Coupled exuviae of the Ordovician *Ovalocephalus* (Pliomeridae, Trilobita) in south China and its behavioral implications (#48931)

First submission

Guidance from your Editor

Please submit by **8 Jun 2020** for the benefit of the authors (and your $200 publishing discount) .

Structure and Criteria
Please read the 'Structure and Criteria' page for general guidance.

Raw data check
Review the raw data.

Image check
Check that figures and images have not been inappropriately manipulated.

Privacy reminder: If uploading an annotated PDF, remove identifiable information to remain anonymous.

Files

Download and review all files from the materials page.

5 Figure file(s)

Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this PDF and upload it as part of your review

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

BASIC REPORTING

- Clear, unambiguous, professional English language used throughout.
- Intro & background to show context. Literature well referenced & relevant.
- Structure conforms to PeerJ standards, discipline norm, or improved for clarity.
- Figures are relevant, high quality, well labelled & described.
- Raw data supplied (see PeerJ policy).

EXPERIMENTAL DESIGN

- Original primary research within Scope of the journal.
- Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
- Rigorous investigation performed to a high technical & ethical standard.
- Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- Impact and novelty not assessed. Negative/inconclusive results accepted. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
- All underlying data have been provided; they are robust, statistically sound, & controlled.
- Speculation is welcome, but should be identified as such.
- Conclusions are well stated, linked to original research question & limited to supporting results.

Standout reviewing tips

The best reviewers use these techniques

Tip	*Example*
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

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

Ruiwen Zong Corresp. 1

1 State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Wuhan, Hubei, China

Corresponding Author: Ruiwen Zong
Email address: zongruiwen@cug.edu.cn

Ecdysis was a vital process during the lives of trilobites, and in addition to reflecting the morphological changes in trilobite ontogeny, it also 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. Based on the morphology of the exuviae, this preserved pattern was caused by the active behavior of the trilobites. It is speculated that these exuvial clusters, combined with the overlying phenomenon, 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 herding behavior of trilobites, representing a behavioral response of the trilobites to choose a nearby safe zone in a crisis situation.

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

Ruiwen Zong

State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Wuhan, Hubei, China

Corresponding Author:

Ruiwen Zong

Lumo Road, No.388, Wuhan, Hubei, 430074, China

Email address: zongruiwen@cug.edu.cn

Abstract

Ecdysis was a vital process during the lives of trilobites and in addition to reflecting the morphological changes in trilobite ontogeny, it also 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. Based on the morphology of the exuviae, this preserved pattern was caused by the active behavior of the trilobites. It is speculated that these exuvial clusters, combined with the overlying phenomenon, 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 herding behavior of trilobites, representing a behavioral response of the trilobites to choose a nearby safe zone in a crisis situation.

Introduction

The chitin exoskeletons of arthropods will hinder 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 thoracopygidium usually occurred during molting (Speyer, 1985; Wang and Han, 1997), and some genera had multiple exuvial modes (Brandt, 1993; Budil and Bruthansova, 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 shed their shells by hiding in empty shells or burrows of other animals (Davis et al., 2001; Chatterton et al., 2003; Chatterton and Fortey, 2008; Zong et al., 2016), and even molted infaunally (Rustan et al., 2011), reflecting the hiding behavior of trilobites. Some phacopids may also have exhibited asymmetric behaviors during molting (Zong and Gong, 2017). Other trilobites collectively shed their shells, which may have been related to molting–mating behavior (Speyer and Brett, 1985; Speyer, 1990).

South China is an important area for trilobite fossils; a large number of exuviae have been reported in the region's Cambrian to Devonian strata in the past (Jiang and Han, 1995; Wang and Han, 1997; Han and Wang, 2000a; Han, 2006; Han and Zhang, 2006; Han and Chen, 2007; Chen et al., 2008; Chen, 2011; Sun et al., 2013), and the classification of exuvial modes has been studied (Han and Wang, 2000b). There are abundant Ordovician trilobites in Hubei Province, but few reports on exuvial specimens and correlation research. Only photographs of exuvial specimens were attached to the identification of genera and species in the paleontological literatures; these exuvial specimens have not been systematically described, their patterns have not been classified and explained, and the behavioral strategy of these trilobites during molting has not been analyzed (Han and Wang, 2000b). Here, I collected many exuviae of *Ovalocephalus tetrasulcatus* (Phacopida, Pliomeridae) from the Upper Ordovician in central Hubei. Some of the specimens were found with two or three in a line, or preserved partly or even completely overlapping; these patterns are regarded as representing the active behavior of trilobites during molting, and may be related to the herding behavior of trilobites. They provide new materials and understanding for the study of the exuvial techniques of trilobites, and the behavioral responses of trilobites during molting.

