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Injuries and molting interference in a trilobite from the Cambrian (Furongian) of South China

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ABSTRACT

An injured *Shergoldia laevigata* Zhu, Hughes & Peng, 2007 (Trilobita, Asaphida) was collected from the Furongian of Guangxi, South China. The injuries occurred in the left thoracic pleurae possessing two marked V-shaped gaps. It led to substantial transverse shortening of the left pleural segments, with barely perceptible traces of healing. This malformation is interpreted as a sub-lethal attack from an unknown predator. The morphology of injuries and the spatial and temporal distribution of predators indicated that the predatory structure might have been the spines on the ganathobase or ganathobase-like structure of a larger arthropod. There were overlapped segments located in the front of the injuries, and slightly dislocated thoracic segments on the left part of the thorax, suggesting that the trilobite had experienced difficulties during molting. The freshly molted trilobite had dragged forward the old exuvia causing the irregular arrangement of segments. This unusual trilobite specimen indicates that the injuries interfered with molting.

Subjects Animal Behavior, Evolutionary Studies, Paleontology

Keywords Sub-lethal attack, *Shergoldia*, Predator-prey interactions, Sandu formation, Guangxi

INTRODUCTION

Numerous trilobite exoskeleton deformities have been documented, including abnormal healing, hyperplasia, deformation, and missing or fractured segments. The causes of these deformities are usually thought to be injuries, developmental disorders, and diseases (Owen, 1985; Babcock, 1993; Pates et al., 2017; Bicknell & Pates, 2020). The evaluation of injuries caused by predator attack is useful for presenting the interactions between predators and trilobites, and for reconstructing the food web and ecological structure in deep time (Klomp maker et al., 2019). Furthermore, such predatorial injuries are used to uncover behavioral information (Babcock & Robison, 1989; Babcock, 1993; Pates et al., 2017; Bicknell, Paterson & Hopkins, 2019). The injuries caused by predators have mainly been detected on the edges of trilobites, especially in the thoraces and pygidia, and are generally considered to have been non-lethal (Babcock, 2003; Babcock, 2007), while cephalic attacks are more often fatal (Pates & Bicknell, 2019). Although numerous studies have evaluated injured trilobites (e.g., Owen, 1985; Rudkin, 1985; Babcock, 1993; Babcock, 2003; Babcock, 2007; Zhu et al., 2007; Schoenemann, Clarkson & Høyberget, 2017; Bicknell & Paterson, 2018; Bicknell & Pates, 2020; Bicknell & Holland, 2020; Zong, 2020), most predators remain

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unidentified, except some carnivores with trilobite fragments in their guts or coprolites (Vannier & Chen, 2005; Vannier, 2012; Zacaï, Vannier & Lerosey-Aubril, 2016; Bicknell & Paterson, 2018; Kimmig & Pratt, 2018). The shapes of the Cambrian trilobite injuries suggest that some predators may have been radiodonts (Babcock & Robison, 1989; Babcock, 1993; Nedin, 1999). Other predator candidates include cephalopods, echinoderms, fish, and other larger arthropods (Bruton, 1981; Briggs & Collins, 1988; Babcock, 1993; Fatka, Budil & Grigar, 2015; Jago, García-Bellido & Gehling, 2016; Bicknell & Paterson, 2018; Bicknell et al., 2018a; Zhai et al., 2019).

Moreover, although it has been inferred that injuries did interfere with daily activities of trilobites, there are rare direct fossil records (Šnajdr, 1985). Herein, I discuss an injured *Shergoldia laevigata* Zhu, Hughes & Peng, 2007 from the Cambrian (Furongian) of Jingxi, Guangxi, South China. The exoskeletal injuries suggest that the predatory structure might have been the spines on the gnathobase or gnathobase-like structure of a larger arthropod. In addition, the findings indicate that these injuries would have caused difficulties for trilobite during molting, but did not cause molting failure.

MATERIALS & METHODS

The described *Shergoldia laevigata* specimen, housed in the State Key Laboratory of Biogeology and Environmental Geology, China University of Geoscience (Wuhan), was discovered from the Cambrian (Furongian)-aged Sandu Formation of Guole Town, Jingxi County, Guangxi Zhuang Autonomous Region, South China (Fig. 1) (Zhu, Hughes & Peng, 2007). The Sandu Formation is represented by calcareous mudstones, siltstones, and argillaceous banded limestones, which formed most probably in the uppermost part of the continental slope (Lerosey-Aubril, Zhu & Ortega-Hernández, 2017). The Sandu Formation is richly fossiliferous, containing abundant, well-preserved articulated trilobites (Han et al., 2000; Zhu, 2005; Zhu, Hughes & Peng, 2007; Zhu, Hughes & Peng, 2010), non-trilobite arthropods (Lerosey-Aubril, Ortega-Hernández & Zhu, 2013; Lerosey-Aubril, Zhu & Ortega-Hernández, 2017), echinoderms (Han & Chen, 2008; Chen & Han, 2013; Zamora et al., 2017; Zamora, Zhu & Lefebvre, 2013; Zhu, Zamora & Lefebvre, 2014), brachiopods, graptolites (Zhan et al., 2010), hyolithids, cnidarians, algae, and some exceptionally preserved soft-bodied fossils (Zhu et al., 2016).

