Exploring abnormal Cambrian-aged trilobites in the Smithsonian collection

Russell D.C. Bicknell¹ and Stephen Pates²

¹ Palaeoscience Research Centre, School of Environmental and Rural Science, University of New England, Armidale, NSW, Australia
² Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, Boston, United States of America

ABSTRACT

Biomineralised trilobite exoskeletons provide a 250 million year record of abnormalities in one of the most diverse arthropod groups in history. One type of abnormality—repaired injuries—have allowed palaeobiologists to document records of Paleozoic predation, accidental damage, and complications in moulting experienced by the group. Although Cambrian trilobite injuries are fairly well documented, the illustration of new injured specimens will produce a more complete understanding of Cambrian prey items. To align with this perspective, nine new abnormal specimens displaying healed injuries from the Smithsonian National Museum of Natural History collection are documented. The injury pattern conforms to the suggestion of lateralised prey defence or predator preference, but it is highlighted that the root cause for such patterns is obscured by the lumping of data across different palaeoecological and environmental conditions. Further studies of Cambrian trilobites with injuries represent a key direction for uncovering evidence for the Cambrian escalation event.

INTRODUCTION

The Cambrian Explosion—a rapid and stunning increase in animal diversity and disparity during the earliest Paleozoic, over 500 million years ago—likely resulted from a combination of biological, ecological, and environmental factors (Smith & Harper, 2013; Zhang et al., 2014; Bicknell & Paterson, 2018). Among the ecological factors, the rise of predation has been considered a key evolutionary innovation that helped drive and shape morphological and diversity trajectories of different Cambrian groups (Vermeij, 1989; Conway Morris, 1998; Bengtson, 2002; Babcock, 2003; Wood & Zhuravlev, 2012; Bicknell & Paterson, 2018; Pates & Bicknell, 2019), including the rise of biomineralisation in the exoskeletons and shells of prey animals (Vermeij, 1989; Vermeij, 2013; Conway Morris & Jenkins, 1985; Babcock, 1993; Babcock, 2003; Conway Morris & Bengtson, 1994; Bicknell & Paterson, 2018). This biomineralisation also permitted the documentation of failed predation events, complications during moulting, as well as genetic, developmental and/or behavioural malfunctions in trilobites and other animals (Owen, 1985; Babcock, 1993; Babcock, 2007; Bicknell & Paterson, 2018).

How to cite this article Bicknell RDC, Pates S. 2020. Exploring abnormal Cambrian-aged trilobites in the Smithsonian collection. PeerJ 8:e8453 http://doi.org/10.7717/peerj.8453
Trilobites were an abundant, diverse, and disparate group of Paleozoic animals with biomineralised exoskeletons (Webster, 2007) that commonly record abnormal features. A range of Cambrian-aged trilobite abnormalities are known and have been used as a model system for exploring Cambrian predator–prey interactions (Owen, 1985; Conway Morris & Jenkins, 1985; Babcock & Robison, 1989; Babcock, 1993; Babcock, 2003; Lee, Choi & Pratt, 2001; Pates et al., 2017; Bicknell & Paterson, 2018; Vinn, 2018; Pates & Bicknell, 2019). Here, nine new examples of abnormal specimens from the Paleontological collection of the Smithsonian National Museum of Natural History (USNM PAL) are presented; a collection from which abnormal trilobites have previously been reported (Babcock, 1993; Bicknell, Pates & Botton, 2018d). These specimens aid the recent pulse in documentation of Cambrian predation traces and other abnormalities (Fatka, Budil & Grigar, 2015; Pates et al., 2017; Bicknell, Pates & Botton, 2018d; Bicknell & Pates, 2019; Klompmaker et al., 2019; Pates & Bicknell, 2019).

METHODS
Cambrian-aged trilobite specimens in the USNM PAL were reviewed for evidence for abnormalities, as originally defined by Owen (1985). This definition has subsequently been used and further refined in studies of other abnormal arthropods (Babcock, 1993; Bicknell & Paterson, 2018; Bicknell & Pates, 2019; see section ‘Terminology’). Specimens were photographed using a Canon EOS REBEL T2i under LED (light-emitting diode) lighting. Measurements of abnormalities were made from photographs using ImageJ (version 1.52a; Schneider, Rasband & Eliceiri, 2012). Specimen ages were determined from the age of the host rock and comparisons to the literature, using the most recent geological timescale (Peng, Babcock & Cooper, 2012).

Terminology

Cicatrisation
Thickening of the exoskeleton over an injury which occurred in same inter-moult period that the injury was sustained (Ludvigsen, 1977; Owen, 1985).

Injuries
Abnormal features that record unsuccessful predation, complications during burrowing, mating, or moulting (Bicknell, Pates & Botton, 2018d). They are indicated by exoskeletal repair, substantial exoskeletal deformity. They can have ‘U’-, ‘V’-, ‘W’-, or ‘L’-shapes impacting multiple sections of the exoskeleton, or be expressed as single segment injuries (SSIs): the shortening and possible rounding of the distal margin of singular thoracic segments (formally referred to as single spine injuries, Pates & Bicknell, 2019).

Regeneration
Regrowth of an injured area, over a series of moults (Owen, 1985; Pates et al., 2017).
RESULTS

Elliptocephala asaphoides Emmons, 1844, USNM PAL 18350a, Browns Pond Formation (=Schodack Formation) (Cambrian Stage 2, Series 4, age taken from Skovsted & Peel, 2007), eastern New York, USA. Figures 1A, 1B.

USNM PAL 18350a is preserved as an external mould with a ‘U’-shaped abnormality that truncates pleurae by 8 mm. Abnormality begins at thoracic segment 6, extends into thoracic segment 8, and is 15 mm long. The margin of the abnormality is cicatrised along thoracic segment 6, while thoracic segments 7 and 8 show no evidence for cicatisation.

