Palaeogeography, Palaeoclimatology, Palaeoecology 520 (2019) 163–172

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

A poorly preserved fish-like animal from the Chengjiang Lagerstätte (Cambrian Series 2, Stage 3)

Jun Zhao[a,b], Guo-Biao Li[a,b,*], Paul A. Selden[c,d]

[a] State Key Laboratory of Environmental Geology and Biogeology, China University of Geosciences, Beijing 100083, China
[b] School of Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China
[c] Department of Geology, University of Kansas, 1457 Jayhawk Boulevard, Lawrence KS66045, USA
[d] Natural History Museum, Cromwell Road, London SW7 5BD, UK

ARTICLE INFO

Keywords:
Myllokunmingiid
Organic decay
Slow accumulation
Event mudstone beds

ABSTRACT

Specimens of a poorly preserved animal, including individuals and body parts, have been discovered from the Chengjiang Lagerstätte. These specimens are interpreted to be a fish-like animal and are described as an unnamed myllokunmingiid. The morphologies and preservation of individuals and body parts are described, and the relative decay patterns are briefly discussed. These specimens are from the event mudstone beds of the Maotianshan Shale Member, but exhibit the classic preservation of organisms in the background mudstone beds: slow accumulation, and this might indicate that different preservation modes of organisms co-exist in the event mudstone beds. Based on the facts that lenses cannot be discerned on all the specimens of myllokunmingiids, their visual organs may have been more like eyespots than true eyes.

1. Introduction

More than three decades have passed since the first soft-bodied fossils from the Chengjiang Lagerstätte were discovered, during which time countless fossils in high-quality preservation have been excavated and described. The sedimentology and taphonomy of the Chengjiang Lagerstätte have also been described and discussed (Zhu et al., 2001, 2005; Hu, 2005; Zhao and Zhu, 2007; Zhang et al., 2008; Zhao et al., 2009, 2012a), and it was concluded that a series of superimposed couplets of background and event mudstone beds in the Chengjiang deposits were the main beds to produce the Chengjiang fossils (Zhao and Zhu, 2007; Zhao et al., 2009, 2012a). The background mudstone beds represent normal sedimentation and slow accumulation (Zhu et al., 2001; Hu, 2005; Zhao et al., 2009), fossils from which generally exhibit a certain degree of decay (Hu, 2005). The event mudstone beds represent distal mud tempestites (Zhu et al., 2001; Hu, 2005) and rapid sedimentation (Hu, 2005), fossils from which are generally in a high quality of preservation with almost complete hard parts (e.g. tergites of arthropods) and soft tissues (e.g. eyes, limbs).

Primitive fish-like animals (Shu et al., 1999) were among the most fascinating discoveries of the Chengjiang Lagerstätte; they have been further investigated and, to some extent considered to be representatives of early vertebrates (e.g. Javier, 1999; Holland and Chen, 2001; Hou et al., 2002; Shu et al., 2003; Conway Morris and Caron, 2014; Williams et al., 2016). To date, three genera (*Myllokunmingia*, *Haikouichthys*, *Zhongjianichthys*), one family (Myllokunmingiida) and one order (Myllokunmingiidae) have been erected (Shu et al., 1999, Shu, 2003). Likewise, these primitive fish-like animals also came from the event mudstone beds and are preserved in almost complete form with internal organs. Distinguished from these well-preserved ones, the fossils documented and illustrated herein are rather poorly preserved: all have suffered mass decay, none is in complete profile, and body parts are separately preserved, although the host rocks also belong to the event mudstone beds. After all the body parts are fitted back together, like a jigsaw puzzle, the identity of these fossils is revealed as a fish-like animal. Comparative analysis between decay patterns of these body remains and the data of decay experiments on extant chordates (Sansom et al., 2011, 2013) reveals that all these fossils belong to later stages of decay, with some even beyond the last stage. In other words, these fish-like animals experienced different timespans of decay prior to burial, indicating that they possibly died at different times. Therefore, these specimens possibly represent a process of slow accumulation, the classic preservation mode of organisms in the background mudstone beds. These provide new evidence for re-investigating the preservation of the fossils in the event mudstone beds of the Chengjiang deposits: different preserving modes may co-exist (rapid burial is accompanied by slow accumulation), at least in the preservation of fish-like animals. The absence of lenses indicates that the eyes of myllokunmingiids might

* Corresponding author at: State Key Laboratory of Environmental Geology and Biogeology, China University of Geosciences, Beijing 100083, China.
E-mail addresses: zhaojunpaleo@126.com (J. Zhao), liguobiao@cugb.edu.cn (G.-B. Li), selden@ku.edu (P.A. Selden).

https://doi.org/10.1016/j.palaeo.2019.02.005
Received 2 November 2018; Received in revised form 6 February 2019; Accepted 6 February 2019
Available online 10 February 2019
0031-0182/

be close to eyespots instead of true eyes. The morphology and preservation of all the specimens are described and discussed below.

2. Materials and methods

2.1. Materials

The fossils described herein were collected in the first three months of 2018, and comprise two slabs with many individuals (YN-JS-200) and body parts (YN-JS-201) and one slab (YN-JS-202) with only one individual being preserved. All specimens came from the event mudstone beds of the Maotianshan Shale Member of the Yu'anshan Formation (Cambrian Series 2, Stage 3, *Eoredlichia-Wutingaspis* Trilobite Assemblage Zone) at the Jianshan section (24.77036°N, 102.57877°E), the same section with *Zhongjianichthys*, and ~2 km from the locality where *Haikouichthys* was first discovered, in Haikou, Yunnan Province, China. The Yu'anshan Formation is generally composed of four parts (in ascending order): the Black Siltstone Member, the Black Shale Member, the Maotianshan Shale Member and the Upper Siltstone Member (Chen et al., 1996; Zhu et al., 2001). At the Jianshan section, the Yu'anshan Formation only exposes the first three parts, with the uppermost part being overlain unconformably by the Middle Devonian Haikou Formation and the lowermost part being underlain conformably by the Shiyantou Formaton (Fig. 1).

2.2. Methods

Some individuals were prepared using a fine needle under a binocular microscope, revealing parts covered by the matrix. In order to investigate the sedimentological structures of the host rock, one end of specimen YN-JS-200 was cut perpendicular to the bedding and the cut surface was dry polished with sandpaper. The black patches in the left eye of YN-JS-202 were chosen for energy dispersion spectrum (EDS) analysis. Digital photographs were taken by using a Cannon EOS 5D MkIII camera and 50 mm macro lens, dry under cross-polarized light and processed in Adobe Photoshop CS 6. Line drawings of some specimens were made using CorelDRAW X8. Terminology follows Shu et al. (Shu et al., 1999, 2003; Shu, 2003).

2.3. Repository and institutional abbreviation

The specimens are housed at the School of Earth Sciences and Resources, China University of Geosciences (Beijing) (CUGB). The abbreviations in the specimen number refer to the location of the fossil section (YN, the province of Yunnan; JS, the quarry of Jianshan).

3. Systematic palaeontology

Phylum Chordata Bateson, 1885
Subphylum Vertebrata Lamarck, 1801
Class Agnatha Cope, 1889
Order Myllokunmingiida Shu, 2003
Family Myllokunmingiidae Shu, 2003
Genus and Species uncertain
Figs. 2–8

3.1. Materials

Three slabs (YN-JS-200, YN-JS-201 and YN-JS-202) with many incomplete individuals and body parts preserved.

