

Soft-bodied biota from the middle Cambrian (Drumian) Rockslide Formation, Mackenzie Mountains, northwestern Canada

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Abstract.—A new Burgess Shale-type Lagerstätte is described from the middle Cambrian (Series 3, Drumian) Rockslide Formation of the Mackenzie Mountains, Northwest Territories, Canada. The Rockslide Formation is a unit of deeper water ramp to slope, mixed carbonate, and siliciclastic facies deposited on the northwestern margin of Laurentia. At the fossil-bearing locality, the unit onlaps a fault scarp cutting lower Cambrian sandstones. There it consists of a succession of shale and thick-laminated to thin-bedded lime mudstone, calcareous sandstone, and greenish-colored calcareous mudstone, overlain by shallower water dolostones of the Avalanche Formation, which is indicative of an overall progradational sequence. The Rockslide Formation is of similar age to the Wheeler and Marjum formations of Utah, belonging to the Bolaspidella Biozone. Only two 1 m thick units of greenish mudstone exhibit soft-bodied preservation, with most specimens coming from the lower interval. However, the biota is common but not as diverse as that of other Lagerstätten such as the Burgess Shale in its type area. The shelly fauna is dominated by the hyolith *Haplophrentis carinatus* Matthew, 1899 along with sparse linguliformean brachiopods, agnostoid arthropods, and ptychoparioid trilobites. The nonmineralized biota includes the macrophytic alga Margaretia dorus Walcott, 1911, priapulid worms, and the carapaces of a number of arthropods. The arthropods belong to Isoxys mackenziensis n. sp., Tuzoia cf. T. guntheri Robison and Richards, 1981; Branchiocaris? sp., Perspicaris? dilatus Robison and Richards, 1981; and bradoriids, along with fragments of arthropods of indeterminate affinities. The style of preservation indicates that most soft parts underwent complete biodegradation, leaving just the more resistant materials such as chitinous arthropod cuticles. The range of preservation and similarity to the coeval biotas preserved in Utah suggests that the composition of this Lagerstätte is probably representative of the community living on the relatively deep-water ramp or slope during middle Cambrian time in Laurentia. This would argue that the extraordinary diversity of the Burgess Shale at Mount Field is anomalous.

Introduction

Biotas exhibiting Burgess Shale-type (BST) preservation have been reported from the Cambrian and Ordovician of most continents and are critical for the understanding of the early evolution of life, because they conserve a greater diversity beyond typical shelly biotas (e.g., Briggs et al., 1994; Edgecombe and Legg, 2013; Caron et al., 2014). Not only do these important deposits open a window that does not exist under normal fossilization conditions, but the degree of complexity of the fossil lineages also suggests that evolution of several main branches of life was extremely rapid, but there is debate as to whether it began prior to or during the earliest Cambrian (e.g., Dohrmann et al., 2013; Erwin and Valentine, 2013; Landing et al., 2013; Lee et al., 2013).

BST deposits pose several fundamental questions, as soft body preservation is exceptional in earth history but does seem to be more common in the early Paleozoic. The nature of the BST taphonomic phenomenon is still controversial and several ideas have been suggested (e.g., Allison, 1988; Butterfield, 1995; Butterfield et al., 2007; Gaines et al., 2012). Another question is to what degree the different BST Lagerstätten represent a typical benthos of the early Paleozoic. Depending on the deposit the biota varies in composition, with only the Burgess Shale in the vicinity of Mount Field, its type area, exhibiting a truly high diversity (e.g., Briggs et al., 1994; Lieberman, 2003; Caron and Jackson, 2008; Edgecombe and Legg, 2013).

Here we present a new Lagerstätte in the Rockslide Formation of the Mackenzie Mountains of northwestern Canada. It is approximately the same age as the Wheeler and Marjum formations of Utah (Drumian stage, *Bolaspidella* Biozone) and, occurring in greenish mudstone, is similar in lithology to the 'phyllopod bed' of the Burgess Shale (Gabbott et al., 2010).

In addition to the hyoliths, linguliformean brachiopods, agnostoids and ptychoparioid trilobites, the soft-bodied fauna is dominated by bivalved arthropods along with priapulids and macrophytic algae, representing a biota similar to that of the Wheeler and Marjum formations. The purpose of this paper is to describe the hyoliths and soft-bodied components of the Rockslide Formation fauna and offer a comparison with similar Lagerstätten.

Geology and fossil locality

The Rockslide Formation is a regionally extensive, relatively deep-water middle Cambrian unit in the Mackenzie Mountains

(Fig. 1; Fritz, 1979; Pratt, 1989). It ranges in age from the *Plagiura–Poliella* Biozone to late *Bolaspidella* or *Lejopyge laevigata* Biozone (Gabrielse et al., 1973). It was deposited on the west-facing continental slope flanking the Selwyn Basin and ultimately the Panthalassic Ocean (Fig. 2; Fritz et al., 1991). The slope was probably seaward of a carbonate platform that has since been planed off. On the other side of the Mackenzie Arch, in the eastern Mackenzie Mountains and Mackenzie River valley, the lower part of the Rockslide Formation is correlative with intrabasinal shales of the upper Mount Cap Formation. To the north, it grades into the Hess River Formation, a thick, deep-water package deposited in the Misty Creek embayment (Cecile, 1982; Chevrier and Turner, 2013).

The new Lagerstätte is located near the headwaters of the Ravens Throat River and was discovered by BRP in 1983, and further collections were made in 1998 and 2004, and by JK in 2012. The Rockslide Formation in this area is about 175 m thick and is a succession of shales that grade upwards into interbedded shale and lime mudstone, and thence to thin-bedded lime mudstone (Fig. 3). It overlies a thin unit of shallow-subtidal limestone and dolomite belonging to the lower Cambrian Sekwi Formation, which in turn rests abruptly on shallow-marine sandstones of the Ediacaran to lower Cambrian (Terreneuvian) Backbone Ranges Formation. At this locality, the Rockslide Formation is gradationally overlain by shallower water dolomites belonging to the Avalanche Formation, which are succeeded by shallow-water limestones and dolomites of the upper Cambrian Broken Skull Formation (Gabrielse et al., 1973; Gordey and Anderson, 1993). To the west, the Rockslide Formation is overlain by deep-water limestones of the Rabbit kettle Formation (Pratt, 1992; Gordey and Anderson, 1993).

