AN IN SITU PRESERVED EARLY CARBONIFEROUS (SERPUKHOVIAN) BRACHIOPOD COMMUNITY IN SOUTHERN GUIZHOU, CHINA

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Abstract. A brachiopod shell bed from the Lower Carboniferous (Serpukhovian) in Guizhou Province of southern China is reported as representing an in situ preserved brachiopod community. The community is characterized by yielding more than 80% complete and articulated specimens preserved in life position and poor size sorting. A new spiriferide species, *Weiningia ziyunensis* n. sp., is described in the community, which contains the other eight species belonging to six genera. Morphology and preservation analysis of *Weiningia ziyunensis* n. sp. suggest that it lived in dense clusters attached to living and dead shells and stablized its position with thickened posterior shell. Size-frequency distribution and survivorship curve are applied to the population dynamics investigation of this species. Large number of juvenile shells accompanied by high mortality reflects that many juvenile individuals suffered from the limited life space and turbid environment generated by dense clusters. The same high adult mortality is the result of more pressure from neighbors that lead to shell malformation and eventually low feeding and cleaning efficiency, whereas the low senior mortality is attributed to their abilities to cope with these problems. Members of the community show great difference in numeric frequency, with *Weiningia ziyunensis* n. sp. being one of the dominant species that was characterized by crowded life strategy. By living in dense clusters on *Striatifera striata* (Fischer de Waldheim, 1837) or other shell fragments, *Weiningia ziyunensis* n. sp. could resist the water current and gradually expand its population.

INTRODUCTION

An in situ preserved fossil assemblage is defined as any group of fossils from a suitably restricted stratigraphic interval and geographic locality, which can be distinguished from those being transported and mixed (Fagerstrom 1964; Brenchley & Harper 1998). In such assemblage, nearly all the specimens are preserved essentially in their original habitats and life position, with approximate sizes

and numbers as when they were alive. The shells of bivalved animals are commonly articulated and weakly damaged. Nevertheless, any life assemblage will undergo a complex preservation history before becoming a fossil one, which may alter the original community structure and composition. Studies showed that 7 to 67% of recent marine organisms without mineralized skeletons have little potential for preservation as fossils (Lawrence 1968; Kidwell & Flessa 1995). Due to the diverse intrinsic properties such as mineralogical composition, body plan, microstructure and life mode, those skeletal organ-
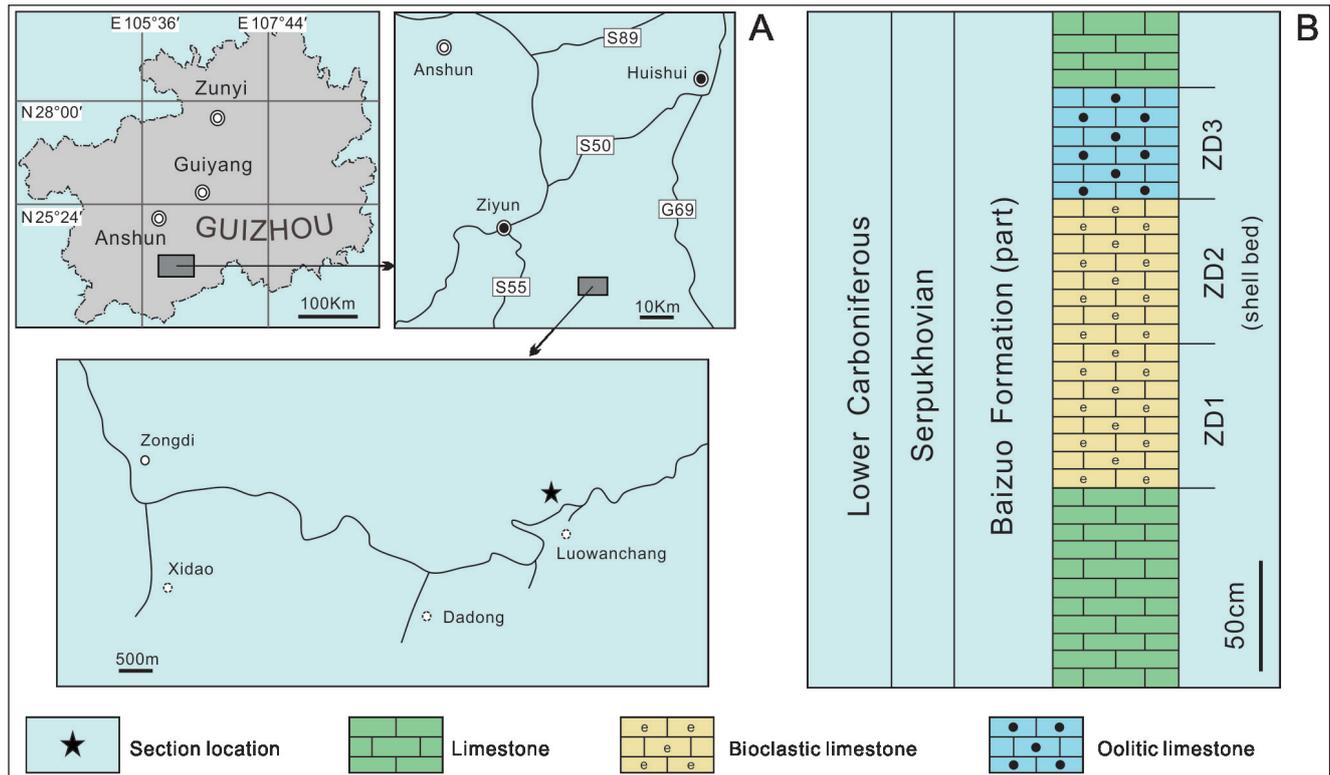
Fig. 1 - Location map (A) and lithological column (B) of the studied section near Luowanchang Village, Zongdi Town, Ziyun County, Guizhou, China.

