Coupled exuviae of the Ordovician *Ovalocephalus* (Pliomeridae, Trilobita) in South China and its behavioral implications

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Abstract

Ecdysis was a vital process during the lives of trilobites, in addition to preserving the morphological changes in trilobite ontogeny, the preservation of its action often captured interesting behavioral information. Abundant exuviae of *Ovalocephalus tetrasulcatus* are preserved in the Ordovician strata in central Hubei, China, and some of them are arranged with two or three together end to end or superimposed. The preserved patterns and burial conditions indicate that these specimens were caused by the active behavior of trilobites. It is speculated that these exuvial clusters were formed by two or three trilobites in line to molt; that is, after one trilobite finished molting, other trilobites molted in front of, behind, or overlying the previously molted shells. This ecdysis strategy is interpreted as related to the postulated herding behavior of some trilobites, representing a behavioral response of the trilobites to choose a nearby safe zone during some risky life activities.

Introduction

The biomineralized or chitinous exoskeleton of arthropods hinders the growth of their bodies; therefore, individuals must shed their old shells many times during growth and development (Moussian, 2013; Daley and Drage, 2016). Trilobites, as an extinct group of arthropods, also needed to shed their shells as they grew (Fortey, 2014). Different trilobites exhibited different molting techniques (Henningsmoen, 1975); most trilobites shed their shells through separating the librigenae from the cranidium (McNamara and Rudkin, 1984; Whittington, 1990), whereas for trilobites with librigenae fused with the cranidium, separation of the cephalon from the thoracopygon usually occurred during molting (Speyer, 1985; Wang and Han, 1997), and some genera had multiple exuvial modes (Brandt, 1993; Budil and Bruthansová, 2005). In addition to ecdysis reflecting the ontogenetic development process of trilobites, some exceptionally preserved trilobite specimens also contain behavioral information. For example, some trilobites

48   shed their shells by hiding in empty shells or burrows of other animals (Davis et al., 2001;
49   Chatterton et al., 2003; Chatterton and Fortey, 2008; Zong et al., 2016), and even molted
50   infaunally (Rustán et al., 2011), reflecting the hiding behavior of trilobites. Some phacopids may
51   also have exhibited asymmetric behaviors during molting (Zong and Gong, 2017). Other
52   trilobites collectively shed their shells, which may have been related to molting–mating behavior
53   (Speyer and Brett, 1985; Speyer, 1990).
54   South China is an important area for trilobite fossils, and abundant Ordovician trilobites
55   have been collected from Hubei Province (Lu, 1975; Zhou and Zhen, 2008). However, there are
56   few reports on exuvial specimens and correlation research. Only photographs of exuvial
57   specimens were attached to the identification of genera and species in the paleontological
58   literature; these exuvial specimens have not been systematically described, their patterns have
59   not been classified and explained, and the behavioral strategy of these trilobites during molting
60   has not been analyzed (Han and Wang, 2000). Here, I collected many exuviae of *Ovalocephalus*
61   *tetrasulcatus* (Phacopida, Pliomeridae) from the Upper Ordovician in central Hubei. Some of the
62   specimens were found with two or three in a line, or preserved partly or even completely
63   overlapping; these patterns are regarded as representing the active behavior of trilobites during
64   molting, and may be related to the herding behavior of some trilobites. They provide new
65   material for understanding exuvial techniques of trilobites, and the behavior of trilobites when
66   molting.

Materials & Methods

68   All specimens were collected from the Upper Ordovician Linhsiang Formation of the Daozimiao
69   section in Jinshan County, central Hubei (GPS: N 30°59′51.49″, E113°06′26.04″) (Fig. 1). The
70   Linhsiang Formation is widely distributed in the middle Yangtze region, and is mainly composed
71   of yellow-green calcareous mudstones with a few siliceous mudstones in the Daozimiao section,
72   but differs from the nodular muddy limestones of the Linhsiang Formation in the type section in
73   Linxiang, Hunan Province. In the Daozimiao section, the Linhsiang Formation is conformably
74   underlain by the muddy limestones of the Upper Ordovician Pagoda Formation and overlain by
75   the graptolite shales of the Upper Ordovician Wufeng Formation. The 1.5-m-thick calcareous
76   mudstones from the top of the Linhsiang Formation (Fig. 1d) yield an abundant and diverse
77   trilobite fauna, including members of the Metagnostidae, Cyclopygidae, Phillipsinellidae,
78   Encrinuridae, Telephinidae, Raphiophoridae, Cheiruridae, Dionididae, Trinucleidae, Asaphidae,
79   Pliomeridae, and Remopleurididae. In addition, the Foliomena fauna (brachiopods) (Zhan and
80   Jin, 2005), ostracods, echinoderms, machaeridians, and trace fossils are also found in the same
81   horizon. Based on the trilobite assemblage, the age of the top of the Linhsiang Formation is
82   constrained to the middle Katian (early Ashgill) (Zhou et al., 2016).
83   The 1.5-m-thick trilobite-bearing calcareous mudstones are homogeneous, without
84   bedding structures. There are no cross-bedding and graded bedding visible in the longitudinal
85   sections of the rocks, but a small amount of authigenic pyrites is preserved in this interval (Fig.
86   2a–d). This evidence suggests the calcareous mudstones formed in a relatively calm and