At the Ravens Throat River locality, the Rockslide Formation onlaps a syndepositional fault scarp cutting the Backbone Ranges Formation (Fig. 4.1). The thin unit belonging to the Sekwi Formation has dropped down and rotated on this normal fault. A change in dip at 19 m above the base of the Rockslide Formation suggests another phase of movement on the fault. The fault scarp is about 750 m north of the ridge that comprises section 19 of Gabrielse et al. (1973) which is unfaulted (Pratt, pers. obs.). Faulting is also absent at the type section 50 km to the east (section 16 of Gabrielse et al., 1973). The fault can be traced to the mountainside across the valley to the north of the Lagerstätte locality. It is likely listric in nature (cf. Collom et al., 2009; K. Johnston et al., 2009) and it probably a localized feature, forming an inclined surface cut into the gentle slope and broadly U-shaped in plane view.

There are two approximately 1-m-thick units that exhibit the distinctive lithology containing soft-bodied preservation, 134 m and 162 m above the top of the Sekwi Formation respectively, with the lower one yielding virtually all of the fossils that were recovered during excavation. Agnostoids and trilobites indicate this interval belongs to the *Bolaspidella* Biozone (Series 3, Drumian). It is therefore younger than the Burgess Shale is but approximately correlative with the Marjum and Wheeler formations of the Great Basin of Utah. The Burgess Shale is of middle Cambrian (Series 3, Stage 5) age, within the *Bathyuriscus–Elrathina* Biozone. Robison and Babcock (2011) placed *Elrathina* Resser, 1937 in synonymy with *Ptychoparella* Poulsen, 1927 but for the time being the traditional biozone name is retained.

Because the exposure is located on a steep cliff (Fig. 4.2), most specimens were collected systematically from the scree slope below it, comprising an area that covers about 1500 m². The host facies is a laminated, light greenish-colored, slightly calcareous mudstone. X-ray diffraction analysis indicates that is composed of quartz, chlorite, calcite, and dolomite. There are interbedded lenses of lime mudstone; scour surfaces and crosslamination are absent. This lithology has not been encountered at the type section of the Rockslide Formation to the east (Gabrielse et al., 1973; Pratt, pers. obs.) or in sections to the west and north (Pratt, pers. obs.). It appears to be localized perhaps in a depression that persisted long after movement of the synsedimentary fault.

Systematic paleontology

The fossils were photographed under water using a Nikon D80 camera with a 60 mm Nikkor macro lens. Latex casts were made of molds and dusted with ammonium chloride. Because the original specimens are mostly dark greenish-gray in color and similar to the host mudstone, photographic images were manipulated in Adobe Photoshop for optimal tone and contrast.

Specimens are housed in the paleontological collection of the Royal Tyrrell Museum, Drumheller, Alberta, Canada (TMP).

Kingdom Animalia Linnaeus, 1758 Phylum Arthropoda von Siebold, 1848

Remarks.—The name Arthropoda is correctly attributed to von Siebold (Hegna et al., 2013). The higher-level taxonomy of Cambrian bivalved arthropods is problematic. Early views considered most species to be crustaceans, whereas studies that are more recent indicate that many belong to the most basal arthropod taxa (Stein, 2010; Legg et al., 2012, 2013; Legg and Caron, 2014). For this reason, the higher-level affiliations of the arthropod genera in the Rockslide Formation are left open.

> Class, Order, and Family uncertain Genus *Isoxys* Walcott, 1890

Type species.—Isoxys chilhoweanus Walcott, 1890, by original designation.

Other species.—Isoxys acutangulus Walcott, 1908; I. carbonelli Richter and Richter, 1927; I. longissimus Simonetta and Delle Cave, 1975; I. communis Glaessner, 1979; I. auritus Jiang, 1982 (in Luo et al. 1982); I. paradoxus Hou, 1987; I. bispinatus Cui, 1991 (in Huo et al. 1991); I. zhurensis Ivantsov, 1990; I. volucris Williams, Siveter and Peel, 1996; I. elongatus Luo and Hu, 1999 (in Luo et al. 1999); I. curvirostratus Vannier and Chen, 2000; I. wudingensis Luo and Hu, 2006 (in Luo et al. 2006); I. minor Luo et al., 2008; I. glaessneri García-Bellido et al. 2009; I. shandongensis Wang et al. 2010; I. granulus Yuan, Peng and Zhao, 2011; I. mackenziensis n. sp.

Diagnosis.—See García-Bellido et al. (2009).



Figure 1. Location of the Ravens Throat River locality (asterix; 63°10'N, 127° 55'W), Mackenzie Mountains, northwest territories, Canada: (1), regional map; (2), topographic map.



Figure 2. Regional cross-section across the Mackenzie Mountains (modified from Aitken et al., 1973).

Occurrence.—China, Australia, Siberia, Europe, Laurentia (including Greenland), lower and middle Cambrian, Series 2 and 3, Stages 3–5 and Drumian.

Remarks.—Isoxys species are known from all major BST deposits of late early and early middle Cambrian age and some are known from their soft tissues in addition to the carapace (García-Bellido et al., 2009). The different species have usually been distinguished based on carapace shape although in general individual valves are sub-oval in outline, tapering anteriorly, and vary in the relative widths of the posterior and anterior ends of the valve and in the length of the anterolateral and posterolateral spines. Intraspecific variation and sexual dimorphism, however, may be present (Fu et al., 2013). Despite widespread occurrence and soft-tissue detail, higher-level taxonomic relationships are still unclear (Legg and Vannier, 2013).

Isoxys mackenziensis new species Figure 5.1–5.6

Holotype.—One complete laterally compressed valve (TMP 2013.101.0038).

Material.—Two complete and five partial valves in lateral view (TMP 2013.101.0030, 2013.101.0038–2013.101.0043).

Diagnosis.—Isoxys with elongated carapace, anterior wider than posterior; ratio of length to maximum width about 1:4. Dorsal line with dorsally directed flexure; anterolateral and posterolateral spines short with respective spine to carapace length ratios of 1:7 and 1:10.5.

