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Injures and molting interference in a trilobite from the Cambrian Furongian of South China

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

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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 wounds occurred in the left pleural region possessing two marked V-shaped gaps in the thorax. It led to substantial transversal shortening of the left pleural segments, with barely perceptible traces of healing. This malformation is

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Introduction

Numerous trilobite exoskeleton deformities have been documented, including abnormal healing, hyperplasia, deformation, and missing or fractured somites. 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 injury caused by predator attack is ~~most~~ useful for proving the interactions between predators and trilobites, and for reconstructing the food chain and ecological structure in deep time (*Klompmaker et al., 2019*). Furthermore, ~~such~~ predatorial injuries are used to elucidate behavioral information (*Babcock & Robison, 1989*; *Babcock, 1993*; *Pates et al., 2017*; *Bicknell, Paterson & Hopkins, 2019*). The wounds 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, 2007*). Although numerous studies have evaluated injured trilobites (e.g., *Owen, 1985*; *Rudkin, 1985*; *Babcock, 1993, 2003, 2007*; *Zhu et al., 2007*; *Bicknell & Paterson, 2018*; *Bicknell & Pates, 2020*; *Bicknell & Holland, 2020*), the predators remain unidentified. The shapes of the trilobite wounds suggest that some predators may have been radiodonts (*Babcock & Robison, 1989*; *Babcock, 1993*; *Nedin, 1999*; *Bicknell & Pates, 2020*; *Bicknell & Holland,* *2020*). Other predator candidates include cephalopods, echinoderms, fish, and other larger arthropods (*Bruton, 1981*; *Briggs & Collins, 1988*; *Babcock, 1993*; *Fatka, Budil & Grigar, 2015*).

It is also unclear whether injured trilobites experienced certain interferences with their activities of living. Although it has been inferred that injuries did interfere with daily activities, direct fossil records are rare. Herein, I discuss an injured *Shergoldia laevigata* Zhu, Hughes & Peng 2007 ~~(*Zhu, Hughes & Peng, 2007*)~~ from the Cambrian (Furongian) of Jingxi, Guangxi, South China. The exoskeleton wounds suggest that the predatory structure might have been the frontal appendages of larger arthropod or arthropod-like organism. In addition, the findings indicate that these injuries would have caused difficulties during the trilobite molting process, 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 thin-middle bedded 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, 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 ~~so far~~ (*Zhu, 2005*; *Zhu, Hughes & Peng, 2007, 2010*); however, only six abnormal specimens have been ~~found in~~ this formation (five *Tamdaspis jingxiensis* and one *Guangxiaspis guangxiensis*) (*Zhu, 2005*; *Zhu et al., 2007*; *Zong, 2020*). The injured *Shergoldia laevigata* was collected from the grey-yellow calcareous mudstones. ~~The age of the specimen is limited to 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. All figures were completed in CorelDRAW X7.

Results

The injured *Shergoldia laevigata* is preserved as a nearly complete dorsal exoskeleton (30.5 mm long) without librigena; ~~such configuration was considered as~~ an exuvia (*Daley & Drage, 2016*; *Drage, 2019*). The posterior of the cranidium overlies the first three thoracic segments, especially on the left side ~~of the body~~ (Fig. 2). The malformation is ~~present~~ on the left part of exoskeleton, while the medial and right sections are ~~normal.~~ There are two wounds: one on the third to fourth thoracic segments, and one on the seventh thoracic segment. The left thoracic segments are shorter than those on the right side and show limited healing. The left pleural segments are only about half as long as the normal segments because of the first wound; the most seriously damaged part is the contact site of the two thoracic segments, where there is a V-shaped wound. The second wound caused the left pleural ~~part~~ of the seventh thoracic ~~segment~~ to be half as long as normal, with the wound presenting as an asymmetric V-shape. The lack of regeneration (e.g., swelling, elongation, or bending of the thoracic tergites) suggests that these malformations occurred during the most recent post- or inter-molt stage.