87 deepwater environment, which is consistent with the results of the characteristics of the
88 brachiopod association found in the same interval (Zhan and Jin, 2005). *Ovalocephalus*
89 *tetrasulcatus* (Kielan 1960) is the only pliomerid trilobite in the Linhsiang Formation of Jingshan.
90 *Ovalocephalus* is largely restricted to peri-Gondwana, but is widely distributed in the Ordovician
91 of China (Zhou et al., 2010). In the Linhsiang Formation of Jingshan, most specimens of
92 *Ovalocephalus tetrasulcatus* are articulated or nearly articulated exoskeletons, as well as enrolled
93 specimens. This pattern suggests that the trilobites were not transported by current before burial,
94 and were buried in situ. Although some biotic burrows can be observed in the calcareous
95 mudstones (Fig. 2e, f), no traces of burrows have been found near the trilobites (Fig. 2b, c),
96 which rules out the likelihood that trilobites were affected by biotic disturbance before burial or
97 preserved in burrows.
98   I collected more than 100 specimens containing articulated or nearly articulated
99 exoskeletons from the calcareous mudstones at the top of the Linhsiang Formation of Jingshan,
100 including 13 specimens that showed two exoskeletons end to end or overlapping one another,
101 and three specimens that show three exoskeletons end to end or two of them overlapping one
102 another, which obviously differed from isolated single exoskeletons preserved in the same
103 interval. The fossils in Fig. 3 were whitened with magnesium oxide powder, and all photographs
104 were captured using a Nikon D5100 camera with a Micro-Nikkor 55 mm F3.5 lens. The axial
105 azimuth measurements of the trilobites and the rose chart were completed in CorelDRAW X7.

Results

107 In the present work, complete exoskeletons include all specimens with articulated cephala,
108 thoraces, and pygidia or enrolled exoskeletons, indicating that they are fossilized carapaces of
109 *Ovalocephalus tetrasulcatus*. Among these nearly complete exoskeletons, a portion of them are
110 articulated thoraces and pygidia, but with the cephala separated and preserved nearby (Fig. 3a),
111 which are considered exuviae (Han and Wang, 2000). Another kind has librigenae separated
112 from the cranidia, but the cranidia and thoracopyga are still articulated, or the cranidia are
113 separated from the thoraces and slightly rotated. These specimens include those with two
114 librigenae separated from cranidia, but still preserved nearby (Fig. 3b), and a portion of these
115 librigenae were inverted or rotated (Fig. 3d); in addition, some specimens have one librigena
116 separated from the cranidium and inverted, but another still in situ (Fig. 3c). Both types of
117 inverted or rotated librigenae separated from the cranidium are similar to the exuvial mode of
118 many trilobites (Henningsmoen,1975; McNamara and Rudkin, 1984), indicating that they are
119 most likely exuviae of *Ovalocephalus tetrasulcatus*, rather than corpses that were broken up by
120 bottom currents and/or organisms, and the natural decomposition of the corpses. This indicates
121 that there is more than one exuvial mode in *Ovalocephalus tetrasulcatus*; i.e., separation of the
122 cephalon from the thoracopygon, separation of the librigenae from the cranidium, or both
123 existing at the same time. A similar diversity of exuvial patterns has been found in other
124 phacopid trilobites (Brandt, 1993; Budil and Bruthansová, 2005; Chen, 2011).

125   In the sixteen specimens with two or three exoskeletons partly superimposed or end to end,
126   all the specimens show separation of the cephalon or librigenae, and the separated cephala or
127   librigenae are still preserved near the thoracopyga (Fig. 4), indicating that all of these specimens
128   are exuviae of *Ovalocephalus tetrasulcatus*. The central axis of the most frontal *Ovalocephalus*
129   *tetrasulcatus* in the exuvial clusters was used as the directrix to calculate the axial azimuth of the
130   posterior trilobites. The results showed that there was an obvious dominant orientation; that is,
131   the axial azimuth of the trilobites in these clusters had obvious consistency (Fig. 5), indicating
132   they were not the result of accidental burial events. The separated librigenae preserved near the
133   cranidia may also preclude them from being the result of postmortem transport. Therefore, these
134   exuviae are inferred to have been caused by the active behavior of trilobites.