Materials & Methods

All specimens were collected from the Upper Ordovician Linhsiang Formation of the Daozimiao section in Jinshan County, central Hubei (Fig. 1). The Linhsiang Formation is widely distributed in the middle Yangtze region, and is mainly composed of yellow-green calcareous mudstones with a few siliceous mudstones in the Daozimiao section, but differs from the nodular muddy limestones of the Linhsiang Formation in the type section in Linxiang, Hunan Province. In the Daozimiao section, the Linhsiang Formation is conformably underlain by the muddy limestones of the Upper Ordovician Pagoda Formation and overlain by the graptolite shales of the Upper Ordovician Wufeng Formation. The 1.5-m-thick calcareous mudstones from the top of the

Linhsiang Formation (Fig. 1d) yield trilobites with the high abundance and diversity, including members of the Metagnostidae, Cyclopygidae, Phillipsinellidae, Encrinuridae, Telephinidae, Raphiophoridae, Cheiruridae, Dionididae, Trinucleidae, Asaphidae, Pliomeridae, and Remopleurididae. In addition, the Foliomena fauna (brachiopods) (Zhan and Jin, 2005), ostracods, echinoderms, and machaerids are also found in the same horizon. Based on the trilobite assemblage, the age of the top of the Linhsiang Formation is constrained to the middle Kaitian (early Ashgill), and the deposits formed in a relatively deepwater environment based on the characteristics of the brachiopod association (Zhan and Jin, 2005).

There is only one species of pliomerid in the Linhsiang Formation of Jingshan, named *Ovalocephalus tetrasulcatus* (Kielan 1960). *Ovalocephalus* is an important trilobite genus largely restricted to peri-Gondwana, and is widely distributed in the Ordovician of China (Zhou et al., 2010). In the Linhsiang Formation of Jingshan, most specimens of *Ovalocephalus tetrasulcatus* are articulated or nearly articulated exoskeletons, as well as enrolled specimens; only a few specimens are scattered cephala, pygidia, and thoracic segments. This pattern reflects that the trilobites were not transported long distances by currents before burial, and were buried quasi-in situ. I collected more than 100 specimens containing articulated or nearly articulated exoskeletons from the calcareous mudstones at the top of the Linhsiang Formation of Jingshan, including 13 specimens that showed two exoskeletons end to end or overlapping together, and three specimens that showed three exoskeletons end to end or two of them overlapping together, which obviously differed from isolated single exoskeletons preserved in the same horizon. The fossils in Fig. 2 were whitened with magnesium oxide powder, and all photographs were captured using a Nikon D5100 camera with a Micro-Nikkor 55 mm F3.5 lens. The axial azimuth measurements of the trilobites and the rose chart were completed in CorelDRAW X7.

Results

In the above materials, complete exoskeletons included all specimens with articulated cephala, thoraces, and pygidia or enrolled exoskeletons, indicating that they are fossilized corpses of *Ovalocephalus tetrasulcatus*. Among these nearly complete exoskeletons, a portion of them are articulated thoraces and pygidia, but with the cephala separated and preserved nearby (Fig. 2a), which are considered exuviae (Han and Wang, 2000b). Another kind has librigenae separated from the cranidia, but the cranidia and thoracopygidia are still articulated, or the cranidia are separated from the thoraces and slightly rotated. These specimens include those with two librigenae separated from cranidia, but still preserved nearby (Fig. 2b), and a portion of these librigenae were inverted or rotated (Fig. 2d); in addition, some specimens has one librigena separated from the cranidium and inverted, but another still in situ (Fig. 2c). Both types of inverted or rotated librigenae separated from the cranidium are similar to the exuvial mode of many trilobites (Henningsmoen,1975; McNamara and Rudkin, 1984), indicating that they are most likely exuviae of *Ovalocephalus tetrasulcatus*, rather than corpses that were broken up by currents. This indicates that there is more than one exuvial mode in *Ovalocephalus tetrasulcatus*; i.e., separation of the cephalon from the thoracopygidium, separation of the librigenae from the

cranidium, or both existing at the same time. A similar diversity of exuvial patterns has been found in other phacopid trilobites (Brandt, 1993; Budil and Bruthansová, 2005; Chen, 2011). In the sixteen specimens with two or three exoskeletons partly superimposed or end to end, all the specimens show separation of the cephalon or librigenae, and the separated cephala or librigenae are still preserved near the thoracopygidia (Fig. 3), indicating that all of these specimens are exuviae of *Ovalocephalus tetrasulcatus*. The central axis of the most frontal *Ovalocephalus tetrasulcatus* in the exuvial clusters was used as the directrix to calculate the axial azimuth of the posterior trilobites. The results showed that there was an obvious dominant orientation; that is, the axial azimuth of the trilobites in these clusters had obvious consistency (Fig. 4), indicating they were not the result of accidental burial events. The separated librigenae preserved near the cranidia may also preclude them from being the result of postmortem transport. Therefore, these exuviae are inferred to have been caused by the active behavior of trilobites.

