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First confident evidence of moulting in eodiscid trilobites from the Cambrian Stage 3 of South China

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Abstract

Trilobite moulting behaviour has been extensively investigated. However, exuviae in eodiscid trilobites are poorly known. Here, we report two eodiscid trilobite specimens, *Tsunyidiscus niutitangensis* and *Tsunyidiscus* sp., showing Somersault configuration from the Niutitang Formation and Mingxinsi Formation of South China, respectively (Cambrian Series 2, Stage 3). The arrangements of the exoskeletons indicate that the two specimens are the slightly disturbed and undisturbed exuviae. The impression of the lower cephalic unit (LCU) displays the rostral plate in *Tsunyidiscus niutitangensis*. The exuviae showing the LCU inverted anteriorly under the trunk. The opening of the facial and rostral sutures would have allowed the emergence of the post-ecdysial trilobite with the partial enrolment of exoskeleton. Moreover, our discovery indicates a Somersault configuration which employed the facial and rostral sutures to create an anterior exuvial gape that also exists in eodiscid trilobites besides redlichiid trilobites, corynexochid trilobites and ptychopariid trilobites during the Cambrian.

1. Introduction

Ecdysis refers to the process by which the exoskeleton is shed during growth in the clade Ecdysozoa which includes arthropods, nematodes and several other phyla (Henningsmoen, 1975; Telford *et al.* 2008; Daley & Drage, 2016). Exploring the moulting process from the fossil record is important, since the developmental strategy of Ecdysozoa might have imparted constraints on morphology throughout their evolution, up to modern animal groups (Daley & Drage, 2016). Apart from this, more biological information on growth and development in deep time can be assessed, which can help resolve the affinity of enigmatic taxa early in the evolution of animals (Daley & Drage, 2016). Additionally, some specimens preserved midway through moulting can provide insight for understanding ecology as one of the only examples of direct evidence of behaviour preserved in the fossil record (García-Bellido & Collins, 2004; Daley & Drage, 2016; Yang *et al.* 2019). Trilobites represent one of the main arthropod groups through the Palaeozoic. However, despite the fact that the trilobite moulting behaviour has been intensively studied in most of the trilobite orders (e.g. Henningsmoen, 1975; McNamara & Rudkin, 1984; Speyer, 1985; Whittington, 1990; Brandt, 2002; Daley & Drage, 2016; Drage *et al.* 2018; Drage, 2019; Wang *et al.* 2020, 2021), a lack of confidence about whether we are looking at real moults or disarticulated carcasses is present in some of them. One possible reason is that many of these works focused on disarticulated and isolated specimens (i.e. Museum collections) without a sedimentological and taphonomical context (see Corrales-García *et al.* 2020). The associated behaviour dealing with moults such as cryptic or synchronized moulting also has been explored and discussed (Rustán *et al.* 2011; Zong *et al.* 2016; Zong & Gong, 2017; Corrales-García *et al.* 2020; Zong, 2021; Zong & Gong, 2022). However, so far, only one record of moulting in eodiscid trilobites has been reported from the Kaili biota (Lin & Yuan, 2009).

Herein, we report two eodiscid trilobite exuviae belonging to the genus *Tsunyidiscus* (Zhang, 1966) from the early Cambrian of South China. These new finds shed new light first on the ecdysial sutures and second about the exuviating procedure of eodiscid trilobites.

2. Materials and methods

Two typically proparian eodiscid trilobites belong to the genus *Tsunyidiscus* (Zhang, 1966) and the holaspid specimens of this genus bear three thoracic tergites. The pygidium is similar in size to the cephalon (i.e. isopygous). The specimens were collected from the Cambrian Stage 3 Niutitang Formation and Mingxinsi Formation in north-central and central Guizhou Province, respectively, South China (Fig. 1), and are housed in the Guizhou Research Centre for

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Palaeontology, Guizhou University, China (KSNT-78-1958A, GZU-2022-1). The photograph of the first specimen (KSNT-78-1958A) was taken using a Canon 5D maker IV camera fitted with a Canon MP-E65mm f/2.8 1-5x. This specimen was not covered with ammonium chloride because the small size prevent to see the morphology once it is covered. The second specimen (GZU-2022-1) that comes from the Mingxinsi Formation has been coated with ammonium chloride sublimate. Pictures were taken using a Nikon D7100 fitted with a Nikon AF Micro-Nikkor 60 mm lens. Images were processed using CorelDRAW 2017 (a free trial version) to adjust tone, contrast, and brightness. Line drawings and measurements were based on high-resolution photographs in CorelDRAW 2017 (a free trial version).