3.2. Remarks

The identified body parts in the specimens documented herein include the myomeres, eyes, notochord with arcualia, branchial arches and fin-fold. Putting together all the identified body parts, the overall morphology of these specimens can be obtained: a fish-like animal with more-or-less fusiform body, a pair of anteriorly located large eyes, antero-dorsally located notochord, serially arranged myomeres and, all of which basically fit with the diagnoses of Myllokunmingiida and Myllokunmingiidae (Shu, 2003). The identity at genus- or species-level cannot be confirmed due to the absence of some informative body parts, such as dorsal fin with fin-radials, gonads, olfactory organ, pericardial cavity, etc. Therefore, an interpretation of these incomplete individuals and body parts as an unnamed myllokunmingiid is reasonable. Considering these body parts may belong to different myllokunmingiids, this interpretation remains tentative.

4. Preservation and interpretation

4.1. General preservation

Specimen YN-JS-200 is a slab with many individuals preserved superimposed and more or less parallel to the surface of the host rock (Fig. 2A); the exact number of individuals is hard to ascertain. These individuals are randomly positioned and all are incomplete. Only body parts are preserved on specimen YN-JS-201 (Fig. 2B), and specimen YN-JS-202 is a slab with only one individual preserved (Fig. 3A). The exact size of any individual cannot be obtained due to the incompleteness; the most complete one (Fig. 3C) is ~12 mm in length and 1–2 mm in width.

Compared to the specimens of fish-like animals described and documented from Chengjiang biota (Shu et al., 1999; Hou et al., 2002; Shu et al., 2003; Zhang and Hou, 2004), the specimens documented herein have mass traces of decay, which are comparable to those of *Pikaia gracilens* Walcott, 1911 from the Burgess Shale (Conway Morris and Caron, 2012, fig. 5). These decay traces can be discerned from the apparently disorganized myomeres in a flabby S-shape, and obscured surfaces of the remainder of the body, such as the posterior section of YN-JS-200-1 (Fig. 3C) and the anterior section of YN-JS-200-2 (Fig. 4A). YN-JS-200-3 (Fig. 5) is composed of many superimposed individuals, whose bodies are obscured by decay, except for a few eyes. YN-JS-202 (Fig. 3A) exhibits variable levels of decay in the same body: the posterior section is comparatively lightly decayed with myomeres being easily discernible, while the anterior section is heavily decayed with few structures can be clearly identified except for the paired eyes.

4.2. Myomeres

Similar to *Myllokunmingia fenjiaoa* (Shu et al., 1999) and *Haikouichthys ercaicunensis* (Luo et al. in Shu et al., 1999), the unnamed myllokunmingiid described herein also has a 'naked' body, which is mainly composed of the serially arranged myomeres. Among all the preserved body parts, these are the most informative structures and easiest to identify. Individuals on specimens YN-JS-200 and YN-JS-202 show that myomeres are in a slightly flabby S-shape (e.g. Fig. 6A), and are possibly deformed due to decay and the dorsal and ventral margins of the body being missing.

4.3. Eyes

Eyes are the best preserved organs and greatest in number among the body parts. At least 45 eyes can be discerned, most of which are paired (e.g. Fig. 7B–C). Unpaired eyes also exist, but are few in number (e.g. Fig. 7D–E). Generally, most of the eyes, including the paired and unpaired, are preserved separately, and only a few are attached to the body (the assemblage of myomeres herein) (e.g. Fig. 3C), indicating the anterior end of the remains. Among the paired eyes, some are preserved partially overlapped (Fig. 7A), while others are connected by something preserved in a similar way with the eye stains (Fig. 7B–C). The assumed lens in the eyes of *Metaspriggina walcotti* Simonetta and Insom, 1993 (Conway Morris and Caron, 2014, fig. 1.f) another fish-like animal from the Cambrian, cannot be found in the specimens herein, and only one

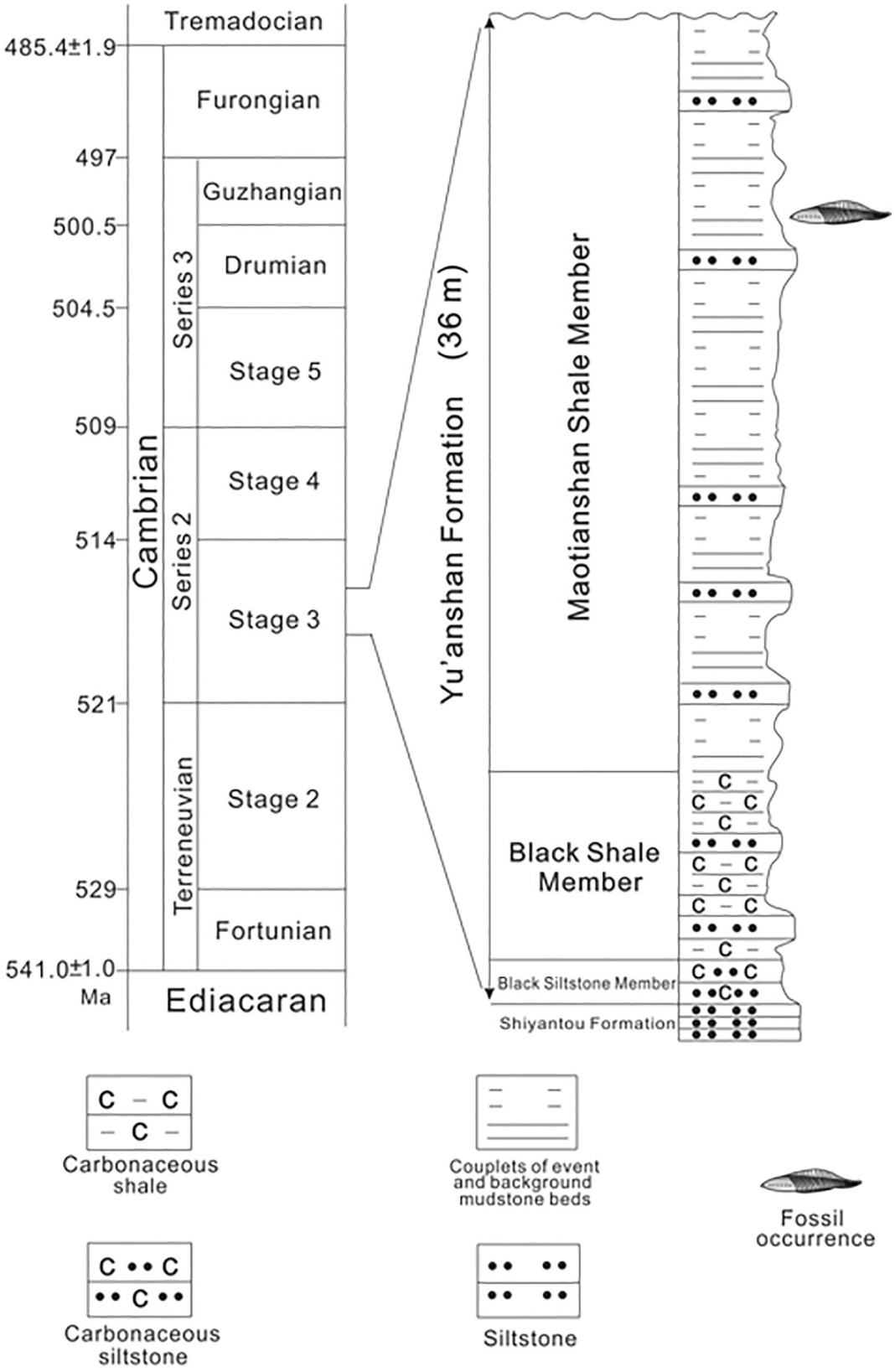

Fig. 1. Simplified schematic stratigraphic column of the Jianshan section.

specimen shows a black circular area located in the center of the eye (Fig. 7A), but it is evidently formed due to the breakdown of the covered mineralized patches.