isms may also be preserved differently (Best & Kidwell 2000; Lazo 2004; Tomašových & Rothfus 2005; Tomašových & Zuschin 2009; Kosnik et al. 2011). Postmortem transportation by current (Tomašových 2004; Zuschin et al. 2004a, 2004b; Chen et al. 2010; Pan et al. 2012; Fürsich et al. 2016), storm (Zuschin et al. 2005; Tomašových 2006) and biotic behavior (Noble & Logan 1981; Shimoyama 1985; Zuschin & Oliver 2003; Yanes 2012), as well as dissolution (Davies et al. 1989; Brachert & Dullo 2000; Wright et al. 2003; Tomašových 2004; Erthal et al. 2011, 2015) and replacement (Fagerstrom 1964) are highlighted to affect the composition of fossil communities. In order to distinguish the autochthonous and the allochthonous assemblages, some taphonomic criteria are used, including the ratios of articulated shells and opposite valves, fragmentation and reorientation (Zuschin et al. 2003; Nielsen 2004; Tomašových 2006; Webster et al. 2008; Balseiro et al. 2011; Pan et al. 2012; Yanes 2012; El-Sabbagh et al. 2015). Besides, time-averaging that is pervasive in fossil assemblages and can influence the fidelity of species abundance and diversity should also be considered (Fürsich & Aberhan 1990; Flessa et al. 1993; Behrensmeyer et al. 2000; Kidwell & Holland 2002;

Pan et al. 2012; Yanes 2012; Kidwell & Tomašových 2013; Weber & Zuschin 2013; Zuschin & Ebner 2015; Fürsich et al. 2018). So far, many studies have revealed that autochthonous fossil assemblages were not rare and they could well provide the significant information about life habits of organisms, paleoenvironment and their interaction (e.g. Angiolini 2007; Fürsich et al. 2009; Lauridsen et al. 2009; Chen et al. 2010; Wang et al. 2012; Abdelhady & Fürsich 2014; Bassi et al. 2015; Nolan et al. 2017; Buscalioni et al. 2018; Posenato et al. 2018; Yang et al. 2018; Salama & Özer 2019; Zacaríasa et al. 2019).

