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New records of Burgess Shale-type taxa from the middle Cambrian of Utah

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Abstract.—Cambrian strata of the Laurentian craton contain numerous examples of Burgess Shale-type faunas. Although displaying a more or less concentric distribution around the cratonal margin, most faunal occurrences are in present-day western North America, extending from the Northwest Territories to California. Nevertheless, the soft-bodied and lightly skeletalized fossils in most of these Lagerstätten are highly sporadic. Here, we extend knowledge of such Middle Cambrian occurrences in Utah with reports of four taxa. An arthropod from the Marjum Formation, *Dytikosicula desmatae* gen. et sp. nov., is a putative megacheiran. It is most similar to *Dicranocaris guntherorum*, best known from the younger Wheeler Formation, but differs primarily in the arrangement of pleurae and overall size. Along with a specimen of *?Yohoia* sp., a new species of *Yohoia*, *Y. utahana* sp. nov., is described. It differs from the type and only known species, *Y. tenuis*, principally in its larger size and shorter exopods; it is the first description of this genus from outside the Burgess Shale. A new species of a stem-group lophotrochozoan from the Spence Shale, *Wiwaxia herka* sp. nov., possesses a palisade of dorso-lateral spines that are more robust and numerous than the type species of *Wiwaxia*, *W. corrugata*. Another notable taxon is *Eldonia ludwigi* from the Marjum Formation, which is interpreted as a primitive ambulacrarian (assigned to the cambroernids) and a new specimen of the ?cnidarian *Cambrorhytium* from the Wheeler Shale is illustrated.

Introduction

The soft-bodied and lightly skeletalized fossils of the Burgess Shale-type biotas have had a profound impact on our understanding of the major radiations of the early metazoans, an event colloquially referred to as the Cambrian “explosion” (e.g., Conway Morris, 1998; Marshall, 2006). To date, only three occurrences are especially prolific. These are the type locality in British Columbia, Canada (and adjacent outcrops, see Collins et al., 1983), the Chengjiang localities around Kunming, Yunnan, China (e.g., Chen and Zhou, 1997; Zhang et al., 2008), and Sirius Passet, Peary Land, North Greenland (e.g., Conway Morris and Peel, 1995, 2008; 2010; Budd, 2011; Daley and Peel, 2010; Ineson and Peel, 2011; Peel and Ineson, 2011). This is not to say that other localities do not have very considerable potential: most notable in this respect are faunas from the Emu Bay Shale of South Australia (e.g., Paterson et al., 2010, 2011; Edgecombe et al., 2011) and in South China both the Kaili deposits from Guizhou, (e.g., Zhao et al., 2003, 2005; Lin, 2006; Yang et al., 2011) and new assemblages (Guanshan, Xiaoshiba) adjacent to Kunming (e.g. Hu et al., 2010; Yang et al., 2013).

Although these localities rightly enjoy the lion’s share of attention, in terms of present-day geography, the lower and middle Cambrian Burgess Shale-type faunas (broadly construed: Conway Morris, 1989; Butterfield, 1995) are widely distributed, with records from western Canada (e.g., Copeland, 1993;

Butterfield and Nicholas, 1996; Randell et al., 2005; Johnston et al., 2009; Caron et al., 2010; Kimmig and Pratt, 2015), eastern United States (e.g., Skinner, 2005; Schwimmer and Montante, 2007; Conway Morris and Peel, 2010), Russia (e.g., Repina and Okuneva, 1969; Friend et al., 2002; Ivantsov et al., 2005), Australia (e.g., Jago and Anderson, 2004; Ortega-Hernandez et al., 2010), Europe (e.g., Conway Morris and Robison, 1986; Chlupáč and Kordule, 2002; García-Bellido et al., 2011; Gámes Vintaned et al., 2011), and China (e.g., Steiner et al., 2012; Xiao et al., 2005; Zhang and Hua, 2005; Liu, 2013; Sun et al., 2013).

It remains the case, however, that in a significant number of these latter Burgess Shale-type localities, the quality of preservation may be impressive, but the range of material is relatively limited and has only been obtained as the result of intensive and protracted seasons of collecting. This applies, for example, to a series of localities in the western United States, most of which are in Utah. Outcrops in the Latham Shale (Gaines and Droser, 2002), Poleta Formation (English and Babcock, 2010), Pioche Formation (e.g., Webster et al., 2008), Spence Shale (e.g., Conway Morris and Robison, 1988; Liddell et al., 1997; Gaines and Droser, 2005; Garson et al., 2012), Wheeler Formation (e.g., Conway Morris and Robison, 1986; Gaines et al., 2005; Halgedahl et al., 2009; Stein et al., 2011), Marjum Formation (e.g., Gaines and Droser, 2010), and Weeks Formation (e.g., Bonino and Kier, 2010; Robison and Babcock, 2011; Lerosey-Aubril et al., 2013) have yielded a

series of Burgess Shale-type fossils. These include non-trilobite arthropods, priapulids, sponges and chancelloriids, as well as several taxa, notably the medusiform *Eldonia* and cataphract *Wiwaxia*, whose systematic positions have been more contentious. To the existing literature on these localities scattered across the Great Basin (e.g., Rigby, 1983; Gunther and Gunther, 1981; Briggs and Robison 1984; Robison, 1991; Conway Morris and Robison, 1986, 1988; Rigby et al., 1997; Waggoner and Hagadorn 2004; Briggs et al., 2005; Cartwright et al., 2007; Halgedahl et al., 2009; Moore and Lieberman, 2009; Conway Morris and Peel, 2010; Gaines and Droser, 2010) we now add some significant new finds. These include an articulated specimen of a new species of *Wiwaxia* (Spence Shale), arthropods in the form of *Dytikosicula desmatae* gen. et sp. nov. (Marjum Formation), as well as specimens of *?Yohioia* sp. and *Yohioia utahana* sp. nov. (Spence Shale), and a large specimen of *Eldonia* (Marjum Formation). In passing, we also draw attention to a specimen of the questionable cnidarian *Cambrorhytium* (Wheeler Formation).

Methods

Specimens were photographed with Canon 5D MkII and MkIII cameras (Canon U.S.A. Inc., Melville, NY) mounted on Leica MZ12.5 and MZ16 stereomicroscopes, either dry or under 70% ethanol, and in cross-polarized light using a ring light and/or low-angle illumination with polarizing filters, and a polarizing filter in front of the objective lens. For each specimen, several photographs were taken at different levels of focus and then stacked using Adobe Photoshop CS6 (Adobe Systems Inc., San Jose, CA) to ensure all parts of each specimen were in focus. For some larger specimens, a mosaic of photographs was taken and these were then merged using Photoshop (see Selden, 2014 for further details). Drawings were made using camera lucida attachments to the microscopes and digitized using iDraw 2.4 (www.indeco.com).

Systematic paleontology

Specimens are housed in the University of Kansas Natural History Museum, Lawrence, Kansas (KUMIP prefix) and the Sedgwick Museum, University of Cambridge (SM prefix).

