SERIES

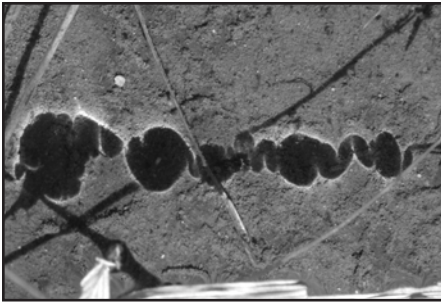## Great Canadian *Lagerstätten* 2. Macro- and Microfossils of the Mount Cap Formation (Early and Middle Cambrian, Northwest Territories)

Thomas H. P. Harvey and Nicholas J. Butterfield
Department of Earth Sciences
University of Cambridge
Downing Street, Cambridge, UK, CB2 3EQ
E-mail: thph2@cam.ac.uk

SUMMARY
The Early–Middle Cambrian Mount Cap Formation, NWT, hosts a diverse range of exceptionally preserved fossils. Like the celebrated Burgess Shale of British Columbia, the Mount Cap contains carbonaceous compression fossils of animals that lacked mineralized hard parts, as well as the fully articulated skeletons of shelly taxa. Its unique importance, however, lies in exceptional carbonaceous preservation at a microscopic scale. Acid-extracted microfossils from the 'Little Bear biota' of the Mackenzie Mountains reveal important details of problematic groups including chancelloriids and hyolithids, and provide direct evidence of Cambrian diets in the form of faecal strings. A complementary microfossil assemblage from the subsurface of the Colville Hills region contains an extraordinary diversity of exquisitely preserved arthropod cuticle, and constitutes the oldest known record of complex crown-group crustaceans. We discuss the wider significance of the Mount Cap fossils, and describe some new forms that point to the potential for future discoveries.

SOMMAIRE
La Formation de Mount Cap dans les T.N.-O. qui va du début de Cambrien jusqu'au Cambrien moyen renferme une gamme diverse de fossiles exceptionnellement bien préservés. Comme dans le cas des schistes de Burgess de Colombie-Britannique, la Formation de Mount Cap renferme des fossiles de compression carbonés d'animaux exempts de parties dures minéralisées, de même que de squelettes pleinement articulés de taxons coquillers. Cependant, son importance unique tient à sa préservation carbonée exceptionnelle à l'échelle microscopique. Les microfossiles obtenus par extraction à l'acide sur le « biote de Little Bear » des monts Mackenzie montrent d'importants détails sur des groupes controversés incluant les chancelloriidés et les hyolithidés, ainsi que des indices directs de la diète cambrienne sous la forme de trainées fécales. Un assemblage microfossile complémentaire du sous-sol de la région de Colville contient une extraordinaire diversité de cuticules d'arthropode très finement préservées, constituant ainsi la plus ancienne archive du groupe-couronne complexe de crustacés. Nous commentons à grands traits la signification de l'existence des fossiles de Mount Cap, et décrivons quelques formes nouvelles qui laissent penser que d'autres découvertes sont possibles.

INTRODUCTION
The Cambrian 'explosion' of diverse shelly fossils and sedimentary traces marks the onset of the modern Phanerozoic biosphere, but presents a deeply unrepresentative account of the underlying diversity and dynamics. Many important evolutionary innovations were limited to 'soft' body parts and organisms, which only became fossilized in rare instances of 'exceptional preservation' – most famously in the Burgess Shale, which was discovered in SE British Columbia in 1909 (see Collins 2009). Since then, comparable and complementary fossil-*Lagerstätten* have been described from China, Greenland, Australia, the United States and elsewhere in Canada (see Hagadorn 2002). Although 'Burgess Shale-type' (BST) biotas are particularly well documented in the southern and central Canadian Rockies (e.g. Collins et al. 1983; Copeland 1993; Butterfield 2000; Johnston et al. 2009; Caron et al. 2010), they have also been encountered much farther north, in the Early to Middle Cambrian Mount Cap Formation of the Northwest Territories (Butterfield 1994; Butterfield and Nicholas 1996; Harvey and Butterfield 2008). As well as being of paleogeographic significance, the Mount Cap fossils have provided a unique view of early metazoan evolution via their (exceptional) preservation of micro-anatomy, and yield both key data points and an important new paleontological search image. Here we present a current summary of the Mount Cap biota, and champion its place among 'great Canadian *Lagerstätten*.'
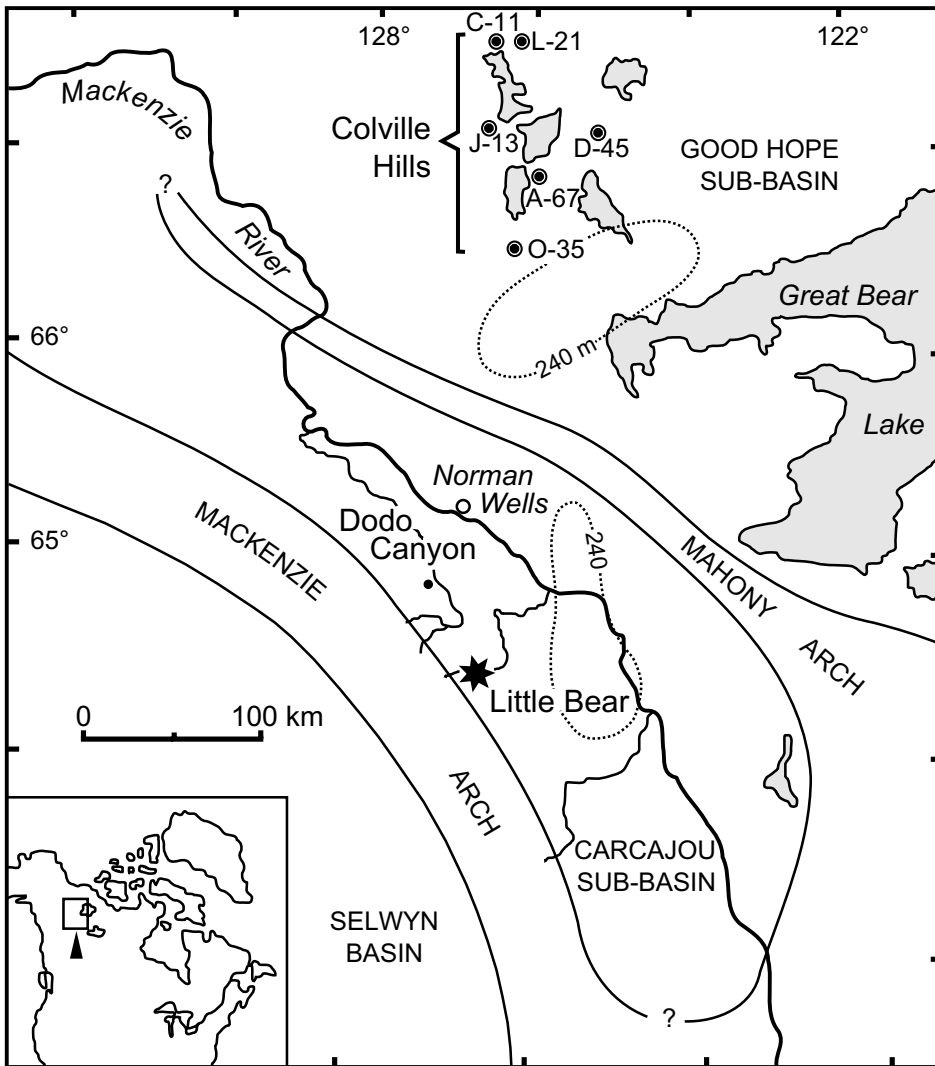
Figure 1. Map showing the principal localities for exceptional fossils in the Mount Cap Formation, including the Little Bear section (Carcajou sub-basin) and subsurface occurrences in the Colville Hills region (Good Hope sub-basin). After Pugh (1993), Butterfield (1994), and Butterfield and Nicholas (1996).