The organs between the eyes in the fish-like animals from the Chengjiang biota are possibly the nasal sacs seen in *Haikouichthys* and *Zhongjianichthys* (Shu, 2003; Shu et al., 2003). The morphology of the median structures in the specimens herein is apparently different from a nasal sac: two specimens (Fig. 7B–C) show that the eyes are connected

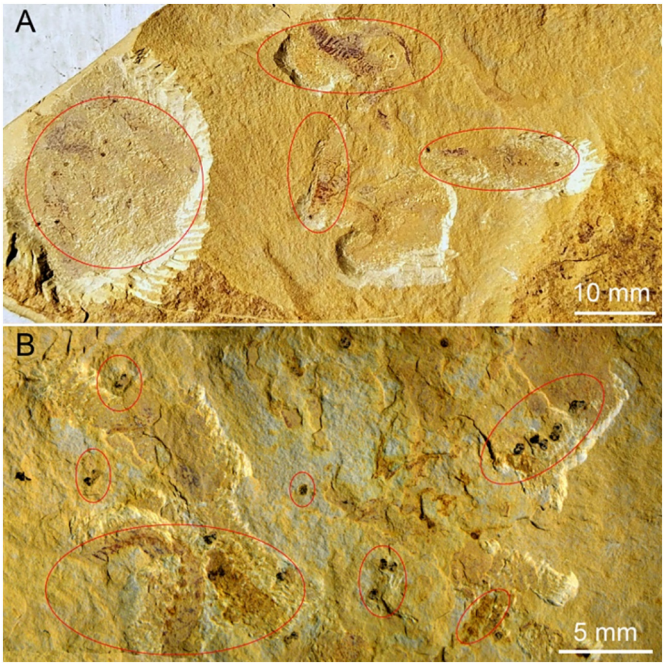

Fig. 2. Two slabs with individuals or body parts preserved in groups.
A. Specimens of incomplete individuals of the unnamed Myllokunmingiid on the slab of YN-JS-200.
B. Specimens of the body parts of the unnamed myllokunmingiid on the slab of YN-JS-201. Red circles indicate fossils on the slabs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

directly by a black band-like unit. These eyes, with an average diameter of 0.5 mm, are sub-circular or oval in shape and covered by black mineralized patches. Some patches have peeled off, exposing the underlying gray-yellow host rock (e.g. Fig. 7B–C).

4.4. Notochord

Specimen YN-JS-200-1 (Fig. 3C–D) shows an incomplete structure: positioned antero-dorsally on the body, it comprises two subcircular parts which are connected together by a cylindrical structure through the center. These structures probably correspond to the arcualia and the notochord respectively seen in *Haikouichthys ercaicunensis* (Shu et al., 2003, fig. 1.g–1.i). Another specimen (YN-JS-201-2, ~2.5 mm in length) is separately preserved and comprises four arcualia and the notochord (Fig. 6B–D).

4.5. Branchial structures

Some incomplete structures (Fig. 3C–D) are preserved antero-ventrally on the individual with the notochord (YN-JS-200-1), including a few curved lines and three sub-oval units with filament-like structures. In terms of the morphology and position on the body, these structures possibly represent the branchial structures discerned in *Haikouichthys ercaicunensis* (Shu et al., 1999; Shu and Chen, 2000; Shu et al., 2003). More specifically, the three sub-oval units with filament-like structures are comparable to the gill pouches and gill filaments identified in *Haikouichthys ercaicunensis* (Shu et al., 1999; Zhang and Hou, 2004). Because of the decay and collapse of the body, these branchial structures might have been displaced from their original positions.

A fragmentary body (Fig. 8A) is preserved on slab YN-JS-201, on which are five subcircular structures (average diameter ~0.5 mm) on

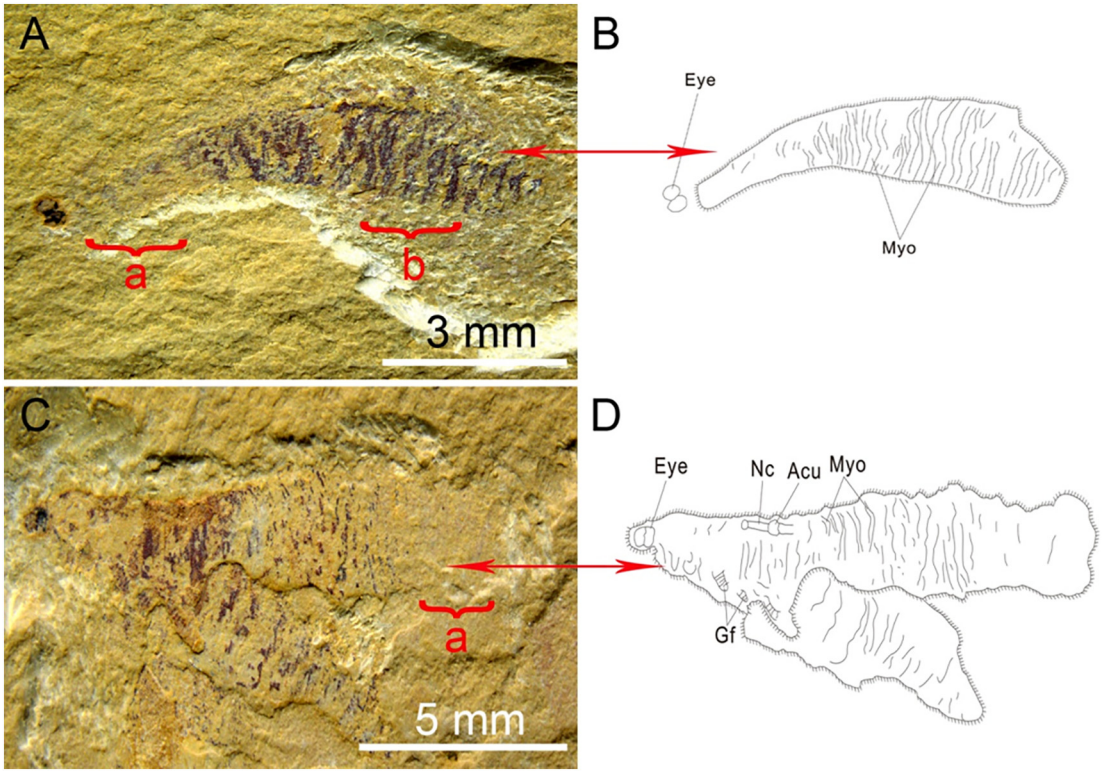

Fig. 3. Specimens of the unnamed myllokunmingiid.
A. Single specimen on the slab of YN-JS-202. Brace (a) refers to the anterior body section suffered comparatively much from decay; brace (b) refers to the posterior body section suffered comparatively less from decay;
B. Line drawing of A;
C. The specimen of YN-JS-200-1; Brace (a) refers to the posterior body surface suffered much from decay;
D. Line drawing of C. Acu, arcualia; Gf, gill filaments; Myo, myomere; Nc, notochord.

