Moulting behaviour in the trilobite *Oryctocephalus indicus* from the Cambrian Miaolingian Series (Wuliuan Stage) of Jianhe, South China (#85684)

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Moulting behaviour in the trilobite *Oryctocephalus indicus* from the Cambrian Miaolingian Series (Wuliuan Stage) of Jianhe, South China

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The accurate interpretation of trilobite moulting behaviour relies on a comprehensive understanding of their moult configurations, yet the focus has commonly been limited to a brief description of the exuviae, and how differences in moulting behaviour further impact the preservation of exuviae is often ignored. This study investigates the configuration, style, and process of moulting in *Oryctocephalus indicus* through analysis of 88 exuviae collected from the Kaili Formation (Cambrian Miaolingian Series and Wuliuan Stage) in Guizhou Province, South China. The moult configurations of *O. indicus* are typically characterised by the lower cephalic unit (LCU), which comprises the librigenae and rostral-hypostomal plate connected as a whole, detached from the cephalon and positioned anterior to the thoracopygon, while the cranidium is mostly absent. Through detailed observations and descriptions of the available material, we believe that *O. indicus* completes moulting by the exuvial gape. Although many exuviae exhibited an opening at the cephalothoracic joint — disjunction of this joint commonly accompanied by fractures in both the facial and rostral sutures — the Salter's configuration produced by the 'Salterian' mode of moulting has not been observed. Additionally, the structural characteristics of Henningsmoen's configuration, Harrington's configuration, and Somersault's configuration are discussed based on the exuviae of *O. indicus*. Henningsmoen's configuration has been categorized into three types according to the different states of fossil preservation. In this paper, apart from promoting further research on moulting behaviour in *O. indicus*, we also provide a supplement for moult configuration based on the exuviae, which offers new materials for studying moulting behaviour in oryctocephalid trilobites.

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Abstract

The accurate interpretation of trilobite moulting behaviour relies on a comprehensive understanding of their moult configurations, yet the focus has commonly been limited to a brief description of the exuviae, and how differences in moulting behaviour further impact the preservation of exuviae is often ignored. This study investigates the configuration, style, and process of moulting in *Oryctocephalus indicus* through analysis of 88 exuviae collected from the Kaili Formation (Cambrian Miaolingian Series and Wuliuan Stage) in Guizhou Province, South China. The moult configurations of *O. indicus* are typically characterised by the lower cephalic unit (LCU), which comprises the librigenae and rostral-hypostomal plate connected as a whole, detached from the cephalon and positioned anterior to the thoracopygon, while the cranidium is mostly absent. Through detailed observations and descriptions of the available material, we believe that *O. indicus* completes moulting by the exuvial gape. Although many exuviae exhibited an opening at the cephalothoracic joint — disjunction of this joint commonly accompanied by fractures in both the facial and rostral sutures — the Salter's configuration produced by the 'Salterian' mode of moulting has not been observed. Additionally, the structural characteristics of Henningsmoen's configuration, Harrington's configuration, and Somersault's configuration are discussed based on the exuviae of *O. indicus*. Henningsmoen's configuration

has been categorized into three types according to the different states of fossil preservation. In this paper, apart from promoting further research on moulting behaviour in *O. indicus*, we also provide a supplement for moult configuration based on the exuviae, which offers new materials for studying moulting behaviour in oryctocephalid trilobites.

Introduction

In a similar way to modern arthropods, trilobites shed their exoskeletons periodically as part of their growth process (Miller & Clarkson, 1980). Comprehending the moulting behaviour and processes of trilobites is imperative, as they played a pivotal role in ancient marine ecosystems with intricate evolutionary histories shaped by their ecdyse capability (Daley & Drage, 2016). Moulting is believed to have been an opportunistic behaviour for trilobites, which employ various strategies for moulting (Brandt, 2002). The diversity and prevailing types of moult configurations seem to be a function of the overall body morphology rather than the actual phylogenetical relations of the species (Budil & Bruthansová, 2005). The moulting behaviour, movements during exuviation, and moult configurations exhibit significant variability across all Trilobita (Drage, 2019), each study on trilobite moulting feeds into a more significant aggregation of occurrences and behavioural descriptions, which can be analysed to interpret evolutionary trends for the group (Drage & Daley, 2016).

Oryctocephalus indicus Reed (1910) is a small, cosmopolitan oryctocephalid trilobite with a wide distribution range across South China, India, western North America, and Siberia (Zhao *et al*., 2019). The first appearance of this species defines a conterminous base of the global Cambrian Miaolingian Series and Wuliuan Stage (Zhao *et al*., 2019), and it is necessary to deepen our understanding of the Cambrian trilobite taxa through a detailed study of their moulting behaviour. As one of the exceptionally preserved Konservat Lagerstätte worldwide, the Kaili Biota (Wuliuan Stage) in Guizhou Province has yielded numerous trilobite fossils and exuviae, providing excellent materials for studying the moulting behaviour of trilobites (Chen *et al*., 2021, 2022). The previous research on trilobite moulting has mainly primarily focused on specimen descriptions, with only a few publications discussing the moulting process (*e.g*., McNamara & Rudkin, 1984; Speyer, 1985; McNamara, 1986; Whittington, 1990; Rustán *et al*., 2011). Chen, Han & Zhao (2008) provided some explanations for the moulting behaviour of *O. indicus*, but only focusing on a description of moult configurations, and new materials are needed to further explore the moulting style and process. A comprehensive account was provided regarding the moult configurations and style of 88 newly discovered exuviae specimens from *O. indicus*, which elucidated the moulting process and complemented the investigation on the moulting behaviour of *O. indicus*.

Materials & Methods

The *Oryctocephalus indicus* specimens selected for this study were obtained from Kaili Formation of the Miaobanpo section in Jianhe County, Guizhou Province (Fig. 1), which is located at 26°45.014'N latitude and 108°24.982'E longitude. All specimens have been deposited at the Guizhou Research Centre for Palaeontology, Guizhou University.