Mummaspis oblisooculatus Fritz, 1992, USNM PAL 443790, Mural Formation (Cambrian Series 2, Stage 4, age taken from Ortega Hernández, Esteve & Butterfield, 2013), Alberta, Canada. Figures 2A–2C.

USNM PAL 443790 is preserved as an external mould and displays a possible bilateral thoracic abnormality. Thoracic segments 3 and 4 on the left side have been truncated into an asymmetric ‘V’-shaped abnormality that is 3 mm long and slightly cicatrised (Fig. 2B). The thoracic segments are truncated pleurae by 9 mm. On the right side of the thorax, there is a potential SSI on thoracic segment 6 (Fig. 2C). However, closer examination of the specimen highlights that there are likely traces of more parts of the pleural spine. In
Figure 2  *Mummaspis oblisooculatus* Fritz, 1992, USNM PAL 443790, Mural Formation (Cambrian Series 2, Stage 4). Specimen was figured in Fritz (1992, pl. 17, fig. 4). (A) Complete specimen showing an injury and evidence for taphonomic alteration. (B) Close up of abnormality on the left side of the thorax illustrating pleural truncation and ‘V’-shape. (C) Close up broken thoracic segment on the right thoracic lobe. Dotted white line shows where part of a spine is preserved.

In this case, this feature reflects taphonomic alteration to the specimen, or poor breakage of the rock.

*Olenellus thompsoni* (Hall, 1859), USNM PAL 729428, Parker Formation (Cambrian Stage 2, Series 4, age taken from Webster & Landing, 2016), Vermont, USA. Figures 3A, 3B.

USNM PAL 729428 is preserved as an external mould with little relief and shows two abnormalities on the right posterior thorax. The more anterior abnormality has a ‘U’-shape, is observed on thoracic segments 7–9, and is slightly cicatrised. Thoracic pleurae 7 and 8 are fused together at the abnormality margin. The second abnormality is ‘W’-shaped, spans thoracic segments 11–13, and has a cicatrised margin. Both abnormalities truncate the thoracic pleurae by 6 mm.

*Olenellus getzi* Dunbar, 1925, USNM PAL 729422, Kinzers Formation (Cambrian Series 2, Stage 4), Pennsylvania, USA. Figures 4A, 4B.

USNM PAL 729422 is a partial specimen preserved as an external mould and displays two abnormalities on the right side of the thorax. The more anterior abnormality is an SSI on the 6th thoracic segment that shows no evidence of cicatrisation and truncates the pleura by 6 mm. Thoracic segment 7 shows possible evidence of two thoracic pleurae developing from the one thoracic segment. The split between these spines occurs ~24 mm from the midline of the specimen. As the upper of the two pleurae shows terraced lines indicative of the ventral surface (*Lieberman, 1999*), it is possible that this specimen instead represents a fragment retained during moult, or even the chance superimposition of a fragment on a complete specimen. Fragments on the specimen indicate that either of these
two scenarios is possible; however, the alignment of the pleura with the segment, and its relative size, support a biological interpretation.

*Nevadia weeksi* *Walcott, 1910*, USNM PAL 56792a; USNM PAL 56792d, Pioche Formation (Miaolingian Series, Wuliuan, age taken from *Kimmig, Meyer & Lieberman, 2018*), Utah, USA Figs. 5A–5E.

USNM PAL 56792a is a partial specimen preserved as an external mould with an abnormality on the posterior right thorax (Figs. 5A, 5B). The abnormality is an SSI on the 16th thoracic segment. The pleura is terminated 2 mm from the thoracic axial lobe, rounded, and shows no evidence of cicatrisation. This abnormality truncates the pleura by 28 mm.

USNM PAL 56792d preserves the posterior section of the exoskeleton and has a bilaterally expressed injury. The plural spine on the 14th thoracic segment on the left side is an SSI that truncates the pleura by 10 mm (Fig. 5D). On the right thoracic side, the 11th and 12th segments show SSIs. The terminus of the 11th thoracic pleura is not rounded and truncated by at least 7 mm (Fig. 5E). The terminus of the 12th thoracic pleura is slightly rounded and truncated by at least 9 mm (Fig. 5E). No abnormalities on this specimen show evidence of cicatrisation.
**Glossopleura gigantea** *Resser, 1939*, USNM PAL 729419, Spence Shale Member, Langston Formation (Miaolingian Series, Wulian), Utah, USA. Figs. 6A, 6B.

USNM PAL 729419 is preserved as an external mould and displays an abnormal right thorax. Abnormality is an SSI on the 4th thoracic segment that truncates the segment by 8 mm. The margin of the abnormality is rounded and slightly cicatrised.

**Ogygopsis klotzi** *(Rominger, 1887)*, USNM PAL 729421, Stephen Formation (Miaolingian Series, Wulian), British Columbia, Canada. Figures 7A, 7B.

USNM PAL 729421 is preserved as an external mould and displays an abnormality on the left thoracic lobe. The abnormality has a shallow 'W'-shape that begins at the 2nd thoracic segment, ends at 5th thoracic segment, is 10.5 mm long, and truncates the pleurae by 2 mm. Abnormality margin shows no evidence of cicatrisation. Thoracic pleurae 3 and 4 are fused together at the abnormality margin, while the margins of pleurae 2 and 5 are distorted about the fused section.

**Elrathia kingii** *Meek, 1870*, USNM PAL 729417, Wheeler Formation (Miaolingian Series, Drumian), western Utah, USA. Figures 8A, 8B.

