

New records of injured Cambrian and Ordovician trilobites

Russell D.C. Bicknell,^{1*} Patrick M. Smith,^{2,3} Thomas F. Howells,⁴ and John R. Foster⁴

¹Palaeoscience Research Centre, School of Environmental and Rural Science, University of New England, Armidale, New South Wales 2351, Australia <rdcbicknell@gmail.com>

²Paleontology Department, Australian Museum Research Institute, Sydney, New South Wales 2010, Australia <Patrick.Smith@australian.museum>

³Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109, Australia

⁴Utah Field House of Natural History State Park, Museum Collections, Vernal, Utah 84078, USA <tomfh2@gmail.com>
<johnfoster@utah.gov>

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

*Corresponding author.

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-occurred 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 (Forrey 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

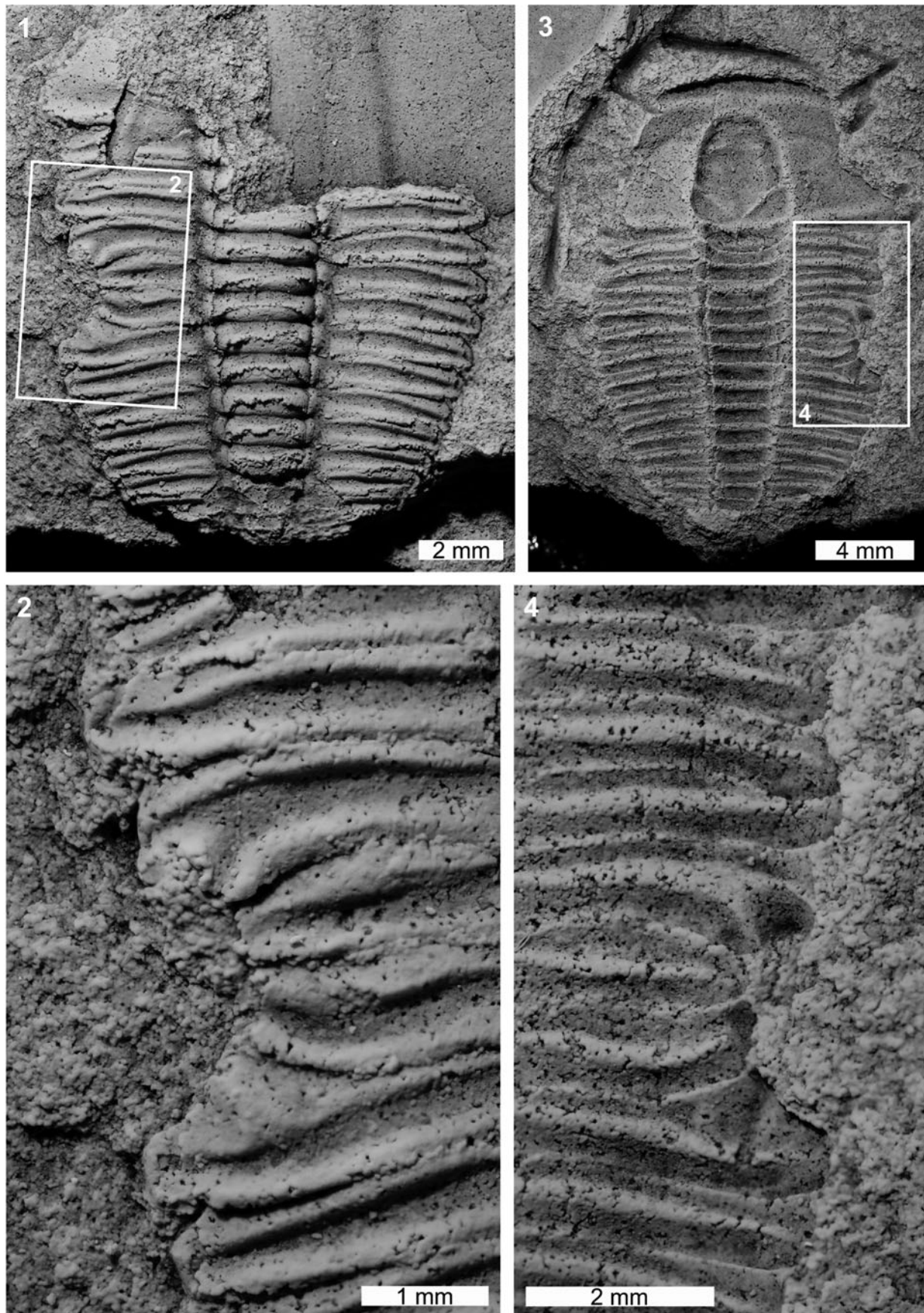


Figure 1. Malformed *Lyriaspis sigillum* Whitehouse, 1939, Beetle Creek Formation (Miaolingian, Wuliuan): (1, 2) AM F34209: (1) complete specimen; (2) detail of abnormality in box in (1) showing U-shaped injury; (3, 4) AM F33980: (3) complete specimen; (4) detail of abnormality in box in (3) showing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