In arthropods, exoskeletons can become disarticulation due to decay or physical processes, and the intra-specific variability of moult configurations can only be preserved under exceptional in-situ preservation conditions (Drage *et al*., 2018). The Kaili Formation in the study area is primarily composed of silty mudstone, calcareous mudstone, and a set of terrigenous clastic rocks dominated by shale, with horizontal lamina developed and few ripple marks and disturbed structures (Zhou *et al*., 1979; Yin, 1987). Previous research has indicated that the Kaili Formation in Jianhe, Guizhou Province, was deposited within a tropical slope transition sedimentary environment between the Yangtze platform (carbonate deposition) and Jiangnan Basin (fine-grained deposition) (Peng & Babcock, 2001). Based on the analysis of calcareous claystone lithofacies and carbonate mudstone lithofacies, it is believed that the Kaili Formation was deposited under low-energy conditions below the base surface of a storm wave, and it is the gravity-driven suspension of fine-grained sediment that was established by storm wave disturbance of substrates lying in shallower waters upslope (Gaines *et al*., 2011). In addition, the study of buried facies and the characteristics of biological preservation furthermore indicated that the Kaili Formation had weak hydrodynamic force during deposition, and the redox interface was close to the seafloor but still within the sediments, resulting in the activity of infauna absent or poorly developed (Zhang *et al*., 1996). At the same time, the fine clay deposits protected the intact preservation of organisms enclosed in the mud, and the early diagenetic mineral (pyrite) plays a crucial role in preventing the soft body from rotting and replicating the soft tissue (Zhu, Erdtmann & Zhao, 1999). In summary, the Kaili Formation was deposited in a low-energy environment within the slope transition zone. The weak biological disturbances and favorable diagenetic conditions provided an excellent setting for preserving trilobite exuviae.

Methods

The specimen photos presented in this paper were captured by employing a Canon 5D Mark Ⅳ camera and VHX100K microscope. The orientation of specimens during photography and measurements is primarily with the cranidium, librigenae, or pygidium horizontal.

Not all disarticulated trilobite specimens are the result of moulting behaviour, and non-exuviation factors such as transportation, biological disturbance, and decomposition during burial may also contribute to exoskeleton disarticulation. In the present work, the exuviae identification criteria adhere to those established by Henningsmoen (1975), Whittington (1990), and Daley & Drage (2016), which primarily encompass: 1) The preservation of exuviae should consider the impact of sedimentary environments; 2) Evidence shows suture opening; and 3) Moult configurations exhibit a systematic, repetitive, and characteristic arrangement of structural units. According to the identification criteria, exuviae of *Oryctocephalus indicus* were selected and classified into Henningsmoen's configuration, Harrington's configuration, and Somersault's configuration. It is noteworthy that Somersault's configuration (Figs. 2D–2F) was first reported in *O. indicus*.

Some of the nomenclatures used to describe the studied material are listed below. The Axial shield (As) (Fig. 2B), is a single unit that includes the cranidium, thorax and pygidium (Henningsmoen, 1975; Drage *et al*., 2018). Thoracopygon (TP) (Fig. 2B), the thorax and pygidium are joined as a single unit (Henningsmoen, 1975; Speyer, 1985). Cephalothoracic joint (CTJT) (Fig. 2B), articulation connecting the cephalon to the thoracopygon (Drage, 2019). Lower Cephalic Unit (LCU) (Fig. 2C), all parts of the cephalon except the cranidium, joined by integument or partially fused facial sutures (Henningsmoen, 1975; Drage *et al*., 2018). For other definitions of the nomenclatures (*e.g*., moult configuration, moult style and exuvial gape), refer to Drage (2019, and references therein).

Results

The moult configurations of *Oryctocephalus indicus*

Henningsmoen's configuration shows a slight displacement of the LCU and a cranidium displacement that is associated with the thoracopygon (Drage et al., 2018). We found 80 specimens of Henningsmoen's configuration in *Oryctocephalus indicus*, which accounted for most of the material studied. According to the preservation characteristics of the exuviae, the moult specimens preserved in Henningsmoen's configuration are classified into three types in this paper: Type Ⅰ (consisting of 7 pieces) showed an intact thoracopygon, while the LCU was slightly displaced and displayed the cranidium on one side, partial specimens (3 pieces) displayed an inverted cranidium; Type II (consisting of 58 pieces) demonstrated that the thoracopygon remained connected, with a slight displacement of the LCU to connect with the thorax, and an absence of the cranidium; Type III (consisting of 15 pieces) is similar to Type II in that it absence the cranidium, but its LCU displacement is greater than of Type II.

In Type Ⅰ (figs. 3A–3C), the most significant difference between figure A and figure B–C is that the cranidium is inverted in the latter, while in figure C, the cranidium is inverted and contacts the anterior end of the LCU. This discovery suggests that the initial position of the dehiscence during trilobites moulting occurred at the junction line between the cranidium and thorax, with subsequent spliting of facial and rostral sutures to form the exuvial gape. Eventually, when the trilobite climbed out of its old exoskeleton, the cranidium was inverted to the anterior end of the LCU. Due to the specimen fragmentation during field collection, only the cranidium (internal model) and thoracopygon (external model) were retained (fig. 3B). The preservation state of this specimen was that the cranidium had flipped over and covered the right thorax. Suppose the exuviae are not quickly buried after moulting, the cranidium inverted at the front of the LCU may also be transported (*e.g*., fig. 3A). Further disturbance could result in the absence of the cranidium, leading to Type II formation from Henningsmoen's configuration.

Most of the exuviae of *Oryctocephalus indicus* preserved in Henningsmoen's configuration were identified as Type II (figs. 3D–3F), with a total of 58 specimens discovered during this study. In the complete specimens of *O. indicus*, the LCU is not connected to the thorax but instead attaches to the cranidium through the facial and rostral suture (fig. 2A). In Type II, the LCU was slightly posteriorly displaced and make contact with the first thoracic tergite due to the absence of the cranidium (figs. 3D–3F). The cranidium was probably absent because the trilobite carried it away during the moulting process. Otherwise, transportation would have caused damage marks on both the entire LCU and rear thoracopygon. The exuviae consist of a mineralised exoskeleton connected by the articulatory membranes and the unmineralised cuticle (Whittington, 1990). The presence of these articulatory membranes and the unmineralised cuticle well indicates that the LCU was preserved in-situ (or near-situ) and lay in anterior to the thoracopygon after separating from the cephalon, unlike case where there is an absence of the cranidium.

