

Injured trilobites within a collection of dinosaurs: Using the Royal Tyrrell Museum of Palaeontology to document Cambrian predation

Russell D. C. Bicknell and Brayden Holland

ABSTRACT

Biomineralised exoskeletons of trilobites are ideal for recording abnormalities, documenting injuries from failed attacks, and understanding predation in the fossil record. The illustration of new injured Cambrian-aged trilobites is particularly important for elucidating aspects of early Paleozoic predator-prey systems and identifying groups that were targets of this early predation. We document six new abnormal trilobite specimens from the Royal Tyrrell Museum of Palaeontology, including the first evidence for injuries on the corynexochid trilobite *Hemirhodon amplipyge*. These new data highlight the importance of museum collections in uncovering unique and informative specimens for studies of predation on early animals.

Russell D. C. Bicknell. Palaeoscience Research Centre, School of Environmental and Rural Science, University of New England, Armidale, New South Wales, 2351, Australia. rdcbicknell@gmail.com
Brayden Holland. Palaeoscience Research Centre, School of Environmental and Rural Science, University of New England, Armidale, New South Wales, 2351, Australia. blongle2@myune.edu.au

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INTRODUCTION

Trilobites were an exceptionally diverse group of Paleozoic arthropods, with over 22,000 species, that are characterised primarily by their biomineralised dorsal exoskeletons; a feature that resulted in a high preservational potential (Webster, 2007; Paterson, 2019). These exoskeletons also

preserve an unprecedented record of abnormal features, which can be attributed to injuries, developmental aberrations, diseases, and parasites (Owen, 1985; Babcock, 1993, 2003, 2007; Bicknell and Paterson, 2018; Vinn, 2018; Bicknell and Pates, 2020). The Cambrian origin of trilobites, and presence of such specimens with abnormalities,

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have made the group central to understanding the rise of predation (Babcock and Robison, 1989; Babcock, 1993; Pates et al., 2017; Pates and Bicknell, 2019). Curiously, abnormalities on Cambrian-aged trilobites have been documented more than any other time-period, which may reflect a higher intensity of research on injuries from this time period, a prevalence of material, and/or a true biological signal (Pates et al., 2017; Bicknell and Paterson, 2018). Regardless, new abnormal specimens provide key information for developing our knowledge of predation, moulting complications, and pathological developments (Owen, 1985; Bicknell and Pates, 2020). Under-explored museum collections are ideal for identifying important specimens, as they often house new examples of abnormal specimens, often from new localities (Bicknell and Pates, 2019, 2020). Museum collections have also been used to identify abnormality stereotypy (Babcock and Robison, 1989; Babcock, 1993).

Canada's rich fossil record has been on show at the Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta (TMP) for over 30 years, and this has made the museum one of the central hubs of Canadian palaeontological research. This museum, and associated research output, is most famous for its extensive vertebrate collection, particularly the remains of Late Cretaceous dinosaurs from Alberta (e.g., Ryan and Evans, 2005; Eberth et al., 2013). As such, there are thousands of specimens housed at the TMP that have greatly increased knowledge of extinct vertebrates (Currie and Koppelhus, 2015). Despite the primary focus on dinosaur and other vertebrate groups, the TMP collection also houses an array of invertebrate taxa (Motz et al., 2001). To expand the use of this diverse collection, and to align with recent research documenting Cambrian predation (Fatka et al., 2015; Pates et al., 2017; Bicknell et al., 2018c; Bicknell and Pates, 2019; Klompmaker et al., 2019; Pates and Bicknell, 2019), Cambrian-aged fossils were reviewed for abnormal trilobite specimens. We present six new examples of abnormal trilobites, representing the taxa *Gabriellus kierorum*, *Ogygopsis klotzi*, *Modocia typicalis*, and the first record of an abnormal *Hemirhodon amplipyge*. This highlights the importance of mining museum collections to increase our knowledge of abnormal and predated animals throughout the Phanerozoic.

