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# New records of injured Cambrian and Ordovician trilobites

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**Abstract.**—Records of abnormal fossil arthropods present important insight into how extinct forms responded to traumatic damage and developmental complications. Trilobites, bearing biomineralized dorsal exoskeletons, have arguably the most well-documented record of abnormalities spanning the Cambrian through the end-Permian. As such, new records of malformed, often injured, trilobites are occasionally identified. To further expand the documentation of abnormal specimens, we describe malformed specimens of *Lyriaspis sigillum* Whitehouse, 1939, *Zacanthoides* sp. indet., *Asaphiscus wheeleri* Meek, 1873, *Elrathia kingii* (Meek, 1870), and *Ogygiocarella debuchii* (Brongniart, 1822) from lower Paleozoic deposits. In considering these forms, we propose that they illustrate examples of injuries, and that the majority of these injuries reflect failed predation. We also considered the origin of injuries impacting singular segments, suggesting that these could reflect predation, self-induced damage, or intraspecific interactions during soft-shelled stages. Continued examination of lower Paleozoic trilobite injuries will further the understanding of how trilobites functioned as prey and elucidate how disparate trilobite groups recovered from failed attacks.

## Introduction

Abnormal trilobites represent a primary means of understanding how a group of wholly extinct euarthropods responded to, and recovered from, injuries and developmental or genetic malfunctions (Owen, 1985; Babcock, 1993, 2007; Bicknell and Pates, 2020). The historical record of abnormal trilobites extends back to the middle nineteenth century (Portlock, 1845) with more detailed documentation arising during the later twentieth century (see Bergström and Levi-Setti, 1978; Šnajdr, 1978a, 1979, 1985; Rudkin, 1979, 1985; Conway Morris and Jenkins, 1985; Owen, 1985; Babcock and Robison, 1989; Babcock, 1993). In the last decade alone, a marked surge in publications documenting these abnormal specimens has occurred. The majority of these works have considered abnormal specimens in the context of trilobite paleobiology and paleoecosystems (Budil et al., 2010; Zamora et al., 2011; Fatka et al., 2015, 2021; Cheng et al., 2019; Bicknell and Pates, 2020; Bicknell and Smith, 2021; Bicknell et al., 2021b; Foster, 2021; Zong, 2021a, b). Population-based data have been presented to explore injury patterns and lateralization in the trilobite fossil record (Pates et al., 2017; Bicknell et al., 2019; Pates and Bicknell, 2019). Finally, limited publications have collated these observations to understand patterns of predation across the Paleozoic (Bicknell and Paterson, 2018; Vinn, 2018; Klompmaker et al., 2019). To further the examination of abnormal trilobites, and bolster evidence that is useful for large meta-analyses, we present seven new examples of abnormal specimens: one *Lyriaspis sigillum* Whitehouse, 1939 from the Wuliuan of Australia; one *Zacanthoides* sp. indet. (of Walcott, 1888) from the Wuliuan of the USA; two *Asaphiscus wheeleri* Meek, 1873, and two *Elrathia kingii* (Meek, 1870) from the Drumian of the USA; and one *Ogygiocarella debuchii* (Brongniart, 1822) from the Darriwilian of Wales.

## Geological context

The *Lyriaspis sigillum* specimen (AM F33980 and AM F34209) was collected from the Beetle Creek Formation, Georgina Basin at the type section (proximal to the Templeton River headwaters), Mt. Isa, western Queensland, Australia. There the unit consists of 15 m of siliceous shale, fine sandstone, thin calcareous beds, and chert horizons that were likely deposited below a storm wave base, at the oceanward shelf edge of a large epeiric sea (Fleming, 1977; Kruse, 2002). This portion of the formation is occasionally referred to as the 'Lower Siltstone Member' (Russell, 1967), or the 'undifferentiated Beetle Creek Formation' (sensu Dunster et al., 2007). At the type locality, the unit unconformably overlies the Proterozoic rocks of the basin and is overlain by the Wuliuan-aged Inca Formation (Southgate and Shergold, 1991; Dunster et al., 2007). Presence of the

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trilobite species *Deiradonyx* sp. aff. *D. collabrevis* Öpik, 1982 (likely *D. collabrevis*) suggests placement in the *Pentagnostus praecurrens* Biozone—the latter taxon co-occurs with the eponym in the 'White Shale' member of the Coonigan Formation, Gnalta Shelf, western New South Wales (originally described as *P. veles* Öpik, 1979, later synonymized by Laurie, 1988). Further support comes from close faunal ties to the Jigaimara Formation (Laurie, 2006b), Arafura Basin, Northern Territory and the lithological correlations to the lower Arthur Creek Formation, southeastern Georgina Basin (Laurie, 2004, 2006a; Dunster et al., 2007). The Australian *Pentagnostus praecurrens* Zone sits within early Templetonian Stage, equivalent to the Wuliuan Stage (Sundberg et al., 2016, Peng et al., 2020 and references therein).