GEOLOGICAL SETTING

Unlike most of the units bearing BST assemblages to the south, the Mount Cap Formation was deposited in an intracratonic basin, separated from the open ocean to the west by the Mackenzie Arch (Fig. 1). The sedimentary succession is represented by 100–300 metres of mostly shallow water glauconitic sandstones, siltstones, shales and minor carbonates that crop out discontinuously in the Mackenzie and Franklin mountain belts (Aitken et al. 1973; Serié et al. 2009), and are intersected locally in the subsurface by exploration boreholes (Pugh 1993; Wielens et al. 1990; Dixon and Stasiuk 1998). The NW–SE trending Mahony Arch defines two localized depocen-

tres: the Carcajou sub-basin, which includes the cordilleran outcrops; and the Good Hope sub-basin, which lies to the east of any orogenic deformation and is known primarily from drillcore (Fig. 1). In both areas, trilobite biostratigraphy identifies a late Early Cambrian (*Bonnia-Olenellus* Zone) to Middle Cambrian (*Glossopleura* Zone) depositional age for the Mount Cap Formation.

Burgess Shale-type fossils were first discovered in drillcore from the Colville Hills area (Butterfield 1994) and only subsequently identified in outcrop, some 300 km to the south, in the front ranges of the Mackenzie Mountains (Butterfield and Nicholas 1996). Because of their marked geo-

graphical, geological and paleontological differences, we recognize two distinct fossil assemblages: the Early Cambrian 'Colville Hills biota' (Good Hope sub-basin), and the Middle Cambrian 'Little Bear biota' (Carcajou sub-basin).

THE LITTLE BEAR BIOTA: 'BURGESS SHALE-TYPE' FOSSILS AT MACRO- AND MICROSCOPIC SCALES

The Little Bear locality, on the Little Bear River in the Mackenzie Mountains (section U-13 of Aitken et al. 1973; section 2 of Serié et al. 2009; Fig. 2), has yielded a variety of exceptionally preserved fossils (Butterfield and Nicholas 1996). Entirely non-biomineralizing animals are represented by the claws of anomalocaridids (Fig. 3a) and the carapaces of bivalved arthropods, including *Isoxys* (Butterfield and Nicholas 1996, fig. 2.3). In addition, animals with mineralized skeletons that typically disarticulate after death are often preserved intact at Little Bear; examples include trilobites, sponges, and two problematic extinct groups: the mollusc-like hyolithids (Fig. 3b) and sponge-like chancelloriids (Fig. 3c). The chancelloriids are preserved as articulated scleritomes with traces of integument, while the hyolithids often retain their operculum and one or both arm-like helens; one hyolithid preserves a simple looped gut (see Butterfield 2003, fig. 2A).

The Little Bear macrofossils are typically defined by a silvery carbonaceous film. Both the non-mineralizing and the shelly forms possess substantial films, indicating that even biomineralized body parts can follow a Burgess Shale-type taphonomic pathway under particular diagenetic conditions (Butterfield and Nicholas 1996). One consequence of this robust carbonaceous expression is that comparatively intact specimens can be isolated from the rock matrix using a gentle hydrofluoric acid technique. Such processing has revealed the fine-scale features of larger Little Bear fossils, and allows the recovery of small specimens that would otherwise go unnoticed.

Significantly, the recovery of carbonaceous constituents in the Little Bear biota offers a complementary new view of familiar shelly fossils (Fig. 4). Cuticle fragments of olenellid trilo-
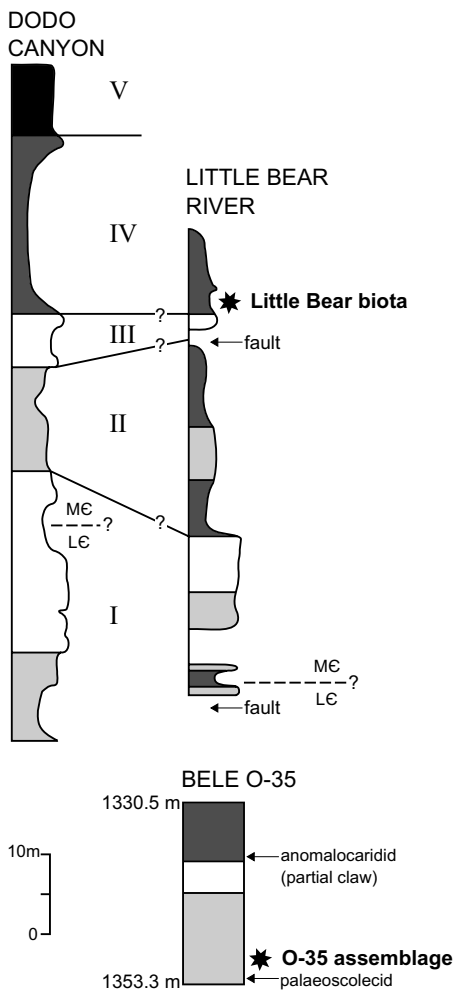
DODO
CANYON

LITTLE BEAR
RIVER

★ **Little Bear biota**

← fault

★ **O-35 assemblage**
← palaeoscolecid

← anomalocaridid
(partial claw)

BELE O-35
1330.5 m
1353.3 m
10m
0

Figure 2. Stratigraphic context of the Mount Cap fossils. The Little Bear biota comes from the Little Bear River section (GSC locality O-108351), which is correlated here with the Dodo Canyon section via a succession of (I) bioturbated coarse clastics and carbonates; (II) grey/green nodular shales; (III) laminated carbonates; (IV) black shales with minor carbonates; and (V) interbedded black carbonates, shales and cherts. The exceptional fossils occur at Little Bear near the base of unit IV, along with trilobites of the Middle Cambrian *Glossopleura* Zone; trilobites of the Lower Cambrian *Bonnia-Olenellus* Zone are restricted to the base of the section (for Dodo Canyon, see Aitken et al. 1973). In the Colville Hills region, the key horizon for exceptional microfossils is a thin dark mudstone among glauconitic siltstones and sandstones at ~ 1351 m in Bele O-35 (GSC locality C-248325); occurrences of *Wanneria* indicate a position within the *Bonnia-Olenellus* Zone (Butterfield 1994). (Logs courtesy of Chris Nicholas).

bites, for example, reveal minute pores and the details of terrace ridges (Butterfield and Nicholas 1996, figs 3.1–2), while shell layers from organo-phosphatic brachiopods exhibit a concentric accretionary pattern and sometimes a porous or granular texture (Fig. 4a). More surprisingly, acid-extraction has recovered structures that had not been known to possess substantial carbonaceous components, including the isolated sclerites of chancelloriids (Fig. 4c) and the conchs, helens and opercula of hyolithids (Fig. 4b, d). In both cases, the carbonaceous specimens reveal details that are not evident in conventional shelly fossils, but bear on the mode of growth and, in turn, the phylogenetic affinities of these problematic groups (see Butterfield and Nicholas 1996; Butterfield 2003; Mus and Bergström 2007; Porter 2008; Harvey et al. in press). The assemblage also contains narrow ornamented cones that resemble the 'small shelly fossils' *Rushtonites* and *Mongolitubulus*

(Fig. 4f). Like many of the smaller acid-extracted brachiopods, hyolithids and chancelloriid sclerites, the cones lack both remnant three-dimensionality and brittle fractures, and may have been only weakly mineralized in life, if at all. This implies a strong bias in the conventional (shelly) fossil records of these groups (Butterfield and Nicholas 1996).

In addition to body fossils, the Little Bear biota contains novel trace fossil evidence of diet and behaviour. Most notably, fecal pellets (and possibly other types of bromalite such as regurgitated material, or isolated gut contents) occur in a variety of sizes, shapes, and modes of preservation. At the macroscopic scale, Little Bear faecal pellets occur as either carbonaceous compressions (Butterfield and Nicholas 1996, fig. 2.4) or as three-dimensional phosphatized structures (Butterfield 2001, figs. 1.3.2.1e). The compression fossils exhibit regular ovoid outlines and a pseudo-segmented structure, but

yield no direct clues to the identity of their producer or its diet. The phosphatized examples, in contrast, are elongate to round in outline and variably 'segmented' or spiriform; one specimen contains numerous brachiopod shell fragments and was clearly produced by a predator or scavenger.