Southern China is an important area for the study of Carboniferous stratigraphy and paleontology. As a part of it, Guizhou Province is characterized by extended outcrops of Carboniferous strata, which contain abundant bryozoans, crinoids, brachiopods and other fossils. Sun & Baliński (2008, 2011) reported a remarkably diverse brachiopod fauna from the Mississippian (Tournaisian) Muhua Formation, including some endemic taxa such as *Muhuathyris* and *Muhuarina* (Sun et al. 2004; Baliński & Sun 2005). *Weiningia*, a martiniid brachiopod genus ranging from Serpukhovian to Bashkirian (Liao 2013), was widespread in Guizhou, Guangxi, Yun-

nan and Xinjiang Province of China (Jin & Liao 1974; Li 1987; Liao et al. 1990; Liao 2013), Japan and Russian (Alexandrov & Solomina 1973; Yanagida & Matsusue 1990, 1995). This genus is often discovered as monospecific fauna forming shell beds (Liao 2013). Little attention has been paid to the paleoecology of *Weiningia* except the consideration of two species described by Yanagida and Matsusue (1990, 1995). Based on asymmetrical shell form and sedimentary facies, the authors referred that *Weiningia* may have lived on the fine sediments that deposited among small patch reefs. Nevertheless, the dense preservation of disarticulated shells indicates that the specimens had been transported, which precluded the further paleoecological investigation. In this study, we report a newly found locality with mass occurrence of *Weiningia* within a brachiopod shell bed in the Lower Carboniferous Baizuo Formation in Guizhou Province. Taphonomic analysis, including low disarticulation ratio, non-reorientation and poor size sorting, indicates the in situ burial of this brachiopod community. Most specimens are preserved in life position and some exhibit clear biotic interactions, providing a good chance for detailed paleoecological investigation. *Weiningia ziyunensis* n. sp., one of the dominant species, forms patchy clusters in the shell bed and displayed a similar life strategy to some recent pediculate brachiopods. Its settlement behavior probably reveals the development of this community.

GEOLOGIC SETTING AND SAMPLING

During Middle Devonian to Carboniferous, the transgression expanded progressively from southwest to north and northeast on the Yangtze plate, resulting in a widely distributed carbonate deposition in most areas of southern China (Wan 2003). In Guizhou Province, the Carboniferous is mainly restricted in the southern and western parts. The Lower Carboniferous is geographically distributed in Dushan-Weining, Langdai-Luodian and Pu'an-Mawei regions representing the shallow water, deep water and the transitional environment respectively (Wu 1976).

The studied materials were collected from the Lower Carboniferous Baizuo Formation exposed along a road-cut near Luowanchang Village, Zongdi Town of Ziyun County (geographic coor-