Discussion

Possible causes of coupled exuviae

Preservation of two together preserved *Ovalocephalus tetrasulcatus* together is similar to preservation of an arthropod in the middle of the act of molting (García-Bellido and Diamond, 2004), but the latter case includes one corpse and one exuvia, whereas all these specimens from Jingshan are exuviae, without corpses; thus, the possibility that the *Ovalocephalus tetrasulcatus* individuals were buried when molting can be excluded. Several cases of queuing of trilobites have been reported in the past, but most of these case are corpse fossils, and the number of trilobites is typically more than three; thus, they are regarded as representing unexpected burial during the migration of trilobites (Radwański et al., 2009; Błażejowski et al., 2016; Vannier et al., 2019). Chatterton and Fortey (2008) reported trilobites aligned for molting, but they were preserved in burrows. In Jingshan, there are no biological burrow near the *Ovalocephalus tetrasulcatus* specimens, and the number of exuviae per specimens is only two or three, in contrast with the former. Since Speyer and Brett (1985) first reported synchronous ecdysis in Middle Devonian phacopids in New York, this behavior has been identified in some other trilobites (Paterson et al. 2007), usually with many trilobites concentrated in a certain place to shed their shells, which is thought to be related to gregarious behavior and is probably associated with the copulation and reproduction of trilobites (Speyer, 1990). A similar pattern may exist in *Ovalocephalus tetrasulcatus*, and pairs of exuviae are relatively easy to understand for mating behavior after molting. However, there are obvious differences of sizes in some exuviae in the same cluster (Fig. 3d). Moreover, there are also cluster with three exuviae (Fig. 3g–i); thus, so it is difficult to explain these exuvial clusters as the result of molting–mating behavior. A single trilobite molting repeatedly in the same place has also been reported (Zwanzig and Liebermann, 2012), but the sizes of exuviae may be similar or vastly different in the exuvial clusters from Jingshan (Fig. 3); for trilobites that grow by molting, it seems difficult to explain these specimens as products of repeated molting.

I speculate that these specimens may reflect a particular exuvial behavior of *Ovalocephalus tetrasulcatus*; because superposition (Fig. 3b) and even almost complete overlapping (Fig. 3c, h–i) exist in the exuvial cluster, it is unlikely that two or three trilobites shed their shells synchronously. Instead, they may have shed their shells in lines; that is, after one trilobite finished molting, the others shed their shells as well. Alternatively, perhaps the first trilobite finished molting and left an empty shell, and then latter, other trilobites come to the same place to molt. The consistency of the long axes of the exuviae may be related to the seabed topography at that time; for example, molting could have occurred in a narrow shallow gully or on a gentle slope. This is may have been somewhat similar to the molting of extant cicadas on trees, where they occasionally molt in line or overlapping (Fig. 5).

Implications for the behavioral strategy of trilobites

Arthropods are weak during and after molting, which leaves them vulnerable to predators and even other members of their species. Living shrimps and crabs usually hide in rock crevices or water plants for molting. Trilobites would also have needed a quiet and undisturbed environment when they shed their shells (Henningsmoen, 1975; Han, 2006). For example, some trilobites used the empty shells of cephalopods and gastropods as shelter for molting (Brandt, 1993; Davis et al., 2001; Zong et al., 2016), some even shed their shells under the empty shells of larger trilobites (Gutiérrez-Marco et al., 2009), and others molted in burrows of other animals (Chatterton et al., 2003; Chatterton & Fortey, 2008). The Upper Ordovician strata in Jingshan have yielded a large number of cephalopods, and I also found nautilus fossils in the Linhsiang Formation. These predators would have threatened great harm to molting trilobites, and the trilobites therefore would have needed to find safe places for ecdysis. However, when there was no shelter on the seafloor, or insufficient space to hide, possibly, they may have chosen to follow congeneric trilobites nearby to molt; alternatively, the remaining exuviae of other trilobites might have suggested that the location was suitable or safe for molting, thus attracting the later trilobites to molt in the same position, thus forming exuvial clusters. It is worth noting that there are only two or three exuviae in each cluster, which may be because the posterior trilobites adopted the principle of proximity when choosing the molting site. This is similar to the herding behavior of animals in crisis situations, indicating that *Ovalocephalus tetrasulcatus* would take the initiative to choose the nearest safe area to carry out vulnerable life activities.

Conclusions

The exuviae of *Ovalocephalus tetrasulcatus* from the Upper Ordovician Linxiang Formation presented two types: separation of the librigenae from the cranidium, and separation of the cephalon from the thoracopygidium, reflecting the diversity of the exuvial modes. Some specimens have two or three exuviae arranged end to end, and some have partly and even completely superimposed exuviae together in clusters. The preserved patterns and burial conditions indicate that these specimens are products of the active behavior of trilobites, rather than mechanical transport by currents, unexpected burial in the middle of the act of molting, repeated ecdysis of the same trilobite, or collective molting before mating. The preserved

patterns and overlapping phenomena of the exuviae indicate that these clusters were formed by two or three trilobites lining up to shed their shells in a long and narrow feature of seafloor topography. They likely represent the behavioral response that the trilobites chose to follow in a crisis situation, indicating that herding behavior existed in these Ordovician trilobites.