Fecal structures also occur among the acid-extracted microfossils (Butterfield and Nicholas 1996; Wilson 2004), where they take the form of more or less coherent strings of compressed carbonaceous material up to a few millimetres long and from 20 to 450 μm wide ($n > 70$). In overall shape they vary from straight to looped, coiled or sinuous (Fig. 5a–d), sometimes with an internal structure of aligned pellets (Fig. 5a). Most specimens consist of amorphous material of indeterminate origin, but a few are densely packed with sphaeromorphic acritarchs (Fig. 5d, e). The acritarchs are uniformly small (< 10 μm diameter), which suggests that they represent primary productivity ('algal' cysts) rather than (for example) the egg cases of metazoans, and so the pellets can be assigned to an herbivorous metazoan grazer, and possibly a member of the zooplankton. Although an alternative, benthic ecology is difficult to rule out, the high abundance of intact pellets in dark shale samples suggests that they were exported from an open water column overlying an undisturbed, probably anoxic sediment surface.

THE COLVILLE HILLS BIOTA: SUBSURFACE MOUNT CAP *LAGERSTÄTTEN*

Of the seven boreholes that intersect the Mount Cap Formation in the Colville Hills area, we have identified Burgess Shale-type fossils in six, from numerous horizons (Butterfield 1994). Not surprisingly, macroscopic forms are rarely encountered in the cores, but include semi-articulated arrays of sponge spicules and, in Bele O-35, a poorly preserved anomalocaridid claw and a palaeoscolecid worm fragment (see Fig. 2). As in the Little Bear biota, however, it is the microfossils that stand out. Systematic acid processing has identified the widespread occurrence of *Wiwaxia* sclerites and *Rushtonites*-like spines in the subsurface, in
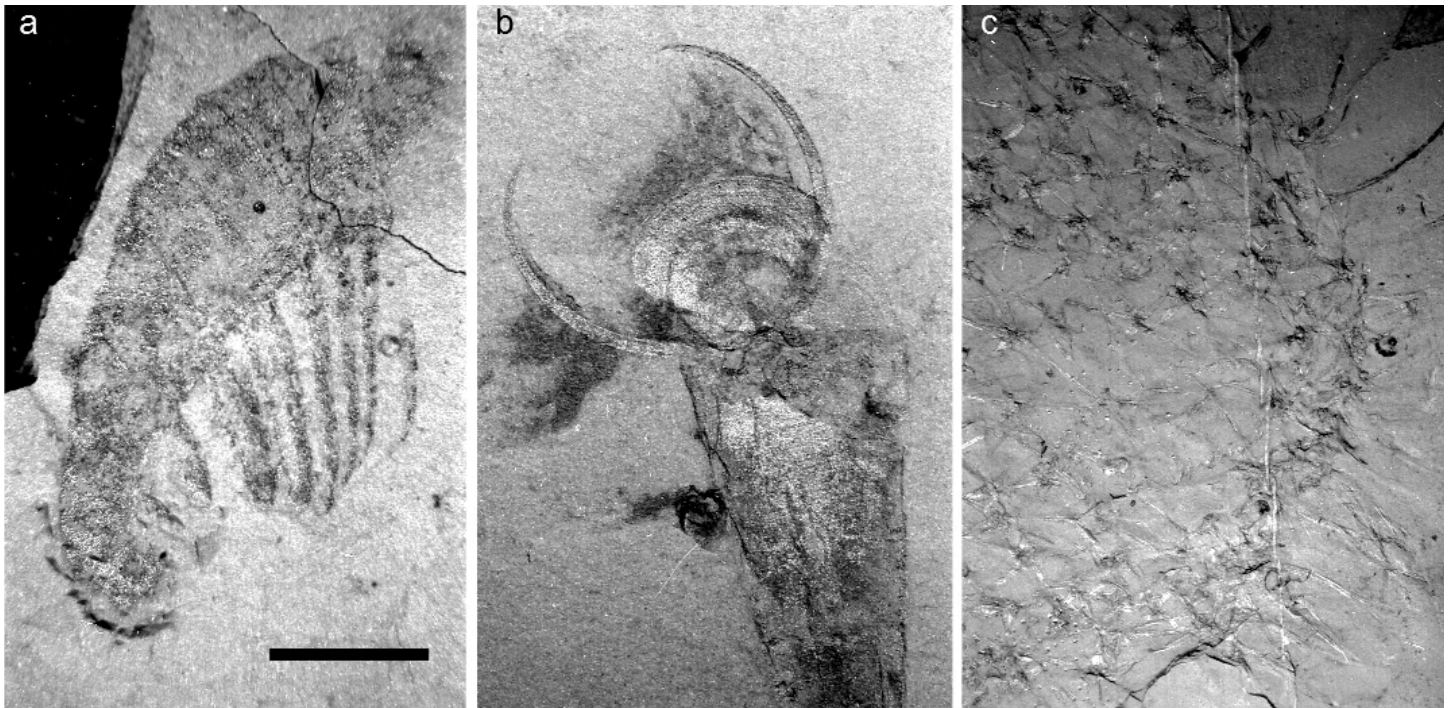
Figure 3. Macrofossils from the Little Bear biota (Middle Cambrian *Glossopleura* Zone; Little Bear River). Specimens in this and subsequent figures are stored at the Geological Survey of Canada (GSC), 601 Booth Street, Ottawa, Ontario, Canada. a. Anomalocaridid claw (GSC 135494); b. Hyolithid conch with articulated operculum and pair of helens (GSC 135495); c. Articulated chancelloriid scleritome (GSC 135496). Scale bars: a. 3 mm; b. 4 mm; c. 7.5 mm.
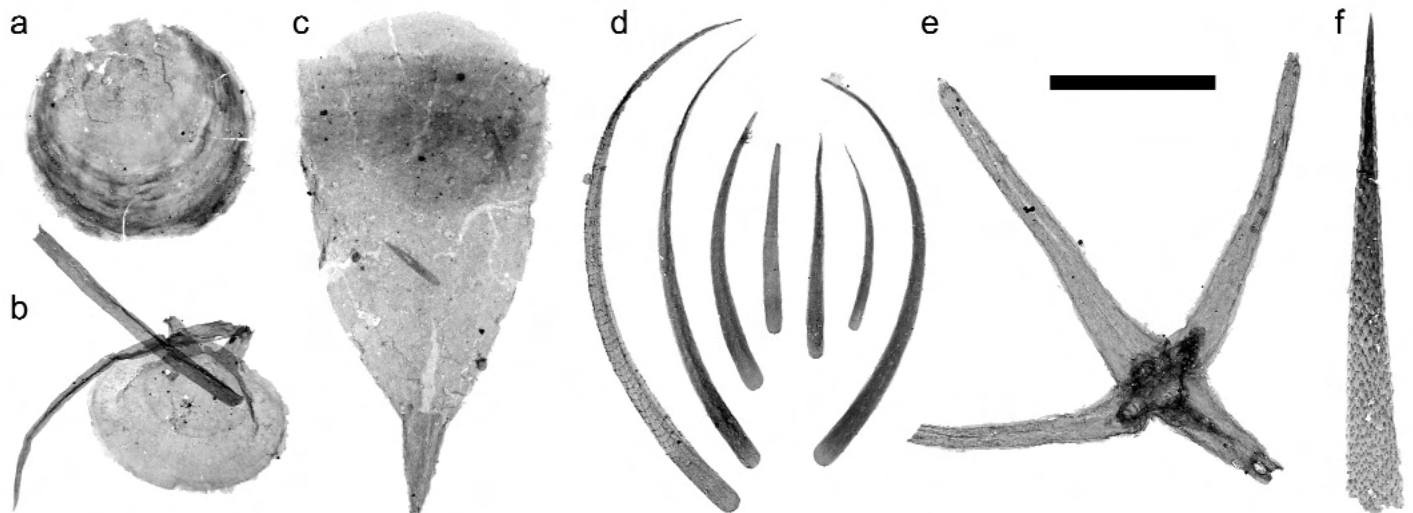

