Brachiopod-dominated communities and depositional environment of the Guanshan Konservat-Lagerstätte, eastern Yunnan, China

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Abstract: The Guanshan Biota is an unusual early Cambrian Konservat-Lagerstätte from China and is distinguished from all other exceptionally preserved Cambrian biotas by the dominance of brachiopods and a relatively shallow depositional environment. However, the faunal composition, overturn and sedimentology associated with the Guanshan Biota are poorly understood. This study, based on collections through the best-exposed succession of the basal Wulongqing Formation at the Shijiangjun section, Wuding County, eastern Yunnan, China recovered six major animal groups with soft tissue preservation; brachiopods vastly outnumbered all other groups. Brachiopods quickly replace arthropods as the dominant fauna following a transgression at the base of the Wulongqing Formation. A transition from a bafstdordiidae-, coobolidae- and acrothelidae-dominated brachiopod assemblage occurs up-section. Four episodically repeated lithofacies reveal a relatively low-energy, offshore to lower shoreface sedimentary environment at the Shijiangjun section, which is very different from the Wulongqing Formation in the Malong and Kunming areas. Multiple event flows and rapid obduction are responsible for faunal overturn and fluctuation through the section. A detailed lithofacies and palaeontological investigation of this section provides a better understanding of the processes and drivers of faunal overturn during the later phase of the Cambrian Explosion.

Supplementary material: Composition and comparison of the Malong Fauna and the Guanshan Biota is available at: https://doi.org/10.6084/m9.figshare.c.5080799

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Discoveries of spectacular soft-bodied animal assemblages from Cambrian Konservat-Lagerstätten around the world have provided incredible insights into the anatomy, behaviour, ecology and early evolution of complex metazoans (Paterson et al. 2011; Hu et al. 2013; O’Brien and Caron 2016; Aria and Caron 2017; Hou et al. 2017; Yang et al. 2018; Liu et al. 2020; Z.F. Zhang et al. 2020a). Early Cambrian Konservat-Lagerstätten from China – such as the Niuhtitang Fauna, Chengjiang Biota, Guanshan Biota, Shipai Biota, Balang Fauna, KaiBiota and the newly discovered Qingjiang Biota (Peng et al. 2005; Zhao et al. 2005; Hu et al. 2013; J. Liu et al. 2016; Hou et al. 2017; Fu et al. 2019) – span a wide range of geological time and provide a unique opportunity to map changes in early Cambrian ecological communities over time (Chen et al. 2019). The Guanshan Biota (Cambrian Series 2, Stage 4) is one of the oldest Konservat-Lagerstätten from South China, occurs in the Wulongqing Formation (Hu et al. 2013) in eastern Yunnan. Younger than the famous Chengjiang and Malong biotas (Cambrian Series 2, Stage 3), but older than the Kaii and Burgess Shale biotas (Miaolingian Series, Wulian Stage), the Guanshan Biota is a significant evolutionary bridge in our understanding of the chronology of the Cambrian radiation and its aftermath (J. Liu et al. 2012a; Hu et al. 2013). Recent intensive, although preliminary, excavations reveal that the Guanshan Biota is composed of 14 major animal groups and various ichnotaxa (Hu et al. 2010, 2013; Chen et al. 2019). Uniquely, the Guanshan Biota is dominated by brachiopods, which serves to distinguish it from all other Cambrian Konservat-Lagerstätten, which are dominated (in terms of diversity and relative abundance) by euarthropod groups. Faunal overturn between the Chengjiang, Malong and Guanshan biotas suggests that the sessile benthic members of the assemblages are affected by the same factors that affect mobile trilobites (Luo et al. 2008; Chen et al. 2019). Furthermore, the Wulongqing Formation is characterized by bioturbated, thinly bedded sandstones, siltstones and mudstones, which crop out widely in eastern Yunnan, South China (Fig. 1) and represent a transgressive systems tract directly after the Hongjingshao Formation (Hu et al. 2010). Previous, very generalized, sedimentological work on the Wulongqing Formation suggests a relative shallow (shoreface to offshore transitional) depositional environment (Hu et al. 2010; Chen et al. 2019), which is distinct from the generally deeper water (in some cases slope to basin) setting of most other early Cambrian deposits that preserve soft tissues (Ivantsov et al. 2005; Colllom et al. 2009; Peel and Ineson 2011).

Continuous exploration and research in the Guanshan Biota has led to the discovery of multiple new localities and increased systematic descriptions of the fossil taxa (Hu et al. 2010, 2013; J. Liu et al. 2012a, 2016; Hopkins et al. 2017; Li et al. 2017; Chen et al. 2019). In Ineson (1), including documentation of one of the oldest examples of kleptoparasitism in the fossil record (Z.F. Zhang et al. 2020a). The Wulongqing Formation is generally poorly exposed at most sites and artificial cover by urban landscaping has obscured many of the classic flat-lying sites. There has been a dearth of even
basic ecological analyses of the faunal assemblages from the Guanshan Biota, and the detailed sedimentology and lithology of the succession are very poorly resolved.

This paper aims to comprehensively document the lithofacies and sedimentology of the basal part of the Wulongqing Formation hosting soft-bodied fossils at the Shijiangjun section, the best-exposed succession in Wuding county, eastern Yunnan (Fig. 1). These data will help to decipher the relationships between microfacies, sedimentary events and faunal overturn after transgression and how fluctuations in depositional environments affect the faunal composition during the later stages of the Cambrian evolutionary radiation.

The uppermost Hongjingshao and lower Wulongqing formations are exposed in the new section with a very clear conformable stratigraphic contact (Figs 2 and 3). This provides an opportunity to document temporal changes in the faunal composition and sedimentary environments at the centimetre scale based on lithological, sedimentological, palaeontological and ichnological evidence. This detailed study enables an interpretation of the depositional environment associated with the lower Wulongqing Formation and facilitates a better resolution of the process and drivers of faunal overturn that distinguish the Guanshan faunas from the Wuding, Malong and Kunming areas (Hu et al. 2013; Chen et al. 2019).
Materials and methods

The Shijiangjun section (25° 35′ 11″ N, 102° 22′ 22″ E) was measured through the uppermost Hongjingshao and lower Wulongqing formations and large-scale sedimentary features were noted. A total of 2988 fossil specimens were collected in one four-week field season sequentially and independently from ten contiguous siltstone and mudstone layers varying in thickness from 6 to 110 cm (Fig. 2; Table 1). Whole fossils were identified and classified to the phylum level and, where applicable, brachiopod genera were identified. Faunal relative abundances are based on all the well-preserved fossils, whereas trace fossils and fragmentary...
unidentifiable specimens, as well as all shell concentrations, were excluded.