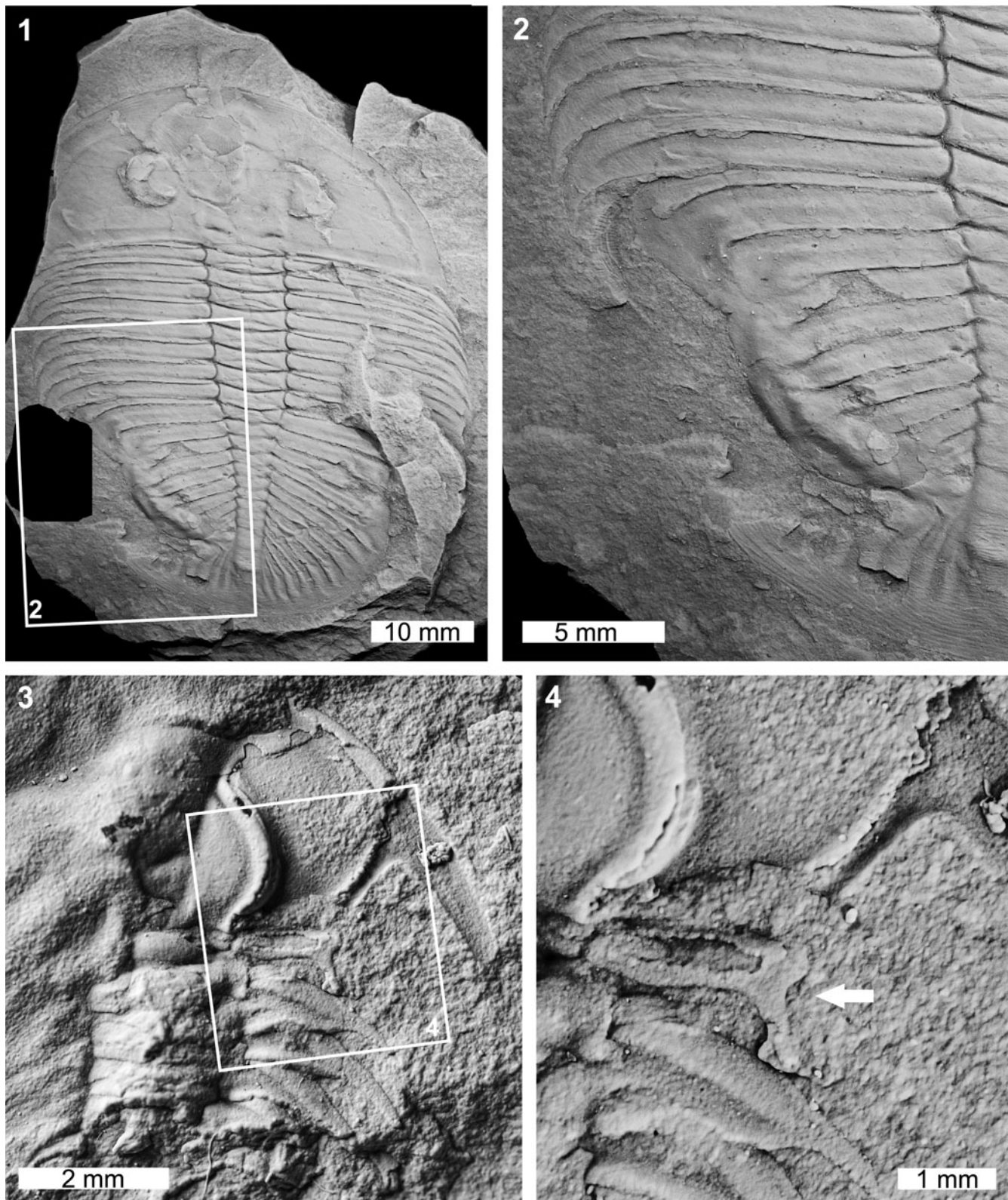


Figure 2. Malformed *Ogygiocarella debuchii* (Brongniart, 1822) and *Zacanthoides* sp. indet. (of Walcott, 1888): (1, 2) *Ogygiocarella debuchii* from the Llanfawr Mudstones (Middle Ordovician, Darriwilian), AM F128230: (1) complete specimen; (2) detail of abnormality in box in (1) showing W-shaped indentation 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.

