity and Fe_{HR}/Fe_T values (Hammarlund *et al.* 2019). The intervals of low-oxygen water-column conditions thus directly correlate with preserved biodiversity. Although reducing bottom water conditions are expected to associate with favourable preservational conditions, this is by no means the only requirement (Gaines 2014). Thus, the presence and preservation of the Lagerstätte fauna was most probably facilitated by additional factors of biological, geological or taphonomical character, or a combination of them.

The seemingly contradictory observations at Sirius Passet, with significant *in situ* animal preservation and yet the general absence of vertical bioturbation other than superficial burrow systems, can be

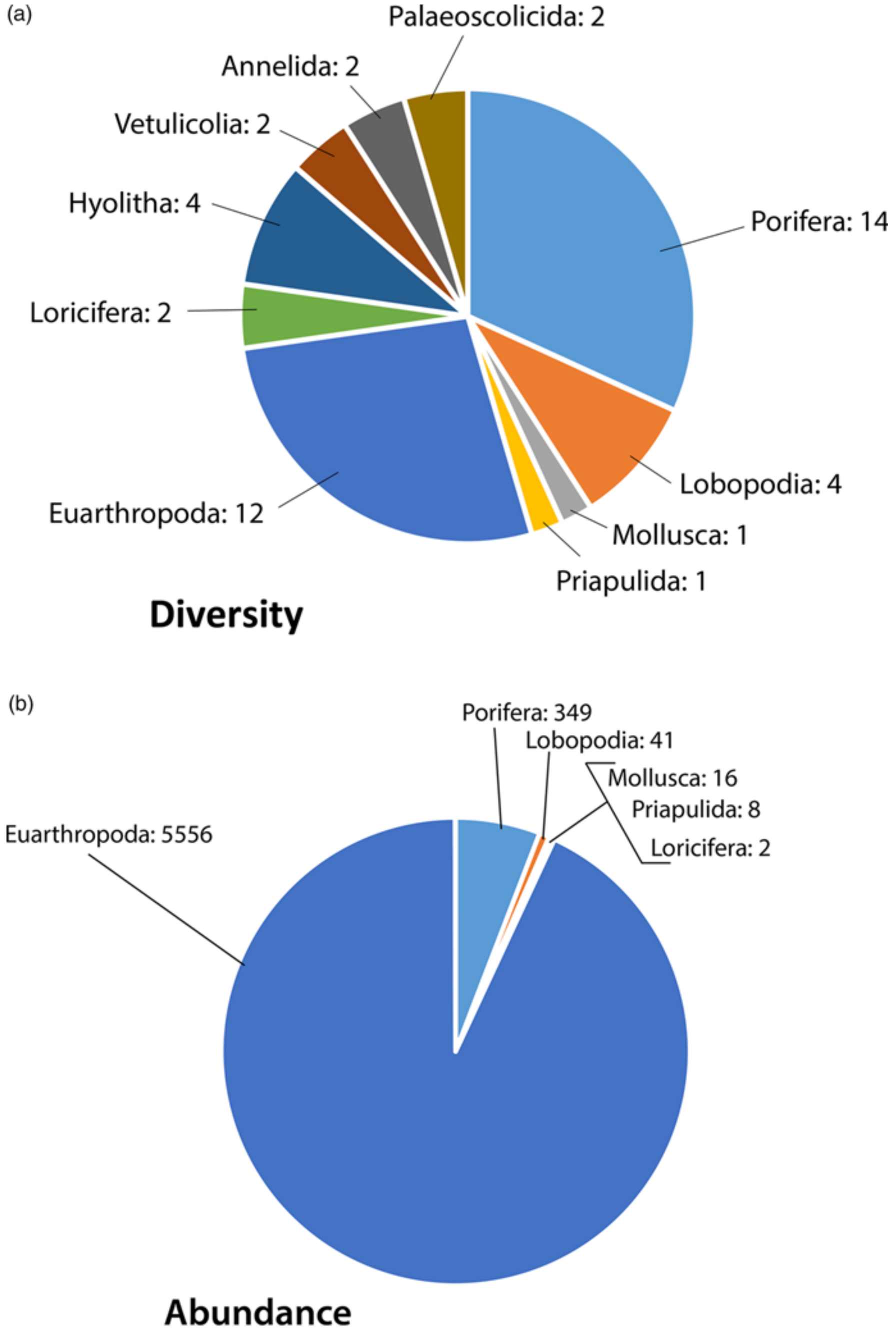

Fig. 7. (**a**) Diversity of taxa based on published data (Table 1). (**b**) Abundance of taxa based on bed-by-bed sampling during the 2011 expedition.