The morphological terminology applied to the description of the studied material is a combination of those in Henningsmoen (1975), Whittington (1990), Whittington and Kelly (1997), Drage *et al.* (2018), some of them with brief statements below.

Exoskeleton unit:

Axial shield. The cranidium, thorax and pygidium are joined as a single unit (Henningsmoen, 1975; Drage *et al.* 2018).

Lower cephalic unit (LCU) is the cephalic integument with exception of cranidium and the joined LCU comprising the librigenae (doublure), rostral plate (if present) and hypostome, but sometime lacking the hypostome in some specimens (Henningsmoen, 1975; Drage *et al.* 2018).

Moult configuration:

Somersault configuration in *Tsuniyidiscus* is the specimen showing LCU disarticulated from the cranidium and anteriorly inverted lying beneath the trunk (Whittington, 1990; Drage *et al.* 2018).

3. Results

Tsuniyidiscus niutitangensis (Chang, 1964) (= *Hebediscus niutitangensis* Zhang, 1964) (KSNT-78-1958A).

KSNT-78-1958A is a partly disarticulated (but complete) meraspid specimen (meraspid degree 2), the cranidium shows one genal spine with two thoracic tergites (Fig. 2a, b). The lateral margin of right side of the cranidium is not well preserved. Although the left inverted librigena lies beneath the trunk, the impression of the left inverted librigena and ventral exoskeleton can be observed in the specimen. The specimen displays the inverted LCU (librigenae and ventral cephalic structures) lying beneath the trunk with minor anticlockwise rotation.

Tsuniyidiscus sp. (GZU-2022-1).

GZU-2022-1 is a partly disarticulated (but complete) holaspid specimen with three thoracic tergites (Fig. 2c, d). The specimen is stereoscopic. The cranidium, the thorax and the pygidium join together tightly. The LCU (librigenae and possible ventral cephalic structures) inverted anteriorly lying beneath the trunk in this specimen. Both sides of the thoracic tergites in the specimen is broken allowing to see the inverted librigenae. Two librigenae are inverted simultaneously and symmetrically. The position and arrangement of inverted librigenae indicate that there is connection between two librigenae, and this structure was hidden beneath the dorsal exoskeleton.

4. Discussion

Corrales-García *et al.* (2020) described several clusters with hundreds of individuals and interpreted them as synchronized moulting behaviour showing all the moulting configurations and

behaviours described by Daley and Drage (2016), Drage *et al.* (2018) and Drage (2019). However, Corrales-García *et al.* (2020) suggested that such high diversity of moulting configuration may be not related to behaviour. Wang *et al.* (2020) considered two configurations in particular to be confidently related to behaviour in moults of *Arthricocephalites xinzhaiheensis*, one of these being the Somersault configuration. This supports the moult assignment of the two specimens described here in the Somersault configuration. Given the degree of articulation in both specimens and the position of the LCU, we argue that they represent slightly or almost undisturbed exuviae. Physical disturbance may or may not lead to random and irregular configurations and fragments, but the specimens in Somersault configuration which meet the criteria for identifying moults (Henningsmoen 1975; Whittington 1990; Daley & Drage 2016; Drage *et al.* 2018; Wang *et al.* 2020) can hardly have been produced by chance. Thus, we can state that these represent confident moult configuration with enough biological information.