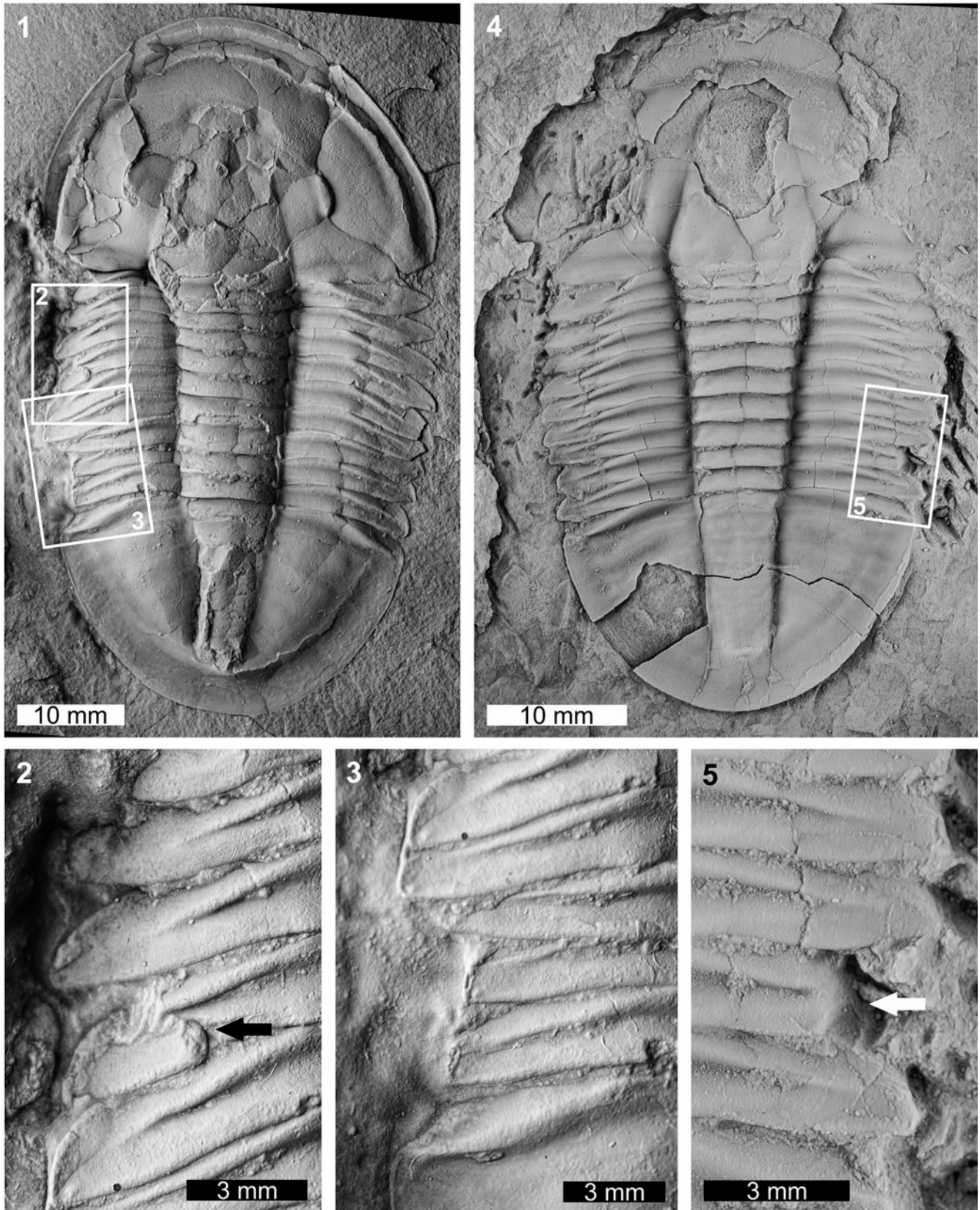


Figure 3. Malformed *Asaphiscus wheeleri* Meek, 1873, House Range, Wheeler Formation (Miaolingian, Drumian): (1–3) MWC 9973: (1) complete specimen; (2) detail of abnormality in box in (1) showing L-shaped injury and pinched pleural region (black arrow); (3) detail of abnormality in box in (1) showing 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.

