

# Trilobites of the Cranbrook Lagerstätte (Eager Formation, Cambrian Stage 4), British Columbia

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**Non-technical Summary.**—Regarded as a low-diversity, Burgess Shale-type Lagerstätte deposit, the Eager Formation (Cambrian Series 2, Stage 4) of the Cranbrook area, British Columbia, contains abundant, sometimes beautifully preserved, trilobites and rare non-biomineralized taxa. Although trilobites from this area were first reported just over a century ago, they have received little study. This paper describes the trilobites of the Cranbrook Lagerstätte. A minimum of eight trilobite species are recognized: four species of olenelloids (two of which are new) are by far the most abundant elements of the fauna, and at least two species of dorypygids and two species of “ptychoparioids” are also present. Trilobite diversity in the Cranbrook Lagerstätte is comparable to that within other Lagerstätten from Cambrian Stage 4 of Laurentia. Preservation attributes of the trilobites and sedimentological data suggest that the assemblage experienced minimal transportation prior to fossilization, and that the local environment was at least occasionally able to support a “typical” seafloor trilobite community. The Cranbrook Lagerstätte is demonstrated to lie within the middle Dyeran Stage of Laurentia, within what was a substantial stratigraphic gap in the distribution of Burgess Shale-type Lagerstätten.

**Abstract.**—The Eager Formation (Cambrian Stage 4) of the Cranbrook area, British Columbia, contains abundant, sometimes beautifully preserved, trilobites and rare non-biomineralized taxa. Trilobites were first reported just over a century ago but have received little research attention, resulting in uncertainty in the number and identity of species within the assemblage and ambiguity in the age of the fauna. The trilobites of the Eager Formation in the Cranbrook area are described herein based largely upon material collected in 2015. A minimum of eight (and perhaps up to 11) trilobite species are recognized. The four species of olenelloids (*Olenellus santuccii* Webster n. sp., *Olenellus? schofieldi*, *Mesonacis eagerensis*, and *Wanneria cranbrookense* Webster n. sp.) are by far the most abundant elements of the fauna. At least two, and perhaps as many as five, species of dorypygid are present, as are two species of “ptychoparioids”. Paucity and poor preservational quality of specimens mean that the various dorypygid and “ptychoparioid” species are left in open nomenclature. Trilobite diversity in the Cranbrook Lagerstätte is comparable to that within other Lagerstätten from Cambrian Stage 4 (Series 2) of Laurentia. The diversity and abundance of trilobites, combined with biostratigraphic and trace fossil data, suggest that the assemblage is autochthonous and/or parautochthonous, and that the local environment was at least periodically able to support a “typical” benthic trilobite community. The age of the Cranbrook Lagerstätte is constrained to lie within the middle Dyeran Stage of Laurentia, within what was a substantial stratigraphic gap in the distribution of Burgess Shale-type Lagerstätten.

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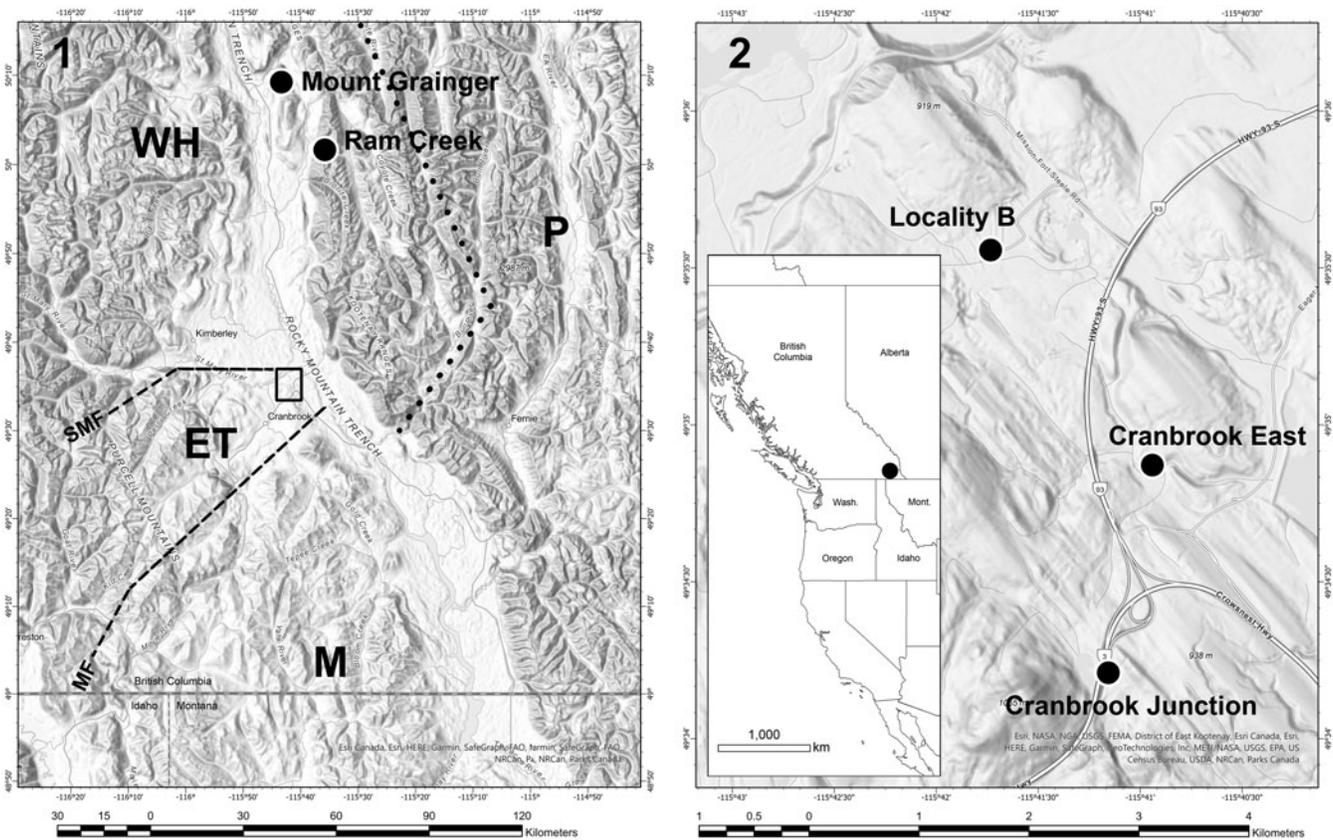
## Introduction

Trilobites from the Eager Formation (Cambrian Series 2, Stage 4) of the Cranbrook area of southeastern British Columbia were first reported just over a century ago (Schofield, 1921, 1922). With further collecting it was soon realized that the Eager Formation contained a Burgess Shale-type fossil assemblage: the

first fossils of non-biomineralized *Tuzoia* Walcott, 1912, and *Anomalocaris* Whiteaves, 1892, from Cranbrook were described less than ten years later (Resser, 1929). One of the earliest localities to be discovered, herein referred to as “Locality B” (Fig. 1), remains a productive fossil-bearing site in the Cranbrook area and has yielded non-biomineralized taxa in addition to trilobites. The rare fossils of non-biomineralized organisms from the Cranbrook area have been mentioned, figured, and/or described in several papers (e.g., Resser, 1929; Briggs, 1979; Briggs and Mount, 1982; Conway Morris, 1989; Copeland, 1993;

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**Figure 1.** Location of fossil-bearing sites discussed herein. (1) Map of southeastern British Columbia showing location of Cranbrook on west side of Rocky Mountain Trench. Moyie Fault (MF) and St. Mary Fault (SMF) approximately mark southern and northern limits, respectively, of Eager Trough (ET) between paleogeographic highs of Montania (M) and Windermere High (WH) that influenced Cambrian sedimentation in the region. Dotted line shows approximate western limit of shelf platform deposits (P) on Laurentia during Cambrian; note westward deflection of platform margin associated with transition onto northern edge of promontory of Montania. Mount Grainger and Ram Creek localities (mentioned in text) lie within western Hughes Range to north of Cranbrook. Rectangle shows location of (2). (2) Location of the three fossil-bearing sites northeast of Cranbrook discussed herein. These three sites together constitute the Cranbrook Lagerstätte. See text for details. Inset map shows location of Cranbrook (circle) within southeastern British Columbia; neighboring provinces and states are identified (abbreviations: Mont., Montana; Wash., Washington).

Lieberman, 2003a; Vannier et al., 2007). In contrast, the far more abundant and sometimes beautifully preserved trilobites of the Eager Formation have received relatively little research attention, despite being represented in many museum, university, and private collections across North America and having been illustrated in popular books (e.g., Fortey, 1991; Levi-Setti, 1993, 2014; Ludvigsen and Bohach, 1996). The dearth of published scientific studies means that the identity and diversity of the Eager Formation trilobites are unsettled, and their paleobiology and taphonomy are essentially unstudied.

The primary source for published documentation of the Cranbrook trilobites remains that by Best (1952b), who identified five trilobite species—the olenelloids *Olenellus gilberti* Meek in White, 1874; *Olenellus eagerensis* Best, 1952b; *Olenellus schofieldi* Best, 1952b; *Wanneria walcottana* (Wanner, 1901); and the dorypygid *Bonnia columbensis* Resser, 1936—but illustrated only the first three (although specimens of the latter two were illustrated in his unpublished M.S. thesis [Best, 1952a]). That list has formed the basis of subsequent summaries of trilobite diversity and age determination of the Eager Formation (e.g., Okulitch, 1956). Best's (1952b) work has experienced only two minor modifications in the published literature over the subsequent 70 years. Firstly, Hu (1985) described the ontogeny

of "*Olenellus gilberti*" from Cranbrook but commented that it might not be conspecific with the type material of that species from Nevada; both Palmer (1998a) and Webster (2015) also concluded that "*Olenellus gilberti*" from Cranbrook represents a new species. Secondly, *Olenellus eagerensis* was reassigned to the genus *Mesonacis* Walcott, 1885, by Lieberman (1999).

However, unpublished work and gray literature hinted at greater diversity and a need for formal taxonomic revision of the Cranbrook trilobite assemblage. In particular, the doctoral dissertations of both Best (1959) and Bohach (1997) deserve meritorious mention. Both those dissertations described the specimens previously identified as "*Olenellus gilberti*" as a new species of *Olenellus* Hall in Billings, 1861a (see also the conclusions by Hu [1985], Palmer [1998a], and Webster [2015]), and both also described the specimens previously identified as "*Wanneria walcottana*" as a new species of *Wanneria* Walcott, 1910. Furthermore, Bohach (1997) tentatively reassigned *Olenellus schofieldi* to the genus *Mesonacis* (a similarity also noted by Lieberman, 1999, p. 39–40), and recognized three species of dorypygid—none of which was identified as *Bonnia columbensis*—and one species of ptychoparioid within the assemblage. Unfortunately, neither of those dissertations was published, and the nomenclatural changes that they

proposed have no formal validity (although the invalid names can be found on the internet and have occasionally crept into the literature; e.g., Levi-Setti, 2014, pl. 112).

A restudy of the Cranbrook trilobites is necessary for several reasons. Firstly, the Eager Formation of that area yields abundant and well-preserved olenelloid trilobites, including articulated specimens and morphologically immature specimens. Such material offers rare insight into the paleobiology and ontogeny of these early trilobites, providing information that will be critical to ongoing studies of their phylogeny. Secondly, detailed study of the biostratigraphy of the trilobites can shed light on the hitherto poorly understood depositional environment of the Cranbrook Lagerstätte. Thirdly, modern systematic treatment of the trilobites is necessary for accurate age determination of the fossil-bearing strata. Although the presence of *Olenellus* and *Mesonacis* is sufficient to demonstrate that the fossiliferous Eager Formation strata lie within the Dyeran Stage of Laurentia (and within Cambrian Stage 4 in the global chronostratigraphic sense; Palmer, 1998b; Peng et al., 2020), a more precise age determination is currently equivocal (see also Conway Morris, 1989). *Olenellus gilberti* and *Wanneria walcottana* are known from the upper Dyeran of the southwestern United States and the middle-to-upper Dyeran of Pennsylvania, respectively, but because the supposed occurrence of both of those species in the Eager Formation is now suspect, the age of the Eager Formation assemblage, including Locality B with its non-mineralized taxa, is not well constrained.

Recognizing the need for a thorough examination of the Eager Formation biota, its preservation, and its paleoenvironmental setting, a Royal Ontario Museum-led expedition (JBC), involving researchers from the University of Chicago (MW), Pomona College, and the University of Saskatchewan conducted a detailed excavation during the summer of 2015 of the Cranbrook Lagerstätte at Locality B (Webster et al., 2015; Caron et al., 2024). Additional fieldwork in the Cranbrook area and adjacent regions of southeastern British Columbia was conducted by MW during 2018. Detailed documentation of the non-trilobite body fossils, the trace fossils, the taphonomy, the sedimentology, and the microstratigraphy of the site will be published elsewhere. The present paper (1) provides a formal description of the trilobites of the Eager Formation in the Cranbrook area, highlighting some features of their ontogenetic development and mature morphology that are phylogenetically conserved and others that are phylogenetically novel (thus improving our understanding of early trilobite evolution and disparity); (2) compares the (increased) trilobite diversity of the Cranbrook Lagerstätte to that of other Lagerstätten from Cambrian Series 2; (3) infers aspects of the depositional environment from consideration of the biostratigraphy of the trilobites; and (4) discusses biostratigraphic constraints on the age of the Cranbrook Lagerstätte.

## Geological background

*Paleogeography and general depositional setting.*—Regional stratigraphy and mapping of the Cranbrook area and neighboring districts was pioneered in the first half of the twentieth century (e.g., Schofield, 1915, 1921, 1922; Walcott, 1924; Rice, 1937, 1941; Leech, 1954, 1958a, b). More recent work has deepened

understanding of the complex tectonostratigraphic setting of the region. Cambrian strata of the Cranbrook area were deposited on the continental margin of Laurentia and are categorized as being of miogeoclinal nature (Patchett and Gehrels, 1998; Colpron et al., 2007). Following the Proterozoic breakup of Rodinia, the Cordilleran margin of Laurentia is often considered to have been passive during the Cambrian. However, volcanism and faults associated with the waning phase of the rift-to-drift transition were sporadically active. Block faulting produced topographic highs and lows that affected Cambrian sedimentation patterns in and around the Cranbrook area.

On a broad tectonostratigraphic scale, the Cambrian rocks of the Cranbrook area lie within the Omineca Belt of western Canada, inboard of the parautochthonous Kootenay Terrane (Wheeler et al., 1991; Colpron et al., 2002, 2007). Cambrian sediments of the Kootenay Terrane were sourced from Laurentia and accumulated in a basinal setting on or immediately adjacent to the craton margin (Colpron and Price, 1995; Patchett and Gehrels, 1998; Colpron et al., 2007). Both the Kootenay Terrane and the Omineca Belt preserve evidence of active Cambrian tectonism. On the Kootenay Terrane, in the Selkirk Mountains and Purcell Mountains to the north and west of the Cranbrook area (Figs. 1.1, 2), rift-related metavolcanic rocks occur in the Neoproterozoic to lower Cambrian Hamill Group (Devlin, 1989; Kubli and Simony, 1992; Colpron et al., 2002; Larson and Price, 2006). In the Omineca Belt east of Cranbrook, volcanism also occurred during deposition of the upper Cambrian McKay Group (Larson and Price, 2006).

On a more local scale, the Cranbrook area lies in the structural St. Mary Block (Benvenuto and Price, 1979), which consists of a northeasterly plunging anticline between the Moyie Fault to the south and the St. Mary Fault to the north (Fig. 1.1). The subparallel, roughly northeast–southwest trending Moyie and St. Mary thrust faults are Mesozoic reactivations that follow basement structures that were active during the Proterozoic and Cambrian. The Moyie Fault approximates the northern limit of Montania, which was a high-relief, oceanward-projecting part of the Laurentian craton during the Paleozoic (Deiss, 1941; North, 1953; Norris and Price, 1966; Benvenuto and Price, 1979; Price, 1994; Larson and Price, 2006). Montania was intermittently tectonically active during the early Paleozoic, and strongly influenced local sedimentation patterns during the Cambrian. The Cambrian succession is very thin on Montania; indeed, on the crest of Montania, Upper Devonian strata rest unconformably on Proterozoic (Purcell Supergroup) strata and Cambrian strata are absent (North, 1971; Benvenuto and Price, 1979). The St. Mary Fault lies just south of the southern margin of the Windermere High, a high-standing, eastward-tilted crustal fault block within the miogeocline (Larson and Price, 2006, and references therein). The Windermere High formed during Proterozoic rifting of the Cordilleran margin and was present as a topographic feature during the early Cambrian (and, indeed, to the Middle Devonian; North, 1953; Benvenuto and Price, 1979; Kubli and Simony, 1992; Larson and Price, 2006). The Cranbrook area lay on the outer shelf between these two paleo-highs in a more basinal setting—the northeast-trending “Eager Trough” (North, 1953; Larson and Price, 2006; Fig. 1.1)—and is represented by a thicker Cambrian succession than is present on the paleo-highs.

System	Global		Laurentia		Kootenay Terrane (Purcell & Selkirk Mts.)	Eager Trough (Cranbrook)	Windermere High (western Hughes Range)	Shelf (Main Ranges, Rockies)
	Series	Stage	Series	Stage				
Cambrian	Series 2	Stage 4	Lin.	Del.	Lardeau Group	?	Jubilee Formation	Mount Whyte Fm.
			Waucoban	Dyeran	Badshot Fm.	?	?	Peyto Fm.
					Mohican Fm.	Eager Formation	Eager Formation	St. Piran Fm.
					Hamill Group upper sandstone unit	?	?	Lake Louise Fm.
		Stage 3	Montezuman	Cranbrook Formation		Cranbrook Formation	Cranbrook Formation	Fort Mountain Fm.
	?				?	?		
	Terreneuvian	Fortunian	Stage 2	Begadean	?	?	?	?
						Hamill Group greenstone - graded sandstone unit	Purcell to Windermere	Miette Group
						lower sandstone unit		
						?		
?								
Proterozoic					Purcell Supergroup	Purcell Supergroup	?	

**Figure 2.** Provisional lithostratigraphic correlation chart for the lower Cambrian units in southeastern British Columbia. Asterisks indicate approximate stratigraphic position of Cranbrook Lagerstätte as described herein. Shaded gray regions indicate unconformities. Vertical scale is arbitrary and non-linear; relative thicknesses of lithostratigraphic units are distorted. Approximate position of as-yet-undefined global chronostratigraphic series and stage boundaries shown as dashed lines. Correlations based on references cited in text, Desjardins et al. (2010), and unpublished observations; question marks indicate poorly constrained positions of lithostratigraphic boundaries. Abbreviations: Del., Delamarian; Fm., Formation; Lin, Lincolnian.

*The Cambrian succession in the Eager Trough.*—The oldest Cambrian deposit in the Eager Trough is the Cranbrook Formation (Schofield, 1922; Fig. 2), which is a quartz arenite with conglomeratic sandstones; a basal conglomerate contains clasts of the Mesoproterozoic Purcell Supergroup units, which it overlies with angular unconformity (Schofield, 1922; Rice, 1937, 1941). The Cranbrook Formation is almost everywhere devoid of body fossils, although Leech (1954, p. 7) reported olenelline trilobites identified (by R.V. Best) as “*Callavia* and possibly *Nevadia*” from approximately 30 meters below the top of the formation at a locality in the Canal Flats area of the western Hughes Range (~60 km NNE of Cranbrook, deposited on the Windermere High). The specimens collected by Leech cannot be located, but if the identification of a nevadiid is correct then a Montezuman age is indicated for the upper portion of the formation (Palmer, 1998b; Hollingsworth, 2011). Consistent with this hypothesis, the Cranbrook Formation has been correlated with the upper sandstone member of the Hamill Group (on the Kootenay Terrane), which are rift-related metavolcanics within the unconformably underlying middle member of the Hamill Group having a maximum age of

569.6 ± 5.3 Ma (Colpron et al., 2002; Larson and Price, 2006). Isopachs plotted on palinspastic restorations (Kubli and Simony, 1992, fig. 14; Larson and Price, 2006, fig. 5) showed that the lower Cambrian sandstone unit formed by the combined Cranbrook Formation and upper member of the Hamill Group generally thickens westwards away from the craton; superimposed on this general trend, the unit is locally thicker within the Eager Trough and thinner over the Windermere High. The Cranbrook Formation is ~180 meters thick in the Cranbrook area (Schofield, 1922).

Above the Cranbrook Formation lies the Eager Formation (Schofield, 1922; Fig. 2), which consists of shale and siltstone with some minor calcareous beds. Sandstones and carbonates are more prevalent within the Eager Formation on the Windermere High, as seen in the western Hughes Range (Schofield, 1922; Walcott, 1924; Leech, 1954; Bohach, 1997; Larson and Price, 2006). The Eager Formation is a structurally incompetent unit, and typically exhibits tectonic strain (see Morphometric Data, below). The contact between the Cranbrook and Eager formations is rarely exposed, but usually has been interpreted as conformable and gradational (Schofield, 1922; Rice, 1941;

Leech, 1954; Larson and Price, 2006). Rice (1937) suggested that it might be unconformable, but later rescinded the idea (Rice, 1941). On the Windermere High to the north and northeast of Cranbrook, the Eager Formation is unconformably overlain by cliff-forming carbonates of the middle to upper Cambrian Jubilee Formation (Leech, 1954; Larson and Price, 2006). The unconformity presumably resulted from uplift and erosion of the Windermere High during the middle Cambrian (Larson and Price, 2006). Strata above the Eager Formation are absent in the Cranbrook area. Nevertheless, the preserved portion of the Eager Formation thickens from the Windermere High southwards into the Eager Trough (North, 1953; Larson and Price, 2006). In the Cranbrook area the Eager Formation can be up to 2,000 meters thick (Rice, 1937, 1941; North, 1953).

Age constraints for the Eager Formation come from the trilobites in the Cranbrook area (Schofield, 1921, 1922; Best, 1952b) and from similar trilobite faunas collected in the western Hughes Range (Walcott, 1924; Leech, 1954; Ludvigsen and Bohach, 1996; also unpublished collections made by Bohach [1997] and MW [discussed below]). These trilobites unambiguously demonstrate a Dyeran age for the fossiliferous strata (see below for a more precise constraint). It is unknown whether the younger portion of the Eager Formation above the fossiliferous strata, which includes that portion ultimately removed by erosion below the unconformity at the base of the Jubilee Formation, spanned into the Delamarian Stage.

### Fossil-bearing localities in the Cranbrook area

The Eager Formation crops out in several places in the vicinity of Cranbrook (Rice, 1937; Leech, 1958a). However, exposures are typically isolated and of very limited spatial and stratigraphic extent. The contact with the underlying Cranbrook Formation is rarely exposed, and the bases and tops of exposures are almost invariably fault-bound or covered by glacial drift. Rampant small-scale faulting combined with the absence of distinctive marker beds hinders precise correlation of the exposures. As a result, it is rarely possible to tightly constrain the position of a particular exposure within the Eager Formation.

Numerous exposures in the Cranbrook area have yielded fossils (Appendix). There is little to no distinction among the localities in their trilobite fauna, suggesting that either the localities are all more-or-less correlative within the Eager Formation, and/or that a single trilobite assemblage persisted throughout deposition of the entire fossiliferous interval. A more varied stratigraphic succession of trilobite assemblages—of greater biostratigraphic utility—is found in sections in the western Hughes Range.

Here, we focus on a limited number of fossil-bearing localities lying in an outcrop belt approximately 8–10 km northeast of Cranbrook (Fig. 1). Details of these and other localities are provided in the Appendix. This focal outcrop belt contains the sites from which fossils were first collected, including Locality B.

*Fossil localities on or near the Old Cranbrook–Fort Steele wagon road.*—Fossils from the Eager Formation of the Cranbrook area were first mentioned by Schofield (1921, 1922). Schofield (1922, p. 9) described the original collection site as being in a roadstone excavation “six miles east of

Cranbrook, B.C., on the Cranbrook–Fort Steele wagon road”. A map of the area (Schofield, 1922, fig. 2) highlighted three fossil-bearing localities, the southernmost of which fits the description as being on the roadside. The road layout has changed over the subsequent century, but comparison to other maps and aerial images indicates that this original locality lay at what is now the southwest end of the modern-day interchange between Kootenay Highway and Crowsnest Highway. This site (“locality C” in Caron et al., 2024) is herein referred to as “Cranbrook Junction” (Fig. 1.2; Appendix).

A second fossil-bearing locality was shown by Schofield (1922, fig. 2, easternmost locality) as being just north of the old Cranbrook–Fort Steele wagon road, ~1.2 km NNE of the southernmost locality. This site remains accessible today and still yields fossils; it is herein referred to as “Cranbrook East” (Fig. 1.2; Appendix).

Best (1952a, b) discussed two fossil localities, one of which (his “Locality A”; Appendix) falls very close to both Cranbrook Junction and Cranbrook East (see the map in Best, 1952a). It is unclear whether Best’s Locality A refers to one or both of these sites, or perhaps even represents a third, now lost, site in that vicinity.

As described by Schofield (1921, p. 666; 1922, p. 12), trilobites from Cranbrook Junction (and perhaps Cranbrook East and other nearby sites) were collected by Col. C.H. Pollen and subsequently by Schofield and sent to C.D. Walcott for identification. The precise provenance of the specimens was not specified, but regional surveying by Schofield showed that they were sourced from an interval of “chocolate-brown shales” over 15 meters thick, the base of which was reported as being more than 91 meters stratigraphically above a disconformity with the Precambrian rocks (Schofield, 1921).

*Locality B.*—A productive outcrop of the Cranbrook Lagerstätte within the Eager Formation is on a small hill sandwiched today between a shooting range and an archery range, ~8 km northeast of Cranbrook (Fig. 1.2; Appendix). This is the northernmost fossil locality marked on the map of Schofield (1922, fig. 2) and was referred to as “Locality B” by Best (1952a, b); Bohach (1997, p. 391–392) referred to the site as “Locality 5”. We herein refer to the site as “Locality B”, following Best (1952a, b). The site is on crown land owned by the provincial government; it is well known to and frequently visited by amateur collectors. Although trilobites are by far the most common fossils, the site has yielded several specimens of *Tuzoia* and *Anomalocaris* as well as rare sponges and a pterobranch hemichordate (Caron et al., 2024).

Resser (1929) described several species of *Tuzoia* and *Anomalocaris* from the Cranbrook area. He stated that the specimens were collected from “five miles northeast of Cranbrook” and referred to the locality as USNM Locality 67 g (Resser, 1929, p. 2–3; Appendix). The occurrence of *Tuzoia* and *Anomalocaris* might suggest that USNM Locality 67 g is synonymous with Locality B. However, given Resser’s (1929, p. 3) declarations that Walcott had previously been made aware of the site and that some of the fossils were collected by Col. Pollen, it is conceivable that Resser used USNM Locality 67 g to refer to another of the localities mentioned by Schofield (1922, fig. 2; i.e., to Cranbrook Junction or Cranbrook East herein) or perhaps

he used it as an undifferentiated catch-all term for all the fossil-bearing localities northeast of Cranbrook.

Despite the abundance of trilobites—some in a state of full articulation—and the presence of non-biomineralized taxa, the Cranbrook Lagerstätte had not been the subject of a focused paleontological or sedimentological study. The diversity of the biota, the trace fossils, the taphonomy of the fossils, the depositional environment, and the age of the deposit were therefore poorly understood. To remedy that deficiency, a multi-institutional team of researchers including JBC and MW (see Acknowledgments) conducted a detailed excavation and study of the Lagerstätte at Locality B in July 2015, as now summarized.

The bedrock at the site is almost everywhere covered by a thick veneer of soil and talus. A mechanical backhoe was therefore employed to excavate a trench down to bedrock. Following the protocol employed during the study of other Lagerstätten (e.g., Caron and Jackson, 2006, 2008; Webster et al., 2008; Zhao et al., 2009), a working surface several square meters in area was exposed in the floor of the trench. Over the course of 11 days a stratigraphic section spanning 2.65 meters of the Eager Formation was thoroughly examined by progressively stripping off beds, centimeter by centimeter. The taxonomic identity and horizon of occurrence (to the nearest centimeter) were recorded for every body fossil found within the section (more than 2,600 in total). Detailed biostratigraphic data were documented for every specimen ( $N = 104$ ) within a 3,004 cm<sup>2</sup> area on a single bedding surface 94 cm below the zero-meter datum in the section. Trace fossil occurrences within the trench were also recorded. Blocks of the section were examined in thin-section in order to reveal sedimentological and microstratigraphic details. As required by our permit from the British Columbia Government and the Royal Ontario Museum, the trench was backfilled upon completion of the fieldwork; casual collecting of fossils from the site is thus once again restricted to surface collecting from talus. All specimens recovered during the fieldwork are housed in the Royal British Columbia Museum, Victoria (RBCM).

Herein, we focus solely on the trilobite body fossils, which made up > 98% of the body fossils encountered in the measured section. Preliminary results of the fieldwork—including brief descriptions of the rest of the biota, the trace fossils, the taphonomy, the sedimentology, and the microstratigraphy—are provided elsewhere (Webster et al., 2015; Caron et al., 2024).

## Material, methods, and terminology

*Material.*—Individual trilobites (total of 545) collected from Locality B during the 2015 excavation, including the best-preserved specimens found in situ within the measured section and several well-preserved and/or interesting specimens found in talus at the site, were selected for detailed examination at the University of Chicago. Many specimens from historical collections made at Locality B and other localities in the Cranbrook area were also examined. Total sample size upon which the descriptions are based was almost 600 specimens.