Trilobites from the Sandu Formation have been classified into at least 25 genera (Zhu, 2005; Zhu, Hughes & Peng, 2007; Zhu, Hughes & Peng, 2010); however, only six abnormal specimens have been documented from this formation (five *Tamdaspis jingxiensis* Zhu et al., 2007 and one *Guangxiaspis guangxiensis* Zhou in Zhou et al., 1977; Zhu, 2005; Zhu et al., 2007; Zong, 2020). The injured *Shergoldia laevigata* was collected from the grey-yellow calcareous mudstones. The specimen is from the *Probinacunaspis nasalis*–*Peichiashania hunanensis* Zone of the Furongian, Jiangshanian (Peng, 2009; Zhu et al., 2016).

The fossil in Fig. 2C was whitened with magnesium oxide powder, and all photographs were captured using a Nikon D5100 camera with a Micro-Nikkor 55 mm F3.5 lens.

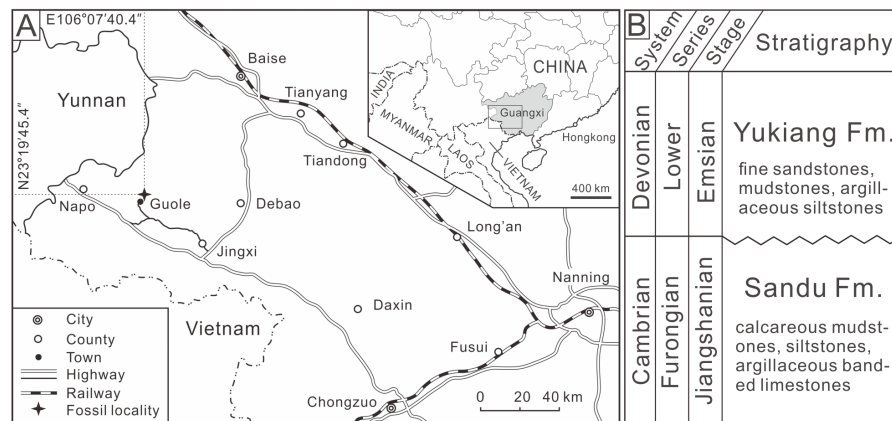


Figure 1 (A) Map of fossil locality at Guole Town, Jingxi County, Guangxi, South China; (B) stratigraphic sketch showing relative position and age of the Sandu Formation.

[Full-size DOI: 10.7717/peerj.11201/fig-1](https://doi.org/10.7717/peerj.11201/fig-1)

RESULTS

The injured *Shergoldia laevigata* is preserved as a nearly complete dorsal exoskeleton (30.5 mm long) without librigena, suggesting an exuvia (Daley & Drage, 2016; Drage, 2019). The posterior of the cranidium overlies the first two thoracic segments, this is most pronounced on the left side (Fig. 2). In addition, the first thoracic segment covered most of the left pleural segment of the second thoracic segment, as well as the anterior margin of the right pleural segment. Similarly, most of the first thoracic segment was covered by the posterior area of the fixigena, particularly on its left side. Moreover, the left pleural segments of the fourth to eighth thoracic segments presented an interlaced arrangement, i.e., the anterior margin of the fourth thoracic segment extended upon the third thoracic segment, and the seventh extended upon the sixth (Fig. 2), while there was a typical imbricated arrangement in the right pleural region.

The malformation is on the left part of the exoskeleton, while the medial (axial) and right sections are undamaged. The left thoracic segments are shorter than those on the right side and show limited healing. There are two injuries: one on the third to fourth thoracic segments, and one on the seventh thoracic segment. Two pleural segments are truncated by 3.3 mm because of the first asymmetric V-shaped injury; the most seriously damaged part is the contact site of the two thoracic segments, where there is a V-shaped injury. The second injury truncates the left pleural section of the seventh thoracic segment by 3.5 mm.