Figure 4. Carbonaceous remains of 'shelly' taxa from the Little Bear biota (Middle Cambrian *Glossopleura* Zone; Little Bear River). a. Brachiopod (GSC 135497); b–d. hyolithid skeletal elements, including an operculum with articulated pair of helens (b, GSC 135498); a conch with enclosed pair of helens (c, GSC 135499); and isolated helens of various sizes (d, GSC 135500-135506); e. chancelloriid sclerite (GSC 135507); f) ornamented cone 'cf. *Rushtonites*' (GSC 135508). Scale bars: a. 200 µm; b. 300 µm; c. 110 µm; d. 340 µm; e, f. 200 µm.

rock types ranging from sandy, glauconitic siltstones to pale, medium and dark grey mudstones. By far the richest assemblage, however, comes from a single 5-cm-thick band of conspicuously dark and fine-grained mudstone in Bele O-35, at a depth of 1351 m (Fig. 2).This contains exceptionally well-preserved fragments of arthropod cuticle in extraordinary abundance, and arguably qualifies as a (micro) *Lagerstätte* in its own right.

Most of the O-35 arthropod fossils (Fig. 6a to r; *n* ~ 3800) consist of highly disarticulated appendage fragments. Even so, their original functions and anatomical positions can often be reconstructed by virtue of the exceptionally fine-scale (sub-micron) preservation of various cuticular specializations, including a great variety of
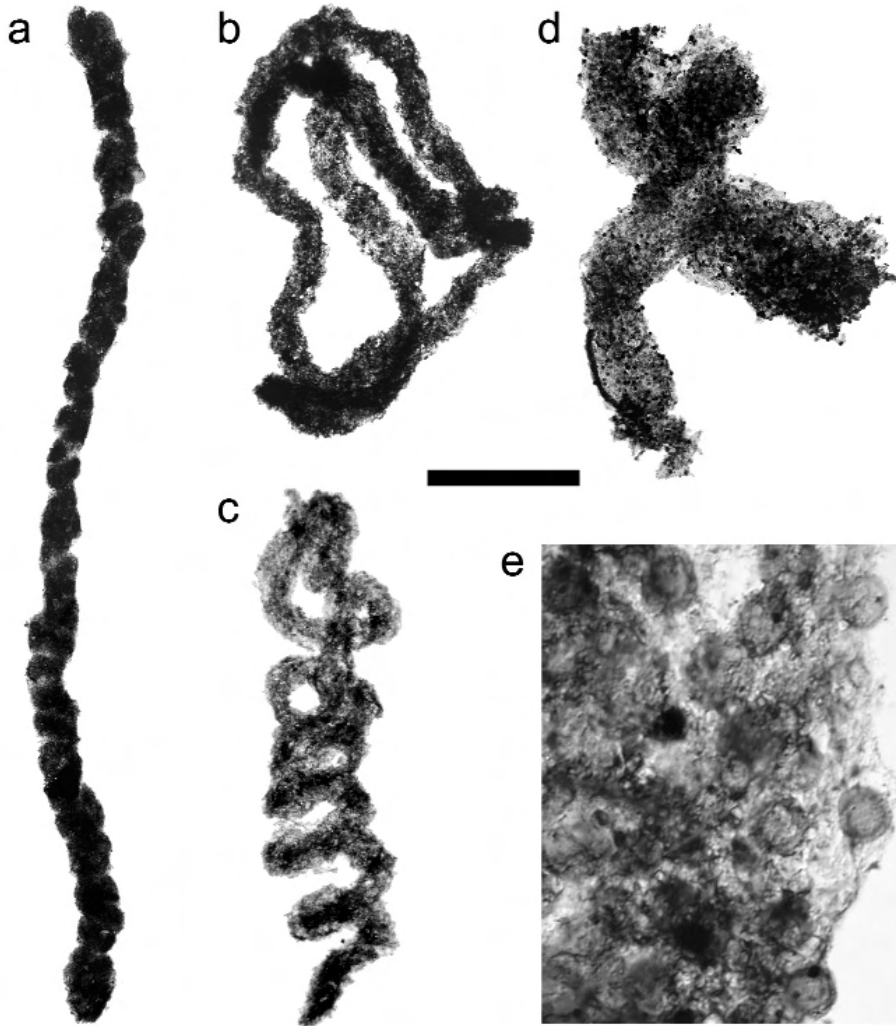
Figure 5. Carbonaceous faecal strings from the Little Bear biota (Middle Cambrian *Glossopleura* Zone; Little Bear River). a. A string of aligned pellets (GSC 135509); b–d. strings that are looped (b, GSC 135510), coiled (c, GSC 135511) or sinuous (d, GSC 135512); e. detail of (d) to show the high density of sphaeromorphic acritarchs contained within the faecal string. Scale bars: a. 450 μm; b, c. 150 μm; d. 225 μm; e. 17 μm.

bility in an arthropod of relatively large body size (estimated length of 5 cm). Although the Mount Cap crustacean may have been active in the plankton (Butterfield 1994) – perhaps producing the sorts of acritarch-packed faecal strings that are known from the Little Bear biota – the various robust setal armatures suggest a lifestyle that involved benthic substrate-scraping activities, at least in part (Harvey and Butterfield 2008).

The exceptionally fine-scale preservation in the Mount Cap (O-35) assemblage has provided novel insights into the phylogeny and ecology of early crustaceans, even in the absence of articulated remains. This is partly because comparable detail is not preserved, or at least not observable, in the various macroscopic Cambrian fossils that have sometimes been interpreted as crustaceans, including a number of BST taxa (e.g. Hou and Bergström 1997; but see Walossek 1999; Budd 2008) and also a possible Cambrian phyllocarid preserved via coarse moulding in sandstone (Collette and Hagadorn 2010). The Mount Cap fossils also contrast with crustaceans known from phosphatic 'Orsten-type' preservation (e.g. Maas et al. 2006), which are similarly detailed but exhibit comparatively simple and unspecialized morphologies. This may be explained by the small body size of the Orsten individuals, which do not exceed 2 mm in length. In contrast, the Mount Cap fossils provide a microscopic view of macroscopic Cambrian crustaceans, and thus substantially augment our knowledge of early crustacean form, function, and phylogeny.

The O-35 assemblage is dominated overwhelmingly by crustacean remains, but has also yielded a modest diversity of unrelated fossils, several of which are attributable to lophotrochozoan animals (the group that includes annelids and molluscs, among others). The most abundant are sclerites of *Wiwaxia* (Fig. 7a; $n = 111$; Butterfield 1994), which are comparable in shape and microstructure to those from the Burgess Shale but are notably better preserved (cf. Butterfield 1990). The fine-scale structure of the sclerites, which is only apparent in acid-isolated material, continues to figure prominently in discussions of

spines, setae and setules ('hairs'). Among the most informative specimens are groups of co-planar setae with a strict biserial arrangement of closely spaced setules (Fig. 6q), and various elongate, fringed elements (Fig. 6l–n) that bear a distinctive microstructure of aligned cuticular scales (Fig. 6r). Both structures have near-identical counterparts among living crustaceans, respectively in the filter plates used to collect suspended particles of food, and in the molar surfaces of mandibles ('jaws') that grind food prior to ingestion (Butterfield 1994; Harvey and Butterfield 2008).