Lithological samples \((n = 41)\) in oriented plaster jackets were collected at intervals from mudstone and sandstone layers through the section (Fig. 2; Table 2). All the samples collected for rock slabs and thin sections were cut and polished at the Shaanxi Key Laboratory of Early Life and Environments, China and revealed the vertical internal organization of the physical and biogenic sedimentary structures. Scanning of the polished slabs was achieved using an Epson V370 photo-scanner at Macquarie University, Australia. Following the methodology outlined by Dorador et al. (2014) and Dorador and Rodríguez-Tovar (2018), Adobe Photoshop was used to digitally improve the visibility (contrast) of the sedimentary and ichnological structures. Sedimentary characteristics, including grain size, lithology, sedimentary structures and vertical bioturbation intensity were recorded (Fig. 2;
Table 2). The percentage bioturbation in each sample was evaluated using Adobe Photoshop (Cao et al. 2015; Gougeon et al. 2018). The bioturbation area was selected using the lasso tool and recorded through the measurement log in pixels. This was then divided by the total area in pixels to determine the percentage of bioturbation. These percentages were then used within the bioturbation index (BI) scheme of Taylor and Goldring (1993). All the rock samples and fossil specimens investigated are deposited in the Early Life Institute (ELI) and the Department of Geology, Northwest University, Xi’an China.

Fig. 3. Field photographs of the lower Wulongqing Formation at the Shijiangjun section. Yellow upper case letters mark the layers yielding a fossil assemblage in accordance with Figure 2. (a) General view of the lower part of the section. The yellow line on the bottom of the section indicates the lithological contact between the Hongjingshao and Wulongqing formations. (b) Load casts at the bottom of the sandstone deposits. (c) Wavy bedding structure above layer C. (d) Normal graded bedding from fossil-yielding layer D, scale bar: 1 cm. (e) Gutter casts, lenticular bedding and wavy ripples at the Shijiangjun section. (f) Plan view of gutter casts from fossil-yielding layer F. (g) The simplified palaeoenvironmental reconstruction for the Guanshan Biota from Wuding area. HJS, Hongjingshao Formation; WLQ, Wulongqing Formation.
and cycle throughout the section, as shown in Figures 2 features, the section is divided into four distinct facies that repeat (Fig. 2). Based on lithological, sedimentary and ichnological 5.3 m) accompanying the only identified trace fossil bioturbated beds occurring in the middle part of the section (3.3 has an overall low level of bioturbation, with some highly bioturbated beds existing in layer M25. Bioturbation is rare (BI = 0), with the percentage bioturbation never exceeding 1% (Fig. 2; Table 2).

The absence of rheological surfaces on the silty mudstone packages indicates a relatively low-energy hydrodynamic system (Zavala et al. 2012). Abundant sub-parallel to oblique brachiopod and/or trilobite fragments within the mudstone indicate transportation by currents (Fürsich et al. 1992).

Interpretation. High rates of fallout or other unobservable environmental stressors (e.g. oxygen, salinity or temperature) may be responsible for the relative absence of bioturbation. As a result, the relatively structureless silty mudstone packages are interpreted as deposited from rapid fallout from suspension during quiet periods of fair weather conditions (Maceachern et al. 1999).

Facies 3: low to highly bioturbated glauconitic sandstones

Facies 3 consists of very fine to very coarse sandstone with rare granule- to pebble-sized clasts (Fig. 4d–g). The granules and pebbles predominately occur in samples S2–S6, S9 and S16 (Figs 2 and 4c; Table 2). The medium- to very coarse-grained sand beds from the lower and upper part of this section are characterized by very poorly to poorly sorted grains distributed within the intervals 0–2.1 m and 4.6–5.0 m (Figs 4d, e and 5d, g). Coarse grains are mainly angular to subrounded and dominated by low to medium sphericity (Fig. 5d, g). Although the very fine- to medium-grained sand beds from interval 2.2–4.2 m are mainly moderately sorted (Fig. 4f), few beds show medium to high sphericity. Two beds (S15

Table 1. Relative abundance and diversity of fossil taxa collected from the lower Wulongqing Formation at the Shijiangjun section, Wuding county

| Animal groups | Taxa | A | B | C | D | E | F | G | H | I | J | Total |
|---------------|------|---|---|---|---|---|---|---|---|---|---|------|
| Brachiopoda   | Neoobolus | 16 | 96 | 238 | 23 | 48 | 386 | 3 | 2 | 3 | 815 | 2030 |
|               | Eoobolus | 16 | 49 | 63 | 54 | 30 | 155 | 109 | 70 | 25 | 16 | 587 |
|               | Westonia | 12 | 43 | 3 | 4 | 9 | 5 | 192 | 93 | 70 | 64 | 147 | 553 |
|               | Lunarrasoria | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 |
|               | Kutorgina | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 |
|               | Nisasia | 5 | 1 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 |
| Arthropoda    | Trilobites | 72 | 260 | 80 | 2 | 1 | 87 | 4 | 33 | 34 | 573 | 699 |
|               | Guangweicaris | 9 | 31 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 |
|               | Pandalonga | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
|               | Issyis | 2 | 14 | 14 | 14 | 14 | 14 | 14 | 14 | 14 |
|               | Tuxia | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
|               | bradoriids | 14 | 14 | 14 | 14 | 14 | 14 | 14 | 14 |
|               | Leancholla | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Hyolitha       | Linevitus | 1 | 12 | 142 | 25 | 6 | 7 | 24 | 7 | 3 | 227 | 227 |
| Anomalocaridids | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| Veturicolida   | 4 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| Priapulida     | Palaeoscolecidae | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
|               | Total | 132 | 512 | 530 | 111 | 91 | 748 | 318 | 139 | 174 | 233 | 2988 |

Results

Geological setting, locality and section

The stratigraphic section is 8 m thick and composed of distinctive intercalated beds of thin to thick (5–60 cm), very fine to very coarse sandstone, siltstone and mudstone (Fig. 3a). Rare gravels and isolated pebbles occur in sandstone samples S2, S3, S4, S5, S6, S9 and S16, in addition to two layers of purple muddy medium to coarse sandstone (S15 and S16), which contained 3–5% oolite grains (Fig. 2; Table 2). Commonly developed primary sedimentary structures include massive bedding, normal graded bedding (Fig. 3d), lenticular bedding and wavy bedding (Figs 2, 3c, e). The contacts between the sandstones and mudstones are sharp. The most common local erosion structures include gutter casts, erosional scour and low ripple marks (Figs 2, 3b, e, f). The measured section has an overall low level of bioturbation, with some highly bioturbated beds occurring in the middle part of the section (3.3–5.3 m) accompanying the only identified trace fossil Teichichnus? isp. documented in two samples (Fig. 2). The medium maturity of the sand/silt laminations probably indicates a certain degree of winnowing and transportation.

Interpretation. The interbedded mudstone and sandstone reflect an alternation of quiet water sediment fallout (low energy) combined with relatively high-energy flows (Buatois et al. 2012; Majid et al. 2017).