MATERIALS AND METHODS

Specimens from Cambrian-aged deposits within the TMP collection were reviewed for trilobites

showing some form of abnormality; features identified by their aberrant morphology (see discussions in Owen, 1985; Bicknell et al., 2018c; Bicknell and Pates, 2019; and references therein). Within the ~5500 examined specimens, six abnormal individuals were identified. Specimens were photographed with a Canon EOS 5DS camera under LED light using a Canon MP-E 65 mm 1—5x macro lens and a Sigma 50mm f/1.4 DG HSM lens.

RESULTS

Gabriellus kierorum Corbacho and López-Soriano, 2013 TMP.1983.021.0034; TMP.1983.021.0039, Atan Group; Rosella Formation? (Series 2, Stage 4), British Columbia, Canada (Figure 1).

Two *Gabriellus kierorum* specimens were identified with abnormalities. TMP.1983.021.0034 is preserved as a complete dorsal exoskeleton (82 mm long) with an abnormality in the centre of the left pleural lobe (Figure 1A, B). The pleurae of thoracic segments 5 and 6 are truncated by ~15 mm relative to the other pleurae on the specimen. The pleurae on these segments are show minute tips, indicating a degree of regeneration (Pates et al., 2017).

TMP.1983.021.0039 is preserved as a complete dorsal exoskeleton (55 mm long) with abnormalities on the posterior sections of the left and right pleural lobes (Figure 1C). Pleural spines on the 7th–9th thoracic segments of the left pleural lobe are truncated. The 7th and 8th spines are truncated by 13 mm relative to undamaged spines, have rounded edges, and appear to be slightly cicatrised (white arrows, Figure 1D). The 9th segment shows some degree of spine recovery and is ~50% the length of undamaged spines (black arrow, Figure 1B). On the right pleural lobe, the pleural spines on the 7th and 8th thoracic segments are truncated by ~11 mm relative to other spines and partly fused together (Figure 1E). This has produced a 'V'-shaped indentation. There is no evidence of cicatrisation or regrowth along the margin of this abnormality.

Ogygopsis klotzi (Rominger, 1887) TMP1983.142.0002; TMP1983.257.0001, Stephen Formation (Miaolingian Series, Wuliuan), British Columbia, Canada (Figure 2).

Two specimens of *Ogygopsis klotzi* with abnormalities were identified. Both specimens lack free cheeks and are therefore examples of axial shield moults (Daley and Drage, 2016; Drage et al., 2018; Drage, 2019).