The particular style of molar ornamentation links the Mount Cap fossils to a clade of crown-group (pan)crustaceans that includes branchiopods, malacostracans, and hexapods, and thus provides a crucial calibration point for arthropod phylogeny, as well as the earliest record of an arthropod with a sophisticated particle-feeding ecology (Harvey and Butterfield 2008). Though now disarticulated, the molars and co-occurring filter plates and other armatures are likely to have constituted a single complex feeding apparatus in life. They would have worked together to generate, harvest and efficiently process extremely small particles of food – an impressive capa-
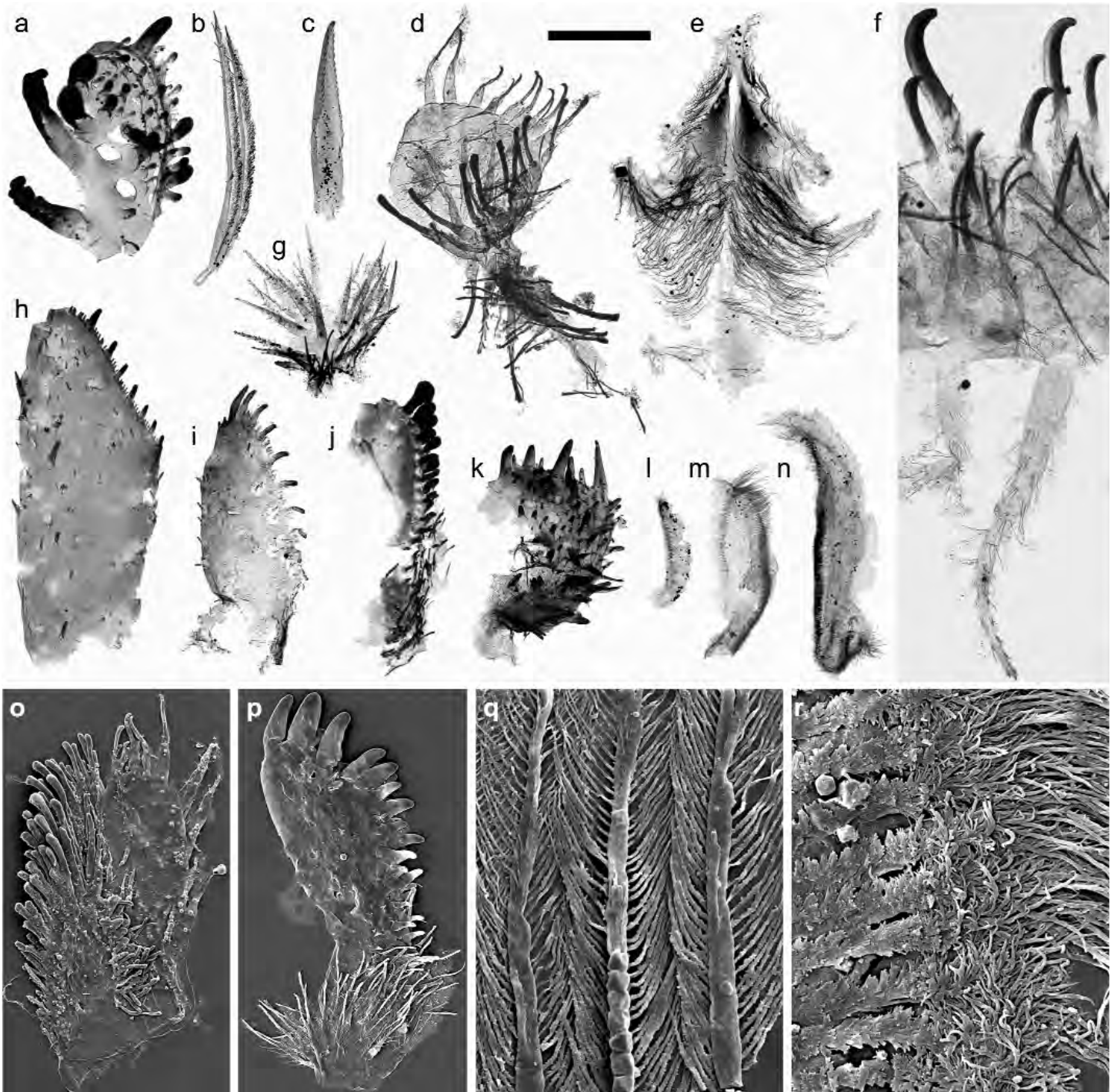
Figure 6. Carbonaceous crustacean cuticles from the O-35 assemblage, Colville Hills biota (Bele O-35 at 1351 m; Lower Cambrian *Bonnia-Olenellus* Zone). Among the various appendage fragments are lobes bearing either robust spines (a, h–k, o, p) or more delicate associations of scraping setae (d, f), as well as various disarticulated spines and setae (b, c, g), probable labrums (e), mandibular molar surfaces (l–n), and filter plates (q). Images o–r are scanning electron micrographs; note the crystals of diagenetic pyrite that lie on and within the cuticular projections. Scale bars: a, d, e, i. 100 μm; b, c, g, h, j–n. 200 μm; f. 40 μm; o. 130 μm; p. 110 μm; q. 16 μm; r. 10 μm. GSC specimen numbers: a) 135513; b) 135514; c) 135515; d) 108964; e) 109201; f) 34928; g) 135516; h) 34933; i) 34932; j) 34939; k) 34940; l) 34934; m) 135517; n) 34935; o) 34947; p) 34946; q) 135518; r) 34936.

lophotrochozoan phylogeny and the emergence of modern-type molluscs and annelids (Scheltema et al. 2003; Eibye-Jacobsen 2004; Butterfield 2006).

A small number of specimens in the Colville Hills biota apparently represent the feeding structures of early lophotrochozoans (Fig. 7b–f). Some can be assigned to a radula-like apparatus of a type known from the Early Cambrian Mahto Formation of Alberta (Butterfield 2008) and the Middle Cambrian Bright Angel Shale of Arizona (Strother et al. 2004). A single articulated array of seven 'boot-shaped
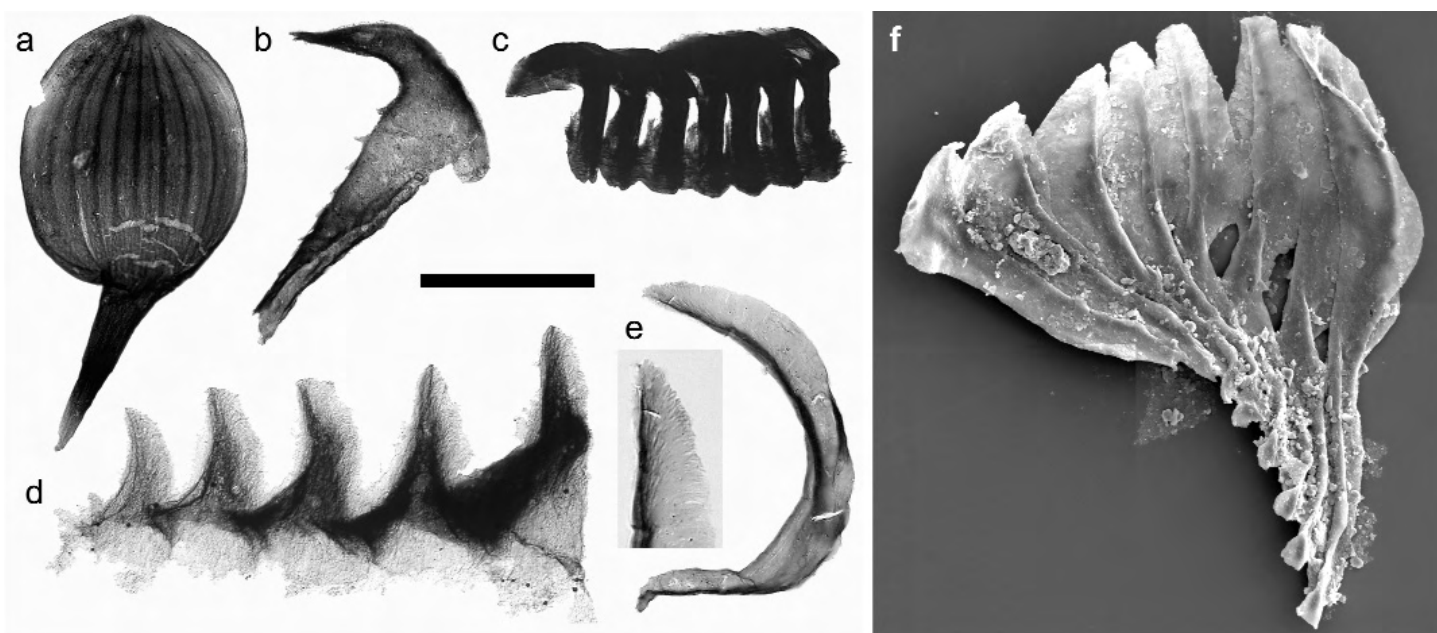
Figure 7. Sclerites and possible feeding structures of lophotrochozoans from the O-35 assemblage, Colville Hills biota (Bele O-35 at 1351 m; Lower Cambrian *Bonnia-Olenellus* Zone). a) Sclerite of *Wiwaxia* (GSC 108957); b, c) probable elements of a radula-like feeding apparatus (GSC 135519; 135520); d) possible lophotrochozoan 'jaw' (GSC 135521); e, f) probable isolated blade (e, GSC 135522) comparable to elements of the feeding apparatus of *Odontogriphus*, and articulated array (f, GSC 135523, scanning electron micrograph). The detail in (e) shows the internal fibrous microstructure. Scale bars: a. 200 µm; b–d. 100 µm; e. 50 µm (inset 30 µm); f. 40 µm.