Description.—The valve is elongate ovate in outline, the anterior wider than the posterior. The ratio of length to width about

is 1:4. The largest specimen is 85 mm long and 22 mm wide, whereas the smallest is 30 mm long and 8 mm wide; maximum width occurs at about one-third the total length from the anterior end as measured along the dorsal hinge. The dorsal hinge is nearly straight but has a gentle, dorsally directed flexure at about one-third the length from the anterior end. Each valve has an anterolateral and posterolateral spine. The anterior spine is shorter, with the longest 10 mm in length and a maximum thickness of about 2 mm at the base. The posterior spine is longer, with the longest 15 mm in length and a maximum thickness of about 1.5 mm. The dorsal surface is smooth.

Etymology.—After the Mackenzie Mountains.

Occurrence.—Rockslide Formation, Ravens Throat River area, Mackenzie Mountains, Northwest Territories, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone.

Remarks.-The valve of Isoxys mackenziensis n. sp. differs from those of I. chilhoweanus, I. acutangulus, I. zhurensis, I. auritus, I. glaessneri, I. carbonelli, I. curvirostratus, I. communis, I. wudingaspis, I. minor, I. volucris and I. bispinatus by being more slender, in that it is narrower and more elongated. In contrast to these species, the posterior end is also narrower and the dorsal hinge has a dorsally directed flexure that is lacking in other species. It differs from I. longissimus and I. paradoxus by having shorter anterolateral and posterolateral spines. The valves of the new species are larger in comparison with the other described species but this is not taken as diagnostic at present. A fragmentary specimen belonging to Isoxys was recovered from older strata in the Mount Cap Formation exposed on the east side of the Mackenzie Arch (Butterfield and Nicholas, 1996). It has a longer and stouter posterolateral spine.

Avalanche Fm. Guzhangian 150 Series 3 Drumian Rockslide Formation middle Cambrian 100 ? 50 5 Stage 0 Sekwi Fm. Series 2 lower Cambrian Ranges Fm. Backbone Terren. lithology silty shale with dolomite **BST** fossils silty shale limestone . . . black shale sandstone

Figure 3. Generalized stratigraphy of the Rockslide Formation in the Ravens Throat river area (upper part of section and contact with overlying Avalanche Formation is not exposed). Star indicates main fossil bed.

Order Canadaspidida Novozhilov *in* Orlov, 1960 Family Perspicaridae Briggs, 1978 Genus *Perspicaris* Briggs, 1977 *Type species.—Canadaspis dictynna* Simonetta and Delle Cave, 1975, by original designation.

Other species.—Perspicaris recondita Briggs, 1977; P.? dilatus Robison and Richards, 1981; P.? ellipsopelta Robison and Richards, 1981.

Diagnosis.—See Briggs (1977).

Occurrence.—Laurentia, middle Cambrian, Series 3, Stage 5 and Drumian.

Remarks.---Most of the taxonomically important features used to differentiate Canadaspis and Perspicaris and their species are based on the soft tissues (Briggs, 1977; Lieberman, 2003). Therefore, Perspicaris? dilatus and P.? ellipsopelta are questionably assigned to the genus because these species are based only on isolated carapaces. Perspicaris differs by possessing true, elongate lateral telson process-bearing spines, whereas Canadaspis has a pair of spinose projections on the ventrolateral margin of the telson. In addition, the eyes of Perspicaris are larger. However, the valves are closely similar and may well be indistinguishable. Lieberman (2003), however, suggested that in Perspicaris, the maximum width is further posterior, the anterior and posterior processes are larger, the muscle scar is more ventrally located, and the height-to-length ratio is smaller. Consequently, we assign most valves in the Rockslide Formation to Perspicaris? rather than Canadaspis.

> *Perspicaris? dilatus* Robison and Richards, 1981 Figures 6.1–6.9, 7.1–7.6, 9.4, 9.6, 11.3, 11.4, 11.6

1981 *Perspicaris? dilatus* Robison and Richards, p. 4, pl. 1, fig. 4, pl. 2, figs. 5–7.

2003 ?Perspicaris dilatus; Lieberman, p. 677, fig. 1.2.

Material.—24 valves in lateral view and one complete carapace in dorsal view (TMP 2013.101.0001–2013.101.0015).

Diagnosis.—Perspicaris? with valve sub-ovate in outline, posterior process larger than anterior process.

Description.—Valve is sub-ovate in outline; posterior portion moderately wider than anterior, with maximum width is about two-thirds along the length of the hinge line from the anterior margin. Maximum length is 65 mm and maximum width is 45 mm, with the smallest 11 mm in length and 8 mm in width. The posterior process is slightly larger than the anterior process, and exhibits an angle of about 100° . Hinge line is straight. The circular muscle scar is inconspicuous in larger valves; on one smaller specimen (Fig. 7.5, 7.6) it is located close to the anterior margin and three times its diameter from the hinge line.

Occurrence.—Comet Shale Member, Pioche Formation, Nevada, middle Cambrian, Series 3, Stage 5, *Eokochaspis nodosa* Biozone; Wheeler Formation, Utah, middle Cambrian, Series 3, Drumian, *Ptychagnostus atavus* Biozone; Rockslide Formation, Ravens Throat River area, Mackenzie Mountains,



Figure 4. The outcrop area near the headwaters of the Ravens Throat River: (1), panorama looking west; (2), left side of outcrop showing the synsedimentary fault (black line; formations labeled; stratigraphic position of fossil-bearing unit shown by arrow); (3), close-up of the fossiliferous thin-bedded mudstone (hammer circled).

Northwest Territories, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone.

Remarks.—The specimens from the Ravens Throat River area are conspecific with *P.? dilatus* and not *P.? ellipsopelta* based on the outline of the valves (Fig. 8) with the maximum width being more posterior, the relatively larger posterior process, and the more anterior location of the muscle scar. However, these are rather small differences and it is possible that larger collections may show that *P.? ellipsopelta* is a junior synonym. Some isolated soft-tissue fragments (Fig. 8.2, 8.3) might represent *P.? dilatus*.

One specimen (Fig. 6.3) shows some simple, seemingly non-branching burrows under the valve. These are preserved as grooves, indicating that they were originally empty tubes, probably from post-mortem bioturbation. They are similar to those described by Mángano et al. (2012; see also Robison and Richards, 1981, pl. 1, fig. 4; Chlupáč and Kordule, 2002).