Facies 1: low–medium bioturbated and interbedded mudstones–siltstones/sandstones

Facies 1 consists of thinly bedded mudstone with thin to thick laminated siltstone and/or very fine sandstone (Figs 4a, b and 5a). The silt and sand grains are medium to well sorted, mainly angular to subrounded, low to high sphericity with increasing sphericity up-section (Fig. 5a). Fine to medium sandstone intercalations occur as lenticular and wavy bedding (Fig. 4a). Laterally discontinuous millimetre-scale (mainly 3–5 mm with some 1–2 mm) silt laminations are common. Graded laminations (4–10 mm) manifest either as a sharp horizontal contact or an erosional base (sole marks) (Figs 4b and 5b). The contact between sand and mud is nearly always sharp. Bioturbation is generally indistinct and unidentifiable, with Teichichnus? isp. documented in two samples (Fig. 2). The bioturbation index ranges from 0 to 3, with a predominant index of 0–1 (up to 4.89% disturbance). More heavily bioturbated beds exist locally (M5 and M20) with indexes of 2–3 recording up to 40% sedimentary fabric disturbance (Fig. 2; Table 2). The graded laminations and erosive bases suggest deposition from decelerating flows (Bouma 1962; Kneller 1995).

Facies 2: Silty mudstones

Facies 2 is represented by uniform mudstones with occasional millimetre-scale silt laminations (≤1 mm) (Fig. 4c). The silt grains are moderately sorted, angular to subrounded (low content) and of low sphericity (Fig. 5c). Interestingly, the M10 layer (Fig. 2) contains a higher concentration of muscovite than any other layer. Fragmentary shelly fossils are often present and are preserved parallel or oblique to bedding, with a particularly high concentration of trilobite fragments documented in layer M25. Bioturbation is rare (BI = 0), with the percentage bioturbation never exceeding 1% (Fig. 2; Table 2).
| Sample number | Sample thickness (mm) | Lithology | Sedimentary structures | Taphonomy | Fossil concentrations | Bioturbation index | Soft tissue |
|---------------|-----------------------|-----------|------------------------|-----------|-----------------------|------------------|-------------|
| M25           | 40                    | Yellowish green silty mudstone | Parallel laminations, discontinuous silt laminations | Abundant fragments are sub-parallel, parallel or oblique to the bedding plane | A large number of fossil fragments are oblique to the bedding plane | 0               |            |
| M24           | 21                    | Yellowish green mudstone intercalated with brick red silt–very fine sandstone, sand grains are moderately sorted, angular to sub-angular, few subrounded grains, low–medium sphericity | Weakly normal graded lamination, sole marks, wavy lamination, erosion bottom surface, top and bottom boundary of sandstone are sharp | Few fossil (fragments) are parallel to sub-parallel to the bedding plane within mud background | Trilobite fragments concentration, high fragmentation | 0               |            |
| M23           | 39                    | Greyish green mudstone intercalated with brick red silt–very fine (feldspathic) sandstone | Weakly normal graded lamination, sole marks, wavy lamination | Few fossils (brachiopods and unknown) are sub-parallel to oblique to the bedding plane within mud background | Westonia concentration, shells within mudstone are low fragmentation, random orientation, poorly sorted, parallel–oblique to the bedding plane | 1               | ×           |
| M22           | 27                    | Purple silty mudstone, some spicular mineral | Massive bedding | No fossils | Westonia concentration, shells within mudstone are low fragmentation, random orientation, poorly sorted, parallel–oblique to the bedding plane | 0               |            |
| M21           | 49                    | Yellowish green silty mudstone | Tiny sole marks, parallel lamination (silt), massive mudstone bed | Many fossils (brachiopods and unknown fragments) are parallel to sub-parallel to the bedding plane within mud background | Westonia concentration, Shell fragments distributed close to the boundary between mud and sand | 0               | √           |
| M20           | 25                    | Lavender mudstone interbedded with purple silt–very fine sandstone, sand grains are well-sorted, angular to subrounded, medium–high sphericity | Massive bedding (bioturbated) | Few fossils (brachiopods and unknown) are parallel to sub-parallel to the bedding plane within mud background, one shell concave-up | Eoobolus concentration, Westonia concentration | 3               | √           |
| S16           | 40                    | Purple, muddy, very coarse sandstone, c. 2% granules (up to 3 mm), 1% ooid, grains very poorly sorted, angular to subrounded, low–medium sphericity, grains’ long axis are usually vertical–oblique to bedding plane; grains are spherical, equant, square, triangle, rod-like and irregular shape | Massive bedding | No fossils | Westonia concentration, shells within mudstone are low fragmentation, random orientation, poorly sorted, parallel–oblique to the bedding plane | 0               | ×           |
| S15           | 35                    | Purple matrix-supported muddy medium–coarse sandstone, 3–5% oolite, 1–2% glauconite, grains are moderately sorted, angular to subangular, low sphericity; grains are square, triangular, rod-like and irregular shape; glauconite grains are subrounded | Truncated and scoured tops of mud with parallel oolite (elongated–rounded), mud clasts | Shell fragments distributed close to the boundary between mud and sand | Westonia concentration, shells within mudstone are low fragmentation, random orientation, poorly sorted, parallel–oblique to the bedding plane | 2               |            |
| S14           | 32                    | Greyish green muddy glauconitic sandstone, grain size from fine to coarse, 3% coarse glauconite grains, grains are moderately sorted, angular to sub-angular, low sphericity, triangular, square, round, tabular, rod-like shapes | Massive bedding (bioturbated), rip up clasts (microbial mats?) | Few fossil (brachiopods and unknown) are parallel to sub-parallel to the bedding plane within mud background | Westonia concentration, shells within mudstone are low fragmentation, random orientation, poorly sorted, parallel–oblique to the bedding plane | 4               |            |
| M19           | 46                    | Greyish mudstone interbedded with brick red silt and very fine sandstone | Normal graded bedding, lenticular lamination, sole marks | Few fossil (brachiopods and unknown) are parallel to sub-parallel to the bedding plane within mud background | Westonia concentration, shells within mudstone are low fragmentation, random orientation, poorly sorted, parallel–oblique to the bedding plane | 0               | √           |
| Sample number | Sample thickness (mm) | Lithology | Sedimentary structures | Taphonomy | Fossil concentrations | Bioturbation index | Soft tissue |
|---------------|----------------------|-----------|------------------------|-----------|----------------------|-------------------|-------------|