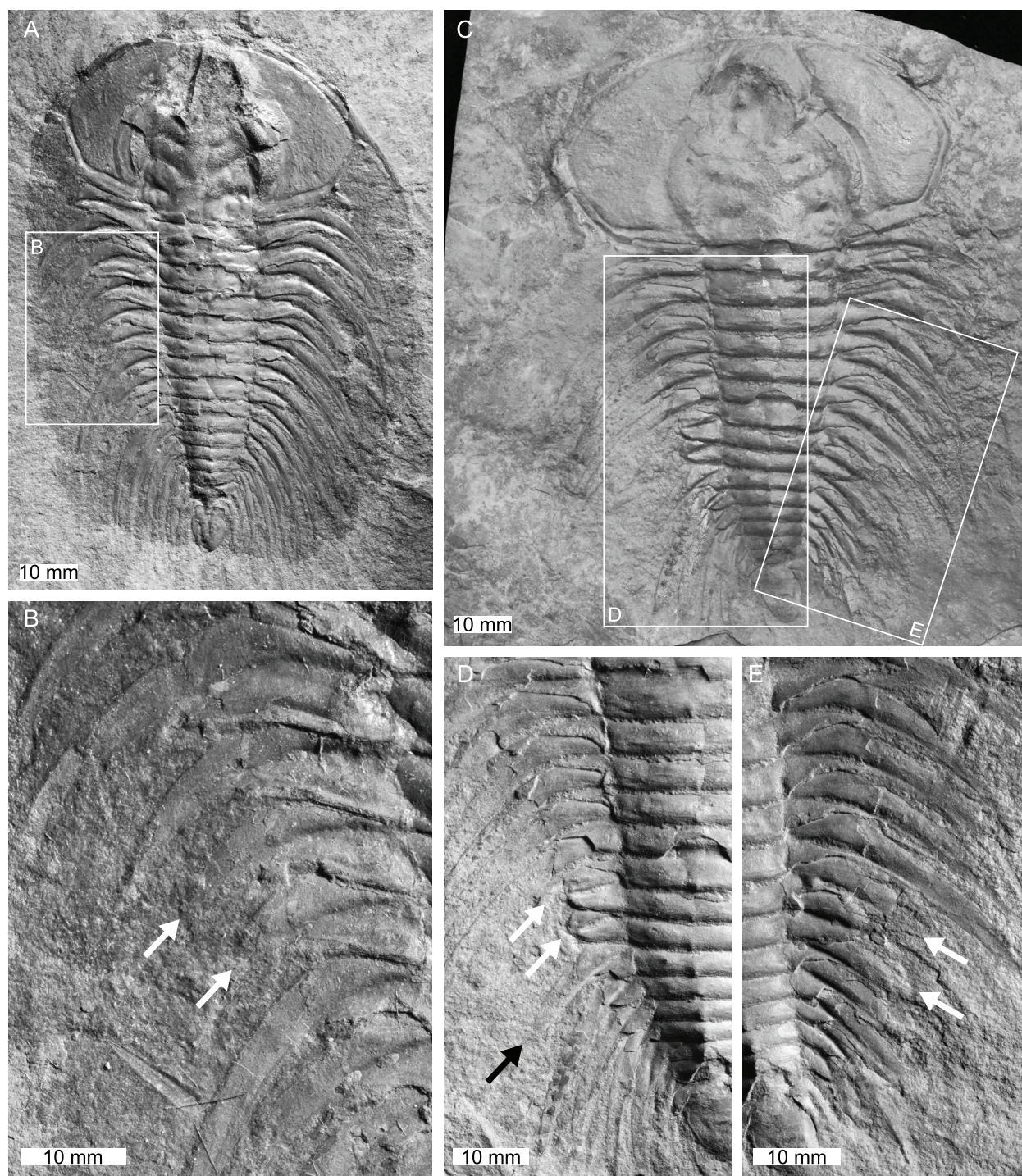


FIGURE 1. *Gabriellus kierorum* specimens from the (?)Rosella Formation. **A, B.** *Gabriellus kierorum* with truncation of left pleural spines on the fifth and sixth thoracic segment (TMP.1983.021.0034). **A:** Complete specimen. **B:** Close up of abnormality (white arrows). **C–E:** *Gabriellus kierorum* with bilaterally expressed thoracic abnormalities (TMP.1983.021.0039). **C:** Complete specimen. **D:** Close up of abnormality on the left side of the specimen (white arrows) and the partly recovered spine (black arrow). **E:** Close up of abnormality on the right side of the specimen (white arrows).