USNM PAL 729417 is preserved as an external mould and displays an abnormality on the posterior right thorax that extends into the anterior pygidium. The abnormality has a 'U'-shape, begins at the 10th thoracic segment, ends within the first 1 mm of the pygidium, is 4.6 mm long, and truncates the affected thoracic segments by 1.5 mm. The abnormality margin is slightly cicatrised and deforms thoracic segments 10–11.
DISCUSSION

Comparing the nature of the abnormalities documented here with examples in other publications suggests that the specimens described in this contribution display repaired injuries, rather than examples of developmental or genetic aberrations (Owen, 1985; Conway Morris & Jenkins, 1985; Babcock & Robison, 1989; Babcock, 1993; Babcock, 2003; Bicknell and Pates, 2020).
Babcock, 2007; Robison, Babcock & Gunther, 2015; Bicknell & Paterson, 2018; Bicknell, Paterson & Hopkins, 2019; Pates & Bicknell, 2019). The injuries that affect more than one thoracic segment and are located on thoracic areas that are unlikely to have been damaged by chance (Babcock & Robison, 1989; Babcock, 1993; Pates et al., 2017; Bicknell & Paterson, 2018) represent healed injuries, likely attributable to predation. Those injuries showing exoskeletal cicatrisation reflect an attack that occurred recently within the same intermoult period, as observed in modern arthropods (Ludvigsen, 1977; Bursey, 1977; Owen, 1985; Rudkin, 1985; Halcrow & Smith, 1986). Injuries that occurred during a soft-shelled stage, when individuals were likely more vulnerable to attacks, would likely have wrinkled and deformed the exoskeleton as it would not have been fully mineralised (Conway Morris & Jenkins, 1985; Bicknell & Paterson, 2018). Injuries lacking cicatrisation and showing partial regeneration likely occurred in prior moult stages (Owen, 1985; Pates et al., 2017). The SSIs observed in the studied sample may record attacks or moultting complications. In particular, the injuries on Nevadaia weeksi likely reflect complications during moultting as the most elongated thoracic pleurae that would catch or not exit the old exoskeleton cleanly during ecdysis (Snajdr, 1978; Owen, 1983; Conway Morris & Jenkins, 1985).
The studied sample presents possible evidence for injury patterns in an entirely qualitative context. This assessment provides potential support for an interpretation of injuries to trilobites caused by predators showing location specificity for the right side; if all injuries do indeed represent failed attacks (e.g., Babcock & Robison, 1989; Babcock, 1993). Six specimens have right-sided injuries, two specimens have potential bilateral injuries and one specimen has a left-sided injury. Although this sample size is too small to test for statistical significance, these data align with the thesis that either Cambrian predators attacked prey from the right side, Cambrian prey orientated themselves to have the right side attacked, or a combination of both (Babcock & Robison, 1989; Babcock, 1993; Eaton, 2019). Evidence for lateralised injury patterns in trilobite systems was also recently presented in the Silurian-aged Rochester Shale (Bicknell, Paterson & Hopkins,
Conversely, Pates et al. (2017) and Pates & Bicknell (2019) reported no statistical evidence for this pattern in their studies of individual Cambrian taxa. As Pates & Bicknell (2019) outlined, studies of injury lateralisation that pool data on injuries from different time periods do not allow researchers to distinguish between potential causes of injuries, as the studied taxa are from different deposits. The true taxon-specific palaeoecological signal is therefore masked by variation in temporal and geographical conditions and it is unlikely that they all were under the same predatory selection pressures (Pates et al., 2017; Bicknell, Paterson & Hopkins, 2019; Pates & Bicknell, 2019). The identification of both Cambrian (Babcock, 1993; Eaton, 2019) and Silurian signals (Bicknell, Paterson & Hopkins, 2019), with the failure to detect a Cambrian signal (Pates et al., 2017; Pates & Bicknell, 2019), and post-Cambrian signal in other cases (Babcock, 1993) demonstrates that the causes of injury lateralisation are best considered on a case-by-case basis. Such an approach provides the best chance of identifying the root causes of an interesting ecological interaction.

No cephalic injuries were reported in this study. This rarity of cephalic injuries has been noted by previous workers (e.g., Owen, 1985; Babcock, 1993; Pratt, 1998). Biological explanations for this pattern could be that predators targeted the thorax and pygidium preferentially, a higher mortality rate of injuries to the head region, and/or trilobites protecting the head region through behavioural actions such as enrolment (Ortega Hernández, Esteve & Butterfield, 2013; Bicknell & Paterson, 2018; Pates & Bicknell, 2019). It is unlikely that it represents sampling bias, as specimens have been collated from a
large number of collectors, and trilobite cephala and cranidia provide a wide range of taxonomic, morphometric, and phylogenetic characters and landmarks (e.g., Lieberman, 1999; Webster, 2015). Furthermore, in a bulk sample with no collection bias injured cephala were significantly rarer than thoracic injuries (Pates & Bicknell, 2019).

Potential predators

Injuries could have been produced by either self-injury during moulting, or the action of predators (Owen, 1985; Babcock, 1993). The traditional perspective is that radiodonts were likely the culprits for Cambrian sublethal, healed trilobite injuries (Radkin, 1979; Nedin, 1999; Leighton, 2011; Zamora et al., 2011). This group of nektonic Paleozoic stem-group euarthropods (Daley et al., 2009) have often been referred to as ‘anomalocaridids’ or ‘anomalocarids’ in reference to the family Anomalocarididae and the first documented radiodont: Anomalocaris canadensis Whiteaves, 1892 (Whittington & Briggs, 1985). The raptorial appendages known to anomalocaridids and amplectobeluids have been highlighted as possible tools for grasping, flexing and breaking trilobite exoskeletons (Babcock, 1993; Nedin, 1999). While some sublethal injuries were potentially caused by this group, the shell-crushing (durophagous) effectiveness of appendage morphologies has been questioned (Pratt, 1998; Bicknell & Paterson, 2018). The slender and elongate auxiliary spines in some Anomalocaris species (Anomalocaris magnabasis Pates et al., in press and A. saron Hou, Bergström & Ahlberg, 1995) is not indicative of a purely durophagous feeding mode (Pates et al., in press). Furthermore, Radiodonta are now considered a group of arthropods with a diverse range of ecologies, from raptorial predation in Anomalocarididae and Amplectobeluidae (e.g., Daley & Edgecombe, 2014; Liu et al., 2018), to sediment sifting in Hurdiidae (e.g., Daley, Budd & Caron, 2013; Moysiuk & Caron, 2019), and filter feeding in Hurdiidae and Tamisiocarididae (Vinther et al., 2014; Van Roy, Daley & Briggs, 2015; Lerosey-Aubril & Pates, 2018). The diversity of feeding modes is supported by the discovery of multiple radiodonts with different inferred ecologies from the same site (Daley & Budd, 2010; Pates & Daley, 2019; Pates et al., in press).