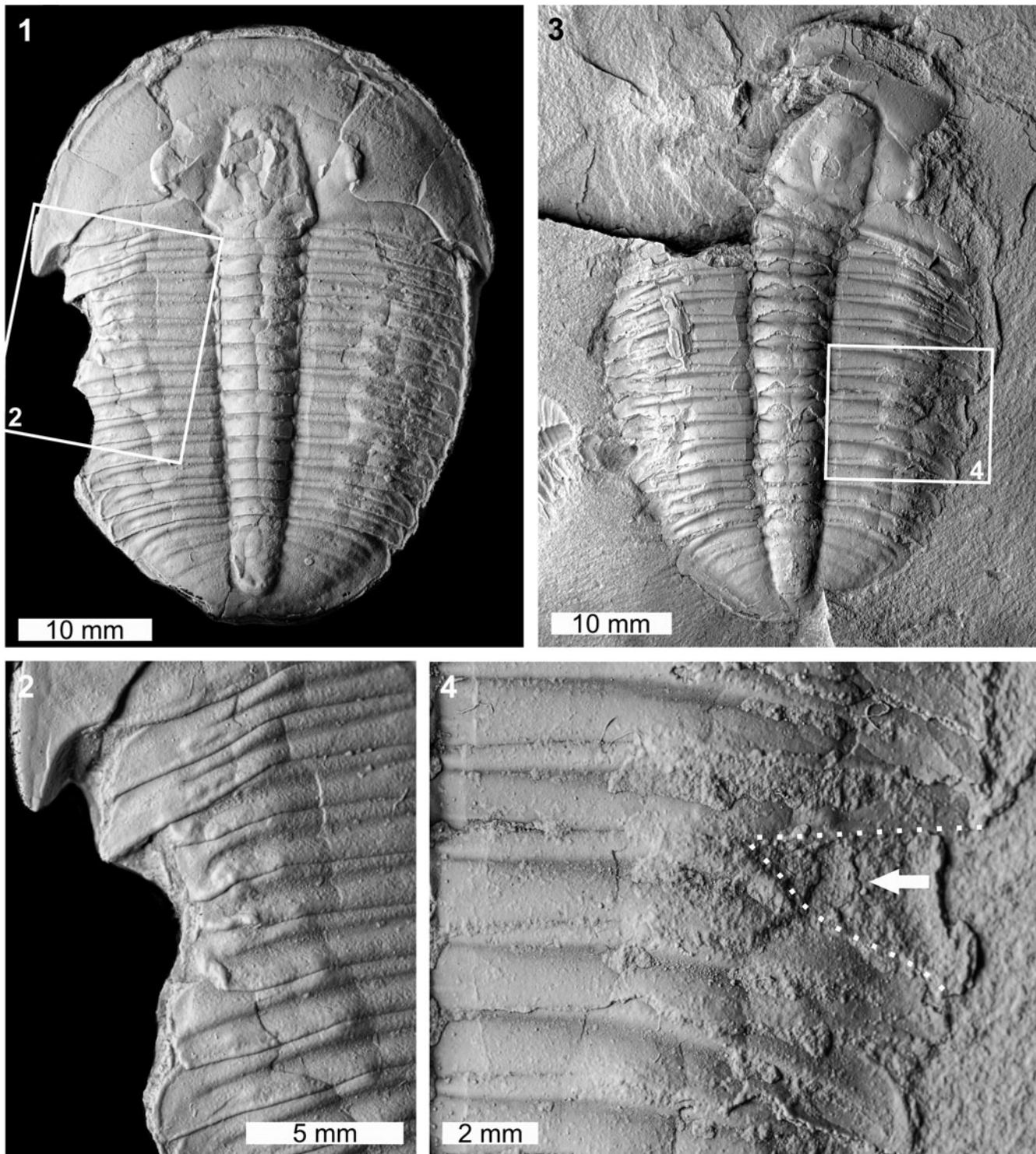


Figure 4. Malformed *Elrathia kingii* (Meek, 1870), Wheeler Formation (Miaolingian, Drumian): (1, 2) MWC 9972, House Range outcrop: (1) complete specimen; (2) detail of abnormality in box in (1) showing large W-shaped indentation; (3, 4) FHPR 16640, Drum Mountains outcrop: (3) complete specimen; (4) 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

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., *Nevadina 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 (Zacai 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; Zacai 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.

Acknowledgments

This research was funded by an Australian Research Council grant (DP200102005), a University of New England Postdoctoral Fellowship (to RDCB), a Karl Hirsch Memorial Grant (to RDCB), and an Australian Museum AMF/AMRI Visiting Research Fellowship (to RDCB). Field work facilitated in part by US Bureau of Land Management permits UT16-014S and N-86224 (to JRF), with thanks to field crew members A.R.C. Milner, R. Hunt-Foster, J. Lehane, M. Perry, and T. Lawrence. MWC specimens were collected by D. Dayvault, and we thank J. McHugh for loan of this material. We thank S. Pates for discussions regarding causes of trilobite injuries. Finally, we thank R.-W. Zong and D. Rudkin for their thorough reviews that substantially improved the text.

References

- Babcock, L.E., 1993, Trilobite malformations and the fossil record of behavioral asymmetry: *Journal of Paleontology*, v. 67, p. 217–229.
- Babcock, L.E., 2007, Role of malformations in elucidating trilobite paleobiology: A historical synthesis, in Mikulic, D.G., Landing, E., and