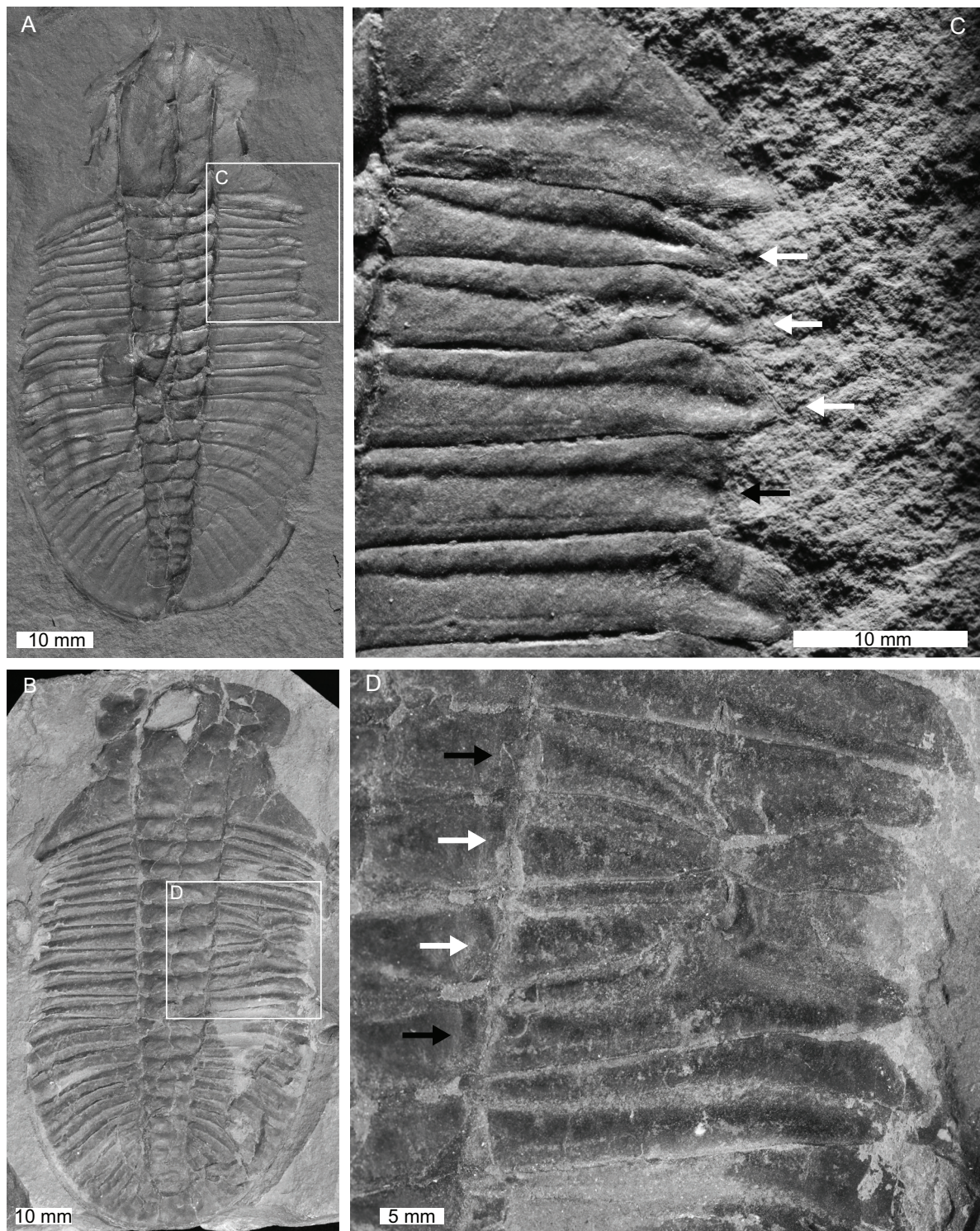


FIGURE 2. *Ogygopsis klotzi* specimens from the Stephen Formation with thoracic abnormalities. **A, C:** *Ogygopsis klotzi* showing truncation of the first four pleural spines of the right thoracic pleural lobe (TMP.1983.142.0002). **A:** Complete specimen. **C:** Close up of truncation of the right pleural spines. Note the 'L'-shaped injury formed by 1st–3rd thoracic segments (white arrows), and the more notable truncation of the 4th segment (black arrow). **B, D:** *Ogygopsis klotzi* with an abnormality on the right pleural lobe that impacts the 4th–7th pleural spines (TMP. 1983.257.0001). **B:** Complete specimen. **D:** Close up of abnormality on the right pleural spines, showing pinching of the 5th and 6th segments (white arrows) and warping of the 4th and 7th segments (black arrows).