DISCUSSION

Possible origin of the injuries and potential predatory structure

Trilobites that are malformed due to predatory attacks have typically V-, U-, or W-shaped injuries (Owen, 1985; Babcock, 1993; Pratt, 1998; Jago & Haines, 2002; Zamora et al., 2011; Pates et al., 2017; Bicknell & Paterson, 2018; Bicknell & Pates, 2020), with a few showing in bay-shaped injuries (Fatka, Budil & Grigar, 2015). Furthermore, there is occasionally signs

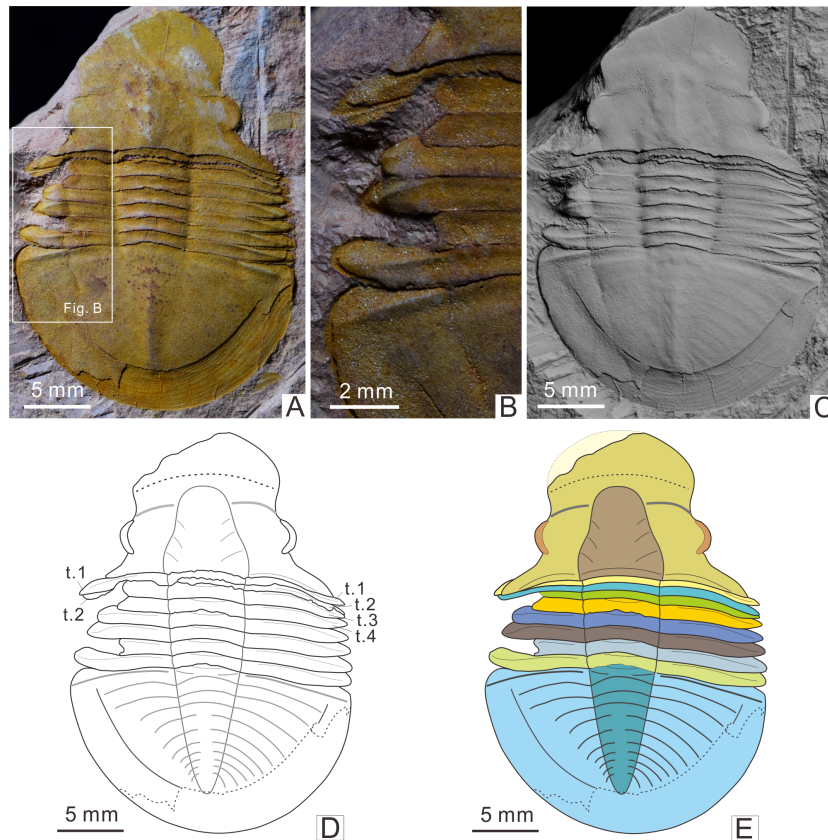


Figure 2 Malformed trilobite *Shergoldia laevigata* from the Cambrian Furongian of Jingxi, Guangxi (Specimen No. CUG-GJ-2015-01). (A) Uncoated specimen; (B) close-up of abnormality in box in (A); (C) specimen whitened by the magnesium oxide powder; (D) sketch of the (A); (E) picture after recovery of the cranidium and the first three thoracic segments, showing the superposed relationship between the posterior area of the fixigena and thoracic segments.

Full-size [DOI: 10.7717/peerj.11201/fig-2](https://doi.org/10.7717/peerj.11201/fig-2)

of healing or regeneration (Rudkin, 1979; McNamara & Tuura, 2011; Pates et al., 2017). In the present specimen, the injuries have traces of healing and are therefore considered evidence of a predatory attack. The two injuries have a similar degree of healing without any regeneration, suggesting that these injuries may have been incurred in the same inter-molt stage.

In the past, the most commonly suggested Cambrian predators are considered to have been the radiodonts, especially anomalocaridids and amplexobeluids, as their frontal appendages and oral cone were extremely effective predatory structures (Whittington & Briggs, 1985; Babcock, 1993; Zamora et al., 2011). Cambrian arthropods or arthropod-like organisms with gnathobases are also considered possible predators, similar to the modern horseshoe crab (Bicknell et al., 2018a; Bicknell et al., 2021). Some amplexobeluid genera have been documented with gnathobase-like structures (Cong et al., 2017; Cong et al., 2018), suggesting that amplexobeluid radiodonts may have been predators of Cambrian trilobites (Bicknell & Pates, 2020). In addition, some trilobites and predatory arthropods with reinforced gnathobasic spines on the protopodal sections of their walking legs are

also considered as potential predators ([Bruton, 1981](#), [Conway Morris & Jenkins, 1985](#); [Zacai, Vannier & Lerosey-Aubril, 2016](#); [Bicknell et al., 2018a](#); [Bicknell et al., 2018b](#); [Bicknell, Paterson & Hopkins, 2019](#); [Bicknell & Holland, 2020](#)).