Specimens were cleaned and prepared as necessary. Latex casts were made of external molds. Each specimen was examined under high magnification using a binocular microscope

and its morphological details were recorded. Specimens were coated with ammonium chloride sublimate and mounted for digital photography in the standard orientation of Shaw (1957), with the dorsal surface of the ocular lobes in a horizontal plane below a vertically mounted camera. Each specimen was photographed using a Canon EOS 5D camera with either a 100 mm or 65 mm macrolens, as appropriate, mounted to a macro rail. To maximize depth of field, a series of digital images was taken with vertical spacing between sequential images between 60  $\mu\text{m}$  and 100  $\mu\text{m}$ , depending on specimen size; those image stacks were rendered into a single composite image using Zerene Stacker for the Macintosh (<https://zerenesystems.com>).

*Morphometric data.*—To assist in species delimitation and description, numerous length and angle measurements were extracted from the digital images using ImageJ software (<https://imagej.nih.gov/ij/>). Values for some variables were estimated on incompletely preserved specimens, but only when those estimates were replicable within a small margin of error (typically < 0.05 mm on large cephalata). Values for variables relating to transverse measurements that span the sagittal axis were obtained on some specimens by doubling a transverse measurement from the sagittal axis to one endpoint of that measurement. Measurement error introduced through these approximations is likely to be minimal; nevertheless, such estimates are designated as “approximate” values in the systematic descriptions.

Variation in these morphometric data represents the combined effects of biology (phenotypic variation among specimens, including that attributable to ontogeny), taphonomy (because all specimens have been deformed by compaction and almost all specimens show some evidence of mild tectonic deformation), and measurement error (which is deemed to be unbiased and trivial compared to interspecific disparity).

Tectonic strain introduces a potential problem for using morphometric data to quantitatively delimit species. Tectonic deformation will affect all morphometric measurements, but some variables or ratios between variables are expected to be more severely affected than others. For example, idealized simple tectonic strain (often depicted as a strain ellipse) of a specimen would cause all linear measures to deviate from their original (pre-strain) values to some extent, but should not affect the proportional ratio between parallel linear measurements. The ratio of two (ex)sagittal length measurements should therefore be a reasonably reliable estimate of the pre-strain ratio, even though the absolute values of those measurements might have been increased or decreased by the tectonic strain. Conversely, linear measures that were not parallel to each other would be differentially distorted by tectonic strain; their ratio would be maximally modified from the pre-strain ratio if those measurements were orthogonal to each other. Angular measurements will always be modified by tectonic deformation except under an extremely limited set of conditions (e.g., when the angle between the features was originally 90° and those features happened to be perfectly aligned with the major and minor axes of the strain ellipse).

No effort was made herein to analytically remove these taphonomic overprints on morphology. This is because tectonic

deformation of the specimens is mild, especially in comparison to the effects on fossil morphology of the ubiquitous compaction-related deformation. Although many analytical methods have been proposed that attempt to retrodeform data from tectonized fossils, none overcomes the measurement distortions that result from compaction. In an effort to increase the ratio of biological signal to taphonomic overprint in the data, morphometric data were not collected from strongly deformed specimens. Although variation in the morphometric data reported herein undoubtedly includes some component that is due to taphonomy, it is encouraging that species-diagnosing distinctions are evident (see plots of morphometric data). Visualization and analyses of morphometric data were performed in R (R Core Team, 2023).

*Stratigraphic terminology.*—Pending formal definition of the global boundary between Cambrian Stage 3 and Stage 4, the less-ambiguous chronostratigraphic series and stage names proposed for the Cambrian of Laurentia (Fig. 2; Palmer, 1998b) are used herein in preference to the global chronostratigraphic units (Peng et al., 2020). The trilobite taxa that define the stages of the Laurentian Waucoban Series are provincial, and it is unlikely that the Montezuman–Dyeran stage boundary of Laurentia will exactly coincide with the base of global Stage 4. Nevertheless, much or all of the Dyeran Stage of Laurentia will surely fall within Stage 4 of the global chronostratigraphic scheme once the latter is defined (Fig. 2).

*Taxonomic terminology.*—Olenelline, olenelloid, and olenellid refer to the successively less-inclusive Suborder Olenellina, Superfamily Olenelloidea, and Family Olenellidae, respectively. The traditional libristomate “Order Ptychopariida” is at best paraphyletic and probably polyphyletic, and has been abandoned (Adrain, 2011). Pending phylogenetic resolution, many families that had been traditionally assigned to that order are currently treated as “Order Uncertain” (Adrain, 2011). Furthermore, several families within that former order, including the Ptychopariidae and Antagmidae, are poorly diagnosed (see discussions by Webster, 2011a; Geyer and Peel, 2017; Sundberg and Webster, 2022). Accordingly, family-level assignment of such trilobites is at present impossible, and they are here referred to informally as “ptychoparioids”. Systematics of the trilobites described herein should be attributed to MW.

*Morphological terminology.*—Morphological terminology follows that of recent work on olenellines (Webster, 2007a, b, 2009, 2015; Webster and Bohach, 2014; Webster and Landing, 2016). A “preocular furrow” is a shallow glabellar furrow anterior to S3 that runs inwards and often forwards from the lateral glabellar margin, contacting the lateral margin of LA at or close to the contact between the outer margin of the ocular lobe and LA (Webster and Bohach, 2014). The preocular furrow could be equivalent to S4, but such putative homology is equivocal. A “transocular furrow” is a shallow furrow running posteriorly and slightly inwards from the preocular furrow to S3, essentially marking the line of contact between the ocular lobe and the glabella (Webster and Bohach, 2014). An “extraocular platform” is a prominent,

steep-walled, flat-topped bulge on the inner portion of the extraocular area, upon which the ocular lobe and eye socle are located (Webster and Bohach, 2014). The platform is differentiated from the rest of the extraocular area by a break in slope.

Genal spine advancement is measured by finding the point at which the axial furrow is intersected by a transverse line drawn between the inner margins of the genal spine bases where they contact the posterior cephalic margin. The systematic descriptions express the qualitative location of that point of intersection relative to the contact of the glabellar lobes and furrows with the axial furrow. Unless otherwise stated, divergence of the ocular lobe from an exsagittal line is measured as the angle between an exsagittal line and a line drawn from the posterior tip of the ocular lobe to the contact of the inner margin of the ocular lobe with the lateral margin of L3.

The trunk is considered to be divided into a prothorax and opisththorax when there is a sharp contrast in pleural morphology between successive segments, with the first opisththoracic segment having much smaller pleurae and pleural spines in comparison to the trend exhibited in more anterior (prothoracic) segments (Whittington, 1989; Whittington in Whittington et al., 1997; Webster and Bohach, 2014).

The five successive phases of ontogenetic development of the olenelloid cephalon as defined by Webster (2007a, b, 2009, 2015; Webster et al., 2001; Webster and Bohach, 2014) are followed here. Specimens younger than phase 3 of cephalic development, which is characterized by possession of genal spines and a glabella that is parallel-sided or anteriorly tapered between SO and S3, were not recovered during the present study. Entry into phase 4 of cephalic development was defined by the onset of pronounced lateral widening (tr.) of L3 relative to L2, so that the glabella became transversely narrowest at L2. Entry into phase 5 was defined by the onset of pronounced lateral widening (tr.) of L2, so that the glabella became transversely narrowest at S1. In some olenelloids S2 subsequently became isolated from the axial furrow, permitting the delimitation of early (pre-isolation) versus late (post-isolation) portions of phase 5.

*Repositories and institutional abbreviations.*—Specimens studied herein are housed at the Cranbrook History Centre, British Columbia (CBK), the Field Museum, Chicago (FMNH), the Institute for Cambrian Studies, Department of the Geophysical Sciences, University of Chicago (ICS), the Museum of Comparative Zoology, Harvard University (MCZ), the Royal British Columbia Museum, Victoria (RCBM), the Geology Museum, University of California, Riverside (UCR), and the Smithsonian Institution, United States National Museum, Washington D.C. (USNM).

## Systematic paleontology

- Order Redlichiida Richter, 1932
- Suborder Olenellina Walcott, 1890
- Superfamily Olenelloidea Walcott, 1890
- Family Olenellidae Walcott, 1890
- Genus *Olenellus* Hall in Billings, 1861

*Type species.*—*Olenus thompsoni* Hall, 1859, from the Parker Formation (Dyeran Stage of Laurentia, Cambrian Stage 4) of Vermont.

*Remarks.*—Palmer and Repina (1993; Palmer and Repina in Whittington et al., 1997) recognized five subgenera within *Olenellus*, and Palmer (1998a) suggested that at least two distinct species groups might be represented within one of those subgenera. Cladistic analyses by Lieberman (1998, 1999) led to the raising of two of those subgenera (*Mesonacis* and *Mesolenellus* Palmer and Repina, 1993) to genus level, and the abandonment of another two—*Paedeumias* Walcott, 1910, which could not be diagnosed from *Olenellus* (*Olenellus*) without rendering the latter paraphyletic; and *Angustolenellus* Palmer and Repina, 1993, which was synonymized into *Mesonacis*. As a result of those revisions, 42 species are currently assigned to *Olenellus* and the genus ranges from the middle Dyeran to the uppermost Dyeran.

Unfortunately, Lieberman's (1998, 1999) cladistic analyses were compromised by numerous coding errors (see Webster, 2007a, 2009; Webster and Bohach, 2014; Webster and Landing, 2016) and by the failure to consider ontogenetic data (see discussions by Webster and Bohach, 2014, and Webster, 2015). A new phylogenetic analysis and systematic revisions of these taxa are currently being conducted (MW in preparation) with the goal of clarifying the diagnosis and species-level composition of *Olenellus* and closely related taxa such as *Mesonacis*. To that end, several key taxa have recently been redescribed, including the type species of *Olenellus*, *Paedeumias*, and *Mesonacis* (Webster and Landing, 2016) and other information-rich species such as *Olenellus gilberti* (Webster, 2015). The present paper describes several other species that yield valuable ontogenetic information and that will be crucial for resolving the phylogenetic relationships among olenellids. Pending completion of the new phylogenetic analysis, generic assignment of the species described herein should be considered provisional.

*Olenellus santuccii* Webster new species  
Figures 3–5, 6.1–6.5, 6.10, 6.11, 7, 8, 10

- 1921 *Mesonacis gilberti* (Meek in White, 1874); Schofield, p. 666.  
?1921 *Callavia* cf. *nevadensis* Walcott, 1910; Schofield, p. 666.  
1922 *Mesonacis gilberti*; Schofield, p. 12.  
?1922 *Callavia* cf. *nevadensis*; Schofield, p. 12.  
1952b *Olenellus gilberti*; Best, p. 17–18, pl. 1, figs. 13–17.  
1956 *Olenellus gilberti*; Okulitch, p. 715.  
1956 *Paedumias* [sic] *nevadensis*; Okulitch, p. 715.  
1985 *Olenellus gilberti*; Hu (part), p. 121–123, 125–129, text-fig. 2, pl. 1, figs. 1–14, 16–23 only [not pl. 1, fig. 15 = *Mesonacis eagerensis*].  
1991 “one of the earliest trilobites”; Fortey, photograph on p. 153.  
1993 *Olenellus fremonti* Walcott, 1910; Levi-Setti, pl. 52, 53a, b.  
1996 *Olenellus* sp.; Ludvigsen and Bohach, p. 52, figs. 4.2a–c, 4.6.  
1998a *Olenellus* n. sp.?; Palmer, p. 668.

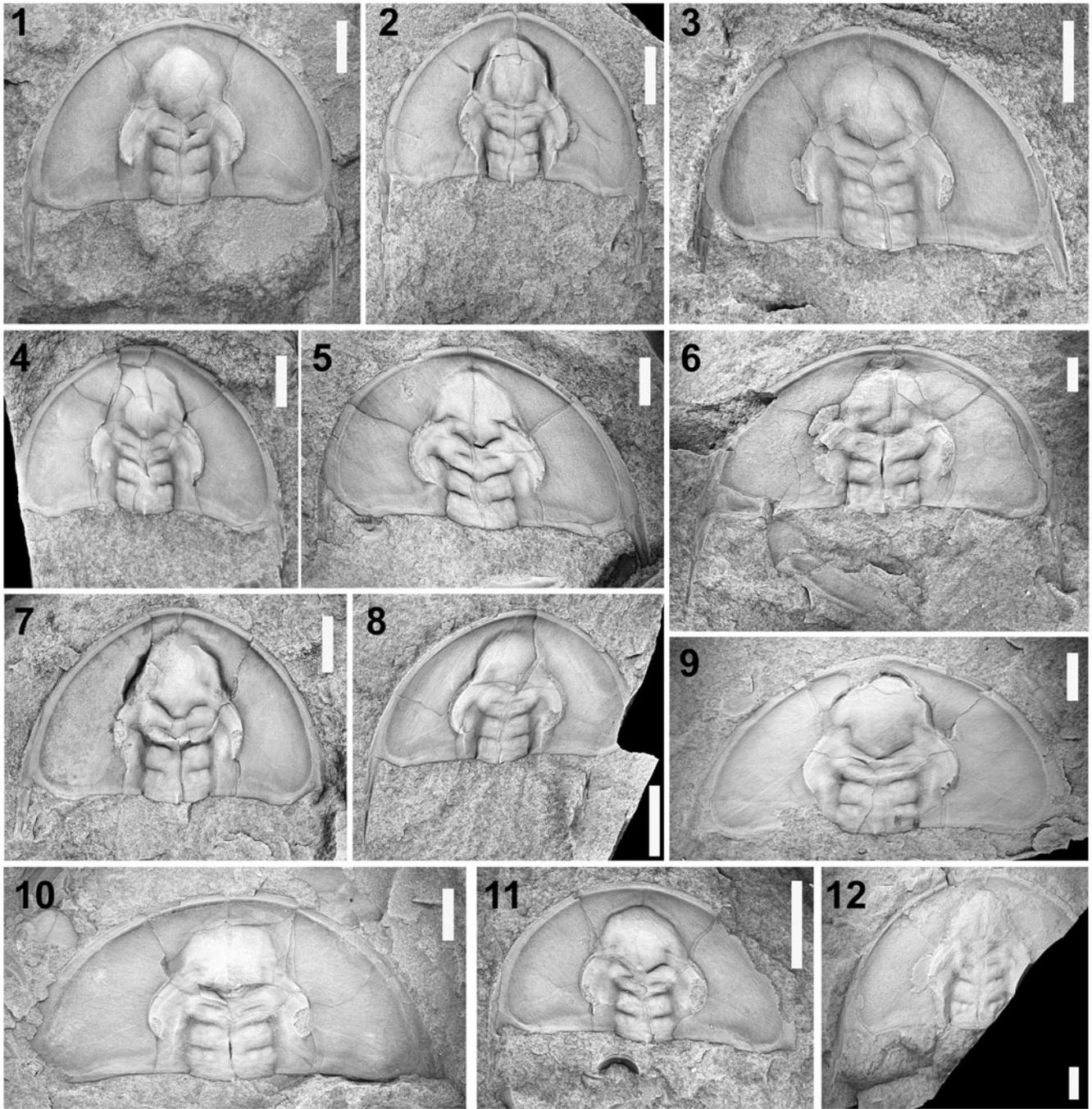
- 2011 *Olenellus* sp. aff. *Olenellus gilberti* Meek in White, 1874; Retallack, fig. 4a.

*Holotype.*—Cephalon RBCM.EH2015.013.0252.003 (Fig. 3.1), from Eager Formation (Cambrian Stage 4), Locality B, Cranbrook, British Columbia.

*Diagnosis.*—Base of genal spines transversely opposite lateral margins of LO, posterior margin of glabella, or slightly posterior to posterior margin of glabella. Radial length of anterior border opposite junction of ocular lobes with LA approximately 37% (range 28–51%) length (exsag.) of LO. Preglabellar field approximately twice length (sag.) of anterior border. Plectrum present. Posterior tip of ocular lobe transversely opposite mid- to posterior portion of lateral margin of L1, rarely SO. Axial node on at least T3 to T14, sometimes also T1 and T2, increasing in size posteriorly down thorax.

*Occurrence.*—*Olenellus santuccii* Webster n. sp. is the most abundant species at Locality B; more than 2,100 specimens were found during the 2015 excavation, of which almost 400 were photographed and examined in detail to provide the description herein. The species is also known from Cranbrook East, Cranbrook Junction, Locality A of Best (1952a, b), MCZ Locality 4790, Rock Point, USNM Locality 67g, and from unspecified localities in the Cranbrook area (Appendix). Levi-Setti (1993, pl. 52, 53) figured two specimens as “*Olenellus fremonti*” that were stated to be from the St. Piran Sandstone (Peyto Limestone Member); those specimens are herein assigned to *Olenellus santuccii* Webster n. sp.

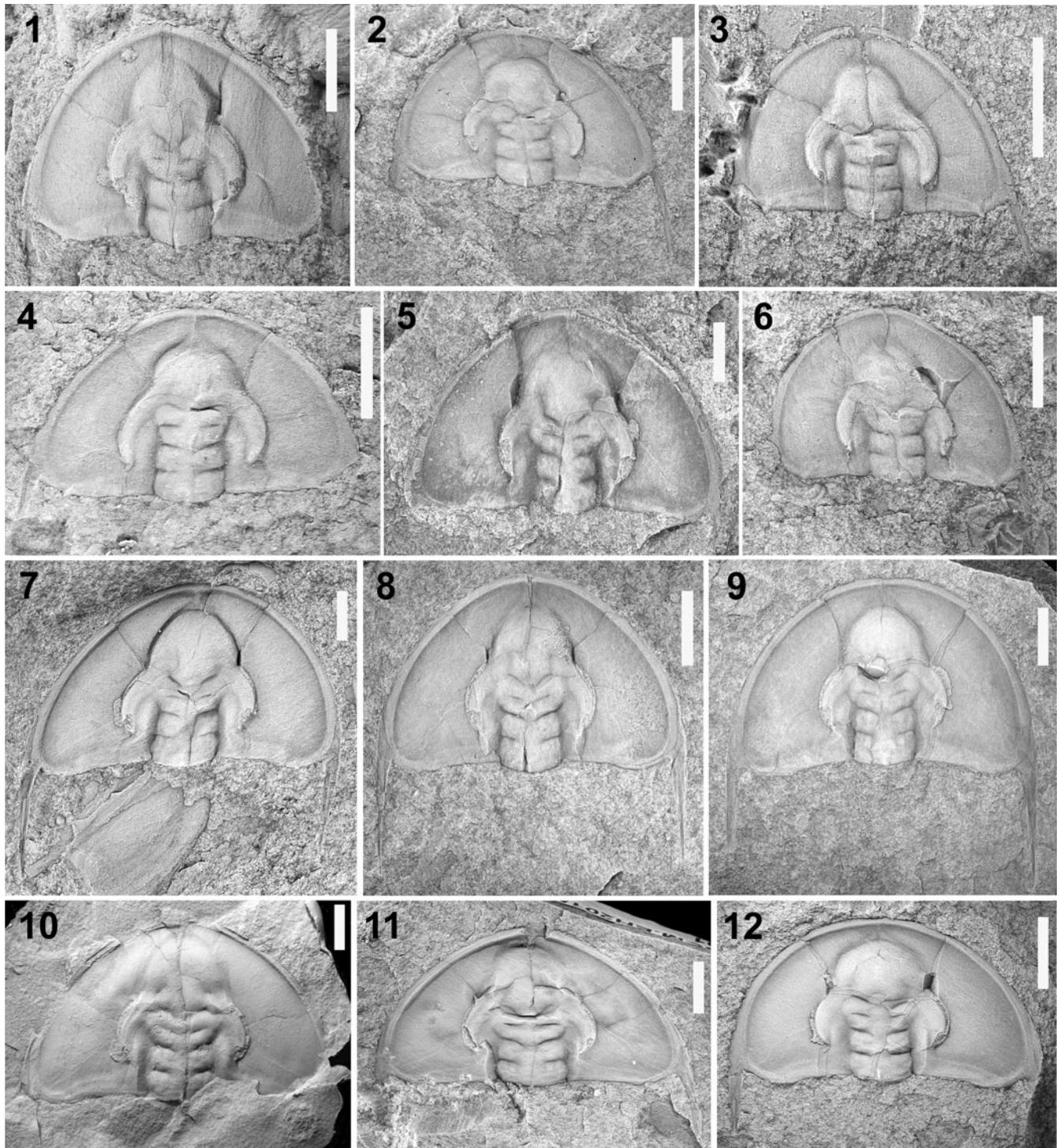
*Description (morphologically mature specimens; sagittal cephalic length > 5 mm).*—Cephalon roughly semicircular in outline, widest (tr.) at base of genal spines. Proximal portion of posterior cephalic margin oriented posteriorly by 0–18° relative to a transverse line when traced distally (typically more strongly posteriorly oriented on larger specimens), distal portion flexed anteriorly by approximately 19° (range 8–33°) relative to proximal portion at broadly rounded adgenal angle located approximately 63% of distance from axial furrow to base of genal spine. Greatest observed cephalic length approximately 24.7 mm (sag.) (Fig. 3.6). Genal spine slender, length approximately 60% of sagittal cephalic length; base transversely opposite lateral margins of LO, posterior margin of glabella (Figs. 3.12, 4.10), or slightly posterior to posterior margin of glabella (Figs. 3.4, 4.9); posterior tip opposite axial ring of T5 (Fig. 5.1, 5.5). Intergenal spine represented on small cephalia by spinelet on posterior cephalic border approximately midway between adgenal angle and base of genal spine or closer to adgenal angle (Fig. 4.1–4.4), on larger cephalia this is reduced to a small node or swelling; can be very subtle (Fig. 3.7) or absent on large cephalia. Cephalic border flat-topped dorsally, well defined around entire cephalon by distinct border furrow; radial length of anterior border (measured perpendicular to margin) opposite junction of ocular lobes with LA approximately 37% (range 28–51%) length (exsag.) of LO. Glabella weakly constricted at S1; approximately 86% of cephalic length (sag.) having increased



**Figure 3.** Morphologically mature cephalons of *Olenellus santucci* Webster n. sp. from the Cranbrook Lagerstätte. (1) Internal mold, holotype, RBCM.EH2015.013.0252.003. (2) Internal mold, RBCM.EH2015.013.0213.001. (3) Internal mold, RBCM.EH2015.013.0007.001. (4) Internal mold, RBCM.EH2015.013.0144.001. (5) Internal mold, RBCM.EH2015.013.0039.001. (6) Largest studied cephalon, internal mold, RBCM.EH2015.013.0113.001. (7) Internal mold, RBCM.EH2015.013.0185.001. (8) Internal mold, RBCM.EH2015.013.0008.001. (9) Latex peel of external mold, RBCM.EH2015.013.0003.001. (10) Internal mold, RBCM.EH2015.013.0092.002. (11) Internal mold, RBCM.EH2015.013.0094.007. (12) Latex peel of external mold, RBCM.EH2015.013.0009.001. All scale bars 5 mm. All from Eager Formation at Locality B.

through ontogeny, preglabellar field well developed, typically approximately twice length (sag.) of anterior border width having decreased through ontogeny. Plectrum present; often fades posteriorly and can broaden to merge with anterior of LA (Fig. 4.7–4.9, 4.12). Maximum width of LA wider than basal glabellar width (tr.) (123–165%). Posterior margin of glabella weakly convex, with adaxial portion sometimes more-or-less straight.

SO deep only abaxially, abaxial end slightly anterior to adaxial end. LO subtrapezoidal, slightly narrows anteriorly, length (exsag.) approximately 16% glabellar length (sag.); rarely with weak lateral swelling (Fig. 3.9). S1 deepest abaxially, very shallow over axis; deeply incised portions approximately parallel to those of SO but slightly arcuate (weakly convex anteriorly). L1 subtrapezoidal, slightly narrows anteriorly; length (exsag.) approximately 16% glabellar length (sag.). S2 deepest



**Figure 4.** Morphologically mature cephalons of *Olenellus santucci* Webster n. sp. from the Cranbrook Lagerstätte. (1) Latex peel of external mold, RBCM.EH2015.013.0032.002. (2) Internal mold, RBCM.EH2015.013.0216.006. (3) Internal mold, RBCM.EH2015.013.0188.002. (4) Latex peel of external mold, RBCM.EH2015.013.0102.007. (5) Internal mold, RBCM.EH2015.013.0092.004. (6) Internal mold, RBCM.EH2015.013.0143.007. (7) Internal mold, RBCM.EH2015.013.0057.006. (8) Internal mold, RBCM.EH2015.013.0263.001. (9) Internal mold, RBCM.EH2015.013.0268.001. (10) Latex peel of external mold, UCR 10825.1, from unknown locality near Cranbrook. (11) Internal mold, RBCM.EH2015.013.0015.001. (12) Internal mold, RBCM.EH2015.013.0131.001. Scale bars 3 mm in (1–7), 5 mm in (8–12). All from Eager Formation at Locality B unless otherwise stated.

midway between sagittal line and axial furrow, isolated from axial furrow, very shallow or absent over axis (sometimes exaggerated by compaction), abaxial end of well-incised portion slightly anterior to adaxial end of well-incised portion. L2 and

L3 confluent distally, widen (tr.) anteriorly to point of contact with ocular lobes. S3 deepest midway between sagittal line and axial furrow, shallow over axis (depth often exaggerated by compaction-related deformation), isolated from axial furrow,

oriented anterolaterally away from axis to point of contact with ocular lobes. S2 and S3 sometimes shallower than SO and S1 (Figs. 3.8, 4.6). Axial furrow shallow at lateral margins of L3. LA slightly wider (tr.) than long (sag.), approximately 42–53% glabellar length (sag.), lateral margins separated from extraocular area by a sharp break in slope, dorsal convexity uncertain due to taphonomic compaction but probably weakly convex; widest point at intersection with anterior margin of ocular lobes. Weak parafrontal band sometimes present around lateral margin of LA immediately anterior to intersection with ocular lobe, fades anteriorly (Fig. 3.5). Small axial node on posterior margin of LO. Ocular lobes diverge from exsagittal line at approximately 20° (range 14–38°), crescentic, flat-topped, posterior tip transversely opposite mid- to posterior portion of lateral margin of L1, rarely SO (Fig. 4.5, 4.6), proportionally shortening through ontogeny (see below); proximal portion of inner margin flush against and often smoothly merged with anterolateral margin of L3; very shallow ocular furrow, deepest anteriorly, inner band slightly wider (tr.) than outer band. Nature of contact between ocular lobes and LA unclear due to compaction-related deformation; inner band of ocular lobe appears to merge smoothly into LA on better-preserved specimens; some specimens with putative shallow transocular furrow (Fig. 3.2, 3.4) and/or preocular furrow (Fig. 3.5, 3.9–3.11), but either might be artifact of or exaggerated by compaction; some specimens show a dimple-like depression isolated from the axial furrow in the presumed location of the adaxial limit of the preocular furrow (Figs. 3.7, 4.8, 4.10). Interocular area shelf-like or sloping down inwards, slightly narrower to wider (tr.) than ocular lobes (78–192%) and approximately 18–38% width (tr.) of extraocular area opposite S1; some specimens with subtle interocular swelling transversely opposite L1 (Figs. 3.11, 5.1). Extraocular genal caeca present on some specimens (Figs. 3.3, 3.5, 4.6, 4.10, 5.1). Weak intergenal ridge at least occasionally present (Figs. 4.11, 5.1); many specimens show ridge on posterodistal portion of extraocular area that represents either intergenal ridge or posterior ocular line (identification uncertain due to proximal fading of ridge). Genal ridge typically present. Terrace lines or lirae sometimes present on dorsal surface of anterior and lateral cephalic border, extending onto base of genal spine (Figs. 3.1–3.4, 3.6, 3.7, 3.10, 4.8, 4.11, 6.5); rarely on posterior cephalic border (Fig. 3.10, 3.11); sometimes on posterior portion of LO (Figs. 3.1, 3.4, 3.6, 3.7, 3.10, 4.8, 5.2). Terrace lines or lirae on cephalic doublure (Figs. 3.3–3.5, 3.9, 3.10, 4.5, 5.1) and ventral surface of genal spines (Fig. 5.1). Impression of crescentic rostral plate preserved on some specimens (Figs. 5.2, 5.4, 5.6, 6.1–6.3), but too poorly known for description.