In the moult specimens of *Oryctocephalus indicus* collected for this study, Henningsmoen’s configuration of Type III shows a more significant displacement of the LCU (figs. 3G–3I). Judging from the preservation state of each structural unit of *O. indicus*, it appears that Type III in Henningsmoen's configuration (lacking a cranidium and with LCU displacement) is more susceptible to burial than Types I and II described above, without considering the effect of moulting behaviour on exuviae preservation. Specimen GTBM9-5-4110 (fig. 3G) exhibits a lateral displacement of the LCU and an absence of the cranidium, while the thoracopygon remains intact and unfractured.

Based on the materials discovered thus far, the exuviae of *Oryctocephalus indicus* are mainly preserved in Henningsmoen’s configuration, with a lesser number of exuviae being preserved in alternative configurations. The specimen shows *O. indicus* with an Axial shield (fig. 4A), which is characterised by maintaining a connexion between the cranidium and the thoracopygon, yet lacking an LCU. Strictly speaking, the Axial shield is not a moult configuration *per se*, as it may be generated by other moult configurations (Drage *et al*., 2018). Unlike many exuviae of Henningsmoen’s configuration, which exhibit a separation between the cranidium and the thoracopygon, the Axial shield and Harrington’s configuration of *O. indicus* suggest an extraordinary phenomenon of mutual connexion between these two structures. These specimens (figs. 4B, 4C) show the preservation of *O. indicus* in Harrington’s configuration, wherein the cranidium remains attached to the thoracopygon throughout the exoskeleton arrangement, and the LCU is posteriorly displaced under the exoskeleton following disconnexion between facial and rostral sutures.

So far, Somersault’s configuration is firstly identified from the *Oryctocephalus indicus* here. In this configuration, the librigenae are turned forward so that the genal spine points forward, if the rostral-hypostomal plate does not drop off, it may be connected to the librigenae as an intact LCU (Drage *et al*., 2018). In specimen GTBM9-5-1024 (fig. 4F), the LCU underwent a clockwise rotation of approximately 90° upon inversion and was subsequently positioned beneath the left side of the thorax, while the cranidium became detached from the thoracopygon and rotated 45° clockwise to face anteriorly. Perhaps owing to the distinct structures of trilobites, in Somersault’s configuration as demonstrated by *O. indicus*, the cranidium was typically detached from the thoracopygon. Only two specimens exhibit preservation of the cranidium (figs. 4D, 4F), while in other specimens (fig. 4E) solely the LCU was inverted and superimposed beneath the thorax.

The moult style of *Oryctocephalus indicus*

Based on the exuviae of *Oryctocephalus indicus* preserved in Henningsmoen's configuration, Harrington's configuration, and Somersault's configuration, it is evident that the moulting behaviour involves shedding of the cranidium and/or LCU, indicating that the moulting activity through the exuvial gape. It is noteworthy that *O. indicus* exhibits variations in moult suture selection between exuviae in Henningsmoen's configuration and those in Axial shield, Harrington's configuration, and Somersault's configuration. Henningsmoen's configuration stressed the importance of the junction line between the cephalon and thorax in the moulting behaviour, where the LCU is in-situ mainly of the whole exoskeleton and does not change with moulting activity. In others, the exuvial gape is primarily formed by the disconnexion of the facial and rostral suture, while trilobite activity during moulting causes displacement and/or inversion of LCU.

Discussion

The reliability of moult configurations in *Oryctocephalus indicu*s

Describing patterns of ecdysis in the fossil record necessitates the ability to distinguish preserved exoskeleton moults from carcasses (Daley & Drage, 2016). With the development of trilobite research, numerous moult configurations have been proposed (*e.g*., Richter, 1937; Henningsmoen, 1957, 1975; Drage *et al*., 2018), but further demonstration is required to ensure the reliability of certain configurations. In the following section, we will discuss the reliability of moult configurations by providing a comprehensive description of *Oryctocephalus indicu*s.

In Henningsmoen's configuration, trilobites can expand their exuvial gape by shedding the cranidium from the thoracopygon (Drage *et al*., 2018; Corrales-García *et al*., 2020; Wang *et al*., 2020). The significant prevalence of *Oryctocephalus indicus* in our research underscores the pivotal role played by the opening at the cephalothoracic joint, as well as the facial and rostral sutures, in forming the exuvial gape. We propose that specimens exhibiting only cranidium displacement or absence, but with relatively intact structural units and minimal displacement, should be classified as exuviae rather than mere products of physical disturbance. Figure 3C illustrates an example of prompt burial of the exuviae after moulting behavior. The cranidium is inverted and contacts the anterior end of the LCU in this peculiar arrangement shown by portions of the exoskeleton in the moult configuration, suggesting that they were not formed by chance during transport and burial. As preserved mentioned, in the exuviae of *O. indicus* preserved of type II in Henningsmoen's configuration, the presence of intact of LCU and thoracopygon negates the absence of the cranidium resulting from transportation. Little is known about the burial of most specimens considered to be moult configurations (Speyer, 1985, 1987; Whittington, 1990). In type III of Henningsmoen's configuration (figs. 3G–3I), it remains uncertain whether the displacement of LCU was solely attributed to moulting activity, and to what extent these particular specimens were affected by burial.

The formation of the exuvial gape is related to the disjunction of various sutures, which are influenced by the distinct structural properties of trilobites. Therefore, when discussing the moulting behaviour of different trilobites, overall structural features must be taken into consideration. To a certain extent, Harrington's configuration bears resemblance to specimens in which the dehiscence of the librigenae was affected by burial. Noteworthily, in Harrington's configuration exhibited by the exuviae of *Oryctocephalus indicu*s, only the LCU is displaced while the librigenae remain connexion with the rostral-hypostomal plate. The consistency of Harrington's configuration suggests that the formation of this configuration was due to the moulting behaviour of the trilobites (Henningsmoen, 1975). When the structural units, such as the cranidium, thorax, and pygidium, are fully preserved, it becomes challenging to attribute displacement of the LCU solely responsible for non-moulting factors. Further evidence is necessary to establish the reliability of the findings, given that only five specimens of *O. indicus* have been preserved in Harrington's configuration. It is undeniable, however, that the whole backward movement of LCU after detachment from the cephalon plays a specific and positive role in the formation of the exuvial gape.