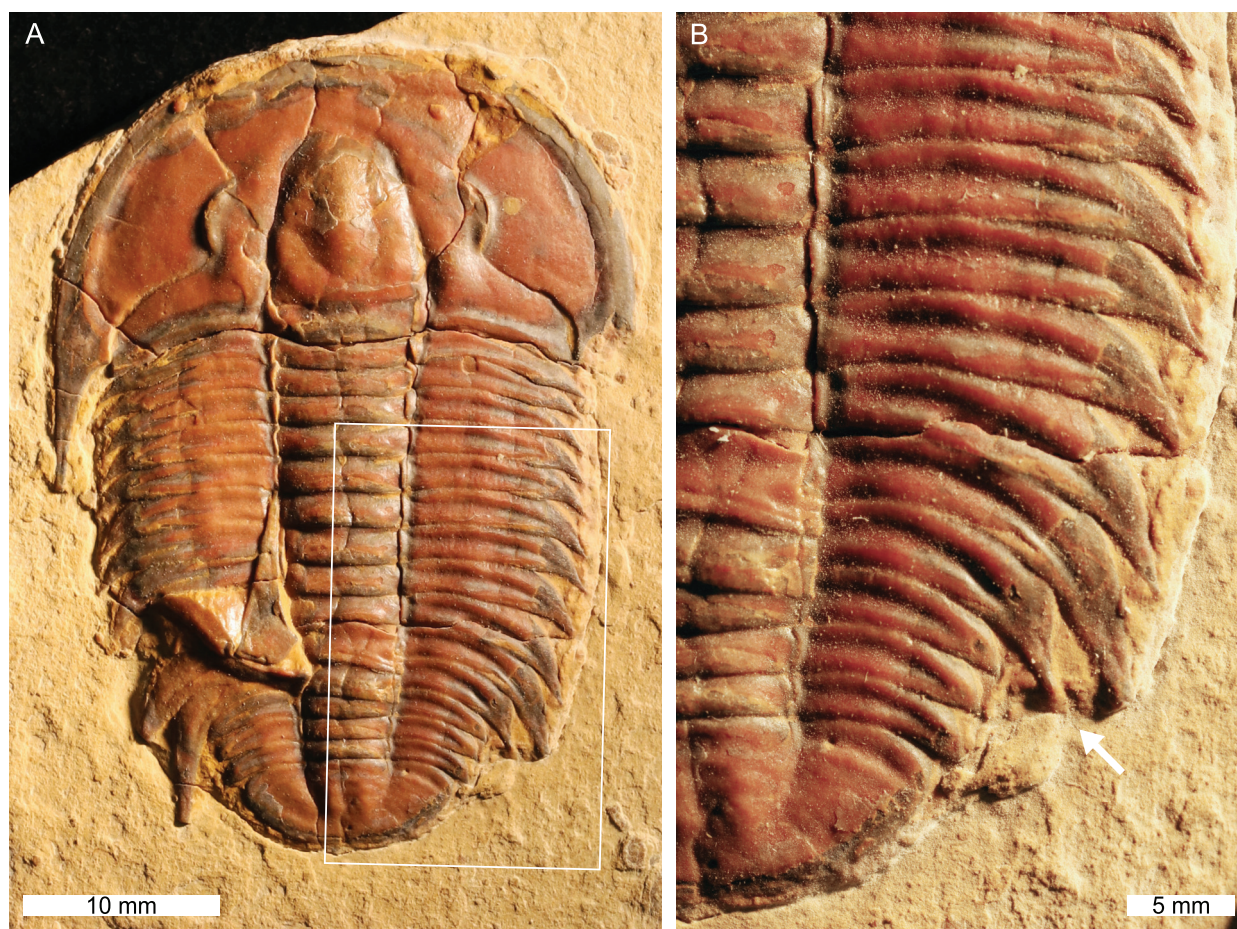


FIGURE 3. *Modocia typicalis* specimen with an abnormality on the right 11th thoracic segment (TMP1984.50.0004). **A:** Complete specimen. **B:** Close up of the truncated pleural spine on the right 11th thoracic segment (white arrow).