Acknowledgements

I would like to thank Qi Liu from Changsha, Hunan, and Guogang Zhang, Qingsong Gao, and Yang Xu, all from Wuhan, Hubei for their help in the field work.

References

Błażejowski B, Brett CE, Kin A, Radwański A, Gruszczyński M. 2016. Ancient animal migration: a case study of eyeless, dimorphic Devonian trilobites from Poland. *Palaeontology* **59:** 743–751 DOI 10.1111/pala.12252.

Brandt DS. 1993. Ecdysis in *Flexicalymene meeki* (Trilobita). *Journal of Paleontology* **67:** 999–1005 DOI 10.1017/S0022336000025312.

Budil P, Bruthansová J. 2005. Moulting in Ordovician dalmanitoid and acastoid trilobites of the Prague Basin. Preliminary observation. *Geologica Acta* **3:** 373–383.

Chatterton BDE., Collins DH, Ludvigsen R. 2003. Cryptic behaviour in trilobites: Cambrian and Silurian examples from Canada, and other related occurrences. *Special Papers in Palaeontology* **70:** 157–173.

Chatterton BDE, Fortey RA. 2008. Linear clusters of articulated trilobites from Lower Ordovician (Arenig) strata at Bini Tin Zoulin North of Zagora, southern Morocco. In: Rábano I, Gozalo R, García-Bellido D, eds. *Advances in trilobite research*. Madrid: Cuadernos del Museo Geominero, 9. Instituto Geológico y Minero de España, 73–78.

Chen GY, Han NR, Zhao YL. 2008. Moulting of the Cambrian trilobite *Oryctocephalus indicus* (Reed, 1910). *Earth Science—Journal of China University of Geosciences* **33:** 783–792.

Chen GY. 2011. *The Silurian trilobite Coronocephalus gaoluoensis Wu from western Hunan: its features, exuviation and abnormalities.* Chinese University of Geosciences, Wuhan, Ph.D. thesis.

Daley AC, Drage HB. 2016. The fossil record of ecdysis, and trends in the moulting behaviour of trilobites. *Arthropod Structure & Development* **45:** 71–96 DOI 10.1016/j.asd.2015.09.004.

Davis RA, Fraaye RHB, Holland CH. 2001. Trilobites within nautiloid cephalopods. *Lethaia* **34:** 37–45.

Fortey R. 2014. The palaeoecology of trilobites. *Journal of Zoology* **292:** 250–259 DOI 10.1111/jzo.12108.

García-Bellido DC, Collins DH. 2004. Moulting arthropod caught in the act. *Nature* **429:** 40 DOI 10.1038/429040a.

Gutiérrez-Marco JC, Sá AA, García-Bellido DC, Rábano I, Valério M. 2009. Giant trilobites and trilobite clusters from the Ordovician of Portugal. *Geology* **37:** 443–446 DOI 10.1130/G25513A.1.

Han NR, Chen GY. 2007. Moulting variability in the Middle Devonian trilobite Ductina from Nandan,Guangxi, China. *Acta Palaeontologica Sinica* **46:** 167–182.

Han NR. 2006. Techniques of exuviations in *Euloma changshanense* Lu (Trilobita) and its palaeoenvironmental significance. *Journal of Palaeogeography* **8:** 17–22.

Han NR, Wang JL. 2000a. Techniques of exuviation in *Hypermecaspis* (Trilobita). *Acta Palaeontologica Sinica* **39:** 419–424.

Han NR, Wang JL. 2000b. The exuvie of trilobites in the literature of palaeontology of China. *Journal of Guilin Institute of Technology* **20:** 137–146.

Han NR, Zhang S. 2006. Taphonomic and molting study of *Leonaspis guangxiensis* Zhou in Zhou and Liu, 1977. *Acta Palaeontologica Sinica* **45:** 108–111.

Henningsmoen G. 1975. Moulting in trilobites. *Fossils and Strata* **4:** 179–200.

Jiang YW, Han NR. 1995. Techniques of exuviation in *Shabaella fengzuensis* (Trilobita). *Acta Palaeontologica Sinica* **34:** 509–517.

McNamara KJ, Rudkin DM. 1984. Techniques of trilobite exuviations. *Lethaia* **17:** 153–173 DOI 10.1111/j.1502-3931.1984.tb01722.x.

Moussian B. 2013. The arthropod cuticle. In: Minelli A, Boxshall G, Fusco G, eds. *Arthropod Biology and Evolution: Molecules, Development, Morphology*. Berlin, Heidelberg: Springer, 171–196.