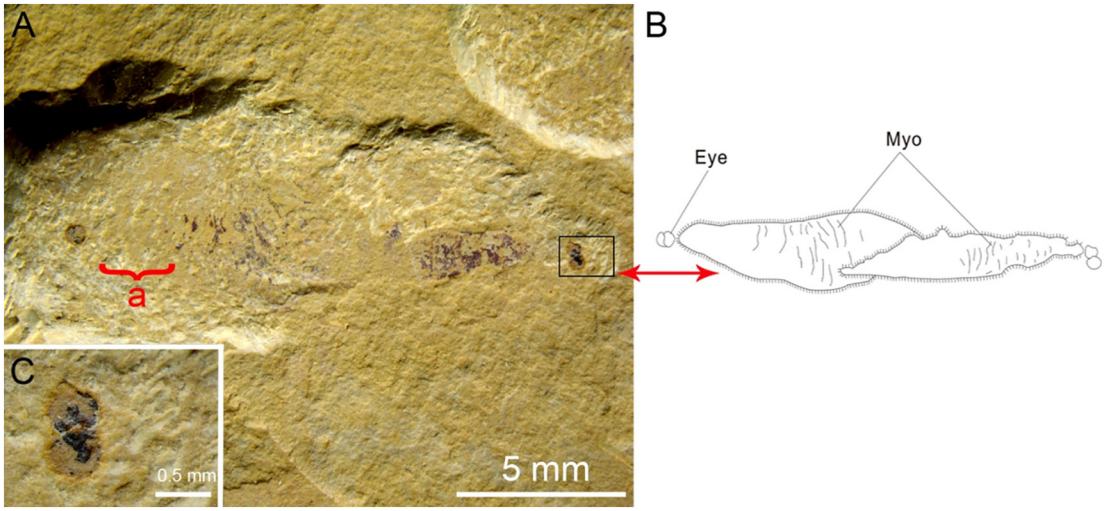

Fig. 4. The specimen of YN-JS-200-2, the unnamed myllokunmingiid.
A. The overall morphology of the specimen. Brace (a) refers to the anterior body surface suffered much from decay;
B. Line drawing of A;
C. Detail of A (position marked by frame). Myo, myomere.

the same horizontal line. No evident connection can be seen in between and, therefore, the possibility of it being the arcualia on the notochord can be removed. Although the exact position for the five units on the body cannot be known, these units are reminiscent of the gill openings in extant lampreys in overall morphology and may have had the same function.

4.6. Fin-fold

A ribbon-like unit attached to a body fragment is preserved on slab YN-JS-200 (Fig. 8B). It is slender in profile and its average width is ~0.8 mm. Although incomplete, the overall morphology of this unit is comparable to the fin-fold seen in *Myllokunmingia fenjiaoa* and *Haikouichthys ercaicunensis* (Shu et al., 1999, 2003; Zhang and Hou, 2004). No evident fin radials can be identified on the surface. Due to the incompleteness and poor preservation, it cannot be confirmed whether it is the dorsal or ventral fin-fold.

5. Discussion

5.1. The most fragmentary specimens of fish-like animals from the Chengjiang Lagerstätte

Shu et al. (1999) first described fish-like animals from the Chengjiang Lagerstätte, including *Myllokunmingia fengjiaoa* and *Haikouichthys ercaicunensis*. The holotype of the former is preserved in a more or less S shape and the body profile is complete; the only incompleteness of the posterior tip was assumed to be formed by post-mortem folding (Shu et al., 1999); the holotype of the latter is almost complete with the posterior region being lost, which was interpreted to possibly represent

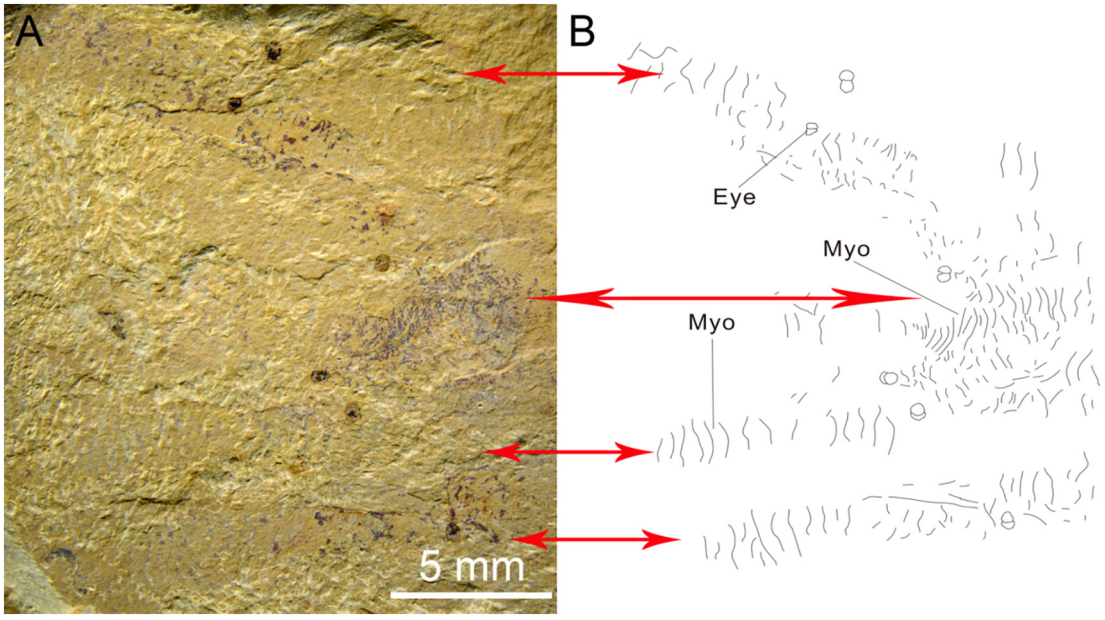

Fig. 5. The specimen of YN-JS-200-3, the superimposed individuals.
A. The overall morphology of the specimen;
B. Line drawing of A. Myo, myomere;

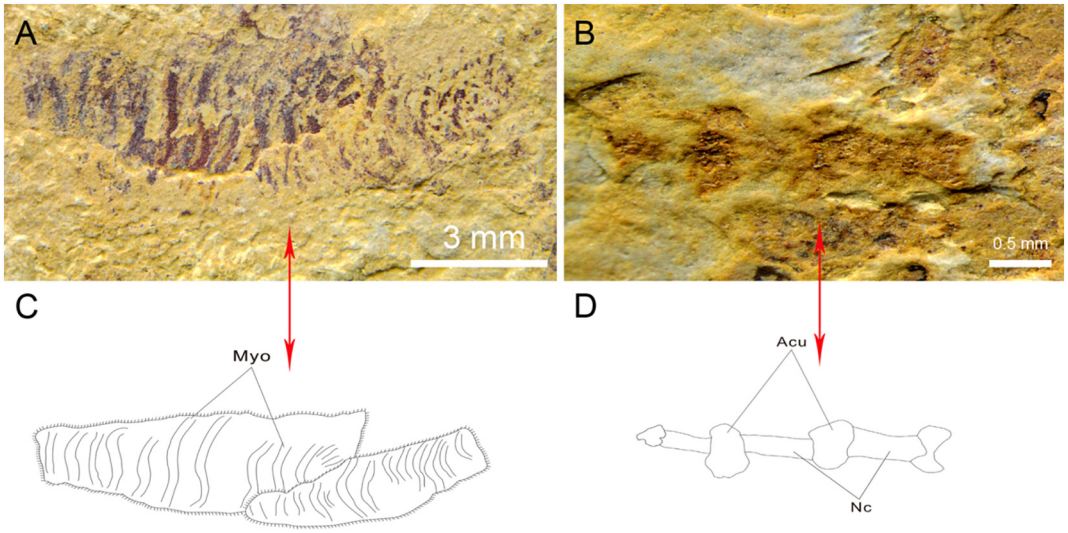

Fig. 6. Specimens of the unnamed myllokunmingiid.
A. The specimen of YN-JS-200-4;
B. The specimen of YN-JS-201-2, a separately preserved notochord;
C. Line drawing of A;
D. Line drawing of B. Acu, arcualia; Myo, myomere; Nc, notochord.