Phylum Arthropoda von Siebold, 1848
Family Yohoiidae Henriksen, 1928
Genus *Yohioia* Walcott, 1912

Type species.—*Yohioia tenuis* Walcott, 1912.

Yohioia utahana new species
Figure 1.1–1.4

Diagnosis.—Relatively large (approximately 30 mm), tergites 10–13 bear tergopleurae, exopods short with large spines, and mostly covered by tergopleurae.

Description.—Large *Yohioia*, body length 30.9 mm (including telson, excluding great appendage); straight trunk; head shield with median smooth portion, and large lateral area with strongly

curved margins divided into three regions. Anterior border of median part of head shield expanded slightly anteriorly, beyond procurved line (Fig. 1.1, 1.2). Pair of eyes situated anteriorly beyond anterior margin of head shield. Great appendage consisting of proximal element emerging from beneath anterior head shield between eyes, extending downwards not beyond lateral edges of head shield, followed by distal element extending upwards. Trunk of 13 segments, increasing in length from approximately 1.0 mm (1), through approximately 1.5 mm (5–9) to approximately 2.0 mm (11–13), and telson. Tergites show slight posterior imbrication. Tergopleura of tergite 1 lobate, narrower (transversely) than other tergites, partly covered by posterior margin of head shield. Tergopleurae 2–9 lobate, with recurved anterior margin, curved tip, procurved posterior margin (Fig. 1.1, 1.2). Curvature of anterior and posterior margins increases posteriorly, so tergopleurae of more posterior tergites appear more swept back. Tergopleura 10 with recurved anterior margin, short pointed posterior angle. Tergopleurae 11–13 narrower (transversely), with short sharply pointed posterior angles. Trunk limbs with exopod and endopodal rami. At least 6 endopods, associated with trunk segments 1–5, 8 (Fig. 1.3, 1.4); exopods on trunk segments 1–9, not seen on segments 10–13. Endopods slender, at least distally where seen protruding from beneath head shield or tergopleurae, tapering distally. Exopods appear as fan of stout bristles, connected by organic material (?setules), curving backwards and downwards, extending only slightly beyond margins of tergopleurae. Telson spatulate, lineations on surface, straight posterior margin bearing zigzag pattern of short spines.

Holotype.—KUMIP 357406, only known specimen (collected by PMJ), part and counterpart.

Etymology.—After Utah, the state in which the specimen was found.

Occurrence.—Spence Shale Member, Langston Formation (Hintze, 1988, Chart 15), lower Middle Cambrian, polymerid *Glossopleura* Zone (Robison, 1976). Locality is about 35 m above base of Spence Shale, Miner's Hollow, Wellsville Mountain, Box Elder County, Utah.

Remarks.—Terminology follows Haug et al. (2012). It is not straightforward differentiating morphology from abiogenic marks in the matrix, such as with a scattering of darker patches, particularly near the anterior of the specimen. A suboval patch near the apex of the head shield resembles an eye. However, in cross-polarized light, the putative eye shows a slightly different coloration, indicating that the suboval patch is matrix. Similarly, matrix patches align with the endopods but these, too, are not thought to be part of the animal.

The body is laterally compressed. Anteriorly, however, the head region has rotated longitudinally. Previous reconstructions of *Yohioia* (Whittington, 1974; Haug et al., 2012) show the eyes to be near the top of the head shield, adjacent to the base of the lateral area of the head shield. In this specimen, the eye position is similarly adjacent to the base of the lateral area of the head shield, but the head shield extends further dorsally from the eye

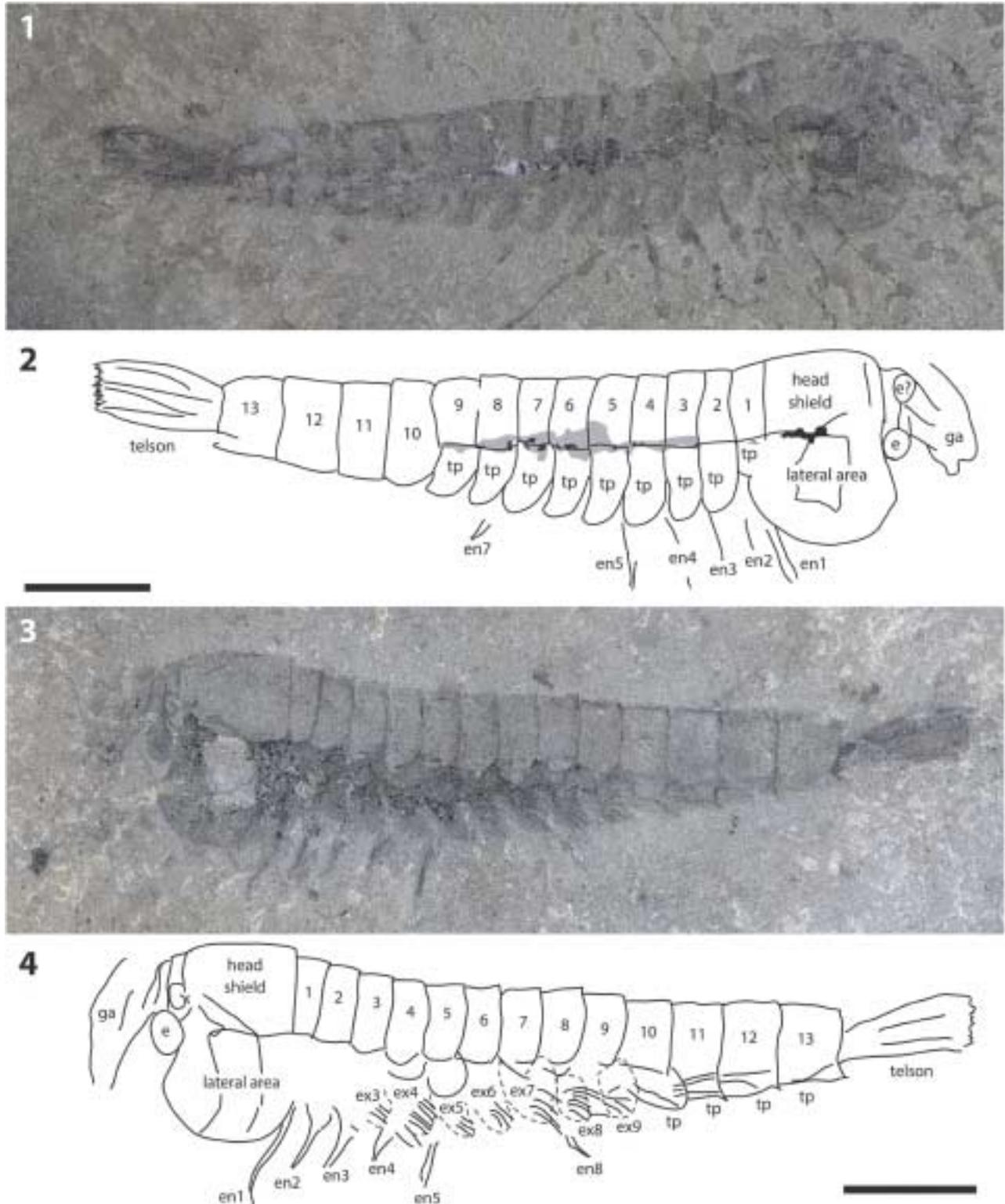


Figure 1. *Yohoia utahana* sp. nov., holotype, KUMIP 357406. (1) photograph of part; (2) interpretative camera-lucida drawing of part; (3) photograph of counterpart; (4) interpretative camera-lucida drawing of counterpart. e, eye; ex1, ex2, etc. exopods; en1, en2, etc., endopods; ga, great appendage; tp, tergopleura. Grey areas indicate possible gut trace; black shows black particles within possible gut (Fig. 1.2). Dashed lines on Figure 1.4 indicate outline of darker color representing organic material between exopod spines. Scale bars represent 5 mm.