Previous research has indicated that preservation of trilobite exuviae exhibiting the Somersault's configuration is uncommon, as it necessitates a strong dorsal flexure during the moulting process and prompt burial after exuviation (Whittington, 1990; Drage *et al*., 2018; Wang *et al*., 2020). In the Somersault's configuration observed in the exuviae of *Eosoptychopara guizhouensis*, the cranidium usually remains connected to the thoracopygon while the LCU is inverted and overlain under the thorax (Chen *et al*., 2022; fig. 3). The prevalence of Henningsmoen's configuration in exuviae of *Oryctocephalus indicu*s, characterised by the absence of the cranidium, suggests that the junction line between the cephalon and thorax is prone tobreakage during the moulting activity, which resulted in some of the exuviae preserved in the Somersault's configuration exhibiting the separation of the cranidium from the thoracopygon. The weakest link in exuviae is between the cranidium and the first thoracic segment, and the cranidium might have been dislocated, inverted, or carried away from the remainder of the exuviae in the course of burial (Whittington, 1990). Therefore, the structural characteristics of *O. indicus* specimens (figs. 4E, 4F) exhibiting separation between cranidium and thoracopygon slightly different from Somersault's configuration documented in previous studies.

The speculated moult process of *Oryctocephalus indicus*

The repeated occurrence of particular exoskeletal configurations ~~or constellations~~ and their agreement with inferred ecdysial openings can reveal how exuviation occurred in a given species (Henningsmoen, 1975). After the preceding discussion of the moult configurations and style of *Oryctocephalus indicus* preserved in Henningsmoen's configuration, Somersault's configuration, and Harrington's configuration, we present a preliminary analysis of the formation process of these three configurations based on information from the exuviae. The information provided by the Axial shield regarding the moulting process is limited, and it is possible that this structure formed subsequent to other moult configurations being transported. Therefore, there is no discussion of the formation process of the Axial shield in this context.

This study has discovered a total of 80 exuviae of *Oryctocephalus indicus* preserved in the Henningsmoen's configuration, with numerous specimens exhibiting a unique moulting process. In the detailed discussion of moult configurations above, we have observed that Henningsmoen's configuration has highlighted the importance of the junction line between cephalon and thorax in moulting behaviour. However, Somersault's configuration and Harrington's configuration primarily generate exuvial gape through disconnexion of facial and rostral sutures. The distinct processes of formation exhibited by moulting specimens of *O. indicus* in Henningsmoen's configuration are depicted (figs. $5B_1$, $5B_2$). Here, we are referring to the moulting process proposed by Whittington (1990), in which trilobites bend themselves to open the suture and create an exuvial gape. However, discrepancies in moulting behaviour result in different configurations of exuviation. Perhaps the initial suture that opened during moulting was located at the cephalothoracic joint, and then, the exuvial gape was further expanded by the disconnexion of both facial and rostral suture due to moulting activity (figs. $5B_1$, $5B_2$). Finally, the trilobite crawls out of its old exoskeleton while flipping the cranidium so that its front area intersects with the front end of the rostral-hypostomal plate. The difference between Figures $5B_1$ and $5B_2$ lies in the displacement of the cranidium in Figure $5B_2$. Since the LCU in specimen GTBM17-1866 (fig. 3A) intersects almost at the front of the thoracopygon, only cranidium displacement occurred, which excludes the possibility that intense transport caused the displacement of cranidium. Otherwise, the LCU with a smaller size would be more susceptible to transport than the cranidium. ~~After excluding the influence of non-moulting factors, we find out the moulting process (fig. $5B_2$).~~ During the moulting process, *O. indicus* disarticulates the facial suture, rostral suture, and cephalothoracic junction to separate the cranidium from its exoskeleton. Then the trilobite crawled out of its old exoskeleton through the exuvial gape, displacing the cranidium and leaving behind the LCU and the thoracopygon. Of course, the moult configuration shown in Figure $5B_2$ in a particular environment could have also occurred after the displacement of cranidium (fig. $5B_1$), which is show this possibility with a dashed line (fig. 5B).

The exuviae of *Oryctocephalus indicus*, preserved in Somersault's configuration and Harrington's configuration have certain similarities during the moulting process. Both of them completed the moulting through the exuvial gape created by the separation of LCU from cephalon, but their divergent moulting behaviours resulted in distinct moult configurations. In the exuviae of *O. indicus* preserved in Somersault's configuration (fig. 5C), disconnexion of both facial and rostral sutures results in a separation between the LCU and cranidium, creating an exuvial gape beneath the cephalon for ecdysis. When the trilobite crawled out of its old exoskeleton, it compelled the LCU to move in the direction indicated by the arrow and ultimately assumed Somersault's configuration, which its thorax and pygidium connected while the LCU was inverted and pressed under the thorax (fig. 5C). The cranidium was easily separated from the thorax in *O. indicus*, resulting in a significant absence or displacement of most of the cranidium in Somersault's configuration. However, we hypothesize that the Harrington's configuration observed in *O. indicus* (fig. 5D) may be attributed to insufficient dorsal flexure during the moulting process, and that the moulting behaviour of the trilobite failed to cause the LCU to overturn after breaking the facial and rostral suture. Instead, the LCU was pushed backwards by the forward movement of the trilobite, eventually forming Harrington's configuration in which the cranidium, thorax and pygidium were connected, while the LCU was displaced below the thorax.