Analysis of the radiodont oral cone has not provided any definitive evidence to support a durophagous lifestyle for these animals (Whittington & Briggs, 1985; Hou, Bergström & Ahlberg, 1995; Hagadorn, 2009; Hagadorn, Schottenfeld & McGowan, 2010; Daley & Bergström, 2012), despite suggestions that the shape might be suitable for producing ‘W’-shaped injuries (e.g., Babcock & Robison, 1989; Nedin, 1999). These lines of evidence, combined with the lack of any hard-parts in known radiodont guts (e.g., Daley & Edgecombe, 2014), has led to suggestions that radiodonts may not have fed on hard-shelled taxa at all (with some potential exceptions discussed below).

Cambrian-aged trilobites and other artiopodans that display gnathobases on protopodal sections of thoracic appendages were potentially durophagous predators that fed like horseshoe crabs (Babcock, 2003; Bicknell et al., 2018a; Bicknell et al., 2018b; Bicknell et al., 2018c; Bicknell, Pates & Botton, 2018d; Bicknell & Paterson, 2018; Holmes, Paterson & Garcia-Bellido, in press). An example of this is Sidneyia inexpectans Walcott, 1911 that is known to have shelly cololites (Bruton, 1981; Zacaï, Vannier & Lerosey-Aubril, 2016; Peel, 2017; Bicknell & Paterson, 2018) and fortified gnathobasic spines for effective durophyag
This was confirmed with recent 3D biomechanical modelling (Bicknell et al., 2018b). Other possible durophagous predators include *Utahcaris orion* Conway Morris & Robison, 1988 that has also been noted with fragmented sclerites in the gut tract (Conway Morris & Robison, 1988; Babcock, 2003; Legg & Pates, 2017). Beyond these arthropodan groups, amplectobeluid genera *Amplectobelua* Hou, Bergström & Ahlberg, 1995 and *Ramskoeldia* Cong et al., 2018 have been documented with gnathobase-like structures near the mouth (Cong et al., 2017; Cong et al., 2018), and three species of the genus *Caryosyntrips* Daley & Budd, 2010 possess stiff appendages with short and robust spines (Daley & Budd, 2010; Pates & Daley, 2017). This suggests that amplectobeluid radiodants, and *Caryosyntrips* (currently unassigned to a family) were potentially capable of consuming harder prey. Nonetheless, such ideas need quantitative testing, as done for *S. inexpectans* (Bicknell et al., 2018b).

One final consideration regarding possible predators is the idea that injuries may have been inflicted by shell hammering, as opposed to shell crushing (Pratt, 1998). It has been suggested that raptorial frontal appendages of *Yohoia tenuis* Walcott, 1912 would have been effective at breaking biomineralised exoskeletons, using similar mechanics to modern-day mantis shrimps (Pratt, 1998; Haug et al., 2012; Bicknell & Paterson, 2018). Analyses of such morphologies with comparisons to extant stomatopods may highlight the effectiveness of such Cambrian shell hammering (Crane et al., 2018).

**Escalation and predation**

Escalated evolution reflects selective pressure placed on individuals by predators, parasites, competitors and dangerous prey (Vermeij, 1994; Vermeij, 2013). Such pressures drive the development of adaptive features in prey to avoid, escape, or defend against predators (Vermeij, 1994; Vermeij, 2013; Thompson, 1999; Baumiller & Gahn, 2004). The record of prey escalation includes changes to external shell ornamentation, fluctuation in predation intensity, and prey regeneration frequency (Vermeij, Schindel & Zipser, 1981; Kelley & Hansen, 1996; McShea, 1998; Alexander & Dietl, 2001; Baumiller & Gahn, 2004; Whitenack & Herbert, 2015). Vermeij (1989) suggested that escalation was a major component of evolution during the Cambrian Explosion and that escalated predation pressures drove the variety of defensive features in prey (Vermeij, 1989; Bengtson, 2002; Brett & Walker, 2002; Babcock, 2003; Marshall, 2006; Vendrasco et al., 2011; Wood & Zhuravlev, 2012; Voje et al., 2015). However, there is limited quantitative evidence for this evolutionary explanation (Bicknell & Paterson, 2018). The Cambrian escalation event could potentially be demonstrated by documenting changes in defensive adaptations of Cambrian trilobites. To conduct such a study, specimens of the same species from different stratigraphic levels within the same formation could be examined for injuries and responses to predation. If Cambrian trilobites did experienced escalated evolution, innovation in defensive features, such as increased exoskeletal thickness, or changes to hypertrophied spines (Pates & Bicknell, 2019), would be observed, and their role in response to the predation tested. An increased number of injured specimens at particular levels within the section would indicate that a higher survival rate from attacks (Vendrasco et al., 2011). Trilobites, with their excellent fossil record, high diversity, high disparity, abundance, and long record of
predation, therefore represent a suitable system for understanding the Cambrian escalation event.

CONCLUSIONS

The current study of abnormal Cambrian trilobites within the Paleontological collection of the Smithsonian National Museum of Natural History presents nine new examples of injured specimens. These injuries display a range of morphologies that are attributed to failed predation and complicated moulting. The possible predatory groups are discussed, and euarthropods with gnathobases and other forms of robust spines are considered as the most probable predators. It is also highlighted that trilobites represent an ideal study system for documenting quantitative evidence for the Cambrian escalation event and responses of prey items to the first durophages.