than would be the case if it were strictly a lateral compression. At the opposite end of the animal, the telson also presents a dorso-ventral aspect, similarly suggesting a degree of rotation.

The body is straight with neither curvature nor a distinct bend which would indicate a tail region. In life, however, it was clearly flexible because adjacent tergites imbricate. Cephalic

appendages include a poorly preserved great appendage and a pair of eyes. With respect to the former the great appendage is poorly preserved, but appears to show a downward part emerging from the anterior of the head between the eyes, and beyond this an upward-sweeping part (the claw element). In the case of the eyes one is located between the great appendage and the head shield; the other eye is less obvious but on the part is superimposed on the base of the great appendage (Fig. 1.1, 1.2). Scattered black patches along the trunk (most obvious on segments 3–9) may be remains of the gut; the line of these coincides with the junction between the main part of each tergite and its tergopleura (Fig. 1.1, 1.2). A similar line of dark patches can be seen in the *Yohioia* specimens figured by Haug et al. (2012; fig. 3).

Interpretation of the tergopleurae and exopods is problematic. The part (Fig. 1.1, 1.2) shows lateral tergopleurae which extend at least the same distance from their junction with main tergite as the width of the latter. In contrast, in the type species the tergopleurae are relatively shorter than the large, flap-like structures that extend beyond the tergite edges and have been interpreted as exopods (Whittington, 1974; Haug et al., 2012). On the counterpart (Fig. 1.3, 1.4) radiating lines resemble the fringing setae of the exopods, but they are much sparser and stouter. Moreover, rather than forming a fringe they are almost completely covered by the tergopleurae. Thus, in the new species, the exopods are shorter than in *Y. tenuis* (see Haug et al., 2012, fig. 9). In *Y. utahana*, the tips of the tergopleurae do not extend beyond the lateral edge of the head shield, as do the ends of the radiating lines. The tergopleurae (in the part; Fig. 1.1, 1.2) seem, therefore, to be real, whereas the underlying radiating lines (in the counterpart, Fig. 1.3, 1.4) likely represent exopodal spines. On the counterpart (Fig. 1.3, 1.4), the matrix shows a darker hue between the exopodal spines (outlined in dashed lines on the drawing), which possibly represents organic material—perhaps masses of setules—connecting the exopodal spines.

Compared with the type and only known species of *Yohioia* (*Y. tenuis* Walcott, 1912), this is larger, with a body length of 30.9 mm. Length of tergites 3–5 (I1 of Haug et al., 2012) is 4.2 mm, length of the head shield (I2 of Haug et al., 2012) is 4.6 mm. Plotting I1/I2 (Fig. 2) on the graph of similar measurements for *Y. tenuis* (Haug et al., 2012, fig. 2) shows *Y. utahana* to lie well beyond the scatter of points, at more than twice the mean for both measurements of the type species. The lateral areas of the head shield show strongly curved margins, in which respect it differs from the type species, in which these lateral areas are subquadrate (Whittington, 1974, text-fig. 2; Haug et al., 2012). As in *Y. tenuis*, the lateral area is divided into three parts, and the trunk consist of 13 segments and a telson which is almost indistinguishable from that of *Y. tenuis* (Whittington, 1974).

Related genera (Stein et al., 2013) from the Lower Cambrian Chengjiang biota of China include *Fortiforceps* Hou and Bergström, 1997, which has somewhat similar exopods but lacks tergopleurae and has 20 tergites, and *Jianfengia* Hou, 1987, which has even more (22) tergites. On the other hand *Haikoucaris* Chen, Waloszek and Maas, 2004 has the same number of postcephalic tergites as *Yohioia* (13) and possibly similar exopods (albeit on all trunk segments), but lacks tergopleurae and has a distinct telson. *Yohioia* differs from all

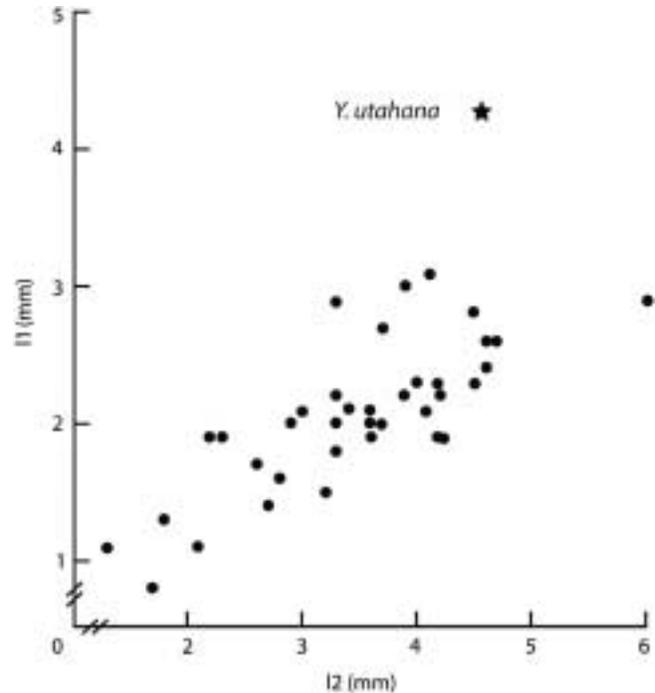


Figure 2. Scatterplot of lengths of tergites three to five (I1) versus length of head shield (I2) of: ● *Yohioia tenuis* Walcott, 1912, and ★ *Yohioia utahana* sp. nov. *Yohioia tenuis* data from Haug et al. (2012, fig. 2).

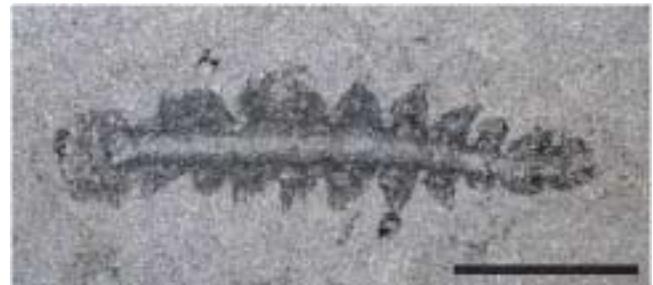


Figure 3. ?*Yohioia* sp., SM X.50206; photograph under ethanol. Scale bar represents 5 mm.

of these related genera in its distinctive head shield with the large, tripartite, lateral area, and spatulate telson composed of a single plate.