Discussion

Possible origin of the wounds and potential predatory structure

Trilobites that are malformed due to predatory attacks have ~~typical~~ V-, U-, or W-shaped wounds (*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 irregularly shaped wounds (*Fatka, Budil & Grigar, 2015*)~~, in addition to certain~~ signs of healing or regeneration (*Rudkins, 1979; Pates et al., 2017*). In the present specimen, the ~~two wounds with~~ traces of healing ~~were classified as the result of predator~~ attack. The two wounds have a similar degree of healing without any regeneration, suggesting that these injuries may have been incurred at the same time.

The most superior Cambrian predators are considered to have been the radiodonts, especially anomalocaridids and amplectobeluids, as their frontal appendages and oral cone were extremely effective predatory structures (*Whittington & Briggs, 1985*; *Babcock, 1993*; *Zamora et al., 2011*). These Cambrian predators preyed on mineralized and non-mineralized trilobites (*Nedin, 1999*). Cambrian arthropods or arthropod-like organisms with gnathobases are also considered possible predators, similar to the modern horseshoe crab (*Bicknell et al., 2018a*). Some amplectobeluid genera have been documented with gnathobase-like structures (*Cong et* al., 2017, 2018), suggesting that amplectobeluid 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; Zacaï, Vannier & Lerosey-Aubril, 2016; Bicknell et al., 2018a, b; Bicknell & Holland, 2020; Bicknell, Paterson & Hopkins, 2019).

Despite these predatory advantages, Cambrian animals with gnathobases did not cause the wounds in the *Shergoldia laevigata* specimen. Ganathobases 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). However, the *Shergoldia laevigata* specimen had two V-shaped wounds and was missing one or two separate thoracic segments, which rules out the gnathobases of predators as a cause of injury. These wounds were instead cause by predatory structure similar to the frontal appendages of radiodonts. It is likely that the exoskeleton of the trilobite was attacked by a radiodont with variously sized ventral spines of the frontal appendages, which produced the different types of injuries (Fig. 3A-B). Ventral spines of various sizes have been discovered on the frontal appendages of some radiodonts, such as *Anomalocaris* (Wang, Huang & Hu, 2013). The two wounds may have been caused by the larger ventral spines of the frontal appendages, while the smaller ventral spines may have not damaged the *Shergoldia laevigata*. While the arthropods *Aglaspella sanduensis* (Lerosey-Aubril, Ortega-Hernández & Zhu, 2013) and *Glypharthrus trispinicaudatus*, *Mollisonia*-like arthropods, unnamed aglaspidid-like arthropods, and *Perspicaris*-like bivalve arthropods (Zhu et al., 2016; Lerosey-Aubril, Zhu & Ortega-Hernández, 2017) were discovered in the Sandu Formation at the same site, none of these have sufficiently strong frontal appendages. Therefore, the tracking down the predator who attacked on studied *Shergoldia laevigata* specimen is still unsuccessful; it is not excluded that other, so far unknown arthropods or arthropod-like organisms with strong frontal appendages occurred in Sandu Formation.

Interference with the molting of trilobite

Pervious studies have reported abundant injured trilobites and presented the possible identity of the predators, including information about their behavior (*Babcock, 1993, 2007*; *Pates et al., 2017*; *Bicknell, Paterson & Hopkins, 2019*). However, there are few direct fossil records showing that injury has disturbed the molting of trilobites (*Šnajdr, 1985*). The trilobite specimen from Guangxi has an apparent overlap of tergites along with the wounds 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 third thoracic ~~segment~~ with part of the wound was covered by the second thoracic segment without breaking or being lost (Fig. 2A-D), indicating that the wound formed before the overlap of the tergites. 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. The recuperative terminal of the posterior area of the fixigena covered the second thoracic segment (Fig. 2E). In addition, 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. All abnormal arrangements of the segments appeared near the wound, and the overlapped part of the somites was only located before the most serious wound (on the third to fourth thoracic segments). Based on the above mentioned descriptions, it is speculated that all of the irregular patterns were caused by molting of *Shergoldia laevigata*. Namely, the new exoskeleton could not be smoothly separated from the old one due to the unbalanced body with wounds (*Drage, 2019*). The trilobite dragged forward the old shell to get rid of the exuvia, which led to the overlap of somites 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 the arthropod *Marrella* (*García-Bellido & Desmond, 2004*), 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 wounds complicated the molting process, which, however, was successful and the molted trilobite left 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 wounds incurred during a sub-lethal predator attack. The degree of healing in both wounds and the distribution of the wounds show that they were caused simultaneously by the same predatory structure. Based on the morphology of the wounds, the structure may have been the frontal appendage of larger arthropod or arthropod-like organism. The conspicuous overlapping of the somites and dislocated arrangement of the thoracic segments, especially in the left pleural region and near the wounds, shows that the injured *Shergoldia laevigata* encountered certain obstacles during the molting process. The trilobite dragged the old exuvia forward, which lead to the irregular arrangement of the somites. Such configuration can demonstrate that even provisionally healed injury can cause certain complication of the molting process in trilobites.