elements' (Fig. 7c) is the most obviously comparable specimen (see Butterfield 2008, fig. 1), but there are also two recurved structures, one with secondary spination (Fig. 7b), that are similar to the 'spinose elements' of the Mahto assemblage (see Butterfield 2008, fig. 6). These specimens would be difficult to interpret without reference to the much larger Mahto sample, but can now be recognised as among the earliest radulas on record.

Two further specimens from the O-35 assemblage deserve attention as possible lophotrochozoan 'jaws'. The first is at least superficially jaw-like in that it consists of a jagged array of five robust, conical size-graded 'teeth' (Fig. 7d). A lophotrochozoan affinity is hinted at by the construction of the teeth from apically directed fibres, which is suggestive of secretion by microvilli (see Butterfield 2008). By contrast, the second specimen is interpreted on the basis of its specific morphology as well as its general characteristics. It consists of a fan-shaped array of eight partially imbricating elements, each of which expands from a narrow base into a paddle- or leaf-shaped blade with a thickened longitudinal axis

(Fig. 7f). Possible examples of similar but isolated blades from the O-35 sample ($n = 3$) have been viewed using transmitted light and reveal an underlying fibrous construction (Fig. 7e), consistent with lophotrochozoan-type secretion. Indeed, there are similarities in outline and microstructure to particular extracellular 'tough parts' in living polychaete annelids, including the fans of abdominal chaetae in various sabellids (although the Mount Cap elements are not fused proximally; cf. Knight-Jones and Fordy 1979, figs. 52–68), and the 'maxillary plates' of certain dorvilleids (ignoring the marginal serrations; cf. Tzetlin and Purschke 2005, fig. 10F, G). However, the closest comparisons are with the feeding apparatuses of *Wiwaxia* and *Odontogriphus* as they appear in articulated Burgess Shale macrofossils (see Butterfield 2006; Caron et al. 2006, 2007), which exhibit two (sometimes three) transverse 'tooth rows' of imbricating blade-like elements. The Mount Cap array conceivably represents one half of one such tooth row, based on its similar number of elements and their pattern of shape and length variation. Similarities in the finer scale character-

istics of the 'teeth', in so far as they can be resolved in the Burgess Shale macrofossils, include the variably rounded or truncated shape of the broad end, and the thickened longitudinal axis (compare the *Odontogriphus* specimen in Caron et al. 2007, fig. 1B). If a genuine relationship exists between the Mount Cap microfossils and their apparent macroscopic counterparts, there is clear potential for a newly detailed understanding of the feeding apparatus in *Wiwaxia* and *Odontogriphus*. This would greatly clarify the phylogenetic significance of these pivotal early lophotrochozoans (see Caron et al. 2006, 2007; Butterfield 2006).

THE MOUNT CAP COMPARED TO OTHER BST *LAGERSTÄTTEN*

The Mount Cap Formation is notable for extending the known geographic, temporal and palaeoenvironmental scope of Burgess Shale-type preservation. It contains the most northerly occurrence of BST macrofossils in Canada, and stands apart from the cluster of localities in the southern Canadian Rockies (e.g. Collins et al. 1983; Copeland 1993; Butterfield 2000;

Johnston et al. 2009; Caron et al. 2010). As well as being geographically distinct, the Mount Cap partly lies within the latest Early Cambrian (latest Series 2), an interval that contains comparatively few BST occurrences worldwide, in contrast to the dense sampling both above and below (e.g. Hagadorn 2002; Zhu et al. 2006). Furthermore, the comparatively shallow, intracratonic setting of the Mount Cap contrasts with the deeper water, shelf-edge settings of the Burgess Shale and many other BST sites (e.g. Conway Morris 1989).

That said, BST macrofossils are comparatively rare in the Mount Cap and fall within the more recalcitrant end of the preservational spectrum, which is dominated by biomineralizing forms and heavily cuticularized body parts such as claws (anomalocaridids) and carapaces (e.g. *Isoxys*). Comparable remains occur, often abundantly, in the Burgess Shale and at many other localities worldwide (e.g. Hagadorn 2002). Similarly, macroscopic fecal pellets/bromalites are documented from a number of Cambrian deposits in North America, Australia and China (see Conway Morris and Robison 1988; Nedin 1999; Vannier and Chen 2005). In contrast, the Mount Cap microfossils from both outcrop and subsurface horizons are truly exceptional in terms of preservational quality and paleobiological significance.

Comparisons across an increasing sample of carbonaceous microfossil assemblages from Cambrian marine mudrocks (e.g. Butterfield 2008; Harvey 2010; Harvey et al. in press) suggest that the particular value of the Mount Cap lies in a combination of favourable early diagenesis and quiescent post-depositional history. For example, acid-extractable specimens from the Burgess Shale include a comparatively low diversity of animal remains (Butterfield 1990; Gostlin 2006) and rather amorphous fecal pellets (Robbins et al. 1985), and are mostly fragmentary, blackened and brittle – a reflection of their associated greenschist-grade metamorphism (Butterfield et al. 2007). In contrast, assemblages from the Middle Cambrian Kaili Formation of south China (Harvey et al. in press) and the Early Cambrian

Forteau Formation of western Newfoundland (Harvey 2010, and unpublished data) are less thermally altered and contain a greater variety of recoverable microfossils, including Little Bear-type remains of chancelloriid sclerites and hyolithid helens. These specimens, however, lack the finest-scale features of their Mount Cap counterparts and are notably rare, which points to constraints in early diagenesis (see Harvey et al. in press). A closer comparison to Mount Cap-type preservation is provided by the crustacean cuticles recently discovered in the Earlie/Deadwood Formation (Middle to Late Cambrian) of Saskatchewan (Harvey et al. 2010). Even so, the O-35 assemblage remains unequalled in terms of abundance and anatomical diversity.

Through detailed taphonomic analysis of assemblages in the Burgess Shale and elsewhere, it is becoming clear that the original expression of BST fossils was predominantly carbonaceous (e.g. Butterfield et al. 2007; Gaines et al. 2008). At most localities, however, the carbon has been secondarily reduced through metamorphism and/or oxidative weathering (Lin and Briggs 2010), with the loss of both resolvable detail and recoverable microfossils. In this light, the value of the Mount Cap lies in its exceptional and exceptionally *unaltered* taphonomy, which reveals the contrasting strengths and biases of macro- vs. microscopic preservation and thus a distinct perspective on Cambrian paleobiology.