Moulting behaviour has been described and argued in most of the trilobite groups, but moulting in eodiscids is poorly known. Only a single cluster containing 22 pagetiid individuals from the Kaili biota was identified as exuviae (Lin & Yuan, 2009). All specimens in their study with missing librigenae were interpreted as intact exuviae that had undergone minimal transport prior to burial by Lin & Yuan (2009). But the evidence of the identified exuviae is too weak in their study. This monospecific cluster shows clear evidences of current orientation, and the dorsal-ventral attitude was lost which makes it difficult to argue against the currents and establish proper biostratigraphic insights (Speyer & Brett, 1986; Hickerson, 1997; Corrales-García *et al.* 2020). In fact, all specimens show axial shield in their study, and this configuration can originate from complete exuviae or disarticulated carcasses. Thus, it is difficult to distinguish the real exuviae from them. The physical disturbance also led to the loss of moulting information that preserved in slightly disturbed and undisturbed exuviae (Wang *et al.* 2020), even if these specimens were real exuviae.

Until now most of the studies regard the eodiscid hypostome as natant in holaspid (Öpik, 1952; Whittington, 1988; Fortey, 1990) and only doublure and hypostome exist in the ventral cephalic side. The doublure is a continuation of the dorsal exoskeleton on the ventral side and natant hypostome lies freely below the cephalon. Zhang and Clarkson (2012) studied abundant phosphatized material of eodiscoid trilobites from the lower and middle Cambrian of China. These authors showed an early meraspid (meraspid degree 0) cephalon of *Shizhudiscus longquanensis* with fine ridge-bearing doublure underneath the lateral border (see Zhang & Clarkson, 2012; Plate 9, Figure 2, 3). Zhang & Clarkson (op. cit) considered that this structure may become the librigena during subsequent development. Another specimen, a holaspid cephalon of *Tsuniyidiscus yanjiazhaiensis* (see Zhang & Clarkson, 2012; Plate 1, Figure 12), displays the connection of the anterior and genal doublure via the attached librigenae. Apart from these, all librigenae are independent (see Zhang & Clarkson, 2012; Plate 1, Figures 14–16; Plate 9, Figures 6–8; Plate 10, Figures 16, 17; Plate 13, Figures 1, 2; Plate 16, Figures 4–7). These phosphatized specimens indicate that the librigenae are independent in eodiscoid trilobites and the doublure of the librigenae cannot connect one each other. Thus, there is almost no definite suture in the ventral side of eodiscid trilobites. However, the different finding appears in our specimens. The impression of the left inverted librigena and ventral exoskeleton can be observed in *Tsuniyidiscus niutitangensis*

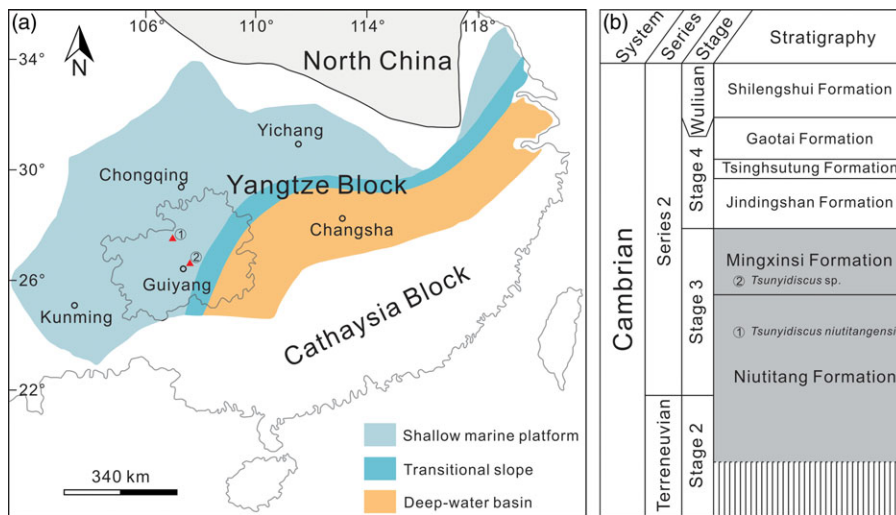


Figure 1. (Colour online) Geological background map of study area and location of the fossil site. (a) The simplified early Cambrian geological map of Yangtze Block and location of the study specimens. (b) Stratigraphic series showing relative position and age of the Niutitang Formation and Mingxinsi Formation. Map modified from Yang and Zhang (2016) and Zhu et al. (2021).