> Order and Family uncertain Genus *Branchiocaris* Briggs, 1976

Type species.—Protocaris pretiosa Resser, 1929, by original designation.

Diagnosis.—See Briggs (1976).

Occurrence.—Laurentia and China, middle Cambrian, Series 3, Stage 5 and Drumian; possibly China, Series 2, Stage 4.

Remarks.—Branchiocaris contains four species and an additional one with question: the type species from the Burgess Shale, three species from the Malong and Guanshan biotas (Honjingshao and Wulongqing formations respectively, lower Cambrian, Series 2, Stage 4), and *B.? yunnanensis* Hou, 1987 from the Chengjiang biota (Yu'anshan Member, Helinpu Formation, China, lower Cambrian, Series 2, Stage 3). The last is known from the carapace only, hence the questionable assignment.

Branchiocaris? sp. Figures 9.1, 9.5, 11.1, 11.5

Material.—One carapace in dorsal view (TMP 2013.101.0022) and four valves in lateral view (TMP 2013.101.21a, b, TMP 2013.101.0045, TMP 2013.101.0046).

Description.—The valve is semicircular in outline; maximum length is 25 mm and maximum width is 13 mm. The anterior process is slightly smaller than the posterior process, and both are relatively small. The anterior muscle scar is indistinct in one specimen (Fig. 9.1) and is located close to anterior margin.



Figure 5. *Isoxys mackenziensis* n. sp. from the Rockslide Formation, middle Cambrian, Ravens Throat River area, Mackenzie Mountains: (1), lateral view of valve and holotype (TMP 2013.101.0038); (2), lateral view of valve (TMP 2013.101.0040); (3), lateral view of valve (TMP 2013.101.0042); (4), lateral view of valve (TMP 2013.101.0039); (5), lateral view of valve (TMP 2013.101.0041); (6), lateral view of valve (TMP 2013.101.0043; surface scratched). Scale bars represent 5 mm.

Occurrence.—Rockslide Formation, Ravens Throat River area, Mackenzie Mountains, Northwest Territories, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone.

Remarks.—Six valves are placed in *Branchiocaris*? because of their semicircular outline, but the absence of soft-tissue attributes necessitates open nomenclature. In the better-preserved valves, the anterior and posterior processes are smaller than in previously described specimens of *B. pretiosa*, which occurs in strata of about the same age (Briggs, 1976; Briggs and Robison, 1984, fig. 9.1–9.4).

Order Tuzoida Simonetta and Delle Cave, 1975 Family Tuzoiidae Raymond, 1935 Genus *Tuzoia* Walcott, 1912

Type species.—Tuzoia retifera Walcott, 1912, by original designation.

Other species.—Tuzoia burgessensis Reeser, 1929; T. canadensis Resser, 1929; T. polleni Resser, 1929; T. dunbari Resser, 1929; T. praemorsa Resser, 1929; T. manchuriensis Resser and Endo in Endo and Resser, 1937; T. nitida Resser and Howell, 1938; T. australis Glaessner, 1979; T. guntheri Robison and Richards, 1981; *T. bispinosa* Yuan and Zhao, 1999; and questionably *T.*? *parva* Walcott, 1912; *T.*? *peterseni* Robison and Richards, 1981.

Diagnosis.—See Vannier et al. (2007).

Occurrence.—Laurentia, China and South Australia, lower and middle Cambrian, Series 2 and 3, Stages 3–5 and Drumian.

Remarks.—Species belonging or possibly belonging to *Tuzoia* are reported from all major BST deposits and is the largest bivalved arthropod known from the Cambrian, with a length up to 180 mm. Only a few specimens with soft body preservation are known (Vannier et al., 2007) and the carapace outline, the arrangement of the spines and spacing in between them, and the valve convexity are used to differentiate species.

Tuzoia cf. *T. guntheri* Robison and Richards, 1981 Figure 9.2, 9.3

- cf. 1981 *Tuzoia guntheri* Robison and Richards, p. 13, pl. 7, figs. 1, 2; pl. 8, figs. 4, 5; pl. 9, fig. 2.
- cf. 1991 Tuzoia guntheri; Robison, p. 84, fig. 7.1.



Figure 6. *Perspicaris? dilatus* from the Rockslide Formation, middle Cambrian, Ravens Throat River area, Mackenzie Mountains: (1), lateral view of valve (TMP 2013.101.0009; cut by two oblique fractures); (2), lateral view of valve (TMP 2013.101.0002; flipped horizontally); (3), lateral view of valve with burrows beneath (latex cast dusted with ammonium chloride; TMP 2013.101.0002); (4), close-up of 3, showing pustular ornament on valve exterior; (5), lateral view of valve (TMP 2013.101.0006; cut by oblique fracture); (7), latex cast of 8 dusted with ammonium chloride; (8), lateral view of small valve (TMP 2013.101.0010); (9), lateral view of weathered partial valve (TMP 2013.101.0011). Scale bars represent 5 mm.

cf. 2003 *Tuzoia guntheri*; Lieberman, p. 679, fig. 1.3.
cf. 2007 *Tuzoia guntheri*; Vannier et al., p. 462, figs. 16, 25.4, 26, 31.

Material.—One partial valve in lateral view (TMP 2013.101.0047).

Diagnosis.—See Vannier et al. (2007).



Figure 7. *Perspicaris? dilatus* from the Rockslide Formation, middle Cambrian, Ravens Throat River area, Mackenzie Mountains: (1), dorsal view of butterflied carapace (TMP 2013.101.0001; surface scratched); (2), same as *1* (dusted with ammonium chloride); (3), lateral views of three complete and one partial valves (TMP 2013.101.0004); (4), lateral views of one complete and two partial valves (latex cast dusted with ammonium chloride; TMP 2013.101.0004); (5), lateral interior view of complete valve, with muscle scar (TMP 2013.101.0008); (6), lateral interior view of complete valve, with muscle scar (latex cast dusted with ammonium chloride; TMP 2013.101.0008; flipped horizontally). Scale bars represent 5 mm.