However, so far, the youngest ampletobeluid and anomalocaridid are from the Drumian and Guzhangian, respectively ([Lerosey-Aubril et al., 2014](#); [Lerosey-Aubril et al., 2020](#)). Most Furongian and Ordovician radiodonts belong to the family Hurdiidae, which do not have endites of alternating size, and all members of this family are considered to be sediment sifters or suspension feeders ([Daley, Budd & Caron, 2013](#); [Daley et al., 2013](#); [Lerosey-Aubril & Pates, 2018](#); [Van Roy, Daley & Briggs, 2015](#); [Pates et al., 2020](#)). Moreover, no radiodonts were discovered in the Sandu Formation. So, the radiodonts are unlikely to have caused the injuries in the *Shergoldia laevigata* specimen. Gnathobases have a slight size gradation of spines along the gnathal edge ([Stein, 2013](#)), or a saw-toothed pattern with spines of alternating sizes ([Bicknell et al., 2018a](#)). These spines may have caused smaller injuries, that is missing one or two separate thoracic segments, on the edges of trilobites. The arthropods *Aglaspella sanduensis* ([Lerosey-Aubril, Ortega-Hernández & Zhu, 2013](#)) and *Glypharthrus trispinicaudatus*, Mollisonia-like arthropods, unnamed aglaspidid-like arthropods, *Perspicares*-like bivalve arthropods ([Zhu et al., 2016](#); [Lerosey-Aubril, Zhu & Ortega-Hernández, 2017](#)), and some larger trilobites ([Zhu, 2005](#)) were discovered in the Sandu Formation at the same site. Therefore, the predator who attacked the studied *Shergoldia laevigata* specimen may be one of these arthropods.

Interference with the molting of trilobite

Previous studies have reported abundant injured trilobites and presented the possible identity of the predators, including information about their behavior ([Babcock, 1993](#); [Babcock, 2007](#); [Pates et al., 2017](#); [Bicknell & Paterson, 2018](#); [Bicknell, Paterson & Hopkins, 2019](#); [Pates & Bicknell, 2019](#)). However, there are few direct fossil records showing that injury has disturbed the molting of trilobites ([Šnajdr, 1985](#)). The studied specimen has an apparent overlap of segments along with the injuries that are mainly present in the posterior of the cranidium and the front of the thorax, especially in the left part of the exoskeleton. The anterior margin of the injured third thoracic segment was covered by the unbroken second thoracic segment ([Figs. 2A–2D](#)), indicating that the injury formed before the overlap of the segments. Bottom currents can also cause the overlap and even disruption of trilobite segments, the Sandu Formation formed in a relatively calm environment ([Lerosey-Aubril, Zhu & Ortega-Hernández, 2017](#)), although there are overlapping segments on the exuvia and carcass of *Shergoldia laevigata* in the same horizon, their thoracic segments still maintain imbricated arrangement ([Zhu, Hughes & Peng, 2007](#)). There is also overlap of thoracic segments on the exuvia of uninjured trilobites ([Daley & Drage, 2016](#)), but it is difficult to determine whether it was caused by molting or other abiotic factors. In contrast to the above two cases, in addition to the overlap of segments in the studied specimen, the left thoracic segments are presented an interlaced arrangement rather than imbricated ([Fig. 2](#)), which seems not to be caused by bottom currents and is rather likely caused by the active behavior of trilobite. Moreover, all abnormal arrangements of the segments appeared near the injury, and the overlapped part of the segments was only located before

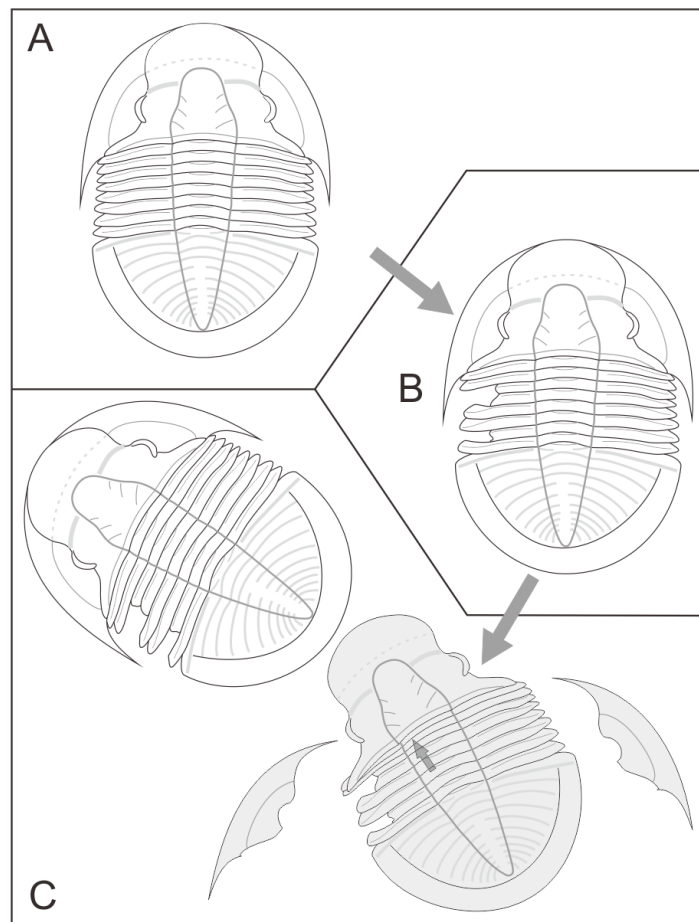


Figure 3 Reconstruction of injury of studied *Shergoldia laevigata* specimen from the Cambrian Furongian of Jingxi, Guangxi. (A–B) Predator attack on *Shergoldia laevigata*, and leading to damage in the exoskeleton. (C) *Shergoldia laevigata* drag forward the old shell during molting, because of the deformation of the exoskeleton. Such condition leads to the overlap of segments and dislocated arrangement of thoracic segments.

