A new bilaterally injured trilobite presents evidence for targeted predation in the Cambrian (#75063)

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A new bilaterally injured trilobite presents evidence for targeted predation in the Cambrian

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Durophagous predation in the Cambrian is typically recorded in malformed shells and trilobites, with rarer evidence in the form of coprolites and shelly gut contents. Reporting novel evidence for this life mode further expands the understanding of where and when in the Cambrian durophage was present. To expand such evidence and present new records of injured trilobites from the Cambrian of China, we present an injured *Redlichia* (*Pteroredlichia*) *chinensis* from the lower Cambrian Balang Formation, western Hunan, South China. The specimen has two distinct injuries along the thorax. The injuries show different degrees of regeneration, suggesting that the specimen was attacked twice. Given this situation, we propose that the individual may have been targeted more readily for the second attack. This predatory approach would have been highly energy efficient and maximizing the predators' net energy gain during attacking.

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Abstract

Durophagous predation in the Cambrian is typically recorded in malformed shells and trilobites, with rarer evidence in the form of coprolites and shelly gut contents. Reporting novel evidence for this life mode further expands the understanding of where and when in the Cambrian durophage was present. To expand such evidence and present new records of injured trilobites from the Cambrian of China, we present an injured *Redlichia* (*Pteroredlichia*) *chinensis* from the lower Cambrian Balang Formation, western Hunan, South China. The specimen has two distinct injuries along the thorax. The injuries show different degrees of regeneration, suggesting that the specimen was attacked twice. Given this situation, we propose that the individual may have been targeted more readily for the second attack. This predatory approach would have been highly energy efficient and maximizing the predators' net energy gain during attacking.

Keywords Predation, Regeneration, *Redlichia*, Cambrian, South China

Introduction

Biomineralized trilobite exoskeleton was constructed from two layers of low magnesium calcite (*Wilmot & Fallick, 1989; Hughes, 2007*). Due to this construction, trilobites had a markedly durable dorsal exoskeleton when composed to most other euarthropods (*Hughes, 2007*). Although this cuticular construction protected the soft-bodied sections, these exoskeletons were still susceptible to damage from shell crushing (durophagous) predators; as recorded in malformed and injured specimens (e.g., *Owen, 1985; Babcock, 1993; Pratt, 1998; Zamora et al., 2011; Pates et al., 2017; Bicknell & Paterson, 2018; Bicknell & Pates, 2020*). These injuries provide insight into Paleozoic predation strategies, predator-prey interactions, evolution of

trilobite morphology and behavior, and Paleozoic foodwebs (*Babcock & Robison, 1989; Babcock, 1993, 2003, 2007; Nedin, 1999; Brett & Walker, 2002; Brett, 2003; Bicknell & Paterson, 2018; Bicknell et al., 2022*).

The majority of trilobites with injuries that have been attributed to failed predation are known from the Cambrian and Ordovician (*Owen, 1985; Babcock, 1993; Bicknell & Paterson, 2018; Bicknell et al., 2021; 2022*). Within this fossil record, most injured specimens show unilaterally expressed injuries (*Babcock, 1993; Bicknell & Paterson, 2018* and their references), with rarer evidence of multiple injuries across the exoskeleton (e.g., *Conway Morris & Jenkins, 1985; Ou et al., 2009; Pates & Bicknell, 2019; Bicknell & Holland, 2020; Bicknell & Pates, 2020; Bicknell et al., 2021, 2022*). Determining whether specimens with multiple injuries reflect one, or multiple failed attacks is complex. However, the degree of exoskeletal regeneration can be a proxy for understanding the timing of attacks and subsequent recovery (e.g., *Cheng et al., 2019; Zong, 2021a*). To expand on this line of enquiry, we describe a malformed redlichiid trilobite from the Cambrian-aged Balang Formation (western Hunan, South China). This specimen, with a bilaterally expressed malformation, is used to explore patterns of trilobite regeneration and present new insight into early Cambrian predation strategies.

MATERIALS AND METHODS

The examined specimen was collected from the Balang Formation, Huayuan County, Xiangxi Autonomous Prefecture, Hunan Province (Fig. 1). The Balang Formation is widely distributed in eastern Guizhou and northwestern Hunan, comprised of fine calcareous clastic rocks with limited limestone interbeds or lens. This indicates that the formation was deposited in