- Kluessendorf, J., eds., *Fabulous Fossils—300 Years of Worldwide Research on Trilobites*: Albany, New York, University of the State of New York, State Education Dept., New York State Museum, p. 3–19.
- Babcock, L.E., and Robison, R.A., 1989, Preferences of Palaeozoic predators: *Nature*, v. 337, p. 695–696.
- Babcock, L.E., Robison, R.A., Rees, M.N., Peng, S., and Saltzman, M.R., 2007, The Global boundary Stratotype Section and Point (GSSP) of the Drumian Stage (Cambrian) in the Drum Mountains, Utah, USA: *Episodes*, v. 30, p. 84–92, <https://doi.org/10.18814/epiugs/2007/v30i2/003>.
- Bell, B.M., and Sprinkle, J., 1978, *Totiglobus*, an unusual new edrioasteroid from the middle Cambrian of Nevada: *Journal of Paleontology*, v. 52, p. 243–266.
- Bergström, J., and Levi-Setti, R., 1978, Phenotypic variation in the middle Cambrian trilobite *Paradoxides davidis* Salter at Manuels, SE Newfoundland: *Geologica et Palaeontologica*, v. 12, p. 1–40.
- Bettley, R.M., Fortey, R.A., and Siveter, D.J., 2001, High-resolution correlation of Anglo-Welsh Middle to Upper Ordovician sequences and its relevance to international chronostratigraphy: *Journal of the Geological Society*, v. 158, p. 937–952, <https://doi.org/10.1144/0016-764900-193>.
- Bicknell, R.D.C., and Holland, B., 2020, Injured trilobites within a collection of dinosaurs: Using the Royal Tyrrell Museum of Palaeontology to document Cambrian predation: *Palaeontologia Electronica*, v. 23, p. a33, <https://doi.org/10.26879/1087>.
- Bicknell, R.D.C., and Paterson, J.R., 2018, Reappraising the early evidence of durophagy and drilling predation in the fossil record: Implications for escalation and the Cambrian Explosion: *Biological Reviews*, v. 93, p. 754–784, <https://doi.org/10.1111/brv.12365>.
- Bicknell, R.D.C., and Pates, S., 2020, Exploring abnormal Cambrian-aged trilobites in the Smithsonian collection: *PeerJ*, v. 8, p. e8453, <https://doi.org/10.7717/peerj.8453>.
- Bicknell, R.D.C., and Smith, P.M., 2021, Teratological trilobites from the Silurian (Wenlock and Ludlow) of Australia: *The Science of Nature*, v. 108, p. 1–11, <https://doi.org/10.1007/s00114-021-01766-6>.
- Bicknell, R.D.C., Ledogar, J.A., Wroe, S., Gutzler, B.C., Watson, W.H. III, and Paterson, J.R., 2018, Computational biomechanical analyses demonstrate similar shell-crushing abilities in modern and ancient arthropods: *Proceedings of the Royal Society of London B: Biological Sciences*, v. 285, p. 20181935, <https://doi.org/10.1098/rspb.2018.1935>.
- Bicknell, R.D.C., Paterson, J.R., and Hopkins, M.J., 2019, A trilobite cluster from the Silurian Rochester Shale of New York: Predation patterns and possible defensive behavior: *American Museum Novitates*, v. 39, p. 1–16, <https://doi.org/10.1206/3937.1>.
- Bicknell, R.D.C., Holmes, J.D., Edgecombe, G.D., Losso, S.R., Ortega-Hernández, J., Wroe, S., and Paterson, J.R., 2021a, Biomechanical analyses of Cambrian euarthropod limbs reveal their effectiveness in mastication and durophagy: *Proceedings of the Royal Society of London B: Biological Sciences*, v. 288, p. 20202075, <https://doi.org/10.1098/rspb.2020.2075>.
- Bicknell, R.D.C., Smith, P.M., Bruthansová, J., and Holland, B., 2021b, Malformed trilobites from the Ordovician and Devonian: *PalZ*, <https://doi.org/10.1007/s12542-021-00572-9>.
- Bicknell, R.D.C., Holmes, J.D., Pates, S., García-Bellido, D.C., and Paterson, J.R., 2022, Cambrian carnage: Trilobite predator-prey interactions in the Emu Bay Shale of South Australia: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 591, p. 110877, <https://doi.org/10.1016/j.palaeo.2022.110877>.
- Brongniart, A., 1822, Sur la classification et la distribution des végétaux fossiles: *Mémoires du Muséum d'Histoire Naturelle (Paris)*, v. 8, p. 203–348.
- Bruton, D.L., 1981, The arthropod *Sidneyia inexpectans*, middle Cambrian, Burgess Shale, British Columbia: *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, v. 295, p. 619–656.
- Budil, P., Fatka, O., Zwanzig, M., and Rak, Š., 2010, Two unique Middle Ordovician trilobites from the Prague Basin, Czech Republic: *Journal of the National Museum (Prague), Natural History Series*, v. 179, p. 95–104.
- Cheng, M.R., Han, J., Ou, G., Zhang, Z.F., Guo, J., and Zhang, X.L., 2019, Injured trilobite *Eoredichia intermedia* from the early Cambrian Chengjiang biota: *Acta Palaeontologica Sinica*, v. 58, p. 425–435, <https://doi.org/10.19800/j.cnki.aps.2019.04.001>.
- Conway Morris, S., and Jenkins, R.J.F., 1985, Healed injuries in early Cambrian trilobites from South Australia: *Alcheringa*, v. 9, p. 167–177.
- Conway Morris, S., and Robison, R., 1986, Middle Cambrian priapulids and other soft-bodied fossils from Utah and Spain: *University of Kansas Paleontological Contributions*, v. 117, p. 1–22.
- Cooper, R.A., and Sadler, P.M., 2012, The Ordovician Period, in *Gradstein, F.M., Ogg, J.G., Schmitz, M., and Ogg, G., eds., The Geologic Time Scale 2012*: Amsterdam, Elsevier, p. 489–524.
- Daley, A.C., and Drage, H.B., 2016, The fossil record of ecdysis, and trends in the moulting behaviour of trilobites: *Arthropod Structure & Development*, v. 45, p. 71–96, <https://doi.org/10.1016/j.asd.2015.09.004>.