?*Yohioia* species indeterminate

Figure 3

Description.—Single specimen occurs in dorso-ventral aspect. Most obvious feature is trunk, with at least nine segments, and prominent tergopleurae (Fig. 3). Largest of these at mid-point, and decrease markedly in size toward the presumed posterior. Broad central strand may represent gut trace. It has slight relief, and may be sediment-filled. Alternatively (considering *Yohioia* is not known to have a sediment-filled gut), the specimen may have split at level of tergopleurae but below level of arched dorsum, revealing matrix beneath. Both ends of specimen indistinct, but presumed anterior (head shield) approximately quadrate. Opposite end smaller and appears to be approximately circular. No appendages preserved.

Material.—SM X.50206, collected by PMJ, part only.

Occurrence.—Spence Shale Member, Langston Formation, (Hintze, 1988, Chart 15), lower middle Cambrian, polymerid *Glossopleura* Zone (Robison, 1976). Locality is approximately 16 m above base of Spence Shale, as float, Miner's Hollow, Wellsville Mountain, Box Elder County, Utah.

Remarks.—Attribution to *Yohoia* (see Whittington, 1974) is provisional. Apart from size, its principal similarities are the prominent tergopleurae, and possibly the head-shield. Unlike *Yohoia*, however, the tergopleurae are prominent to the last (visible) trunk segment

Genus *Dytikosicula* new genus

Diagnosis.—As for the species.

Type species.—*Dytikosicula desmatae* new species.

Etymology.—Based on the Greek *dytikos* (west) and small dagger (*sicula*), and is a combined reference to both the geographical area and the recurved paratergal extensions.

Remarks.—This new taxon is similar to *Dicranocaris* (Briggs et al., 2008). Phylogenetic relationships of Cambrian arthropods

are not fully resolved but *Dicranocaris* appears to be a mega-cheiran (Ortega-Hernández et al., 2013; see also Hendricks and Lieberman, 2008).

Dytikosicula desmatae new species
Figures 4.1–4.2, 5.1–5.2

1981 ?*Molaria*-like trilobitomorph, Gunther and Gunther, pl. 48B.

1991 ?*Alalcomenaeus* cf. *cambricus* (Simonetta); Robison, p. 86, fig. 7.10.

2008 ?*Dicranocaris guntherorum* Briggs et al., p. 245, figs 5.4–9 [non figs. 5.1–3].

Diagnosis.—Subcircular head shield and trunk with at least six tergites, all with prominent pleurae. It differs from *Dicranocaris* by trunk segment one bearing pleura, and pleurae more arcuate. Head shield similar, but dorsal outline more circular.

Description.—Single specimen (Figs. 4, 5) preserved in dorsal aspect, lacks posterior section. Head shield suboval in outline, with smooth margins and gently concave posterior margin abutting first thoracic segment. No evidence for eyes. Trunk undifferentiated, but bears six rather prominent pleural

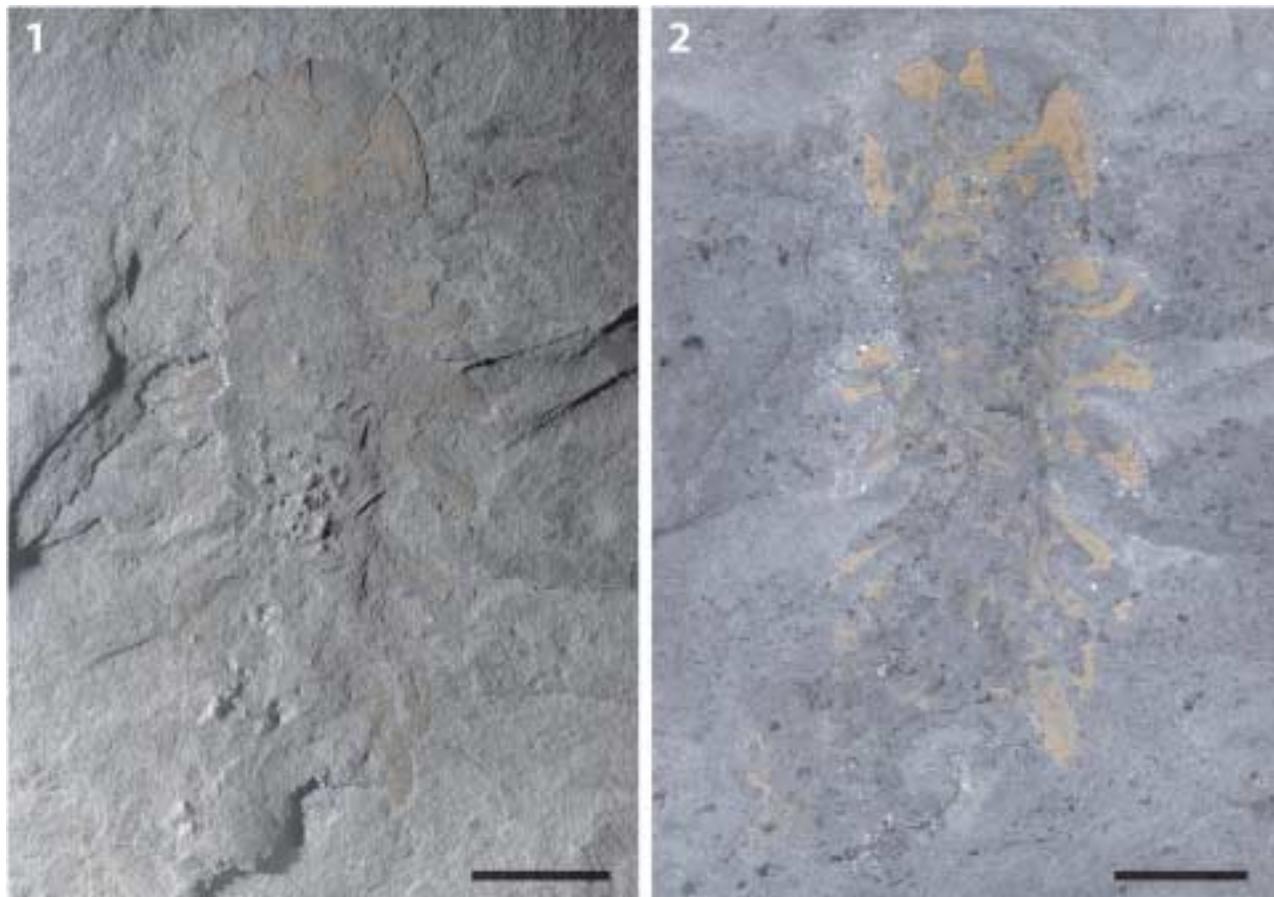


Figure 4. *Dytikosicula desmatae* gen. et sp. nov., holotype, SM X.50203. (1) photograph dry in low-angle light; (2) photograph under ethanol. Scale bars represent 5 mm.