Paterson JR, Jago JB, Brock GA, Gehling JG. 2007. Taphonomy and palaeoecology of the emuellid trilobite *Balcoracania dailyi* (early Cambrian, South Australia). *Palaeogeography, Palaeoclimatology, Palaeoecology* **249:** 302–321 DOI 10.1016/j.palaeo.2007.02.004.

Radwański A, Kin A, Radwański U. 2009. Queues of blind phacopid trilobites *Trimerocephalus*: a case of frozen behaviour of Early Famennian age from the Holy Cross Mountains, Central Poland. *Acta Geologica Polonica* **59:** 459–481.

Rustán JJ, Balseiro D, Waisfeld B, Foglia RD, Vaccari NE. 2011. Infaunal molting in trilobita and escalatory responses against predation. *Geology* **39:** 495–498 DOI 10.1130/G31879.1.

Speyer SE. 1985. Moulting in phacopid trilobites. *Transactions of the Royal Society of Edinburgh, Earth Sciences* **76:** 239–253 DOI 10.1017/S0263593300010476.

Speyer SE. 1990. Gregarious behavior and reproduction in trilobites. In: Boucot AJ, ed. *Evolutionary Paleobiology of Behavior and Coevolution*. Amsterdam: Elsevier, 405–409.

Speyer SE, Brett CE. 1985. Clustered trilobite assemblages in the Middle Devonian Hamilton Group. *Lethaia* **18:** 85–103 DOI 10.1111/j.1502-3931.1985.tb00688.x.

Sun ZY, Yang XL, Zhao YL, Zheng HL, Zhu YJ. 2013. Exuviation of trilobite *Protoryctocephalus arcticus* from the Cambrian Tsinghsutung Formation of Guizhou. *Acta Palaeontological Sinica* **52:** 256–264.

Vannier J, Vidal M, Marchant R, Hariri KE, Kouraiss K, Pittet B, Albani AE, Mazurier A, Martin E. 2019. Collective behaviour in 480-million-year-old trilobite arthropods from Morocco. *Scientific Reports* **9:** e14941, DOI 10.1038/s41598-019-51012-3.

Wang JL, Han NR. 1997. Moulting in *Plagiolaria* (Trilobita) from the Lower Devonian of China. *Geobios* **30:** 831–834 DOI 10.1016/S0016-6995(97)80184-2.

Whittington HB. 1990. Articulation and exuviations in Cambrian trilobites. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **329:** 27–46 DOI 10.1098/rstb.1990.0147.

Zhan RB, Jin JS. 2005. New data on the *Foliomena* fauna (Brachiopoda) from the Upper Ordovician of South China. *Journal of Paleontology* **79:** 670–686 DOI 10.1666/0022-3360(2005)079[0670:NDOTFF]2.0.CO;2.

Zhou ZQ, Zhou ZY, Xiang LW. 2016. *Trilobite fauna from the Ordovician Pagoda Formation of central and western Yangtze block, China*. Beijing: Geological Publishing House.

Zhou ZY, Yuan WW, Zhou ZQ. 2010. Evolutional trends and palaeobiogeography of the Ordovician trilobite *Ovalocephalus* Koroleva 1959. *Proceedings of the Royal Society B, Biological Sciences* **277:** 257–266 DOI 10.1098/rspb.2009.0133.

Zong RW, Fan RY, Gong YM. 2016. Seven 365-Million-Year-Old Trilobites Moulting within a Nautioid Concn. *Scientific Reports* **6:** e34914 DOI 10.1038/srep34914.

Zong RW, Gong YM. 2017. Behavioural asymmetry in Devonian trilobites. Palaeogeography, Palaeoclimatology, *Palaeoecology* **476:** 158–162 DOI 10.1016/j.palaeo.2017.04.003.

Zwanzig M, Liebermann S A. 2012. Silurian Bohemoharpes twice used an empty shell of an orthocone nautiloid as refuge for moulting. In: Budil P, Fatka O, eds. *The 5th Conference on Trilobites and their relatives*. Prague: Czech Geological Survey, 58.

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.