Description.—The specimen is 60 mm long, representing a fragment of an ovate valve about 75 mm long. It has four spines on the posterior margin; the most dorsal is 4 mm long, the mid-posterior spine is 6 mm long, the posteroventral spine is 17 mm long, and the ventral spine is 2 mm long. Exterior surface is covered by somewhat irregular reticulate pattern of fine grooves surrounding slightly convex interiors. The diameter of

the cells is between 0.5 to 2 mm, with the smaller ones towards the periphery.

Occurrence.—Comet Shale Member, Pioche Formation, *Eokochaspis nodosa* Biozone, middle Cambrian, Series 3, Stage 5, Nevada; Marjum Formation, Utah, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone; Rockslide Formation,



Figure 8. Variation in outline of *Perspicaris? dilatus* specimens from the Rockslide Formation, middle Cambrian, Ravens Throat River area, Mackenzie Mountains. (1), TMP 2013.101.0006; (2), TMP 2013.101.0002; (3), TMP 2013.101.0005; (4), TMP 2013.101.0009; (5), TMP 2013.101.0010; (6), TMP 2013.101.0001; (7), TMP 2013.101.0008; (8), TMP 2013.101.0007; (9), TMP 2013.101.0004. Specimens are drawn to scale and anterior is oriented to the left. Scale bar represents 10 mm.

Ravens Throat River area, Mackenzie Mountains, Northwest Territories, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone.

Remarks.—*Tuzoia* cf. *T. guntheri* from the Ravens Throat River area has a posterior arrangement of four spines of short to moderate length, which fits the holotype from the Marjum Formation. As the fragment does not preserve the hinge, dorsal spine, and anterior or posterior processes, the assignment is tentative.

Order Bradoriida Raymond, 1935 Family uncertain bradoriid genus and species indet. 1 Figure 10.1, 10.2

Material.—One carapace (TMP 2013.101.0044).

Description.—Carapace postplete; valve elongate ovate in outline, 16 mm long and 10 mm wide. Possible anterodorsal node present. The anterior margin is transverse. Narrow marginal ridge extends from anterior end of hinge around at least to posterolateral margin and possibly to posterior end of hinge. Exterior surface probably smooth.

Occurrence.—Rockslide Formation, Ravens Throat River area, Mackenzie Mountains, Northwest Territories, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone.

Remarks.—The specimen is flattened and the left valve is slightly dorsoventrally compressed. The outline, presence of narrow marginal ridge, simple convexity and large size of the valve show similarities with species of *Anabarochilina* Abushik, 1960, such as material from the Marjum and Week formations of Utah assigned to *A. cf. A. australis* Hinz-Schallreuter, 1993 (Siveter and Williams, 1997). It is possible that the Rockslide specimen has a similar anterodorsal node but this cannot be determined with certainty.

bradoriid genus and species indet. 2 Figure 10.3

Material.—One valve (TMP 2013.101.0024).

Description.—Valve almost semicircular in outline, 10 mm long and 8 mm wide. Hinge is probably short. Anterior process is short; posterior process unknown. Narrow marginal ridge



Figure 9. Arthropods from the Rockslide Formation, middle Cambrian, Ravens Throat River area, Mackenzie Mountains: (1), *Branchiocaris*? sp., lateral view of valve (TMP 2013.101.0045); (2), *Tuzoia* cf. *T. guntheri*, lateral view of partial valve (TMP 2013.101.0047); (3), *Tuzoia* cf. *T. guntheri*, close-up of 2 showing reticulate ornament on valve exterior surface (TMP 2013.101.0047); (4), small valve of *Perspicaris*? *dilatus* in lateral view (TMP 2013.101.0007); (5), *Branchiocaris*? sp., lateral view of valve (TMP 2013.101.0046); (6), *Perspicaris*? *dilatus*, lateral view of partial valve with broken hinge, possibly two valves overlying each other (TMP 2013.101.0048). Scale bars represent 5 mm.



Figure 10. Bradoriids from the Rockslide Formation, middle Cambrian, Ravens Throat River area, Mackenzie Mountains: (1), bradoriid genus and species indet. 1, complete carapace in dorsal view (TMP 2013.101.0044); (2), latex cast of *1* dusted with ammonium chloride; (3), bradoriid genus and species indet. 2, valve in lateral view (TMP 2013.101.0024). Scale bar represents 5 mm.



Figure 11. Fragmentary arthropods from the Rockslide Formation, middle Cambrian, Ravens Throat River area, Mackenzie Mountains: (1), *Branchiocaris*? sp. lateral views of two disarticulated valves (TMP 2013.101.0021); (2), *Tuzoia* sp. lateral view of partial valve with ornament of cuspate ridges along margin (TMP 2013.101.0018); (3), *Perspicaris? dilatus* lateral view of valve (TMP 2013.101.0019); (4), *Perspicaris? dilatus* lateral view of valve (TMP 2013.101.0017); (5), *Branchiocaris*? sp. butterflied carapace (TMP 2013.101.0022); (6), lateral view of valve, possibly *Perspicaris? dilatus* (TMP 2013.101.0016). Scale bars represent 5 mm.

extends from anterior end of hinge around posterolateral margin and possibly to posterior end of hinge. Exterior surface probably smooth. *Occurrence.*—Rockslide Formation, Ravens Throat River area, Mackenzie Mountains, Northwest Territories, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone.



Figure 12. Arthropod fragments from the Rockslide Formation, middle Cambrian, Ravens Throat River area, Mackenzie Mountains: (1,2), arthropod genus and species indet. 1: (1), posterior portion of thorax with lateral telson process consisting of two processes in dorsal view (TMP 2013.101.0036); (2), posterior portion of thorax with lateral telson process in lateral view (TMP 2013.101.0035); (3), arthropod genus and species indet. 2, isolated lateral telson process (TMP 2013.101.0034); (4), arthropod genus and species indet. 3, possible biramous appendage consisting of endopod(?) and exopod(?) (TMP 2013.101.0037). Scale bars are 5 mm.

Remarks.—The semicircular outline, absence of anterodorsal node, and narrow marginal ridge are similar to *Liangshanella burgessensis* Siveter and Williams, 1997 from the Burgess Shale, but the Rockslide valve is some three times larger.