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the most serious injury (on the third to fourth thoracic segments). It is speculated that all of the irregular patterns were caused by post-injury molting of *Shergoldia laevigata*. Namely, the new exoskeleton could not be smoothly separated from the old one due to the unbalanced body with injuries (Drage, 2019; Drage et al., 2019). The trilobite dragged forward the old shell to get rid of the exuvia, which led to the overlap of segments and the dislocated arrangement of thoracic segments, especially near the injuries (Fig. 3). Some previous studies have reported cases of failed molting of a trilobite (McNamara & Rudkin, 1984) and other ecdysozoans (García-Bellido & Collins, 2004; Drage & Daley, 2016; Yang et al., 2019), in which the new exoskeletons were preserved under the old exuvia. However, none of the fragments of the new exoskeleton were found under or near the exuvia of *Shergoldia laevigata*, which implies that the molting might not have failed. Although the

injuries complicated the molting process, it was successful and the molted trilobite moved away.

CONCLUSIONS

The *Shergoldia laevigata* specimen has substantially shorter pleural segments of the third to fourth and seventh thoracic segments, with signs of lightly healing in the injuries incurred during a sub-lethal predator attack. The degree of healing in both injuries and the distribution of the injuries show that they may have been caused in the same inter-molt stage. Based on the morphology of the injuries and the spatial and temporal distribution of predators, the predatory structure may have been the spines on the gnathobase or gnathobase-like structure of a larger arthropod. The conspicuous overlapping of the segments and dislocated arrangement of the thoracic segments, especially in the left pleural region and near the injuries, shows that the injured *S. laevigata* encountered certain obstacles during molting. The trilobite dragged the old exuvia forward, which led to the irregular arrangement of the segments. Such configuration can demonstrate that even provisionally healed injury can cause certain complication of the molting process in trilobites.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests

The author declares there are no competing interests.

Author Contributions

- Ruiwen Zong 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.

Data Availability

The following information was supplied regarding data availability:

The raw data are photographs in [Figs. 1–3](#).

The specimen is stored in the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Wuhan, China: CUG-GJ-2015-01.