a shelf to slope environment (Fig. 1) (*Yin, 1996; Liang et al., 2017*). The formation is located within the *Arthricocephalus chauveaui-Changaspis elongata* zone, which corresponds to the Cambrian *Series 2, Stage 4* (*Peng, 2009; Qin et al., 2010*). The Balang Formation has yielded a diverse, exceptionally preserved fauna including radiodonts, trilobitomorphs, bivalved arthropods, worms, chancelloriids, cnidarians, echinoderms, and algae (*Peng et al., 2005; Liu & Lei, 2013*). Trilobites from this formation consist of primarily oryctocephalids, redlichiids, and ptychopariids that are arrayed across ten genera (*Peng et al., 2018; Chen, 2019*). The Balang redlichiids consist of four species (including one subspecies) within a *Redlichia* subgenus (*Liang et al., 2017; Chen & Zhao, 2018*), and the dominate taxon is *Redlichia* (*Pteroredlichia*) *chinensis* (*Walcott, 1905*). The dark gray calcareous shale of the Balang Formation in western Hunan yielded a large number of well-preserved *R*. (*Pteroredlichia*) *chinensis*, and malformed individual has been detected in this species (*Zong, 2021b*). The abnormal specimen in this study also belong to *R*. (*Pteroredlichia*) *chinensis*. The specimen was coated with magnesium oxide for photography. All photographs were taken with a Nikon D5100 camera using a Micro-Nikkor 55 mm F3.5 lens. Specimen measurements were made with ImageJ software (*Schneider, Rasband & Eliceiri, 2012*). The specimen is housed in the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (Wuhan) (BGEG).

RESULTS

The described specimen (BGEG-HXB-02) is an articulated exoskeleton lacking free cheeks and is therefore likely an exuviae (*Daley & Drage, 2016; Drage, 2019*). Two malformations along the thorax are noted (Fig. 2A). The more anterior malformation is an asymmetrical V-

shaped indentation along the fourth and fifth pleural segments of the left pleural lobe that shows limited cicatrization along the edge (Fig. 2B). The distal section of the fourth pleural segment is lacking a pleural spine, truncated by ~1.8 mm. The pleural furrow of this segment is slightly S-shaped. The fifth thoracic segment is truncated by ~2.9 mm and reduced abaxially. Distal section of this segment is rounded and reduced by ~50% relative to the undamaged sixth pleural segment. The pleural furrow of this segment is also slightly distorted. The third segment on the left side has been rotated anteriorly to be positioned under the second pleural segment. However, this rotated segment lacks shortening or distortion (Fig. 2C) indicating that this was either a taphonomic alteration or the result of molting (*Zong, 2021a*).

The second malformation is a U-shaped indentation located across the seventh to ninth pleural segments on the right pleural lobe (Fig. 2D, E). The seventh and eight segments are truncated by ~1.8 mm and ~2.6 mm, respectively. The ninth segment is truncated by 2.5 mm, and the distal portion is narrower when compared to the same segment on the left plural lobe. All malformed segments have reduced pleural spines that are ~50% smaller when compared to undamaged segments, indicating pleural spine regeneration (*Pates et al., 2017*).

DISCUSSION

Several factors likely produced malformations in trilobites. These include failed predation or molting resulting in injuries, developmental malformations producing teratologies, and pathological infections (e.g., *Rudkin, 1985; Owen, 1985; Babcock, 1993, 2003; Owen & Tilsley, 1996; Chen, 2011; Fatka, Budil & Grigar, 2015; Bicknell & Pates, 2020; Bicknell & Smith, 2021; Zong, 2021b; De Baets et al., 2022*). Abnormal trilobite specimens with U-, V- or W-

93 shaped breakages, reduced segments, and evidence of cicatrization or regeneration are
94 considered indicative of non-lethal predation (*Babcock, 1993*; *Nedin, 1999*; *Zhu et al., 2007*;
95 *Bicknell & Paterson, 2018*; *Pates & Bicknell, 2019*; *Bicknell & Pates, 2020*; *Zong, 2021b*;
96 *Bicknell et al., 2022*). Two indentations documented here are V- and U-shaped with cicatrization
97 on the left injury and pleural spine regeneration on the right injury. Given this, we confidently
98 assign these indentations to failed predation within the Balang Formation. More importantly,
99 these injuries show distinctly different stages of recovery (Fig. 2).

100 The process of recovering from injuries in trilobites likely had an anteroposterior polarity.
101 This has been documented in more anterior segments showing markedly more recovery than
102 more posterior sections (e.g., *Šnajdr, 1981*; *Conway Morris & Jenkyns, 1985*; *Babcock, 1993*;
103 *McNamara & Tuura 2011*). This pattern is common to modern arthropods and annelids and is
104 controlled by segmentation polarity genes (*McNamara & Tuura, 2011*). In BGEG-HXB-02, the
105 anterior injury shows cicatrization, but no evidence for segment regeneration. This presents an
106 apparent conundrum. If we assume the injuries were incurred at the same time, we directly
107 contradict fundamental theories on arthropod development (*McNamara & Tuura, 2011*). The
108 most parsimonious explanation for the observed pattern is that the posterior injury was incurred
109 first. This injury was able to regenerate before the more anterior injury was incurred.