Conclusions

Based on the established criteria for identifying exuviae in previous studies and the detailed description of *Oryctocephalus indicus* provided in this paper, we propose that the disarticulated specimens presented herein are trilobite exuviae resulting from moulting behaviour rather than simple mechanical transport. The exuviae of *O. indicus* are predominantly preserved in the Henningsmoen's configuration, with some specimens exhibiting Harrington's configuration or Somersault's configuration. Additionally, we have categorized Henningsmoen's configuration into two types (Type I and Type II) based on the presence or absence of the cranidium in the exuviae, and have further distinguished Type III from Type II by examining whether or not the LCU is displaced.

In the exuviae of *Oryctocephalus indicu*s, the LCU was detached from the cephalon and positioned anteriorly to the thoracopygon. The majority of the cranidium was absent, indicating that this is a typical moult style (exuvial gape) of Cambrian oryctocephalid trilobites. In this paper, we examine the reliability of *O. indicus* moult configuration in light of available exuviation information, and suggest that burial-related transport processes may have contributed to variation in moult configuration. Simultaneously, while endeavoring to reconstruct the moulting process of *O. indicus*, it was discovered that variations in trilobite selection during the moulting process may result in diverse moult configurations. With the information gained from studying the moulting behaviour of *O. indicus*, we believe that even for trilobites preserved in recognized moult configurations, it is imperative to consider whether non-moulting factors have affected the preservation state of structural units, in the exuviae prior to complete preservation.

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Figure 1

Figure 1 Location and stratigraphy of the Miaobanpo section.

(A) The lithofacies reconstruction of South China during the earliest Cambrian Miaolingian Series (modified from Feng *et al*. 2004). (B) A simplified sketch map of the fossil locality in Jianhe County, Guizhou Province, South China. (C) The Stratigraphicaln column of the Miaobanpo section (Kaili Formation) displays a horizon that yields *Oryctocephalus indicus* (modified from Zhao *et al*. 2012), the red arrows indicate the main collection horizon of the fossils in this study.

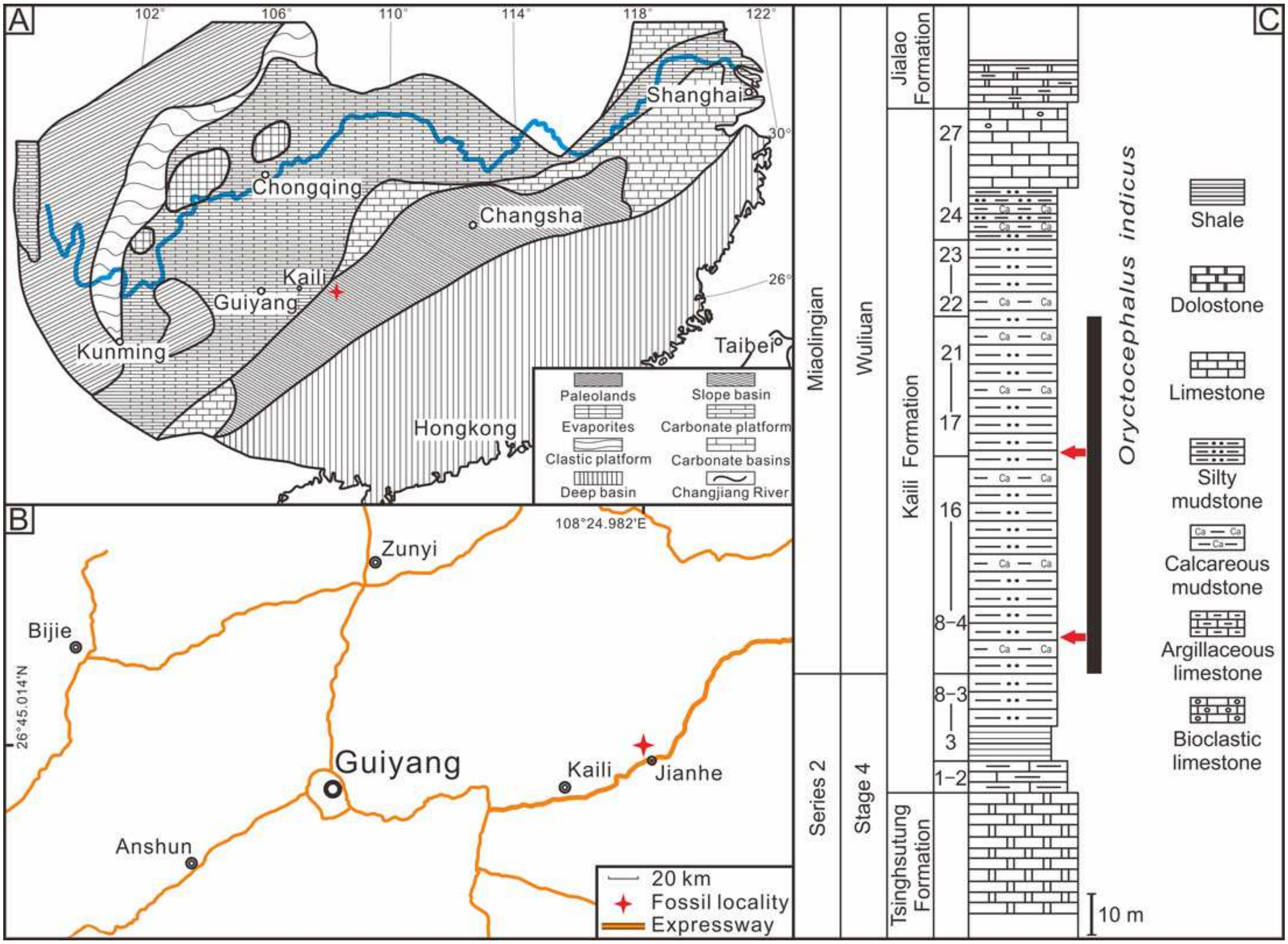


Figure 2

Figure 2 Reconstructions of *Oryctocephalus indicus*.