Prothorax (Figs. 5, 6.1–6.5) of 14 segments; axis slightly narrower (tr.) than inner pleural region on T1, gently tapers posteriorly. Axial node on at least T3 to T14, sometimes also T1 and T2 (Figs. 5.3, 6.3, 6.4), tiny on anteriormost segments, increasing in size posteriorly down trunk. Inner pleural region of T1 transverse, slightly tapered distally, with slightly curved anterior margin; that of T2 parallel-sided with straight margins. T3 macropleural; pleural spine macrospinous, slender, tip opposite posterior of prothorax (Fig. 5.1, 5.3). Inner pleural region of T4 transverse, slightly tapered distally, with anterior margin slightly curved to accommodate lateral expansion (exsag.) of T3; that of

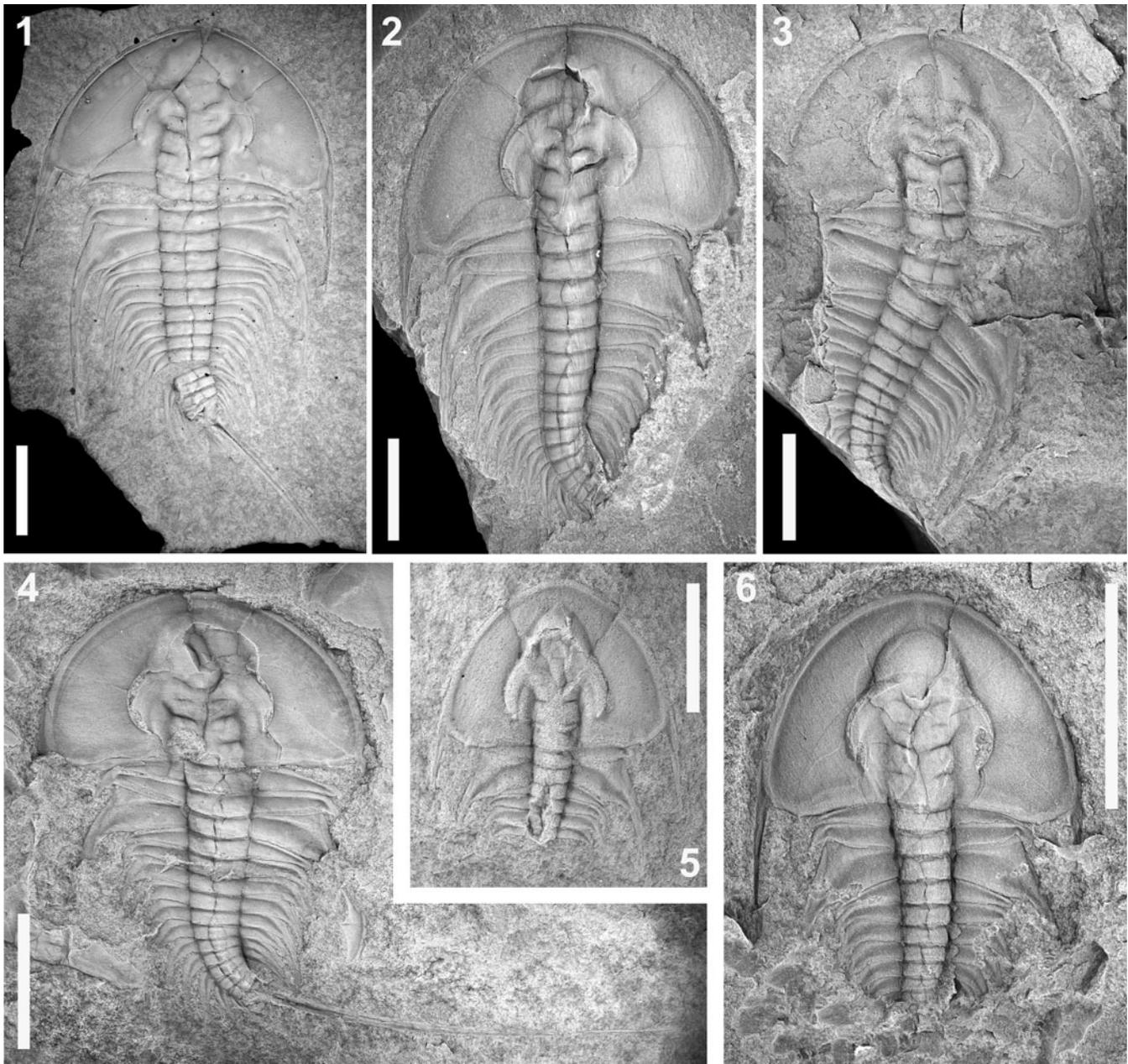
T5 to T8 parallel-sided with straight margins; that of T9 to T14 increasingly divergent to pendent with curved margins. Pleural spine of T1 sentate, that of T2 and T4 sentate to weakly falcate; that of T5 and more posterior segments falcate, increasing in length down thorax. Pleural furrows broad (exsag.), occupying much of inner pleural region; steeper anteriorly; extending onto pleural spine of all segments except T1 and sometimes T2 and T4. Bertillon markings on pleural spine of all prothoracic segments. Long axial spine on T15, length exceeds that of prothorax (Fig. 5.1, 5.4); bears granular ornament. Rest of thorax and pygidium unknown.

*Etymology.*—Named for Guy Santucci of Cranbrook, whose generosity and unwavering enthusiasm was instrumental in establishing and coordinating this research program.

*Ontogeny.*—The smallest studied specimens (sagittal cephalic length 2.33 mm; Fig. 7.1, 7.2) represent phase 4 of cephalic development. Phase 5 of cephalic development was attained by sagittal cephalic length of at least 3.16 mm (Fig. 8.1–8.5).

Relative to the morphologically mature condition (above), specimens in phase 4 of cephalic development exhibit proportionally longer preglabellar field (Figs. 7, 9.1) and a proportionally narrower cephalon. Neither S2 nor S3 are isolated from the axial furrow. The ocular lobes are proportionally longer (Fig. 9.2), with the posterior tip transversely opposite the posterior half of the lateral margin of L1 or SO (Fig. 7). An intergenal spine is prominent, the base of which is located distal to a weak adgenal angle (Fig. 7.2–7.5); the intergenal angle is stronger than the adgenal angle. The full length of the intergenal spine is unknown, but it was probably only slightly shorter than the genal spine (Fig. 7.5). The intergenal spine base is of greater dorsal relief than the posterior cephalic border, and interrupts the border as it crosses from the extraocular area. There are no axial nodes anterior to that on LO.

During phase 5 of cephalic development, the extraocular area (and thus the cephalon) proportionally widened (tr.) (Figs. 8, 9.5). The intergenal angle progressively decreased and the adgenal angle increased in angularity, so that the latter became the prominent deflection of the posterior cephalic margin (compare Fig. 8.1, 8.4, and 8.6 to Figs. 3, 4, 8.8, and 8.10). The base of the genal spine became located relatively farther back on the cephalon (Fig. 9.6). The glabella proportionally elongated (sag.) at the expense of the preglabellar field (Fig. 9.1, 9.3). The ocular lobes proportionally shortened (Fig. 9.2). The intergenal spine reduced in proportional size to become a spinelet, and the dorsal relief of the spine base diminished until it became barely higher than the posterior cephalic border (compare Fig. 8.1–8.4 to Fig. 8.8–8.10). The genal spines proportionally elongated. L3 continued to widen proportionally (tr.), increasing the length of contact between the anterolateral margin of L3 and the inner margin of the ocular lobe. The connection between S3 and the axial furrow shallowed and is more-or-less obsolete on some specimens as small as 4.15 mm in cephalic length (sag.; Fig. 8.7, 8.9). L2 also widened proportionally, especially anteriorly, so that it became increasingly trapezoidal in outline, and the glabella became increasingly constricted at S1. S2 became isolated from the axial furrow (marking entry into late phase 5) on specimens with sagittal cephalic length



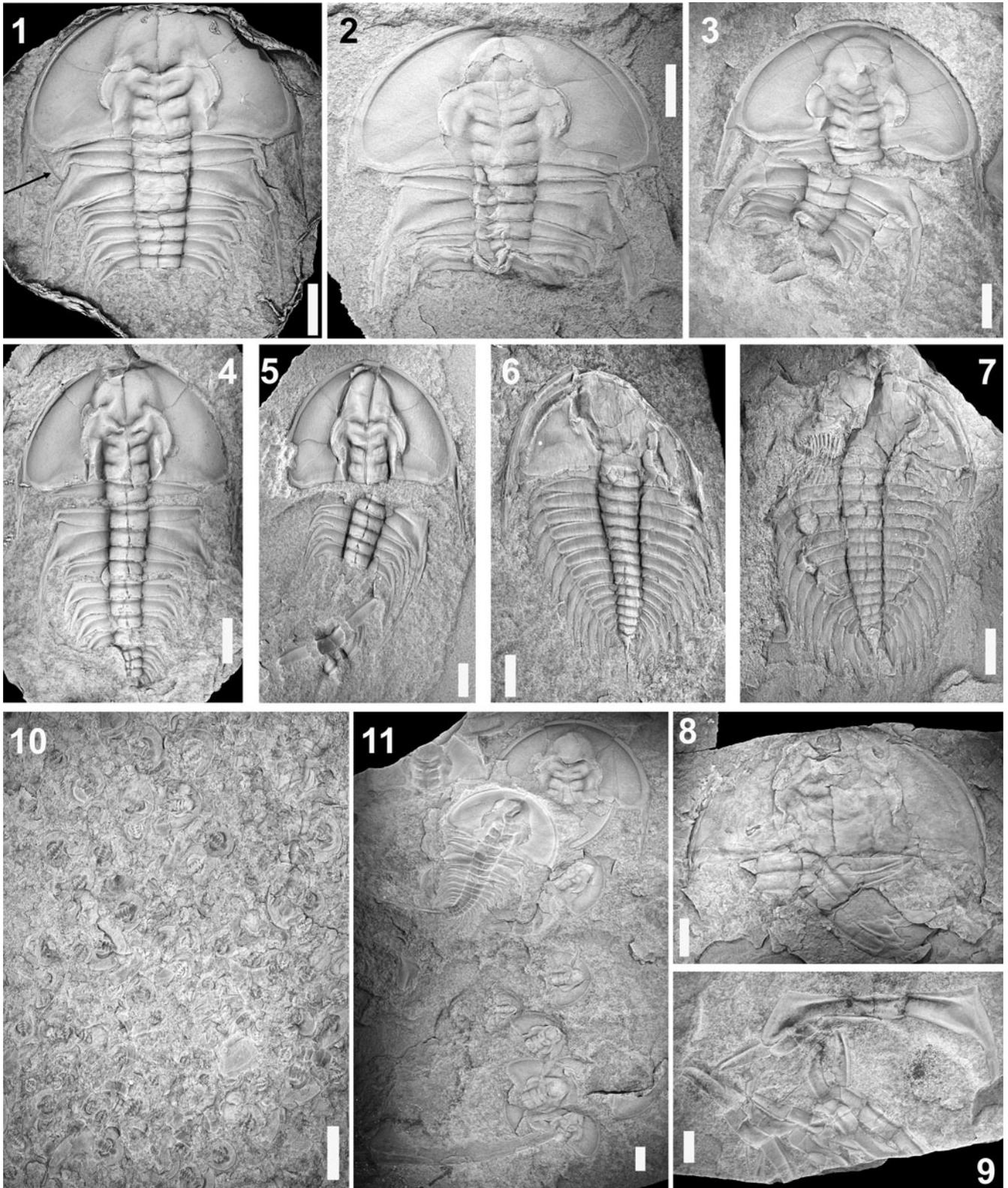
**Figure 5.** Articulated specimens of morphologically mature *Olenellus santuccii* Webster n. sp. from the Cranbrook Lagerstätte. (1) Well-preserved specimen showing slight disarticulations in trunk behind T1 and T10, epoxy cast made from latex peel of internal mold, UBC GT352. This specimen was previously figured by Ludvigsen and Bohach (1996, fig. 4.2c) and Bohach (1997, pl. 20, fig. 8). (2) Specimen with impressions of hypostome and rostral plate more-or-less in life position beneath cephalon, and slight disarticulations behind T12, T13, and T14, RBCM.EH2015.013.0042.001. (3) Specimen with slight disarticulations in trunk behind T1 and T2, RBCM.EH2015.013.0184.001. (4) Specimen with impression of hypostome and rostral plate in slightly displaced positions beneath cephalon, and slight disarticulation at posterior margin of cephalon, RBCM.EH2015.013.0237.004 (see also Fig. 6.11). (5) Specimen with impression of hypostome in life position beneath cephalon, anterior portion of trunk displaced anteriorly beneath posterior margin of cephalon, and disarticulation posterior to T7, latex peel of external mold, RBCM.EH2015.013.0106.005, scale bar 5 mm. (6) Specimen with impression of displaced rostral plate beneath cephalon, RBCM.EH2015.013.0257.001. All scale bars 10 mm unless otherwise stated. All from Eager Formation at Locality B.

as small as 4.90 mm (Fig. 8.7), although some specimens as large as 6.22 mm sagittal cephalic length remained in early phase 5.

Articulated specimens reveal that at least seven thoracic segments were present and that T3 was already macropleural and macrospinous at a sagittal cephalic length of 2.39 mm (Fig. 7.3). The full complement of prothoracic segments and the long axial spine on T15 were present by at least early

phase 5 of cephalic development (sagittal cephalic length 6.2 mm, Fig. 8.8).

**Remarks.**—*Olenellus santuccii* Webster n. sp. is most similar to *Olenellus gilberti*, with which it has historically been confused (Walcott in Schofield, 1921, 1922; Best, 1952a, b). Hu (1985, p. 125) noted that the Cranbrook specimens differed from *Olenellus gilberti* from Nevada, because the latter had “a

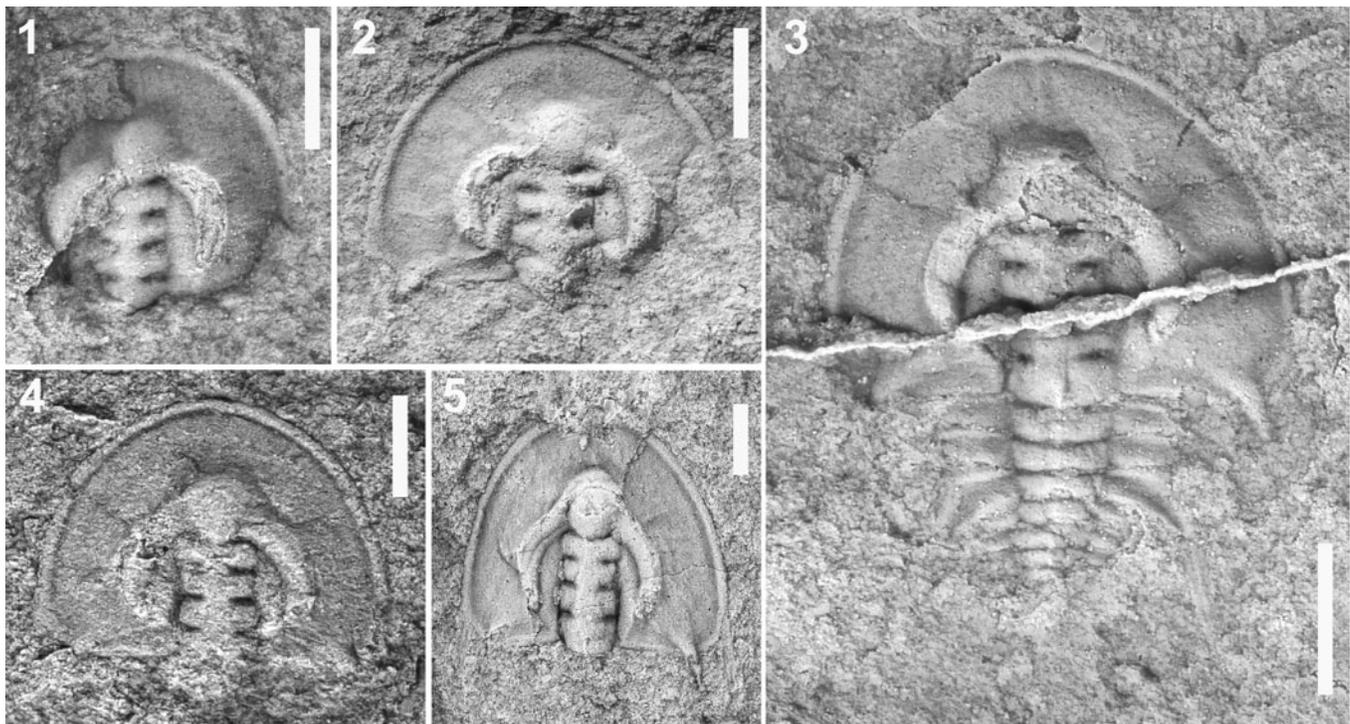


**Figure 6.** Aspects of the preservation and biostratinomy of trilobites at the Cranbrook Lagerstätte. (1–3) Increasingly disrupted sclerite associations of *Olenellus santuccii* Webster n. sp. that might represent exuviae. (1) Specimen with inverted and posteriorly pointing rostral plate (arrowed) in classic ecdysial configuration of olenelloids, lacking trunk posterior to T8, latex peel of external mold, ICS replica # 3788, from USNM Locality 67g; (2) specimen with impression of slightly displaced rostral plate beneath cephalon, and possibly of flipped trunk posterior to T7, latex peel of external mold, RBCM.EH2015.013.0014.001; (3) specimen with impression of slightly displaced rostral plate beneath cephalon, and disarticulated and slightly rotated segments T1 to T7, RBCM.EH2015.013.0192.001. (4, 5) Specimens of *Olenellus santuccii* Webster n. sp. showing closely associated but disarticulated sclerites. (4) “Extended” specimen with disarticulations posterior to T1, T5, T8(?), T9, and T12, latex peel of external mold, USNM PUM78615A, from USNM Locality 67g; (5) specimen with articulated run of T3 to T7 behind and slightly rotated relative to cephalon; inverted segment lying behind T7 might represent T1 or T2 of this individual, and segment immediately behind that segment might represent T7 of this individual, RBCM.EH2015.013.0190.001. (6, 7) Nearly complete specimens of *Wanneria cranbrookense* Webster n. sp. that might represent exuviae. (6) Specimen with impression of slightly displaced rostral plate and hypostome beneath cephalon, and anteriorly displaced thorax with T1 lying below posterior of cephalon, RBCM.EH2015.013.0021.001; (7) specimen with impression of slightly displaced rostral plate beneath cephalon, which is slightly rotated clockwise relative to trunk, RBCM.EH2015.013.0027.001, scale bar 10 mm. (8) Jumble of sclerites of an individual of *Wanneria cranbrookense* Webster n. sp. that is not easily interpreted as an undisturbed ecdysial configuration, RBCM.EH2015.013.0132.001, scale bar 10 mm. (9) Jumble of sclerites (some inverted) of an individual of *Olenellus* sp. indet. that is not easily interpreted as an undisturbed ecdysial configuration, RBCM.EH2015.013.0239.001. (10) “Hash surface” bedding plane with concentration of small cephalae of *Olenellus santuccii* Webster n. sp. and isolated olenellid hypostomes, RBCM.EH2015.013.0182. (11) Surface preserving several specimens of *Olenellus santuccii* Webster n. sp. which seem to show a weak common alignment to the right or upper right, RBCM.EH2015.013.0237 (the articulated specimen, RBCM.EH2015.013.0237.004, is also illustrated as Fig 5.4). All scale bars 5 mm unless otherwise stated. All from Eager Formation at Locality B unless otherwise stated.

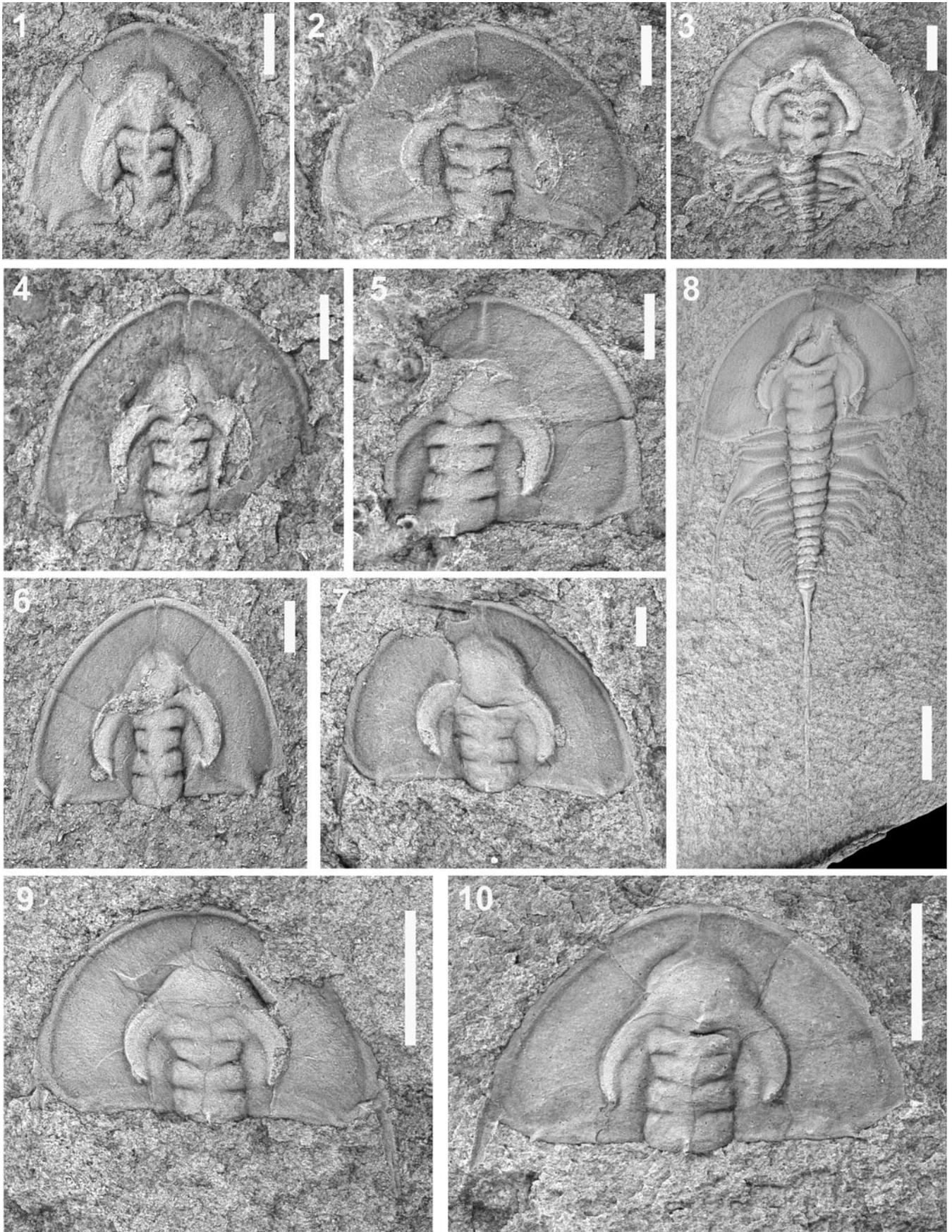
rather transverse cephalic shield, and a large ocular ring [sic, perhaps meaning ocular lobe], which posteriorly protrudes”. However, Hu (1985) was using as his point of comparison the silicified material of “*Olenellus gilberti*” described by Palmer (1957), which has since been reassigned to *Olenellus* aff. *O. fowleri* (Webster, 2011b, c, 2015).

*Olenellus santuccii* Webster n. sp. can be distinguished from *Olenellus gilberti* sensu stricto by several features. Over the sampled portion of ontogeny, *Olenellus santuccii* Webster n. sp. has proportionally shorter (exsag.) ocular lobes (Fig. 9.2), a proportionally shorter (sag.) glabella (Fig. 9.3), a proportionally longer (sag.) preglabellar field (Fig. 9.1), and a proportionally shorter (sag.) anterior cephalic border (Fig. 9.4) compared to *Olenellus gilberti*. Comparison of

data for specimens of sagittal cephalic length > 10 mm (to reduce the complicating effects of ontogenetic allometry) reveals that the differences are statistically significant: Student’s t-test of relative glabellar length,  $t = 8.339$ ,  $df = 252$ ,  $p < 0.001$ ; Student’s t-test of relative preglabellar field length,  $t = -20.135$ ,  $df = 237$ ,  $p < 0.001$ ; Student’s t-test of relative anterior border length,  $t = 22.326$ ,  $df = 237$ ,  $p < 0.001$ ; Student’s t-test of relative ocular lobe length,  $t = 30.237$ ,  $df = 187$ ,  $p < 0.001$ . On the thorax, *Olenellus santuccii* Webster n. sp. bears axial nodes on at least T3 to T14 (sometimes also T1 and T2), whereas *Olenellus gilberti* never bears axial nodes on T3 to T5 (axial nodes are invariably present on T11 to T14, and variably present or absent on T1, T2, and T6 to T10; Webster, 2015).



**Figure 7.** Morphologically immature specimens of *Olenellus santuccii* Webster n. sp. from the Cranbrook Lagerstätte. All in phase 4 of cephalic development. (1) Cephalon, latex peel of external mold, RBCM.EH2015.013.0002.003. (2) Cephalon, RBCM.EH2015.013.0081.003. (3) Cephalon with partial thorax, latex peel of external mold, RBCM.EH2015.013.0246.001. (4) Cephalon, RBCM.EH2015.013.0006.004. (5), Cephalon, RBCM.EH2015.013.0154.004. All scale bars 1 mm. All from Eager Formation at Locality B.



**Figure 8.** Morphologically immature specimens of *Olenellus santuccii* Webster n. sp. from the Cranbrook Lagerstätte. All in early phase 5 of cephalic development unless otherwise stated. (1) Cephalon in earliest phase 5 of development, RBCM.EH2015.013.0140.001. (2) Cephalon in earliest phase 5 of development, RBCM.EH2015.013.0107.001. (3) Cephalon in earliest phase 5 of development with partial thorax, latex peel of external mold, RBCM.EH2015.013.0090.001. (4) Cephalon, RBCM.EH2015.013.0182.001. (5) Cephalon, RBCM.EH2015.013.0208.001. (6) Cephalon, RBCM.EH2015.013.0130.001. (7) Cephalon in late phase 5 of cephalic development, RBCM.EH2015.013.0193.001. (8) Almost complete dorsal exoskeleton, latex peel of external mold, RBCM.EH2015.013.0002.001. (9) Cephalon, RBCM.EH2015.013.0007.002. (10) Cephalon, RBCM.EH2015.013.0100.004. Scale bars 1 mm in (1–7), 3 mm in (8–10). All from Eager Formation at Locality B.

Differences between what is here formally named *Olenellus santuccii* Webster n. sp. and *Olenellus gilberti* were also previously noted in the theses by Best (1952a, 1959) and Bohach (1997). Best (1952a, p. 35–37, frontispiece, pl. 2, figs. 6–10 and p. 44–45, pl. 2, figs. 1–5) referred to the Canadian form as “*Olenellus cf. gilberti*” and “*Paedeumias nevadensis*” and later (Best, 1959, p. 95–96, pl. 1, fig. 1) described it as an informal new species “*Olenellus garretti*”; Bohach (1997, p. 199–203, pl. 29, figs. 5–8, 12, pl. 21, figs. 1–11, text-fig. 42) described it as an informal new species “*Olenellus ricei*”. However, neither of those proposed names were published, and they are thus nomina nuda.

*Olenellus santuccii* Webster n. sp. differs from *Mesonacis fremonti* most obviously by possessing a well-developed preglabellar field (which is absent or extremely short in the latter species), and by possessing a proportionally shorter (measured perpendicular to margin) anterior and lateral cephalic border. The ocular lobes of *Mesonacis fremonti* are typically proportionally shorter than those of *Olenellus santuccii* Webster n. sp., although some overlap occurs.

The ontogenetic development of *Olenellus santuccii* Webster n. sp. is similar to that of *Olenellus gilberti*. Over the portion of ontogeny that is known for both species, the two species underwent homologous patterns of glabellar shape change (i.e., phases 4 and 5 of cephalic development are applicable to both species) and achieved the transition between those phases of development at similar size: the sagittal cephalic length at which *Olenellus santuccii* Webster n. sp. transitioned into phase 5 (i.e., 3.16 mm) closely matches that at which *Olenellus gilberti* underwent the same transition (i.e., somewhere between 3.13 mm and 3.57 mm; Webster, 2015). The ontogenetic changes in other aspects of cephalic shape (above) are also seen in *Olenellus gilberti* (Fig. 9.1–9.4; Webster, 2015). This indicates a strong degree of evolutionary conservatism between these closely related species in these aspects of cephalic growth.

No thoracic segments posterior to T15 were observed on the specimens of *Olenellus santuccii* Webster n. sp. studied herein, and the opisthothorax and pygidium are therefore treated as unknown. However, Best (1952b, p. 18; see also Hu, 1985, p. 128) stated that “rudimentary [i.e., opisthothoracic] segments were observed doubtfully on only one specimen; no less than three appear to be present” (this observation was subsequently qualified as “very doubtfully recorded” by Best [1959, p. 96]), and Bohach (1997, p. 201) noted that “an indication of two opisthothoracic segments is present on one specimen”. It is therefore possible that scrutiny of the vast number of specimens of this species in the collections of the University of British Columbia, or in private collections, would yield more information regarding the posterior of the trunk.

The large sample size of *Olenellus santuccii* Webster n. sp. allows assessment of intraspecific variation among morphologically

mature specimens. Like *Olenellus gilberti* (Webster, 2015, p. 57–60), *Olenellus santuccii* Webster n. sp. shows intraspecific variation in the presence or absence (and sometimes prominence) of qualitative cephalic features such as extraocular genal caeca, intergenal ridge, and terrace lines or lirae. The course of the genal ridge can be strongly asymmetric on the left versus the right side of the cephalon (Fig. 10). Such asymmetry is evident in other olenelloids (e.g., Palmer and Repina, 1993, fig. 13). Documentation of variation and asymmetry in such traits is crucial for robust species delimitation and for accurate coding of phenotypic characters in cladistic analyses (see Webster, 2015, p. 64); it can also be pertinent to the investigation of mechanisms and constraints of phenotypic evolution (Webster, 2007c, 2015, 2019).