ACKNOWLEDGEMENTS

We thank Mark Florence for access to the USNM collection and use of the USNM photographic facilities. Finally, we thank the editor Bruce S Lieberman, and the reviewers Loren Babcock, Oldřich Fatka and Brain Pratt for their helpful comments that thoroughly improved this contribution.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding
This research was supported by funding from an Australian Research Council Discovery Project (DP200102005), a UNE Postdoctoral Research Fellowship (to Russell Dean Christopher Bicknell), a Charles Schuchert and Carl O. Dunbar grants-in-Aid award (to Russell Dean Christopher Bicknell) and an Alexander Agassiz Postdoctoral Fellowship (to Stephen Pates). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures
The following grant information was disclosed by the authors:
Australian Research Council Discovery Project: DP200102005.
UNE Postdoctoral Research Fellowship.
Charles Schuchert and Carl O. Dunbar grants-in-Aid award.
Alexander Agassiz Postdoctoral Fellowship.

Competing Interests
The authors declare there are no competing interests.

Author Contributions
• Russell D.C. Bicknell conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
Stephen Pates performed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability
The following information was supplied regarding data availability:
The raw data are photographs presented in Figs. 1–8.
The specimens are housed in the Paleontological collection of the Smithsonian National Museum of Natural History (USNM PAL):

- *Elliptocephala asaphoides* USNM PAL 18350a,
- *Mummaspis oblisoculatus* USNM PAL 443790,
- *Olenellus thompsoni* USNM PAL 729428,
- *Olenellus getzi* USNM PAL 729422,
- *Nevadia weeksi* USNM PAL 56792a; USNM PAL 56792d,
- *Glossopleura gigantea* USNM PAL 729419,
- *Ogygopsis klotzi* USNM PAL 729421,
- *Elrathia kingii* USNM PAL 729417.

REFERENCES

Alexander RR, Dietl GP. 2001. Shell repair frequencies in New Jersey bivalves: a recent baseline for tests of escalation with Tertiary, Mid-Atlantic congeners. *Palaios* 16(4):354–371 DOI 10.1669/0883-1351(2001)016<0354:SRFINJ>2.0.CO;2.

Babcock LE. 1993. Trilobite malformations and the fossil record of behavioral asymmetry. *Journal of Paleontology* 67(2):217–229 DOI 10.1017/S0022336000032145.

Babcock LE. New York. 2003. Trilobites in Paleozoic predator–prey systems, and their role in reorganization of early Paleozoic ecosystems. In: Kelley P, Kowalewski M, Hansen TA, eds. *Predator—prey interactions in the fossil record*. New York: Springer, 55–92.

Babcock LE. 2007. Role of malformations in elucidating trilobite paleobiology: a historical synthesis. In: Mikulic DG, Landing E, Kluessendorf J, eds. *Fabulous fossils—300 years of worldwide research on trilobites*. New York: University of the State of New York, State Education Dept. New York State Museum, 3–19.

Babcock LE, Robison RA. 1989. Preferences of Palaeozoic predators. *Nature* 337(6209):695–696.

Baumiller TK, Gahn FJ. 2004. Testing predator-driven evolution with Paleozoic crinoid arm regeneration. *Science* 305(5689):1453–1455 DOI 10.1126/science.1101009.

Bengtson S. 2002. Origins and early evolution of predation. *Paleontological Society Papers* 8:289–318 DOI 10.1017/S1089332600001133.

Bicknell RDC, Klinkhamer AJ, Flavel RJ, Wroe S, Paterson JR. 2018a. A 3D anatomical atlas of appendage musculature in the chelicerate arthropod *Limulus polyphemus*. *PLOS ONE* 13(2):e0191400 DOI 10.1371/journal.pone.0191400.

Bicknell RDC, Ledogar JA, Wroe S, Gutzler BC, Watson III WH, Paterson JR. 2018b. Computational biomechanical analyses demonstrate similar shell-crushing abilities
in modern and ancient arthropods. Proceedings of the Royal Society B: Biological Sciences 285(1889):20181935 DOI 10.1098/rspb.2018.1935.

Bicknell RDC, Paterson JR. 2018. Reappraising the early evidence of durophagy and drilling predation in the fossil record: implications for escalation and the Cambrian explosion. Biological Reviews 93(2):754–784 DOI 10.1111/brv.12365.

Bicknell RDC, Paterson JR, Caron J-B, Skovsted CB. 2018c. The gnathobasic spine microstructure of Recent and Silurian chelicerates and the Cambrian arthropod Sidneyia: functional and evolutionary implications. Arthropod Structure & Development 47(1):12–24 DOI 10.1016/j.asd.2017.12.001.

Bicknell RDC, Paterson JR, Hopkins MJ. 2019. A trilobite cluster from the Silurian Rochester Shale of New York: predation patterns and possible defensive behavior. American Museum Novitates 39(3937):1–16 DOI 10.1206/3937.1.

Bicknell RDC, Pates S. 2019. Abnormal extant xiphosurids in the Yale Peabody Museum Invertebrate Zoology collection. Bulletin of the Peabody Museum of Natural History 60(1):41–53 DOI 10.3374/014.060.0102.

Bicknell RDC, Pates S, Botton ML. 2018d. Abnormal xiphosurids, with possible application to Cambrian trilobites. Palaeontologia Electronica 21(2):1–17.

Brett CE, Walker SE. 2002. Predators and predation in Paleozoic marine environments. Paleontological Society Papers 8:93–118 DOI 10.1017/S1089332600001078.

Bruton DL. 1981. The arthropod Sidneyia inexpectans, Middle Cambrian, Burgess Shale, British Columbia. Philosophical Transactions of the Royal Society of London Series B, Biological Sciences 295(1079):619–656 DOI 10.1098/rstb.1981.0164.

Bursey CR. 1977. Histological response to injury in the horseshoe crab, Limulus polyphemus. Canadian Journal of Zoology 55(7):1158–1165 DOI 10.1139/z77-150.