dinates: 25°34'52.92"N, 106°22'10.68"E; Fig. 1). The Baizuo Formation is the youngest unit of the Lower Carboniferous in Dushan-Weining region, and it distinguishes from the underlying Shangsi Formation by the disappearence of the rugosa coral *Kueichouphyllum*, the first appearance of the productide *Gigantoproductus* and occurrence of numerous productide *Striatifera* (GZGMRB 1987). It distinguishes from the overlying Huashiban Formation by the first appearance of the fusulinids *Pseudostaffella* and *Profusulinella* (GZGMRB 1987), or the disappearence of the brachiopods *Gigantoproductus edelburgensis* Phillips, 1836 and *Gondolina* (Yang 1978). The Baizuo formation is widely distributed in southern Guizhou with a thickness varying from 4 to 582 m. The formation is mainly composed of massive limestone, dolomitic limestone and dolostone, deposited in a shallow bay environment (Yang 1978). More than 30 brachiopod genera are recognized within this lithostratigraphic unit in Guizhou province, many of them are extended from the underlying formations (Yang 1978). Two brachiopod assemblages were established in the Baizuo Formation: *Striatifera striata* (Fischer de Waldheim, 1837) - *Gigantoproductus edelburgensis* assemblage in the lower and *Gondolina weiningensis* Jin & Liao, 1966 - *Striatifera angusta* Janischewsky, 1910 - *Gigantoproductus edelburgensis* assemblage in the upper, and they are yielded in Dewuan Stage which is dated to the Serpukhovian (GZGMRB 1987; Jin et al. 2000). In the studied area, the formation is 100-200 m thick. Beds are almost horizontally exposed along a road-cut near Luowanchang Village of Zongdi Town, with brachiopods, foraminifers, ammonoids and other fossils. At about 3 m above the road, a 0.3-0.4 m-thick bed is filled with numerous brachiopods, which are locally highly concentrated to form some 0.3 to 0.4 m high and ca. 1.5 m to several meters long clusters intermittently distributed along the strike.

MATERIAL AND METHOD

Brachiopod specimens statistically studied in this paper were obtained from the shell bed shown in Figs. 1 and 2A-D. Two bulk samples were collected, with over 60 kg from one cluster (ZDA) and 30 kg from its nearby non-cluster patch (ZDB). Two other bulk samples, 12 kg of each, were collected from the underlying and overlying beds (non-shell bed, ZD1 and ZD3 respectively). Specimens that were extracted by physically splitting and breaking slabs are housed at the Geological Museum of Peking University, Beijing, China (PKUM). Those pertaining to this study were coated with ammo-

Samples / Taxa	ZDA	ZDB	Total
Megachonetes zimmermanni	3	8	11
Striatifera striata	735	288	1023
Echinoconchella elegans	0	2	2
Gigantoproductus schajenwanensis	0	1	1
Gigantoproductus edelburgensis	0	1	1
Gigantoproductus moderatus	7	9	16
Fluctuaria undata	0	3	3
Cleiothyridina submabranacea	35	8	43
Weiningia ziyunensis n. sp.	914	5	919
Total	1694	325	2019

Tab. 1 - Numeric distribution of brachiopods in the shell bed from the Baizuo Formation.

Total counted shells (number)	Articulated shells (number and percent)	Disarticulated shells (number and percent)	Ventral valves (number)	Dorsal valves (number)	Valve ratio (ventral / dorsal)
962	813, 84.5%	149, 15.5%	962	887	1.08

Tab. 2 - Disarticulation and dorsal/ventral valve ratios of biconvex brachiopods (*Cleiothyridina submabranacea* and *Weiningia ziyunensis* n. sp.) in the shell bed from the Baizuo Formation.

Species richness (S)	Individual	Simpson dominance (D)	Simpson diversity (1-D)	Shannon-Wiener (H')	Pielou's equitability (J)
9	2019	0.46	0.54	0.88	0.40

Tab. 3 - Several diversity indices of brachiopods in the shell bed.

nium chloride and photographed under Nikon SMZ 1500 binocular equipped with a Nikon DS-Fi3 microscope camera. The images were further processed under Adobe Photoshop CS4. Furthermore, thin sections were processed for the investigation of sedimentary environments in the four sampled places. Over 24 kg samples were processed with acetic and formic acids to obtain conodonts for biozone determination of the beds.