Fig. 8. (**a**) *Buenellus higginsi* Blaker, 1988, MGUH 33376, scale bar 1 cm. (**b**) *Arthroaspis bergstroemi* Stein, Budd, Peel & Harper, 2013, MGUH 33377, scale bar 3 cm. (**c**) *Campanamuta mantoni* Budd, 2011, MGUH 33378, scale bar 2 cm. (**d**) *Kleptothule rasmusseni* Budd, 1995, MGUH 33379, scale bar 5 mm. (**e**) *Buenaspis forteyi* Budd, 1999, MGUH 33380, scale bar 5 mm. (**f**) *Isoxys volucris* Williams, Siveter & Peel, 1996, MGUH 33381, scale bar 5 mm. (**g**) *Kiisortoqia soperi* Stein 2010, MGUH 33382, scale bar 5 mm. (**h**) *Sirilorica carlsbergi* Peel 2010*b*, MGUH 33383, scale bar 5 mm. (**i**) *Xystoscolex boreogyrus* Conway Morris & Peel, 2010, MGUH 33384, scale bar 5 mm. (**j**) *Lenica hindei* (Dawson, 1896), MGUH 33385, scale bar 1 cm.

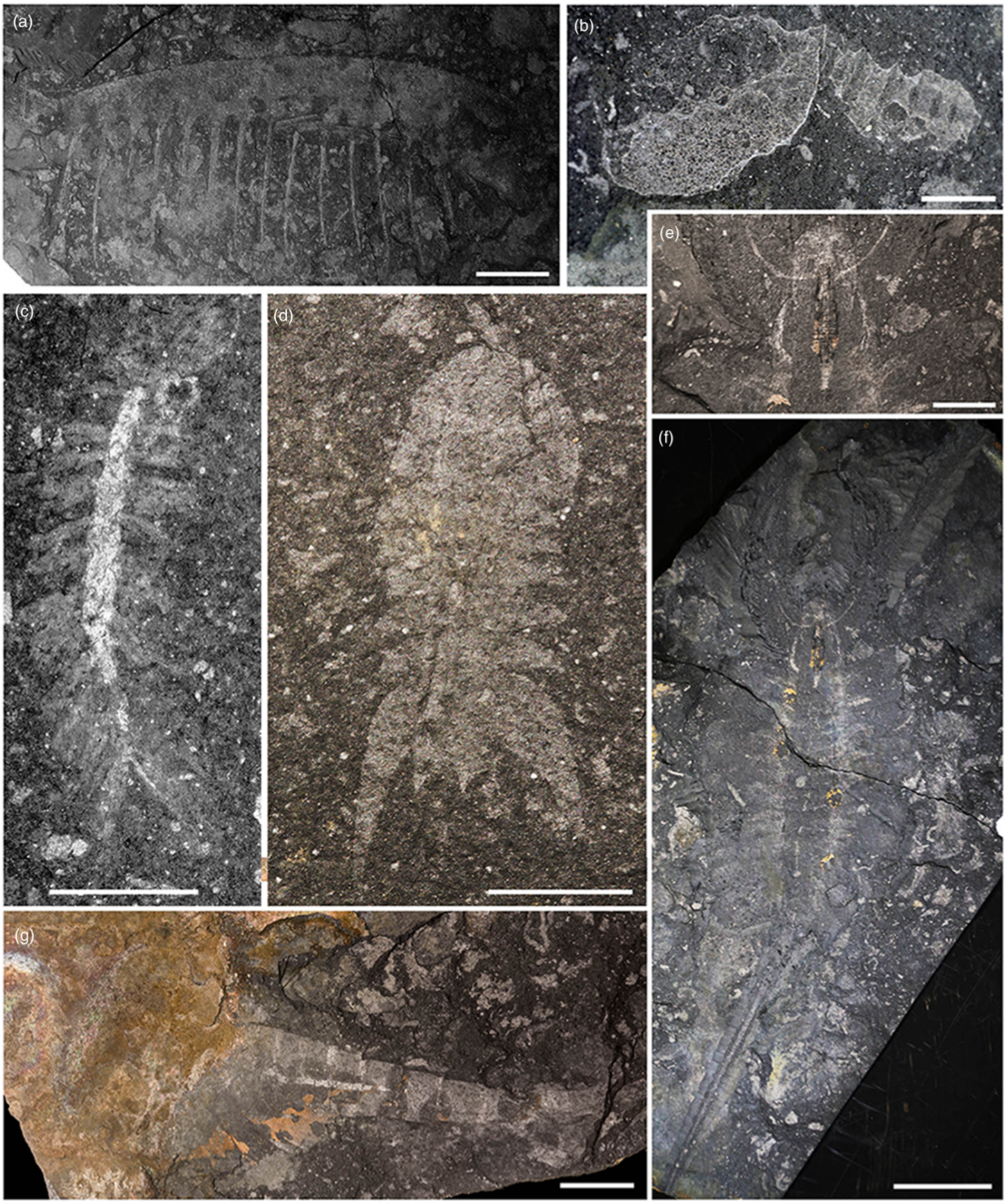

Fig. 9. (**a**) *Tamisiocaris borealis* Daley & Peel, 2010, MGUH 30500, scale bar 2 cm. (**b**) *Ooedigera peeli* Vinther, Smith & Harper, 2011*b*, MGUH 29279, scale bar 5 mm. (**c**) *Pygocirrus butyricampum* Vinther, Eibye-Jacobsen & Harper, 2011*a*, MGUH 29288, scale bar 5 mm. (**d**) *Aaveqaspis inesoni* Peel & Stein, 2009, MGUH 33386, scale bar 5 mm. (**e**, **f**) *Kergymachela kierkegaardi* Budd, 1993, MGUH 32048a ((e) close-up of head region, scale bar 5 mm; (f) plan view, scale bar 2 cm). (**g**) *Pauloterminus spinodorsalis* Taylor, 2002, MGUH 33387, scale bar 1 cm.

understood by comparison with modern low-oxygen ecosystems. The lack of bioturbation but the presence of horizontal trace makers, pioneering species and chemosynthesis-based nutrition are all observations that may be reconciled with extremely low-oxygen settings (Levin 2003). Modern Oxygen Minimum Zones (OMZs) also share certain ecological characteristics with the Sirius Passet biota. For example, a generally low diversity characterized by large predators and detrivores, and a short food chain (Levin 2003) are observed in both settings. Taken together, we interpret the Sirius Passet Lagerstätte as having been deposited in a dynamic setting, experiencing both intermittent turbulence (with sediment gravity flows punctuating quieter background sedimentation) and fluctuating oxygen concentrations. The geochemical and palaeontological data from Sirius Passet are comparable with those in modern OMZs