The *Zacanthoides* sp. indet. specimen (FHPR 17618) was collected from the Half Moon Mine locality, Chisholm Formation, Lincoln County, eastern Nevada. The Chisholm Formation there consists of 17–35 m of tan to gray to light reddish calcareous shale with some thin (0.05–3 m) interbedded carbonates (Sundberg, 2011). It is a relatively thin, slope-forming unit overlying the Lyndon Limestone and underlying the Highland Peak Formation. The examined specimen co-occured with trilobite genera, e.g., *Amecephalus* Walcott, 1924, *Athabaskia* Raymond, 1928, and *Glossopleura* Poulsen, 1927; echinoderms (*Gogia* Walcott, 1917); and the edrioasteroid *Totiglobus* Bell and Sprinkle, 1978 (Sundberg, 2011; Foster and Gaines, 2016). This fauna indicates that, at the Half Moon Mine, the Chisholm Formation is from the *Glossopleura walcotti* and *Pentagnostus praecurrens* biozones of the Wuliuan Stage (Sundberg, 2011; Peng et al., 2020).

The *Asaphiscus wheeleri* and *Elrathia kingii* specimens were collected from the Wheeler Formation, Millard County, western Utah, USA. The *A. wheeleri* (FHPR 16702, MWC 9973) and one *E. kingii* (MWC 9972) are from the House Range (Wheeler Amphitheater site), whereas another *E. kingii* (FHPR 16640) is from the Wheeler Formation in the Drum Mountains. The Wheeler Formation is up to 277 m of gray to olive to pinkish calcareous shale (Hintze and Davis, 2002, 2003). The formation overlies the Swasey Limestone and underlies the Marjum Formation in the House Range and the Pierson Cove Formation (a carbonate-rich, Marjum Formation equivalent) in the Drum Mountains. Restriction of the Wheeler Formation to the House Range and Drum Mountains reflects infilling of the middle Cambrian House Range Embayment—a fault-bounded, deep-water bathymetric feature of the Laurentian shelf that was surrounded on three sides by shallow carbonate belt deposits (Rees, 1986; Foster and Gaines, 2016). The deeper-water setting of the Wheeler Formation within the embayment allowed preservation of articulated trilobites and soft-bodied taxa (Robison et al., 2015). The examined specimens from the House Range are from the upper Wheeler Formation, and the Drum Mountains specimen is also from the upper portion of the same formation, ~7 m below the Pierson Cove Formation. This places the material in the *Bolaspidella* and *Ptychagnostus atavus* biozones of the Drumian Stage (Babcock et al., 2007; Peng et al., 2020).

The *Ogygiocarella debuchii* specimen (AM F128230) originated from a Llanfawr quarry near the township of Llandrindod Wells, central Wales, UK. These quarries are known for complete *O. debuchii* specimens, as well as other well-preserved trilobites (Hughes, 1969, 1971, 1979; Owens, 1981, 2002; Sheldon, 1987a). The specimen was from the lower Llanfawr Mudstones (Sheldon, 1987b; Owens, 2002) of the Builth Inlier. The Llanfawr Mudstones layer is relatively thick (> 200 m at some localities) and dominated by fine mudstone and siltstone that were deposited in relatively quiet, middle to outer shelf depths (Fortey and Owens, 1987; Owens, 2002). *Ogygiocarella debuchii* ranges through the entire formation, between the upper *Didymograptus murchisonii* and lower *Nemagraptus gracilis* biozones. However, the specimens reported here are likely from the regional Llandeilian Stage (*Hustedograptus*? *teretiusculus* Biozone) (Sheldon, 1987b), correlating with the upper Middle Ordovician, Darriwilian (Bettley et al., 2001; Cooper and Sadler, 2012; Bicknell et al., 2021b).