Class, Order, and Family uncertain arthropod genus and species indet. 1 Figure 12.1, 12.2

Material.—Two telsons, one preserved in dorsoventral view (TMP 2013.101.0036) and the other in lateral view with abdominal segments (TMP 2013.101.0035).

Description.—In dorsoventral view (Fig. 12.1), telson (and possible short abdominal somite) is 26 mm long and 9 mm wide. It consists of a pair of posteriorly directed, nearly straight to slightly inward-curving pair of lateral telson processes 20 mm in length, Base of the lateral telson process narrow then expanding abruptly, becoming elongated blade-like in outline.

In lateral view (Fig. 12.2), the telson and nine abdominal segments is 37 mm long and 13 mm wide. Abdominal segments are uniformly about 1 mm in length, transverse in outline, and terminate laterally to short, backward-curving spines. Lateral telson process projects from a rounded surface and is 13 mm long and slightly curved.

Occurrence.—Rockslide Formation, Ravens Throat River area, Mackenzie Mountains, Northwest Territories, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone.

Remarks.—The two specimens are considered to belong to the same taxon but represent different views. The telson of Perspicaris dictynna from the Burgess Shale has two wider lateral telson processes and there is a row of short marginal secondary spines (Briggs, 1977). By contrast, the telson of Canadaspis perfecta consists of a fringe of spines (Briggs, 1978, fig, 162; Lieberman, 2003). No telson belonging to Tuzoia has been described (Vannier et al., 2007). One small specimen from the Burgess Shale possesses a pair of narrow spines (Briggs, 1977, pl. 72, fig. 8). However, it is not clear if that specimen is a juvenile or belongs to a different arthropod group such as the Bradoriidae (Vannier et al., 2007). No soft tissues are known for P? dilatus but it is also possible that these specimens could belong to that species. On the other hand, the lateral telson processes are distinctly narrower than the lateral telson process of arthropod genus and species indet. 2 (Fig. 12.3). Another possibility is that it belongs to Branchiocaris, B. pretiosa from the Wheeler Formation is similar (Briggs et al., 2008), as are some specimens from the Burgess Shale (D. A. Legg, pers. obs.).

> arthropod genus and species indet. 2 Figure 12.3

Material.—One fragmentary telson preserving one lateral telson process (TMP 2013.101.0034).

Description.—The lateral telson process is a 20 mm long and 5 mm wide at its maximum. For most of its length it tapers



Figure 13. *Haplophrentis carinatus* from the Rockslide Formation, middle Cambrian, Ravens Throat River area, Mackenzie Mountains: (1), conch with operculum and helens (TMP 2013.101.0058); (2), conch with operculum and one helen (TMP 2013.101.0059); (3), conch (TMP 2013.101.0063); (4), conch (TMP 2013.101.0064); (5), conch with operculum and one helen (TMP 2013.101.0065); (6), conch with operculum (TMP 2013.101.0066); (7), conch with operculum and partial helen (TMP 2013.101.0067); (8), three conches (TMP 2013.101.0068a, b, c); (9), two conches, one possible juvenile specimen (TMP 2013.101.0070a, b); (10), two juxtaposed conches (TMP 2013.101.0071a, b); (11), conch (TMP 2013.101.0072). Scale bar represents 2 mm.



Figure 14. Priapulids from the Rockslide Formation, middle Cambrian, Ravens Throat River area, Mackenzie Mountains. Possible gut contents or residual soft tissues appear as dark patches. (1–3), priapulid genus and species indet. 1: (1), curved specimen, with partially extended proboscis to left (TMP 2013.101.0051); (2), coiled specimen, with anterior end at bottom (TMP 2013.101.0052); (3), coiled specimen, with anterior end at bottom (TMP 2013.101.0053); (4–6), priapulid genus and species indet. 2: (4), sinuous specimen, anterior ends unknown (TMP 2013.101.0055); (6), Elongated specimen (TMP 2013.101.0055); (6), Elongated specimen (TMP 2013.101.0056). Scale bar is 5 mm.

gently posteriorly, until close to it terminus where it tapers sharply to a blunt point.

Occurrence.—Rockslide Formation, Ravens Throat River area, Mackenzie Mountains, Northwest Territories, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone.

Remarks.—This lateral telson process differs from the narrower forms that have been assigned to *Canadaspis perfecta*, but it resembles those of *Perspicaris dictynna* Briggs, 1977 while lacking the marginal spines present in that species. Given the co-occurring carapaces, this lateral telson process could belong to either *P.? dilatus* or *Branchiocaris?* sp.

arthropod genus and species indet. 3 Figure 12.4

Material.—One fragment of a possible biramous appendage (TMP 2013.101.0037).

Description.—A slender 'anterior ramus' (exopod?) appears to be joined to a wider 'posterior ramus' (endopod?) forming an angle of about 30°. The former is straight and uniform in thickness, possibly segmented, terminating in a slightly wider, backward-curving 'claw'; it is 11 mm long and 1.5 mm at its widest point. The latter consists of a wide backward curving 'claw,' 10 mm long and 3 mm at its widest point. Broken lateral margin of the specimen is more or less transverse.

Occurrence.—Rockslide Formation, Ravens Throat River area, Mackenzie Mountains, Northwest Territories, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone.

Remarks.—The isolated specimen appears to be biramous but this could be coincidental overlapping of two separate objects. It resembles biramous appendages lacking the gills of trilobites, for example.

Phylum Mollusca Cuvier, 1797 Class Hyolitha Marek, 1963 Order Hyolithida Matthew, 1899 Family Hyolithidae Nicholson, 1872 Genus *Haplophrentis* Matthew, 1899

Type species.—Haplophrentis carinatus Matthew, 1899, by original designation.

Other species.—Haplophrentis reesei Babcock and Robison, 1988.

Diagnosis.—Hyolithid with weak, longitudinal, dorsomedial septum in conch. Lateral longitudinal sulci singly paired on dorsum and venter. One pair of curved helens. (Modified from Babcock and Robison, 1981).

Occurrence.—Laurentia, middle Cambrian, Series 3, Stage 5 and Drumian.