TMP1983.142.0002 is 73 mm long with an abnormality on the anterior section of the right pleural lobe (Figure 2A). The pleurae of thoracic segments 1–4 are truncated by 2 mm relative to other segments (Figure 2C). Segments 1–3 form an 'L'-shaped injury that shows limited thoracic recovery (these segments are ~75% the length of undamaged sections) and does not show evidence of cicatrisation. Further, the 4th segment is more truncated than segments 1–3 (2.5 mm). The margin of this abnormality is not obviously cicatrised. The degree of indentation suggests that this abnormality likely occurred more recently than the more anterior segments.

TMP1983.257.0001 is 101 mm long and has an abnormality on the centre of the right pleural lobe that affects thoracic segments 4–7 (Figure 2B). Segments 5 and 6 are pinched together and segments 4 and 7 are warped about this point (Figure 2D). There is no evidence of cicatrisation along the margin of this abnormality.

Modocia typicalis (Resser, 1938), TMP 1984.50.0004. Wheeler Formation (Miaolingian Series, Drumian), Utah, USA (Figure 3).

TMP 1984.50.0004 is preserved as a complete dorsal exoskeleton (40 mm long) with an abnormality on the posterior part of the right pleural lobe. The hypertrophied pleural spine on the 11th thoracic segment is truncated by 4 mm relative to the same spine on the left side. This truncation forms a single segment injury (SSI, sensu Bicknell and Pates, 2020) that is slightly rounded and shows evidence of cicatrisation along the margin.

Hemirhodon amplipyge Robison, 1964; TMP.2006.036.0102. Duchesnay Member, Chancellor Formation (Miaolingian Series, Drumian); British Columbia, Canada (Figure 4).

TMP.2006.036.0102 is preserved as a complete dorsal exoskeleton (87 mm long) with an abnormality on the anterior section of the left side of the pygidium. The abnormality truncates the pygidial margin by 3.9 mm. The abnormality is