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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.

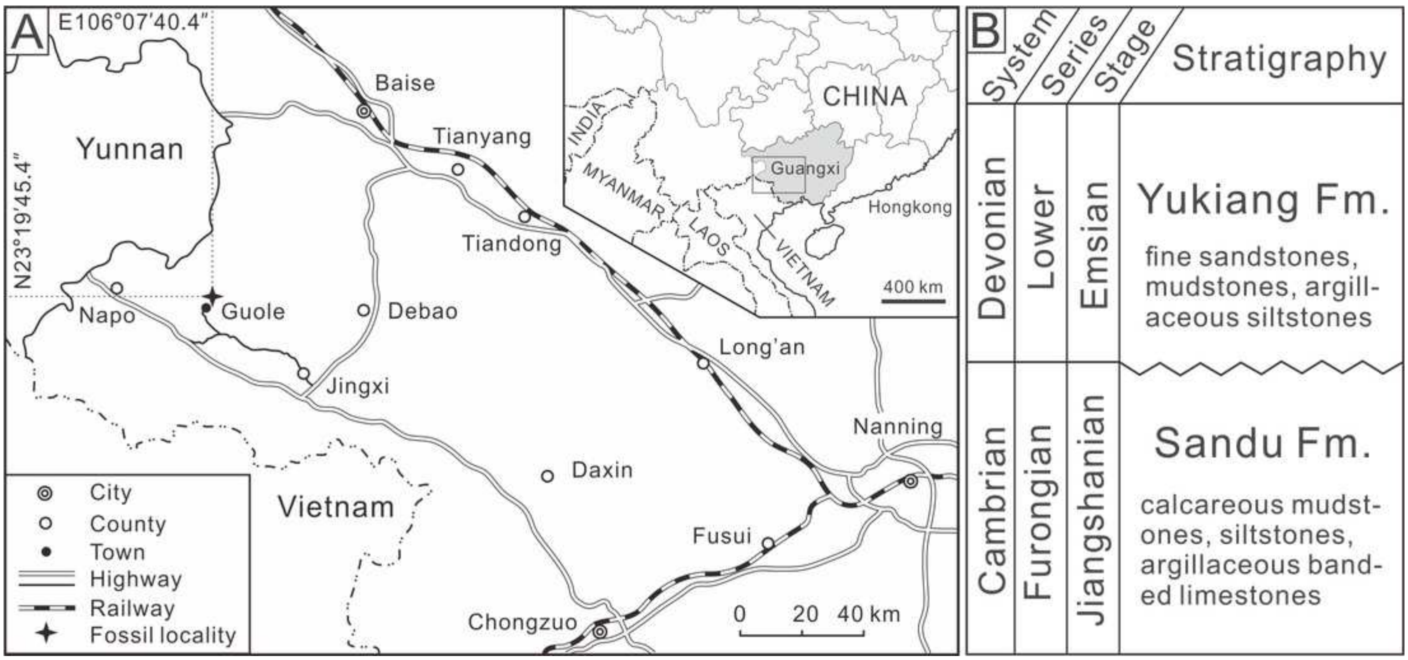


Figure 2

Malformed trilobite *Shergoldia laevigata* from the Cambrian Furongian of Jingxi, Guangxi (Specimen No. CUG-GJ-2015-01).

(A) The uncoated specimen; (B) close-up of abnormality in box in figure (A); (C) the specimen whitened by the magnesium powder; (D) a sketch of the figure (A); (E) the 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.