#### *Olenellus? schofieldi* Best, 1952

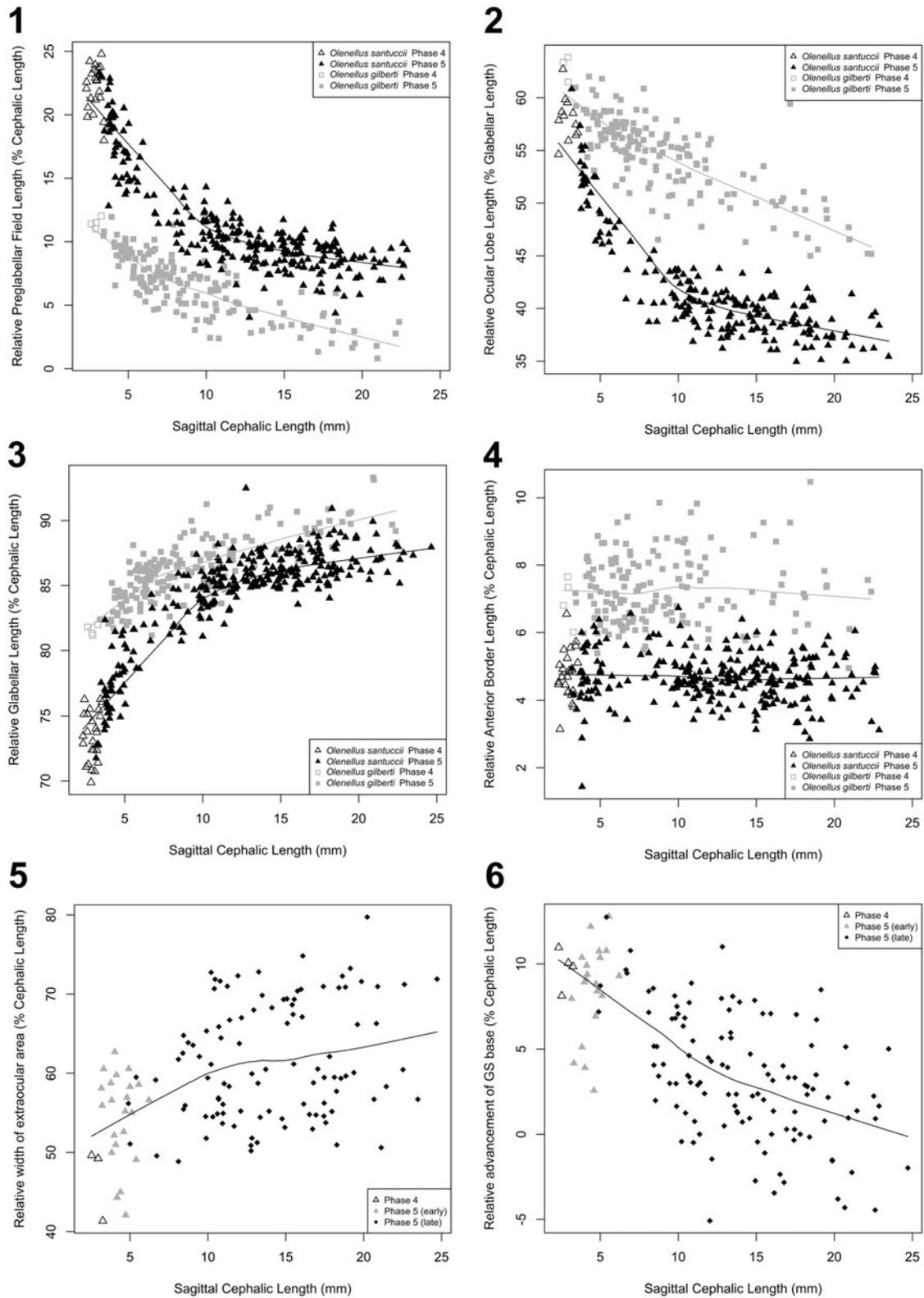
##### Figure 11

- ?1921 *Olenellus cf. fremonti* Walcott, 1910; Schofield, p. 666.
- ?1922 *Olenellus cf. fremonti*; Schofield, p. 12.
- 1952b *Olenellus schofieldi* Best, p. 13, 16–19, pl. 1, figs. 1–4.
- 1956 *Olenellus schofieldi*; Okulitch, p. 715.
- 1992 *Olenellus schofieldi*; Fritz, p. 19.
- 1999 *Olenellus schofieldi*; Lieberman, p. 39–40.

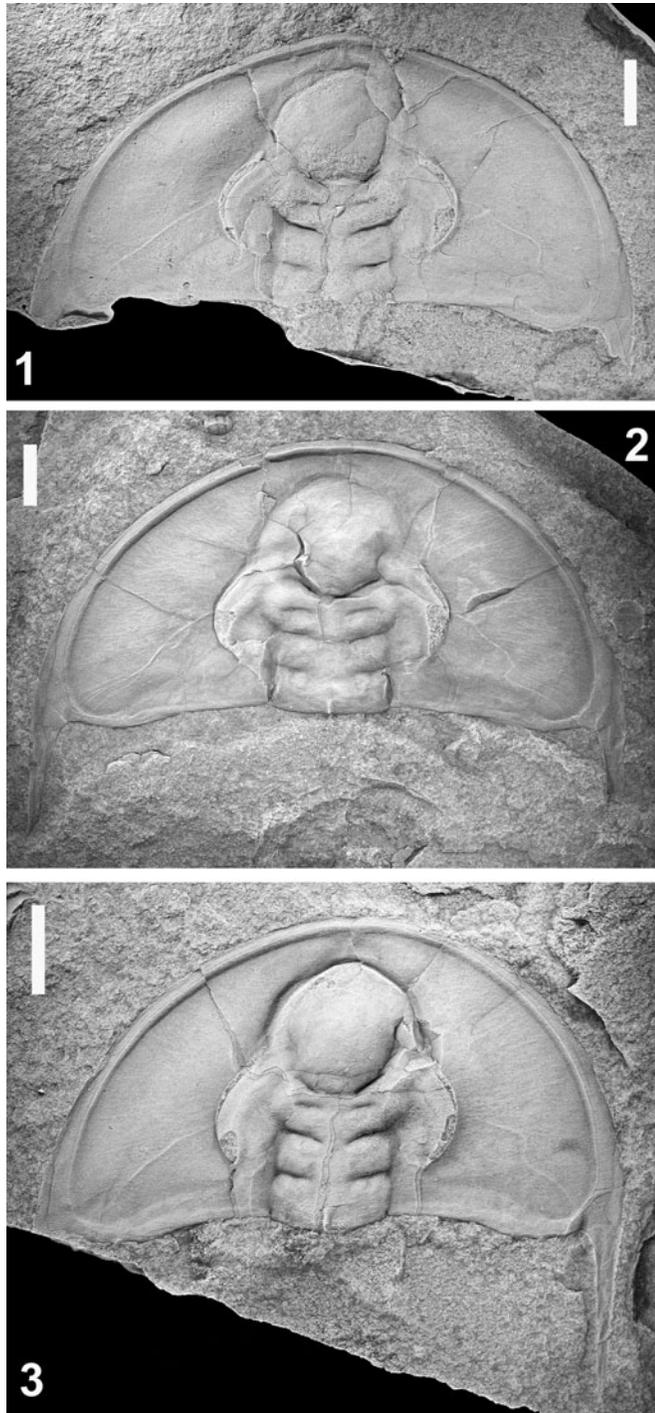
**Holotype.**—Almost complete dorsal exoskeleton UBC GT201 (Fig. 11.1), from Eager Formation (Cambrian Stage 4), Locality B, Cranbrook, British Columbia.

**Diagnosis.**—Base of genal spine transversely opposite posterior portion of lateral margins of LO. Intergenal spine represented by spinelet or small node on posterior cephalic border approximately midway between adgenal angle and base of genal spine. Cephalic border short, approximately 25% length (exsag.) of LO. Preglabellar field very short (sag.) or absent; when present, approximately as long as cephalic border; plectrum absent. Basal glabellar width (tr.) approximately 22% of distance between genal spine bases. Posterior tip of ocular lobe transversely opposite anterior half of lateral margin of L1. Elongate interocular swelling transversely opposite L1. Axis of T1 marginally narrower (tr.) than inner pleural region. Axial node on posterior margin of all known thoracic segments. Pleural spines slender. Pleural furrows broad (exsag.), occupying much of inner pleural region; extending onto pleural spines of at least T1 to T11.

**Occurrence.**—*Olenellus? schofieldi* is a rare species, known from very few specimens at Locality B and from an inferred occurrence at Cranbrook Junction (Appendix). Only two specimens of the species were recovered during the 2015 excavation of Locality B; those two specimens happened to be on the same slab. The ontogeny of the species is unknown.



**Figure 9.** Ontogenetic change in linear dimensions of *Olenellus santuccii* Webster n. sp. from the Cranbrook Lagerstätte. All plots are fitted with a LOWESS regression line for ease of visualization. (1) Proportional length of the preglabellar field (sag., relative to sagittal cephalic length), with data for *Olenellus gilberti* (in gray) for comparison. (2) Proportional length of the ocular lobe (exsag., relative to sagittal length of the glabella), with data for *Olenellus gilberti* (in gray) for comparison. (3) Proportional length of the glabella (sag., relative to sagittal cephalic length), with data for *Olenellus gilberti* (in gray) for comparison. (4) Proportional length of the anterior cephalic border (sag., relative to sagittal cephalic length), with data for *Olenellus gilberti* (in gray) for comparison. (5) Proportional width of the extraocular area (measured as the transverse distance between the base of the genal spine [GS] and the axial furrow at the posterior of the glabella, relative to sagittal cephalic length). This variable is calculated as the ratio between a transverse width and a sagittal length and is therefore more prone to distortion by tectonic deformation than the other variables plotted in this figure. (6) Proportional advancement of the genal spine (GS) base (measured as the exsagittal anterior displacement of the genal spine base from the posterior margin of the glabella, relative to cephalic length).

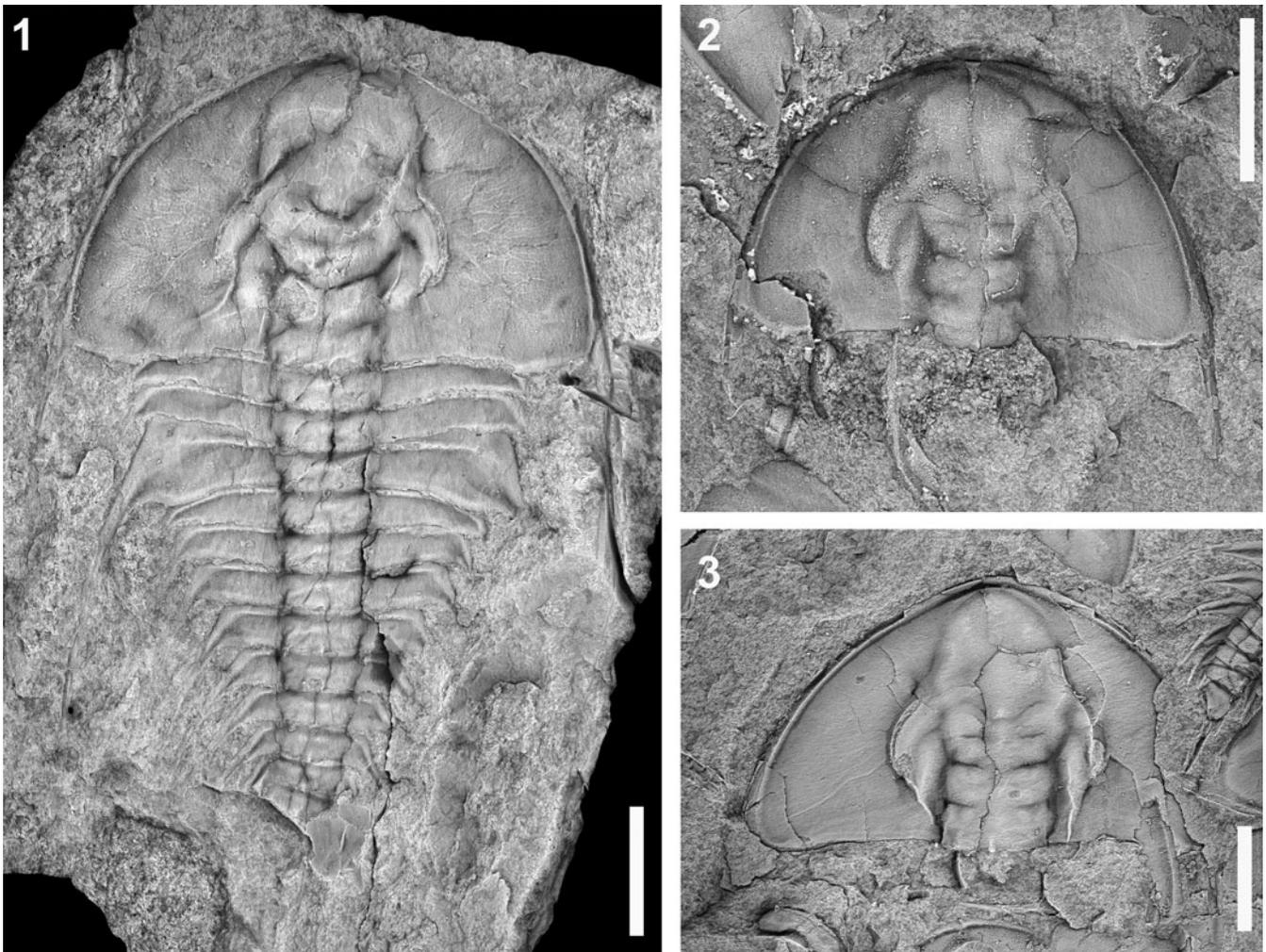


**Figure 10.** Morphologically mature cephalons of *Olenellus santuuccii* Webster n. sp. from the Cranbrook Lagerstätte showing asymmetrical genal ridges. (1) Latex peel of external mold, RBCM.EH2015.013.0264.001. (2) Internal mold, RBCM.EH2015.013.0249.001. (3) Internal mold, RBCM.EH2015.013.0228.001. All scale bars 5 mm. All from Eager Formation at Locality B.

**Description.**—Cephalon roughly semicircular in outline, widest (tr.) at base of genal spines. Proximal portion of posterior cephalic margin oriented slightly posteriorly when traced distally, distal portion flexed slightly anteriorly relative to proximal portion at weak adgenal angle estimated to lie roughly two-thirds to three-quarters of distance from axial furrow to

base of genal spine. Greatest observed cephalic length approximately 13.5 mm (sag.; Fig. 11.3); although Best (1952a) mentioned a specimen with cephalic length of 17.1 mm, not seen by the present authors. Genal spine slender, length approximately 30–40% of sagittal cephalic length; base transversely opposite posterior portion of lateral margins of LO; posterior tip opposite axial ring of T2 or T3. Intergenal spine represented by spinelet or small node on posterior cephalic border approximately midway between adgenal angle and base of genal spine. Cephalic border weakly convex dorsally, well defined around entire cephalon by distinct border furrow; radial length of anterior border (measured perpendicular to margin) opposite junction of ocular lobes with LA approximately 25% length (exsag.) of LO. Glabella weakly constricted at S1; approximately 95% of cephalic length (sag.), preglabellar field very short (sag.) or absent; when present, approximately as long as cephalic border; plectrum absent. Maximum width of LA approximately considerably wider than (132–152%) basal glabellar width (tr.). Posterior convexity of posterior margin of glabella difficult to determine due to taphonomic fracturing.

SO deep only abaxially, abaxial end slightly anterior to adaxial end. LO subtrapezoidal, slightly narrows anteriorly, length (exsag.) approximately 15% glabellar length (sag.). S1 deepest abaxially, very shallow over axis; deeply incised portions approximately parallel to those of SO but slightly arcuate (weakly convex anteriorly). L1 subtrapezoidal, slightly narrows anteriorly; length (exsag.) approximately 15% glabellar length (sag.). S2 deepest midway between sagittal line and axial furrow, isolated from axial furrow, probably absent over axis (condition complicated by compaction), abaxial end of well-incised portion transversely opposite or very slightly anterior to adaxial end of well-incised portion. L2 and L3 confluent distally, widen (tr.) anteriorly to point of contact with ocular lobes. S3 deepest midway between sagittal line and axial furrow, probably shallow over axis (depth exaggerated by compaction-related deformation), isolated from axial furrow, oriented anterolaterally away from axis to point of contact with ocular lobes. Glabellar furrows S2 and S3 slightly shallower than SO and S1 on some specimens (Fig. 11.2, 11.3). LA slightly wider (tr.) than long (sag.), approximately 48–50% glabellar length (sag.), separated from extraocular area by a sharp break in slope, dorsal convexity uncertain due to taphonomic compaction but probably weakly convex; widest point at intersection with anterior margin of ocular lobes. Low ridge around anterolateral margin of LA on one specimen (Fig. 11.3) might represent weak parafrontal band or taphonomic artifact. Small axial node on posterior margin of LO. Ocular lobes diverge from exsagittal line at approximately 20°, crescentic, flat-topped, posterior tip transversely opposite anterior half of lateral margin of L1; proximal portion of inner margin flush against anterolateral margin of L3 but separated from it by shallow continuation of axial furrow that fades anteriorly; shallow ocular furrow, deepest anteriorly, inner band slightly wider (tr.) than outer band. Inner band of ocular lobe merges smoothly into LA; shallow preocular furrow present on at least one specimen (Fig. 11.2). Interocular area gently arched in transverse section and sloping down inwards, slightly narrower to wider (tr.) than ocular lobes (88–130%) and approximately 25% width (tr.) of extraocular area opposite S1; subtle, elongate interocular swelling transversely opposite L1. Extraocular genal



**Figure 11.** Morphologically mature specimens of *Olenellus? schofieldi* Best, 1952b, from the Cranbrook Lagerstätte. (1) Almost complete dorsal exoskeleton, epoxy cast made from latex peel of internal mold, holotype, UBC GT201. This specimen was previously figured by Best (1952a, pl. 1, fig. 14; 1952b, pl. 1, fig. 1) and Bohach (1997, pl. 23, fig. 8). (2) Cephalon, internal mold, RBCM.EH2015.013.0029.003. (3) Cephalon, internal mold, RBCM.EH2015.013.0029.002. All scale bars 5 mm. All from Eager Formation at Locality B.

caeca and genal ridge present. Posterior ocular line and intergenal ridge at least occasionally present (Fig. 11.1, 11.3).

Thorax of at least 12 segments (Fig. 11.1); axis marginally narrower (tr.) than inner pleural region on T1, gently tapers posteriorly. Axial node on posterior margin of all known segments, tiny on anterior segments, larger on more posterior segments (Fig. 11.1). Inner pleural regions of T1 and T2 transverse, with straight margins; T1 slightly tapered distally. T3 macropleural; pleural spine macrospinous, slender, tip opposite axial ring of T10 (Fig. 11.1). Inner pleural region of T4 roughly transverse, slightly tapered, margins slightly curved to accommodate lateral expansion (exsag.) of T3. Inner pleural regions of T5 to T10 transverse, parallel-sided, with straight margins; those of T11 slightly divergent with curved margins; those of T12 unknown. Pleural spines of T1, T2, and T4 sentate, very slender, divergent; those of T5 to T10 slender, falcate, increasing in length to at least T9 (tips not preserved on T10 to T12). Pleural furrows broad (exsag.), occupying much of inner pleural region; steeper anteriorly; extending onto pleural spines of at least T1 to T11. Rest of thorax, rostral plate, and pygidium unknown.

**Remarks.**—*Olenellus schofieldi* has not yet been included in a cladistic analysis, and its generic assignment is uncertain. It has variously been assigned to *Olenellus* (Best, 1952a, b; Fritz, 1992; tentatively by Lieberman, 1999), to *Mesonacis* (tentatively, in the unpublished thesis by Bohach, 1997, p. 215–217, pl. 23, figs. 6–8), and to *Olenellus (Fremontia)* in the unpublished thesis by Best (1959, p. 128). It shares many traits with *Mesonacis eagerensis* and *Mesonacis vermontanus* (Hall, 1859), including a proportionally short cephalic border, a very short to absent preglabellar field, a proportionally narrow thorax, broad (exsag.) thoracic pleural furrows, and slender pleural spines. However, several of those traits are also shown by species such as *Olenellus terminatus* Palmer, 1998a. Pending completion of a new phylogenetic analysis, the species is tentatively assigned to *Olenellus* following Lieberman (1999, p. 39–40).

*Olenellus terminatus* differs from *Olenellus? schofieldi* most obviously by having a proportionally longer preglabellar field, by having strongly developed Bertillon markings on the extraocular area, by having longer ocular lobes (posterior tip

typically transversely opposite the lateral margin of SO or anterior portion of LO), and by having shorter pleural spines on the non-macropleural thoracic segments. No other species of *Olenellus* shares the combination of proportionally short cephalic border, very short to no preglabellar field, and proportionally short ocular lobes exhibited by *Olenellus? schofieldi*.

Differences among *Olenellus? schofieldi*, *Mesonacis eagerensis*, and *Mesonacis vermontanus* are more subtle. The posterior portion of the glabella is proportionally narrower in *Olenellus? schofieldi*: the basal glabellar width (tr.) is approximately 22% of the distance between the genal spine bases in *Olenellus? schofieldi*, compared to 29–33% in *Mesonacis eagerensis* and 29–31% in *Mesonacis vermontanus*. The base of the genal spine is typically more strongly advanced in *Mesonacis eagerensis* (transversely opposite the lateral margins of LO, SO, or posterior portion of L1) than in *Olenellus? schofieldi* (transversely opposite posterior portion of lateral margins of LO), although there is some overlap when described in a qualitative sense. The thoracic pleural spines of *Mesonacis eagerensis* of T1, T2, and T4 to T10 are shorter than those of *Olenellus? schofieldi*, and the pleural furrows of T1, T2, and T4 to T8 do not extend onto the pleural spines in *Mesonacis eagerensis*, but do so in *Olenellus? schofieldi*. The thoracic pleurae of *Mesonacis vermontanus* decrease in proportional width (tr., relative to the transverse width of the corresponding axial ring) less strongly down the thorax than do those of *Olenellus? schofieldi*, so that the pleurae of segments posterior to T6 are markedly less well developed (relative to the axis) in the latter species. The interocular area of both species is dorsally arched, but *Mesonacis vermontanus* lacks the interocular swelling transversely opposite L1 that is often developed in *Olenellus? schofieldi*.

#### Genus *Mesonacis* Walcott, 1885

*Type species*.—*Olenus vermontana* Hall, 1859, from the Parker Formation (Dyeran Stage of Laurentia, Cambrian Stage 4) of Vermont.

*Remarks*.—Palmer and Repina (1993, Palmer and Repina in Whittington et al., 1997) treated *Mesonacis* as a subgenus of *Olenellus*, but Lieberman (1999) recognized *Mesonacis* as a distinct genus. *Fremontia* Raw, 1936 (type species *Olenellus fremonti* Walcott, 1910) and *Angustolenellus* Palmer and Repina, 1993 (type species *Olenellus hamoculus* Cowie and McNamara, 1978) are currently considered to be junior synonyms of *Mesonacis* (following Lieberman, 1998, 1999). The genus currently includes seven named species (Lieberman, 1999; Gapp and Lieberman, 2014).

Assignment of species to olenellid genera such as *Olenellus* or *Mesonacis* can be problematic (see remarks for *Olenellus* and *Olenellus? schofieldi*, above). It is likely that such genera comprise more than one distinct species group (see also Palmer, 1998a). Within *Mesonacis* (as currently defined), species such as *Mesonacis fremonti* show marked differences from *Mesonacis vermontanus*, which suggests a closer affiliation to *Olenellus*, and it is likely that a new phylogenetic analysis (MW, in preparation) will shuffle species assignments between existing (and new or re-established) genera. However, Lieberman's (1999) cladistic analysis supported a sister-species relationship between

*Mesonacis eagerensis* and *Mesonacis vermontanus*, and generic assignment of *Mesonacis eagerensis* is likely to be robust even if some other species are ultimately excluded from *Mesonacis*.

#### *Mesonacis eagerensis* (Best, 1952)

##### Figures 12, 13

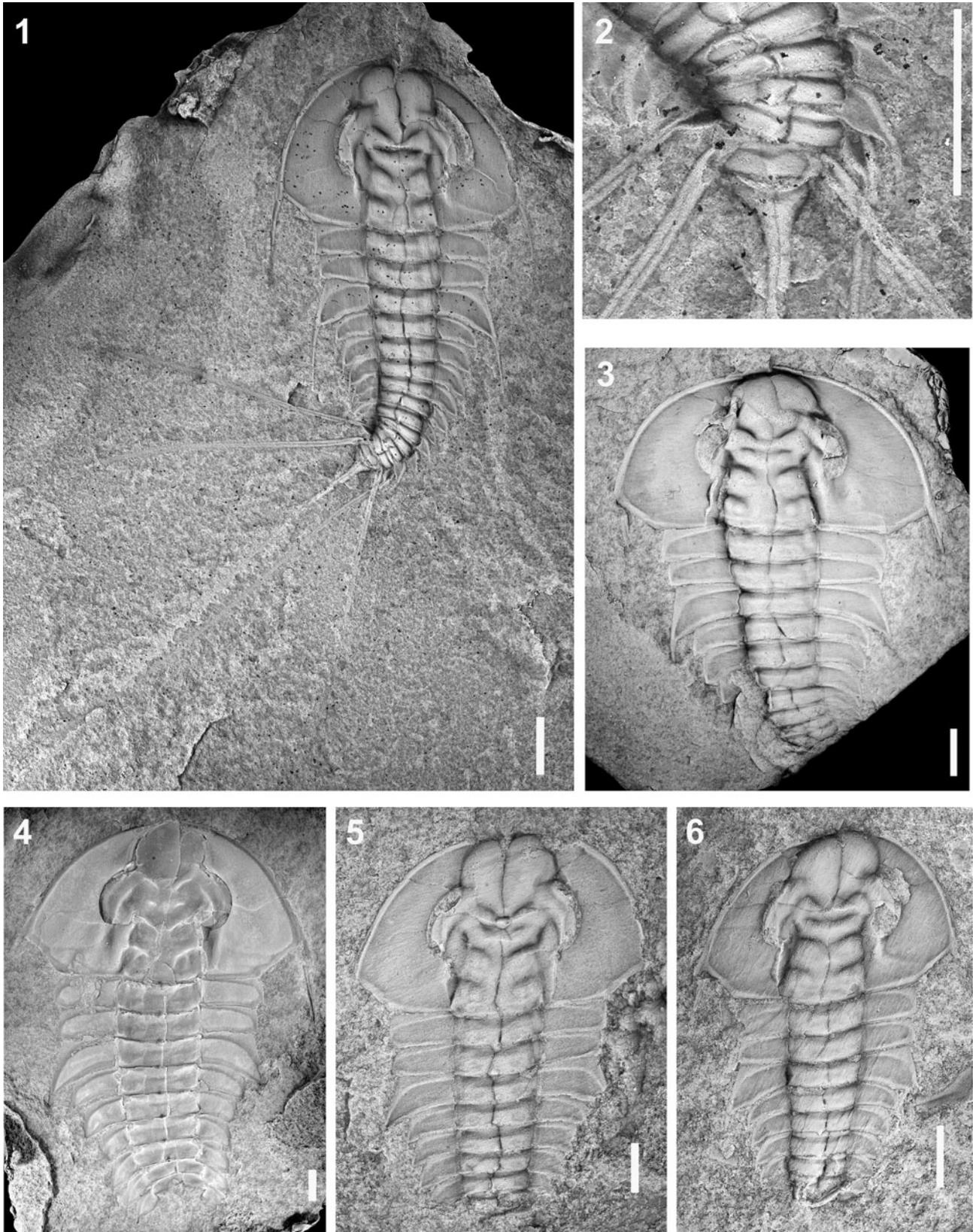
- 1952b *Olenellus eagerensis* Best, 1952b, p. 13, 16–20, pl. 1, figs. 5–12.  
 1956 *Olenellus eagerensis*; Okulitch, p. 715.  
 1978 *Olenellus eagerensis*; Cowie and McNamara, p. 630.  
 1978 *Olenellus (Olenellus) eagerensis*; McNamara, p. 642, 650–651.  
 1985 *Olenellus gilberti* Meek in White, 1874; Hu (part), pl. 1, fig. 15 only.  
 1999 *Mesonacis eagerensis*; Lieberman, p. 38, 40, 43–44.  
 2002 *Mesonacis eagerensis*; Lieberman, p. 699.  
 2003b *Mesonacis eagerensis*; Lieberman, p. 63.  
 2014 *Mesonacis eagerensis*; Gapp and Lieberman, p. 486.

*Holotype*.—Cephalon and anterior prothorax UBC GT101 (Fig. 12.4), from Eager Formation (Cambrian Stage 4), Locality B, Cranbrook, British Columbia.

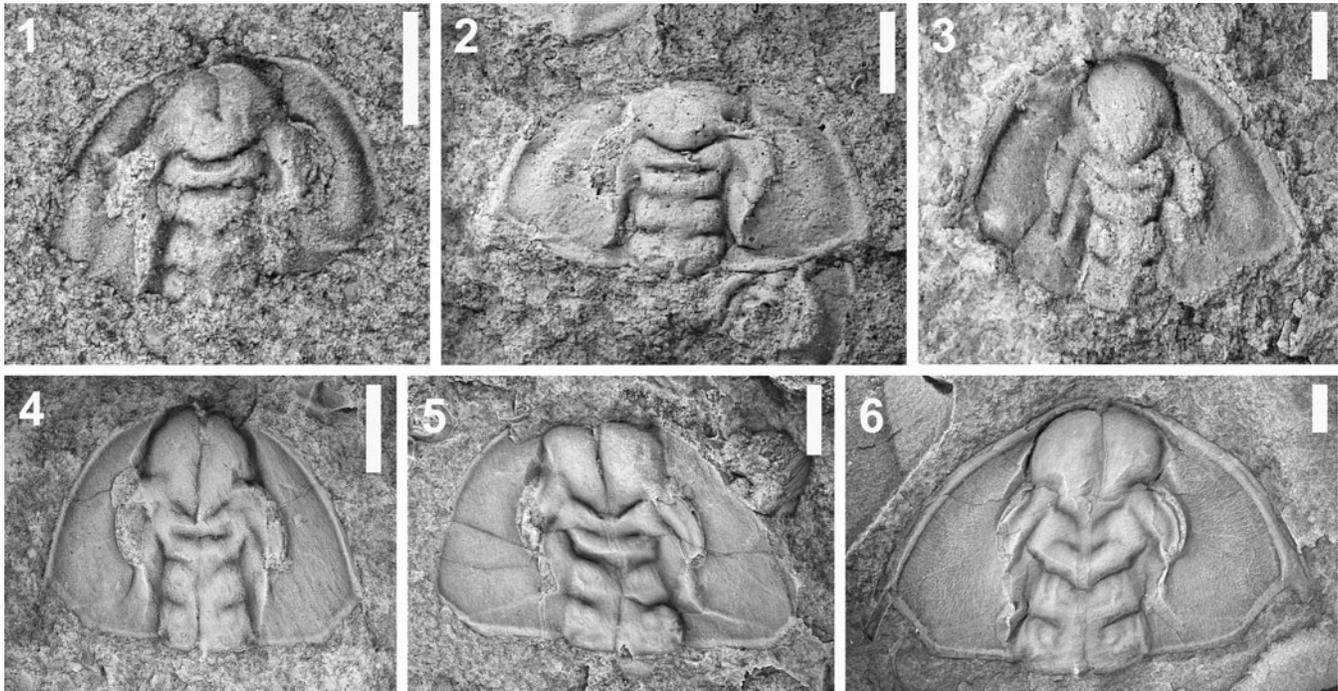
*Diagnosis*.—Base of genal spine transversely opposite lateral margins of LO, SO, or posterior portion of L1. Intergenal spine absent or represented by small node or dorsal swelling on posterior cephalic border approximately midway between adgenal angle and base of genal spine. Cephalic border short, approximately one-fifth length (exsag.) of LO. Preglabellar field absent. Basal glabellar width (tr.) approximately 30% of distance between genal spine bases. Posterior tip of ocular lobe transversely opposite distal tip of S1 or anterior portion of lateral margin of L1. Elongate interocular swelling transversely opposite L1. Axis of T1 wider (tr.) than inner pleural region. Axial node on posterior margin of all known thoracic segments. Pleural spines slender; those of T1, T2, and T4 to T9 sentate; those of T13 and T14 dolichospinous. Pleural furrows broad (exsag.), occupying much of inner pleural region; extending onto pleural spines of T3 and T9 to T14.