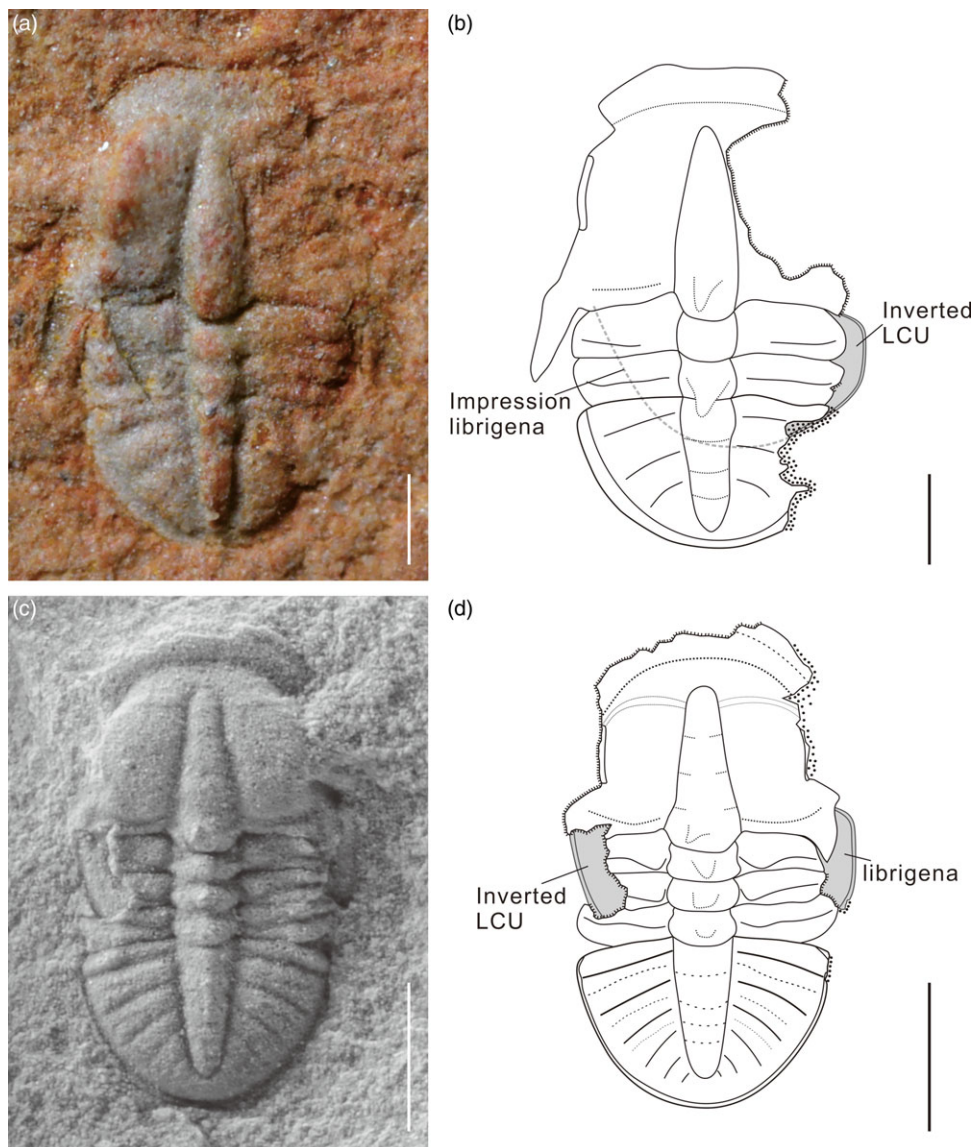


Figure 2. (Colour online) Somersault configuration in *Tsuniyidiscus niutitangensis* and *Tsuniyidiscus* sp. from the Cambrian Stage 3 Niutitang Formation and Mingxinsi Formation respectively, Guizhou Province, South China. (a) Specimen (KSNT-78-1958A) of *Tsuniyidiscus niutitangensis* showing Somersault configuration. (b) Line drawing of the specimen (KSNT-78-1958A). (c) Specimen (GZU-2022-1) of *Tsuniyidiscus* sp. showing Somersault configuration. (d) Line drawing of the specimen (GZU-2022-1). Scale bars: 0.2 mm (a, b); 1 mm (c, d). Additional abbreviations: LCU, the cephalic integument with exception of cranium. Grey areas indicate the inverted exoskeletal unit.