ACKNOWLEDGEMENTS

REFERENCES

Aitken, J.D., Macqueen, R.W., and Usher, J.L., 1973, Reconnaissance studies of Proterozoic and Cambrian stratigraphy, Lower Mackenzie River area (Operation Norman), District of Mackenzie: Geological Survey of Canada Paper, v. 73-9, p. 1-178.

Budd, G.E., 2008, Head structure in upper stem-group euarthropods: Palaeontology, v. 51, p. 561-573.

Butterfield, N.J., 1990, A reassessment of the enigmatic Burgess Shale fossil *Wiwaxia corrugata* (Matthew) and its relationship to the polychaete *Canadia spinosa* Walcott: Paleobiology, v. 16, p. 287-303.

Butterfield, N.J., 1994, Burgess Shale-type fossils from a Lower Cambrian shallow-shelf sequence in northwestern Canada: Nature, v. 369, p. 477-479.

Butterfield, N.J., 2000, The oldest? and the youngest? Burgess Shale assemblages in North America, Jasper National Park, Alberta, Canada (abstract): Geological Society of America, Abstracts, v. 32, p. 301.

Butterfield, N.J., 2001, Cambrian food webs, in Briggs, D.E.G. and Crowther, P.R., eds., Palaeobiology II: Blackwell Science Ltd., Malden, MA, p. 40-43.

Butterfield, N.J., 2003, Exceptional fossil preservation and the Cambrian explosion: Integrative and Comparative Biology, v. 43, p. 166-177.

Butterfield, N.J., 2006, Hooking some stem-group "worms": fossil lophotrochozoans in the Burgess Shale: Bioessays, v. 28, p. 1161-1166.

Butterfield, N.J., 2008, An Early Cambrian radula: Journal of Paleontology, v. 82, p. 543–554.

Butterfield, N.J., and Nicholas, C.J., 1996, Burgess Shale-type preservation of both non-mineralizing and 'shelly' Cambrian organisms from the Mackenzie Mountains, northwestern Canada: Journal of Paleontology, v. 70, p. 893-899.

Butterfield, N.J., Balthasar, U., and Wilson, L.A., 2007, Fossil diagenesis in the Burgess Shale: Palaeontology, v. 50, p. 537-543.

Caron, J.-B., Scheltema, A., Schander, C., and Rudkin, D., 2006, A soft-bodied mollusc with radula from the Middle Cambrian Burgess Shale: Nature, v. 442, p. 159-163.

Caron, J.-B., Scheltema, A., Schander, C., and Rudkin, D., 2007, Reply to Butterfield on stem-group 'worms': fossil lophotrochozoans in the Burgess Shale: Bioessays, v. 29, p. 200-202.

Caron, J.-B., Gaines, R.R., Mángano, M.G., Streng, M., and Daley, A.C., 2010, A new Burgess Shale-type assemblage from the 'thin' Stephen Formation of the southern Canadian Rockies: Geology, v. 38, p. 811-814.

Collette, J. H., and Hagadorn, J. W., 2010, Three-dimensionally preserved arthropods from Cambrian Lagerstätten of Quebec and Wisconsin: Journal of Paleontology, v. 84, p. 646-667.

Collins, D., 2009, Misadventures in the Burgess Shale: Nature, v. 460, p. 952-

953.

Collins, D., Briggs, D., and Conway Morris, S., 1983, New Burgess shale fossil sites reveal Middle Cambrian faunal complex: Science, v. 222, p. 163-167.

Conway Morris, S., 1989, The persistence of Burgess Shale-type faunas: Implications for the evolution of deeper-water faunas: Transactions of the Royal Society of Edinburgh, v. 80, p. 271-283.

Conway Morris, S., and Robison, R.A., 1988, More soft-bodied animals and algae from the Middle Cambrian of Utah and British Columbia: University of Kansas Paleontological Contributions, v. 112.

Copeland, M.J. 1993. *Anomalocaris* [of unknown affinity] and *Tuzoia* [a possible arthropod] from the Lower Cambrian Eager Formation near Cranbrook, British Columbia: Geological Survey of Canada, Bulletin, v. 444, p. 1-5.

Dixon, J., and Stasiuk, L.D., 1998, Stratigraphy and hydrocarbon potential of Cambrian strata, Northern Interior Plains, Northwest Territories: Bulletin of Canadian Petroleum Geology, v. 46, p. 445-470.

Eibye-Jacobsen, D., 2004, A re-evaluation of *Wiwaxia* and the polychaetes of the Burgess Shale: Lethaia, v. 37, p. 317-335.

Gaines, R.R., Briggs, D.E.G., and Zhao, Y., 2008, Cambrian Burgess Shale-type deposits share a common mode of fossilization: Geology, v. 36, p. 755-758.

Gostlin, K.E., 2006, Sedimentology and palynology of the Middle Cambrian Burgess Shale: Unpublished PhD thesis, University of Toronto, 245 p.

Hagadorn, J.W., 2002, Burgess Shale-type localities: The global picture, in Bottjer, D.J., Etter, W., Hagadorn, J.W. and Tang, C.M., eds., Exceptional Fossil Preservation: A Unique View on the Evolution of Marine Life: Columbia University Press, New York, p. 91-116.

Harvey, T.H.P., 2010, Carbonaceous preservation of Cambrian hexactinellid sponge spicules: Biology Letters, v. 6, p. 834-837.

Harvey, T.H.P., and Butterfield, N.J., 2008, Sophisticated particle-feeding in a large Early Cambrian crustacean: Nature, v. 452, p. 868-871.

Harvey, T.H.P., Velez, M., and Butterfield, N.J., 2010, Microfossil evidence for diverse macroscopic crustaceans in the middle Cambrian Earlie Formation of Saskatchewan (abstract): Palaeontological Association Annual Meeting 2010, Palaeontological Association Newslet-

ter, v. 75, p. 52.

Harvey, T.H.P., Ortega-Hernández, J., Lin, J.-P., Zhao, Y., and Butterfield, N.J., in press, Burgess Shale-type microfossils from the middle Cambrian Kaili Formation, Guizhou Province, China: Acta Palaeontologica Polonica, doi: 10.4202/app.2011.0028.

Hou, X.-G., and Bergström, J., 1997, Arthropods of the Lower Cambrian Chengjiang fauna, southwest China: Fossils and Strata, v. 45, p. 1-116.

Johnston, K.J., Johnston, P.A., and Powell, W.G., 2009, A new, Middle Cambrian, Burgess Shale-type biota, *Bolaspidella* Zone, Chancellor Basin, southeastern British Columbia: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 277, p. 106-126.

Knight-Jones, P., and Fordy, M.R., 1979, Setal structure, functions and interrelationships in Spirorbidae (Polychaeta, Sedentaria): Zoologica Scripta, v. 8, p. 119-138.

Lin, J.-P., and Briggs, D.E.G., 2010, Burgess Shale-type preservation: A comparison of naraoiids (Arthropoda) from three Cambrian localities: Palaios, v. 25, p. 463-467.

Maas, A., Braun, A., Dong, X.-P., Donoghue, P.C.J., Müller, K.J., Olempska, E., Repetski, J.E., Siveter, D.J., Stein, M., and Waloszek, D., 2006, The 'Orsten' – more than a Cambrian Konservat-Lagerstätte yielding exceptional preservation: Palaeoworld, v. 15, p. 266-282.

Mus, M.M., and Bergström, J., 2007, Skeletal microstructure of helens, lateral spines of hyolithids: Palaeontology, v. 50, p. 1231-1243.

Nedin, C., 1999, *Anomalocaris* predation on nonmineralized and mineralized trilobites: Geology, v. 27, p. 987-990.

Porter, S.M., 2008, Skeletal microstructure indicates chancelloriids and halkieriids are closely related: Palaeontology, v. 51, p. 865-879.