135   ## Discussion

136   **Possible causes of coupled exuviae**
137   Preservation of two *Ovalocephalus tetrasulcatus* exoskeletons preserved together is similar to
138   the preservation of an arthropod in the middle of the act of molting (García-Bellido and Collins,
139   2004), but the latter case includes one corpse and one exuvia, whereas all these specimens from
140   Jingshan are exuviae, without corpses; thus, the possibility that the *Ovalocephalus tetrasulcatus*
141   individuals were buried when molting can be excluded. Several cases of queuing of trilobites
142   have been reported in the past, but most of these cases involve corpse fossils, and the number of
143   trilobites is typically more than three; thus, they are regarded as representing unexpected burial
144   during the migration of trilobites (Radwański et al., 2009; Błażejowski et al., 2016; Vannier et al.,
145   2019). Chatterton and Fortey (2008) reported trilobites aligned for molting, but they were
146   preserved in burrows. In Jingshan, there are no biological burrows near the *Ovalocephalus*
147   *tetrasulcatus* specimens (Fig. 2b, c), and the number of exuviae per specimens is only two or
148   three, in contrast with the former. Since Speyer and Brett (1985) first reported synchronous
149   ecdysis in Middle Devonian phacopids in New York, this behavior has been identified in some
150   other trilobites (Paterson et al. 2007), usually with many trilobites concentrated in a certain place
151   to shed their shells, which is thought to be related to gregarious behavior and is probably
152   associated with the copulation and reproduction of trilobites (Speyer, 1990). A similar pattern
153   may exist in *Ovalocephalus tetrasulcatus*, and pairs of exuviae are relatively easy to understand
154   for mating behavior after molting. However, there are obvious differences of sizes in some
155   exuviae in the same cluster (Fig. 4d), or in different clusters (Fig. 4b, e). More importantly, there
156   are also clusters with three exuviae (Fig. 4g–i), and the superposition (Fig. 4b) even almost
157   complete overlapping (Fig. 4c, h–i) is visible in the exuvial clusters, it is unlikely that two or
158   three trilobites shed their shells synchronously, given the time interval likely represented (a few
159   hours or days). Thus, it is difficult to explain these exuvial clusters as the result of molting–
160   mating behavior.
161   I speculate that these specimens may reflect a particular exuvial behavior of *Ovalocephalus*
162   *tetrasulcatus*; because superposition (Fig. 4b) and even almost complete overlapping (Fig. 4c, h–
163   i) exist in the exuvial clusters, it is unlikely that two or three trilobites shed their shells
164   synchronously. Instead, they may have shed their shells in lines; that is, after one trilobite

165   finished molting, the others shed their shells as well. Alternatively, perhaps the first trilobite
166   finished molting and left an empty shell, and then later, other trilobites came to the same place to
167   molt. The consistency of the long axes of the exuviae may be related to the seabed topography at
168   that time; for example, molting could have occurred in a narrow shallow gully or on a gentle
169   slope. This is may have been somewhat similar to the molting of extant cicadas on trees, where
170   they occasionally molt in line or overlapping (Bobo, 2016; Muchen, 2016; Zhu and Wang, 2017).
171   **Implications for the behavioral strategy of trilobites**
172   Arthropods are weak during and after molting, which leaves them vulnerable to predators and
173   even other members of their species. Living shrimps and crabs usually hide in rock crevices or
174   water plants for molting. Trilobites would also have needed a quiet and undisturbed environment
175   when they shed their shells (Henningsmoen, 1975; Han, 2006). For example, some trilobites
176   used the empty shells of cephalopods and gastropods as shelter for molting (Chatterton, 1971;
177   Brandt, 1993; Davis et al., 2001; Zong et al., 2016), some even shed their shells under the empty
178   shells of larger trilobites (Gutiérrez-Marco et al., 2009), and others molted in burrows of other
179   animals (Chatterton et al., 2003; Chatterton & Fortey, 2008). The Upper Ordovician strata in
180   Jingshan have yielded a large number of cephalopods, and I also found nautiloid fossils in the
181   Linhsiang Formation. These predators would have threatened great harm to molting trilobites,
182   and the trilobites therefore would have needed to find safe places for ecdysis. However, when
183   there was no shelter on the seafloor, or insufficient space to hide, possibly, they may have chosen
184   to follow congeneric trilobites nearby to molt; alternatively, the remaining exuviae of other
185   trilobites might have suggested that the location was suitable or safe for molting, thus attracting
186   the later trilobites to molt in the same position, thus forming exuvial clusters. It is worth noting
187   that there are only two or three exuviae in each cluster, which may be because the posterior
188   trilobites adopted the principle of proximity when choosing the molting site. This is similar to the
189   herding behavior of animals in crisis situations, indicating that *Ovalocephalus tetrasulcatus*
190   would take the initiative to choose the nearest safe area to carry out vulnerable life activities.