| S13           | 50                   | Brick red very fine–fine sandstone interbedded with greyish-green mudstone, 1–2% medium glauconite, elongate minerals, feldspathic sandstone, grains are moderately sorted, angular to subrounded, low–medium sphericity, triangular, square, round, tabular, rod-like shapes | Wavy lamination, lenticular lamination, massive bedding (bioturbated) | Few fossil (brachiopods and unknown) are parallel–oblique to the bedding plane within mud background, one shell concave-down | 3 | X |
| M18           | 42                   | Greyish green mudstone interbedded with silt–very fine sandstone, grains are moderately sorted, angular to subrounded, medium sphericity | Weakly normal graded bedding, lenticular bedding (very fine sandstone), sole marks | Few fossil (brachiopods and unknown) are parallel–oblique to the bedding plane | 0 |  |
| S12           | 45                   | Yellowish green muddy very fine–fine sandstone, 1% medium-grained glauconite, grains are moderately sorted, angular to subrounded, high sphericity | Massive bedding (bioturbated) | Eoobolus concentration, Westonia concentration | 5 | X |
| S11           | 50                   | Brick red muddy very fine sandstone, few fine–medium sand grains, few glauconite grains, grains are well-sorted, high sphericity, most of them are sub-angular | Massive bedding (bioturbated) | Westonia and Eoobolus concentration, shells are random orientation, low fragmentation, poorly sorted (1–12 mm), parallel to sub-parallel to the bedding plane, conjoined; few Neobolus preserved with tubeworm | 4 |  |
| M17           | 35                   | Yellowish green, thin-bedded silty mudstone with very fine sandstone | Lenticular lamination (very fine sand), tiny sole marks, low angle wavy lamination (non-parallel) | Few fossils (conjoined brachiopod valves and unknown) are parallel or oblique to the bedding plane within mud background | 0 | √ |
| M16           | 36                   | Yellowish green mudstone | Discontinuous, parallel silt lamination | Several fossils are parallel to the bedding plane distributed within the mud background | Larval or juvenile Neobolus concentration |  |
| M15           | 25                   | Yellowish green mudstone intercalated with grey siltstone and very fine sandstone, sand grains are well-sorted, medium sphericity, angular to subrounded, tabular grains are usually parallel to bedding, few oblique to the bedding plane | Lenticular lamination, sole marks | Few fossil (brachiopods and unknown) are parallel to sub-parallel to the bedding plane within mud background | Westonia concentration, larval or juvenile Neobolus concentration, shells are low fragmentation, parallel to the bedding plane, poorly sorted (1–13 mm), random orientation, conjoined | 1 |
| M14           | 43                   | Greyish green mudstone interbedded with brick red siltstone | Normal graded lamination, lenticular bedding, parallel lamination, sole marks | Fossils are parallel to sub-parallel to the bedding plane, a few shells concave-down | Westonia concentration, Neobolus concentration, shells are parallel to the plane, poorly sorted, most are conjoined and a few are disarticulated |  |
| M13           | 45                   | Greyish green, very thin-bedded mudstone interbedded with very fine sandstone and siltstone | Normal graded lamination, lenticular bedding, sole marks | A few fossils are parallel to the bedding plane | Neobolus concentration, shells are low fragmentation, parallel to the bedding plane, conjoined, poorly sorted (0.5–4 mm), random orientation | 0 |
| S10           | 65                   | Brick red, thin-bedded, very fine sandstone, few glauconite grains, grains are well-sorted, angular-rounded, medium–high sphericity | Massive bedding, mud clasts? | One fossil oblique to the bedding plane | 0 | X |
| M12           | 26                   | Dark green, thin-bedded mudstone intercalated with medium laminated grey siltstone | Normal graded lamination | | 0 | X |
| Page | Code | Description | Bedding Type | Notes |
|------|------|-------------|--------------|-------|
| S9   | 48   | Brick red, muddy, fine–medium sandstone, grains are poorly sorted, angular to sub-rounded, low–medium sphericity; coarse grains up to c. 10%, granules are c. 1–2%; quartz grains > dark minerals > feldspar grains > lithic fragments; spherical, rod-like, triangular, square and irregular shapes | Massive bedding (bioturbated?) | 0 | × |
| M11  | 35   | Yellowish green silty mudstone, few fine sandstone, grains are poorly sorted, angular to sub-angular, low sphericity; spherical, square, tabular, irregular shapes | Massive bedding | Few fossils (brachiopod and trilobites? hyoliths, unknown rounded?) are parallel to the bedding plane | Neobolus and Eoobolus and Westonia and Redlichia and Palaeolenus and hyoliths fragment concentration, fragments are poorly sorted, oblique to perpendicular to the bedding plane | 0 | × |
| S8   | 30   | Brick red, medium sandstone, few very coarse quartz grains, poorly sorted, angular–sub-angular, few sub-rounded, low sphericity, grains, long axis are usually oblique–parallel to the bedding plane, quartz > black minerals > feldspar | Weakly normal graded lamination | 0 | × |
| S7   | 35   | Brick red, medium–coarse sandstone, grains are poorly sorted, angular to sub-rounded, low–medium sphericity, spherical, tabular, rod-like shapes | Weakly normal graded lamination, sole marks? | 1 |
| S6   | 45   | Brick red, coarse–very coarse sandstone, few granules, grains are poorly–very poorly sorted, angular to sub-rounded, low sphericity; quartz, feldspar, lithic fragment, dark minerals | Massive bedding | 0 |
| S5   | 35   | Brick red coarse sandstone, granules up to 10–20%, small pebbles up to 5%, very poorly sorted, sub-angular–rounded, medium sphericity, spherical and bladed shapes; the lower part is thin very fine–fine sandstone (very coarse sand grains up to 5%, mud up to 5%) and mudstone | Sharp boundary, massive lamination/bedding | 0 |
| M10  | 25   | Greyish green silty mudstone, silt grains are dark minerals (spherical, tabular, bladed and rod-like shapes), parallel–oblique to bedding plane, few are vertical, angular–sub-rounded (low content), low sphericity, higher content of white mica than other beds | Massive bedding | Few fossils (round, flat, crescent-shaped, irregular) are sub-parallel to oblique to the bedding plane | Trilobite fragment concentration | 0 | √ |
| M9   | 33   | Greyish green silty mudstone, silt grains are dark minerals (spherical, tabular, bladed and rod-like shapes), parallel–oblique to bedding plane, angular–sub-rounded (low content), low sphericity | Massive bedding | Few fossils are sub-parallel to oblique to bedding plane | Neobolus and Redlichia and Palaeolenus and hyoliths fragment concentration | 0 |
| M8   | 35   | Yellowish green mudstone intercalated with white siltstone, silt grains are dark minerals (spherical, tabular, bladed and rod-like shapes), parallel–oblique to bedding plane, angular–sub-rounded (low content), low sphericity | Weakly normal graded bedding, parallel lamination, lenticular lamination, tiny sole marks | Many fossils (brachiopod shells and unknown fragments) are preserved parallel–sub-parallel to the bedding plane | Neobolus and Redlichia and Palaeolenus and hyoliths fragment concentration | 0 |