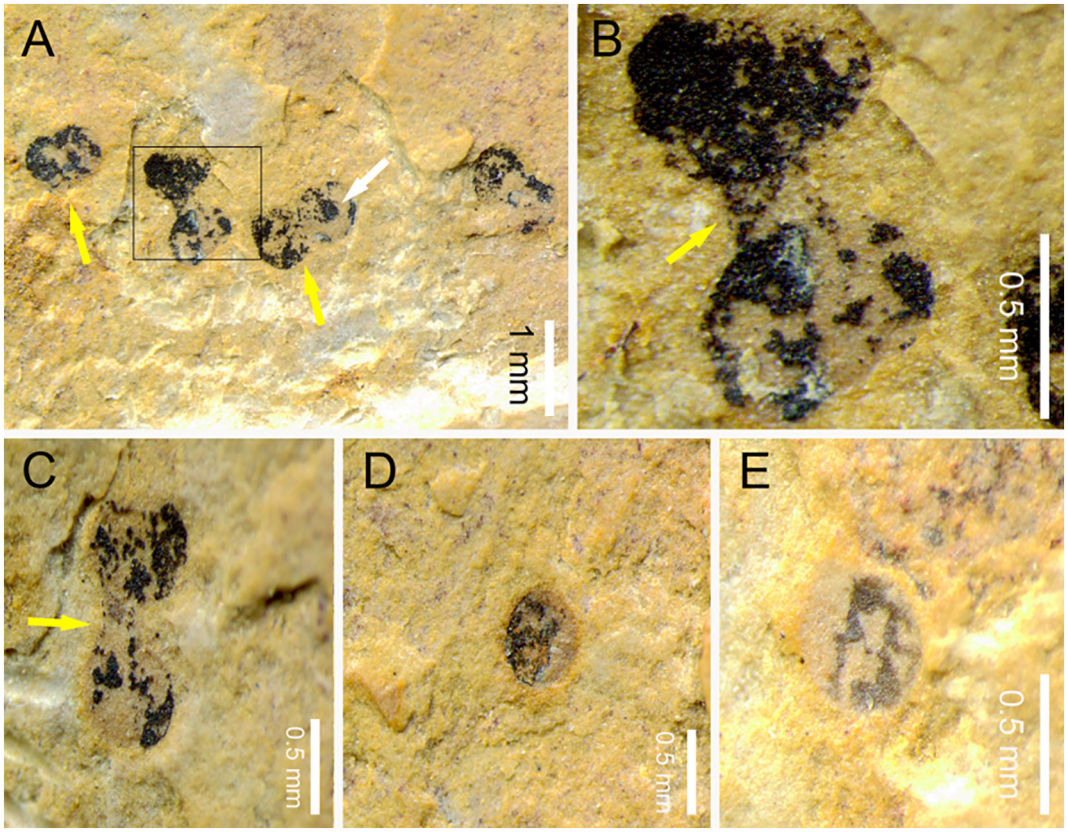

Fig. 7. Separately preserved eyes of the unnamed myllokunmingiid on the slab of YN-JS-201.
A. The specimen of YN-JS-201-4, yellow arrows point to the partially overlapped paired eyes and white arrow points to the circular area;
B. Detail of A (position marked by frame), yellow arrow points to the connection between the eyes;
C. The specimen of YN-JS-201-5, yellow arrow points to the connection between the eyes;
D. The specimen of YN-JS-201-6;
E. The specimen of YN-JS-201-7. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

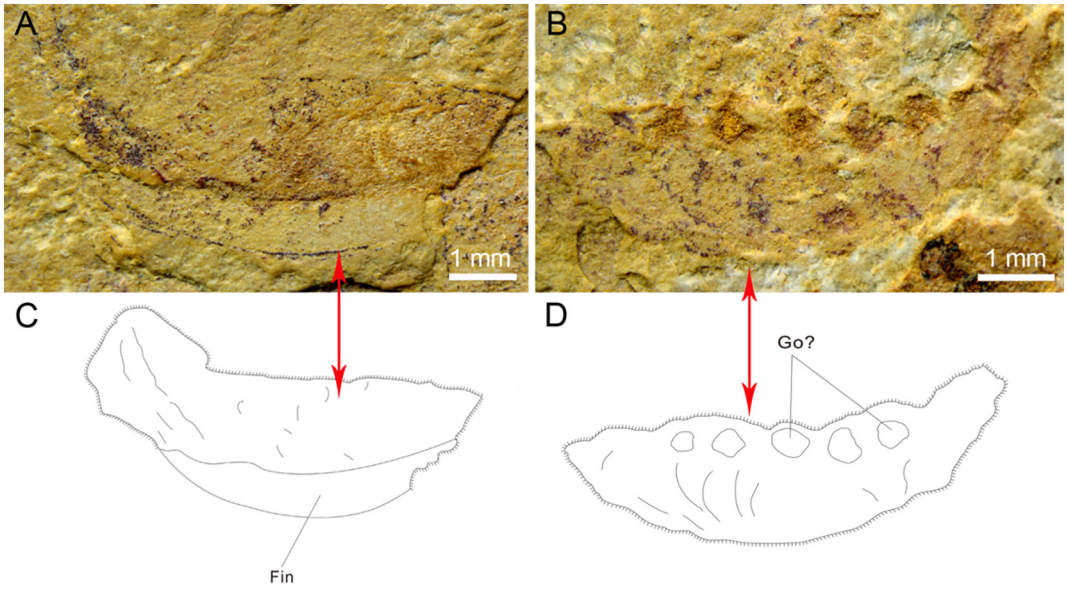

Fig. 8. Specimens of the unnamed myllokunmingiid.
A. The specimen of YN-JS-200-5, the fin-fold of the unnamed myllokunmingiid;
B. The specimen of YN-JS-201-3, the possible gill openings;
C. Line drawing of A;
D. Line drawing of B. Go?, possible gill openings; fin, fin-fold.

decay of the body (Shu et al., 1999; Shu and Chen, 2000). Hou et al. (2002) and Zhang and Hou (2004) restudied the fish-like animals from the same biota, and the described specimens also had almost complete body profiles. In addition, these specimens meticulously captured some internal organs, such as the branchial structures, gonads, gut/intestine, etc. According to the data of decay experiments on chordates (Sansom et al., 2010, 2011, 2013), these characters are decay prone, indicating that these fossils had been buried alive or decayed for a rather limited time before burial.