Conclusions

192   The exuviae of *Ovalocephalus tetrasulcatus* from the Upper Ordovician Linxiang Formation
193   presented two types: separation of the librigenae from the cranidium, and separation of the
194   cephalon from the thoracopygon, reflecting the diversity of the exuvial modes. Some specimens
195   have two or three exuviae arranged end to end, and some have partly and even completely
196   superimposed exuviae together in clusters. The preserved patterns and burial conditions indicate
197   that these specimens are products of the active behavior of trilobites, rather than mechanical
198   transport by currents, unexpected burial in the middle of the act of molting, or collective molting
199   before mating. The preserved patterns and overlapping phenomena of the exuviae indicate that
200   these clusters were formed by two or three trilobites lining up to shed their shells in a long and
201   narrow feature of seafloor topography. They likely represent the behavioral response that the
202   trilobites chose to follow in certain risky life activities, indicating that herding behavior existed
203   in these Ordovician trilobites.

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Figure 1

Locality map of the fossil site and stratigraphic horizon of *Ovalocephalus tetrasulcatus* in Jingshan County, Hubei

a–b. Location of the fossil locality of *Ovalocephalus tetrasulcatus* in the Daozimiao section, Jingshan; c. stratigraphic column of the Upper Ordovician Linhsiang Formation and stratigraphic distribution of trilobites in the Daozimiao section (graptolite Zone after Zhou et al., 2016); d. photo showing the 1.5-m-thick calcareous mudstone from the top of the Linhsiang Formation in Daozimiao section.
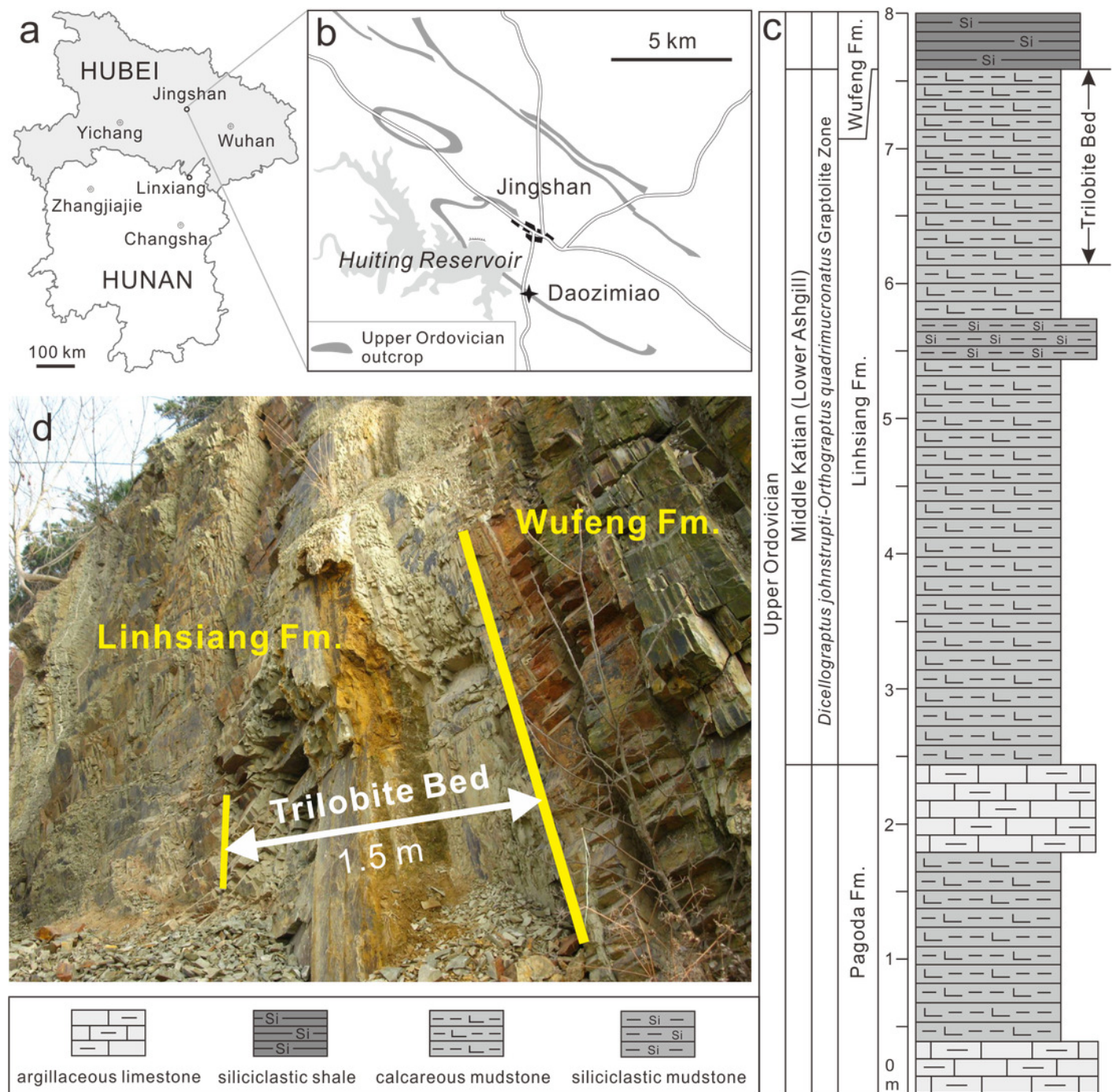
Figure 2