## Materials and methods

Trilobite specimens within the AM, FHPR, and MWC were reviewed for abnormalities by RDCB and JRF. A total of seven specimens were identified. Specimens were coated in magnesium oxide and photographed under low angle LED light with a Canon EOS 5DS (AM specimens) or a Canon EOS 5D Mark IV (FHPR and MWC specimens). All measurements of specimens were made using ImageJ (Schneider et al., 2012).

*Repositories and institutional abbreviations.*—AM = Australian Museum, Sydney, New South Wales, Australia; FHPR = Utah Field House of Natural History State Park Museum, Vernal, Utah, USA; MWC = Museums of Western Colorado, Dinosaur Journey Museum, Fruita, Colorado, USA.

## Results

The *Lyriaspis sigillum* specimen is articulated internal (AM F34209) and external (AM F33980) molds, and AM F33980 is more complete (Fig. 1). The specimen has a U-shaped indentation on the left thoracic pleural lobe (Fig. 1.1, 1.2). The indentation impacts thoracic segments 3–6, truncates pleurae by 1 mm, and is 2.6 mm long. The abnormality margin is cicatrized and thoracic segments 4 and 5 are pinched distally (Fig. 1.1, 1.4).

The *Zacanthoides* sp. indet. specimen is a partial internal mold showing the anterior right cephalic and thoracic regions (FHPR 17618; Fig. 2.3, 2.4). The first thoracic pleural spine of the specimen has been truncated by 1.3 mm (Fig. 2.3, 2.4). The spine also has a U-shaped indentation with a reduced, posteriorly directed spine (Fig. 2.4). This reduced section likely records abnormal regrowth of the segment through subsequent molting events.

Two abnormal *Asaphiscus wheeleri* specimens were considered. The first specimen is a complete internal mold (MWC 9973; Fig. 3.1–3.3). MWC 9973 has two abnormalities on the left thoracic pleural lobe. The anterior abnormality truncates the thoracic pleurae 1–4 by ~1.5 mm when compared to the right pleural lobe and shows an L-shaped morphology (sensu Bicknell and Pates, 2020). This region shows evidence of possible regrowth of the anteriormost pleurae. Further, the fourth thoracic pleura has a

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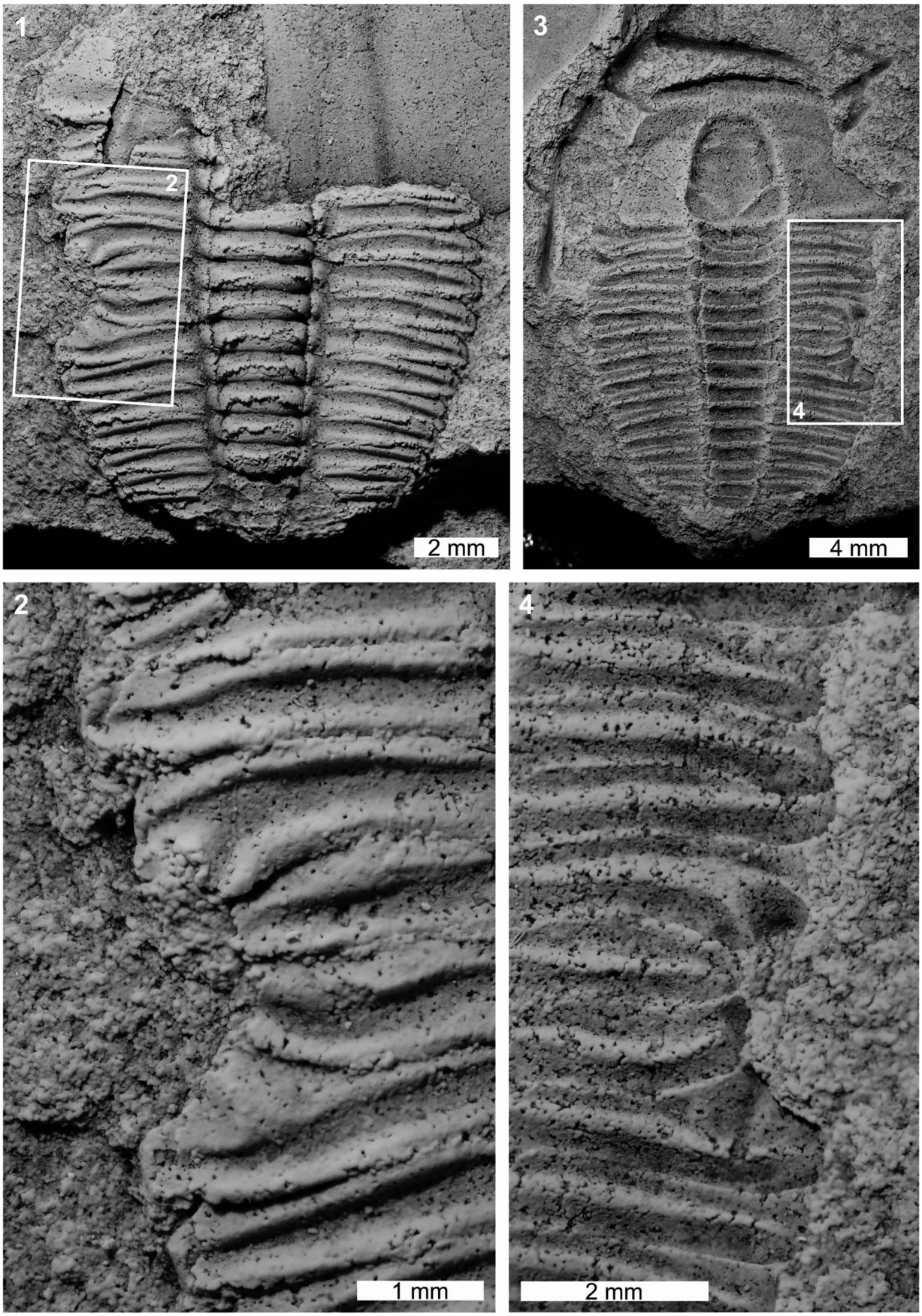