The specimens described herein are the most poorly preserved and suffered the most decay. Neither body profile nor internal organs have been fully captured. In terms of primitive fish-like animals, the overall preservation of these specimens is similar to *Metaspriggina walcotti* Simonetta and Insom, 1993 (Conway Morris and Caron, 2014), which is also preserved in unpleasant conditions, e.g. some myomeres are highly disorganized because of decay. The morphological decay stage of most of the specimens herein corresponds to stage four or five (late stage of decay) in the decay experiments of Sansom et al. (2010). The preservation of these specimens indicate that this unnamed myllokunmingiid from the event mudstone beds of Maotianshan Shale Member had experienced a rather long period of decay prior to burial, leaving obscured and highly disorganized bodies.

5.2. Decay patterns of individuals and body parts

Purnell et al. (2018) analyzed and discussed the processes of decay, fossilization and preservation of soft-tissues or non-biomineralized tissues of organisms. In addition, Sansom et al. (2011, 2013) conducted decay experiments on extant chordates, and proposed that the resulting data could help recognize and interpret the anatomy of non-biomineralized fossil vertebrates. In analyzing the specimens of the unnamed myllokunmingiid herein, we believe these analyses and data are instructional. The comparative analyses of decay stages of the body remains are discussed below.

Of all the specimens, YN-JS-200-1 (Fig. 3C), YN-JS-200-2 (Fig. 4) and YN-JS-202 (Fig. 3A) preserve both the overall body profile (assemblage of some myomeres herein) and eyes. In addition, YN-JS-200-1 also preserves the notochord with arcualia and branchial structures. Its decay stage roughly corresponds to stage four of the adult lamprey studied by Sansom et al. (2011). Although being preserved together, eyes and body remains are slightly disarticulated from each other on the other two specimens, while the notochord, one of the most decay resistant characters (Sansom et al., 2011, 2013), is not present on either specimen. And this possibly indicates a long-period decay process, during which the notochord might get displaced due to the collapse of the body. The decay stages of these two specimens are beyond the last stage of the decay experiments of Sansom et al. (2011, 2013).

YN-JS-200-3 (Fig. 5) is a specimen with many individuals preserved superimposed. Body profiles have been lost, and only a few myomeres can be discerned. Some paired eyes are preserved on the same specimen, but they are apparently disarticulated from the body remains. The decay stages of these individuals are even higher than those of YN-JS-200-2 and YN-JS-202.

YN-JS-200-4 (Fig. 6A) is a specimen with two body remains being partially overlapped. Nothing but myomeres can be discerned. It is unquestionable that the two individuals are at later stages of decay, and also beyond the last stage.

YN-JS-200-5 (Fig. 8B) preserves a rather obscured body fragment and an attached fin-fold. The overall preservation of this specimen indicates a later stage of decay, similar to YN-JS-200-4. The decay experiments of Sansom et al. (2013) showed that a fin with fin radials is more decay resistant and can persist into the later stages. No traces of fin radials can be discerned on this specimen, which might suggest that without fin radials, the fin-fold of the unnamed myllokunmingiid could also be decay resistant.

YN-JS-201-2 (Fig. 6B) preserves only a notochord with four arculia, which is possibly disarticulated from a decayed body. Although incomplete, the profile of the notochord can be clearly discerned. According to the decay experiments of extant chordates (Sansom et al., 2011, 2013), the notochord is rather decay resistant. This resulting data is confirmed here in the fossil record of the primitive fish-like animal.

YN-JS-201-3 (Fig. 8A) preserves five possible gill openings on a highly fragmentary body. The overall preservation of this specimen also indicates a later stage of decay.

Many eyes, paired and unpaired, are preserved on YN-JS-201 (e.g. Fig. 7). They must have been disarticulated from collapsed bodies, and

this, again, indicates a later stage of decay. Although separately preserved, these eyes are perfect in profile and no apparent traces of loss can be discerned, which indicates a strong resistance against decay.

Based on the analyses above, all the specimens documented herein belong to later stages of decay, among which three more specific stages can be figured out. The first stage is shown by YN-JS-200-1, which preserves not only the eyes and myomeres but also branchial structures and notochord. The second stage is shown by YN-JS-200-2 and YN-JS-202, which only preserve eyes and myomeres. The third stage is shown by YN-JS-200-3, with eyes having been disarticulated from the body remains and the myomeres having become obscured. The specimens of separately preserved characters, such as the notochord and fin, wholly exhibit later stages of decay. It can be concluded from these decay patterns of characters that individuals of this unnamed myllokunmingiid had died at different times and experienced decay processes of different timespans before burial, the longest of which could possibly last for more than 300 days according to the results of decay experiments of Sansom et al. (2011, 2013). Therefore, these specimens show a process of slow accumulation, instead of a rapid burial (Fig. 10).

5.3. Different preservation modes of organisms may co-exist in the event beds

Chengjiang fossils mainly come from the superimposed couplets of background and event mudstone beds in Maotianshan Shale Member, Yu'anshan Formation (Zhao et al., 2010, 2012a, 2014). The background bed is black (fresh) or dark gray (weathered) mudstone with a comparatively high content of organics, and represents normal sedimentation and slow accumulation (Zhu et al., 2001; Hu, 2005; Zhao et al., 2009), the period of which could be as long as several years or hundreds of years (Hu, 2005). Fossils from the background beds are of low species richness (Hu, 2005; Zhao and Zhu, 2007; Zhao et al., 2009) and generally exhibit a certain degree of decay prior to burial (Hu, 2005). The event bed is dark gray (fresh) or gray-yellow (weathered) mudstone and represents distal mud tempestites (Zhu et al., 2001; Hu, 2005), which are the main beds which produce the exceptionally-well preserved soft-bodied fossils of the Chengjiang Lagerstätte (Zhu et al., 2001; Zhao and Zhu, 2007; Zhao et al., 2009). Articulated soft-bodied organisms comprise most of the fossil assemblages from the event mudstone beds, indicating rapid burial (within hours or days) and minimal transportation (Zhao et al., 2009).

To date, all of the specimens of fish-like animals from Chengjiang Lagerstätte come from the event mudstone beds and nearly all of them exhibit the classic preservation mode of rapid burial (possibly being buried alive). Only one specimen of *Haikouichthys ercaicunensis* shows some signs of decay (Fig. 4, Shu et al., 1999), the stage of which seems to be rather early according to the data of decay experiments on chordates (Sansom et al., 2011, 2013). The specimens of the unnamed myllokunmingiid described herein also come from the event mudstone beds, and the sedimentary facies of these specimens (Fig. 9) show no obvious difference with those studied by Zhao et al. (2009, 2012a, 2012b, 2014): the event mudstone hosting the unnamed myllokunmingiid is structureless upward and shares a gradational boundary with the overlying background mudstone. But, as analyzed above, these specimens not only experienced rather long decay processes but also had different decay stages. Taken together, it can be concluded that the preservation of these specimens indicates a slow, rather than a fast, accumulation, which is the classic preservation mode of organisms in the background mudstone beds. In the preservation of organisms in the event mudstone beds, rapid burial is thus possibly accompanied by slow accumulation. That mudstones deposited in the same palaeoenvironment bear specimens preserved in obviously different conditions might indicate that different preservation modes of organisms, at least in myllokunmingiids, co-exist in the event mudstone beds of Chengjiang deposits.

The cause of death of this unnamed myllokunmingiid cannot be confirmed based only on these specimens. If it was a natural death, traces of scavenging and bioturbation should be present, but these specimens do not show any such signs. Therefore, an unnatural death seems to be more likely, the cause of which might be closely related to changes of physiochemical conditions in the water column.