Remarks.—Haplophrentis broadly resembles *Hyolithes*, d'Eichwald (1840) and *Linevitus* Syssoiev, 1958, but differs from these and other hyolithids in having an inner dorsomedial





Figure 16. Relative abundance of specimens of metazoan taxa in all samples collected from the fossilifereous unit of the Rockslide formation (both in situ and from the scree slope), middle Cambrian, Ravens Throat River area, Mackenzie Mountains.

septum and longitudinal sulci on the dorsum and venter (Babcock and Robison, 1988).

Haplophrentis carinatus Matthew, 1899 Figure 13.1–13.11

- *Hyolithes carinatus* Matthew, p. 42, pl. 1, figs. 5a, b. *Haplophrentis carinatus*; Babcock and Robison, p. 15,
- fig. 7. [see for synonomy]
- 1994 *Haplophrentis carinatus*; Briggs et al., p. 113, fig. 62. cf. 2011 *Haplophrentis* cf. *carinatus*; Zhao et al., p. 112, figs.
- 114–118.
- cf. 2014 Haplophrentis cf. carinatus; Caron et al., p. 4, fig. 3.

Material.—66 specimens, some with associated operculum and helens (TMP 2013.101.0056–TMP 2013.101.0121).

Description.—Conch conical exhibits an apical angle about 25°. Average length without the ligula is 12.4 mm, the smallest being 6 mm and the longest 20 mm. Average width is 4.8 mm, the smallest being 2.5 mm and the largest 7 mm. The conical shield of the opercula has an apical angle of about 125°. Cardinal processes are 0.5–0.8 mm in length. Conch with fine, straight transverse growth lines; these are arcuate in the ligula and opercula. Line spacing varies: they are closer together near the apex, and the distance becomes uniform after about one-third the length of the conch. Helens are curved.

Occurrence.—Burgess Shale, southern British Columbia, middle Cambrian, Series 3, Stage 5, *Bathyuriscus–Elrathina* Biozone; Marjum and Wheeler formations, Utah, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone; Rockslide Formation, Ravens Throat River area, Mackenzie Mountains, Northwest Territories, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone.

Remarks.—Hyoliths are the most abundant elements in the fossiliferous beds, but most specimens are preserved as isolated conches. The specimens are assigned to *H. carinatus* based on the apical angle of the conch and the conical shield of the operculum. This species differs from *H. reesei* by its wider conch, larger apical angle, presence of faint longitudinal grooves on the dorsum, and stronger rugae on the operculum (Babcock and Robison, 1988).

Phylum Priapulida Théel, 1906 priapulid genus and species indet. 1 Figure 14.1–14.3

Material.—3 specimens (TMP 2013.101.0051–TMP 2013.101.0053).

Description.—Shape is curved or coiled into a single whorl; anterior portion is narrower than posterior. The longest specimen is 65 mm long and 6 mm at its widest point. Poorly preserved proboscis is partially extended in one specimen (Fig. 14.1).

Occurrence.—Burgess Shale, southern British Columbia, middle Cambrian, Series 3, Stage 5, *Bathyuriscus–Elrathina* Biozone; Marjum and Wheeler formations, Utah, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone; Rockslide Formation, Ravens Throat River area, Mackenzie Mountains, Northwest Territories, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone.

Remarks.—These specimens resemble *Ottoia prolifica* because they show the enlarged posterior region and the curved to coiled shape which is characteristic of this species when contracted. However, the preservation is such that other features are not discernible, especially the trunk annulation and details of the proboscis. Black carbonaceous films in the specimens may be remains of gut contents or residues from the soft tissues.

 Table 1. Occurrence of Ravens Throat River taxa in other western Laurentian Lagerstätten: Pioche Formation (series 3, stage 5); Burgess Shale (series 3, stage 5); Marjum Formation (series 3, Drumian); Wheeler Formation (series 3, Drumian).

Species of the Ravens Throat River Lagerstätte	Pioche Formation		Burgess Shale		Wheeler and Marjum Formations	
	Genus	Species	Genus	Species	Genus	Species
Isoxys mackenziensis Branchiocaris? sp. Perspicaris? dilatus Tuzoia cf. T. guntheri Haplophrentis carinatus Margaretia dorus	x x x x	$\begin{array}{c} x \\ x \\ \\ \\ \\ x \\ x \\ x \end{array}$		x x x 		

 $\sqrt{}$ = represented, x = not represented.

Figure 15. *Margaretia dorus* from the Rockslide Formation, middle Cambrian, Ravens Throat River area, Mackenzie Mountains: (1), partial branch (TMP 2013.101.0130); (2), partial branch (TMP 2013.101.0131); (3), branching specimen (TMP 2013.101.0132); (4), partial branch (TMP 2013.101.0133); (5), partial branch (TMP 2013.101.0134); (6), partial branch (TMP 2013.101.0135); (7), two partial branches (TMP 2013.101.0136); (8), partial branch (TMP 2013.101.0137); (9), partial branch (TMP 2013.101.0138); (10), partial branch (TMP 2013.101.0139); (11), partial branch (TMP 2013.101.0140). Scale bar is 10 mm.

The fossiliferous beds yield many poorly preserved, elongate objects visible as patchy dark films. These most likely belong to *Margaretia dorus* or worms, but identification is impossible.

priapulid genus and species indet. 2 Figure 14.4–14.6

Material.—3 specimens in lateral view (TMP 2013.101.0054– TMP 2013.101.0056).

Occurrence.—Rockslide Formation, Ravens Throat River area, Mackenzie Mountains, Northwest Territories, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone.

Remarks.—Poorly preserved specimens vary in width along the length of the trunk somewhat as in *Ottoia prolifica*, but although they are similar in size and two are sinuous in attitude, they are not coiled.

Kingdom Plantae Haeckel, 1866 Division Chlorophyta Reichenbach, 1834 Class Chlorophyceae Wille *in* Warming, 1884 Family Caulerpaceae Kützing, 1843 Genus *Margaretia* Walcott, 1931

Type species.—Margaretia dorus Walcott, 1931, by original designation.

Other species.—Margaretia chamblessi Waggoner and Hagadorn, 2004.

Diagnosis.—See Waggoner and Hagadorn (2004).

Occurrence.—Laurentia, middle Cambrian Series 3, stage 5 and Drumian.

Remarks.—Margaretia dorus and *M. chamblessi* differ in that the former exhibits more frequent anastomosis of the longitudinal fibers in the cortex, and the papillae are sparser in *M. chamblessi*.