**Figure 1.** Malformed *Lyriaspis sigillum* Whitehouse, 1939, Beetle Creek Formation (Miaolingian, Wuliuan): (**1, 2**) AM F34209: (**1**) complete specimen; (**2**) detail of abnormality in box in (**1**) showing U-shaped injury; (**3, 4**) AM F33980: (**3**) complete specimen; (**4**) detail of abnormality in box in (**3**) showing injury. All specimens coated. All images converted to grayscale.

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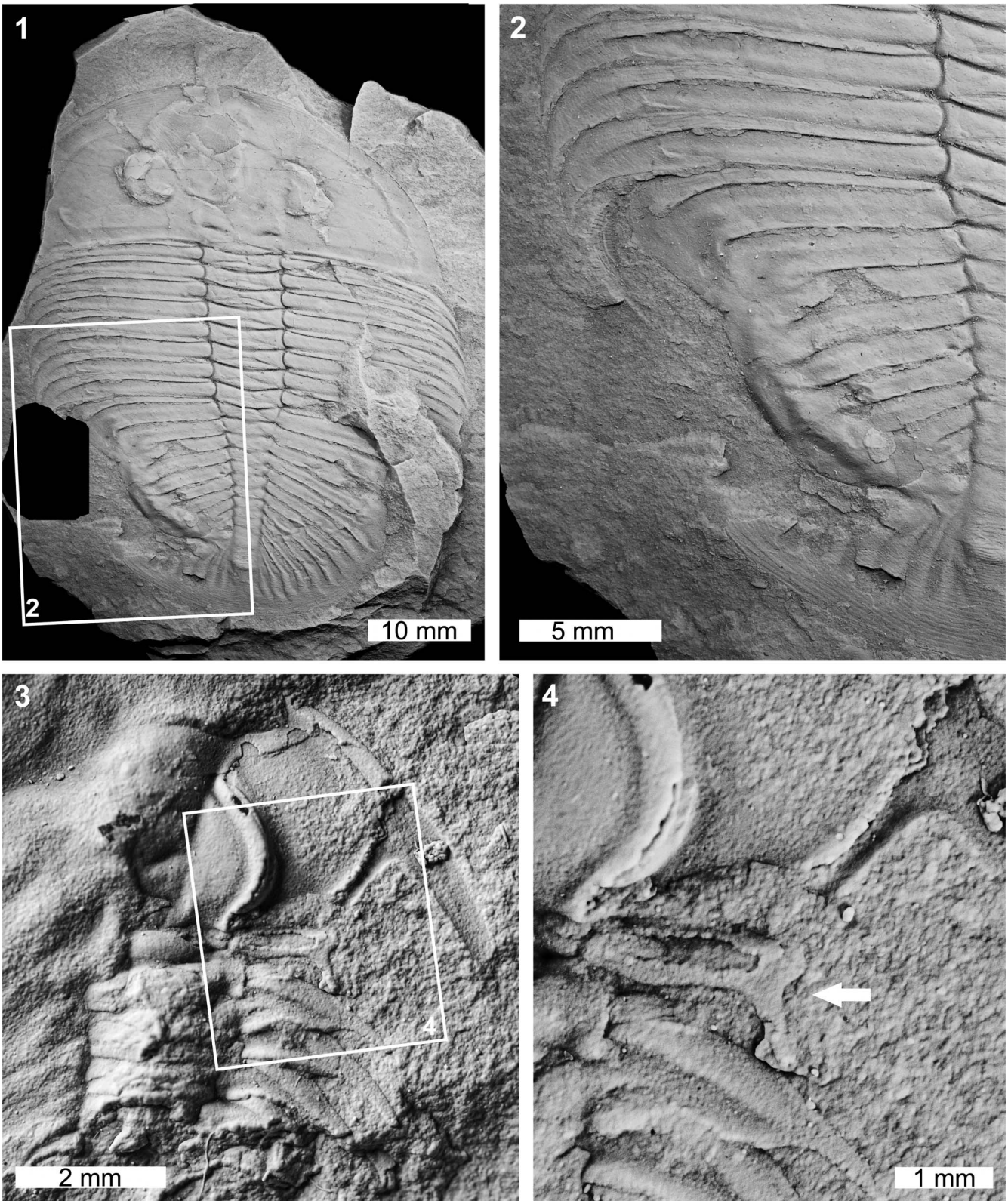