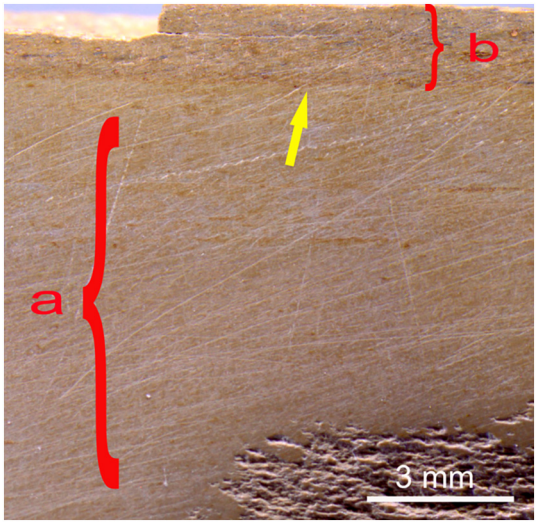

Fig. 9. The polished slab from specimen of YN-JS-200, brace (a) refers to the event mudstone bed hosting the unnamed myllokunmingiid; brace (b) refers to the overlying background mudstone bed; yellow arrow points to the gradational boundary in between. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5.4. Preservation mode and possible identity of eyes of myllokunmingiids

Of all the body parts, the spherical eyes are the best preserved and appear more decay resistant. Nearly all of the eyes are covered by black patches, and EDS analysis shows that they are mainly composed of O (40.56%), C (32.80%), Si (12.89%), Al (6.27%), Fe (3.88%), K (2.47%), Mg (0.76%). Zhu et al. (2005) discussed the fossilization modes of Chengjiang fossils and detected carbon in specimens of *Stellostomites*, *Paleoscolex* and one of the terminal spines of the grasping appendages of *Anomalocaris*. In addition, Forchielli et al. (2012) and Yun et al. (2017) discerned traces of carbon in sponges and chancelloriids respectively from the same biota. The relatively high concentration of carbon in the eyes documented herein, again, indicates that carbon film is common in the preservation of Chengjiang fossils and plays an important role in helping preserve the complete profiles of non-biomineralized soft-tissues during taphonomy and diagenesis.

Lenses have not been found in any specimen of myllokunmingiid ever found, nor herein. According to the decay experiments of Sansom et al. (2011, 2013), lenses are rather decay resistant and can persist after collapse and disarticulation. This might indicate that the eyes of these primitive fish-like animals from Chengjiang Lagerstätte are possibly not true eyes but visual organs close to the eye spots of amphioxus in morphology and function. Accompanied by lenses, eyes can get clear pictures of objects at various distances, and its absence in myllokunmingiids possibly indicate that these fish-like animals in early Cambrian have not yet developed good vision.

6. Conclusions

The fossils described herein are a kind of ‘naked’ fish-like animal with notochord and arcualia. Due to the poor preservation, the identity at genus- or species-level is unknown. Based on the morphologies exhibited by these specimens, we tentatively interpret it as an unnamed myllokunmingiid. Two kinds of preservation (rapid burial and slow

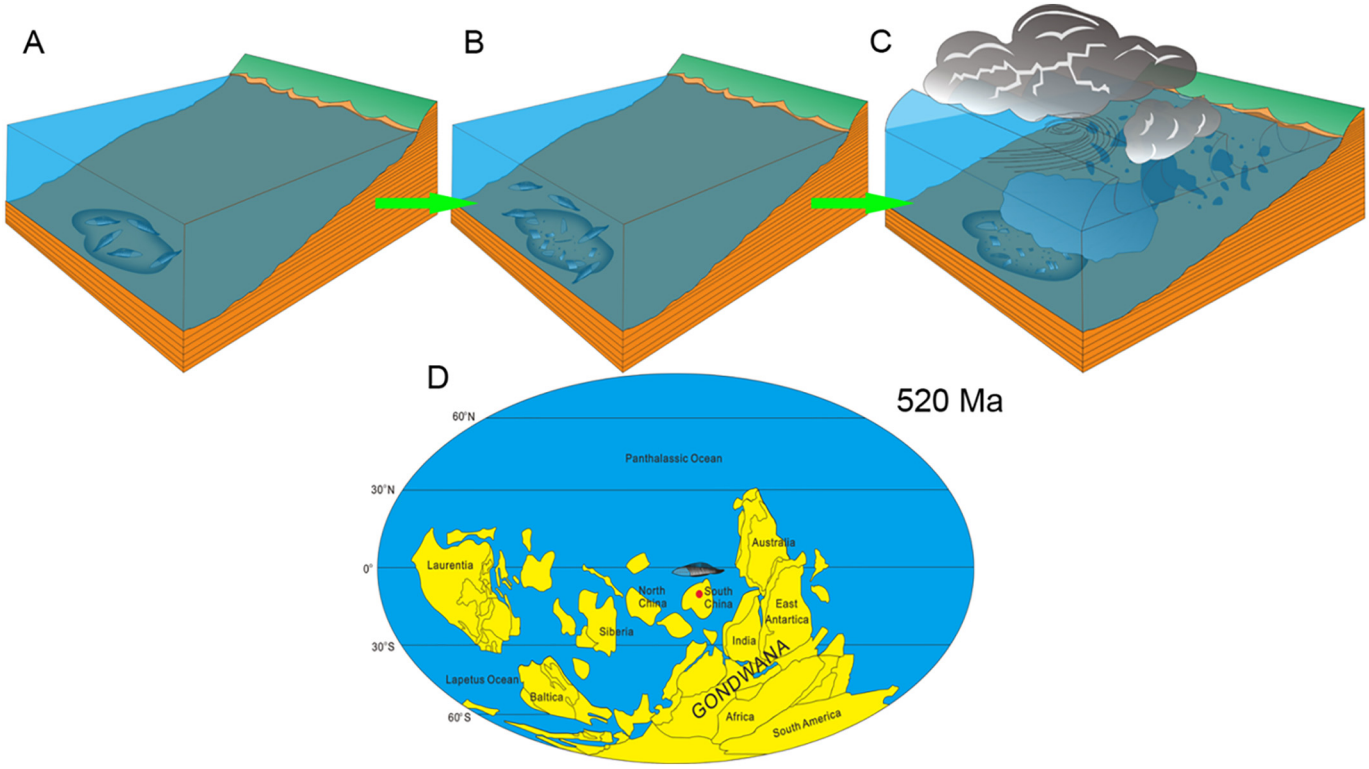

Fig. 10. A–C. the putative formation of the preservation of the unnamed myllokunmingiid in event mudstone bed; D. the fossil occurrence of the unnamed myllokunmingiid is on the South China microplate in the early Cambrian (520 Ma).
(Modified from Hou et al., 2017).

accumulation) of Chengjiang fossils might co-exist in the event mudstone beds from the Maotianshan Shale Member, Yu'anshan Formation, and this can be confirmed by all specimens of myllokunmingiid ever found, and herein. Visual organs of myllokunmingiids from the Chengjiang Lagerstätte may be more akin to eyespots in morphology and function.

Acknowledgments

This research is supported by the Strategic Project of Science and Technology of Chinese Academy of Sciences (XDB03010403) and the State Scholarship Fund of China (41272030, 40972026). We appreciate the constructive comments from the reviewers and the editor that helped improve the manuscript significantly. We thank L. Fei and H. Ming for the assistance during field work.