(continued)
| Sample number | Sample thickness (mm) | Lithology | Sedimentary structures | Taphonomy | Fossil concentrations | Bioturbation index | Soft tissue |
|---------------|-----------------------|-----------|------------------------|-----------|-----------------------|-------------------|-------------|
| S4            | 40                    | Dark green fine–medium sandstone, few granules, grains are poorly sorted, angular to subrounded, most of them are angular to subangular, low sphericity; c. 90–95% are quartz grains, followed by feldspar and others | Massive bedding (sandstone), sole mark, sharp boundary | Many fossils (one conjoined and many dorsal or ventral brachiopod shells and unknown fragments) are preserved parallel–sub-parallel to the bedding plane | Palaeolenus fragment concentration | 0 | × |
| M7            | 30                    | Yellowish thin-bedded mudstone | Weakly normal graded bedding | Many fossils (one conjoined and many dorsal or ventral brachiopod shells and unknown fragments) are preserved parallel–sub-parallel to the bedding plane | Palaeolenus and Redlichia concentration, parallel to the bedding plane, Palaeolenus low fragmentation | 0 | √ |
| M6            | 40                    | Yellowish green mudstone | Weakly normal graded bedding | Plentiful fossils (brachiopod shells, trilobites and unknown fragments) are preserved parallel to sub-parallel to the bedding plane, few are oblique, few shells concave-up | Palaeolenus and Redlichia concentration, parallel to the bedding plane, Palaeolenus low fragmentation | 0 | √ |
| M5            | 50                    | Yellowish green mudstone interbedded with grey fine sandstone, grains are medium sorted, the quartz grains are sub-angular to subrounded, low sphericity | Lenticular lamination (fine sandstone), sole marks | Several fossils are preserved parallel–sub-parallel to the bedding plane, few fossils are oblique to the bedding plane, two conjoined fossils | Palaeolenus and Redlichia fragment concentration | 2 | |
| M4            | 50                    | Yellowish green mudstone interbedded with grey fine–medium sandstone, poorly sorted, the quartz grains are angular to subrounded, most are angular to sub-angular, low sphericity | Weakly normal graded bedding, wavy lamination, lenticular lamination, sole marks | Fossils are preserved parallel to sub-parallel to the bedding plane, few shells concave-up | Palaeolenus and Redlichia fragment concentration | 1 | |
| S3            | 53                    | Greyish green medium–coarse sandstone, few granules, poorly sorted, the granules are angular to subrounded; low–medium sphericity; c. 95% are quartz grains, very few are detritus and feldspar | Fining-upwards | | | 0 | |
| S2            | 63                    | Greyish green mudstone interbedded with medium grey fine sandstone, grains are poorly sorted, angular-rounded, medium–high sphericity | Massive bedding | | | 0 | × |
| M3            | 45                    | Greenish mudstone interbedded with medium grey fine sandstone, grains are poorly sorted, angular-rounded, medium–high sphericity | Weakly normal graded lamination, wavy lamination, lenticular lamination (0.1–0.4 mm thick), sole marks | Few fossils (on top close to the upper sandstone) are parallel to the bedding plane within silt or clay, few shells concave-down | Linnaeusonia concentration, low fragmentation, poorly sorted | 0 | √ |
| M2            | 40                    | Greenish silty mudstone, unidentified spicules (mineral or sponge?) | Tiny rip-up clasts | | | 0 | |
| M1            | 40                    | Yellowish mudstone interbedded with purple fine–medium sandstone, grains are medium sorted, sub-angular–subrounded, low sphericity | Lenticular lamination | | | 1 | |
| S1            | 55                    | Grey fine–medium sandstone, moderately sorted, subrounded–well rounded, spherical | Massive bedding | | | 0 | |
and S16) contain 1–5% elongate ooids. Most of the ooids are oval and few are rounded.

The sandstone beds are either characterized by a homogeneous uniform grain size or high bio-disturbance, which has destroyed the original sedimentary structures. Only levels S7 and S8 show weakly normal graded bedding. Sand beds S11–S15 show a relatively higher content of mud and a higher percentage of bio-disturbance (BI = 2–5) (Fig. 2; Table 2). The bioturbation index and bio-disturbance reach a peak of BI = 5 and 98.76% within S12 (Figs 4f and 5f), followed by S11 (80.88%) and S14 (76.16%) (Fig. 4g). However, more than half of the sandstones below S11 show scarce or no bioturbation (Fig. 2; Table 2).

The occurrence of syngenetic glauconite grains within the sandstones of Facies 3 is unique (Fig. 4f, g; Table 2). These grains were identified based on their green colour, random microcrystalline internal texture and aggregate polarization (Baioumy and Boulis 2012). They are, in some instances, coated and replaced by iron oxides (mostly hematite and goethite). These grains occur in every sandstone interbed at relatively low contents (Fig. 2; Table 2). The grains are usually medium sorted, subrounded to rounded and of medium sphericity (Fig. 5e). Although glauconite cannot be used as a specific environmental indicator (Mcrae 1972; Chafetz and Reid 2000; Chafetz 2007), it is commonly associated with transgressive systems tracts (Delamette 1989; Garzanti et al. 1989; Amorosi et al. 2012; Banerjee et al. 2012, 2017; Rudmin et al. 2017). Different types of glauconite (i.e. autochthonous, paraautochthonous and detrital) can be determined based on the criteria proposed by Amorosi (1997). The glauconite that usually occurs in detrital granular and sand facies lacks a diffuse green pigmentation, which often alternates between glauconite-rich and glauconite-free layers, and can be interpreted to indicate an allochthonous (e.g. paraautochthonous or detrital) origin (Amorosi 1997; Baioumy and Boulis 2012). By contrast, the low compositional and structural maturity of Facies 3, as well as a lack of

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**Fig. 4.** Polished slabs of the lower Wulongqing Formation at the Shijiangjun section, with facies classification and sample numbers in parentheses. (a, b) Slabs of Facies 1 showing wavy laminations, graded lamination, lenticular lamination and erosive base. (c) Silty mudstone without sedimentary structures representing Facies 2. (d–g) Massive sandstone deposits representing Facies 3. (d) Poorly sorted, angular to sub-angular clasts with few granules. (f, g) Highly bioturbated sandstone with glauconite grains. (h) Mudstone without structures (Facies 4). Scale bars 5 mm.
glauconite in the older Hongjingshao Formation, implies a parautochthonous origin (Amorosi 1997; Baioumy and Boulis 2012), in which the autochthonous glauconites have been transported a short distance from their original location by waves, storm currents and/or gravity flow processes.

Local observations of Facies 3 show that these sandstones have a low compositional and textural maturity, which suggests that the sediments were deposited with minimal traction and clast collisions from a proximal sediment source. Therefore the clasts retain their immature, angular texture (Henstra et al. 2016). Storm deposits are generally understood to consist of well-sorted sand with a fining-upwards sequence that reflects the waning storm waves (Swift et al. 1983; Saito 1989; Duke et al. 1991; Cheel and Leckie 1993; Meldahl 1993). The storm flow usually converts to a turbidity current as the power of the storm flow weakens near the storm wave base, resulting in the suspended mud and gravel depositing together with fine suspended sediments during recessive periods (X. Liu et al. 2012b).

**Interpretation.** The common occurrence of poor bedding and disordered accumulation indicate fairly rapid suspension fall out without winnowing (Stow 2005), probably affected by gravity flow deposition in relatively deeper water (Wu et al. 2016). The sharp contacts at the lower and upper boundaries between the sandstones and mudstones show that each sandstone layer represents a single event. However, the changing grain size inside the thin sandstone units shows an unstable hydrodynamic environment. Facies 3 is interpreted to have been deposited within lower shoreface zone formed near the storm wave base and was affected by multiple pulses of gravity flows.