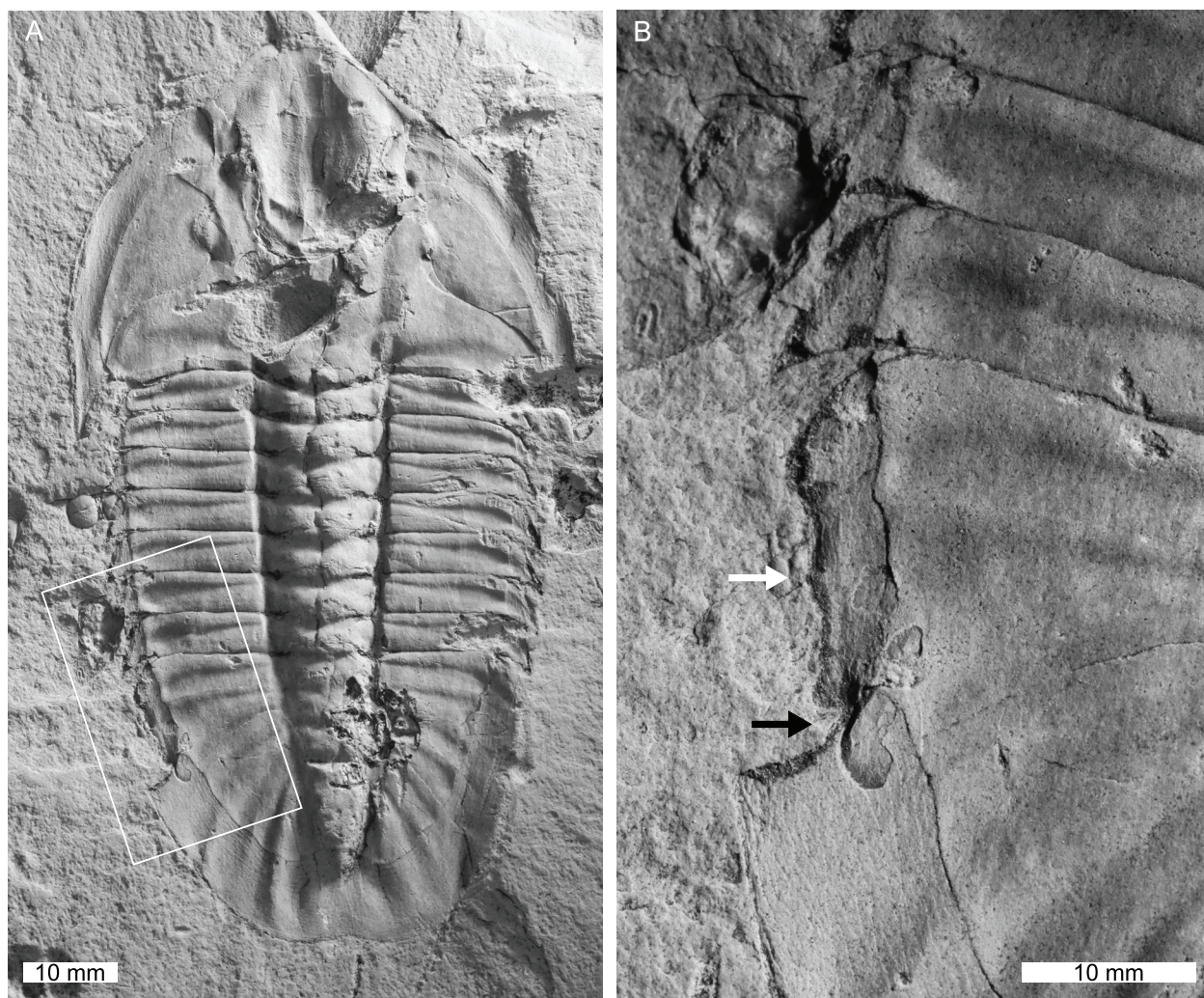


FIGURE 4. The first record of a *Hemirhodon amplipyge* specimen with an abnormality (TMP.2006.036.0102). **A:** Complete specimen. **B:** Close up of the abnormality on left side of pygidium, showing a truncated 'W'- (white arrows) and 'V'-shape (black arrow) on pygidial margin.

expressed as a shallow "W"-shape indentation next to a more posterior, deeper, and acute "V"-shape (white and black arrows, respectively, in Figure 4B). The margin of the abnormality is cicatrised.

DISCUSSION

The abnormalities considered here are morphologically similar to examples that have been attributed to injuries (Šnajdr, 1978; Owen, 1985; Bicknell and Paterson, 2018; Bicknell and Pates, 2020). These abnormal specimens are therefore interpreted either as individuals that experienced failed predation, or individuals who injured themselves as a result of a moulting complication or other behaviour (Owen, 1985). The cicatrised abnormality observed on the *Ogygopsis klotzi* specimen TMP1983.142.0002 (Figure 2A, C) is

morphologically similar other *O. klotzi* injuries that were attributed to failed attacks (Table 1). Further, the 'W'-shaped morphology and cicatrised nature of the injury to the *Hemirhodon amplipyge* specimen is comparable to other injuries, suggestive of at least one failed attack (Figure 4). One of the most curious specimens examined here is the *Ogygopsis klotzi* specimen TMP1983.257.0001 (Figure 2B, D) that has warped thoracic segments; an abnormality previously unknown in this group, but has been reported in other trilobite taxa (Šnajdr, 1955). The disruption of these segments may reflect an injury from moulting, deformation during a soft-shelled stage, or potentially a developmental issue. It seems unlikely that *O. klotzi* experienced complications from moulting as the taxon lacks large pleural spines (Conway Morris and Jenkins, 1985). We therefore suggest that the individual either experi-

TABLE 1. Examples of previously documented abnormal *Ogygopsis klotzi* and the suggested predator groups.