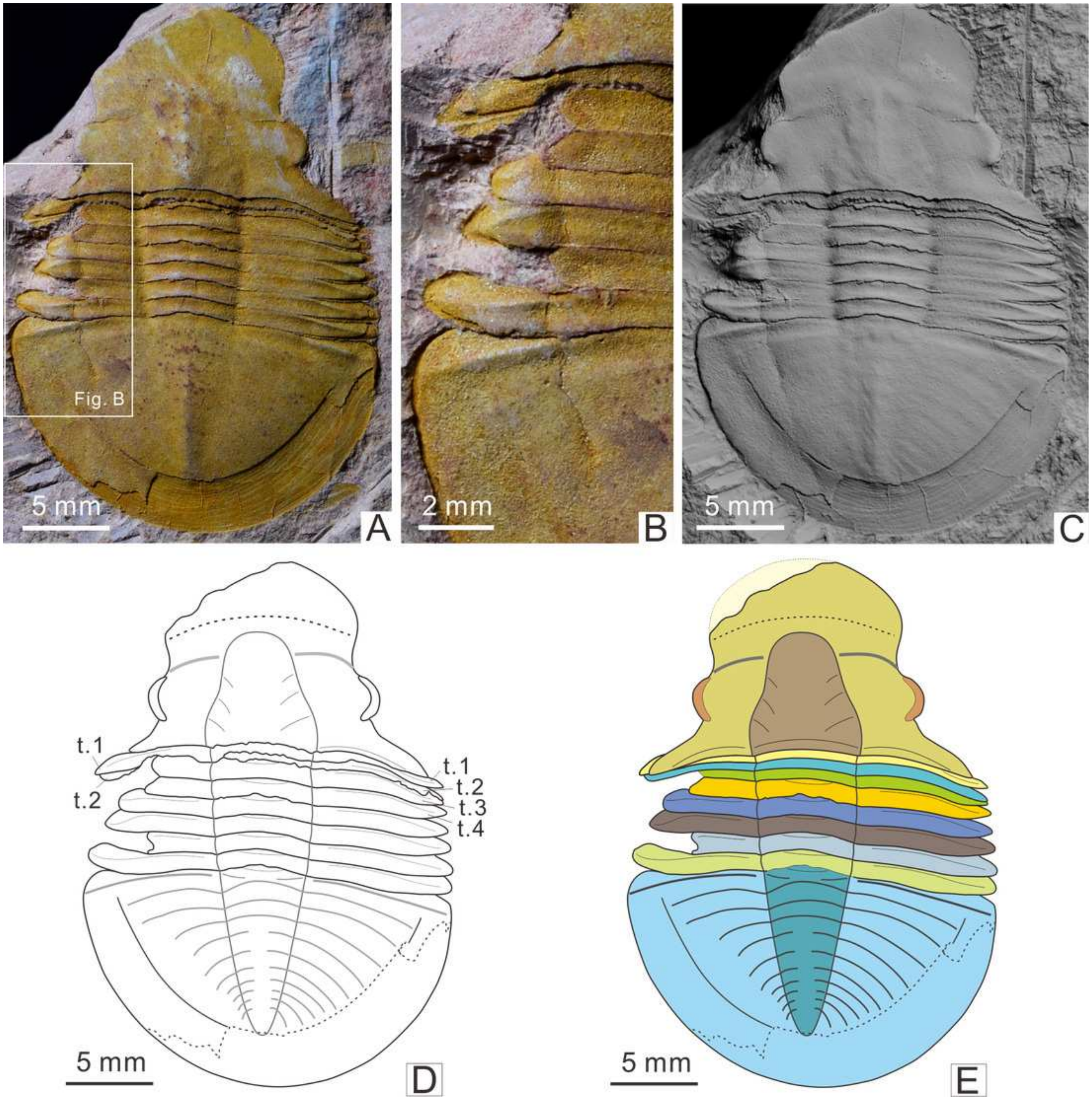
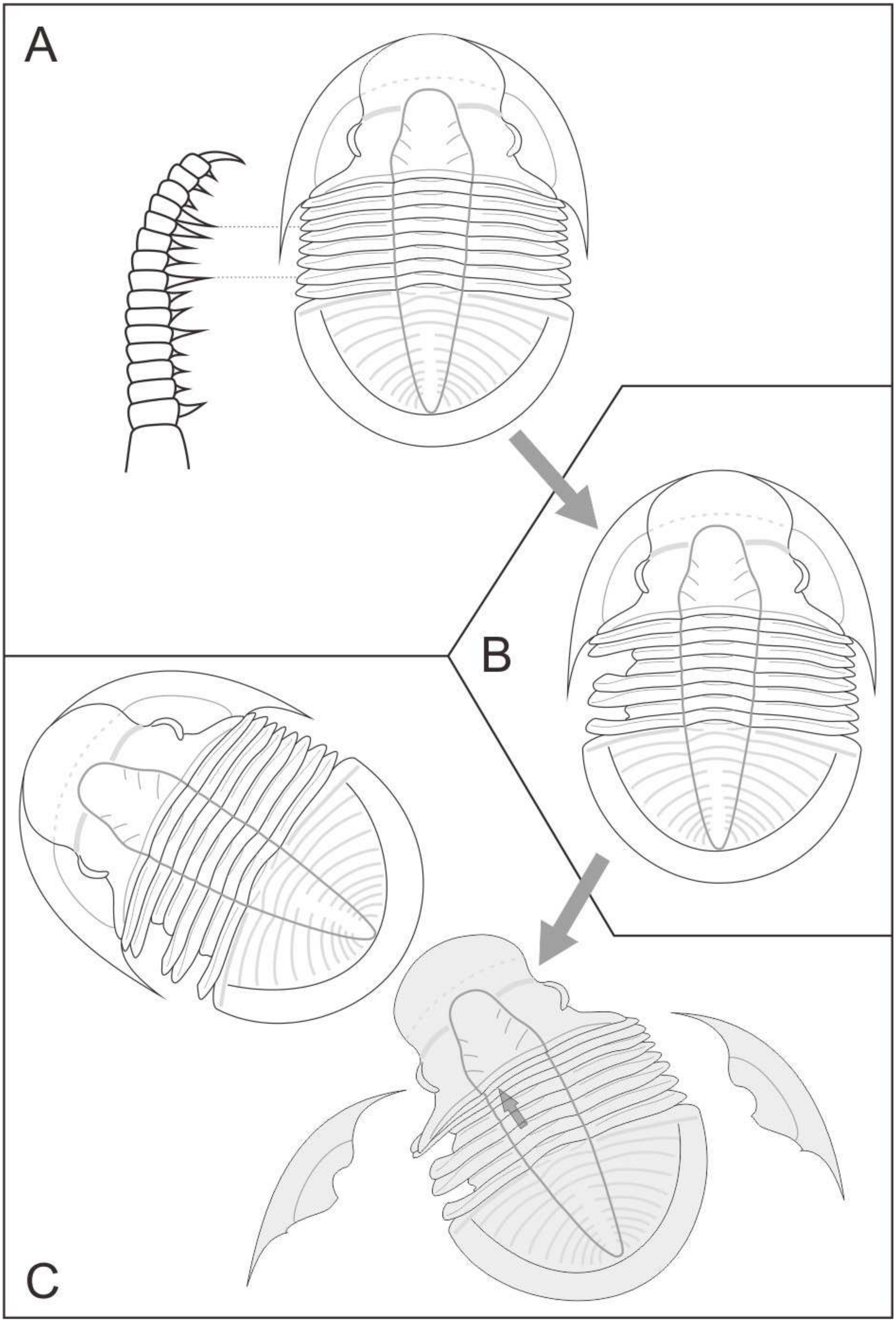


Fig. B
5 mm
A
2 mm
B
5 mm
C
t.1
t.2
t.1
t.2
t.3
t.4
5 mm
D
5 mm
E

Figure 3

Reconstruction of injured of studied *Shergoldia laevigata* specimen and possible predatory structure of unknown predator from the Cambrian Furongian of Jingxi, Guangxi.

(A–B) Predatory frontal appendage with variable-sized ventral spines attacking 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 somites and dislocated arrangement of thoracic segments.


A
B
C