Cong P, Daley AC, Edgecombe GD, Hou X. 2017. The functional head of the Cambrian radiodontan (stem-group Euarthropoda) Amplectobelua symbrachiata. BMC Evolutionary Biology 17(1):208 DOI 10.1186/s12862-017-1049-1.

Cong P, Edgecombe GD, Daley AC, Pates S, Hou X. 2018. New radiodontans with gnathobase-like structures from the Cambrian Chengjiang Biota and implications for the systematics of Radiodonta. Papers in Palaeontology 4(4):605–621 DOI 10.1002/spp2.1219.

Conway Morris S. 1998. The Crucible of Creation: the Burgess Shale and the rise of animals. New York: Oxford University Press.

Conway Morris S, Bengtson S. 1994. Cambrian predators: possible evidence from boreholes. Journal of Paleontology 68(1):1–23 DOI 10.1017/S0022336000025567.

Conway Morris S, Jenkins RJF. 1985. Healed injuries in early Cambrian trilobites from South Australia. Alcheringa 9(3):167–177 DOI 10.1080/03115518508618965.

Conway Morris S, Robison RA. 1988. More soft-bodied animals and algae from the Middle Cambrian of Utah and British Columbia. 12: 21–48.

Crane RL, Cox SM, Kisare SA, Patek SN. 2018. Smashing mantis shrimp strategically impact shells. Journal of Experimental Biology 221(11):jeb176099 DOI 10.1242/jeb.176099.
Daley AC, Bergström J. 2012. The oral cone of *Anomalocaris* is not a classic “peytoia”. *Naturwissenschaften* **99**(6):501–504 DOI 10.1007/s00114-012-0910-8.

Daley AC, Budd GE. 2010. New anomalocaridid appendages from the Burgess Shale, Canada. *Palaeontology* **53**(4):721–738 DOI 10.1111/j.1475-4983.2010.00955.x.

Daley AC, Budd GE, Caron J-B. 2013. Morphology and systematics of the anomalocaridid arthropod *Hurdia* from the Middle Cambrian of British Columbia and Utah. *Journal of Systematic Palaeontology* **11**(7):743–787 DOI 10.1080/14772019.2012.732723.

Daley AC, Budd GE, Caron J-B, Edgecombe GD, Collins D. 2009. The Burgess Shale anomalocaridid *Hurdia* and its significance for early euarthropod evolution. *Science* **323**(5921):1597–1600 DOI 10.1126/science.1169514.

Daley AC, Edgecombe GD. 2014. Morphology of *Anomalocaris canadensis* from the Burgess Shale. *Journal of Paleontology* **88**(1):68–91 DOI 10.1666/13-067.

Dunbar CO. 1925. Antennae in *Olenellus getzi* n. sp. *American Journal of Science* **52**:303–308.

Eaton K. 2019. Lethal and sublethal predation on cambrian trilobites from North America. Undergraduate Thesis, Ohio State University.

Emmons E. 1844. *The taconic system; based on observations in New-York, Massachusetts, Maine, Vermont and Rhode-Island*. New York: Carroll and Cooke, Printers.

Fatka O, Budil P, Grigar L. 2015. A unique case of healed injury in a Cambrian trilobite. *Annales de Paléontologie* **101**(4):295–299 DOI 10.1016/j.annpal.2015.10.001.

Fritz WH. 1992. Walcott’s Lower Cambrian olenellid trilobite collection 61K, Mount Robson area, Canadian Rocky Mountains. *Geological Survey of Canada Bulletin* **432**:1–65.

Hagadorn JW. 2009. Taking a bite out of *Anomalocaris*. In: *Walcott 2009 International Conference on the Cambrian Explosion*, 33–34.

Hagadorn JW, Schottenfeld MT, McGowan D. 2010. Putting *Anomalocaris* on a soft-food diet? *Geological Society of America Abstracts* **42**:320.

Halcrow K, Smith JC. 1986. Wound closure in the crab *Carcinus maenas* (L.). *Canadian Journal of Zoology* **64**(12):2770–2778 DOI 10.1139/z86-401.

Hall J. 1859. Remarks upon the trilobites of the shales of the Hudson-River Group, with descriptions of some new species of the genus *Olenus*. *Natural History of New York, Paleontology* **3**:525–529.

Haug JT, Waloszek D, Maas A, Liu Y, Haug C. 2012. Functional morphology, ontogeny and evolution of mantis shrimp-like predators in the Cambrian. *Palaeontology* **55**(2):369–399 DOI 10.1111/j.1475-4983.2011.01124.x.

Holmes JD, Paterson JR, García-Bellido DC. 2019. 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* 1–40 In Press DOI 10.1080/14772019.2019.1605411.

Hou XG, Bergström J, Ahlberg P. 1995. *Anomalocaris* and other large animals in the Lower Cambrian Chengjiang fauna of southwest China. *GFF* **117**(3):163–183 DOI 10.1080/11035899509546213.
Kelley PH, Hansen TA. 1996. Naticid gastropod prey selectivity through time and the hypothesis of escalation. *Palaios* 11(5):437–445 DOI 10.2307/3515211.

Kimmig J, Meyer RC, Lieberman BS. 2018. *Herpetogaster* from the early Cambrian of Nevada (Series 2, Stage 4) and its implications for the evolution of deuterostomes. *Geological Magazine* 156(1):172–178.

Klompmaker AA, Kelley PH, Chattopadhyay D, Clements JC, Huntley JW, Kowalewski M. 2019. Predation in the marine fossil record: studies, data, recognition, environmental factors, and behavior. *Earth-Science Reviews* DOI 10.1016/j.earscirev.2019.02.020.

Lee JG, Choi DK, Pratt BR. 2001. A teratological pygidium of the Upper Cambrian trilobite *Eugonocare* (*Pseudeugonocare*) *bispinatum* from the Machari Formation, Korea. *Journal of Paleontology* 75(1):216–218 DOI 10.1017/S0022336000032005.