- De Baets, K., Budil, P., Fatka, O., and Geyer, G., 2021, Trilobites as hosts for parasites: From paleopathologies to etiologies, in De Baets, K., and Huntley, J.W., eds., *The Evolution and Fossil Record of Parasitism: Coevolution and Paleoparasitological Techniques*: Cham, Switzerland, Springer International Publishing, p. 173–201, https://doi.org/10.1007/978-3-030-52233-9_6.
- Drage, H.B., 2019, Quantifying intra- and interspecific variability in trilobite moulting behaviour across the Palaeozoic: *Palaeontologia Electronica*, v. 22, p. 1–39, <https://doi.org/10.26879/940>.
- Drage, H.B., Holmes, J.D., García-Bellido, D.C., and Daley, A.C., 2018, An exceptional record of Cambrian trilobite moulting behaviour preserved in the Emu Bay Shale, South Australia: *Lethaia*, v. 51, p. 473–492, <https://doi.org/10.1111/let.12266>.
- Dunster, J.N., Kruse, P.D., Duffett, M.L., and Ambrose, G.J., 2007, Geology and resource potential of the southern Georgina Basin: Northern Territory Geological Survey, Digital Information Package DIP007, CD-ROM.
- Fatka, O., Szabad, M., and Budil, P., 2009, Malformed agnostids from the middle Cambrian Jince Formation of the Pøřbram-Jince Basin, Czech Republic: *Bulletin of Geosciences*, v. 84, p. 121–126, <https://doi.org/10.3140/bull.geosci.1107>.
- Fatka, O., Budil, P., and Grigar, L., 2015, A unique case of healed injury in a Cambrian trilobite: *Annales de Paléontologie*, v. 101, p. 295–299, <https://doi.org/10.1016/j.annpal.2015.10.001>.
- Fatka, O., Budil, P., and Zicha, O., 2021, Exoskeletal and eye repair in *Dalmanitina socialis* (Trilobita): An example of blastemal regeneration in the Ordovician?: *International Journal of Paleopathology*, v. 34, p. 113–121, <https://doi.org/10.1016/j.ijpp.2021.05.011>.
- Fleming, P.J.G., 1977, Faunas, lithologies, and the origin of phosphorites in parts of the middle Cambrian Beetle Creek Formation of northwest Queensland: Geological Survey of Queensland Publication, v. 364, p. 21.
- Fortey, R.A., and Owens, R.M., 1987, The Arenig Series in South Wales: *Bulletin of the British Museum, Natural History (Geology)*, v. 41, p. 69–307.
- Foster, J.R., 2021, Abnormal pygidial spine in an injured (?) trilobite (*Tricrepicephalus texanus*) from the Weeks Formation (Cambrian, Guzhangian), House Range, Utah: *New Mexico Museum of Natural History and Science Bulletin*, v. 82, p. 71–74.
- Foster, J.R., and Gaines, R.R., 2016, Taphonomy and paleoecology of the ‘middle’ Cambrian (Series 3) formations in Utah’s West Desert: Recent finds and new data: *Utah Geological Association Publication*, v. 45, p. 291–336.
- Hintze, L.F., and Davis, F.D., 2002, Geologic map of the Tule Valley 30’ x 60’ quadrangle and parts of the Ely, Fish Springs, and Kern Mountains 30’ x 60’ quadrangles, northwest Millard County, Utah: *Utah Geological Survey, Map 186*, scale 1:100,000, 1 sheet, 1 p. text.
- Hintze, L.F., and Davis, F.D., 2003, *Geology of Millard County, Utah*: *Utah Geological Survey, Bulletin*, v. 133, p. 1–305.
- Holmes, J.D., Paterson, J.R., and García-Bellido, D.C., 2020, The trilobite *Redlichia* from the lower Cambrian Emu Bay Shale Konservat-Lagerstätte of South Australia: Systematics, ontogeny and soft-part anatomy: *Journal of Systematic Palaeontology*, v. 18, p. 295–334, <https://doi.org/10.1080/14772019.2019.1605411>.
- Hughes, C.P., 1969, Ordovician trilobite faunas from central Wales, part I: *Bulletin of the British Museum of Natural History (Geology)*, v. 18, p. 39–103.
- Hughes, C.P., 1971, Ordovician trilobite faunas from central Wales, part II: *Bulletin of the British Museum of Natural History (Geology)*, v. 20, p. 115–182.
- Hughes, C.P., 1979, Ordovician trilobite faunas from central Wales, part III: *Bulletin of the British Museum of Natural History (Geology)*, v. 32, p. 109–181.
- Jones, P.J., and McKenzie, K.G., 1980, Queensland middle Cambrian Brador-iida (Crustacea): New taxa, palaeobiogeography and biological affinities: *Alcheringa*, v. 4, p. 203–225.
- Klompaker, A.A., Kelley, P.H., Chattopadhyay, D., Clements, J.C., Huntley, J.W., and Kowalewski, M., 2019, Predation in the marine fossil record: Studies, data, recognition, environmental factors, and behavior: *Earth-Science Reviews*, v. 194, p. 472–520, <https://doi.org/10.1016/j.earscirev.2019.02.020>.
- Kruse, P.D., 2002, Biostratigraphic potential of middle Cambrian hyoliths from the eastern Georgina Basin: *Alcheringa*, v. 26, p. 353–398, <https://doi.org/10.1080/03115510208619263>.
- Laurie, J.R., 1988, Revision of some Australian Ptychagnostinae (Agnostida, Cambrian): *Alcheringa*, v. 12, p. 169–205.
- Laurie, J.R., 2004, Early middle Cambrian trilobite faunas from NTGS Elkedra 3 corehole, southern Georgina Basin, Northern Territory: *Memoirs of the Association of Australasian Palaeontologists*, v. 30, p. 221–260.
- Laurie, J.R., 2006a, Early middle Cambrian trilobites from Pacific Oil & Gas Baldwin 1 well, southern Georgina Basin, Northern Territory: *Memoirs of the Association of Australasian Palaeontologists*, v. 32, p. 127–204.
- Laurie, J.R., 2006b, Early middle Cambrian trilobites from the Jigamara Formation, Arafura Basin, Northern Territory: *Memoirs of the Association of Australasian Palaeontologists*, v. 32, p. 103–126.