(A) dorsal view of the exoskeleton. (B) Axial shield (n=2). (C) Cranidium and lower cephalic unit. (D) Henningsmoen’s configuration (n=80). (E) Harrington’s configuration (n=2); (F) Somersault’s configuration (n=4). Structural units under the exoskeleton appear red. Abbreviations: As, Axial shield; Cr, Cranidium; TP, thoracopygon; LCU, lower cephalic unit; CTJT, cephalothoracic joint; L, librigenae; Cs, Connective suture; Rh, rostral-hypostomal plate; Rs, rostral suture.

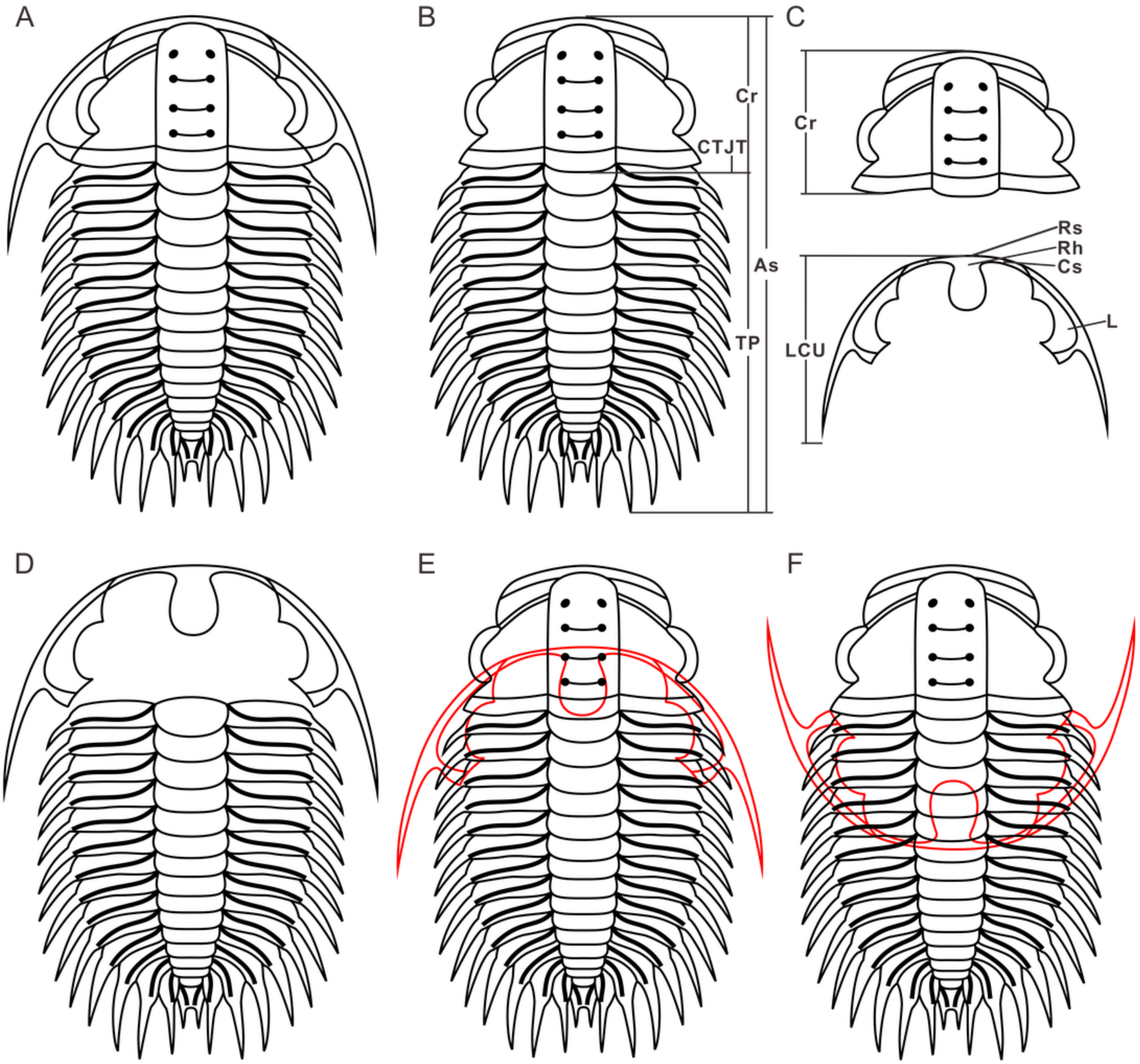

A
B
Cr
CTJT
As
TP
C
Cr
Rs
Rh
Cs
LCU
L
D
E
F

Figure 3

Figure 3 Examples of Henningsmoen’s configuration in *Oryctocephalus indicus* from the Cambrian Kaili Formation of Guizhou Province, South China.

Styles I (A, B, C) shows the preservation of cranidium (Cr); Styles II (D, E, F) shows the lower cephalic unit (LCU) nearly in situ and the displaced cranidium is missing; Styles III (G, H, I) shows the laterally rotated of the LCU and the displaced cranidium is missing. (B) Except for the cranidium is a body fossil, the rest of the structures are external models. (D) Shows the cranidium inverted before the LCU. Specimen No: A, GTBM17-1866; B, GTBM9-3-3706; C, GTBM16-437; D, GTBM9-3-3745; E, GTBM9-2-4282; F, GTBM9-5-4029; G, GTBM9-5-4110; H, GTBM8-5-832; I, GTBM9-3-2110. All scale bars equal 2 mm.