**Facies 4: mudstones**

Facies 4 represents mudstones with occasional interbedded wisps of silt (Figs 4h and 5h). The mud layers are considerably thicker (2.5–3 cm) than in other facies (Fig. 5b). The silt laminations are fairly thin (0.3–1 mm) with sharp erosive bases and a crudely micro-graded lower part and structureless upper part. Shelly fossils preserved within Facies 4 are usually parallel to sub-parallel to the bedding plane. The bio-disturbance within Facies 4 is the lowest among the four facies, only up to 0.15%, resulting in a low bioturbation index (BI = 0) (Fig. 2; Table 2).

**Interpretation.** These sedimentary features, along with the soft tissue preservation associated with Facies 4, suggest a mainly rapid
deposition (obrution) of suspended muds settling from weak storm flows in a relatively low-energy environment (Zhu et al. 2001).

Composition and relative abundance of fossil assemblages

Thousands of well-preserved fossils spanning six key animal groups \((n = 2988)\) were collected from the lower Wulongqing Formation at the Shijiangjun section during one four-week field season. The taxa include brachiopods, arthropods, hyoliths, priapulids, vetulicolians and anomalocaridiids in descending order of rank abundance (Table 1). All these taxa are also found in the Wulongqing Formation from the Kunming and Malong areas (Hu et al. 2013; Chen et al. 2019). Brachiopods, arthropods and hyoliths form the three main components, with up to 98.9% of the total number of specimens (Table 1; Fig. S1). Even though the anomalocaridiids, vetulicolians and priapulids are rare in this section, they are very important elements of Cambrian Burgess Shale-type Lagerstätten (Zhao et al. 2010; Paterson et al. 2011; Smith 2015). Four genera of organophosphatic brachiopods, including Neobolus, Eoobolus, Westonia (Luo et al. 2008), Linnarssonia (Duan et al. 2020) and two calcareous taxa (Kutorgina and Nisusia) occur throughout the section. Neobolus is the most abundant genus (40.2%), followed by Eoobolus (28.9%) and Westonia (27.2%). However, arthropods remain the most diverse group, composed of trilobites, bradoriids, Guangweicaris, Panlongia, Isoxys, Tuzoia and Leanchoilia. Among these, trilobites are the most abundant taxon (82%) (Table 1).

Fossil data from every mudstone layer was obtained during four weeks of intensive fieldwork in 2018 (Table 1). The fossil
composition within assemblages A and B is similar, consisting of five animal groups, while faunal diversity decreases in assemblages C–F. This is followed by an increased diversity associated with faunal assemblages G–J. Faunal assemblage I has the highest diversity, with almost all taxa known from the entire section concentrated in this assemblage. Assemblage F has the greatest abundance of fossils \((n = 748)\) accounting for 25% the total number of individuals, followed by assemblages C, B, G and J (Fig. 2; Table 1).

The relative abundance of individual specimens from ten sampling layers was obtained (Fig. 2; Table 1) to gauge the baseline assemblage structure. Assemblages A and B are dominated by arthropods, accounting for 63.6 and 59.8%, respectively. Brachiopods dominate all other assemblages from layers C–J, with some fluctuation of composition in the relative abundance between brachiopod taxa. The abundance of brachiopods reaches a peak within assemblage F. Hyoliths, a common early Cambrian group, occur throughout the entire section, except for assemblage G. Anomalocaridids, vetulicolians and priapulids are interspersed irregularly within the assemblages.

The relative abundance of six genera of brachiopods throughout the section is very instructive (Fig. 2; see also Fig. 7b). Assemblage A is composed, almost equally, of three genera (Neobolus, 36.4%; Eoobolus, 36.4%; and Linnarssonia, 27.2%), whereas assemblage B contains a higher proportion of Neobolus (51.1%), with the relative abundance of the remaining two taxa 26.1 and 22.8%, respectively. Westonia occurs as a small proportion of assemblage C, whereas Neobolus and Eoobolus together exceed 97%. Assemblages C and D are mainly composed of Eoobolus (20.5 and 62.8%, respectively) and Neobolus (77.3 and 26.7%, respectively) with minor Westonia. By contrast, Westonia reaches a higher relative abundance (26.2%) in assemblage F. Eoobolus dominates assemblages G and H (52.4 and 64.2%, respectively), where Westonia also reaches a higher proportion of the assemblage (44.7% in G). Assemblages I and J are both dominated by Westonia, with 61.5 and 88% relative abundance, respectively; Eoobolus (24 and 9.6%, respectively) ranks second in these assemblages. The rare calcareous brachiopods Kutorgina and Nisusia are restricted to the upper part of the section in assemblages I and J (Figs 6g and 7b).

The lower part of the Wulongqing Formation (0–6 m) at the Shijiangjun section also contains distinctive brachiopod and trilobite fossil concentrations (Fig. 2; Table 2). The concentrations preserved in coarser sandy deposits (especially Facies 3) are highly fragmented (although also fragile and thin) and moderately well-sorted, which indicates a relatively high level of energy and transportation (Table 2). Some well-preserved shell concentrations are also preserved within thin mud beds (e.g. Facies 1 and 4), occasionally restricted to single bedding planes, and in a relative sense these thin shells are characterized by low levels of fragmentation, poor sorting, low to medium disarticulation, and occur sub-parallel to bedding planes with a high ratio (>50%) of conjoined brachiopod shells with more or less soft tissue preservation. These taphonomic proxies indicate a relatively rapid obrution deposit and minimal transportation (Figs 2 and 6a–d;
Table 2). The shell concentrations from the Shijiangjun section are either monospecific or paucispecific, dominated by brachiopods or trilobites (Fig. 6a–d). These concentrations are nearly always restricted to specific layers. For example, abundant Palaeolenus are exclusively found within layer M6 in assemblage B (Fig. 6b), whereas a concentration of Linuralia shells is known within layer M3 in assemblage A (Fig. 6a). The brachiopod concentrations from assemblage F are most abundant and mainly composed of monospecific layers of Neobolus (Fig. 6c) or Westonia (Fig. 6d), respectively. The Eoobolus and Westonia shell concentrations extend to the upper part of the section (Fig. 2). Throughout the section, brachiopod concentrations are completely restricted to Facies 1 and 2, whereas trilobite concentrations are mainly associated with Facies 4, which is restricted to assemblage B (Fig. 2).

Remarkable soft tissue preservation occurs in all assemblages except D and E, demonstrating the high preservation potential within facies at the Shijiangjun section of the Wulongqing Formation in the Wuding area. Tube-dwelling organisms encrusting to Neobolus shells (see Z.F. Zhang et al. 2020a) (with exceptionally preserved setae and soft viscera) are fairly common within the lower part of the section within mudstone beds (layers A, B, C and F) (Fig. 6c). Abundant specimens of Westonia display high-quality soft tissue preservation from assemblage F, including setal fringes and mantle canals (Fig. 6f). Palaeoecoleidcan worms, as an important component of lower Paleozoic soft-bodied assemblages, were found throughout the section, except for assemblage C (Fig. 6h). Relatively rare vetulicolians occur at the base and in the upper part of the section (assemblages A, B, I and J) (Figs 2 and 6f). Anomalocarididans are the rarest element in the section, only preserved as isolated frontal appendages in assemblages I and J. The rare oldest known digestive system of trilobites (Hopkins et al. 2017) have also been preserved in the Wuding area, but only in assemblage B (Fig. 6j).