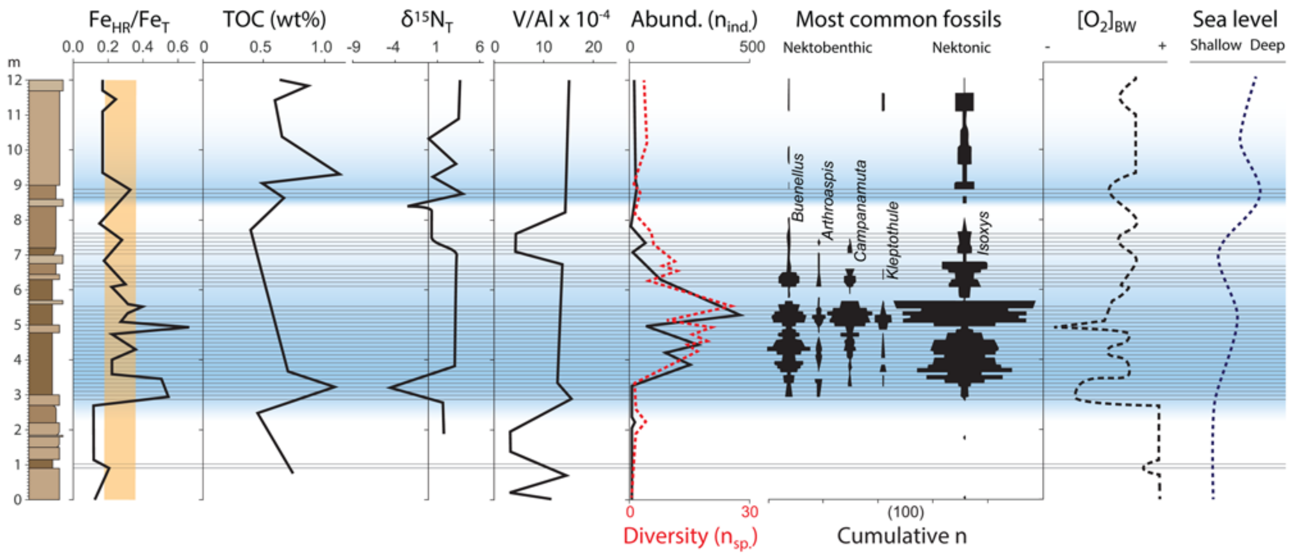

Fig. 10. Correlation of geochemical trends (Fe_{HR}/Fe_T, TOC, $\delta^{15}N_T$, V/Al) in the Sirius Passet section with fossil abundance (black continuous line) and species diversity (red dashed line) next to cumulative abundance ($n = 100$ between individual tick marks) of the five most common fossils (*Buenellus*, *Arthroaspis*, *Campanamuta* and *Kleptothule* (presumed nektobenthic) and *Isoxys* (certainly nektonic)), together with inferred changes (dashed black lines) of bottom water oxygen concentrations $[O_2]_{BW}$ and relative water depth. Yellow zone in Fe_{HR}/Fe_T column brackets intermediate Fe_{HR}/Fe_T values between the Cambrian average value of 0.14 and the 0.38 value that is used to distinguish oxic and anoxic waters. Proposed intervals of periodic anoxia in blue with horizontal ruling. Modified from Hammarlund *et al.* 2019.

(e.g. chemosynthetic nutrition, monospecific communities and short food chain), and are also consistent with an interpretation that oxygen concentrations were variable but consistently low, which restricted bioturbation but were at times sufficient to permit the establishment of a limited nektobenthic community (Fig. 10). Although optimal conditions for preservation were associated with fluctuations in water-column chemistry and sea-level, we envisage that a substantial component of the Sirius Passet animal community also lived at or near the site, tolerating conditions of low water-column oxygen concentrations. The geochemical analysis indicates that the Sirius Passet Lagerstätte represents an early Cambrian biota that, in terms of oxygen, lived at concentrations that we today consider extremely low (Hammarlund *et al.* 2019).

Significance of the fauna

The Sirius Passet biota is one the oldest of the Cambrian Lagerstätten and may form a bridge between Neoproterozoic Ediacara biotas and the diverse communities of the Paleozoic era (Erwin & Valentine 2013). It retains some features of the latest Proterozoic ecosystems, such as a seafloor associated, in places, with microbial mats and a unique style of preservation in some taxa. But in most other features, such as an overwhelming dominance of animals, particularly predators, a highly populated water column and locally abundant trace fossils, the fauna is an early window on the evolution of the Paleozoic biota. The fauna also provides an opportunity to study the early evolution of a number of animal groups, the mode of construction of some of the first animal-based communities and an indication of the environment and seawater chemistry that were associated with the initial stages of the Cambrian Explosion.

The Sirius Passet Lagerstätte preserves remnants of the earliest Cambrian microbial mat community associated with exceptional preservation, predating the Burgess Shale by *c.* 10 myr. A remarkable array of distinctive faunal elements and preservational modes demonstrate that the Sirius Passet represents a unique and significant site on which to study the Cambrian Explosion. These microbial mat communities dissipated with the appearance of abundant mat grazers and burrowers as the Cambrian Explosion intensified, and the seafloor switched from a Neoproterozoic ‘savannah’ to the modern marine seascapes of the Phanerozoic (Budd & Jensen 2015). The Sirius Passet biota thus has considerable significance in understanding the early radiation of metazoan groups, the assembly of the first complex, animal-based communities, their relationship to oxygen and the establishment of modern ecosystems.

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