**Figure 2.** Malformed *Ogygiocarella debuchii* (Brongniart, 1822) and *Zacanthoides* sp. indet. (of Walcott, 1888): (**1, 2**) *Ogygiocarella debuchii* from the Llanfawr Mudstones (Middle Ordovician, Darriwilian), AM F128230: (**1**) complete specimen; (**2**) detail of abnormality in box in (**1**) showing W-shaped indentation on the left side of the pygidium; (**3, 4**) *Zacanthoides* sp. indet. from the Half Moon Mine, Chisholm Formation (Miaolingian, Wuliuan), FHPR 17618: (**3**) complete specimen; (**4**) detail of abnormality in box in (**3**) showing abnormally developed pleural spine (white arrow). All specimens coated. All images converted to grayscale.

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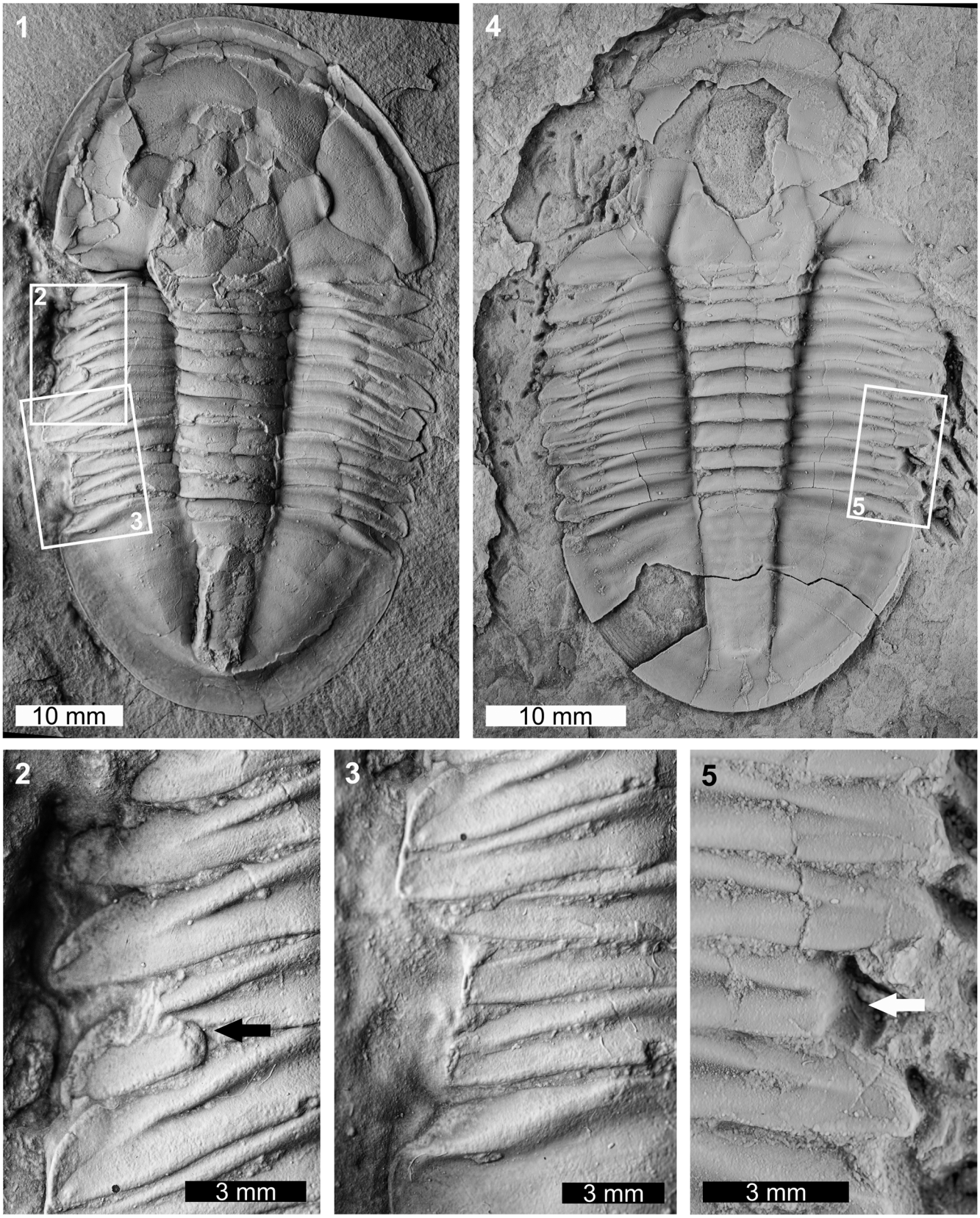


**Figure 3.** Malformed *Asaphiscus wheeleri* Meek, 1873, House Range, Wheeler Formation (Miaolingian, Drumian): (**1–3**) MWC 9973: (**1**) complete specimen; (**2**) detail of abnormality in box in (**1**) showing L-shaped injury and pinched pleural region (black arrow); (**3**) detail of abnormality in box in (**1**) showing U-shaped injury; (**4, 5**) FHPR 16702: (**4**) complete specimen; (**5**) detail of abnormality in box in (**4**) showing SSI (white arrow). All specimens coated. All images converted to grayscale.