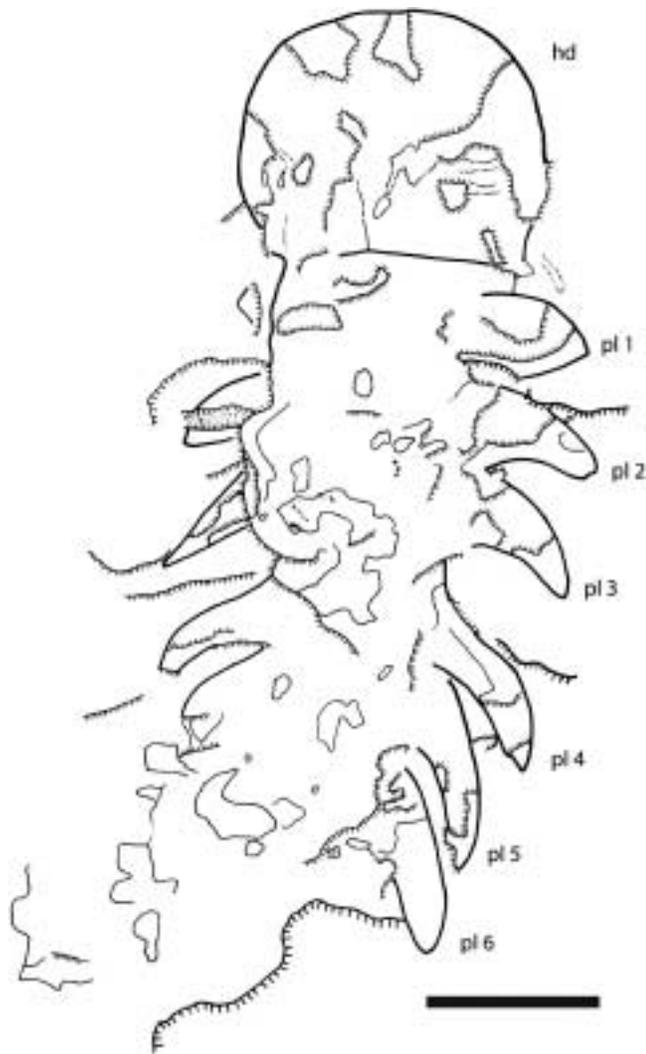


Figure 5. Interpretative camera-lucida drawing of *Dytikosicula desmatae* gen. et sp. nov., compare Figure 4. hd, head shield; pl 1, pl 2, etc., pleurae 1–6. Scale bar represents 5 mm.

extensions, quite strongly recurved posteriorly and well separated. Posterior end incomplete. No appendages preserved.

Holotype.—SM X.50203, holotype and only known specimen, part only. Specimen originally collected by Robert Drachuk, and donated by Charlie Magovern.

Etymology.—Refers to the proposed link (Greek, *desmos*, bond or chain) to other Cambrian megacheirans.

Occurrence.—Marjum Formation, middle Cambrian. Locality is west of Delta, House Range, Utah.

Remarks.—Specimen shows characteristic Burgess Shale-type preservation (e.g. Briggs et al., 2008). Otherwise parts of the fossil have a brownish mineral adhering which may represent the original skeleton, apparently uncalcified. Associated with part of the thorax are granular areas, probably representing diagenetic mineral growth (?pyrite). These are not obviously

consistent with any soft-part anatomy, but may have resulted from decaying tissue.

This new taxon is most similar to the megacheiran *Dicranocaris guntherorum* Briggs et al., 2008, best known from the Wheeler Formation but is also recorded from the Marjum Formation. Detailed comparisons are hindered because the best preserved specimen of *D. guntherorum* is more complete than the sole specimen of *D. desmatae*, and is buried at an oblique angle in comparison to the dorso-ventral attitude of the specimen described here. The most obvious difference is that whereas in *D. guntherorum* the pleural extensions of the trunk are limited to segments 2 to 5, in *D. desmatae* each of the preserved segments bears pleura. In addition and making allowances for the different angles of burial, the head of *D. desmatae* appears to be somewhat more circular. Deciding whether *Dytikosicula desmatae* is a distinct taxon, or better interpreted as another species of *Dicranocaris* is to some extent a matter of judgement. Generic distinction, however, is warranted not only by the differences noted, but also the conspicuously larger size of the holotype. In this context it is tentatively suggested that other material (albeit from the Wheeler Formation) and attributed questionably to *D. guntherorum* by Briggs et al. (2008; figure 5.4–9; see also Gunther and Gunther, 1981; Robison, 1991) not only falls into the same size range of *D. desmatae* but may be better accommodated in this taxon. Thus despite poor preservation these specimens (all in lateral view) show some evidence for a pleuron on the first trunk segment (see also Gunther and Gunther, 1981, pl. 48; the precise interpretation of these structures diverged amongst the authors contributing to Briggs et al. (2008)).

It is also worth noting a possible relationship to the arthropod *Serracaris lineata* Briggs, 1978, which is known only from the Lower Cambrian Kinzers Formation of Pennsylvania. All specimens of this taxon are incomplete, but available material consists of an elongate trunk consisting of at least fifteen tergites with recurved extensions. The most obvious differences are that in *Serracaris* these tergal extensions on either side appear to be double. In addition, one segment towards the anterior end has conspicuously larger extensions, although there they appear to have been single. Briggs (1978, Pl. 1, fig. 4) drew attention to a possible anterior carapace. Because of its unique occurrence he regarded it, however, as probably fortuitous. It does, however, have some similarity to the head shield of *Dytikosicula*, but in *Serracaris* it appears proportionally larger and possibly wider. Although the posterior end of the unique specimen of *D. desmatae* is not preserved, Briggs et al. (2008) drew attention in *D. guntherorum* to “the unique morphology of the telson” (p. 245) with its terminal bifurcation. Although these authors made no comparison, *Serracaris* also possesses a bifurcate telson (Briggs, 1978). *Serracaris* is, of course, stratigraphically somewhat older than *Dytikosicula*. From the Eldon Formation of British Columbia Briggs (1978, text fig. 2a, b) described a more nearly contemporaneous form to *D. desmatae* as *Serracaris*?. The unique specimen is poorly preserved, and appears to have had more spinose tergal projections.

Stem-group Lophotrochozoa

Remarks.—Current consensus regards the wiwaxiids as having a molluscan affinity (e.g. Yang et al., 2014). Our material throws no

further light on this question, and we prefer to take a more agnostic view of their wider relationships, placing them within the lophotrochozoans but not shoe-horning them into a specific phylum.