*Occurrence*.—Known from several specimens at Locality A and Locality B of Best (1952a, b), plus the St. Mary River locality, USNM Locality 67f, USNM Locality 67g, and an unknown site in the Cranbrook area (Appendix). Ten specimens of the species were recovered during the 2015 excavation of Locality B.

*Description (morphologically mature specimens; sagittal cephalic length > 5 mm)*.—Cephalon roughly pentagonal in outline, widest (tr.) at base of genal spines. Proximal portion of posterior cephalic margin oriented more-or-less transversely or weakly anteriorly by up to 6° relative to a transverse line when traced distally, distal portion flexed anteriorly by approximately 38° (range 28–48°) relative to proximal portion at adgenal angle located approximately 60% of distance from axial furrow to base of genal spine. Greatest observed cephalic length approximately 17.5 mm (sag.; Fig. 13.6). Genal spine



**Figure 12.** Morphologically mature specimens of *Mesonacis egerensis* (Best, 1952b) from the Cranbrook Lagerstätte. (1, 2) Almost complete dorsal exoskeleton, latex peel of external mold, RBCM EH96.05.0001. This specimen was previously figured by Bohach (1997, pl. 22, figs. 4, 5); (1) entire specimen, showing array of remarkably long spines on posterior portion of trunk; (2) enlargement of posterior portion of trunk, showing bases of long pleural spines on T13 and T14 and axial spine on T15. (3) Cephalon and anterior prothorax, latex peel of external mold, ICS replica # 3791, from USNM Locality 67g. (4) Cephalon and anterior prothorax, latex peel of internal mold, holotype, UBC GT101. This specimen was previously figured by Best (1952b, pl. 1, fig. 5) and Bohach (1997, pl. 22, fig. 3). (5) Cephalon and anterior prothorax, latex peel of external mold, RBCM.EH2015.013.0195.001. (6) Cephalon and anterior prothorax, RBCM.EH2015.013.0191.001. All scale bars 3 mm. All from Eager Formation at Locality B unless otherwise stated.



**Figure 13.** Cephalons of *Mesonacis egerensis* (Best, 1952b) from the Cranbrook Lagerstätte. (1) Morphologically immature cephalon in phase 4 or 5 of development, internal mold, RBCM.EH2015.013.0086.001. (2) Tentatively assigned morphologically immature cephalon in early phase 5 of development, internal mold, RBCM.EH2015.013.0179.001. (3) Morphologically immature cephalon in early phase 5 of development, internal mold, RBCM.EH2015.013.0162.001. (4) Morphologically mature cephalon, internal mold, RBCM.EH2015.013.0191.002. (5) Morphologically mature cephalon, latex peel of external mold, RBCM.EH2015.013.0199.001. (6) Largest known morphologically mature cephalon, internal mold, RBCM.EH2015.013.0212. Scale bars 1 mm in (1–3), 3 mm in (4–6). All from Eager Formation at Locality B.

slender, length approximately 40% of sagittal cephalic length; base transversely opposite lateral margins of LO, SO (Figs. 12.4, 12.6, 13.4), or posterior portion of L1 (Fig. 13.6); posterior tip opposite axial ring of T2 or T3 (Fig. 12.1, 12.4). Intergenal spine represented by small node or dorsal swelling on posterior cephalic border approximately midway between adgenal angle and base of genal spine; absent on largest cephalon (Fig. 13.6). Cephalic border weakly convex dorsally, well defined around entire cephalon by distinct border furrow; radial length of anterior border (measured perpendicular to margin) opposite junction of ocular lobes with LA approximately one-fifth (16–31%) length (exsag.) of LO. Glabella weakly constricted at S1; approximately 96% of cephalic length (sag.), preglabellar field absent. Maximum width of LA approximately equal to or slightly wider than basal glabellar width (tr.) (99–117%). Posterior convexity of posterior margin of glabella difficult to determine due to taphonomic fracturing.

SO deep only abaxially, abaxial end slightly anterior to adaxial end. LO subtrapezoidal, slightly narrows anteriorly, length (exsag.) approximately 18% glabellar length (sag.); sometimes with weak lateral swelling (Fig. 12.3). S1 deepest abaxially, very shallow over axis; deeply incised portions approximately parallel to those of SO but slightly arcuate (weakly convex anteriorly). L1 subtrapezoidal, slightly narrows anteriorly; length (exsag.) approximately 17% glabellar length (sag.). S2 deepest midway between sagittal line and axial furrow, isolated from axial furrow, very shallow over axis (sometimes exaggerated by compaction), abaxial end of well-incised portion slightly anterior to adaxial end of well-incised portion.

L2 and L3 confluent distally, widen (tr.) anteriorly to point of contact with ocular lobes; axial furrow distinctly changes direction (becoming more strongly divergent anteriorly) at point of confluence. S3 deepest midway between sagittal line and axial furrow, shallow over axis (Fig. 12.3; depth sometimes exaggerated by compaction-related deformation), isolated from axial furrow, oriented anterolaterally away from axis to point of contact with ocular lobes. Axial furrow shallow at lateral margins of L3, sometimes not incised so that distalmost portion of L3 more-or-less confluent with interocular area (Fig. 13.4, 13.5). LA slightly wider (tr.) than long (sag.), approximately 40–47% glabellar length (sag.), separated from extraocular area by a sharp break in slope, dorsal convexity uncertain due to taphonomic compaction but probably weakly convex; widest point at or rarely slightly anterior to (Figs. 12.5, 13.6) intersection with anterior margin of ocular lobes; anterior margin contacts anterior cephalic border furrow and on largest cephalon impinges into and deflects course of anterior cephalic border (Fig. 13.6). Plectrum not developed. Weak parafrontal band sometimes present around lateral margin of LA immediately anterior to intersection with ocular lobe, fades anteriorly (Fig. 12.1, 12.4). Small axial node on posterior margin of LO. Ocular lobes diverge from exsagittal line at approximately 24° (range 14–34°), crescentic, flat-topped, posterior tip transversely opposite distal tip of S1 or anterior portion of lateral margin of L1; proximal portion of inner margin flush against anterolateral margin of L3 but separated from it by shallow continuation of axial furrow, which fades anteriorly; shallow ocular furrow, deepest anteriorly, inner band slightly wider (tr.) than outer band. Nature of contact between ocular lobes and LA unclear due to compaction-related

deformation; inner band of ocular lobe appears to merge smoothly into LA on better-preserved specimens; weak preocular furrow on some specimens (Fig. 12.1, 12.3, 12.4, 12.6) but might be exaggerated by compaction. Interocular area gently arched in transverse section and sloping down inwards, slightly narrower to wider (tr.) than ocular lobes (70–170%) and approximately 25–37% width (tr.) of extraocular area opposite S1; elongate interocular swelling transversely opposite L1. Extraocular genal caeca present on some specimens (Figs. 12.3, 13.6). Weak posterior ocular line at least occasionally present (Fig. 12.4); many specimens show ridge on posterodistal portion of extraocular area that represents either intergenal ridge or posterior ocular line (identification uncertain due to proximal fading of ridge). Genal ridge sometimes present (Figs. 12.1, 12.3, 12.6, 13.5, 13.6). Terrace lines or lirae on dorsal surface of anterior and lateral cephalic border, extending onto base of genal spine (Fig. 12.1, 12.3); rarely on axis of LO and L1 (Fig. 13.6). Terrace lines on cephalic doublure. Hypostome and rostral plate unknown.

Prothorax of 14 segments (Fig. 12.1); axis 34–54% wider (tr.) than inner pleural region on T1, gently tapers posteriorly. Axial node on posterior margin of T1 to T14, tiny on anterior segments, larger on more posterior segments (Fig. 12.1, 12.2, 12.4–12.6). Inner pleural regions of T1 and T2 transverse, parallel-sided, with straight margins. T3 macropleural; pleural spine macrospinous, slender, tip opposite axial ring of T7 or T8 (Fig. 12.1). Inner pleural regions of T4 to T6 roughly transverse, parallel-sided, margins slightly curved to accommodate lateral expansion (exsag.) of T3. Inner pleural regions increasingly divergent and with more strongly curved margins posteriorly from T7 to T14. Pleural spines of T1, T2, and T4 to T9 sentate, very slender, divergent; those of T10 to T12 becoming increasingly falcate; those of T13 and T14 dolichospinous, longer than entire thorax, divergent posteriorly (Fig. 12.1, 12.2). Pleural furrows broad (exsag.), occupying much of inner pleural region; steeper anteriorly; extending onto pleural spines of T3 and T9 to T14. Long axial spine on T15. Rest of thorax and pygidium unknown.

*Ontogeny.*—The smallest specimen of *Mesonacis egerensis* studied herein is an isolated cephalon approximately 2.31 mm in sagittal cephalic length (Fig. 13.1). The specimen is in either phase 4 or early 5 of cephalic development, because L3 is wider (tr.) than L2, but S2 is not isolated from the axial furrow. Poor preservation means that it cannot be determined whether or not L2 widens anteriorly, so it is unclear whether the individual had entered phase 5. The cephalon is probably hexagonal in outline, being widest (tr.) at the base of the genal spines. The base of the genal spine is transversely opposite the lateral margin of L1. The ocular lobe slopes anteriorly down into a broad transocular furrow at the contact with LA. The posterior tip of the ocular lobe is approximately transversely opposite the distal tip of S1. The extraocular area is proportionally narrower (tr.) than the mature condition. The presence or absence and condition of any intergenal spines cannot be determined. The specimen apparently lacks procranial spines but shows a geniculation between the anterior and lateral cephalic border. During the ontogeny of other olenelloids, such a geniculation can indicate the location

of a procranial spine that was present at an earlier developmental stage but has been resorbed (MW, unpublished data). It is therefore possible that *Mesonacis egerensis* possessed procranial spines at smaller (unsampled) cephalic size.

A slightly larger but crushed and distorted cephalon in early phase 5 of development (Fig. 13.2, sagittal cephalic length estimated to have been approximately 2.54 mm), tentatively assigned to this species, shows less-advanced genal spines (base transversely opposite the distal tip of SO) than the smallest specimen. The adgenal angle is weak relative to the mature condition, and the extraocular area is proportionally wider (tr.) than on the smallest specimen. A ridge representing either a posterior ocular line or an intergenal ridge (proximal portion unclear) crosses the posterior cephalic border and runs onto a tiny intergenal spine located along the distal portion of the posterior cephalic border, approximately midway between the adgenal angle and the base of the genal spine.

A slightly larger cephalon in early phase 5 of development (Fig. 13.3, sagittal cephalic length 3.96 mm) shows a more circular LA which is widest (tr.) slightly anterior to the point of contact with the anterior margin of the ocular lobe. The posterior tip of the ocular lobe is transversely opposite the distal margin of S1. The base of the genal spine is not well preserved but is estimated to lie approximately transversely opposite the lateral margins of L1. A geniculation between the anterior and lateral portions of the cephalic border is absent.

*Remarks.*—Best (1952a, b) originally assigned this species to the genus *Olenellus*, but in his unpublished Ph.D. thesis (Best, 1959, p. 134–135, pl. 2, figs. 1–3) he thought that it belonged in *Bristolia* Harrington, 1956, based primarily on its cephalic outline with relatively strongly anteriorly advanced genal spines and its relatively short ocular lobes. However, anteriorly advanced genal spines convergently evolved in many olenelloid genera (see Webster and Bohach, 2014, p. 17–18) and in many cases the degree of anterior advancement is coupled with a shortening of the ocular lobes. Given that, and the lack of features such as a hyperpleural T3, assignment to *Bristolia* is unwarranted. Bohach (1997, p. 211–213, pl. 22, figs. 1–6, text-fig. 43) informally reassigned the species to the genus *Mesonacis* in her unpublished thesis. Lieberman's (1999) cladistic analysis supported a sister-species relationship between *Mesonacis egerensis* and *Mesonacis vermontanus*, and he formally reassigned the species to *Mesonacis*. That reassignment is followed herein.

*Mesonacis egerensis* is most similar to *Mesonacis vermontanus*, from which it differs most obviously by having slightly shorter ocular lobes, a stronger adgenal angle, more anteriorly advanced genal spines, a proportionally narrower (tr.) extraocular area, shorter pleural spines on T1, T2, and T4 to T12, and very long pleural spines on T13 and T14. The thoracic pleurae of *Mesonacis vermontanus* decrease in proportional width (tr., relative to the transverse width of the corresponding axial ring) less strongly down the thorax than do those of *Mesonacis egerensis*, so that the pleurae of segments posterior to T6 are markedly less well developed (relative to the axis) in the latter species. The interocular area of both species is dorsally arched, but *Mesonacis vermontanus* lacks the interocular

swelling transversely opposite L1 that is often developed in *Mesonacis eagerensis*.

*Mesonacis eagerensis* also closely resembles two species that are currently (provisionally) assigned to *Olenellus*. Differences from *Olenellus? schofieldi* are outlined in the remarks for that species. *Olenellus terminatus* differs from *Mesonacis eagerensis* most obviously by having a proportionally longer preglabellar field, by having strongly developed Bertillon markings on the extraocular area, and by having longer ocular lobes (posterior tip typically transversely opposite the lateral margin of SO or anterior portion of LO).

The spectacular, long pleural spines on T13 and T14 are apparently unique to *Mesonacis eagerensis*, expanding our knowledge of olenelloid disparity. Unfortunately, specimens that preserve the posterior portion of the prothorax are extremely rare (MW is aware of only three such specimens, the best of which is figured herein [Fig. 12.1, 12.2]; another is illustrated in Caron et al., 2024).

Family Wanneriidae Hupé, 1953  
Genus *Wanneria* Walcott, 1910

*Type species*.—*Olenellus (Holmia) walcottanus* Wanner, 1901, from the Kinzers Formation (Dyeran Stage of Laurentia, Cambrian Stage 4) of Pennsylvania.

*Remarks*.—In the most recent revision of *Wanneria*, Lieberman (1999, p. 49) stated that the genus was monotypic, having reassigned many previously included species to other genera (Lieberman, 1998, 1999). However, those revisions failed to discuss or reassign several species—such as *Wanneria abnormis* Poulsen, 1958, *Wanneria ellae* Poulsen, 1932, and *Wanneria inermis* Poulsen, 1958—which therefore remain assigned to *Wanneria*. Although some of Lieberman's (1998, 1999) generic reassignments are well supported, others, such as the reassignment of *Wanneria logani* (Walcott, 1910) to *Elliptocephala* Emmons, 1844, are being reconsidered in light of examination of new material (MW, unpublished data). New wanneriid species and genera are being described elsewhere. Characterizing the nature of the genus *Wanneria*, and of the Wanneriidae more generally, is beyond the scope of the present study. However, the new species described below is closely similar to *Wanneria walcottana* and is therefore assigned to the same genus.

*Wanneria cranbrookense* Webster new species  
Figures 6.6–6.8, 14–20

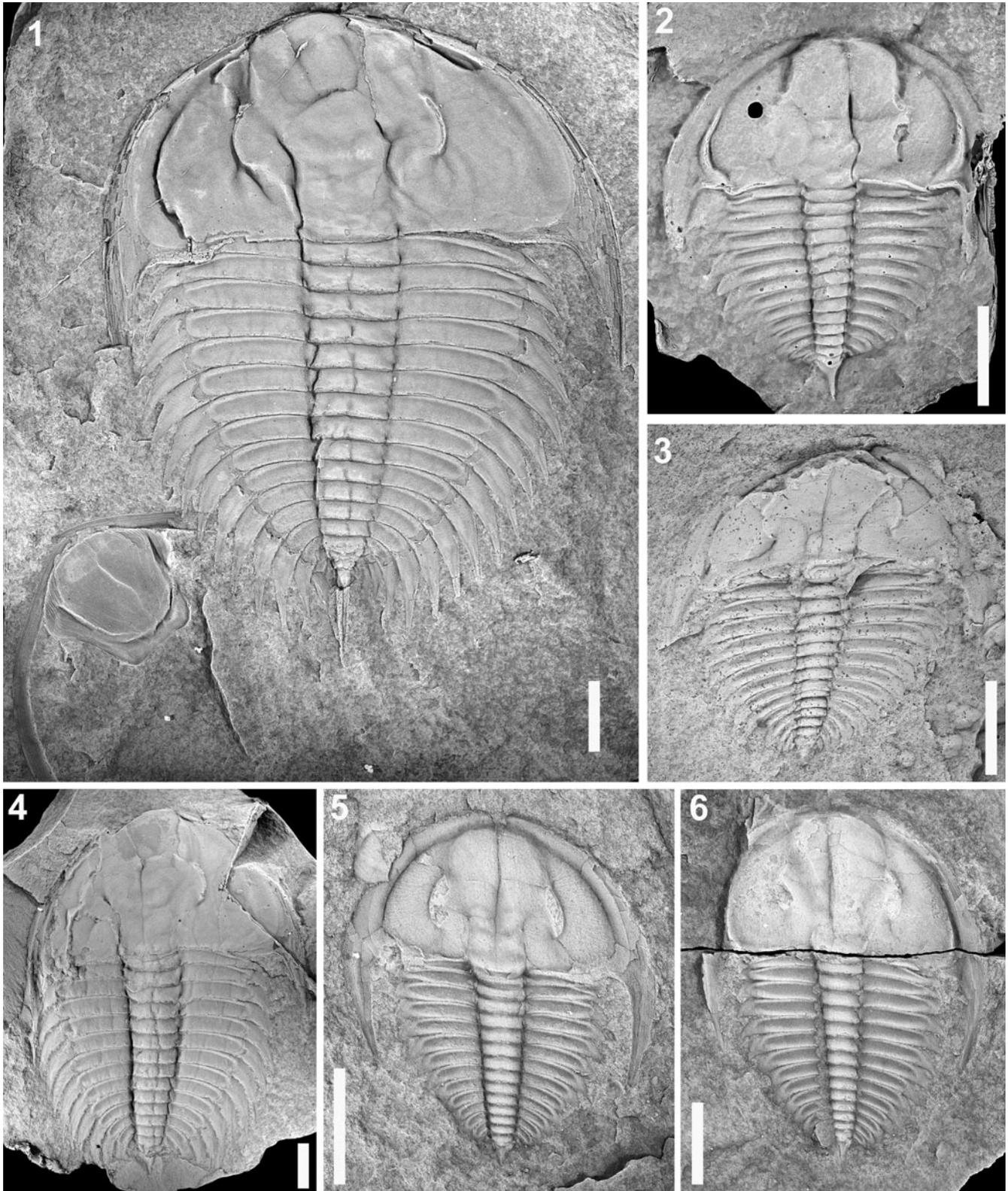
- 1921 *Wanneria* n. sp.?; Schofield, p. 666.  
1921 *Wanneria* cf. *walcottanus* (Wanner, 1901); Schofield, p. 666.  
1922 *Wanneria* n. sp.?; Schofield, p. 12.  
1922 *Wanneria* cf. *walcottanus*; Schofield, p. 12.  
1952b *Wanneria walcottana*; Best, p. 13, 15.  
1956 *Wanneria walcottana*; Okulitch, p. 715.  
1991 *Wanneria walcottana*; Fortey, photograph on p. 85.  
1996 *Wanneria* sp.; Ludvigsen and Bohach, p. 52, 53, figs. 4.3a, b, 4.4c, d.  
2014 *Wanneria* sp.; Levi-Setti, pl. 112.

*Holotype*.—Dorsal exoskeleton and displaced rostral plate and hypostome UBC GT507 (Figs. 14.1, 17.1, 18.1), from Eager Formation (Cambrian Stage 4), Locality B, Cranbrook, British Columbia.

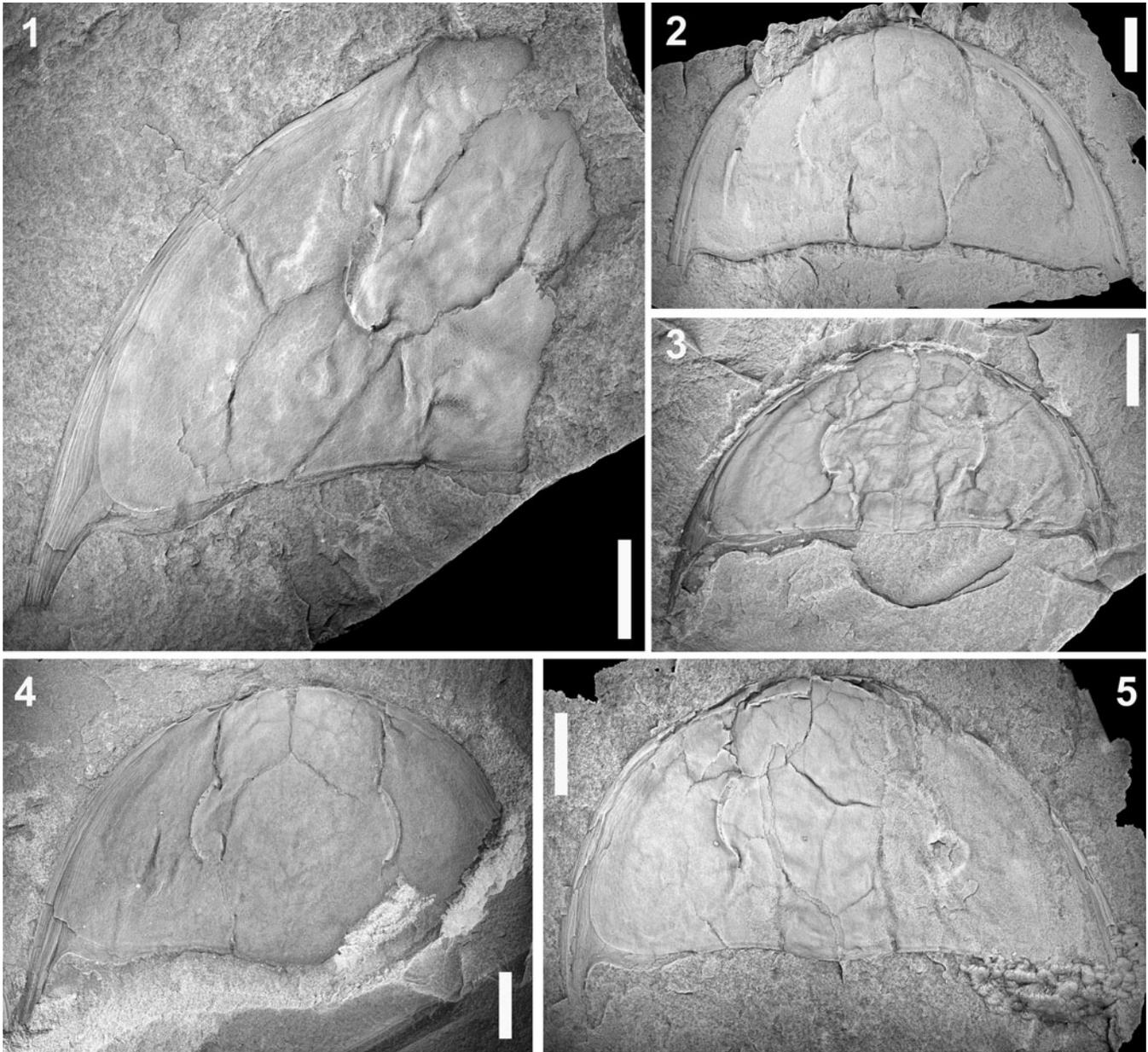
*Diagnosis*.—Broadly rounded intergenal angle; base of genal spine transversely opposite or slightly behind posterior margin of glabella. Glabellar furrows, axial furrow, and cephalic border furrow shallow to almost totally effaced. Thorax of 16 segments. No axial nodes on T1 to T14.

*Occurrence*.—*Wanneria cranbrookense* Webster n. sp. is the second most abundant species at Locality B, with more than 300 specimens recovered during the 2015 excavation (of which more than 100 were photographed and examined in detail to provide the description herein). The species is also known from Locality A of Best (1952a, b), from USNM Locality 67f, from unspecified sites in the Cranbrook area, and from an inferred occurrence at Cranbrook Junction (Appendix). It also occurs in the Eager Formation on the Windermere High in the western Hughes Range at Mount Grainger and Ram Creek (Fig. 1.1; Ludvigsen and Bohach, 1996; Bohach, 1997; Webster, unpublished data; Appendix).

*Description (morphologically mature specimens; sagittal cephalic length > 5 mm)*.—Cephalon roughly semicircular in outline, widest (tr.) at base of genal spines. Proximal portion of posterior cephalic margin curves posterolaterally away from axial furrow to broadly rounded intergenal angle; distal portion of posterior cephalic margin oriented more transversely (Figs. 6.8, 14.1, 15.3) or weakly anterolaterally (Fig. 15.2, 15.4, 15.5) when traced abaxially. Greatest observed cephalic length more than 45 mm (sag.; Fig. 15.1). Genal spine broad-based; tapers to point, tip typically transversely opposite axial ring of T5 or T6 (Fig. 14.1), sometimes T8 (Fig. 14.5, 14.6); proportionally shorter on large cephalia; inner and outer margins curved so that entire spine arcs slightly inwards posteriorly (less so on largest cephalia); base transversely opposite or slightly behind posterior margin of glabella. Intergenal spine absent. Cephalic border poorly defined by shallow, trough-like, broad border furrow; anterior border shortest at sagittal axis, lengthens distally, longest portion of border located at confluence with genal spines; radial length of anterior border (measured perpendicular to margin) opposite junction of ocular lobes with LA 10–1% of glabellar length (exsag.), decreasing through ontogeny; posterior cephalic border shortens (exsag.) adaxially, very short inwards of intergenal angle. Border broadly dorsally arched and sloping down outwards on small cephalon preserved in limestone (Ludvigsen and Bohach, 1996, fig. 4.4c, d), but convexity and slope on larger specimens preserved in shale unclear due to taphonomic compaction. Glabella club-shaped in outline, narrowest at S1; approximately 90–99% of cephalic length (sag.; decreasing through ontogeny [see below]). No preglabellar field; LA impinges into anterior cephalic border, which is reduced to short strip sagittally on large cephalia; plectrum absent. Posterior margin of glabella convex posteriorly (Fig. 16.1, 16.2), sagittal portion can be more-or-less transverse on large cephalia



**Figure 14.** Articulated specimens of morphologically mature *Wanneria cranbrookense* Webster n. sp. from the Cranbrook Lagerstätte. (1) Dorsal exoskeleton and displaced rostral plate and hypostome, latex peel, holotype, UBC GT507 (see also Figs. 17.1, 18.1). This specimen was previously figured by Ludvigsen and Bohach (1996, fig. 4.3b) and Bohach (1997, pl. 7, fig. 8). (2) Almost complete dorsal exoskeleton, latex peel of external mold, ICS replica # 3790. (3) Almost complete dorsal exoskeleton, latex peel of external mold, RBCM.EH2015.013.0048.003. (4) Almost complete dorsal exoskeleton, latex peel of external mold, USNM PUM78552b. (5) Almost complete dorsal exoskeleton, RBCM.EH2015.013.0096.001. (6) Almost complete dorsal exoskeleton, RBCM.EH2015.013.0157.001. All scale bars 5 mm. (1, 3, 5, 6) from Eager Formation at Locality B, (2) from Eager Formation at USNM Locality 67f, (4) from Eager Formation at unknown locality in Cranbrook area.