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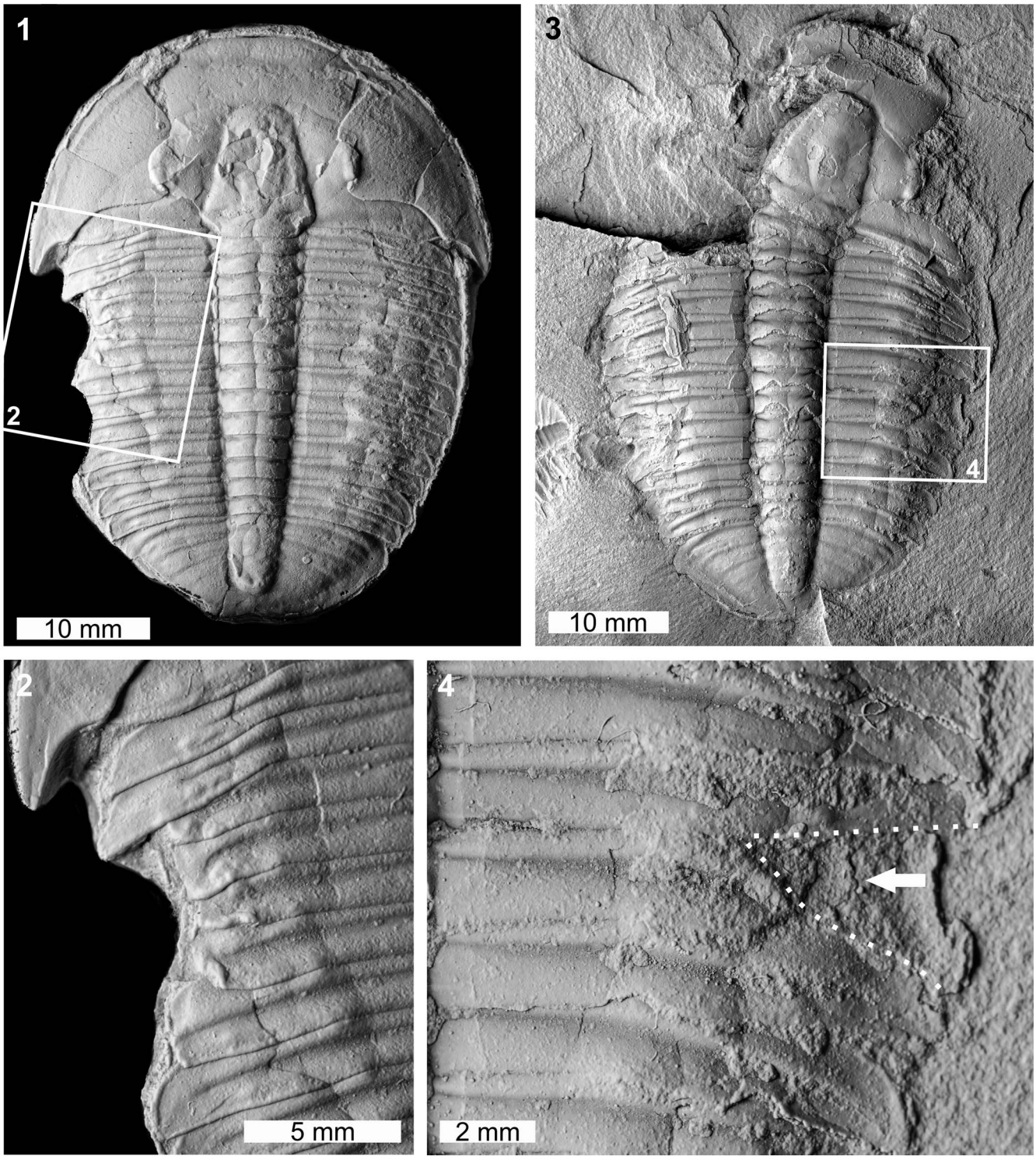


**Figure 4.** Malformed *Elrathia kingii* (Meek, 1870), Wheeler Formation (Miaolingian, Drumian): (**1, 2**) MWC 9972, House Range outcrop: (**1**) complete specimen; (**2**) detail of abnormality in box in (**1**) showing large W-shaped indentation; (**3, 4**) FHPR 16640, Drum Mountains outcrop: (**3**) complete specimen; (**4**) detail of abnormality in box in (**3**) showing V-shaped indentation (dotted white line, white arrow). All specimens coated. All images converted to grayscale.

pinched region (Fig. 3.2). The posterior abnormality is a U-shaped indentation that impacts thoracic pleurae 7–9 and the anteriormost pygidium. The edge of this indentation shows marked cicatrization (Fig. 3.3) and truncates pleurae by 2.5 mm. The second specimen is an internal mold with a damaged cephalon (FHPR 16702; Fig. 3.4, 3.5). The specimen has a single segment injury (SSI) on the eighth pleura on the right pleural lobe. This truncates the pleural spine by 1.7 mm.

Two abnormal *Elrathia kingii* specimens were identified. The first specimen is a complete internal mold (MWC 9972; Fig. 4.1, 4.2). MWC 9972 has a large W-shaped indentation on the left thoracic pleural lobe impacting thoracic pleurae

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1–7. The indentation extends up to 4.3 mm into the specimen and shows evidence of cicatrization (Fig. 4.2). The second specimen is an internal mold and likely represents a molt (Daley and Drage, 2016; Drage et al., 2018; Drage, 2019) (FHPR 16640; Fig. 4.3, 4.4). The specimen has a V-shaped indentation with limited cicatrization that impacts thoracic pleurae 7 and 8 on the right pleural lobe (Fig. 4.4). This indentation truncates pleurae by 4.6 mm.

The *Ogygiocarella debuchii* specimen is an articulated internal mold (AM F128230; Fig. 2.1, 2.2). The specimen has a large W-shaped indentation on the left side of the pygidium that extends across ~75% of the pygidium (Fig. 2.1, 2.2). The malformation is 17.1 mm long and the margin shows extensive fusion of the damaged pygidium. This results in an inflated pygidial border relative to other exoskeletal regions (Fig. 2.2).