Morphology of injury	Proposed predator	Publication
'U'-shaped injury on right side of thorax impacting thoracic segments 3–6	Possibly <i>Anomalocaris</i>	Rudkin (1979, fig. 1A, B)
'W'-shaped injury on left side of thorax impacting thoracic segments 6–8	Possibly <i>Anomalocaris</i>	Rudkin (1979, fig. 1C, D)
'W'-shaped injury on the anterior section of the right side of pygidium	Possibly <i>Anomalocaris</i>	Rudkin (1979, fig. 1E, F)
'V'-shaped injury on right side of thorax impacting thoracic segments 7–8	Possibly <i>Anomalocaris</i>	Rudkin (1979, fig. 1G, H), refigured in Rudkin (2009, fig. 1B)
'U'-shaped injury on posterior right side of thorax impacting thoracic segment 10 and the anterior right pygidium	<i>Anomalocaris</i>	Briggs and Whittington (1985, p. 37)
Cicatrized 'W'-shaped injury on the anterior right side of pygidium	<i>Anomalocaris</i> sp.	Pratt (1998, fig. 1A)
'W'-shaped injury on the right side of thorax impacting thoracic segments 3–6 and minor 'U'-shaped injury on the left side of the thorax impacting thoracic section 5	<i>Anomalocaris</i> sp.	Nedin (1999, fig. 2C)
'W'-shaped injury on the left side of thorax impacting thoracic segments 2–5	Total group euarthropod with gnathobases or gnathobase-like structures; e.g. amplexobeluid radiodonts, trilobites, and other artiopodans	Bicknell and Pates (2020; fig. 7A, B)

enced an injury during a soft-shelled stage that deformed the exoskeleton, or the exoskeleton developed incorrectly.

Evidence for predators that targeted trilobites reiterates the question that has been considered since at least Öpik (1961), Alpert and Moore (1975), and Rudkin (1979): what was predating on Cambrian trilobites? The most likely predators are those trilobites and predatory artiopodans that displayed reinforced gnathobasic spines on protopodal sections of the walking legs, ideal for durophagy, similar to the extant horseshoe crabs (Bruton, 1981; Conway Morris and Jenkins, 1985; Zacaï et al., 2016; Bicknell et al., 2018a, b, 2019; Holmes et al., 2020). Radiodont groups, such as anomalocaridids, may have been capable of attacking those trilobites in a non-biomineralised state using fortified frontal appendages to grab and break prey, perhaps in conjunction with the radial mouthpart (Nedin, 1999; Daley et al., 2013; Bicknell and Paterson, 2018). However, doubt has been cast on shell-crushing ability of mouthparts (Whittington and Briggs, 1985; Hagadorn, 2009; Hagadorn et al., 2010; Daley and Bergström, 2012). Recent studies of other radiodont groups has highlighted the presence of taxa with gnathobasic-like structures on frontal appendages, which may have also been in used in predation (Cong et al., 2017, 2018). While such morphologies are not known from North American deposits, related taxa

are known from the Stage 4 Kinzers Formation and Latham Shale (USA), Wuliuan Burgess Shale (Canada), and Drumian Wheeler Formation (Daley and Budd, 2010; Pates and Daley, 2019; Pates et al., 2019; Lerosey-Aubril et al., 2020). Finally, the raptorial frontal appendages of stem chelicerate *Yohoia tenuis* Walcott, 1912, may have functioned like a hammer and been capable of breaking biomineralised exoskeletons, in a manner comparable to stomatopods (Pratt, 1998; Haug et al., 2012; Bicknell and Paterson, 2018).

CONCLUSIONS

Examination of palaeontological collections that focus primarily on one part of the tree of life often permits the identification of novel palaeoecological data. The Royal Tyrrell Museum of Palaeontology represents a particularly interesting example of this situation; although the museum focuses chiefly on vertebrate research, there is an expansive collection of invertebrate material. We have shown here that examining the arthropod section of the collection has uncovered previously unknown information on Cambrian trilobites. Another part of the invertebrate collection that would undoubtedly lend itself to key research is the molluscan material. Examining this section of the TMP would uncover new trends in predator-prey interactions involving this group across the Meso-

zoic and could potentially be extended to consider further Palaeozoic palaeoecological systems.

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