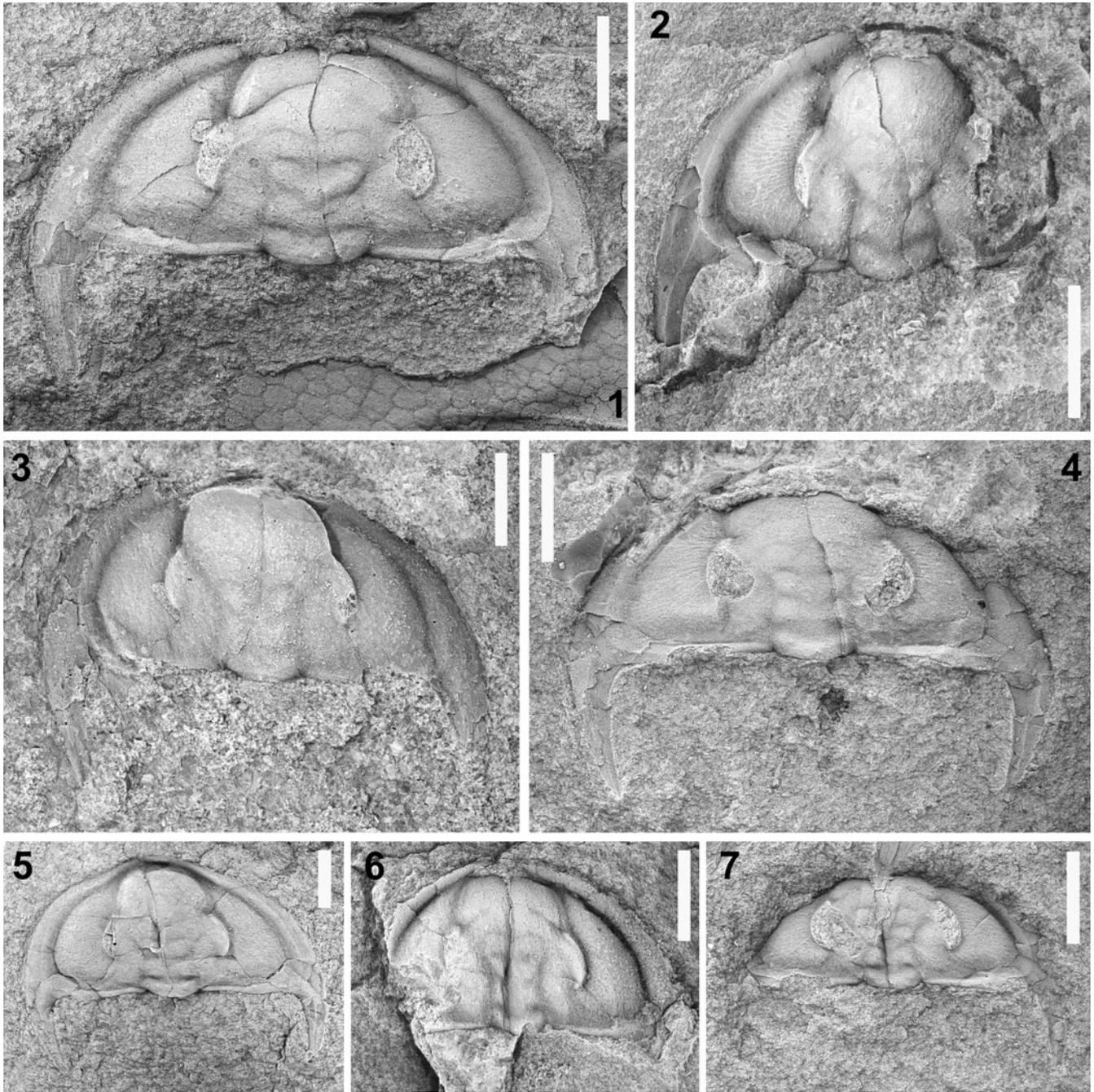


**Figure 15.** Large morphologically mature cephalons of *Wanneria cranbrookense* Webster n. sp. from the Cranbrook Lagerstätte. (1) Largest studied cephalon, internal mold, RBCM.EH2015.013.0150.001. (2) Latex peel of external mold, RBCM.EH2015.013.0231.001. (3) Internal mold, RBCM.EH2015.013.0047.001. (4) Internal mold, RBCM.EH2015.013.0244.001. (5) Latex peel of external mold, RBCM.EH2015.013.0161.001. All scale bars 10 mm. All from Eager Formation at Locality B.

(Fig. 15.2, 15.3). Glabellar furrows and axial furrow extremely shallow; more-or-less effaced, especially on large cephalons (Fig. 15).

SO (when expressed) deepest abaxially, abaxial end slightly anterior to adaxial end, convex anteriorly either side of axis. S1 (when expressed) deepest abaxially, abaxial end anterior to adaxial end. LO and L1 weakly subtrapezoidal, slightly narrowing anteriorly, length (exsag.) of L1 approximately 11% glabellar length (sag.), LO slightly shorter than L1 (exsag.) (Fig. 16.6). L2 and L3 widen (tr.) anteriorly, L3 to a greater extent so that axial furrow kinks outwards anterior to S2. S2 (when expressed) arcuate, convex anteriorly either side of axis, deepest midway between axis and axial furrow, retains shallow connection to axial furrow (Fig. 16.3, 16.6). S3 (when

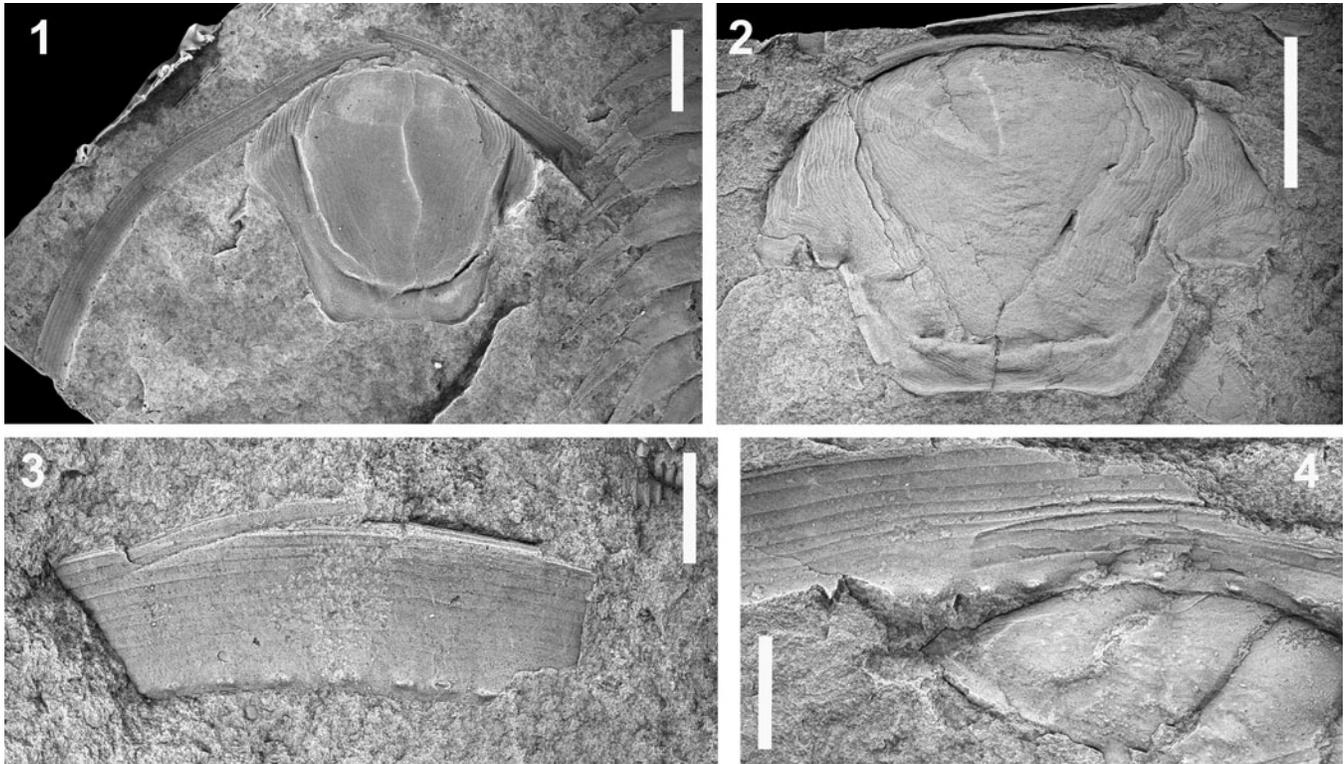
expressed) shallower than S2, arcuate, convex anteriorly either side of axis, deepest distally. LA transversely oblate in outline, anterior margin broadly rounded; approximately 44% glabellar length (sag.), approximately twice as wide (tr.) as long (sag.), widest point at (Fig. 16.3) or slightly anterior to (Fig. 15.4) intersection with anterior margin of ocular lobes, width across contact with outer margins of ocular lobes approximately 178% (range 149–202%) of basal glabellar width (tr.), maximum width approximately 185% (range 170–214%) of basal glabellar width (tr.); weakly dorsally convex and with lateral margins separated from extraocular area by break in slope on small cephalon preserved in limestone (Ludvigsen and Bohach, 1996, fig. 4.4c, d), but convexity on large specimens preserved in shale unclear due to taphonomic compaction. Very shallow preocular



**Figure 16.** Small morphologically mature cephalons of *Wanneria cranbrookense* Webster n. sp. from the Cranbrook Lagerstätte. (1) Internal mold, RBCM.EH2015.013.0094.004. (2) Internal mold, RBCM.EH2015.013.0048.002. (3) Internal mold, RBCM.EH2015.013.0020.005. (4) Internal mold, RBCM.EH2015.013.0057.001. (5) Latex peel of external mold, RBCM.EH2015.013.0080.005. (6) Internal mold, RBCM.EH2015.013.0025.005. (7) Internal mold, RBCM.EH2015.013.0057.002. All scale bars 3 mm. All from Eager Formation at Locality B.

furrow sometimes runs inwards and anteriorly from contact of LA with outer margin of ocular lobes, not incised over axis, but might be exaggerated by or artifact of compaction (Figs. 15.2, 16.6, 16.7). Some specimens appear to show shallow transocular furrow (Fig. 16.3), although this might be artifact of taphonomic distortion. Possible parafrontal band around lateral margins of LA on some cephalons (Figs. 15.1, 15.2, 16.6), but might be artifact of taphonomic distortion. Tiny axial node on posterior portion of LO (Figs. 14.2, 15.1, 16.1). Faint ovoid lateral swelling sometimes present on

anterolateral portion of LO (Fig. 16.7). Ocular lobes diverge from exsagittal line at approximately  $28^\circ$  (range  $18\text{--}36^\circ$ ; measured as a line from most abaxial point on outer margin to point of contact between outer margin and LA), crescentic, posterior tip transversely opposite posterior portion of lateral margin of L2, distal tip of S1, or anteriormost portion of lateral margin of L1 (generally shortening through ontogeny; see below); inner margin poorly differentiated from interocular area. Some specimens with extremely shallow ocular furrow expressed only anteriorly, inner band wider (tr.) than outer band (Figs. 14.1,



**Figure 17.** Ventral sclerites of *Wanneria cranbrookense* Webster n. sp. from the Cranbrook Lagerstätte. (1) Hypostome and rostral plate, latex peel of dorsal surface, holotype, UBC GT507. Inner margin of rostral plate is almost everywhere missing (see also Figs. 14.1, 18.1). (2) Hypostome, ventral surface, latex peel of external mold, RBCM.EH2015.013.0102.005, scale bar 10 mm. (3) Fragment of rostral plate showing row of elongate dorsal projections along inner margin, dorsal surface, RBCM.EH2015.013.0233.001. (4) Portion of incomplete rostral plate showing row of elongate dorsal projections along inner margin (where preserved), dorsal surface, RBCM.EH2015.013.0047.006. Scale bars 3 mm unless otherwise stated. All from Eager Formation at Locality B.

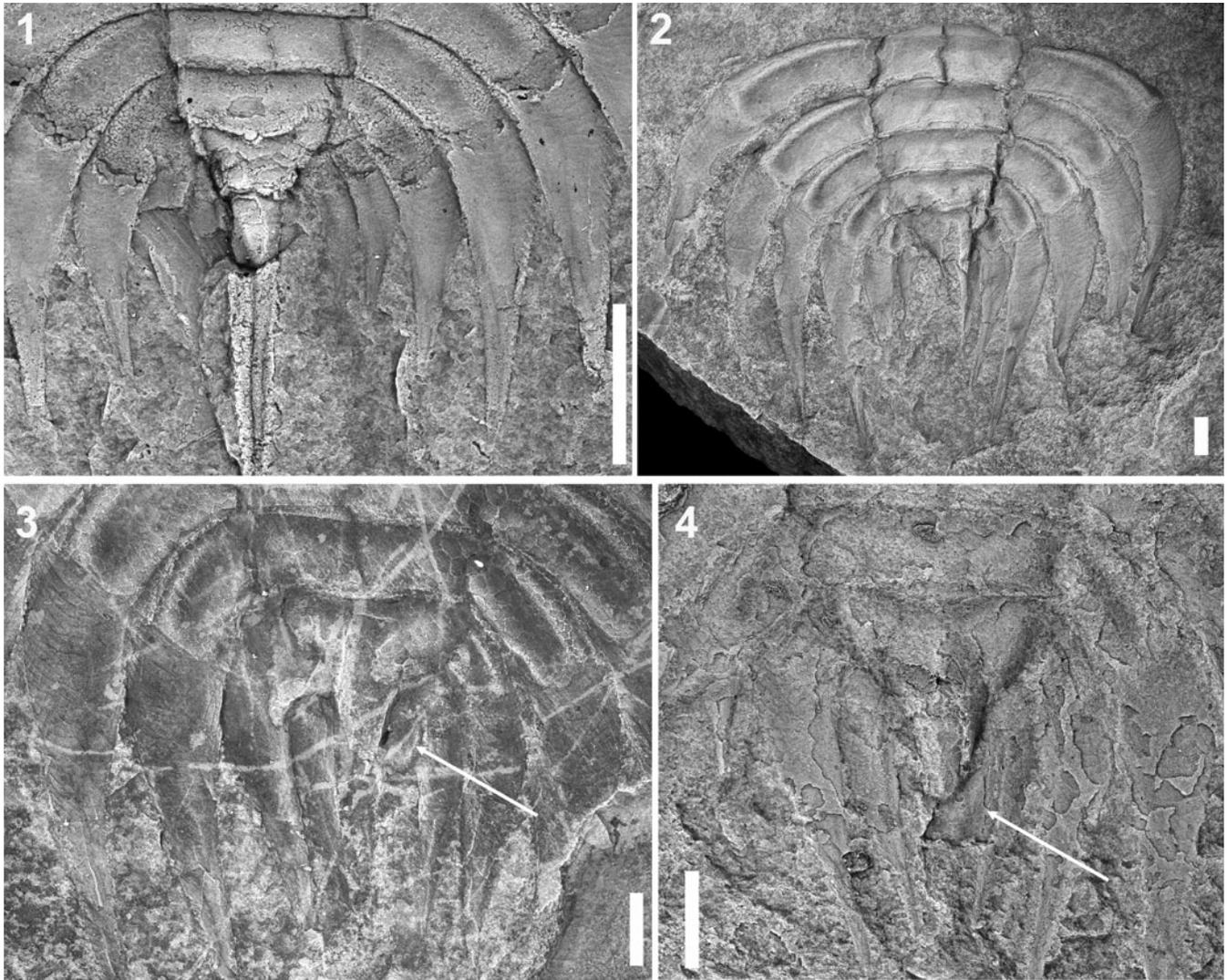
16.2, 16.5, 16.6). Circumocular suture defines large visual surface (not preserved) that occupied much of length of outer wall of ocular lobe; portion of outer wall of ocular lobe below circumocular suture forms prominent, steep eye socle (Figs. 14.1, 14.5, 15.1–15.5, 16.5). Slope of interocular area unclear due to compaction, but surface convex upward, giving arched appearance; approximately twice width (tr.) of ocular lobe and approximately half width (tr.) of extraocular area opposite S2. Dorsal surface of large cephalia covered in reticulate network of raised ridges forming polygonal pattern (Fig. 15.1–15.5), especially clear on interocular area and posterior portion of extraocular area; polygons elongate and grade into Bertillon markings and lirae from inner to outer portions of lateral cephalic border (Fig. 15.1, 15.2, 15.4); some polygons bear a tiny central node (Fig. 15.1, 15.4). Extraocular genal caeca often present (Figs. 14.1, 14.5, 15.3, 16.1, 16.2, 16.4, 16.5, 16.7); caeca contact lateral and anterior cephalic border, interrupting border furrow and giving it a faintly “dimpled” appearance (Fig. 16.2, 16.5; also, Ludvigsen and Bohach, 1996, fig. 4.4c, d). Genal ridge (Figs. 14.1, 16.7) and interocular ridge (Fig. 14.1) present on some specimens. Depression or sometimes crack along position of posterior ocular line (e.g., Figs. 14.3, 14.5, 14.6, 15.3–15.5, 16.1, 16.3); sometimes arcs onto extraocular area giving impression of (taphonomically compacted) extraocular platform (Fig. 16.1, 16.4, 16.7). Terrace lines or lirae on dorsal and ventral surface of genal spines and doublure.

Rostral plate (Figs. 6.6, 6.7, 17.3, 17.4) crescent-shaped in plan view, weakly convex ventrally in cross section. Terrace

lines run concentrically to margins. Elongate, dorsally projecting swellings form a row along inner margin (Fig. 17.3, 17.4).

Mature hypostome conterminant with rostral plate (Figs. 6.6, 17.1), subtrapezoidal in outline. Anterior lobe of middle body subtrapezoidal, occupies approximately 82–90% of sagittal length of hypostome (Fig. 17.2); anterior margin broadly curved; expands laterally onto broad, triangular anterior wings, tips of which are located roughly at hypostomal midlength. Posterior lobe of middle body very short (sag., exsag.), < 10% of hypostome length (sag.), transversely crescentic in outline, widest anteriorly. Anterior border narrow, sagittal width approximately 4% of hypostome length. Lateral and posterior border very narrow, virtually absent sagittally, weakly defined by very shallow furrow. Posterior and lateral margins lack obvious projections (Fig. 17.1, 17.2). Subtle, transversely oblate swelling developed at contact between posterior and lateral border, projects inwards into posterior lobe of middle body (Fig. 17.2). Ornament of concentric, Bertillon terrace lines or lirae on anterior lobe of middle body and anterior wings, grading into reticulations in middle furrow and on posterior lobe of middle body.

Thorax (Figs. 6.6, 6.7, 14) of 16 segments, not differentiated into a prothorax and opisththorax; maximum width (tr.) of trunk across T3 or T4. Axis typically narrower than (92%, range 81–102%) inner pleural region on T1 (tr.), gently tapers posteriorly. Axes of T1 to T14 without node or spine; T15 bears long, broad-based axial spine, tip not preserved so full length unknown but likely to have been shorter than length of prothorax; presence or absence of axial structure on T16



**Figure 18.** Posterior portion of the trunk of *Wanneria cranbrookense* Webster n. sp. from the Cranbrook Lagerstätte. (1) Posterior thoracic segments of articulated specimen, latex peel of external mold, holotype, UBC GT507. Pygidium, if present, is obscured by long axial spine on T15 (see also Figs. 14.1, 17.1). (2) Articulated T11 to T16 showing ornament and base of long axial spine on T15 that obscures axis of T16, internal mold, RBCM.EH2015.013.0113.011. (3) Posterior portion of articulated trunk showing part of pygidium (arrowed) exposed between T15 axial spine and inner margin of T16 pleura, internal mold, RBCM.EH2015.013.0158.001. (4) Posterior portion of articulated trunk showing part of pygidium (arrowed) exposed between T15 axial spine and inner margin of T16 pleura, latex peel of external mold, RBCM.EH2015.013.0241.001. All scale bars 3 mm. All from Eager Formation at Locality B.

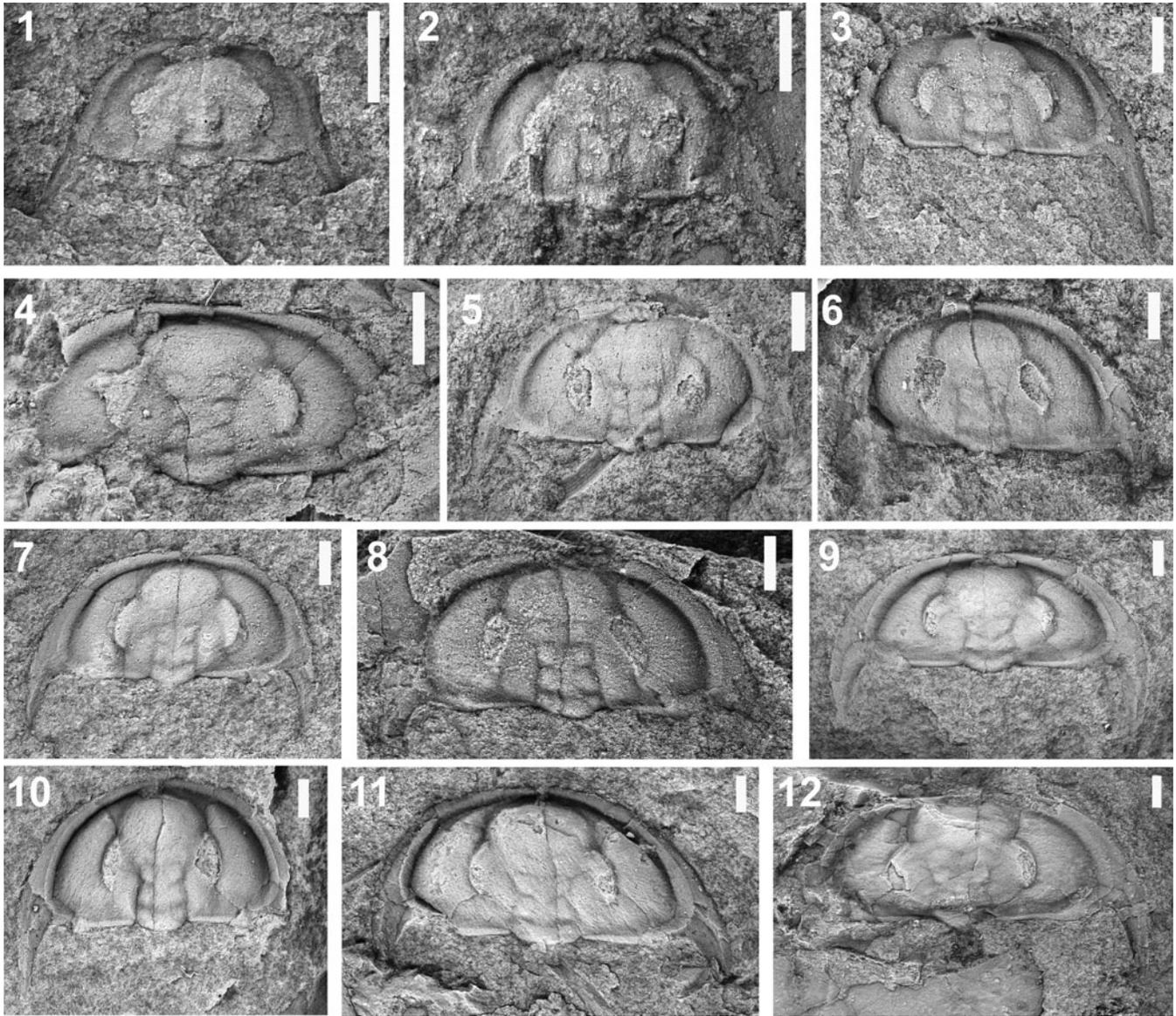
unknown (obscured by T15 axial spine; Fig. 18.1–18.4). Subtle lateral swellings on anterolateral corners of each axial ring, so that lateral margin of each axial ring is sinuous. Inner pleural region of T1 transverse, tapered distally, with slightly curved anterior margin; that of T2 to T5 parallel-sided, transverse, with straight margins; that of T6 to T16 parallel-sided, increasingly divergent (T15 and T16 subpendent), with increasingly curved margins. T3 not macropleural or macrospinous. Pleural spines progressively elongate from T1 to T13 (sentate on T1, falcate on T4), then shorten from T14 to T16. Pleural spines proportionally shorter on smaller specimens (Fig. 14.6). Pleural furrow steeper-walled anteriorly, occupies much of inner pleural region adaxially, tapers distally due to distal widening (exsag.) of anterior band; shallows to terminate more-or-less at base of pleural spine (coincident with inner margin of doublure) on all segments. Dorsal surface of each segment covered in reticulate network of raised ridges forming polygonal pattern. Terrace

lines arc (convex-outward) from anterior to posterior margin on ventral surface of pleural spines of all thoracic segments (Figs. 6.6, 14.1, 18.2).

Pygidium poorly known, typically obscured by T15 axial spine (Fig. 18.3, 18.4). Appears to be elongate, length (sag.) approximately 150% maximum width (tr.); lateral margins slightly bowed outwards. Axial details, including nature of rhachis and presence or absence of sagittal notch in posterior margin, unknown.

*Etymology.*—Named for the town of Cranbrook, British Columbia.

*Ontogeny.*—The smallest studied specimen (sagittal cephalic length approximately 1.44 mm; Fig. 19.1) is poorly preserved but is in either phase 3 or phase 4 of cephalic development. Other small specimens (sagittal glabella length approximately 1.87 mm, sagittal cephalic length < 2.35 mm; Fig. 19.2, 19.3)

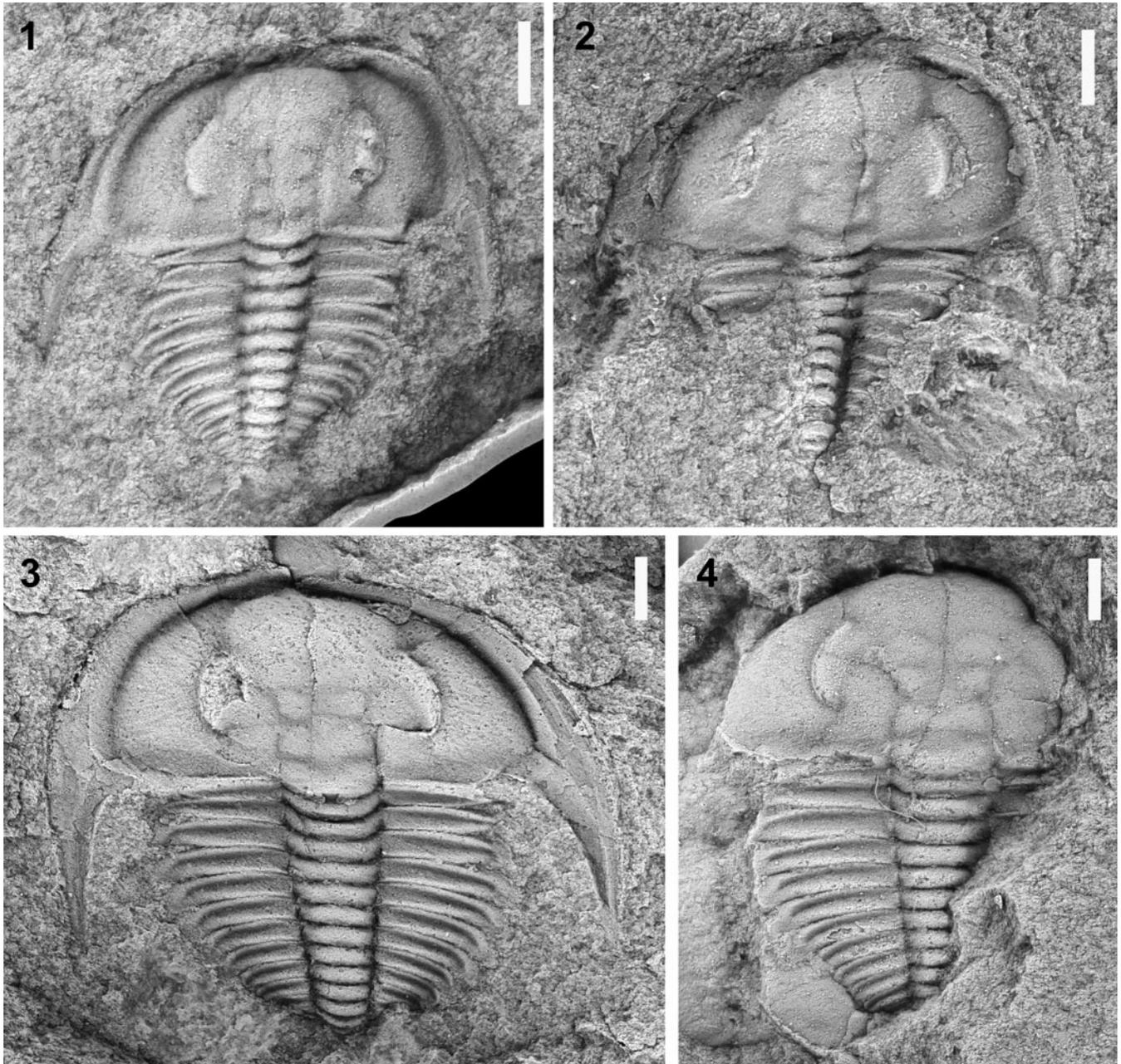


**Figure 19.** Morphologically immature *Wanneria cranbrookense* Webster n. sp. from the Cranbrook Lagerstätte. (1) Smallest known cephalon, in phase 3 or 4 of development, internal mold, RBCM.EH2015.013.0151.003. (2) Cephalon in phase 4 of development, internal mold, RBCM.EH2015.013.0186.001. (3) Cephalon in phase 4 of development, internal mold, RBCM.EH2015.013.0247.002. (4) Cephalon in phase 4 of development, latex peel of external mold, RBCM.EH2015.013.0132.003. (5) Cephalon in phase 4 of development, latex peel of external mold, RBCM.EH2015.013.0132.002. (6) Cephalon in phase 4 of development, internal mold, RBCM.EH2015.013.0182.010. (7) Cephalon in phase 4 of development, internal mold, RBCM.EH2015.013.0127.001. (8) Cephalon in phase 4 of development, internal mold, RBCM.EH2015.013.0062.003. (9) Cephalon in early phase 5 of development, latex peel of external mold, RBCM.EH2015.013.0233.002. (10) Cephalon in early phase 5 of development, latex peel of external mold, RBCM.EH2015.013.0072.004. (11) Cephalon in early phase 5 of development, internal mold, RBCM.EH2015.013.0033.001. (12) Cephalon in early phase 5 of development, internal mold, RBCM.EH2015.013.0057.003. All scale bars 1 mm. All from Eager Formation at Locality B.

represent phase 4 of cephalic development. Phase 5 of cephalic development was attained by sagittal cephalic length of at least 3.2 mm (Fig. 19.9).