References

Bateson, W., 1885. Memoirs: the later stages in the development of Bala-noglossus Kowalevskii, with a suggestion as to the affinities of the Enteropneusta. J. Cell Sci. 2 (S1), 81–122.
Chen, J.Y., Zhou, G.Q., Zhu, M.Y., Yeh, K.Y., 1996. The Chengjiang Biota: A Unique Window of the Cambrian Explosion: Taicung. Taiwan National Museum of Natural Science. (222 pp. (in Chinese)).
Conway Morris, S., Caron, J.B., 2012. *Pikaia gracilens* Walcott, a stem-group chordate from the Middle Cambrian of British Columbia. Biol. Rev. 87, 480–512.
Conway Morris, S., Caron, J.B., 2014. A primitive fish from the Cambrian of North America. Nature 512, 419–422.
Cope, E.D., 1889. The Batrachia of North America. US Government Printing Office (No. 34).
Forchielli, A., Steiner, M., Hu, S.X., Keupp, H., 2012. Taphonomy of Cambrian (Stage 3/4) sponges from Yunnan (South China). Bull. Geosci. 87, 133–142.
Holland, N.D., Chen, J.Y., 2001. Origin and early evolution of the vertebrates: new insights from advances in molecular biology, anatomy, and palaeontology. BioEssays 23, 142–151.
Hou, X.G., Aldridge, R.J., Siveter, D.J., Siveter, D.J., Feng, X.H., 2002. New evidence on the anatomy and phylogeny of the earliest vertebrates. Proc. R. Soc. B 269, 1865–1869.
Hou, X.G., Siveter, D.J., Siveter, D.J., Aldridge, R.J., Cong, P.Y., Gabbott, S.E., Ma, X.Y., Purnell, M.A., Williams, M., 2017. The Cambrian fossils of Chengjiang, China: the flowering of early animal life. John Wiley & Sons, pp. 1–307.
Hu, S.X., 2005. Taphonomy and palaeoecology of the Early Cambrian Chengjiang Biota from Eastern Yunnan, China. Berl. Paläobiologische Abh. 7, 1–197.
Javier, P., 1999. Catching the first fish. Nature 402, 21–22.
Lamarck, J.B.P.A., 1801. Système des Animaux sans Vertèbres. Deterville (432 pp.).
Purnell, M.A., Donoghue, P.J.C., Gabbott, S.E., Mcnamara, M.E., Murdock, D.J.E., Sansom, R.S., 2018. Experimental analysis of soft-tissue fossilization: opening the black box. Palaleontology 61, 317–323.
Sansom, R.S., Gabbott, S.E., Purnell, M.A., 2010. Non-random decay of chordate characters causes bias in fossil interpretation. Nature 463, 797–800.
Sansom, R.S., Gabbott, S.E., Purnell, M.A., 2011. Decay of vertebrate characters in hagfish and lamprey (Cyclostomata) and the implications for the vertebrate fossil record. Proc. R. Soc. Lond. B Biol. Sci. 278, 1150–1157.
Sansom, R.S., Gabbott, S.E., Purnell, M.A., 2013. Atlas of vertebrate decay: a visual and taphonomic guide to fossil interpretation. Palaeontology 56, 457–474.
Shu, D.G., 2003. A paleontological perspective of vertebrate origin. Chin. Sci. Bull. 48, 8725–8735.
Shu, D.G., Chen, L., 2000. Mosaic evolution of the earliest-known vertebrates. Geosciences 14, 315–322 (in Chinese with English summary).
Shu, D.G., Luo, H.L., Conway Morris, S., Zhang, X.L., Hu, S.X., Chen, L., Han, J., Zhu, M., Li, Y., Chen, L.Z., 1999. Lower Cambrian vertebrates from South China. Nature 402, 42–46.
Shu, D.G., Conway Morris, S., Han, J., Zhang, Z.F., Yasul, K., Janvier, P., Chen, L., Zhang, X.L., Liu, J.N., Li, Y., Liu, H.Q., 2003. Head and backbone of the Early Cambrian vertebrate *Haikouichthys*. Nature 421, 526–529.
Simonetta, A.M., Insom, E., 1993. New animals from the Burgess Shale (Middle Cambrian) and their possible significance for the understanding of the Bilateria. Ital. J. Zool. 60, 97–107.
Walcott, C.D., 1911. Middle Cambrian annelids, Smithsonian Miscellaneous Collections. 57, 109–144.
Williams, M., Siveter, D.J., Siveter, D.J., Gabbott, S.E., Ma, X.Y., Purnell, M.A., Cong, P.Y., 2016. The spectacular fossils of the 'water margin': the Cambrian biota of Chengjiang, Yunan, China. Geol. Today 32, 233–237.
Yun, H., Zhang, X.L., Li, L.Y., 2017. Chancelloriid *Allonnia erjiensis* sp. nov. from the Chengjiang Lagerstätte of South China. J. Syst. Palaeontol. 16, 435–444.
Zhang, X.G., Hou, X.G., 2004. Evidence for a single median fin-fold and tail in the Lower Cambrian vertebrate, *Haikouichthys ercaicunensis*. J. Evol. Biol. 17, 1162–1166.
Zhang, X.L., Liu, W., Zhao, Y.L., 2008. Cambrian Burgess Shale-type Lagerstätten in South China: distribution and significance. Gondwana Res. 14, 255–262.
Zhao, F.C., Zhu, M.Y., 2007. Quantitative comparison of the fossil assemblages between the event and background mudstones from the Early Cambrian Chengjiang Lagerstätte, Yunan. Acta Palaeontol. Sin. 46, 75–86 (in Chinese with English

summary).
Zhao, F.C., Caron, J.B., Hu, S.X., Zhu, M.Y., 2009. Quantitative analysis of taphofacies and paleocommunities in the Early Cambrian Chengjiang Lagerstätte. Palaios 24, 826–839.
Zhao, F.C., Zhu, M.Y., Hu, S.X., 2010. Community structure and composition of the Cambrian Chengjiang Biota. Sci. China Earth Sci. 53, 1784–1799.
Zhao, F.C., Hu, S.X., Caron, J.B., Zhu, M.Y., Yin, Z.J., Lu, M., 2012a. Spatial variation in the diversity and composition of the Lower Cambrian (Series 2, Stage 3) Chengjiang Biota, Southwest China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 346–347, 54–65.
Zhao, F.C., Zhu, M.Y., Hu, S.X., 2012b. Diverse responses of Cambrian organisms to sedimentary events: evidence from the Chengjiang Lagerstätte of eastern Yunnan. Acta Palaeontol. Sin. 51, 265–280 (in Chinese with English summary).
Zhao, F.C., Caron, J.B., Bottjer, D.J., Hu, S.X., Yin, Z.J., Zhu, M.Y., 2014. Diversity and species abundance patterns of the early Cambrian (Series 2, Stage 3) Chengjiang Biota from China. Paleobiology 40, 50–69.
Zhu, M.Y., Zhang, J.M., Li, G.X., 2001. Sedimentary environments of the early Cambrian Chengjiang biota: sedimentology of the Yu'anshan Formation in Chengjiang County, eastern Yunnan. In: Zhu, M.Y., Van Iten, H., Peng, S.C., Li, G.X. (Eds.), The Cambrian of South China: Acta Palaeontologica Sinica. 40. pp. 80–105 (suppl.).
Zhu, M.Y., Babcock, L.E., Steiner, M., 2005. Fossilization modes in the Chengjiang Lagerstätte (Cambrian of China): testing the roles of organic preservation and diagenetic alteration in exceptional preservation. Palaeogeogr. Palaeoclimatol. Palaeoecol. 220, 31–46.