Longitudinal sections of the trilobite-bearing calcareous mudstones and trace fossils from the top of the Linhsiang Formation in Jingshan, Hubei

a. Longitudinal sections of the calcareous mudstones, without any cross-bedding or graded bedding; b. longitudinal sections of the trilobite-bearing calcareous mudstones; c. longitudinal sections of the trilobite-bearing calcareous mudstones with authigenic pyrites; d. close up of authigenic pyrites in box in figure c; e–f. biotic burrows in the bedding surface (e) and longitudinal section (f) (white arrows) of calcareous mudstones.
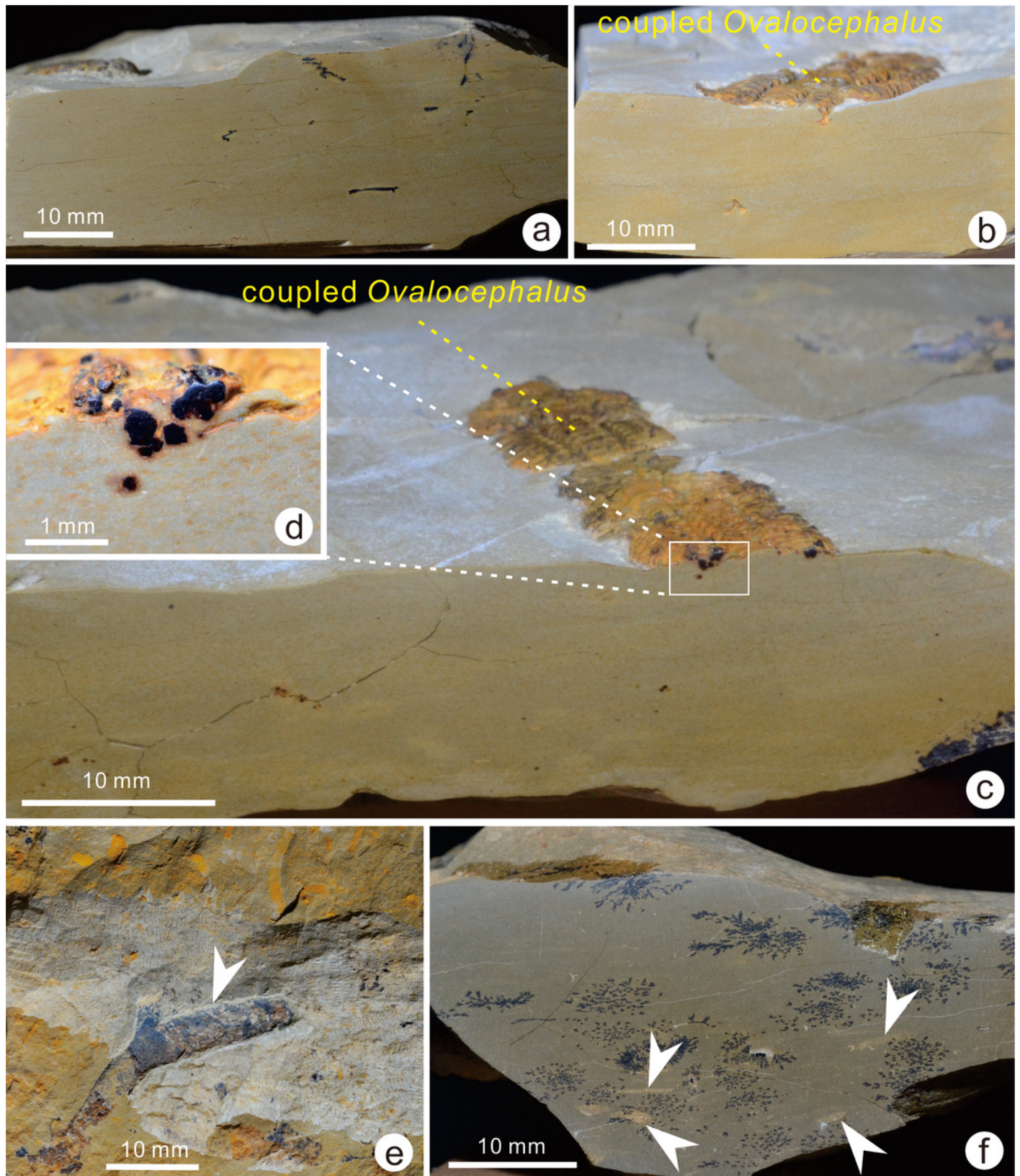
Figure 3