Family *Wiwaxiidae* Walcott, 1911a;

Remarks.—*Wiwaxiids* are best known from articulated material of *Wiwaxia corrugata* (Matthew, 1899) from the Phyllopod Bed of the Burgess Shale (Conway Morris, 1985). Also occurring in this deposit in moderate abundance are isolated sclerites (and rarely partial associations), detached from the cataphract scleritome either by deciduous action or upon death and post-mortem scattering (see also Butterfield, 1990; Mankiewicz, 1992). Sclerites are also known from the Lower and Middle Cambrian of northwestern Canada (e.g. Butterfield and Nicholas, 1996), South China (e.g. Y-L. Zhao et al., 1994, 2005; Harvey et al., 2012; Sun et al., 2014; Yang et al., 2014; F-C. Zhao et al., 2015), Utah (Conway Morris and Robison, 1988), Australia (Porter, 2004), Czech Republic (Fatka et al., 2011) and Siberia (Ivantsov et al., 2005). These records collectively indicate that the individual sclerites were probably robust and relatively resistant to decay. In contrast, articulated *wiwaxiids* are very rare. Apart from the Burgess Shale examples (Conway Morris, 1985) and recent discoveries from the Xiaoshiba Lagerstätte (Yang et al., 2014) and the Kaili Formation (Zhao et al., 1994, 2005, Pl. II, fig. 2; also Sun et al., 2013, fig. 6) in China, our report is the only known occurrence of an articulated specimen from Laurentia.

Genus *Wiwaxia* Walcott, 1911a

Type species.—*Wiwaxia corrugata* (Matthew, 1899).

Wiwaxia herka new species

Figure 6.1–6.8

Diagnosis.—A *wiwaxiid* with a prominent palisade of recurved and stout dorso-lateral spines. Differs from type species in larger number of spines and their degree of robustness.

Description.—Single articulated specimen (Fig. 6.1, 6.2) preserved in approximately lateral view, shows a fairly pronounced dorso-ventral curvature (cf., Conway Morris, 1985, figs. 82, 83, 88). Most obvious feature is palisade of dorso-lateral spines. These are quite stout, posteriorly recurved, closely spaced. Those on the right-hand side (in the part) are clearest, with a total of 13 visible. Near the anterior end, a few spines of the opposite side are visible at a lower level. Three anterior-most spines are somewhat shorter (about half the length of others), whereas remainder longer and sub-equal length, except at posterior where again last one or two shorter. Remaining sclerites, that mantled dorsal and lateral regions of the body, only moderately well preserved, but components of the lateral and ventro-lateral series are identifiable. In addition to the articulated specimen, six isolated sclerites are available. Based on the characteristic recurved shape, three (KUMIP 286300, 286302) are identified as ventro-lateral (equivalent to sciculate; see Conway Morris and Peel, 1995 [Fig. 6.3, 6.7, 6.8]). Another two sclerites (KUMIP 286300, 286301), one of which is poorly preserved, are more elongate and probably represent lateral (= cultrate) sclerites (Fig. 6.4, 6.5). Finally, one sclerite (KUMIP 286301) may be from the dorsal region (Fig. 6.6).

Holotype.—KUMIP 287449, holotype, part and counterpart (Fig. 6.1, 6.2), collected by Glade Gunther. Paratypes, KUMIP 286300 (part with two sclerites, counterpart with opposite side of ?lateral sclerite only) (Fig. 6.3–6.5), 286301 (Fig. 6.6), 286302 (part and counterpart) (Fig. 6.7, 6.8), donated by Lloyd Gunther.

Etymology.—From *herka* (Greek, fence), in reference to the palisade of spines.

Occurrence.—Spence Shale Member, Langston Formation (Hintze, 1988, Chart 15), lower Middle Cambrian, polymerid *Glossopleura* Zone (Robison, 1976). Locality is approximately 3 m below top of Spence Shale, south side of Antimony Canyon on west side of Wellsville Mountain; NW¼ sec. 31, T. 10 N., R. 1 W.; approximately 4 km north of Brigham City, Box Elder County, Utah. Other biota from the same locality, mostly collected by members of the Lloyd Gunther family, include trilobites *Amecephalus idahoense* (Resser, 1939a), *Athabaskia wasatchensis* (Resser, 1939b), *Glossopleura gigantea* ? Resser, 1939a, *Glossopleura* sp., *Kootenia mendosa* Resser, 1939a, and *Zacanthoides idahoensis* Walcott, 1908; other arthropods *Meristosoma paradoxum* Robison and Wiley, 1995, *Hurdia* indet. sp. (Daley et al., 2013) and an undetermined taxon with large axial spine on rear shield; undetermined articulate brachiopods; echinoderms *Ctenocystis utahensis* Robison and Sprinkle, 1969, and *Gogia* sp. nov.; a hemichordate (see Loduca et al., 2013) *Yuknessia simplex* Walcott, 1919; hyolith *Hyolithes carinatus* Babcock and Robison, 1988; sponge *Vauxia gracilentia*? Walcott, 1920; worms *Ottoia prolifica* Walcott, 1911a, and *Selkirkia* sp.; other animal taxa, *Eldonia ludwigi* Walcott, 1911b, and *Scenella* sp.; large coprolites (cf. Conway Morris and Robison, 1988, fig. 32); and algae *Marpolia spissa* Walcott, 1919.

Remarks.—Erection of new species *Wiwaxia herka* is based on a single articulated specimen, seems justified on account of the distinctiveness of its dorso-lateral spines. In contrast to *W. corrugata* (Conway Morris, 1985) spines are more densely arrayed (approximately 12 versus an average of approximately 8) and less elongate. On the unproven assumption that the isolated sclerites (Fig. 6.3–6.8) derive from the same species, the ventro-lateral ones appear similar to those of *W. corrugata*, whereas the ?lateral and ?dorsal sclerites appear to be more elongate. *W. herka* is evidently closely related to *W. corrugata*, but differs more obviously from other lower Cambrian taxa from China (Zhao et al., 1994; Yang et al., 2014) in being substantially larger and possessing spines (also absent in juvenile *W. corrugata*: Conway Morris 1985).