Margaretia dorus Walcott, 1931 Figure 15.1–15.11

- 1931 Margaretia dorus Walcott, p. 2, pl. 1, figs. 1-6.
- 1988 *Margaretia dorus*; Conway Morris and Robison, p. 6, figs. 3, 4. [see for synonomy]
- 1994 Margaretia dorus; Briggs et al., p. 55, fig. 3.
- 2010 Margaretia dorus; Gaines and Droser, p. 653, fig. 5H
- 2012 *Margaretia dorus*; Handle and Powell, p. 306, fig. 2H, 4C–E, 6B–C.

Material.—74 partial specimens (TMP 2013.101.0130–TMP 2013.101.0203).

Diagnosis.—See Conway Morris and Robison (1988).

Description.—Thallus is large, branching, and more or less uniform in branch width. Average width is 7.8 mm, the smallest being 4 mm and the largest 15 mm. Branches extend from the trunk at right angles; branch shape varies from straight to tightly curved (equivalent to one branch width). Papillae are parallel to the axis in rows; they vary from elongate to oval to nearly circular. Most specimens are carbonaceous films but some preserve marked relief.

Occurrence.—Burgess Shale, southern British Columbia, middle Cambrian, Series 3, Stage 5, *Bathyuriscus–Elrathina* Biozone; Spence Shale member of the Langston Formation, Utah, middle Cambrian, Series 3, Stage 5, *Ptychagnostus praecurrens* Biozone; Marjum and Wheeler formations, Utah, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone; Rockslide Formation, Ravens Throat River area, Mackenzie Mountains, Northwest Territories, middle Cambrian, Series 3, Drumian, *Bolaspidella* Biozone.

Remarks.—Margaretia dorus is the only macrophytic alga present. It occurs in the lower fossiliferous unit and in thin beds up to 0.5 m above it, as well as being the only fossil recovered from the upper bed with soft-bodied preservation. The many poorly preserved elongate objects in the fossiliferous beds, if they belong to *Margaretia*, would indicate a greater abundance of these algae.

Discussion

The BST fossil-bearing greenish mudstones of the Rockslide Formation are interpreted to have been deposited below storm wavebase, because of their fine-grained composition and absence of erosional features and cross-lamination. The restriction of the fossils to two thin units in a succession of shales and lime mudstones suggests special, localized geochemical and sedimentological circumstances on the sea floor and maybe also in the water column at the time of deposition. It is at present uncertain if the taphonomic factors that led to softbodied preservation are comparable to those proposed for other Lagerstätten (e.g., Butterfield, 1995; Gaines et al., 2012). However, the quality of preservation does not match that in the Burgess Shale and some of the other Cambrian Lagerstätten. The soft tissues of the arthropods are not preserved and the priapulids show advanced decay. This suggests that biodegradation proceeded more or less normally on the sea floor or under shallow burial before ceasing.

The environmental setting of the Rockslide Formation at the Ravens Throat River locality bears some similarities to that of the Burgess Shale (e.g., Johnston et al., 2009), the lower Cambrian (Series 2, Stage 4) Sirius Passet locality in northern Greenland (Peel and Ineson, 2011) and the Wheeler and Marjum formations of Utah (Rees, 1986) because all are associated with syndepositional block faulting. The significance of this relationship is unclear in terms of its effect on the benthic ecology or the taphonomy of the soft-bodied components. Rare BST fossils have also been reported from strata coeval with and older than the Rockslide Formation that crop out in the Mackenzie River Valley to the east of the Mackenzie Arch (Butterfield, 1994; Butterfield and Nicholas, 1996; Harvey and Butterfield, 2011). These rocks were deposited in a shallow, intra-shelf basin (Dixon and Stasiuk, 1998). Chancelloriids exhibiting BST preservation also occur in the lower Cambrian Sekwi Formation (Randell et al., 2005).

Arthropods, namely carapace-bearing taxa, are represented by the highest diversity of forms. The most common species is *Perspicaris? dilatus*. So far, the carapaces have not been associated with soft-bodied parts, but isolated fragments likely belong to that species. Priapulids and macrophytic algae are also present, along with typical members of the shelly fauna of this age. Simple burrows are observed under some of the arthropod valves. In terms of simple relative abundance, the fauna is dominated by hyoliths (Fig. 16). These early molluscs often occur with their operculum and helens. The biota may represent a fairly typical benthic community of middle Cambrian age in the deeper water ramp or slope region of marginal Laurentia. However, there is an apparent absence of siliceous sponges, which are variably common elsewhere.

The Ravens Throat River Lagerstätte is similar to the BST deposits from the Great Basin. Not only is it of about the same age as the Wheeler and Marjum formations, but it also has several taxa in common with these units, as well as with the older Burgess Shale and Pioche Shale Lagerstätten (Table 1; e.g., Robison and Richards, 1981; Robison, 1991; Briggs et al., 1994, 2008; Lieberman, 2003). The dominance of arthropods over other groups is also observed in the Burgess Shale (e.g., Briggs et al., 1994; Caron and Jackson, 2008), the Chengjiang biota (Hou et al., 2004), and the Kaili biota (Zhao et al., 2005, 2011).

Conclusions

The new middle Cambrian Lagerstätte in the Rockslide Formation of the Mackenzie Mountains of northwestern Canada carries a shelly fauna consisting of common hyoliths, agnostoid arthropods and polymeroid trilobites, and scarce linguliformean brachiopods. It yields a soft-bodied fauna that includes a number of bivalved and other arthropods, especially species belonging to Isoxys, Perspicaris?, Tuzoia, Branchiocaris? and bradoriids, along with the macrophytic alga Margaretia and rare priapulids. Overall, the biota is similar in composition to the known Laurentian BST deposits of similar age in the Great Basin of southwestern U.S.A. Like the Burgess Shale and some other comparable Cambrian Lagerstätten, it is similarly associated with synsedimentary faulting in a deeper water depositional setting. One difference lies in the heterogeneity of the facies that comprise the Ravens Throat River section and the preservation of only the more robust components of its biotic elements restricted to two thin units. This locality affirms that the propensity for BST preservation was more widespread in Laurentia than hitherto understood.

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