REFERENCES

- Babcock LE. 1993.** Trilobite malformations and the fossil record of behavioral asymmetry. *Journal of Paleontology* **67**:217–229 DOI [10.1017/S0022336000032145](#).
- Babcock LE. 2003.** Trilobites in Palaeozoic predator–prey systems, and their role in reorganization of early Paleozoic ecosystems. In: Kelly PH, 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 DG, Landing E, Kluessendorf J, eds. *Fabulous fossils—300 years of worldwide research on trilobites*. New York: The University of State of New York, 3–18.
- Babcock LE, Robison RA. 1989.** Preferences of Palaeozoic predators. *Nature* **337**:695–696 DOI [10.1038/337695c0](#).
- Bicknell RDC, Holland B. 2020.** Injured trilobites within a collection of dinosaurs: using the Royal Tyrrell Museum of Palaeontology to document Cambrian predation. *Palaeontologia Electronica* **23**:a33 DOI [10.26879/1087](#).
- Bicknell RDC, Holmes JD, Edgecombe GD, Losso SR, Ortega-Hernández J, Wroe S, Paterson JR. 2021.** Biomechanical analyses of Cambrian euarthropod limbs reveal their effectiveness in mastication and durophagy. *Proceedings of the Royal Society B: Biological Sciences* **288**:20202075 DOI [10.1098/rspb.2020.2075](#).
- Bicknell RDC, Ledogar JA, Wroe S, Gutzler BC, Watson III WH, Paterson JR. 2018a.** Computational biomechanical analyses demonstrate similar shell-crushing abilities in modern and ancient arthropods. *Proceedings of the Royal Society B: Biological Sciences* **285**: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**:754–784 DOI [10.1111/brv.12365](#).
- Bicknell RDC, Paterson JR, Caron JB, Skovsted CB. 2018b.** The gnathobasic spine microstructure of Recent and Silurian chelicerates and the Cambrian artiopodan *Sidneyia*: functional and evolutionary implications. *Arthropod Structure & Development* **47**: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* 39:1–16 DOI 10.1206/3937.1.
- Bicknell RDC, Pates S. 2020.** Exploring abnormal Cambrian-aged trilobites in the Smithsonian collection. *PeerJ* 8:e8453 DOI 10.7717/peerj.8453.
- Briggs DEG, Collins D. 1988.** A Middle Cambrian chelicerate from Mount Stephen, British Columbia. *Palaeontology* 31:779–798.
- 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* 295:619–656 DOI 10.1098/rstb.1981.0164.
- Chen GY, Han NR. 2013.** New materials of Stylophora from the Upper Cambrian of the Jingxi area, Guangxi, South China. *Acta Palaeontologica Sinica* 52:288–293.
- Cong PY, Daley AC, Edgecombe GD, Hou XG. 2017.** The functional head of the Cambrian radiodontan (stem-group Euarthropoda) *Amplectobelua symbrachiata*. *BMC Evolutionary Biology* 17:208 DOI 10.1186/s12862-017-1049-1.
- Cong PY, Edgecombe GD, Daley AC, Guo J, Pates S, Hou XG. 2018.** New radiodonts with gnathobase-like structures from the Cambrian Chengjiang biota and implications for the systematics of Radiodonta. *Papers in Palaeontology* 4:605–621 DOI 10.1002/spp2.1219.
- Conway Morris S, Jenkins RJF. 1985.** Healed injuries in Early Cambrian trilobites from South Australia. *Alcheringa* 9:167–177 DOI 10.1080/03115518508618965.
- Daley AC, Budd GE, Caron JB. 2013.** Morphology and systematics of the anomalocaridid arthropod *Hurdia* from the Middle Cambrian of British Columbia and Utah. *Journal of Systematic Palaeontology* 11:743–787 DOI 10.1080/14772019.2012.732723.
- Daley AC, Drage HB. 2016.** The fossil record of ecdysis, and trends in the moulting behaviour of trilobites. *Arthropod Structure & Development* 45:71–96 DOI 10.1016/j.asd.2015.09.004.
- Daley AC, Paterson JR, Edgecombe GD, García-Bellido DC, Jago JB. 2013.** New anatomical information on *Anomalocaris* from the Cambrian Emu Bay Shale of South Australia and a reassessment of its inferred predatory habits. *Palaeontology* 56:971–990 DOI 10.1111/pala.12029.
- Drage HB. 2019.** Quantifying intra- and interspecific variability in trilobite moulting behaviour across the Palaeozoic. *Palaeontologia Electronica* 22.2.34:1–39 DOI 10.26879/940.
- Drage HB, Daley AC. 2016.** Recognising moulting behaviour in trilobites by examining morphology, development and preservation: Comment on Błażejowski et al, 2015. *BioEssays* 38:981–990 DOI 10.1002/bies.201600027.
- Drage HB, Vandenbroucke TRA, Van Roy P, Daley AC. 2019.** Sequence of post-moult exoskeleton hardening preserved in a trilobite mass moult assemblage from the Lower Ordovician Fezouata Konservat-Lagerstätte, Morocco. *Acta Palaeontologica Polonica* 64:261–273 DOI 10.4202/app.00582.2018.
- Fatka O, Budil P, Grigar L. 2015.** A unique case of healed injury in a Cambrian trilobite. *Annales de Paléontologie* 101:295–299 DOI 10.1016/j.annpal.2015.10.001.