Pugh, D.C., 1993, Subsurface geology of pre-Mesozoic strata, Great Bear River map area, District of Mackenzie: Geological Survey of Canada Memoir 430, 137 p.

Robbins, E.I., Porter, K.G., and Haberyan, K.A., 1985, Pellet microfossils: Possible evidence for metazoan life in Early Proterozoic time: Proceedings of the National Academy of Sciences of the United States of America, v. 82, p. 5809-5813.

Scheltema, A.H., Kerth, K., and Kuzirian, A.M., 2003, Original molluscan radula: Comparisons among Aplacophora, Polyplacophora, Gastropoda, and the Cambrian fossil *Wiwaxia corrugata*:

Journal of Morphology, v. 257, p. 219-245.

Serié, C., Bergquist, C.L., and Pyle, L.J., 2009, Seventeen measured sections of Cambrian Mount Clark and Mount Cap formations, northern Mackenzie Mountains and Franklin Mountains, Northwest Territories: Geological Society of Canada, Open File 6148, p. 1-38, 37 figures.

Strother, P., Wood, G.D., Taylor, W., and Beck, J., 2004, Middle Cambrian cryptospores and the origin of land plants: Memoirs of the Association of Australasian Palaeontologists, v. 29, p. 99-113.

Tzetlin, A., and Purschke, G., 2005, Pharynx and intestine: Hydrobiologia, v. 535/536, p. 199-225.

Vannier, J., and Chen, J.-Y., 2005, Early Cambrian food chain: New evidence from fossil aggregates in the Maotianshan Shale biota, SW China: Palaios, v. 20, p. 3-26.

Walossek, D., 1999, On the Cambrian diversity of Crustacea, in Schram, F. R. and von Vaupel Klein, J. C., eds., Crustaceans and the Biodiversity Crisis: Proceedings of the Fourth International Crustacean Congress 1998, v. 1, Brill, Leiden, p. 3-27.

Wielens, J.B.W., von der Dick, H., Fowler, M.G., Brooks, P.W., and Monnier, F., 1990, Geochemical comparison of a Cambrian alginite potential source rock, and hydrocarbons from the Colville/Tweed Lake area, Northwest Territories: Bulletin of Canadian Petroleum Geology, v. 38, p. 236-245.

Wilson, L., 2004, Using guano as a tool in unravelling Cambrian palaeoecology (abstract): Palaeontological Association Annual Meeting 2004, Palaeontological Association Newsletter, v. 57, p. 192-193.

Zhu, M.-Y., Babcock, L.E., and Peng, S.-C., 2006, Advances in Cambrian stratigraphy and paleontology: Integrating correlation techniques, paleobiology, taphonomy and paleoenvironmental reconstruction: Palaeoworld, v. 15, p. 217-222.

The Geological Society
serving science & profession

Lyell Collection
Geological Society publications online

New developments for 2012

GEOFACETS.

The Society is collaborating with Elsevier to launch a Lyell Collection module on Geofacets. Selected titles will be available on Geofacet's searchable database of georeferenced geological maps that enables geoscientist working in the early stages of upstream exploration to assess a region's or basin's geological characteristics.

- Intuitive search features designed for geoscientists
- Map overlays
- Access to thousands of georeferenced maps
- Links to associated articles
- For further information please contact sales@geolsoc.org.uk

Special Publication archives

Online archives of the first 300 volumes of the Geological Society's Special Publications are now available for sale on a one-off, perpetual access basis. Prices include a 10% discount for those purchasing the full archive (volumes 1–300)

New titles

Two new archival titles will be launched and made available to Lyell Collection Complete subscribers at no additional charge.

- Transactions of the Edinburgh society
- Transactions of the Glasgow society

What is the Lyell Collection?

Launched in 2007 the Lyell Collection is an online collection comprising the Society's journal titles, Special Publications and key book series. Cutting edge science sits alongside important historical material, all captured and presented to the highest electronic standards and benefiting from the extensive functionality of HighWire Press' H20 platform.

With 240 000 peer-reviewed pages, 25 000 articles and 1000 volumes, the Lyell Collection is an invaluable tool for the researcher and student alike.

- Full text in HTML and PDF format
- Actively linking to cited references
- Free public access to alerts, search functions and abstracts
- Selected open access articles
- Hosted by Highwire Press

The Geological Society

The Geological Society of London was founded in 1807 and is the UK national society for geosciences, with over 10 000 members. It is a global leader in Earth science publishing, dedicated to providing a high-quality service throughout the world.

Lyell Collection for libraries 2012: content and prices

TITLE	2012 Content	Access options	UK price £*	RoW price £*	RoW price US$*
Lyell Collection Complete	All content	Online	£3,661	£3,889	$7,778
		Online + Print	£4,119	£4,375	$8,750
		Online + Special Publications Print**	£3,911	£4,139	$8,278
Special Publications	360+ volumes	Online	£2,158	£2,250	$4,499
		Online + Print	£2,427	£2,531	$5,061
Engineering Geology Special Publications	25+ volumes	*Available as part of Lyell Collection Complete only*			
Memoirs	36+ volumes	*Available as part of Lyell Collection Complete only*			
Petroleum Geology Conference Series	4 volumes	*Available as part of Lyell Collection Complete only*			
Journal of the Geological Society	1845 to current	Online	£842	£935	$1,871
		Online + Print	£948	£1,052	$2,105
Quarterly Journal of Engineering Geology and Hydrogeology	1967 to current	Online	£399	£447	$893
		Online + Print	£449	£502	$1,005
Geochemistry: Exploration, Environment, Analysis	2001 to current	Online	£215	£243	$487
		Online + Print	£242	£274	$548
Petroleum Geoscience	1995 to current	Online	£361	£361	$722
		Online + Print	£406	£406	$813
Scottish Journal of Geology	1965 to current	Online	£200	£200	$400
		Online + Print	£225	£225	$450
Proceedings of the Yorkshire Geological Society	1837 to current	Online	£162	£162	$324
		Online + Print	£183	£183	$365
Journal of Micropalaeontology	1991 to current	Online	£184	£184	$368
		Online + Print	£207	£207	$413
Transactions of the Geological Society	1811 to 1856	*Available as part of Lyell Collection Complete only*			
Transactions of the Edinburgh Geological Society	1870 to 1963	*Available as part of Lyell Collection Complete only*			
Transactions of the Glasgow Geological Society	1863 to 1965	*Available as part of Lyell Collection Complete only*			
Special Publications Archive					
Archive 1	Volumes 1–100	Online	£2,500	£2,500	$5000
Archive 2	Volumes 101–200	Online	£2,500	£2,500	$5000
Archive 3	Volumes 201–300	Online	£2,500	£2,500	$5000
Archive 1 - 3	Volumes 1–300	Online	£6,750	£6,750	$13,500

*VAT rate as applicable at the time of invoicing – please see website for current VAT rates for UK and EU subscribers. **The archives will be hosted on the Lyell Collection, and are not available for local hosting. There will be no ongoing maintenance or access charge. Prices are for single sites only. Please apply for multi-site and consortial pricing.

To order the Lyell Collection or individual journal titles, or request further information or a free trial, please contact:

In UK and Europe: Email: geologicalsociety@accucoms.com Telephone: +31 71 524 7630
In Korea: Email: jkim1@ebsco.com Telephone: 82-2-598-2571 (ext. 230)
In Australian and New Zealand: Email: dviollet@ebsco.com Telephone: +61 7 5453-7675
In South America: Email: info@dotlib.com Telephone: +55 (21) 3431-3430

In USA and Canada: Email: geologicalsociety@pcgplus.com Telephone: +1 617 395 4065
In Japan: Email: kobayashi@ebsco.co.jp Telephone: +81 (0)3 5327 5273
In Taiwan, Hong Kong, Macau, SE Asia: Email: salestw@ebsco.com Telephone: +886 2 8786 0601
All other regions: Email: sales@geolsoc.org.uk Telephone: +44 (0)1225 445046

bp

Foundation Sponsors

For more information visit: www.lyellcollection.org