- Meek, F.B., 1870, Descriptions of fossils collected by the US Geological Survey under the charge of Clarence King, Esq.: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 14, p. 56–64.
- Meek, F.B., 1873, Preliminary paleontological report, consisting of lists and descriptions of fossils, with remarks on the ages of the rocks in which they were found, in U.S. Geological Survey of the Territories, 6th Annual Report: Washington, DC, United States Geological Survey, p. 429–518.
- Nedin, C., 1999, *Anomalocaris* predation on nonmineralized and mineralized trilobites: *Geology*, v. 27, p. 987–990.
- Öpik, A.A., 1975, Templetonian and Ordian xystridurid trilobites of Australia: Bulletin of the Bureau of Mineral Resources, Geology & Geophysics, v. 121, p. 1–84.
- Öpik, A.A., 1979, Middle Cambrian agnostids: Systematics and biostratigraphy: Bulletin of the Bureau of Mineral Resources, Geology & Geophysics, v. 172, p. 1–188.
- Öpik, A.A., 1982, Dolichometopid trilobites of Queensland, Northern Territory, and New South Wales: Bulletin of the Bureau of Mineral Resources, Geology & Geophysics, v. 175, p. 1–85.
- Owen, A.W., 1980, An abnormal cranium of the trilobite *Calyptaulax norvegicus*: *Norsk Geologisk Tidsskrift*, v. 60, p. 87–88.
- Owen, A.W., 1985, Trilobite abnormalities: Transactions of the Royal Society of Edinburgh, Earth Sciences, v. 76, p. 255–272.
- Owens, R.M., 1981, The Ordovician proetacean trilobite *Rorringtonia*: *Geological Magazine*, v. 118, p. 89–94.
- Owens, R.M., 2002, Cyclopygid trilobites from the Ordovician Bulth-Llandrindod Inlier, central Wales: *Palaeontology*, v. 45, p. 469–485.
- Pates, S., and Bicknell, R.D.C., 2019, Elongated thoracic spines as potential predatory deterrents in olenelline trilobites from the lower Cambrian of Nevada: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 516, p. 295–306, <https://doi.org/10.1016/j.palaeo.2018.12.013>.
- Pates, S., Bicknell, R.D.C., Daley, A.C., and Zamora, S., 2017, Quantitative analysis of repaired and unrepaired damage to trilobites from the Cambrian (Stage 4, Drumian) Iberian Chains, NE Spain: *Palaios*, v. 32, p. 750–761, <https://doi.org/10.2110/palo.2017.055>.
- Peng, S., Babcock, L.E., and Ahlberg, P., 2020, The Cambrian Period, in Gradstein, F.M., Ogg, J.G., Schmitz, M.D., and Ogg, G.M., eds., *Geologic Time Scale 2020*, Volume 2: Amsterdam, Elsevier, p. 565–629.
- Portlock, J.E., 1845, Report on the Geology of the county of Londonderry and of parts of Tyrone and Fermanagh: Dublin, A. Milliken, 784 p., 38 pls.
- Poulsen, C., 1927, The Cambrian, Ozarkian and Canadian faunas of northwest Greenland: *Meddelelser om Grønland*, v. 70, p. 233–243.
- Raymond, P.E., 1928, Two new Cambrian trilobites: *American Journal of Science*, v. 5, p. 309–313.
- Rees, M.N., 1986, A fault-controlled trough through a carbonate platform: The Middle Cambrian House Range embayment: *Geological Society of America Bulletin*, v. 97, p. 1054–1069.
- Robison, R.A., Babcock, L.E., and Gunther, V.G., 2015, Exceptional Cambrian fossils from Utah: A window into the age of trilobites: *Utah Geological Survey, Miscellaneous Publication 15-1*, 99 p.
- Rudkin, D.M., 1979, Healed injuries in *Ogygopsis klotzi* (Trilobita) from the middle Cambrian of British Columbia: *Royal Ontario Museum, Life Sciences Occasional Paper*, v. 32, p. 1–8.
- Rudkin, D.M., 1985, Exoskeletal abnormalities in four trilobites: *Canadian Journal of Earth Sciences*, v. 22, p. 479–483.
- Russell, R.T., 1967, Discovery of major phosphate deposits in northwest Queensland: *Queensland Government Mining Journal*, v. 68, p. 153–157.
- Schneider, C.A., Rasband, W.S., and Eliceiri, K.W., 2012, NIH Image to ImageJ: 25 years of image analysis: *Nature Methods*, v. 9, p. 671–675, <https://doi.org/10.1038/nmeth.2089>.
- Sheldon, P.R., 1987a, Parallel gradualistic evolution of Ordovician trilobites: *Nature*, v. 330, p. 561–563.