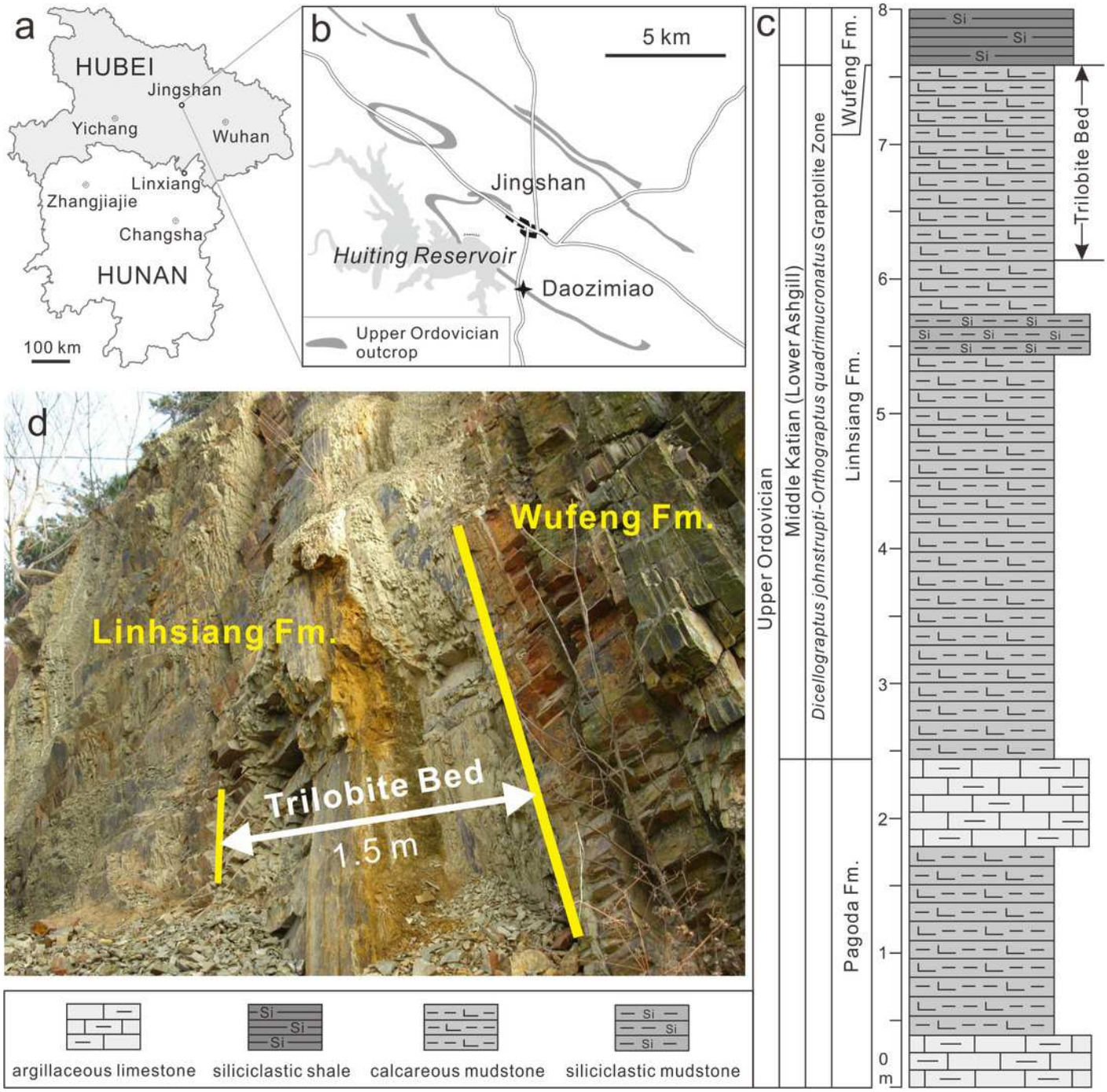
a
HUBEI
Jingshan
Yichang
Wuhan
Linxiang
Zhangjiajie
Changsha
HUNAN
100 km
b
5 km
Jingshan
Huiting Reservoir
Daozimiao
Upper Ordovician outcrop
c
Upper Ordovician
Middle Katian (Lower Ashgill)
Dicellograptus johnstrupti-Orthograptus quadrimucronatus Graptolite Zone
Wufeng Fm.
Linhsiang Fm.
Pagoda Fm.
Trilobite Bed
8
7
6
5
4
3
2
1
0
m
d
Wufeng Fm.
Linhsiang Fm.
Trilobite Bed
1.5 m
argillaceous limestone
siliciclastic shale
calcareous mudstone
siliciclastic mudstone

Figure 2

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

a. Cephalon is separated from the enrolled thoracopygidium, 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.