This new species confirms the basic arrangement of the *wiwaxiid* scleritome, but does not throw further light on their phylogenetic position within the lophotrochozoans. One approach is to treat *wiwaxiids* as stem-group annelids. This is on the dual supposition of the similarities of the sclerite microstructure to annelidan chaetae (Butterfield, 1990; see also Conway Morris and Peel, 1995) and the inferred transformation of the scleritome into parapodial bundles capable of locomotion and defense (Conway Morris and Peel, 1995; Struck, 2011). Arguments, especially on the nature of the radula-like mouth-

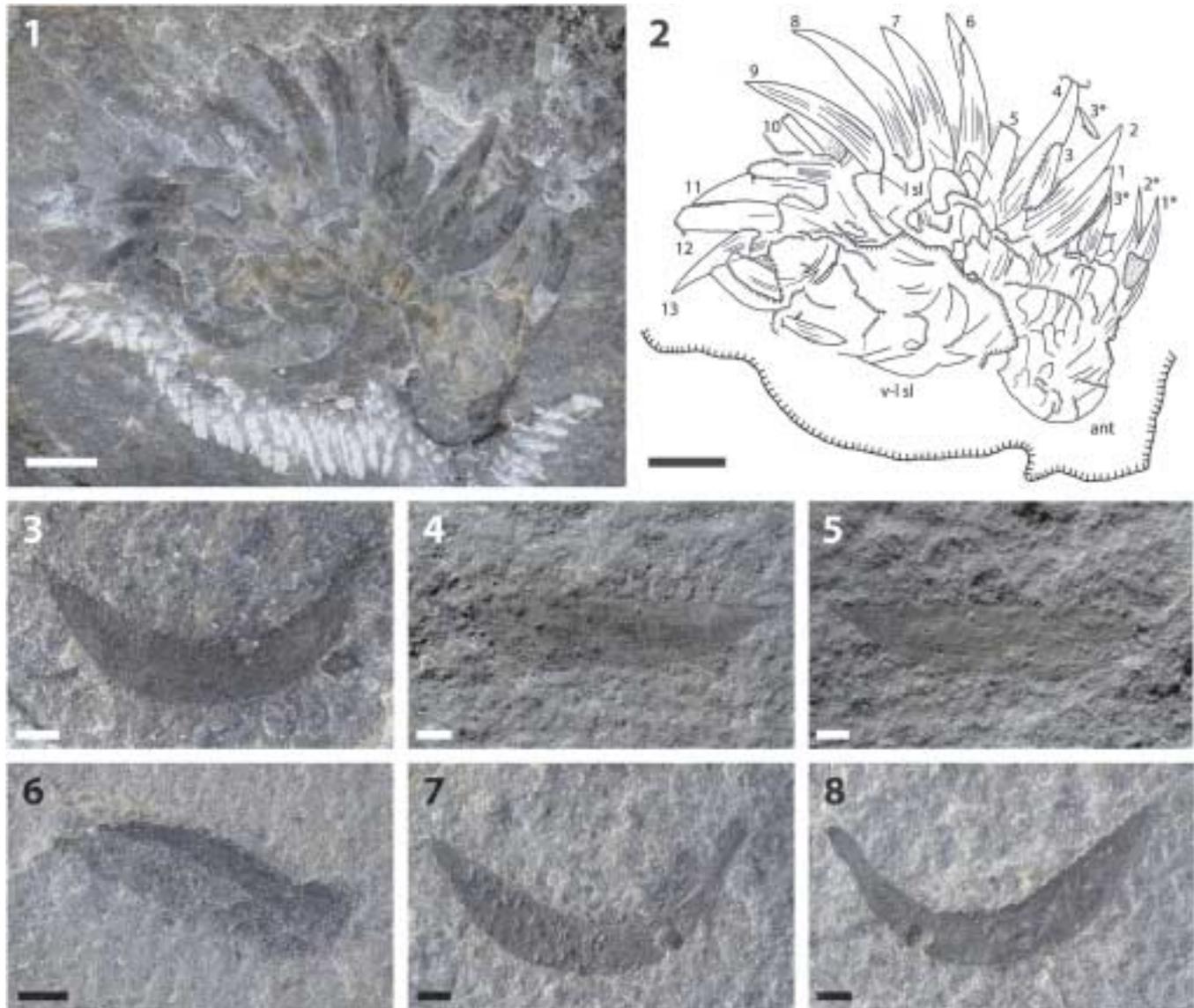


Figure 6. *Wiwaxia herka* sp. nov. (1) holotype, KUMIP 287449; (2) holotype, interpretative camera-lucida drawing, compare Figure 6.1 Fine lines represent striations on sclerites; other lines partial outlines of compressed sclerites. Hachure on lower side is edge of excavated sediment. ant, anterior; l sl, lateral sclerites; v-l sl, ventro-lateral sclerites. Dorsal-lateral spines numbered consecutively from anterior; numbers with asterisks refer to left side, others more complete series on right side; (3–5) KUMIP 286300: (3) isolated ventro-lateral sclerite (part only); (4) isolated ?lateral sclerite, part; (5) isolated ?lateral sclerite, counterpart; (6) KUMIP 286301 isolated ?dorsal sclerite (part only); (7) KUMIP 286302 isolated ventro-lateral sclerite, part; (8) KUMIP 286302, isolated ventro-lateral sclerite, counterpart. All photographs taken dry under cross-polarized illumination. Scale bars represents 5 mm (1, 2), 1 mm (3–8).

parts (Smith, 2012) and similarities to *Odontogriphus* (Caron et al., 2006) on the other hand point to a molluscan affinity (see also Smith, 2014). By itself, *W. herka* can add nothing material to this discussion, but it is worth emphasizing that if the wiwaxiids belong to a stem-group identified as the halwaxiids (Conway Morris and Caron, 2007) then shoe-horning them into a given phylum may serve to obscure how crucial anatomical transitions were achieved among which end-results are the setae of annelids (and brachiopods) or radula of mollusks.

Superphylum Ambulacraria Metschnikoff 1881
Stem-group Cambroernids

Remarks.—The cambroernids is an un-ranked informal stem group (Caron et al., 2010).

Family Eldoniidae Walcott, 1911b
Genus *Eldonia* Walcott, 1911b

Type species.—*Eldonia ludwigi* Walcott, 1911b.

Eldonia ludwigi Walcott, 1911b
Figure 7.1–7.2

Description.—New specimen, part and counterpart, incomplete with slightly more than half disc preserved. Maximum width approximately 80 mm. Principal features (Fig. 7) visible are part of gut (and associated coelomic cavity) and disc. Latter consists of two fairly distinct regions. Inner zone traversed by series of widely spaced radial lines, which are probably on surface of disc. Outer region bears semi-continuous groove (in part) and

otherwise subdued concentric wrinkles. Half of disc, which might have shown the feeding apparatus, not preserved.

Material.—SM X.50204.1 (part) and SM X.50204.2 (counterpart), collected by Paul Jamison.

Occurrence.—Middle part of Marjum Formation, mid-middle Cambrian, *Ptychagnostus punctuosus* Zone. Locality is Marjum Pass, House Range, Millard County, Utah.

Remarks.—Specimen from the same stratigraphic horizon was described by Conway Morris and Robison (1988, figs. 28, 29). To first approximation new specimen is similar, but preserves outer parts of the disc more clearly.