Discussion

Depositional environment

Heterolithic successions consisting of sandstone beds interbedded with mudstones are usually deposited below the fair weather wave base and above the storm wave base (Dott and Bourgeois 1982; Myrow and Southard 1996; Dumas and Arnott 2006; Bullimore et al. 2008; Buatois and Mángano 2011; Eide et al. 2015). These beds are commonly described as tabular (Elliott 1978; Coe et al. 2003) and often show abundant erosive gutter casts (Eide et al. 2015). The alternation of mudstone (Facies 1, 2 and 4) and sandstone (Facies 3) layers – in addition to graded lamination/bedding, wavy bedding, ripple marks and gutter casts from the Shijiangjun section – suggest a depositional environment close to the storm wave base, which underwent multiple depositional events and episodic cycles (Shannumgam 2002; Hu et al. 2010; Buatois and Mángano 2011).

Previous studies have interpreted the sedimentary environment associated with the Guanshan Biota as mainly offshore transition with common storm events (Hu et al. 2010; Chen et al. 2019), which is comparable with the Cambrian Stage 4 Emu Bay Shale from Australia (Paterson et al. 2016) and the Ordovician Fezouata Biota (Martin et al. 2016). However, typical storm-generated structures such as hummocky cross-stratification, an indicator of oscillatory combined flows reflecting deposition under high-energy storm conditions (Arnott and Southard 1990; Cheel 1990; Southard et al. 1990; Cheel and Leckie 1993; Yokokawa et al. 1999; Dumas et al. 2005) are absent in the Wuding succession.

The occurrence of erosive bases, ripple marks, wavy bedding, fine-graded bedding, gutter casts and multiple massive fine to coarse deposits indicates a complex hydrodynamic environment, with less frequent waves and distal storms (Zhu et al. 2001; Buatois and Mángano 2011; X. Liu et al. 2012; Michalik et al. 2013). Periodic subaqueous gravity flows resulted in the deposition of distinctive centimetre-scale sandstone interbeds (Facies 3) at the Shijiangjun section. Hence the sedimentary environment of the lower Wulongqing Formation in the Wuding area is largely the result of fluctuating wave energy, distal storms and gravity flows.

The centimetre-scale conglomerates characterized by high sphericity reported from the Wulongqing Formation at Malong and Kunming represent high-energy channels, probably proximal to the shoreface (Hu et al. 2010; Chen et al. 2019). The absence of basal conglomerates and the occurrence of medium to very coarse sandstones with few granules at the base of the Wulongqing Formation in the Wuding area (Fig. 4e) suggest a relatively deeper and low-energy clastic sedimentary environment than that in the Malong and Kunming areas (Hu et al. 2010; Chen et al. 2019), although this remains to be tested because detailed continuous successions of the Wulongqing Formation have not been studied sedimentologically. Overall, the depositional environment here is interpreted as offshore to lower shoreface as defined by Martin et al. (2016) and the offshore zone of Buatois and Mángano (2011), which slightly extends below the storm wave base (Fig. 3g).

Faunal overturn and assemblage composition

The baseline time series of the fossil data recovered from the lower Wulongqing Formation at the Shijiangjun section reveals a unique transition in the structure of the benthic community over time (Fig. 2; Table 1). The relative abundance of six key animal groups, including six brachiopod genera, from ten sampled layers demonstrates gradual replacement, overturn and fluctuation in the faunal composition (Figs 2 and 7). Although arthropods dominate the base (0–1.1 m) of the section (assemblages A and B), the proportion of brachiopods gradually increases, replacing arthropods as the dominant fauna in assemblages C–J, reaching peak abundance (97.99%) within assemblage F (Figs 2 and 7a). Although there is a fluctuation in the relative abundance of brachiopods through assemblages G–J (c. 60–80%), arthropods maintain a relatively low, but stable, percentage.

There is no doubt that trilobites dominated early Cambrian benthic communities in terms of diversity and abundance, which is demonstrated well in the older Chengjiang Lagerstätte (Zhao et al. 2010; Hou et al. 2017; Paterson et al. 2019) and the Malong Fauna (Luo et al. 2008; Chen et al. 2019). The latter is characterized by extremely abundant and diverse trilobites yielding from the underlying Hongningshao Formation (Fig. S1; Table S1). However, detailed fossil data from the Guanshan Biota in Wuding and Malong areas reveals a community structure that is unique for early Cambrian Konserat-Lagerstätten, with brachiopods dominating the benthic community in abundance, if not diversity, and often forming distinctive concentrations of shell beds in the lower Cambrian Stage 4 of the Wulongqing Formation (Figs 2 and 7a; Fig. S1). The ecological transition from trilobite–brachiopod-dominated communities occurs widely across shallow marine clastic environments across the South China Platform (Fig. 1), coinciding with well-documented transgression events during Cambrian Stage 4 (Luo et al. 2008; Hu et al. 2010, 2013; Chen et al. 2019). Thus organophosphatic brachiopods diversify and become superabundant across the broad ‘shallow’ shelf of the Yangtze Platform during the final stage of the Cambrian Explosion (Z.F. Zhang et al. 2020a). The rise of organophosphatic brachiopods as the numerically dominant element in the lower Cambrian Stage 4 Wulongqing Formation is the oldest brachiopod-dominated soft substrate community known in the fossil record and represents a precursor to more
complex community tiering and brachiopod-dominated benthic communities during the Great Ordovician Biodiversification Event (Bassett et al. 2002; Servais and Harper 2018; Topper et al. 2018; Z.L. Zhang et al. 2018, 2020b; Z.F. Zhang et al. 2020a).

The brachiopods recovered from the section include lingulides (Eoobolus, Neobolus and Westonia), an acrotertid (Linnarssonia) and calcareous kutorginides (Kutorgina and Nisusia) (Table 1). Lingulides occur in high abundance and also form many shell concentrations within several assemblages (Fig. 2). The number of brachiopod concentrations (at least ten thin mud beds) far exceeds those produced by trilobites (only one mud bed). The composition of brachiopod taxa within each assemblage shows a rapid transition through time (Figs 2 and 7b). Neobolus is predominant in the lower part of the section (assemblages A–C, E and F), with Eoobolus (lingulides) and acrotertides common, but subordinate (Figs 2 and 7b). The relative abundance of the acroterloid brachiopods, earlier referred to as ‘Westonia’ gabaiensis, increases gradually up-section, replacing, in part, the lingulides (Eoobolus and Neobolus) and acrotertides. This is partly attributed to the fact that the brachiopods of Eoobolus and Linnarssonia had a much smaller shell (c. 2–5 mm in maximum width) than Westonia. In addition, Westonia has a very wide and circular shell in outline, which is potentially adapted to the shallow seawater environment. In general, the linguliform (e.g. lingulides and acrotertides) brachiopods show a strong control on assemblage dominance, whereas calcareous forms (kutorginides) remain rare (Fig. 7b).