Diverse exuvial techniques of *Ovalocephalus tetrasulcatus* from the Upper Ordovician Linhsiang Formation in Jingshan, Hubei

a. Cephalon is separated from the enrolled thoracopygon, and overlaps in front of the thorax (CUG-HJ19); b. two librigenae (white arrows) are separated from the cranidium and preserved nearby (CUG-HJ01); c. the inverted left librigena (white arrow) is separated from the cranidium, whereas the right librigena is still in situ (CUG-HJ17); d. two inverted librigenae (white arrows) are separated from the cranidium, which is rotated slightly (external mold) (CUG-HJ20). All scales are 5 mm.
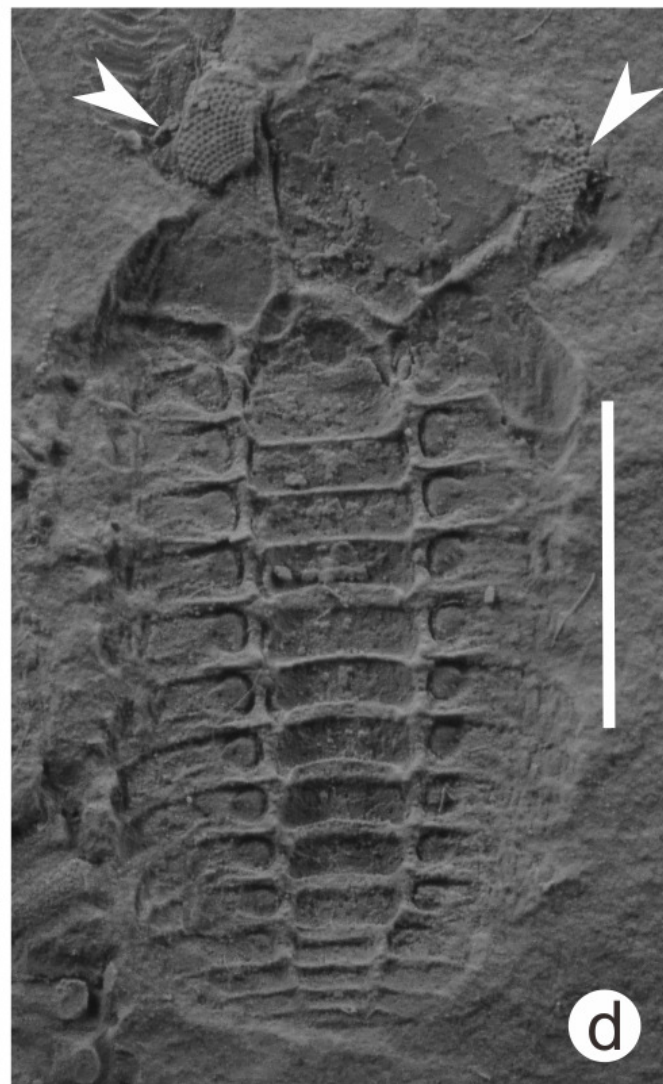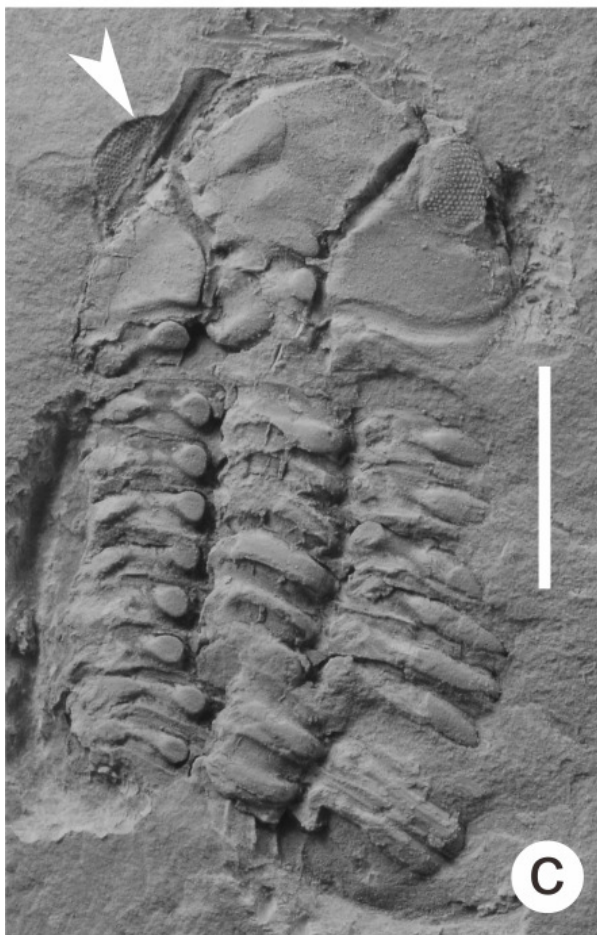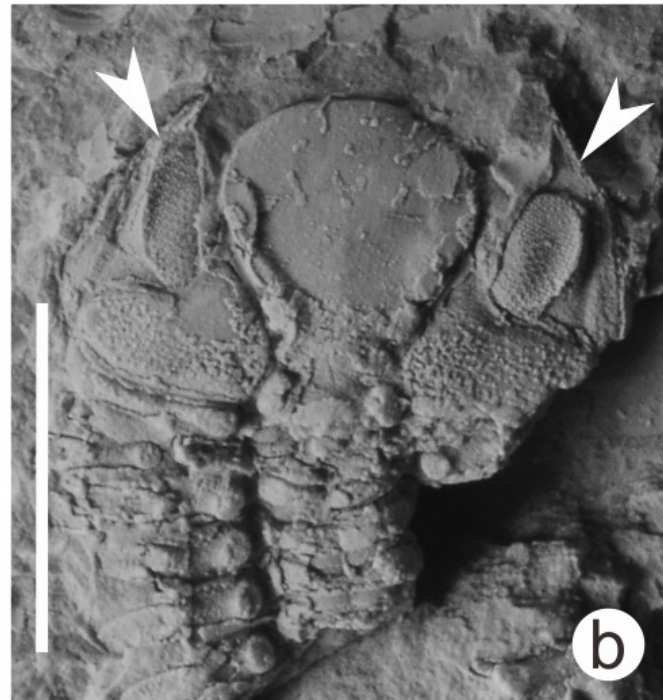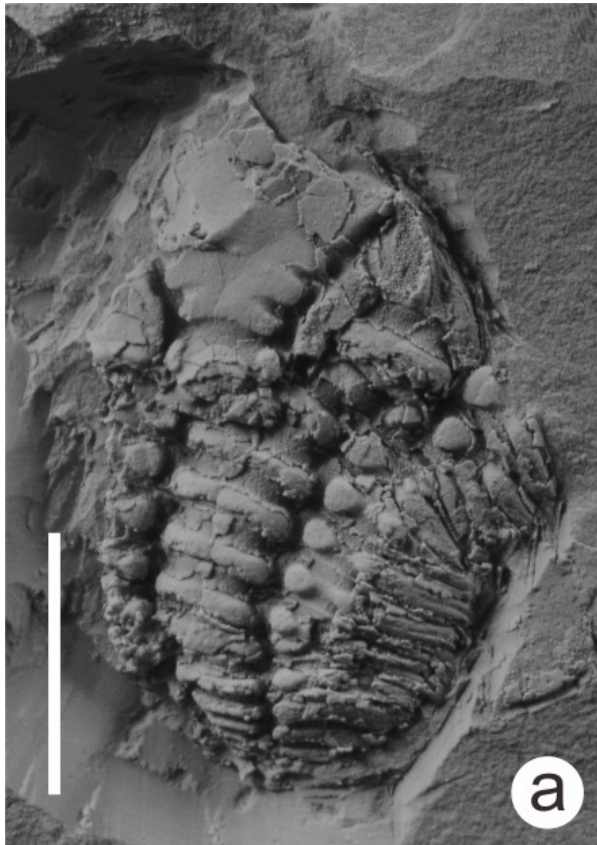
Figure 4