The medusiform eldoniids (and rotadiscids) are a characteristic component of Burgess Shale-type faunas. In addition to their type occurrence in the Burgess Shale (Walcott, 1911b; Durham, 1974; Friend, 1995), this group is recorded from other Lower (e.g., Chen et al., 1995; Chen and Zhou, 1997) and Middle Cambrian localities in China (Zhao and Zhu, 1994; Dzik et al., 1997), Siberia (Friend et al., 2002), Poland (Masiak and Zylińska, 1994), and Utah (Conway Morris and Robison, 1988). Taxonomic affinities of the eldoniids have remained controversial (e.g., Zhu et al., 2002). One suggestion has been to link them to the lophophorates (e.g., Dzik et al., 1997). More popular has been to pursue a relationship either to the echinoderms (e.g., Friend, 1995) or a more specific proposal that they are actual holothurians, an idea that stems back to the time of C.D. Walcott (e.g., Clark, 1912) and has received recurrent support (e.g., Durham, 1974; Hou and Bergström, 2003). The description of the related *Herpetogaster collinsi* from British Columbia (Caron, Conway Morris and Shu, 2010; see also Caron et al., 2010) suggests, however, that this taxon, along with *Eldonia* and *Phlogites*, are stem-group ambulacrarians forming an informal group known as the cambroermids that lies close to the echinoderm-hemichordate divergence.

Wider significance

While these finds augment existing knowledge of otherwise rare taxa, it is worth reviewing some wider implications of this work. First, as noted, *Dytikosicula desmatae* gen. et sp. nov. appears to be a megacheiran, closely related to *Dicranocaris guntherorum*. In the wider context of Cambrian arthropod evolution (e.g., Budd and Telford, 2009; Edgecombe, 2010) the overall diversity of known taxa is striking, and reports of more poorly preserved material (e.g., Halgedahl et al., 2009; Johnston et al., 2009; Caron et al., 2010) that in at least some cases represent new forms (e.g. Legg, 2013) suggest that our documentation of arthropod morphospace is incomplete. Thus, in the context of the description of *Dytikosicula* and its phylogenetic proximity to *Dicranocaris*, this indicates a relatively densely occupied area of morphospace, but a cursory glance at other Cambrian megacheirans (see Hendricks and Liebermann, 2008) suggests otherwise a considerable disparity. So too the identification of a new species of *Yohoia* hints at another more densely populated area of arthropod morphospace.

While the collection of Burgess Shale-type fossils from Middle Cambrian localities in the western United States has proved to be a relatively slow process, these new finds serve two useful purposes. First, they confirm that the diversity of these faunas remains incompletely documented. Second, they reinforce the notion of a Burgess Shale-type fauna that arguably is typical of Cambrian shelf seas, although this is not to dispute environmental controls on the make-up of particular assemblages. In general, however, the Burgess Shale-type faunas differ more in the details rather than general aspect. Although the majority of assemblages were deposited in offshore, even deeper water, and in conditions of low oxygen (e.g., Gaines and Droser, 2010), shallower water locales are also known (e.g., Copeland, 1993; Schwimmer and Montante, 2007; Gehling et al., 2011; see also Masiak and Zylińska, 1994). Collectively, these confirm a broad faunal identity characterized by arthropods, sponges, priapulids as well as eldoniids (and less frequently groups such as chordates, polychaetes and vetulicolians), along with a variety of typical Cambrian shelly taxa (trilobites, hyoliths,

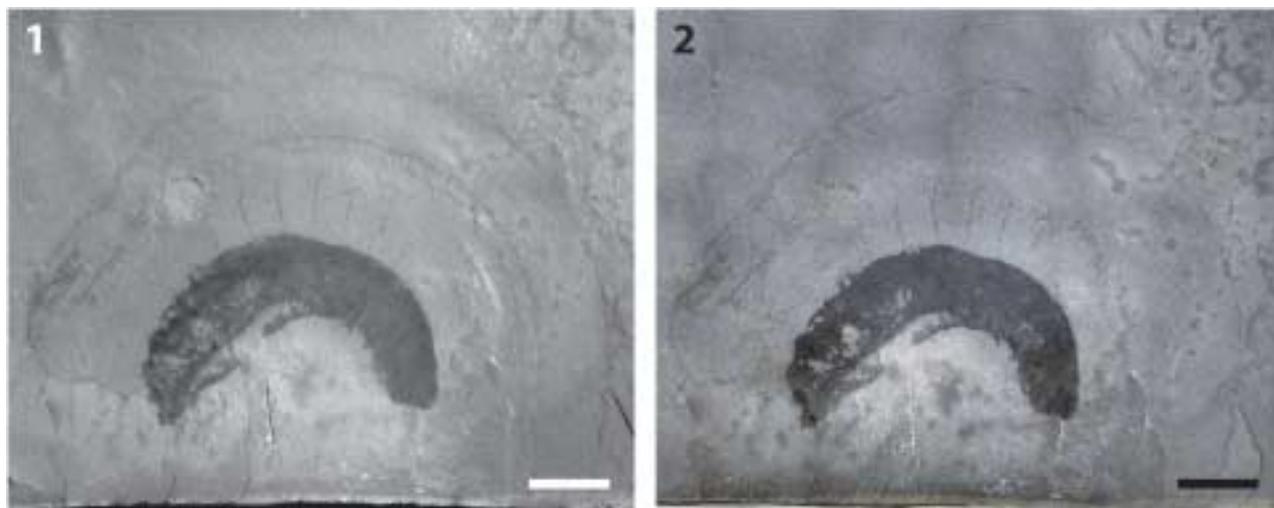


Figure 7. *Eldonia* cf. *ludwigi* Walcott 1911, SM X.50204.1; (1) photographed dry in low-angle light; (2) photographed under ethanol. Scale bars represent 10 mm.



Figure 8. *Cambrorhynchium* sp., SM X.50205.2. Scale bar represents 5 mm.

brachiopods). Despite this common identity, subtle distinctions may ultimately reveal paleoenvironmental controls that may in turn refine our understanding of the ecological preferences of at least some taxa. A useful test case involves the arthropod *Marrella*. Known from an incomplete specimen from the Lower Cambrian Balang Formation of Hunan (Liu, 2013) and slightly more abundantly from the lower Middle Cambrian Kaili Fossil-Lagerstätte of Guizhou (Zhao et al., 2003), prior to these reports *Marrella* was effectively known only from the Phyllopod bed of the Burgess Shale (Whittington, 1971) and immediately adjacent areas (García-Bellido and Collins, 2006), where it occurs in extraordinary abundance (e.g. García-Bellido and Collins, 2006; Caron and Jackson, 2008). It remains conjectural what specific environmental conditions favor the occurrences of *Marrella*, or indeed other highly sporadic occurrences in the Burgess Shale-type faunas, such as the annelids, chordates, or halkieriids.

Conclusions

This report augments our knowledge of Cambrian arthropods, notably in the form of *Yohioia utahana* sp. nov. and *Dytikosicula desmatae* gen. et sp. nov., and illustrates a new species of *Wiwaxia*. It also amplifies the occurrences of *Eldonia*. Finally, we also note briefly a specimen (collected by PMJ) of the

tubicolous ?cnidarian *Cambrorhynchium* (see Conway Morris and Robison, 1988) from the upper Wheeler Shale (Fig. 8) of the Drum Mountains, Millard County, Utah. The specimen (part and counterpart) is relatively small (approximately 1 cm) and at its proximal end shows relatively coarse growth lines (Fig. 8). No associated soft parts are evident.

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