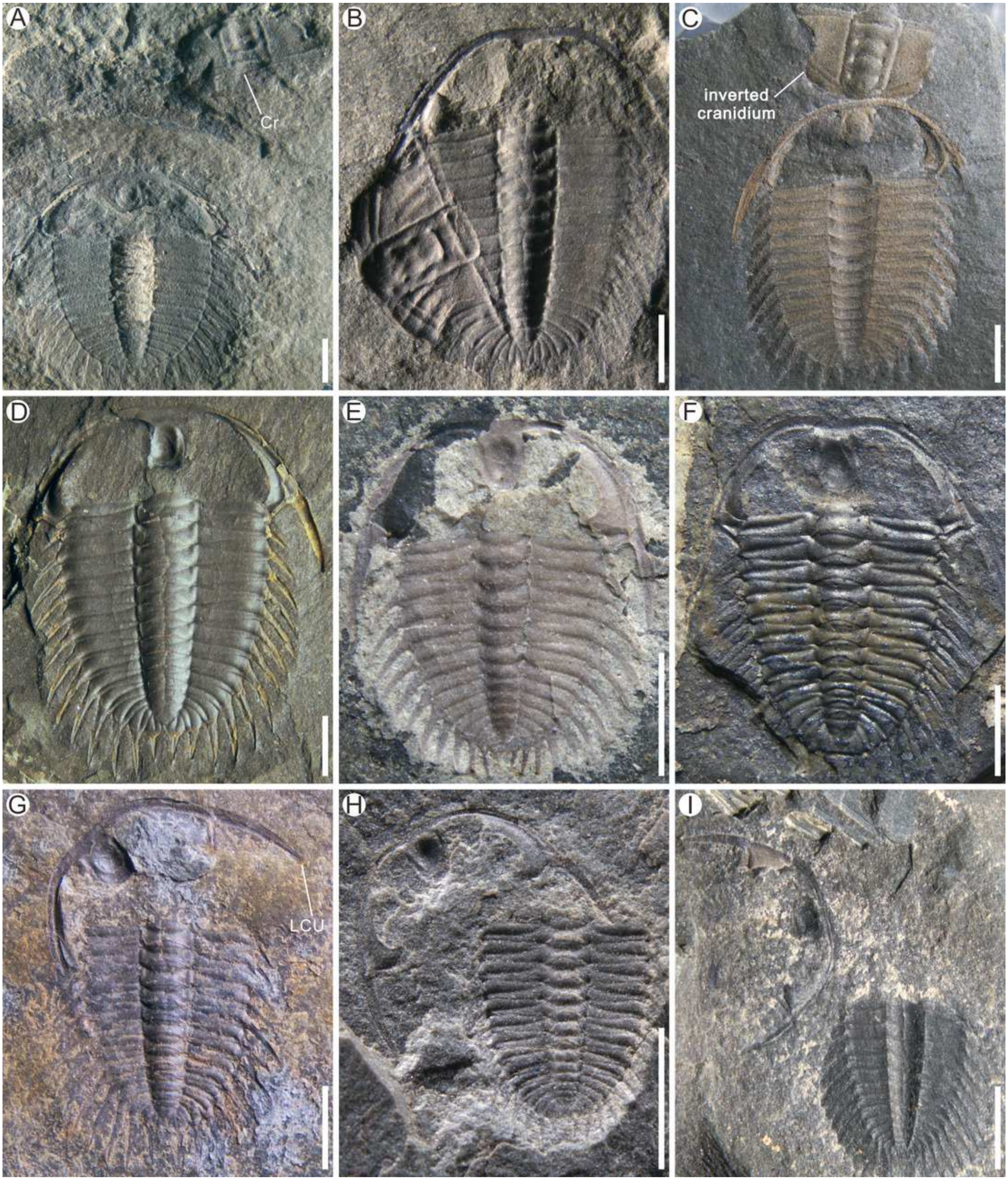

A
Cr
B
C
inverted cranidium
D
E
F
G
LCU
H
I

Figure 4

Figure 4 Examples of moult configurations in *Oryctocephalus indicus* from the Cambrian Kaili Formation of Guizhou Province, South China.

(A) Axial shield; (B-C) Harrington’s configuration shows the backward displacement of the lower cephalic unit (LCU). (D-F) Somersault’s configuration shows the inversion of the LCU and the absence or displacement of the cranidium. (E) shows the rostral-hypostomal plate (Rh) pressed beneath the thorax. A, GTBM9-2-1508; B, GTBM9-2-4316; C, GTBM9-1-752; D, GTBM9-2-2046; E, GTBM17-1578; F, GTBM9-5-1024. All scale bars are equal to 2 mm.