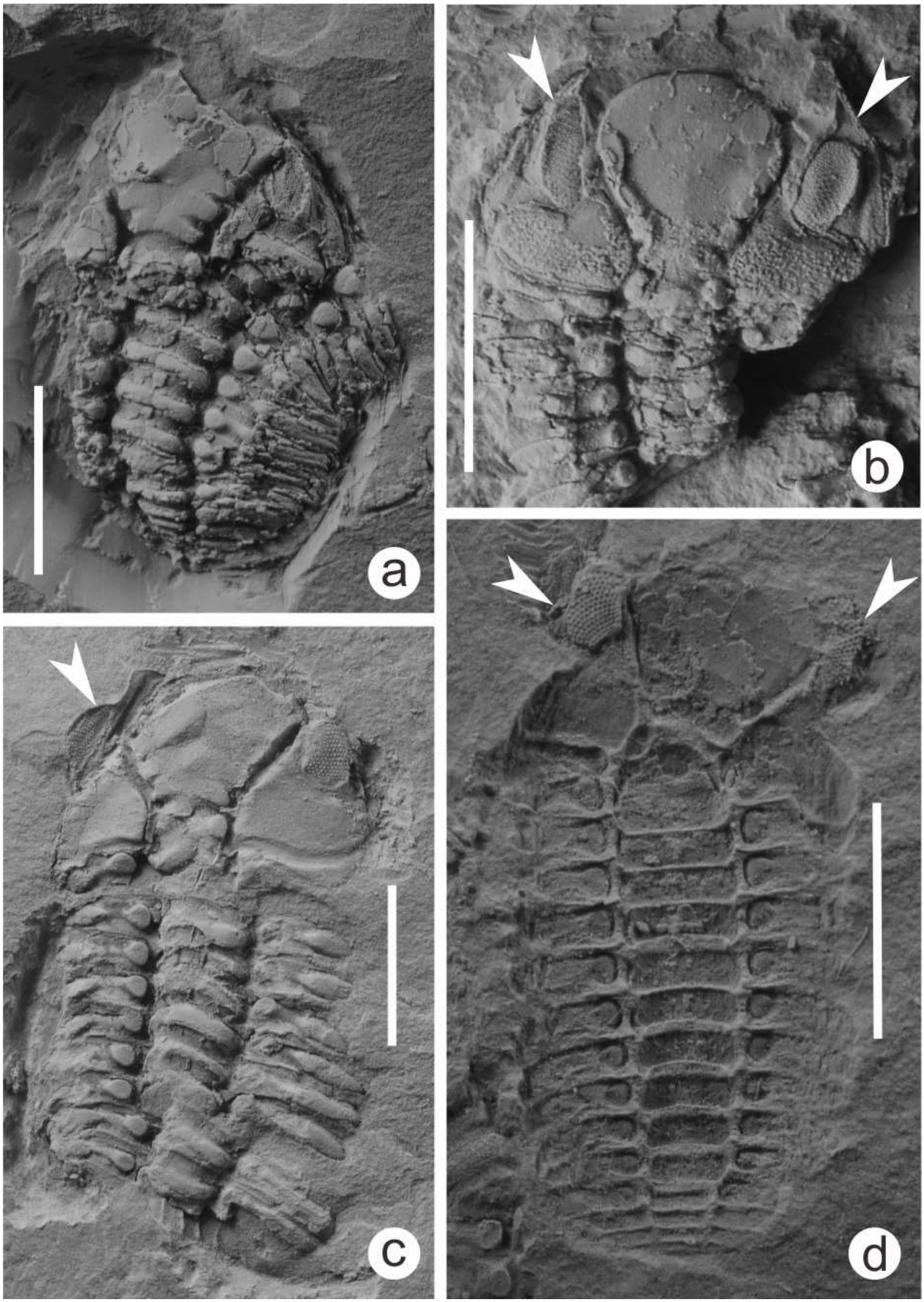
a
b
c
d

Figure 3

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 thoracopygidia, 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