Coupled exuviae of *Ovalocephalus tetrasulcatus* from the Upper Ordovician Linhsiang Formation in Jingshan, Hubei

a. Two exuviae arranged end to end (CUG-HJ14); b. two partially overlapping exuviae with the same axial direction (CUG-HJ05); c. two overlapping exuviae with opposite orientations (CUG-HJ11); d. two exuviae with different sizes arranged end to end (CUG-HJ02); e. two small exuviae arranged end to end, with the cephala separated from the thoracopyga, and the first cephalon overlapping with the anterior two thoracic segments (CUG-HJ08); f. two exuviae arranged in a nearly straight line (CUG-HJ07); g. three exuviae arranged end to end; the first one is quite different from the other two in size (CUG-HJ03); h. three exuviae, with the latter two almost completely overlapping and joined with the first one end to end (CUG-HJ06); i. three exuviae, with the latter two almost completely overlapping and partially overlapping with the first one (CUG-HJ15). The white arrows indicate the separated librigenae, and all scales are 5 mm.
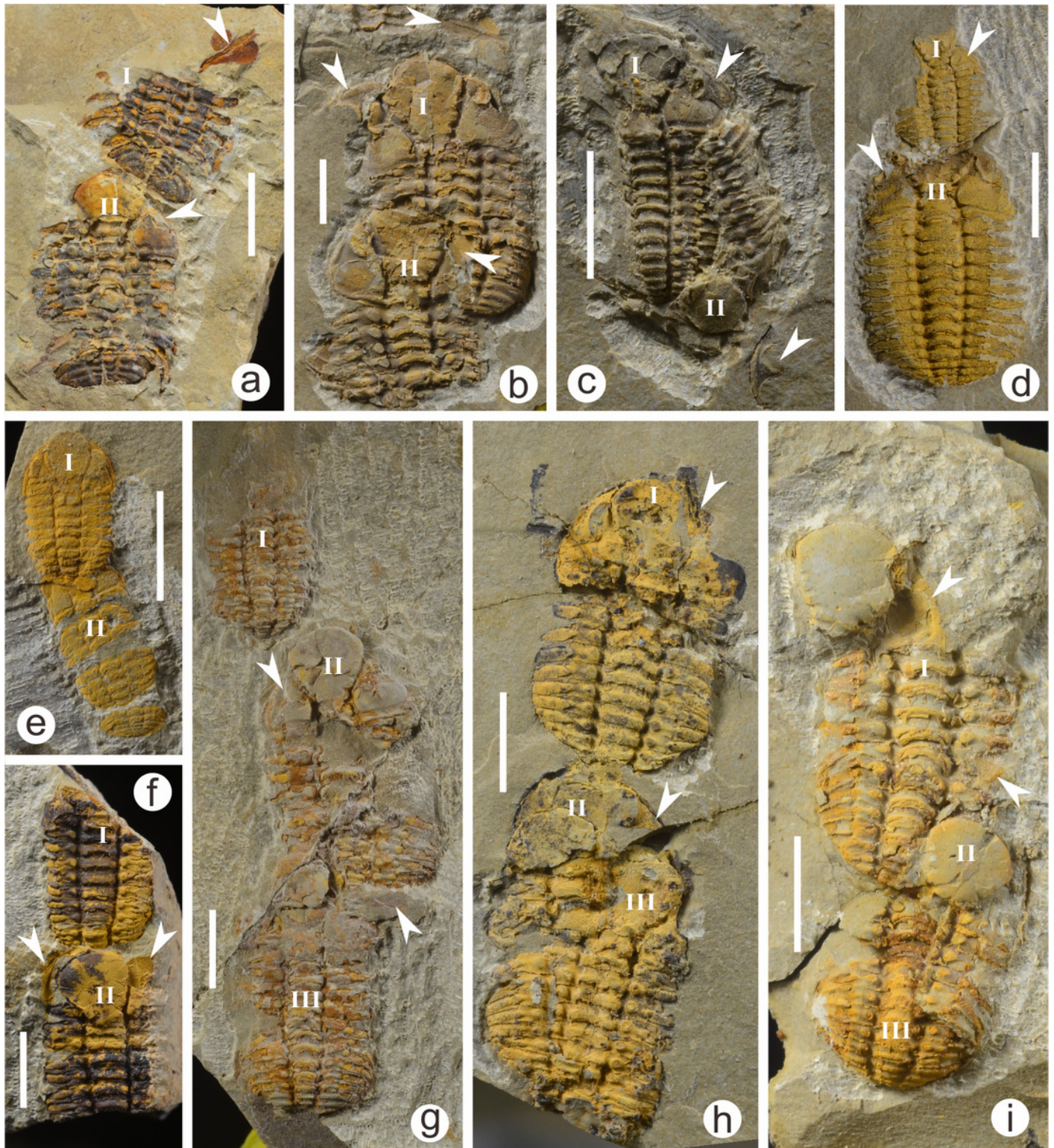
Figure 5

Statistical results of axial azimuth (a) and the corresponding rose diagram (b) for the coupled exuviae of *Ovalocephalus tetrasulcatus* from the Upper Ordovician Linhsiang Formation in Jingshan, Hubei

No.	azimuth of axis of first exuviae	azimuth of axis of second exuviae	azimuth of axis of third exuviae
CUG-HJ01	0°	75.6°	/
CUG-HJ02	0°	2.6°	/
CUG-HJ03	0°	355.3°	1.7°
CUG-HJ04	0°	317.9°	/
CUG-HJ05	0°	4.4°	/
CUG-HJ06	0°	347.9°	4.4°
CUG-HJ07	0°	354.5°	/
CUG-HJ08	0°	336.6°	/
CUG-HJ09	0°	342.5°	/
CUG-HJ10	0°	354.7°	/
CUG-HJ11	0°	163.8°	/
CUG-HJ12	0°	33°	/
CUG-HJ13	0°	30°	/
CUG-HJ14	0°	345.6°	/
CUG-HJ15	0°	12.1°	3°
CUG-HJ16	0°	10.8°	/

a

b