- Sheldon, P.R., 1987b, Trilobite evolution and faunal distribution in some Ordovician rocks of the Builth Inlier, central Wales [Ph.D. thesis]: Cambridge, UK, University of Cambridge, 256 p.
- Šnajdr, M., 1978a, Anomalous carapaces of Bohemian paradoxid trilobites: *Sborník Geologických Věd Paleontologie*, v. 20, p. 7–31.
- Šnajdr, M., 1978b, Pathological neoplasms in the fringe of *Bohemoharpes* (Trilobita): *Věstník Ústředního Ústavu Geologického*, v. 53, p. 49–50.
- Šnajdr, M., 1979, Two trinucleid trilobites with repair of traumatic injury: *Věstník Ústředního Ústavu Geologického*, v. 54, p. 49–50.
- Šnajdr, M., 1981, Bohemian Proetidae with malformed exoskeletons (Trilobita): *Sborník Geologických Věd Paleontologie*, v. 24, p. 37–61.
- Šnajdr, M., 1985, Anomalous exoskeletons of Bohemian encrinurine trilobites: *Věstník Ústředního Ústavu Geologického*, v. 60, p. 303–306.
- Southgate, P.N., and Shergold, J.H., 1991, Application of sequence stratigraphic concepts to middle Cambrian phosphogenesis, Georgina Basin, Australia: *BMR Journal of Australian Geology and Geophysics*, v. 12, p. 119–144.
- Stein, M., 2013, Cephalic and appendage morphology of the Cambrian arthropod *Sidneyia inexpectans*: *Zoologischer Anzeiger*, v. 253, p. 164–178, <https://doi.org/10.1016/j.jcz.2013.05.001>.
- Sundberg, F.A., 2011, Chisholm Shale (*Glossopleura walcottii* Zone, upper Delamaran, Global Stage 5) at the Half Moon Mine, Pioche, Nevada, in Hollingsworth, J.S., Sundberg, F.A., and Foster, J.R., eds., *Cambrian Stratigraphy and Paleontology of Northern Arizona and Southern Nevada*: *Museum of Northern Arizona Bulletin*, v. 67, p. 224–226.
- Sundberg, F.A., Geyer, G., Kruse, P.D., McCollum, L.B., Pegel, T.V., Zylinska, A., and Zhuravlev, A.Y., 2016, International correlation of the Cambrian Series 2-3, Stages 4-5 boundary interval: *Australasian Palaeontological Memoirs*, v. 49, p. 83–124.
- Vinn, O., 2018, Traces of predation in the Cambrian: *Historical Biology*, v. 30, p. 1043–1049, <https://doi.org/10.1080/08912963.2017.1329305>.
- Vorwald, G.R., 1984, Paleontology and paleoecology of the upper Wheeler Formation (late middle Cambrian), Drum Mountains, west-central Utah [M.S. thesis]: Lawrence, University of Kansas, 176 p.
- Walcott, C.D., 1888, Cambrian fossils from Mount Stephen, northwest territory of Canada: *American Journal of Science*, ser. 3, v. 36, p. 163–166.
- Walcott, C.D., 1910, Cambrian geology and paleontology, no. 6: *Olenellus* and other genera of the Mesonacidae: *Smithsonian Miscellaneous Collections*, v. 53, p. 231–422.
- Walcott, C.D., 1917, Cambrian geology and paleontology, 4, Fauna of the Mount Whyte Formation: *Smithsonian Miscellaneous Collections*, v. 67, p. 61–114.
- Walcott, C.D., 1924, Cambrian and Ozarkian trilobites: *Smithsonian Miscellaneous Collections*, v. 75, p. 53–60.
- Whitehouse, F.W., 1939, The Cambrian faunas of north-eastern Australia, part 3: The polymerid trilobites: *Memoirs of the Queensland Museum*, v. 21, p. 179–282.
- Zacáň, A., Vannier, J., and Lerosey-Aubril, R., 2016, Reconstructing the diet of a 505-million-year-old arthropod: *Sidneyia inexpectans* from the Burgess Shale fauna: *Arthropod Structure & Development*, v. 45, p. 200–220, <https://doi.org/10.1016/j.asd.2015.09.003>.
- Zamora, S., Mayoral, E., Esteve, J., Gámez-Vintaned, J.A., and Santos, A., 2011, Exoskeletal abnormalities in paradoxid trilobites from the Cambrian of Spain, and a new type of bite trace: *Bulletin of Geosciences*, v. 86, p. 665–673, <https://doi.org/10.3140/bull.geosci.1275>.
- Zong, R.-W., 2021a, Abnormalities in early Paleozoic trilobites from central and eastern China: *Palaeoworld*, v. 30, p. 430–439, <https://doi.org/10.1016/j.palwor.2020.07.003>.
- Zong, R.-W., 2021b, Injuries and molting interference in a trilobite from the Cambrian (Furongian) of South China: *PeerJ*, v. 9, p. e11201, <https://doi.org/10.7717/peerj.11201>.

Accepted: 10 February 2022