Small specimens exhibit several differences from the morphologically mature condition. On small specimens the glabellar furrows, axial furrow, and cephalic border furrow are less strongly effaced, so that glabellar segmentation is more obvious (Figs. 19, 20). Those specimens also possess a proportionally shorter glabella (sag.; Fig. 21.1) that does not impinge into the anterior cephalic border, which is proportionally longer (sag.; Fig. 21.2). Indeed, on the smallest studied specimens, the anterior margin of the glabella and the anterior cephalic border are

separated by a short preglabellar field (Fig. 19.1–19.4, 19.6, 19.10). The glabella barely tapers (tr.) anteriorly from its posterior margin to S1; and L2 does not widen (tr.) anteriorly. The ocular lobe is proportionally longer (Fig. 21.3), with the posterior tip transversely opposite the middle portion of the lateral margin of L1 (Figs. 19.4, 19.5, 20.1). The extraocular area is proportionally narrower. The genal spine does not curl inwards posteriorly (Fig. 19.1, 19.3). A posterior ocular line is present on the left side of one small cephalon (Fig. 19.4), and weak lateral swellings are evident on the anterolateral corners of LO and L1 of another (sagittal cephalic length approximately 2.57 mm; Fig. 19.5; see also Fig. 20.2, 20.4).



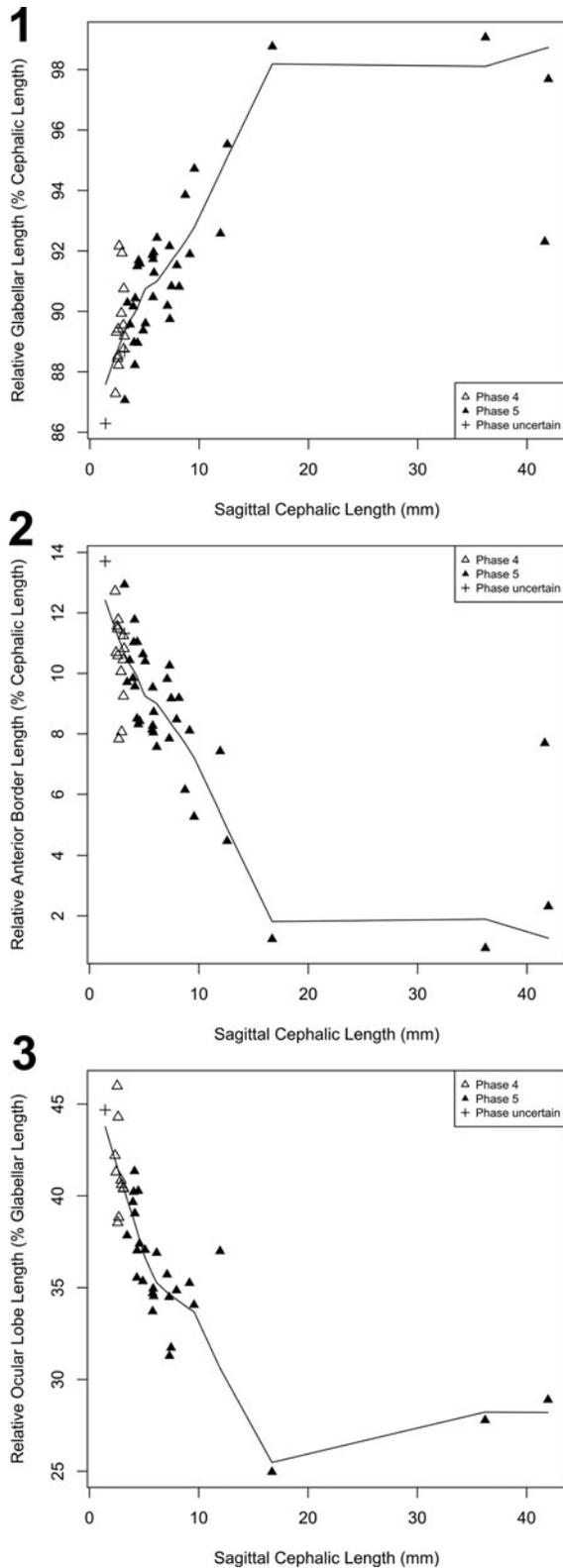
**Figure 20.** Articulated specimens of morphologically immature *Wanneria cranbrookense* Webster n. sp. from the Cranbrook Lagerstätte. (1) Latex peel of external mold, RBCM.EB2015.013.0133.001. (2) Internal mold, RBCM.EH2015.013.0012.001. (3) Internal mold, RBCM.EH2015.013.0055.001. (4) Latex peel of external mold, RBCM.EH2015.013.0123.001. All scale bars 1 mm. All from Eager Formation at Locality B.

Most of the thorax (T1 to at least T12) is preserved on a specimen in phase 4 of cephalic development (sagittal cephalic length approximately 2.53 mm; Fig. 20.1). The third thoracic segment of that specimen is neither macropleural nor macrospinous (see also Fig. 20.2–20.4). The genal spine extends back at least as far as opposite the axial ring of T6 (the tip is obscured). The tip of the genal spine is transversely opposite the axial ring of T8 on a slightly larger specimen that preserves T1 to at least T13 (Fig. 20.3).

During the early portion of phase 5 of development, L2 proportionally widened (tr.) anteriorly, so that the glabella became narrowest at S1 (Fig. 19.9–19.12). S2 shallows as it approaches

the axial furrow but did not become fully isolated from the axial furrow (Fig. 19.11). A tiny intergenal nubbin is present at the intergenal angle on some specimens in earliest phase 5 of cephalic development (Fig. 19.10); this indicates that the deflection in the posterior cephalic margin of mature cephalia represents an intergenal angle rather than an adgenal angle. One specimen in early phase 5 of cephalic development is badly crushed but seems to retain evidence of the presence of an extraocular platform (Fig. 19.12).

Considerable shape change in several features is evident over the sampled portion of ontogeny. The glabella proportionally elongated (sag.; Fig. 21.1), so that the preglabellar field was



**Figure 21.** Ontogenetic change in linear dimensions of *Wanneria cranbrookense* Webster n. sp. from the Cranbrook Lagerstätte. All plots are fitted with a LOWESS regression line for ease of visualization. (1) Proportional length of the glabella (sag., relative to sagittal cephalic length). (2) Proportional length of the anterior cephalic border (sag., relative to sagittal cephalic length). (3) Proportional length of the ocular lobe (exsag., relative to sagittal length of the glabella).

lost and LA became separated from the anterior cephalic border only by a broad, trough-like border furrow (Fig. 19.7, 19.11); continued glabellar elongation led to the progressive impingement of LA into the anterior border (Fig. 21.2). The ocular lobe proportionally shortened (exsag.) relative to glabellar length (sag.; Fig. 21.3), so that the posterior tip of the ocular lobe is transversely opposite the anterior portion of the lateral margin of L1 on some phase 4 cephalons (Figs. 19.7, 19.8, 20.2). The extraocular area proportionally widened (compare Fig. 19.1–19.3 to Fig. 15.1–15.5).

*Remarks.*—*Wanneria cranbrookense* Webster n. sp. is most similar to *Wanneria walcottana*, and some previous workers have treated them as a single species (see synonymy list; also, the unpublished thesis by Best, 1952a, p. 47–49, pl. 2, figs. 11–18). The two species most obviously differ in the stronger degree of effacement of cephalic furrows on morphologically mature specimens of *Wanneria cranbrookense* Webster n. sp.; in the number of thoracic segments (16 in *Wanneria cranbrookense* Webster n. sp., 17 in *Wanneria walcottana*); and in the distribution of axial structures on the thorax (no axial nodes on T1 to T14 in *Wanneria cranbrookense* Webster n. sp., axial nodes on T1 to T14 in *Wanneria walcottana*).

The Cranbrook form was treated as a distinct, new species in the theses by Best (1959, p. 155–157, pl. 4, figs. 5–13, pl. 5, figs. 1–13, informally named “*Wanneria edentata*”) and Bohach (1997, p. 138–141, pl. 6, figs. 10–18, pl. 7, figs. 1–8, pl. 8, figs. 1, 2, text-fig. 26 [top], informally named “*Wanneria dunnae*”). However, neither of those theses were published and the proposed names are thus nomina nuda.

Three aspects of the ontogeny of *Wanneria cranbrookense* Webster n. sp. (above) are noteworthy. Firstly, the sampled portion of ontogeny demonstrates that the species passes through the same phases of cephalic development as other olenelloids (see *Olenellus santuccii* Webster n. sp., above), thus extending the argument for phylogenetic conservatism of these aspects of development to include the Wanneriidae.

Secondly, morphologically immature specimens exhibit relatively clearly incised furrows, so that the nearly effaced condition is attained during late portions of ontogeny (during phases 4 and 5 of cephalic development). A similar pattern of progressive effacement through ontogeny occurs in other olenelloids such as *Pea-chella* Walcott, 1910, and *Biceratops* Pack and Gayle, 1971 (Webster, 2009). In *Wanneria cranbrookense* Webster n. sp., *Pea-chella*, and *Biceratops*, the effacement of glabellar furrows is a developmental feature superimposed upon and independent of a phylogenetically conserved pattern of ontogenetic shape change of the glabella; effacement is not a “peramorphic” extension of glabellar development (contra McNamara, 1986; see Webster, 2009, p. 215–216 for further discussion).

Thirdly, T3 is “normal” (i.e., neither macropleural nor macrospinous) throughout the sampled portion of ontogeny, including on specimens only 2.53 mm in sagittal cephalic length. This stands in contrast to the condition seen in *Elliptocephala asaphoides* Emmons, 1844, where T3 is macropleural and macrospinous on specimens up to at least 4.2 mm in cephalic length but then proportionally shrinks to become “normal” on

larger specimens (Whittington, 1957; MW, personal observation), and in *Olenellus* (e.g., *Olenellus santucci* Webster n. sp. and *Olenellus gilberti* [Webster, 2015]), where T3 is macropleural and macrospinous throughout ontogeny. Taxa apparently achieved a similar condition of T3 at morphological maturity in different ways. Ontogenetic dynamics of traits such as T3 morphology provide an as-yet-untapped source of characters that should be included in phylogenetic analysis.

Another noteworthy feature of *Wanneria cranbrookense* Webster n. sp., which is shared with *Wanneria walcottana*, is the arcuate row of elongate dorsal projections along the inner margin of the rostral plate (Fig. 17.3, 17.4). It is possible that these projections aligned with the faint, ventrally projecting “dimples” that form an arcuate row in the cephalic border burrow visible on some specimens (Fig. 16.2, 16.5; Ludvigsen and Bohach, 1996, fig. 4.4c, d). A similar (and often much more obvious) row of pits in the anterior and lateral cephalic border furrow is seen in some (but not all) members of other, distantly related, olenelline clades such as nevadiids and biceratopsids (MW, personal observation), suggesting that the feature was either lost or gained multiple times within the Olenellina. This is significant because the presence of a similar

structure was used by Adrain (2011) as a synapomorphy for the Order Olenida. The homology and/or the propensity for convergent evolution of the structure across such disparate trilobites should be further investigated.

Order Corynexochida Kobayashi, 1935

Family Dorypygidae Kobayashi, 1935

Genus *Kootenia* Walcott, 1889

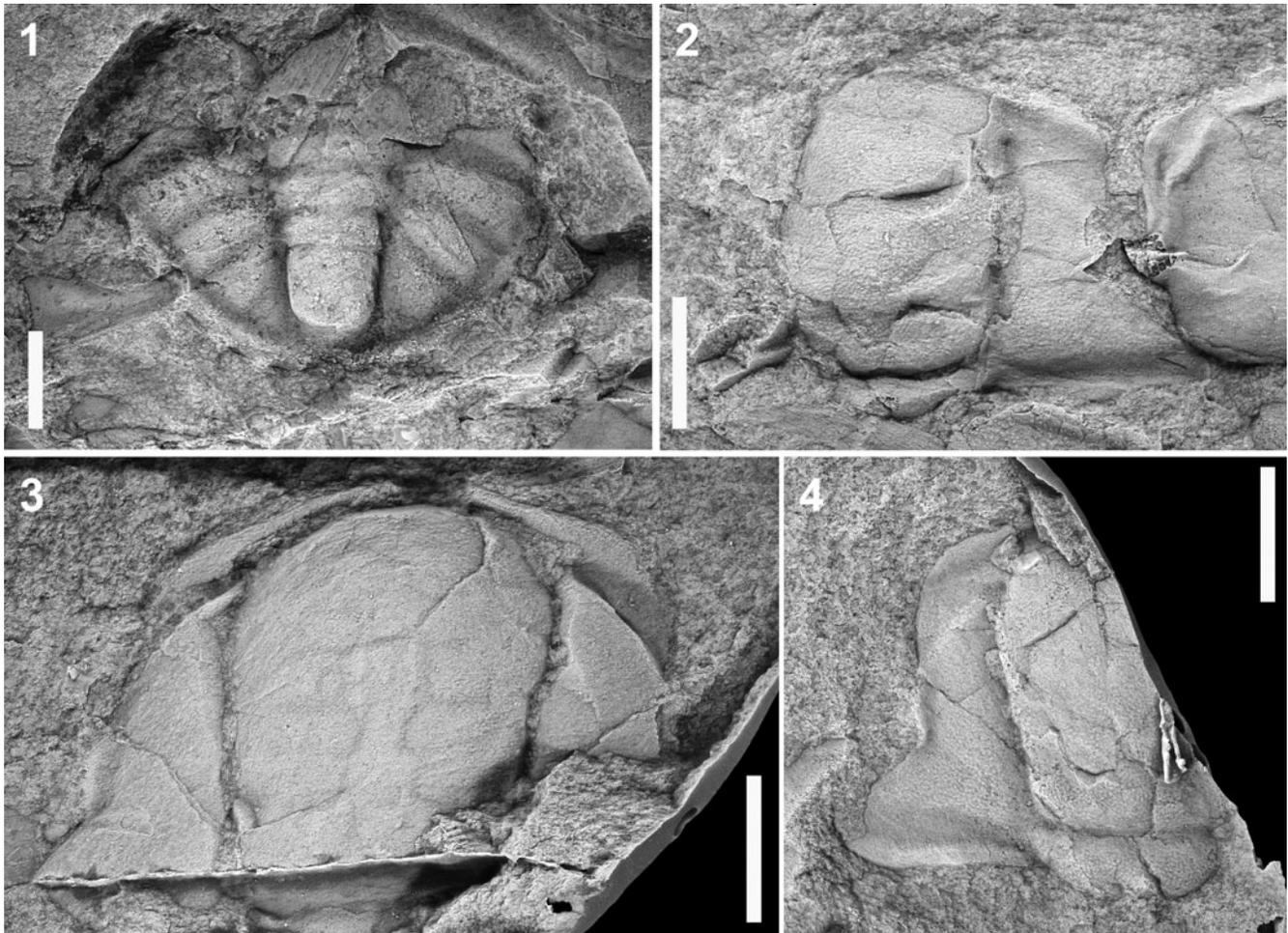
*Type species*.—*Bathyriscus (Kootenia) dawsoni* Walcott, 1889, from the Stephen Formation (Wuliuan Stage), British Columbia, Canada.

*Kootenia?* sp. indet.

Figure 22.1

*Occurrence*.—One pygidium recovered from the 2015 excavation of Locality B, Eager Formation (Cambrian Stage 4), Cranbrook, British Columbia.

*Remarks*.—The pygidium (Fig. 22.1) bears three clearly defined axial rings that sequentially narrow (tr.) posteriorly, plus a



**Figure 22.** Dorypygids from the Cranbrook Lagerstätte. (1) *Kootenia?* sp. indet., pygidium, internal mold, RBCM.EH2015.013.0165.001. (2–4) Dorypygid gen. and sp. indet. (2) Cranidium, latex peel of external mold, RBCM.EH2015.013.0137.001; (3) cranidium, latex peel of external mold, RBCM.EH2015.013.0074.001; (4) cranidium, latex peel of external mold, RBCM.EH2015.013.0219.001. All scale bars 3 mm. All from Eager Formation at Locality B.

poorly defined fourth axial ring and terminal piece that together form an elongate, parallel-sided, structure that extends almost to the border furrow; at least three pleural furrows with barely apparent interpleural furrows; a well-defined pygidial border; and at least five pairs of marginal spines or spinelets (length and curvature unknown). Despite the fragmentary nature and poor preservational quality of the specimen, which negate the possibility of species-level identification, it is tentatively assigned to the genus *Kootenia* Walcott, 1889. This tentative assignment is based on the presence and number of marginal spines (typically absent or fewer in number and extremely short in *Bonnia* Walcott, 1916), the relatively low number of segments (typically greater in *Ogygopsis* Walcott, 1889), and the effacement of the interpleural furrows (typically more strongly incised in *Olenoides* Meek, 1877).

Only one dorypygid pygidium from the Cranbrook area has been illustrated to date (Best, 1952a, pl. 2, fig. 29). That pygidium is poorly preserved (e.g., the presence or absence of marginal spines cannot be determined) but differs from the one illustrated herein in that the entire rhachis is more-or-less parallel-sided (rather than tapering backwards to the anterior margin of the fourth axial ring). Indeed, of the various dorypygid species identified in the Cranbrook area by previous workers (Schofield, 1921, 1922; Best, 1952a, b; Bohach, 1997), none have pygidia that conform to the specimen illustrated herein: they differ in the number of marginal spines and/or the number of interpleural furrows. Regardless of its generic assignment, then, the present specimen apparently represents the first of its kind in the region.

Dorypygid gen. and sp. indet.  
Figure 22.2–22.4

**Occurrence.**—Three fragmentary cranidia recovered from the 2015 excavation of Locality B, Eager Formation (Cambrian Stage 4), Cranbrook, British Columbia.

**Remarks.**—All three cranidia (Fig. 22.2–22.4) show virtually effaced glabellar furrows except for a shallow, transglabellar SO; the axial and border furrows are also shallow. An axial structure is possibly present on the occipital ring of one specimen (Fig. 22.4), but whether this represents the broken base of an occipital node/spine or a taphonomic artifact is uncertain. The ocular ridge diverges backwards abaxially away from the anterior cranial border, so that an outwardly widening triangular strip of exoskeleton separates the two and the anterior branch of the facial suture is relatively long (Fig. 22.4). Lirae are present on the anterior cranial border and anterior portion of the glabella; these grade into elongate granulations on the fixigena and central/posterior portions of the glabella.

These dorypygid cranidia perhaps represent a single species. Regardless, they cannot be unambiguously identified to the genus level. They are unlikely to represent *Bonnia*, because in species of that genus the ocular ridge runs close and more-or-less parallel to the anterior cranial border, so that the anterior branch of the facial suture is short. However, a relatively long anterior branch of the facial suture (as seen in these specimens) occurs in some species of *Kootenia* (e.g., *Kootenia*

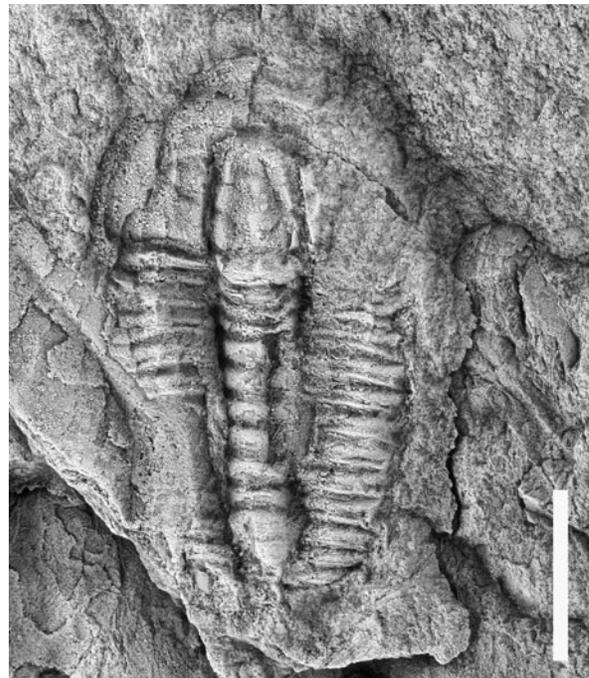
*randolphi* Robison and Babcock, 2011, and *Kootenia youngorum* Robison and Babcock, 2011) and *Ogygopsis* (e.g., *Ogygopsis batis* [Walcott, 1916] and *Ogygopsis klotzi* Rominger, 1887).

Only two dorypygid cranidia from the Cranbrook area have been figured previously (Best, 1952a, pl. 2, fig. 20; Bohach, 1997, pl. 27, fig. 11). Both those specimens differ from the present specimens by possessing a short anterior branch of the facial suture. Indeed, of the various dorypygid species identified in the Cranbrook area by previous workers (Schofield, 1921, 1922; Best, 1952a, b; Bohach, 1997), none have the relatively long anterior branch of the facial suture that characterizes the present specimens. Regardless of its generic assignment, then, the present morphotype has not been previously documented in the region.

It is possible that these cranidia belonged to the same species as the pygidium described as *Kootenia?* sp. indet. (above). However, given the uncertainty of that association, the cranidia are conservatively left in broader open nomenclature.

Order Uncertain  
Family Uncertain  
“Ptychoparioid” genus and species indet.  
Figure 23

**Occurrence.**—No “ptychoparioids” were recovered from Locality B during the 2015 excavation. However, an articulated specimen of a “ptychoparioid” from that site (Eager Formation [Cambrian Stage 4], Cranbrook, British Columbia), held in the personal collection of Dan Kelly, was made available to MW for study (Fig. 23). The specimen was subsequently donated to Cranbrook History Centre.



**Figure 23.** “Ptychoparioid” genus and species indet. from the Cranbrook Lagerstätte. Poorly preserved internal mold, CBK.2023.003. Scale bar 3 mm. From Eager Formation at Locality B.

*Remarks.*—The specimen is a poorly preserved internal mold but represents a unique occurrence and is therefore documented herein. The glabella is weakly tapered anteriorly, with a broadly rounded anterior margin. Glabellar furrows are visible on the internal mold; SO is deepest distally but appears to cross the sagittal axis; L1 is convex anteriorly, oriented inwards and backwards from the axial furrow, and does not appear to be incised over the sagittal axis; S2 is oriented more-or-less transversely adjacent to the axial furrow, but its inwards course and depth cannot be determined. There is a moderately long preglabellar field. The anterior cranial margin is strongly curved, with the anterior border being substantially longer sagittally than exsagittally. It cannot be determined whether the anterior cephalic border furrow deflects posteriorly at the sagittal axis. The adaxial portion of the ocular ridge is oriented more-or-less transversely, the ocular ridge then gently arcs posterolaterally across the interocular area. It is unclear whether the librigena bears a genal spine. At least eleven thoracic segments are preserved behind the cranidium.

Recent work has highlighted the significance of multi-sclerite associations, three-dimensional relief, and surface ornamentation to ptychoparioid systematics (e.g., Webster, 2011a; Geyer and Peel, 2017; Sundberg and Webster, 2022). Such information is not available for the poorly preserved Cranbrook specimen, which therefore cannot be reliably identified to even the genus level. The broad anterior border with strongly curved anterior margin is similar to species of *Crassifimbria* Lochman, 1947, and *Onchocephalus* Resser, 1937. The Cranbrook specimen differs from species such as *Crassifimbria walcotti* (Resser, 1937), *Crassifimbria? metalaspis* (Sundberg and McCollum, 2000), *Onchocephalus thia* (Walcott, 1917), *Onchocephalus buelnaensis* Lochman in Cooper, 1952, and *Onchocephalus mexicanus* Lochman in Cooper, 1952, by possessing a longer preglabellar field.

Bohach (1997, p. 307, 392, pl. 39, figs. 17, 18) identified a “ptychoparioid” from Locality B and illustrated two cranidia. Those cranidia differ from the specimen illustrated herein by possessing a straighter and shorter (sag., exsag.) anterior border, wider (tr.) posterior limb of the fixigenae, and more transversely oriented ocular ridges, and therefore seem to represent a second species of “ptychoparioid” at the site. No specimens of that second species were found or examined during the course of the present study, and it is not illustrated herein.

### Preservation and biostratigraphy of the trilobites, with paleoenvironmental inferences

As noted above, Webster et al. (2015; see also Caron et al., 2024) provided some preliminary observations on the sedimentology and the preservation and biostratigraphy of the Cranbrook Lagerstätte fauna in general. Those authors concluded that the depositional environment was an outer shelf setting below storm wave base but within the photic zone, with sedimentation occurring episodically in the form of turbidity flows sourced from (storm-induced?) disturbance on the shallower shelf. Most flows deposited only muds and clays, but some had sufficient energy to transport sand grains and cause scouring of the seabed. Herein, we summarize observations on the preservation and

biostratigraphy of the trilobites from the site and use those observations to infer the extent to which the assemblage is likely to have been winnowed and/or transported by those flow-induced currents prior to burial.

Trilobites are very abundant at the site, making up >98% of the > 2,600 body fossils recovered from the 2.65-meter section. The trilobites are preserved as internal and external molds. The vast majority are disarticulated, although some more-or-less fully articulated specimens were recovered (e.g., Figs. 5, 6.6, 6.7, 14.2–14.6), as were some specimens showing intermediate degrees of disarticulation (Fig. 6.1–6.5). Some articulated specimens retain all their dorsal sclerites in an essentially intact arrangement and might represent carcasses (Figs. 5.2, 14.2–14.6). Whether those individuals were transported into the site prior to death and burial is unknown. Some specimens (Figs. 5.4–5.6, 6.1, 6.2, 6.6, 6.7, 14.1) show displaced ventral sclerites and/or telescoping of the thorax under the cephalon in a configuration consistent with ecdysis (see Webster, 2015, p. 68 for criteria) and thus might represent essentially undisturbed exuviae. Such consistently arranged, delicate, and biologically interpretable configurations are unlikely to be produced by or survive transportation and are thus strongly indicative of the presence of a trilobite community inhabiting the site of burial. The presence—albeit rarely—of arthropod trackways at Locality B (Caron et al., 2024) is unambiguous evidence of living arthropods at the site of deposition, although a hypothesis that such tracks were produced by live individuals that had been transported into the locale cannot be refuted.

Other specimens show a less well-ordered arrangement of slightly dissociated sclerites perhaps indicative of post-ecdysial disturbance of exuviae (Fig. 6.3). Some curious patterns of sclerite (dis)association are not obviously interpretable in terms of simple molting behavior, decay, or predation/scavenging of a carcass. These include examples of trunks that have been extended by disarticulation (Figs. 5.1, 5.3, 6.4), disruption and/or loss of only a portion of the thorax (Fig. 6.5), and chaotic jumbles of sclerites (Fig. 6.8, 6.9). Such patterns perhaps suggest that articulated remains became disturbed as a result of exposure to weak bottom currents and/or short transportation, although any such exposure to or transport by currents was not sufficient to cause complete disarticulation and dissociation of parts.

Some bedding surfaces show rich concentrations of disarticulated trilobite sclerites (Fig. 6.10). These are interpreted as winnowed or hiatal surfaces and indicate the presence of occasional bottom currents and/or episodic sedimentation. Consistent with the hypothesis of sclerite movement by bottom currents, there is a suggestion of weak preferred alignment of specimens on some surfaces (Fig. 6.11), and the presence of trilobite debris within what had been open burrows (Caron et al., 2024). The failure to observe very small specimens (e.g., cephalons in phases 1 or 2 of development, or small isolated thoracic segments) probably indicates some degree of size-sorting, with tiny sclerites presumably winnowed away.

It is thus deemed likely that the turbid flows that brought in the sediment to Locality B were responsible for the winnowing away of the smallest sclerites and for the disturbance (including possible reorientation) of some trilobite remains. It is conceivable—although by no means certain—that some of the trilobites

were transported into the depositional site by currents. However, the preservation of what appear to be more-or-less undisturbed exuviae (Figs. 5.4–5.6, 6.1, 6.2, 6.6, 6.7, 14.1), specimens with delicate spines (Fig. 12.1), and jumbles of loosely associated (but not entirely isolated) sclerites (Fig. 6.3–6.5, 6.8, 6.9) suggest that trilobites inhabited the site and/or that any transportation was not over a great distance. The assemblage is therefore interpreted as autochthonous and/or parautochthonous.

### Diversity of the trilobite fauna, with comparison to other Lagerstätte

Previous estimates of trilobite diversity within the Eager Formation in the Cranbrook area have varied between five and seven (perhaps eight) species. In his seminal paper, Best (1952b) identified five trilobite species from the Cranbrook area: *Olenellus gilberti*, *Olenellus eagerensis*, *Olenellus schofieldi*, *Wanneria walcottana*, and *Bonnia columbensis*. His unpublished M.S. thesis (Best, 1952a) also identified *Paedeumias nevadensis* (Walcott, 1910), but the specimens attributed to that species in the thesis were assigned to *Olenellus gilberti* in the published paper (Best, 1952b).

Walcott (in Schofield, 1921, 1922) had identified six species of trilobites within the initial collections made in the Cranbrook area: *Callavia* cf. *C. nevadensis*, *Wanneria* n. sp.?, *Mesonacis gilberti*, *Wanneria* cf. *W. walcottanus*, *Olenellus* cf. *O. fremonti* Walcott, 1910, and *Protypus senectus* Billings, 1861b. However, none of the specimens was illustrated and the matching of these earliest identifications to those of subsequent workers (including the present study) involves some speculation. Walcott's *Mesonacis gilberti* (and perhaps *Callavia* cf. *C. nevadensis*, which later became *Paedeumias nevadensis*) presumably correspond to Best's *Olenellus gilberti*; Walcott's two *Wanneria* species presumably equate to Best's (1952b) *Wanneria walcottana*; and the dorypygid identified as *Bonnia columbensis* by Best (1952a, b) is presumably what Walcott had called *Protypus senectus*. It is probable that Best's (1952b) *Olenellus schofieldi* was identified by Walcott as *Olenellus* cf. *O. fremonti*, based on the (near) absence of a preglabellar field and on the relatively short ocular lobes.

Several workers subsequently recognized that Best's (1952a, b) *Olenellus gilberti* actually represents a new species (Best, 1959; Hu, 1985; Bohach, 1997; Palmer, 1998a; Webster, 2015). The unpublished theses of Best (1959) and Bohach (1997) also attributed the specimens previously identified as *Wanneria walcottana* to a new species. Best's (1952b) *Olenellus eagerensis* has been reassigned to *Mesonacis* (Lieberman, 1999; see also Bohach, 1997). Such revisions change the names but not the number of species within the assemblage.