## Discussion

The abnormal trilobites documented here show evidence of removal of exoskeletal sections. Furthermore, no specimens have abnormal growths indicative of genetic malformations (Owen, 1980, 1985; Babcock, 1993; Bicknell and Smith, 2021) or circular/ovate structures indicative of pathologies (Šnajdr, 1978b; Babcock, 1993; De Beats et al., 2021). These specimens therefore show examples of injuries (Owen, 1985; Babcock, 1993; Pates et al., 2017; Bicknell et al., 2021b) that occurred through failed predation, a molting complication, or some other traumatic injury. Trilobites with overdeveloped thoracic spines, e.g., *Nevadia weeksi* (Walcott, 1910), likely experienced molting complications and would have damaged the hypertrophied spines (Conway Morris and Jenkins, 1985; Bicknell et al., 2022). The examined specimens lack these morphologies. Furthermore, L-, U-, V-, and W-shaped indentations are commonly attributed to failed predation (Šnajdr, 1981, 1985; Owen, 1985; Babcock, 1993, 2007; Fatka et al., 2009, 2015; Pates et al., 2017; Bicknell and Holland, 2020). As such, the indentations likely record failed predation.

Explanations for SSIs are therefore worth considering. When SSIs are observed with larger injuries on the opposing side (Conway Morris and Jenkins, 1985; Nedin, 1999; Bicknell et al., 2022), they likely reflect a bilateral predatory attack. When SSIs are not identified with larger injuries, further explanation is needed. It seems unlikely that predators large enough to consume trilobites would damage only one segment (Babcock, 1993). However, smaller predators could have removed a single section while a trilobite was in a soft-shelled stage. Failed predation as an explanation for unpaired SSIs is therefore plausible. An SSI could occur during enrollment—if an individual enrolled too quickly or on an abnormal angle, a segment could be nicked. Furthermore, intraspecific competition during feeding or seeking communal shelter during the postecdysal, soft-shell phase could have resulted in minor damage. As such, consideration of broader paleoecology is needed when proposing explanations for SSIs.

The injured *Lyriaspis sigillum* documented here represents the first record of a malformed trilobite from the Beetle Creek Formation and the second example of predation from the deposit (see Jones and McKenzie, 1980). The degree of exoskeletal warping around the injury in AM F34209/F33980 indicates that the specimen was damaged during a soft-shelled phase and also suggests that durophages were present in the Beetle Creek Formation biota. One of the co-occurring *Xystridura* spp. (four are currently known from the unit) is a possible injury-maker, given the size of the genus (Öpik, 1975). Appendage data is unknown for *Xystridura* Öpik, 1975; however, it was likely comparable to other predatory artiopodans and used gnathobasic spines on walking legs to masticate prey (Zacaï et al., 2016; Bicknell et al., 2018, 2021a). Alternatively, large, nonbiomineralized artiopodans with gnathobasic spines might have produced the injury and the lack of soft-bodied preservation in the Beetle Creek Formation precludes the identification of these forms. Regardless, the rarity of injured *L. sigillum* reflects either an occasional diet of smaller trilobites, or the complete consumption of prey. Shelly coprolites from equivalent *Xystridura*-bearing units (e.g., the Giles Creek Dolostone in the neighboring Amadeus Basin, Northern Territory) would support the second theory (unpublished data, Smith, 2022).

Prior to documentation of the injured *Asaphiscus wheeleri* specimen considered here, only malformed *Asaphiscus wheeleri* pygidia were known (Vorwald, 1984; Babcock, 1993; Bicknell and Paterson, 2018). The addition of thoracic injuries illustrates that *Asaphiscus wheeleri* was subject to more substantial predation than previously thought. Previous records of predation within the Wheeler Formation have been assigned to the activities of priapulid worms (Conway Morris and Robison, 1986), radiodonts (Babcock, 1993), and artiopodans with gnathobasic spines on walking legs (Bicknell and Pates, 2020). However, biomechanical and functional morphological evidence suggest that the last group were the most effective at breaking exoskeletons (Bruton, 1981; Stein, 2013; Zacaï et al., 2016; Bicknell et al., 2018, 2021a; Holmes et al., 2020). Further examination of the morphology and predatory ability of other possible predators from these sites is needed to present more complete paleoecological reconstructions and aid in understanding the role of predation during the earliest marine ecosystems.

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