(KSNT-78-1958A). The *Tsunyidiscus* sp. (GZU-2022-1) displays that both librigenae are inverted simultaneously and symmetrically. The impression and arrangement of inverted librigenae in these specimens indicates: the ventral structure connecting two librigenae and specific ventral suture exist in *Tsunyidiscus*. Cederström et al. (2009, p. 522, pl. 7) figured and described the hypostome of *Calodiscus lobatus* which changes from a conterminant attachment in late meraspid instars of degree 1, to a natant condition within meraspid instars of degree 2. They considered that the anterior border of hypostome was attached to the doublure of the frontal border, but this structure resembles the rostral plate. Although Cederström et al. (2009) found the important information of hypostomal condition in eodiscid trilobites, the relationship between facial sutures and possible ventral suture is still not clear. Zhang and Clarkson (1993) speculated that the additional rostral plate which is possibly uncalcified may exist in eodiscid trilobites because of the narrow doublure in *Pagetia*. If the rostral plate exists in ventral cephalic structures of eodiscid trilobite *Tsunyidiscus*, the impression and arrangement of ventral cephalic structure are easy to explain in our specimens. So, here, we argue that the rostral plate could exist in our specimens.

Although we cannot make an accurate reconstruction of the ventral cephalic structures in eodiscid trilobites, we can state that *Tsunyidiscus niutitangensis* and *Tsunyidiscus* sp., present Somersault configurations, providing confident evidence of moulting processes in the early Cambrian. As many researchers described (McNamara & Rudkin, 1984; Whittington, 1990; Drage et al. 2018; Wang et al. 2020), this process involved the partial flexure or full enrolment of the exoskeleton. Eodiscids could enrol and several examples have been reported (e.g. Jell, 1975; Zhang & Clarkson, 1993; Cederström et al. 2009; Dai et al. 2019). The opening of facial suture and rostral suture would have allowed the emergence forward of the post-ecdysial trilobite. Subsequently, the dragging forward of the exuviae in this withdrawal led to the overturned LCU lying beneath the trunk. These eodiscid exuviae preserving an anteriorly inverted LCU lying beneath the trunk displays the Somersault configuration. Somersault configuration also exists in the Cambrian corynexochid trilobite *Ogygopsis klotzi* (McNamara & Rudkin, 1984, Figure 9; Whittington, 1990, Figures 9–12), *Arthricocephalites xinzhaiheensis* (Wang et al. 2020, Figures 5A, B; Wang et al. 2021, Figures 3A–L), the redlichiid trilobite *Paradoxides davidis* (McNamara & Rudkin, 1984, Figure 12; Whittington, 1990, Figures 7–8), *Bathynotus kueichouensis* (Yang et al. 2021, Figure 8d), the ellipsocephaloid trilobite *Estaingia bilobata* (Drage et al. 2018, Figure 3D), and the ptychopariid trilobite *Nangaops danzhaiensis* (Xu et al. 2020, Figure 2F), *Xingrenaspis xingrenensis* (Chen et al. 2021, Figure 3N) and *Eosoptychoparia guizhouensis* (Chen et al. 2022, Figures 3A–C).

5. Conclusion

Two eodiscids, *Tsunyidiscus niutitangensis* and *Tsunyidiscus* sp., from the Cambrian Stage 3 Niutitang Formation and Mingxinsi Formation respectively, from South China show the horizontally inverted LCU such that it faces the posterior lying beneath the trunk and are slightly disturbed and undisturbed exuviae. The impression of LCU indicates the rostral plate exists in the ventral cephalic structures of *Tsunyidiscus niutitangensis*. The arrangement of exoskeleton, Somersault configuration, in both exuviae suggests that facial and rostral sutures are ecdysial sutures of eodiscid trilobite *Tsunyidiscus* and the exuviating individuals need

to apply flexion (i.e. partial enrolment) of the exoskeleton which lead to the overturned LCU lying beneath the trunk. This work has important implications in our understanding of trilobite evolution and their phylogenetic relationships since we show clear evidence that the same moulting strategy was employed by different trilobite orders.

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Competing interests. The authors report there are no competing interests to declare.

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