Fossil concentrations, although common throughout geological time (Li and Droser 1997; Damborenea and Laniés 2007; Mancou et al. 2015; El-Sabbagh and El Hedeny 2016; García-Ramos and Zuschin 2019), are rarely reported from Burgess Shale-type Lagerstätten (Han et al. 2006). The dominance of brachiopods within the Guanshan Biota, compared with other Cambrian Lagerstätten, is unique (Luo et al. 2008; Zhao et al. 2010; Paterson et al. 2016; Strang et al. 2016; Fu et al. 2019). The in situ preserved brachiopod concentrations in the Wuding area also occur in the Malong and Kunming areas, which indicates a wide geographical distribution (c. 6000 km²) after the rapid transgression at the base of the Wulongqing Formation (Hu et al. 2013; Chen et al. 2019; Z.F. Zhang et al. 2020a).

Overall, the fossil data show that brachiopods quickly replaced arthropods as the dominant fauna following a transgression that led to the deposition of the Wulongqing Formation at Wuding (Figs 2 and 7a; Fig. 51). Different brachiopod genera dominated different assemblages and, in places, formed distinctive shell concentrations (Figs 2 and 7b).

**Guanshan Biota and its environment**

The Guanshan Biota is an exceptionally preserved Konservat-Lagerstätte, uniquely characterized by brachiopod-dominated early Cambrian communities, substantially different from the arthropod-dominated Konservat-Lagerstätten such as the Chengjiang and Burgess Shale biotas (Zhao et al. 2010; O’Brien and Caron 2016; Hou et al. 2017; Nanglu et al. 2020). Although the preservation of soft tissues within biomineralized and sclerotized exoskeletons is common, which is at least partly attributable to the high number of brachiopods, trilobites and hyoliths, completely soft-bodied organisms (e.g. ctenophores) are absent in the Shijiangjun section, which is similar to the Ordovician Fezouata Biota (Saleh et al. 2020). This phenomenon is possibly related to preservation bias because the brachiopods, trilobites and hyoliths are more resistant to decay and much more readily preserved within this Konservat-Lagerstätte, which might lead to an underestimate of the diversity (Saleh et al. 2020) of the Guanshan Biota in the Wuding area. The lack of completely soft-bodied taxa may be due to the lack of an exaroebric preservational trap that typifies the Burgess Shale-type deposits (Gaines and Droser 2005).

The relatively shallow sedimentary environment (lower offshore in Martin et al. 2016 or offshore in Buatois and Mángano 2011) of the Guanshan Biota also separates it from most other Cambrian Lagerstätten worldwide except, perhaps, for the early Cambrian Emu Bay Shale from Australia, which is interpreted to have been deposited in a nearshore micro-basin setting adjacent to an active tectonic margin that generated continual syndepositional faulting and slumping (Paterson et al. 2016). The Guanshan Biota is also comparable with the Ordovician Fezouata Biota, both in terms of depositional environment and shelly faunal composition (Van Roy et al. 2015; Saleh et al. 2018). The latter was deposited mainly in an offshore to lower shoreface setting (Martin et al. 2016).

Gravity, traction and turbiditic flows are responsible for the transitions from arthropod- to brachiopod-dominated assemblages from the lower part of the Wulongqing Formation at the Shijiaguang section. The depositional environment between the fair weather wave base and the storm wave base is usually affected by frequent event flows, such as oscillatory and gravity flows (Kooi and Groen 2001; Majid et al. 2017), which helps to mix oxygen-enriched surface water with stagnant bottom water, providing favourable nutrient-rich conditions for the development of the benthic community (X. Liu et al. 2012b). Transportation from a nearby source, rapid fall out from suspension and the resuspension of seston provides a high nutrient load for suspension feeders such as brachiopods to flourish.

The limited amount of bioturbation throughout most of the section seems to indicate conditions unfavourable for burrowing, resulting from high turbidity, high or low salinity, or the relatively low oxygen content, perhaps explaining the dominance of relatively small, physiological simple filter-feeding brachiopods. The increase in the bioturbation index in the middle part of the section (3–6 m above the basal contact) is coincident with assemblages G–I, indicating more favourable conditions, probably as a result of the relatively shallower depositional environment or fluctuatingoxic conditions (Gaines and Droser 2005). The frequent overturn of fossil assemblages, especially brachiopods, may be attributed to frequent environmental fluctuations and the episodic input of coarser sediments, which probably periodically interrupt the benthic suspension assemblances.

Detailed analysis of the sedimentology, lithology and structures facilitates the identification of distinct lithofacies associated with transgressive systems tracts that directly affected the composition, diversity and relative abundance of faunal assemblages in the transition from the Hongningshao to the Wulongqing deposits (Luo et al. 2008; Chen et al. 2019). Microfacies analysis, the degree of bioturbation and the faunal composition at the lower part of the Wulongqing Formation provide a new understanding of how fluctuations in the depositional environment influenced the faunal overturn in the Guanshan Biota across the Yangtze Platform in eastern Yunnan.

**Conclusions**

This is the first detailed report of the lithofacies, depositional environments and associated relative faunal abundance in the Cambrian Age 4 Guanshan Biota. The new Shijiangjun section through the basal part of the Wulongqing Formation in the Wuding area, eastern Yunnan reveals fossil assemblages composed of six bilaterian groups (Brachiopoda, Arthropoda, Hyolitha, Priapulida, Vetulicola and Anomalocarciidi). Detailed sedimentological, lithological and ichnological characteristics of the section indicate that: (1) hydrodynamic conditions are fluctuating, with episodic changes in energy and current regimes producing periodically coarse sand beds (Facies 3); (2) the sediments are derived from a
relative nearby source and accumulated rapidly; (3) the environment is affected by multi-period hydrodynamic events, such as storm and gravity flows forming obrution deposits (Zhang et al. 2019); and (4) the overall sedimentary environment in the Wuding area represents a deeper offshore to lower shoreline than the Wulongqing Formation outcropping in the Malong and Kangning areas.

The community transitioned from arthropod- to brachiopod-dominated at the first time for the base of the Wulongqing Formation in the Shijianggou section. Within the brachiopod communities, a lingulata-dominated assemblage transitioned to an acrotheloid-dominated assemblage with the new occurrence of calcareous kutorginids up-section. The detailed study and documentation of this transition provides a better understanding of the differences in faunal composition and overturn between the Malong Fauna and Guanshan Biota (Luo et al. 2008; Chen et al. 2019). The unstable sedimentary environment with periodically sandy depositional inputs and muddy obrution deposits is probably closely associated with the observed succession of community assemblages. Brachiopods from the Guanshan Biota generally show a preference for such a fluctuating environment and adapt well to this environmental setting during the final stage of Cambrian evolutionary radiation.

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