- García-Bellido DC, Collins DH. 2004. Moulting arthropod caught in the act. *Nature* 429:40 DOI 10.1038/429040.
- Han NR, Chen GY. 2008. New stylophorans (Echinodermata) from the Upper Cambrian of Guangxi, South China. *Science China Series D: Earth Sciences* 51:181–186 DOI 10.1007/s11430-008-0003-x.
- Han NR, Tang L, Wei RS, Wang GB. 2000. Stratigraphy of Upper Cambrian from Guole, Jingxi, Guangxi. *Journal of Guilin Institute of Technology* 20:350–355.
- Jago JB, García-Bellido DC, Gehling JG. 2016. An early Cambrian chelicerate from the Emu Bay shale, south Australia. *Palaeontology* 59:549–562 DOI 10.1111/pala.12243.
- Jago JB, Haines PW. 2002. Repairs to an injured early Middle Cambrian trilobite, Elkedra area, Northern Territory. *Alcheringa* 26:19–21 DOI 10.1080/03115510208619241.
- Kimmig J, Pratt BR. 2018. Coprolites in the Ravens Throat River Lagerstätte of northwestern Canada: implications for the Middle Cambrian food web. *Palaios* 33:125–140 DOI 10.2110/palo.2017.038.
- Klompmaaker 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* 194:472–520 DOI 10.1016/j.earscirev.2019.02.020.
- Lerosey-Aubril R, Hegna TA, Babcock LE, Bonino E, Kier C. 2014. Arthropod appendages from the Weeks Formation Konservat-Lagerstätte: new occurrences of anomalocaridids in the Cambrian of Utah, USA. *Bulletin of Geosciences* 89:269–282 DOI 10.3140/bull.geosci.1442.
- Lerosey-Aubril R, Kimmig J, Pates S, Skabelund J, Weug A, Ortega-Hernández J. 2020. New exceptionally preserved panarthropods from the Drumian Wheeler Konservat-Lagerstätte of the House Range of Utah. *Papers in Palaeontology* in press DOI 10.1002/spp2.1307.
- Lerosey-Aubril R, Ortega-Hernández J, Zhu XJ. 2013. The first aglaspidid *sensu stricto* from the Cambrian of China (Sandu Formation Guangxi). *Geological Magazine* 150:565–571 DOI 10.1017/S0016756812001045.
- Lerosey-Aubril R, Pates S. 2018. New suspension-feeding radiodont suggests evolution of microplanktivory in Cambrian macronekton. *Nature Communications* 9:3774 DOI 10.1038/s41467-018-06229-7.
- Lerosey-Aubril R, Zhu XJ, Ortega-Hernández J. 2017. The Vicissicaudata revisited—insights from a new aglaspidid arthropod with caudal appendages from the Furongian of China. *Scientific Reports* 7:11117 DOI 10.1038/s41598-017-11610-5.
- McNamara KJ, Rudkin DM. 1984. Techniques of trilobite exuviations. *Lethaia* 17:153–173 DOI 10.1111/j.1502-3931.1984.tb01722.x.
- McNamara KJ, Tuura ME. 2011. Evidence for segment polarity during regeneration in the Devonian asteropygine trilobite *Greenops widderensis*. *Journal of Paleontology* 85:106–110 DOI 10.2307/23019504.
- Nedin C. 1999. *Anomalocaris* predation on nonmineralized and mineralized trilobites. *Geology* 27:987–990 DOI 10.1130/0091-7613(1999)027%3C0987:aponam%3E2.3.co;2.

- Owen AW. 1985.** Trilobite abnormalities. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **76**:255–272 DOI [10.1017/s0263593300010488](https://doi.org/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**:295–306 DOI [10.31233/osf.io/2jr9c](https://doi.org/10.31233/osf.io/2jr9c).
- Pates S, Bicknell RDC, Daley AC, Zamora S. 2017.** Quantitative analysis of repaired and unrepaired damage to trilobites from the Cambrian (Stage 4, Drumian) Iberian Chains, NE Spain. *Palaaios* **32**:750–761 DOI [10.2110/palo.2017.055](https://doi.org/10.2110/palo.2017.055).
- Pates S, Botting JP, McCobb LM, Muir LA. 2020.** A miniature Ordovician hurdiid from Wales demonstrates the adaptability of Radiodonta. *Royal Society Open Science* **7**:200459 DOI [10.1098/rsos.200459](https://doi.org/10.1098/rsos.200459).
- Peng SC. 2009.** Review on the studies of Cambrian trilobite faunas from Jiangnan slope belt, South China, with notes on Cambrian correlation between South and North China. *Acta Palaeontologica Sinica* **48**:437–452.
- Pratt BR. 1998.** Probable predation on Upper Cambrian trilobites and its relevance for the extinction of soft-bodied Burgess Shale-type animals. *Lethaia* **31**:73–88 DOI [10.1111/j.1502-3931.1998.tb00493.x](https://doi.org/10.1111/j.1502-3931.1998.tb00493.x).
- 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**:479–483 DOI [10.1139/e85-047](https://doi.org/10.1139/e85-047).
- Schoenemann B, Clarkson ENK, Høyberget M. 2017.** Traces of an ancient immune system—how an injured arthropod survived 465 million years ago. *Scientific Reports* **7**:40330 DOI [10.1038/srep40330](https://doi.org/10.1038/srep40330).
- Šnajdr M. 1985.** Anomalous exoskeletons of Bohemian encrinurine trilobites. *Vestník Ústředního Ústavu Geologického* **60**:303–306 DOI [10.31233/osf.io/2jr9c](https://doi.org/10.31233/osf.io/2jr9c).
- Stein M. 2013.** Cephalic and appendage morphology of the Cambrian arthropod *Sidneyia inexpectans*. *Zoologischer Anzeiger* **253**:164–178 DOI [10.1016/j.jcz.2013.05.001](https://doi.org/10.1016/j.jcz.2013.05.001).
- Vannier J. 2012.** Gut contents as direct indicators for trophic relationships in the Cambrian marine ecosystem. *PLOS ONE* **7**:e52200 DOI [10.1371/journal.pone.0052200](https://doi.org/10.1371/journal.pone.0052200).
- Vannier J, Chen JY. 2005.** Early Cambrian food chain: new evidence from fossil aggregates in the Maotianshan Shale biota, SW China. *Palaaios* **20**:3–26 DOI [10.2110/palo.2003.p03-40](https://doi.org/10.2110/palo.2003.p03-40).
- Van Roy P, Daley AC, Briggs DE. 2015.** Anomalocaridid trunk limb homology revealed by a giant filter-feeder with paired flaps. *Nature* **522**:77–80 DOI [10.1038/nature14256](https://doi.org/10.1038/nature14256).
- Whittington HB, Briggs DEG. 1985.** The largest Cambrian animal, *Anomalocaris*, Burgess Shale, British Columbia. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **309**:569–609 DOI [10.1098/rstb.1985.0096](https://doi.org/10.1098/rstb.1985.0096).
- Yang J, Ortega-Hernández J, Drage HB, Du KS, Zhang XG. 2019.** Ecdysis in a stem-group euarthropod from the early Cambrian of China. *Scientific Reports* **9**:5709 DOI [10.1038/s41598-019-41911-w](https://doi.org/10.1038/s41598-019-41911-w).