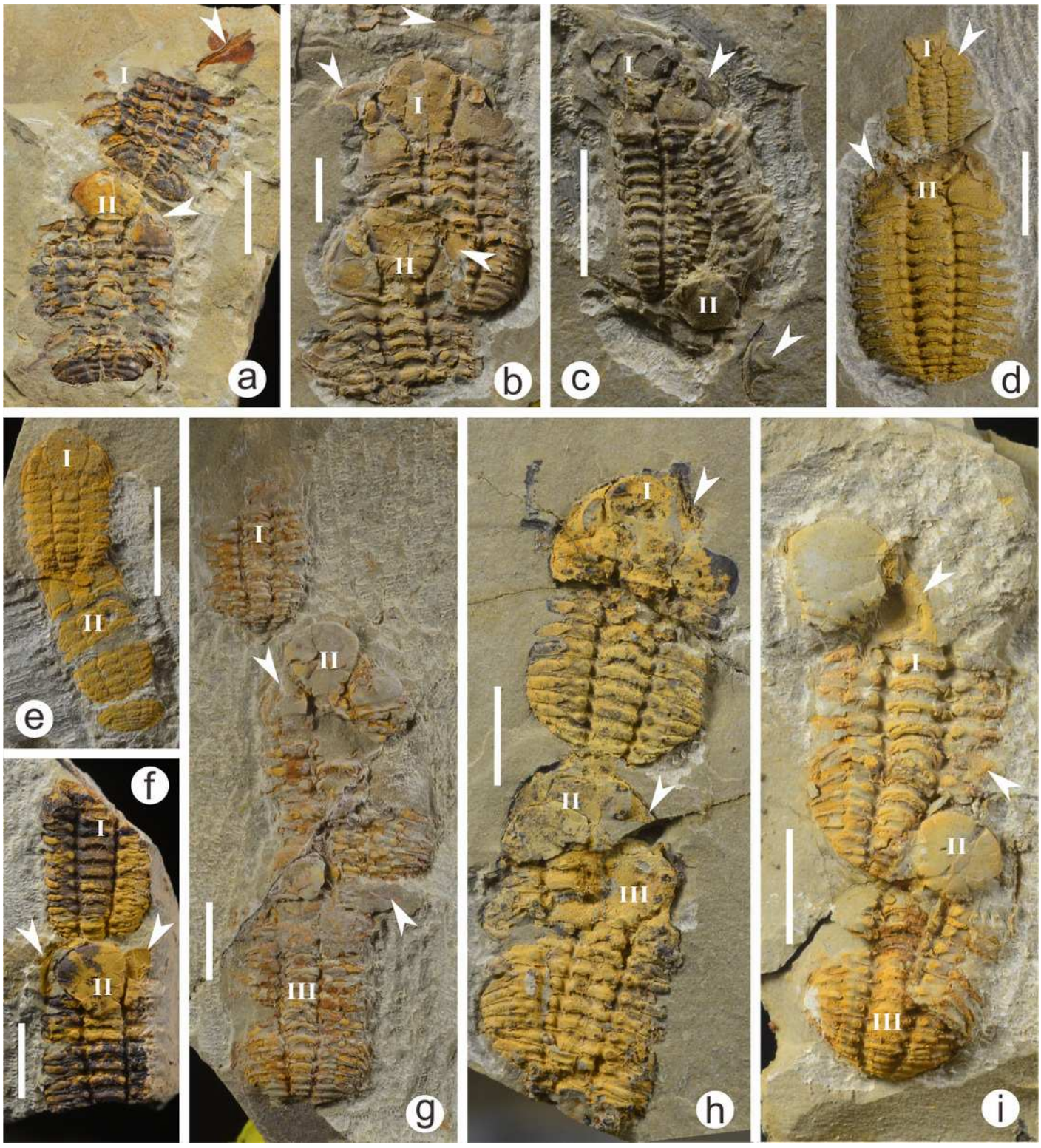
I
II
a
I
II
b
I
II
c
I
II
d
I
II
e
I
II
III
g
I
II
III
h
I
II
III
i
I
II
f

Figure 4

Statistical results of axial azimuth and the corresponding rose diagram 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
Hj01	0°	75.6°	/
Hj02	0°	2.6°	/
Hj03	0°	355.3°	1.7°
Hj04	0°	317.9°	/
Hj05	0°	4.4°	/
Hj06	0°	347.9°	4.4°
Hj07	0°	354.5°	/
Hj08	0°	336.6°	/
Hj09	0°	342.5°	/
Hj10	0°	354.7°	/
Hj11	0°	163.8°	/
Hj12	0°	33°	/
Hj13	0°	30°	/
Hj14	0°	345.6°	/
Hj15	0°	12.1°	3°
Hj16	0°	10.8°	/

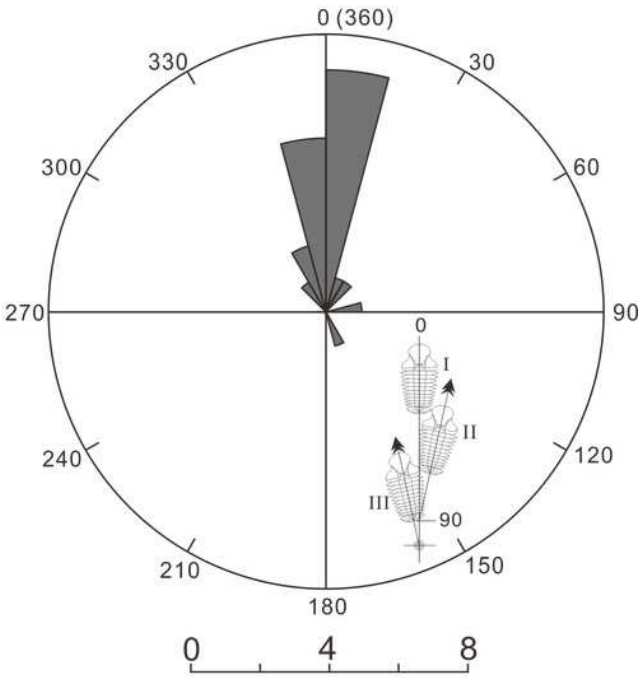

Figure 5

The exuvial behavior of extant cicadas

a. cicada is moulting near an empty shell, picture from http://www.mafengwo.cn/i/5409738.html (photographed by Bobo)b. cicada is moulting overlap on an empty shell, picture from http://bbs.zol.com.cn/dcbbs/d18_46288_0.html (photographed by Muchen)