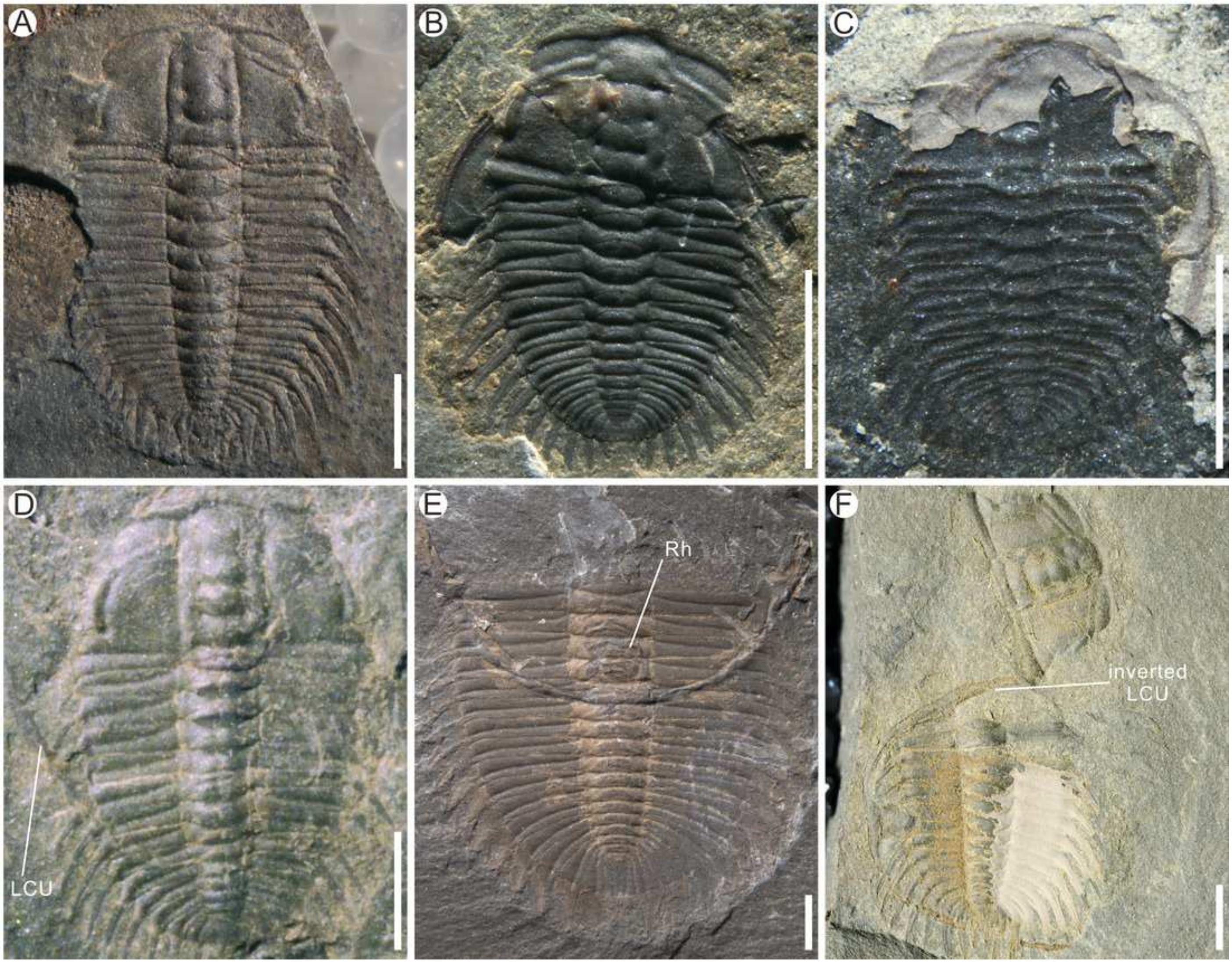
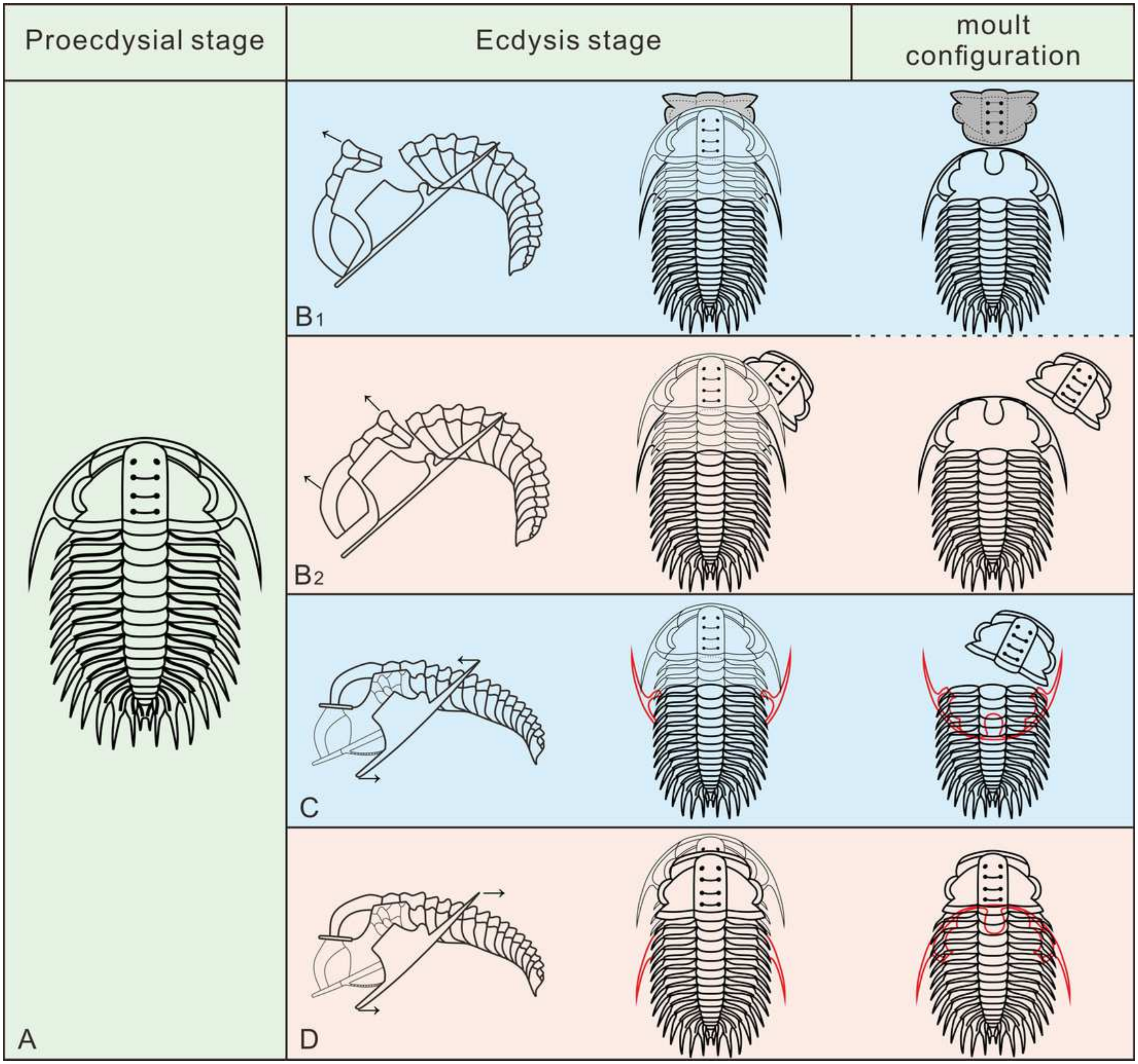


Figure 5

Figure 5 Reconstruction of moult process for *Oryctocephalus indicus* based on specimens.

(A) a complete individual at the proecdysial stage; (B_1) and (B_2) is the formation processes of two different types in the Henningsmoen's configuration, the inverted cranidium in B_1 is shown in grey; (C) the formation process of the Somersault's configuration; (D) the formation process of the Harrington's configuration. After inverted or displacement, structural elements under the thoracopygon are shown in red, and trilobites in the moulting process are plotted in thin lines. The moulting process was modified by Whittington (1990).


Proecdysial stage
Ecdysis stage
moult configuration
B1
B2
C
A
D