Legg DA, Pates S. 2017. A restudy of *Utahcaris orion* (Euarthropoda) from the Spence Shale (Middle Cambrian, Utah, USA). *Geological Magazine* 154(1):181–186 DOI 10.1017/S0016756816000789.

Leighton LR. 2011. Analyzing predation from the Dawn of the Phanerozoic. In: Laflamme M, Schiffauer JD, Dornbos SQ, eds. *Quantifying the evolution of early life*. Dordrecht: Springer, 73–109.

Lerosey-Aubril R, Pates S. 2018. New suspension-feeding radiodont suggests evolution of microplanktivory in Cambrian macronekton. *Nature Communications* 9(1):3774 DOI 10.1038/s41467-018-06229-7.

Lieberman BS. 1999. Systematic revision of the Olenelloidea (Trilobita, Cambrian). *Bulletin of the Yale University Peabody Museum of Natural History* 45:1–150.

Liu J, Lerosey-Aubril R, Steiner M, Dunlop JA, Shu D, Paterson JR. 2018. Origin of raptorial feeding in juvenile euarthropods revealed by a Cambrian radiodontan. *National Science Review* 5(6):863–869 DOI 10.1093/nsr/nwy057.

Ludvigsen R. 1977. Rapid repair of traumatic injury by an Ordovician trilobite. *Lethaia* 10(3):205–207 DOI 10.1111/j.1502-3931.1977.tb00613.x.

Marshall CR. 2006. Explaining the Cambrian explosion of animals. *Annual Reviews in Earth and Planetary Sciences* 34:355–384 DOI 10.1146/annurev.earth.33.031504.103001.

McShea DW. 1998. Possible largest-scale trends in organismal evolution: eight live hypotheses. *Annual Review of Ecology and Systematics* 29(1998):293–318 DOI 10.1146/annurev.ecolsys.29.1.293.

Meek FB. 1870. Descriptions of fossils collected by the US Geological Survey under the charge of Clerence King, Esq. *Proceedings of the Academy of Natural Sciences of Philadelphia* 22:56–64.

Moysiuk J, Caron J-B. 2019. A new hurdiid radiodont from the Burgess Shale evinces the exploitation of Cambrian infaunal food sources. *Proceedings of the Royal Society B* 286(1908):20191079 DOI 10.1098/rspb.2019.1079.

Nedin C. 1999. *Anomalocaris* predation on nonmineralized and mineralized trilobites. *Geology* 27(11):987–990 DOI 10.1130/0091-7613(1999)027<0987:APONAM>2.3.CO;2.
Ortega Hernández J, Esteve J, Butterfield NJ. 2013. Humble origins for a successful strategy: complete enrolment in early Cambrian olenellid trilobites. *Biology Letters* 9(5):20130679 DOI 10.1098/rsbl.2013.0679.

Owen AW. 1983. Abnormal cephalic fringes in the Trinucleidae and Harpeditae (Trilobita). *Special Papers in Paleontology* 30:241–247.

Owen AW. 1985. Trilobite abnormalities. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 76(2–3):255–272 DOI 10.1017/S0263593300010488.

Pates S, Bicknell RDC. 2019. Elongated thoracic spines as potential predatory deterrents in olenelline trilobites from the lower Cambrian of Nevada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 519(2019):295–306.

Pates S, Bicknell RDC, Daley AC, Zamora S. 2017. Quantitative analysis of repaired and un repaired damage to trilobites from the Cambrian (Stage 4, Drumian) Iberian Chains, NE Spain. *Palaios* 32(12):750–761 DOI 10.2110/palo.2017.055.

Pates S, Daley AC. 2017. *Caryosyntrips*: a radiodontan from the Cambrian of Spain, USA and Canada. *Papers in Palaeontology* 3(3):461–470 DOI 10.1002/spp2.1084.

Pates S, Daley AC. 2019. The Kinzers Formation (Pennsylvania, USA): the most diverse assemblage of Cambrian Stage 4 radiodonts. *Geological Magazine* 156(7):1233–1246 DOI 10.1017/S0016756818000547.

Pates S, Daley AC, Edgecombe GD, Cong P, Lieberman BS. 2019. Systematics, preservation and biogeography of radiodonts from the southern Great Basin, USA, during the upper Dyeran (Cambrian Series 2, Stage 4). *Papers in Palaeontology* In Press DOI 10.1002/spp2.1277.

Peel JS. 2017. Mineralized gutfills from the Sirius Passet Lagerstätte (Cambrian Series 2) of North Greenland. *GFF* 139(2):83–91 DOI 10.1080/11035897.2016.1260051.

Peng S, Babcock LE, Cooper RA. 2012. The Cambrian period. In: Gradstein FM, Ogg JG, Schmitz M, Ogg G, eds. *The Geologic Time Scale*. Netherlands: Elsevier, 437–488.

Pratt BR. 1998. Probable predation on Upper Cambrian trilobites and its relevance for the extinction of soft-bodied Burgess Shale-type animals. *Lethaia* 31(1):73–88.

Resser CE. 1939. The Spence Shale and its fauna (with six plates). *Smithsonian Miscellaneous Collections* 98(24):1–72.

Robison RA, Babcock LE, Gunther VG. 2015. Exceptional Cambrian fossils from Utah: a window into the age of trilobites. *Utah Geological Survey, Miscellaneous Publication* 15–1:1–97.

Rominger C. 1887. Description of primordial fossils from Mount Stephens, NW Territory of Canada. *Proceedings of the Academy of Natural Sciences of Philadelphia* 39(1):12–19.

Rudkin DM. 1979. Healed injuries in *Ogygopsis klotzi* (Trilobita) from the Middle Cambrian of British Columbia. *Royal Ontario Museum, Life Sciences Occasional Paper* 32:1–8.

Rudkin DM. 1985. Exoskeletal abnormalities in four trilobites. *Canadian Journal of Earth Sciences* 22(3):479–483.

Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH image to ImageJ: 25 years of image analysis. *Nature Methods* 9(7):671–675 DOI 10.1038/nmeth.2089.
Skovsted CB, Peel JS. 2007. Small shelly fossils from the argillaceous facies of the Lower Cambrian Forteau formation of western Newfoundland. *Acta Palaeontologica Polonica* 52(4):729–748.

Smith MP, Harper DAT. 2013. Causes of the Cambrian explosion. *Science* 341(6152):1355–1356 DOI 10.1126/science.1239450.

Šnajdr M. 1978. Anomalous carapaces of Bohemian paradoxid trilobites. *Sborník Geologických Věd Paleontologie* 20:7–31.

Thompson JN. 1999. Coevolution and escalation: are ongoing coevolutionary meanderings important? *The American Naturalist* 153(S5):S92–S93 DOI 10.1086/303214.

Van Roy P, Daley AC, Briggs DEG. 2015. Anomalocaridid trunk limb homology revealed by a giant filter-feeder with paired flaps. *Nature* 522(7554):77–80 DOI 10.1038/nature14256.

Vendrasco MJ, Kouchinsky AV, Porter SM, Fernandez CZ. 2011. Phylogeny and escalation in *Mellopegma* and other Cambrian molluscs. *Palaeontologia Electronica* 14(2):1–44.

Vermeij GJ. 1989. The origin of skeletons. *Palaios* 4(6):585–589 DOI 10.2307/3514748.

Vermeij GJ. 1994. The evolutionary interaction among species: selection, escalation, and coevolution. *Annual Review of Ecology and Systematics* 25:219–236 DOI 10.1146/annurev.es.25.110194.001251.

Vermeij GJ. 2013. On escalation. *Annual Review of Earth and Planetary Sciences* 41:1–19 DOI 10.1146/annurev-earth-050212-124123.

Vermeij GJ, Schindel DE, Zipser E. 1981. Predation through geological time: evidence from gastropod shell repair. *Science* 214(4524):1024–1026 DOI 10.1126/science.214.4524.1024.

Vinn O. 2018. Traces of predation in the Cambrian. *Historical Biology* 30(8):1043–1049 DOI 10.1080/08912963.2017.1329305.

Vinther J, Stein M, Longrich NR, Harper DA. 2014. A suspension-feeding anomalocarid from the Early Cambrian. *Nature* 507(7493):496–499 DOI 10.1038/nature13010.

Voje KL, Holen ØH, Liow LH, Stenseth NC. 2015. The role of biotic forces in driving macroevolution: beyond the Red Queen. *Proceedings of the Royal Society Series B, Biological Sciences* 282(1808):20150186 DOI 10.1098/rspb.2015.0186.

Walcott CD. 1910. *Olenellus* and other genera of the Mesonacidae. *Smithsonian Miscellaneous Collections* 53(6):231–422.

Walcott CD. 1911. Cambrian geology and paleontology, II. Middle Cambrian Merostomata. *Smithsonian Miscellaneous Collections* 57:17–40.

Walcott CD. 1912. Middle Cambrian Branchiopoda, Malacostraca, Trilobita and Merostomata. *Cambrian Geology and Paleontology II* 57:145–228.

Webster M. 2007. A Cambrian peak in morphological variation within trilobite species. *Science* 317(5837):499–502 DOI 10.1126/science.1142964.

Webster M. 2015. Ontogeny and intraspecific variation of the early Cambrian trilobite *Olenellus gilberti*, with implications for olenelline phylogeny and macroevolutionary trends in phenotypic canalization. *Journal of Systematic Palaeontology* 13(1):1–74 DOI 10.1080/14772019.2013.852903.
Webster M, Landing E. 2016. Geological context, biostratigraphy and systematic revision of late early Cambrian olenelloid trilobites from the Parker and Monkton formations, northwestern Vermont, USA. Australasian Palaeontological Memoirs 49:193–240.

Whiteaves JF. 1892. Description of a new genus and species of phyllocarid crustacea from the Middle Cambrian of Mount Stephen, BC. Canadian Record of Science 5:205–208.

Whitenack LB, Herbert GS. 2015. Did shell-crushing crabs trigger an escalatory arms race in the aftermath of a Late Neogene regional mass extinction event? An experimental test. Palaeogeography, Palaeoclimatology, Palaeoecology 417(2015):57–65 DOI 10.1016/j.palaeo.2014.09.026.

Whittington HB. 1989. Olenelloid trilobites: type species, functional morphology and higher classification. Philosophical Transactions of the Royal Society of London Series B, Biological Sciences 324(1221):111–147 DOI 10.1098/rstb.1989.0041.

Whittington HB, Briggs DEG. 1985. The largest Cambrian animal, Anomalocaris, Burgess Shale, British Columbia. Philosophical Transactions of the Royal Society of London B, Biological Sciences 309(1141):569–609 DOI 10.1098/rstb.1985.0096.

Wood R, Zhuravlev AY. 2012. Escalation and ecological selectively of mineralogy in the Cambrian radiation of skeletons. Earth-Science Reviews 115(4):249–261 DOI 10.1016/j.earscirev.2012.10.002.

Zacaï A, Vannier J, Lerosey-Aubril R. 2016. Reconstructing the diet of a 505-million-year-old arthropod: Sidneyia inexpectans from the Burgess Shale fauna. Arthropod Structure & Development 45(2):200–220 DOI 10.1016/j.asd.2015.09.003.

Zamora S, Mayoral E, Esteve J, Gámez-Vintaned JA, Santos A. 2011. Exoskeletal abnormalities in paradoxid trilobites from the Cambrian of Spain, and a new type of bite trace. Bulletin of Geosciences 86(3):665–673.

Zhang X, Shu D, Han J, Zhang Z, Liu J, Fu D. 2014. Triggers for the Cambrian explosion: hypotheses and problems. Gondwana Research 25(3):896–909 DOI 10.1016/j.gr.2013.06.001.