110 The presence of two injuries from two distinct attacks demonstrates that Cambrian trilobites
111 could have experienced multiple attacks during their life cycle. This has important implications
112 for Cambrian predator-prey systems, especially with comparison to modern systems. Extant
113 predators will target weaker prey within a population as these individuals require less energy in

predation and likely represent a more successful attack (*Temple, 1987; Mesa et al., 1994; Hethcote et al., 2004; Genovart et al., 2010*). It seems that predation targeting more vulnerable individuals had therefore arisen in the Cambrian and may have allowed the first durophages to maximizing net energy gain during predation. Finally, the rarity of trilobite specimens with multiple distinct injuries likely reflects an increased rate of successful predation, and a higher rate of mortality in previously injured individuals.

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Figure 1

Geological background map of study area and location of the fossil site.

(A) Cambrian sedimentary facies zones of South China (modified from Zhao et al., 1993). (B) Map of fossil site at Huayuan County, Xiangxi Autonomous Prefecture, Hunan Province. (C) Stratigraphic series showing relative position and age of the Balang Formation (modified from Zhu et al., 2021).

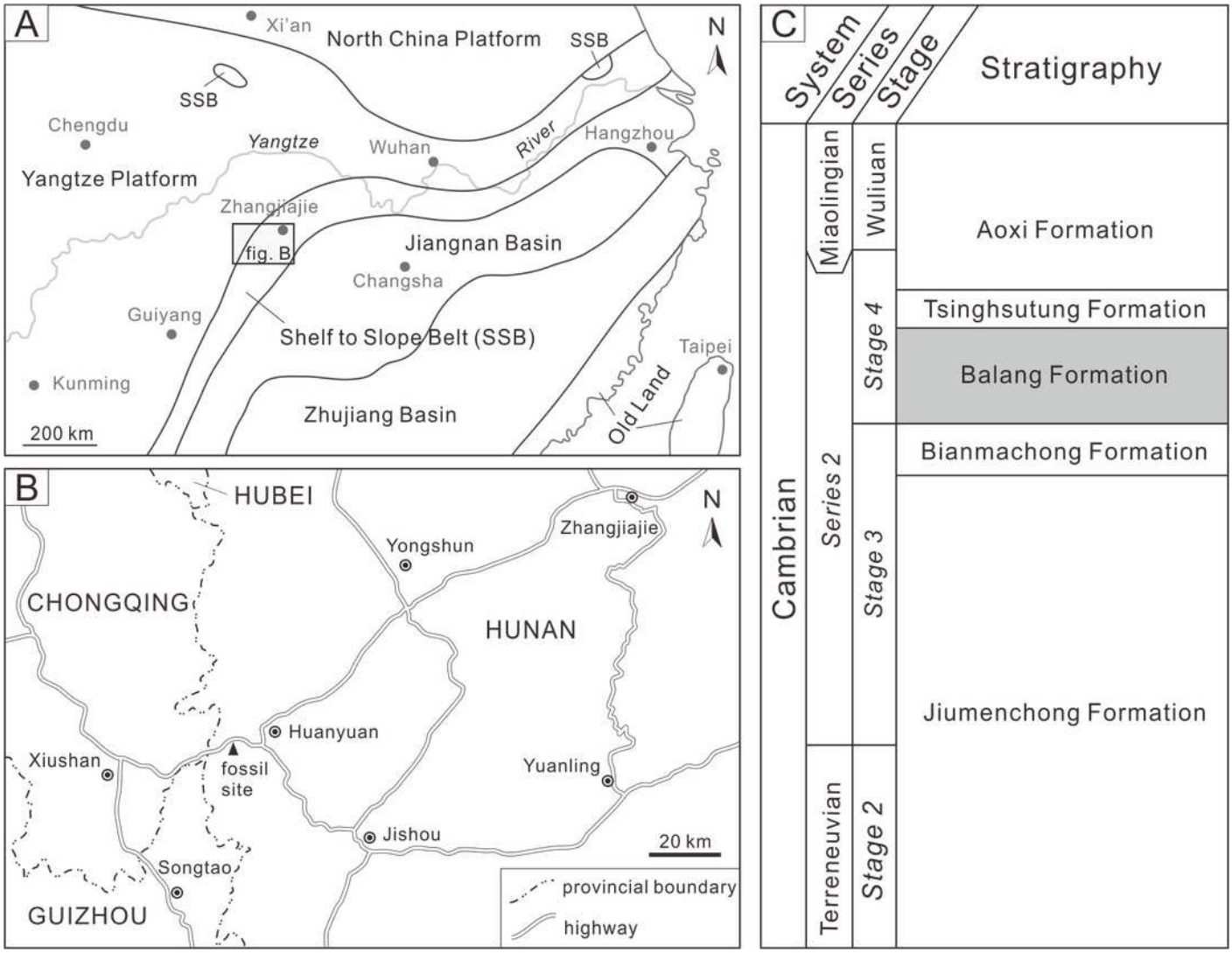
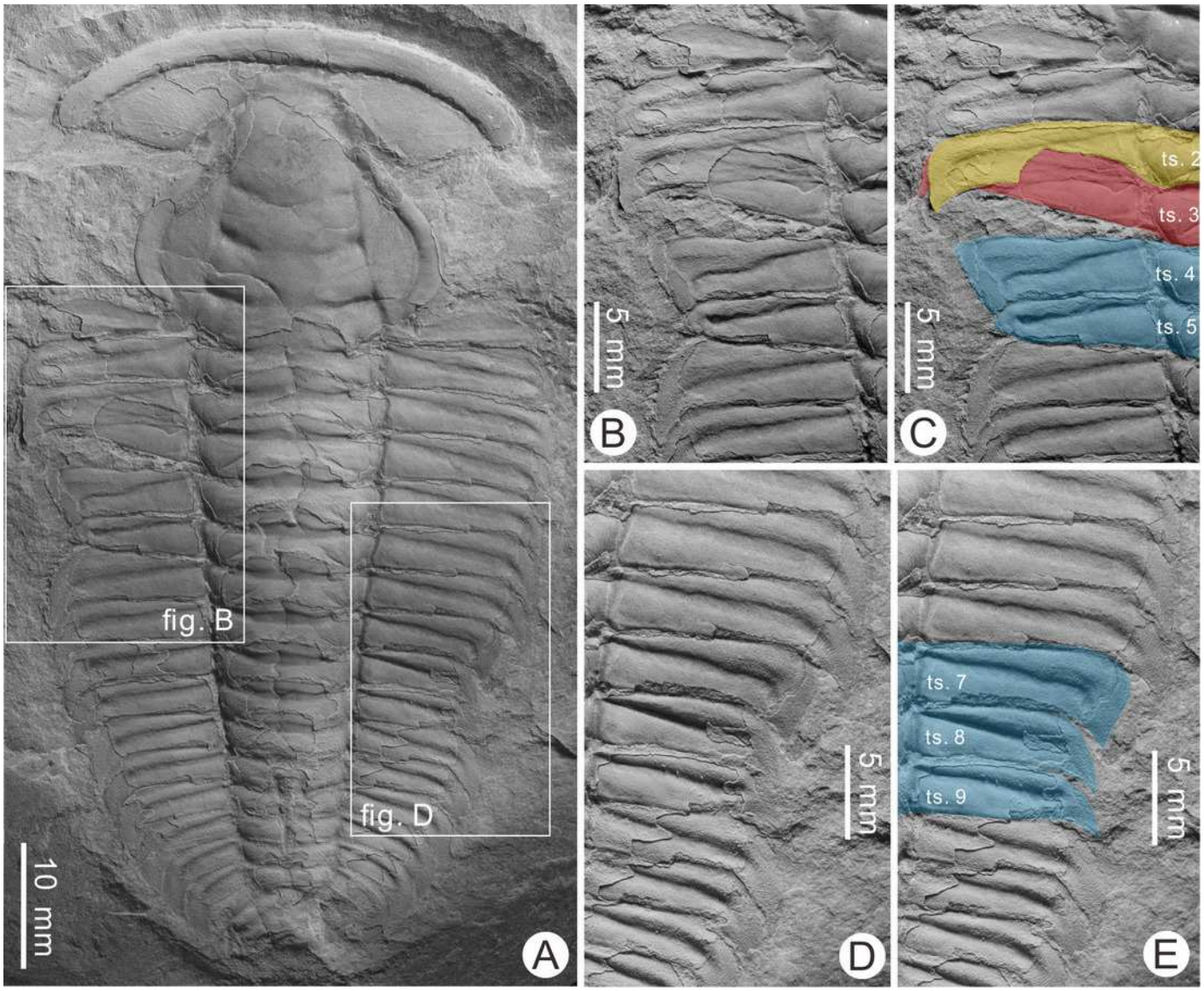


Figure 2

Injured *Redlichia* (*Pteroredlichia*) *chinensis* (Walcott, 1905) from the Balang Formation (Cambrian *Series 2*, *Stage 4*), Hunan, South China.

(A) Complete specimen (BGEG-HXB-02) showing two injuries. (B, C) Close-up of the injury on the left pleural lobe. (B) V-shaped indentation. (C) Same as B showing overlap of the second (yellow) and third (red) pleural segments and injury (blue). (D, E) Close-up of injury on right pleural lobe. (D) U-shaped indentation. (E) Same as D showing injury (blue). Abbreviation: ts.: thoracic segment.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