- Zacai 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**:200–220 DOI [10.1016/j.asd.2015.09.003](https://doi.org/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**:665–673 DOI [10.3140/bull.geosci.1275](https://doi.org/10.3140/bull.geosci.1275).
- Zamora S, Sumrall C, Zhu XJ, Lefebvre B. 2017.** A new stemmed echinoderm from the Furongian of China and the origin of Glyptocystitida (Blastozoa, Echinodermata). *Geological Magazine* **154**:465–475 DOI [10.1017/S001675681600011X](https://doi.org/10.1017/S001675681600011X).
- Zamora S, Zhu XJ, Lefebvre B. 2013.** A new Furongian (Cambrian) echinoderm-Lagerstätte from the Sandu Formation (South China). *Cahiers de Biologie Marine* **54**:565–569.
- Zhai DY, Edgecombe GD, Bond AD, Mai HJ, Hou XG, Liu Y. 2019.** Fine-scale appendage structure of the Cambrian trilobitomorph *Naraoia spinosa* and its ontogenetic and ecological implications. *Proceedings of the Royal Society B: Biological Sciences* **286**:20192371 DOI [10.1098/rspb.2019.2371](https://doi.org/10.1098/rspb.2019.2371).
- Zhan RB, Jin JS, Rong JY, Zhu XJ, Han NR. 2010.** Late Cambrian brachiopods from Jingxi, Guangxi Province, South China. *Alcheringa* **34**:99–133 DOI [10.1080/03115510903522872](https://doi.org/10.1080/03115510903522872).
- Zhou TM, Liu YR, Meng XS, Sun ZH. 1977.** Class Trilobita. In: *Palaeontological atlas of Central and South China. 1, Early Palaeozoic*. Beijing: Geological Publishing House, 104–266.
- Zhu XJ. 2005.** Trilobite faunas from Cambrian Upper Furongian of Guangxi with special notes on malformation, dimorphism and the function of eye ridges. Ph.D. Thesis, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing.
- Zhu XJ, Hughes NC, Peng SC. 2007.** On a new species of *Shergoldia* Zhang & Jell, 1987 (Trilobita), the family Tsinaniidae and the order Asaphida. *Memoirs of the Association of Australasian Palaeontologists* **34**:243–253.
- Zhu XJ, Hughes NC, Peng SC. 2010.** Ventral structure and ontogeny of the late Furongian (Cambrian) trilobite *Guangxiaspis guangxiensis* Zhou, 1977 and the diphyletic origin of the median suture. *Journal of Paleontology* **84**:493–504 DOI [10.1666/09-070.1](https://doi.org/10.1666/09-070.1).
- Zhu XJ, Peng SC, Du SX, Hu YS. 2007.** Ontogeny and malformation of *Tamdaspis jingxiensis* sp. nov. (Trilobite, Cambrian) from Jingxi, Guangxi, China. *Acta Palaeontologica Sinica* **46**:225–231.
- Zhu XJ, Peng SC, Zamora S, Lefebvre B, Chen GY. 2016.** Furongian (upper Cambrian) Guole Konservat-Lagerstätte from South China. *Acta Geologica Sinica (English Edition)* **90**:30–37 DOI [10.1111/1755-6724.12640](https://doi.org/10.1111/1755-6724.12640).
- Zhu XJ, Zamora S, Lefebvre B. 2014.** Morphology and palaeoecology of a new edrioblastoid (Edrioasteroidea) from the Furongian of China. *Acta Palaeontologica Polonica* **59**:921–926 DOI [10.4202/app.2012.0116](https://doi.org/10.4202/app.2012.0116).

Zong RW. 2020. Abnormalities in early Paleozoic trilobites from central and eastern China. *Palaeoworld* in press DOI [10.1016/j.palwor.2020.07.003](https://doi.org/10.1016/j.palwor.2020.07.003).