Bohach (1997) identified a minimum of seven, and perhaps eight, species of trilobite from the Cranbrook area. These included the four olenelloids mentioned above, plus at least two (and a tentative identification of a third) dorypygid species, plus one species of "ptychoparioid" in open nomenclature. Two of the three dorypygid species represented new species of *Bonnia*; the third was *Bonnia fieldensis* Walcott, 1916, which Bohach (1997) proposed should be reassigned to the genus *Bonnaspis* Resser, 1936. Bohach presumably considered Best's (1952a, b) previous record of *Bonnia columbensis* to be

subsumed within one of her newly reported species (probably *Bonnia fieldensis*).

Herein we recognize a minimum of eight species of trilobite within the Eager Formation of the Cranbrook area; that tally might be as high as 11 species depending on the as-yet-undetermined number of dorypygid species. Four species of olenelloids are present: (1) *Olenellus santucci* Webster n. sp., described above and providing a formal name for the species formerly identified as *Olenellus gilberti*; (2) *Olenellus? schofieldi*, redescribed above; (3) *Mesonacis eagerensis*, redescribed above; and (4) *Wanneria cranbrookense* Webster n. sp., described above and providing a formal name for the species formerly identified as *Wanneria walcottana*. At least two, and perhaps as many as five, species of dorypygid are present. The 2015 excavation at Locality B led to the discovery of a previously unrecorded pygidial morphotype (documented above as an indeterminate species tentatively assigned to *Kootenia*) and a previously unrecorded cranidial morphotype (documented above as an indeterminate dorypygid genus and species); these might (or might not) represent sclerites of the same species. Neither of the newly discovered sclerites, however, is conspecific with the previously reported dorypygids which, as summarized above, represent from one to three additional species (Bohach, 1997). Finally, two species of "ptychoparioids" are present: a previously unrecorded form is documented in open nomenclature above, which differs from the single species reported by Bohach (1997).

All eight (or 11) species occur at Locality B, and at least three of the olenelloid species are also known from other localities in the Cranbrook area (Appendix). The species-level diversity of trilobites at the Cranbrook Lagerstätte is comparable to that at other Lagerstätte from the Dyeran on Laurentia, all of which also occur in fine-grained siliciclastic rocks. For example, at least five trilobite species have been recovered from the Lagerstätte in the "Insolens Beds" at Klondike Gap in Nevada (Delamar Member, Pioche Formation; Webster, 2007b, 2011b); standing diversity within the Lagerstätte-bearing Latham Shale of California peaks at seven trilobite species (Webster et al., 2003; Webster, 2011b); the Ruin Wash Lagerstätte in Nevada (Combined Metals Member, Pioche Formation) contains 11 trilobite species (Palmer, 1998a; Webster, 2011b; Webster and Sundberg, 2020); approximately 13 species of trilobite occur at the Parker Quarry Lagerstätte in Vermont (Parker Formation; Webster and Landing, 2016), although the dorypygids and "ptychoparioid" await modern systematic revision; and preliminary data suggest that at least eight trilobite species are present in the Lagerstätte-bearing sites in the Kinzers Formation (Pennsylvania; MW, unpublished data). By comparison, the "unusually diverse" trilobite assemblage described by Palmer (1964) from the carbonates of the Harkless Formation at the Gold Point locality in Nevada consists of 12 species.

The Cranbrook Lagerstätte therefore cannot be described as depauperate in terms of its trilobite species richness. Nor are trilobite remains rare at the site (see above). These facts, along with the evidence from trilobite biostratigraphy (above), indicate that the local environment of the Eager Trough was at least periodically able to support a "typical" (for Cambrian Series 2) benthic trilobite community of olenelloids, dorypygids, and "ptychoparioids". The absence of open-shelf-inhabiting oryctocephalid

trilobites from the Cranbrook assemblage could be relevant to facies interpretation, or it could result from the age of the deposit (perhaps slightly pre-dating the widespread colonization of Laurentia by the group). Factors such as periodic oxygen stress and intervals of high sedimentation rate seem to have limited the diversity, abundance, and/or preservation potential of non-trilobite elements of the biota—both biomineralized (brachiopods and hyoliths) and non-biomineralized—in the Cranbrook Lagerstätte relative to some other Burgess Shale-type Lagerstätte (Caron et al., 2024), but apparently had no marked effect on the trilobite diversity. The preservation of trilobite remains might have been more robust against such factors, or perhaps the trilobites themselves were more tolerant of such factors or were able to colonize the site more quickly during the intervals of more favorable environmental conditions (see Dahl et al., 2019, for a potentially analogous situation).

### Age of the Cranbrook Lagerstätte

The age of the Cranbrook Lagerstätte has, until now, remained poorly constrained. Conway Morris (1989, p. 274) placed the Eager Formation in the upper Dyeran and noted that the age of the Cranbrook Lagerstätte relative to that of other important Lagerstätten such as in the Kinzers Formation of Pennsylvania, the Chilhowee Group of Tennessee, and the Parker Formation of Vermont, could not be resolved, although he noted some circumstantial evidence that the Cranbrook site might be older than the Latham Shale of California.

Recent field work has shed light on the relative ages of some of these other Lagerstätten (Fig. 24). Webster and Hageman (2018) described a new trilobite from the Murray Shale (upper Chilhowee Group, Tennessee), which indicated that the fauna from that unit is of a much older middle to upper Montezuman age. Webster and Landing (2016) constrained the age of the Parker Quarry Lagerstätte (Parker Formation, Vermont) to lie within the *Bolbolonellus euryparia* Zone or overlying *Nephrolenellus multinodus* Zone. Webster (2011b) showed that the Latham Shale spans from the *Arcuolenellus arcuatus* Zone to the *Peachella iddingsi* Zone of the upper Dyeran; unpublished data show that the soft-bodied fossils occur as low as the *Bristolia mohavensis* Zone. Work to more precisely refine the age(s) of the middle to upper Dyeran Kinzers Formation Lagerstätte is in progress (MW, in preparation).

Precise age determination of the Cranbrook Lagerstätte has been hampered or misled by inaccurate identification of the trilobites from the deposit. The previous identification of *Olenellus gilberti* in the Eager Formation implied a species-level correlation to uppermost Dyeran strata of the southwestern United States, where that species occurs in the upper portion of the *Bolbolonellus euryparia* Zone and throughout the *Nephrolenellus multinodus* Zone (Webster, 2011b, 2015). The previous identification of *Wanneria walcottana* in the Eager Formation implied a species-level correlation to middle to upper Dyeran strata of Pennsylvania, where that species occurs in the Emigsville Member of the Kinzers Formation (e.g., Wanner, 1901; Walcott, 1910; Whittington, 1989; Skinner, 2005). Best's (1952a, b) previous identification of *Bonnia columbensis* from Cranbrook would imply a species-level correlation to (middle? to) upper Dyeran strata in the Canadian Rockies of British Columbia

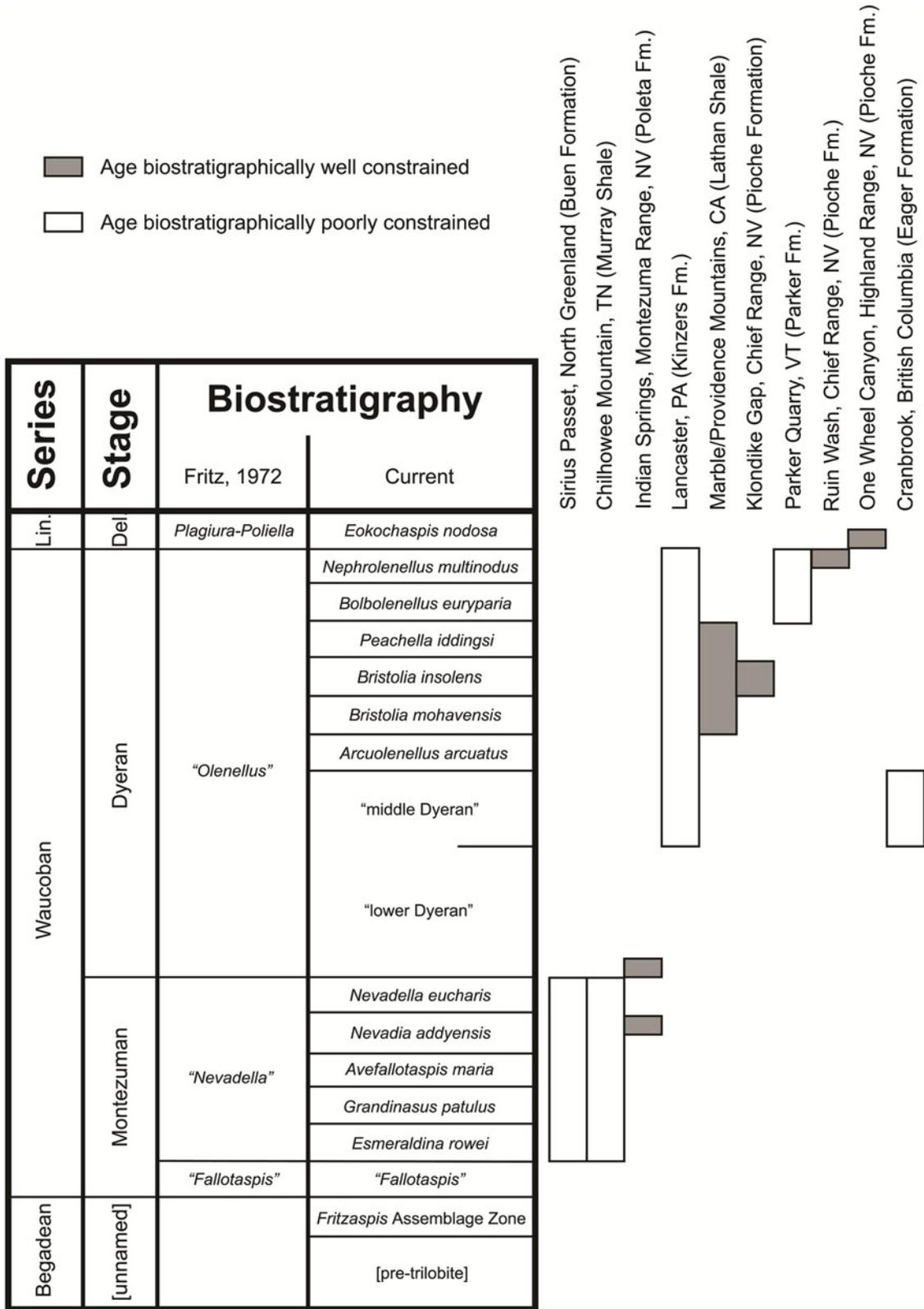
(Walcott, 1917; Rasetti, 1951), the Wernecke Mountains of Yukon Territory (Fritz, 1991), the Sekwi Formation of Yukon Territory (Fritz, 1972), and Clayton Ridge in Nevada (Sundberg and Webster, 2021). However, none of those previous identifications is supported herein, and the correlations that they implied must therefore be reconsidered.

Fortunately, the revised trilobite identifications herein, in combination with unpublished occurrence data from exposures of the Eager Formation in other areas, can better constrain the age of the Cranbrook Lagerstätte within the Dyeran Stage.

At the genus level, *Wanneria*, *Olenellus*, and *Mesonacis* elsewhere on Laurentia all make their lowest stratigraphic occurrence in the middle Dyeran (Palmer and Repina, 1993; Palmer and Repina in Whittington et al., 1997; Webster, 2011b; Landing et al., 2024). *Wanneria* probably ranges into the lower part of the upper Dyeran (Webster, unpublished data), while *Olenellus* and *Mesonacis* range to the uppermost Dyeran (Palmer and Repina, 1993; Palmer and Repina in Whittington et al., 1997; Webster, 2011b; Landing et al., 2024). However, correlations based on genus-level occurrences are less satisfactory than those based on species-level occurrences due to the higher potential for strong diachrony of genus-level occurrences between regions, especially if the species within that genus differ between the regions.

At the species level, the four olenelloid species are all endemic to the Eager Formation and, by themselves, are not useful for inter-regional correlation. However, field work by MW in the Eager Formation on Mount Grainger in the western Hughes Range (on the Windermere High; Fig. 1.1; Appendix) has confirmed Bohach's (1997, p. 355–359) unpublished discovery that *Wanneria cranbrookense* Webster n. sp. occurs at that locality in stratigraphic association with *Elliptocephala logani* (Walcott, 1910). *Elliptocephala logani* is a widely distributed species, occurring in middle Dyeran strata in, for example, the Forteau Formation of Labrador (Walcott, 1910) and the Sekwi Formation of the Northwest Territories (Fritz, 1972). The stratigraphic co-occurrence of *Wanneria cranbrookense* Webster n. sp. and *Elliptocephala logani* on Mount Grainger therefore strongly indicates that *Wanneria cranbrookense* Webster n. sp. is a middle Dyeran species. Based on that finding, and under the assumption that *Wanneria cranbrookense* Webster n. sp. does not have an unusually long stratigraphic range—an assumption supported by all currently available data (Bohach, 1997; MW, unpublished data)—it is thus concluded that the Cranbrook Lagerstätte is of middle Dyeran age (Fig. 24).

Such an age determination makes the Cranbrook Lagerstätte one of the oldest Burgess Shale-type deposits on Laurentia: only the Sirius Passet (Conway Morris et al., 1987; Ineson and Peel, 2011), the Murray Shale, and the Indian Springs Lagerstätten (English and Babcock, 2010) are older (Fig. 24). The Kinzers Formation Lagerstätte might be approximately as old as the Cranbrook Lagerstätte, but the other well-known upper Dyeran Lagerstätten in Vermont, Nevada, and California are demonstrably younger (above). The Cranbrook Lagerstätte therefore lies within what was a substantial stratigraphic gap between the Montezuman-to-lowermost Dyeran Lagerstätten and the upper Dyeran Lagerstätten. The significance of this age determination to our understanding of the stratigraphic ranges of non-biomineralized taxa will be discussed elsewhere.



**Figure 24.** Relative ages of Burgess Shale-type Lagerstätten from the traditional “lower” Cambrian of Laurentia. With the possible exception of the poorly age-constrained Kinzers Formation Lagerstätte, the Cranbrook Lagerstätte is the only middle Dyeran deposit known to yield fossils of non-mineralized taxa. Vertical scale is arbitrary and non-linear. Current biostratigraphic zonation scheme follows Hollingsworth (2011) and Webster (2011b); the now-abandoned genus-level scheme proposed by Fritz (1972) is included for completeness. Work is in progress to establish species-level biostratigraphic zones within the lower and middle portions of the Dyeran Stage (e.g., Webster and Bohach, 2014; Landing et al., 2024). Abbreviations: Del., Delamarian; Fm., Formation; Lin., Lincolnian.

## Conclusions

The Cranbrook Lagerstätte is a hitherto little-studied interval within the Eager Formation (Cambrian Series 2, Stage 4) that crops out 8–10 km northeast of Cranbrook, southeastern British Columbia. It was deposited in the Eager Trough, a basin on the outer shelf between the paleo-highs of the Windermere High and Montania along the Cordilleran miogeocline of Laurentia. The Lagerstätte is dominated by trilobites and has yielded fossils of brachiopods, hyoliths, rare sponges, and several non-biomineralized taxa including *Tuzoia*, *Anomalocaris*, and a pterobranch hemichordate. A detailed excavation and systematic survey in 2015 of a productive site known as Locality B provided new material upon which the trilobites of the Cranbrook Lagerstätte are herein described.

A minimum of eight, and perhaps up to 11, trilobite species occur in the Lagerstätte, making up > 98% of the body fossils at Locality B. Four species of olenelloids are by far the most abundant elements of the fauna; they are described herein as *Olenellus santucci* Webster n. sp., *Olenellus? schofieldi*, *Mesonacis eagerensis*, and *Wanneria cranbrookense* Webster n. sp. Two species of “ptychoparioids” and at least two (perhaps as many as five) species of dorypygids are far rarer and are left in open nomenclature. The other fossil-bearing localities in the Cranbrook area yield the same olenelloid species, suggesting that the sites are all more-or-less correlative within the Eager Formation to the limits of biostratigraphic resolution. Trilobite diversity in the Cranbrook Lagerstätte is comparable to that within other Lagerstätten from Cambrian Stage 4 (Series 2) of Laurentia, even if the diversity of non-trilobite taxa is somewhat subdued.

The diversity and abundance of trilobites, combined with biostratigraphic data such as the preservation of apparently undisturbed exuviae and associations of slightly disarticulated remains, suggest that the assemblage is autochthonous and/or parautochthonous, and that the local environment was at least periodically able to support a “typical” benthic trilobite community. This interpretation is bolstered by the presence of arthropod trackways at Locality B.

The stratigraphic co-occurrence of *Wanneria cranbrookense* Webster n. sp. with the widely distributed and biostratigraphically useful *Elliptocephala walcotti* in the Eager Formation at sites to the north (on the Windermere High) indicates that the Cranbrook Lagerstätte lies within the middle Dyeran Stage of Laurentia. It therefore lies within what was a substantial stratigraphic gap in the distribution of Burgess Shale-type Lagerstätten on Laurentia, between the stratigraphically older Sirius Passet, Chilhowee Mountain, and Indian Springs Lagerstätten (Montezuman and earliest Dyeran), and the stratigraphically younger Lagerstätten in the Latham Shale, Pioche Formation, and Parker Formation (upper Dyeran).

The abundance and generally good preservational quality of olenelloids in the Cranbrook Lagerstätte permits study of the paleobiology and ontogeny of these early trilobites. Such data shed light on the dynamics of development, with important ramifications for studies of olenelloid phylogeny and evolution, as shown by three examples documented herein. Firstly, the successive phases of cephalic development previously documented

in the ontogeny of other olenelloids are also recognized in the Cranbrook species. This suggests a degree of phylogenetic conservatism in the general pattern of ontogenetic cephalic shape change and the cephalic sizes at which those changes occurred. Secondly, mirroring the pattern seen in some other olenelloids, the effacement of cephalic furrows in *Wanneria cranbrookense* Webster n. sp. was progressively achieved through ontogeny, being superimposed upon and independent of a phylogenetically conserved pattern of ontogenetic shape change of the glabella. This is consistent with the hypothesis that effacement was not a peramorphic extension of glabellar development, with implications for character independence in phylogenetic analysis. Thirdly, the third thoracic segment of *Wanneria cranbrookense* Webster n. sp. was “normal” (i.e., neither macropleural nor macrospinous) throughout the sampled portion of ontogeny. This stands in contrast to the condition seen in taxa such as *Elliptocephala asaphoides* (where that segment is macropleural and macrospinous at young developmental stages and proportionally shrinks to become “normal” at morphological maturity) or *Olenellus santucci* Webster n. sp. (where that segment is macropleural and macrospinous throughout ontogeny). This suggests that the ontogenetic dynamics of the segment should be considered in phylogenetic analysis. The Cranbrook Lagerstätte also increases our knowledge of trilobite disparity (e.g., *Wanneria cranbrookense* Webster n. sp. possessed only 16 thoracic segments at morphological maturity, which increases the known disparity of thoracic segmentation within the genus; the striking array of five very long spines radiating from the posterior portion of the trunk of *Mesonacis eagerensis*, which is unique) and intraspecific variation (including within-individual asymmetry, as shown for genal ridge orientation in *Olenellus santucci* Webster n. sp.). Such data are important for robust species delimitation, for accurate coding of phenotypic characters in cladistic analyses, and for the investigation of mechanisms and constraints of phenotypic evolution.

## Acknowledgments

St. Mary’s First Nation band of the Kootenay people generously allowed MW access to the fossil localities on their homeland in 2018. The British Columbia Government approved the permit for excavating Locality B under a Land Act license of occupation (#405166) from the then Ministry of Forests, Lands and Natural Resource Operations. We thank E. Deom (Fossil Management Office) for facilitating the permit application. The fossil material collected during the 2015 expedition is deposited at the Royal British Columbia Museum; special thanks are due to V. Arbour and D. Larson for their assistance with research loans. G. Santucci was instrumental in coordinating and assisting the fieldwork in both 2015 and 2018. The Cranbrook History Centre served as a hub for meetings and logistics during MW’s fieldwork in 2018; Executive Director C. Murray is thanked. R. Gaines (Pomona College) and G. Mángano (University of Saskatchewan) were collaborators on the 2015 excavation of Locality B. Field assistance and advice on that project was generously provided by M. Akrami and J. Moysiuk (ROM), and by local collectors and volunteers C. Bell, D. George, A. Ingleson, C. New, D. Nordby, and H. Whittaker. We also

offer our thanks to Terry the skilled backhoe operator (Bad Ventures earthworks), F. Katay (British Columbia Geological Survey), and B. Robison (TerraLogic Exploration) for logistical support. P. Fenton and M. Akrami (ROM) provided technical support with collections. Field assistance to MW during 2018 was generously provided by J. Jacobs (East Kootenay Chamber of Mines), C. Jenkins, F. Katay, D. Kelly, D. Nordby, P. Ransom, and R. Williams (First Nations). D. Kelly kindly loaned his “ptychoparioid” specimen to MW for study, and then donated it to Cranbrook History Centre. S. Brown (University of Chicago Library) assisted with drafting the maps. This research was funded in part by NSF EAR Integrated Earth Systems grant #1410503 (to MW), Natural Sciences and Engineering Research Council Discovery Grant #341944 (to JBC), ROM internal sources (Peer Review Research Grant, Fieldwork Grant, Casual Salary Grant, Restricted Curatorial Funds), and Pomona College. We thank reviewers F.A. Sundberg and S.R. Westrop and Guest Editor N.C. Hughes for their helpful comments.

### Declaration of competing interests

The authors declare none.

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## Appendix

This appendix lists, in alphabetical order, the fossil-bearing localities within the Eager Formation in the Cranbrook area and the western Hughes Range that are relevant to the present study (Fig. 1).

### Cranbrook East, Cranbrook area

This is the easternmost fossil locality marked on the map of Schofield (1922, fig. 2), just north of the old Cranbrook–Fort Steele wagon road. It is an outcrop at the northern end of a low-lying field, 0.75 km north-northeast of intersection of Kootenay Highway and Crowsnest Highway, ~8 km northeast of Cranbrook (Fig. 1.2; 49°34.865'N, 115°40.906'W). The site was visited by MW and JBC in 2015, and again by MW in 2018. This site might be synonymous with USNM Locality 67f (below).

*Trilobite fauna*.—MW, personal observation, 2015, 2018.  
*Olenellus santuccii* n. sp.

### Cranbrook Junction, Cranbrook area

This is the original locality from which fossils were collected by Pollen and sent to Walcott via Schofield (see Schofield, 1922, fig. 2, southernmost fossil locality). The locality was shown as being on the side of the old Cranbrook–Fort Steele wagon road. This indicates that it was located at the southwest end of the modern-day interchange between Kootenay Highway and Crowsnest Highway, ~8 km northeast of Cranbrook, British Columbia (Fig. 1.2; approximately 49°34.233'N, 115°41.169'W).

*Trilobite fauna*.—Inferred from list by Walcott in Schofield, 1921, 1922 (see text).

*Olenellus santuccii* n. sp.

?*Olenellus? schofieldi* Best, 1952a.

*Wanneria cranbrookense* n. sp.

Dorypygid sp.

### Locality A of Best (1952a, b), Cranbrook area

This site was shown on the map (Best, 1952a) as being more-or-less on the Cranbrook–Fort Steele road. The road layout has been markedly altered in the years since the publication of this map. Nevertheless, the mark on the map of Best (1952a) places this site ~800 m northeast of Cranbrook Junction and ~400 m south of Cranbrook East. It is unclear whether Best's (1952 a, b) Locality A refers to one or both of these localities, or perhaps even represents a third, now lost, site in that vicinity.

*Trilobite fauna*.—Updated from Best (1952a, b).

*Olenellus santuccii* n. sp.

*Mesonacis eagerensis* (Best, 1952b).

*Wanneria cranbrookense* n. sp.

### Locality B of Best (1952a, b), Cranbrook area

This fossiliferous locality was shown by Schofield (1922, fig. 2, northernmost fossil locality) as being almost due north of the prominent hill just north of the road between Cranbrook and Fort Steele, and just south of the wagon road between Fort Steele and the St. Eugene Mission on the southern side of the St Mary River. Today, the locality is accessible as an outcrop on a small hill sandwiched between a shooting range and an archery range (Fig. 1.2; 49°35.458'N, 115°41.906'W). Best (1952a, b) referred to the site as “Locality B” (followed herein); Bohach (1997, p. 391–392) referred to the site as “Locality 5”. This site was excavated and studied in July 2015, as summarized in the text.

*Trilobite fauna*.—Updated from Best, 1952a, b; Ludvigsen and Bohach, 1996; Bohach, 1997; herein. \*At least two, and perhaps as many as five, dorypygid species might be represented among the various specimens in open nomenclature (see text).

*Olenellus santuccii* n. sp. (type locality) (Figs. 3.1–3.12, 4.1–4.9, 4.11, 4.12, 5.1–5.6, 6.2, 6.3, 6.5, 6.10, 6.11, 7.1–7.5, 8.1–8.10, 10.1–10.3).

*Olenellus? schofieldi* Best, 1952b (type locality) (Fig. 11.1–11.3).

*Mesonacis eagerensis* (Best, 1952b) (type locality) (Figs. 12.1, 12.2, 12.4–12.6, 13.1–13.6).

*Wanneria cranbrookense* n. sp. (type locality) (Figs. 6.6–6.8, 14.1, 14.3, 14.5, 14.6, 15.1–15.5, 16.1–16.7, 17.1–17.4, 18.1–18.4, 19.1–19.12, 20.1–20.4).

\**Kootenia?* sp. indet. (Fig. 22.1).

\*Dorypygid gen. and sp. indet. (Fig. 22.2–22.4)\*Dorypygid sp. or spp. (Bohach, 1997, pl. 27, fig. 11).

“Ptychoparioid” genus and species indet. (Fig. 23).

“Ptychoparioid” sp. (Bohach, 1997, pl. 39, figs. 17, 19).

### MCZ Locality 4790, Cranbrook area (from near Cranbrook, British Columbia)

*Trilobite fauna*.—Herein.

*Olenellus santuccii* n. sp.

### Mount Grainger section, western Hughes Range

In her unpublished work, Bohach (1997, p. 348–359) described three measured sections along Mount Grainger in the western Hughes Range (Fig. 1.1), two of which were visited by MW in 2015 and 2018. Bohach's (1997) “MG2” section (50° 08.490'N, 115°43.019'W; see Bohach, 1997, p. 355–359, text-fig. 54 for details) is important to the present study because it documents a stratigraphic co-occurrence of *Wanneria cranbrookense* n. sp. with *Elliptocephala logani* (Walcott, 1910) in collection MG2c. This co-occurrence was confirmed by MW in 2018.

### Ram Creek section, western Hughes Range

This locality in the western Hughes Range (Fig. 1.1) was measured and collected by Bohach (1997, p. 359–362, text-figs. 55, 56). It is important to the present study because it documents an occurrence of *Wanneria cranbrookense* n. sp. (in collection RC4f; Ludvigsen and Bohach, 1996, fig. 4.4c, d; Bohach, 1997, pl. 7, figs. 2, 5) only a short stratigraphic distance above an occurrence of *Elliptocephala logani* (Walcott, 1910) (in collection RC4f; Bohach, 1997, pl. 6, figs. 1, 2, 5, 8).

### Rock Point, Cranbrook area

A roadside exposure of the Eager Formation on the north bank of the St. Mary River, ~2.7 km northeast of Saint Eugene Mission, Kootenay First Nations Reservation (49°36.100'N, 115° 43.702'W). The locality was referred to as “St. Eugene Mission” by Bohach (1997, p. 391). The site was visited by MW in 2018.

*Trilobite fauna*.—Updated from Bohach, 1997; MW, personal observation, 2018.

*Olenellus santuccii* n. sp.

### St. Mary River, Cranbrook area

This locality refers to a series of cliffy outcrops in a pine wood near the St. Mary River (49°36.625'N, 115°55.931'W). This site was referred to as the “Marysville Locality” by Bohach (1997, p. 392). The site was visited by MW in 2018.

*Trilobite fauna*.—Updated from Bohach, 1997; MW, personal observation, 2018.

*Mesonacis eagerensis* (Best, 1952b).—Two specimens mentioned by Bohach, 1997, p. 392.

Trilobite sp. indet.

**USNM Locality 67f, Cranbrook area**

The index card for this locality, stored in the USNM, describes the site as “Eager Formation, six miles northeast of Cranbrook and three miles southwest of Fort Steele, about 100 yards from the road leading from Cranbrook to Fort Steele, and about 50 feet below level of road in a gravel pit, Kootenay River valley, British Columbia.” This suggests that USNM Locality 67f might be synonymous with Cranbrook East (above), but given the ambiguity, the two sites are here kept distinct. The fossils occur in a soft, pinkish, fine-grained sandstone to siltstone, and were collected by S. J. Schofield in 1921.

*Trilobite fauna.*—Herein.

*Mesonacis eagerensis* (Best, 1952b).

*Wanneria cranbrookense* n. sp. (Fig. 14.2).

**USNM Locality 67g, Cranbrook area**

This locality was described as “five miles northeast of Cranbrook” (Resser, 1929, p. 2–3). It is unclear whether Resser used USNM locality 67 g to refer to just one of the localities mentioned by Schofield (1922, fig. 2; Cranbrook Junction, Cranbrook East, or Locality B herein) or whether he used it as an undifferentiated catch-all term for all of the fossil-bearing localities northeast of Cranbrook.

*Trilobite fauna.*—Herein.

*Olenellus santuccii* n. sp. (Fig. 6.1, 6.4)

*Mesonacis eagerensis* (Best, 1952b) (Fig. 12.3)

Accepted: 14 November 2023