To investigate the brachiopod composition in ZD2, the abundance of each species was calculated based on counting the number of articulated shells and half of the total number of disarticulate valves if they occurred. For the broken pieces resulted from sampling and preparation process, only the ones having relatively complete posterior part were counted. Disarticulation and ventral/dorsal valve ratios were applied as taphonomic analysis to recognize an autochthonous fossil assemblage (e.g. Angiolini 2007; Fürsich et al. 2009; Chen et al. 2010; Bassi et al. 2015; Yao et al. 2016; Posenato et al. 2018; Salama & Özer 2019). In the articulation ratio (N/N_0) which was proposed by Boucot et al. (1958), N is the number of disarticulated shells and N_0 is the original number of all shells present before disarticulation. Although most productide shells are clearly observed in articulated forms, it is difficult to count the total number of both valves because some hide in the rocks that cannot be separated from. Here the biconvex taxa (*Cleiothyridina submabranacea* Grabau, 1933 and *Weiningia ziyunensis* n. sp.) were chosen because they were more accessible to collect. The number of *Weiningia ziyunensis* n. sp. is also large enough to represent the whole community (Tab. 1).

As an important part of paleoecological investigation the population dynamics is studied by analyzing the size and age composition of populations. Size-frequency distribution and survivorship curve, the common methods of accessing that information of fossil species (Bitner 2002; Tomašových 2004; Zuschin et al. 2004, 2005; Tomašových 2006; Webster et al. 2008; Pan et al. 2012; Skawina 2013; Lü & Ma 2017; Huang et al. 2018), were undertaken for *Weiningia ziyunensis* n. sp. Since the size is associated with the age of brachiopods, the size-frequency distribution can partly reflect the age structure of the population and it is plotted in a histogram with size (length or width) as horizontal axis and frequency as vertical axis (Dodd & Stanton 1981; Huang et al. 2013). Chen et al. (1994) suggested that the distribution would be essentially the same regardless of the horizontal axis was either the length or the width. In this study, the length of ventral valve was chosen as horizontal axis. As for survivorship curve, it can represent the mortality rate of different growth stages, giving the relative age and frequency as horizontal and vertical axis. The age is derived from the size based on the assumption that the growth rate is initially rapid and decreases during ontogeny, which has been discovered in many recent articulate brachiopods (Paine 1969; Thayer 1975, 1977; Curry 1982; Peck et al. 1995; Brey et al. 1995; Baumgarten et al. 2014) and bivalves (Levinton & Bambach 1970; Schöne et al. 2003; Michaelidis et al. 2005). The equation and methods proposed by Levinton & Bambach (1970) and Dodd & Stanton (1981) were applied in this study. Species richness (S), Simpson index of dominance (D) and Pielou's equitability (J) were used to measure the species evenness of the community (e.g. Zuschin et al. 2005; Forcino 2012). The dominance index (D) indicates the probability that two randomly picked individuals are the same species. It will be close to 1 if there is a single very dominant taxon while it will reach the minimal value 1/S if all taxa are equally common. The equitability index (J), varying from 0 to 1, indicates the difficulty in predicting the species of the next individual collected. It is established based on the Shannon-Wiener index but normalized for the species richness as the Shannon-Wiener index is sensitive to the relative abundances and the number of taxa (Hammer & Harper 2006). Both indexes follow the calculations by Hammer & Harper (2006).

Fig. 2 - Outcrops (A-D) and thin sections of some typical rocks from sampled beds (E-M) of the Baizuo Formation. A) View of the outcrop with location of the shell bed. B) Close view of the sampled beds. Location of ZD1-3, cluster (ZDA) and non-cluster (ZDB) samples are marked. C) Close view of ZDA with numerous *Weiningia ziyunensis* n. sp. (arrows). D) Close view of ZDB with *Striatifera striata* (arrows) parallel to the bedding plane. E, F) Bioclastic grainstone in ZD1. Arrow indicates productide spine. G-I) Bioclastic packstone inside (G, H) and on the edge (I) of ZDA. Arrows indicate productide spines in H and geopetal structure in I. Sparry calcite fills the cavity above the horizontal sediment surface (S), below which the infilling is dominated by micrite grains. J, K) Bioclastic grainstone inside (J) and on the edge (K) of ZDB. L, M) Oolitic grainstone in ZD3. The hammer in B is 30 cm long. The coin in C and D is 24 mm wide. Scale bar in E-M is 0.5 mm long.
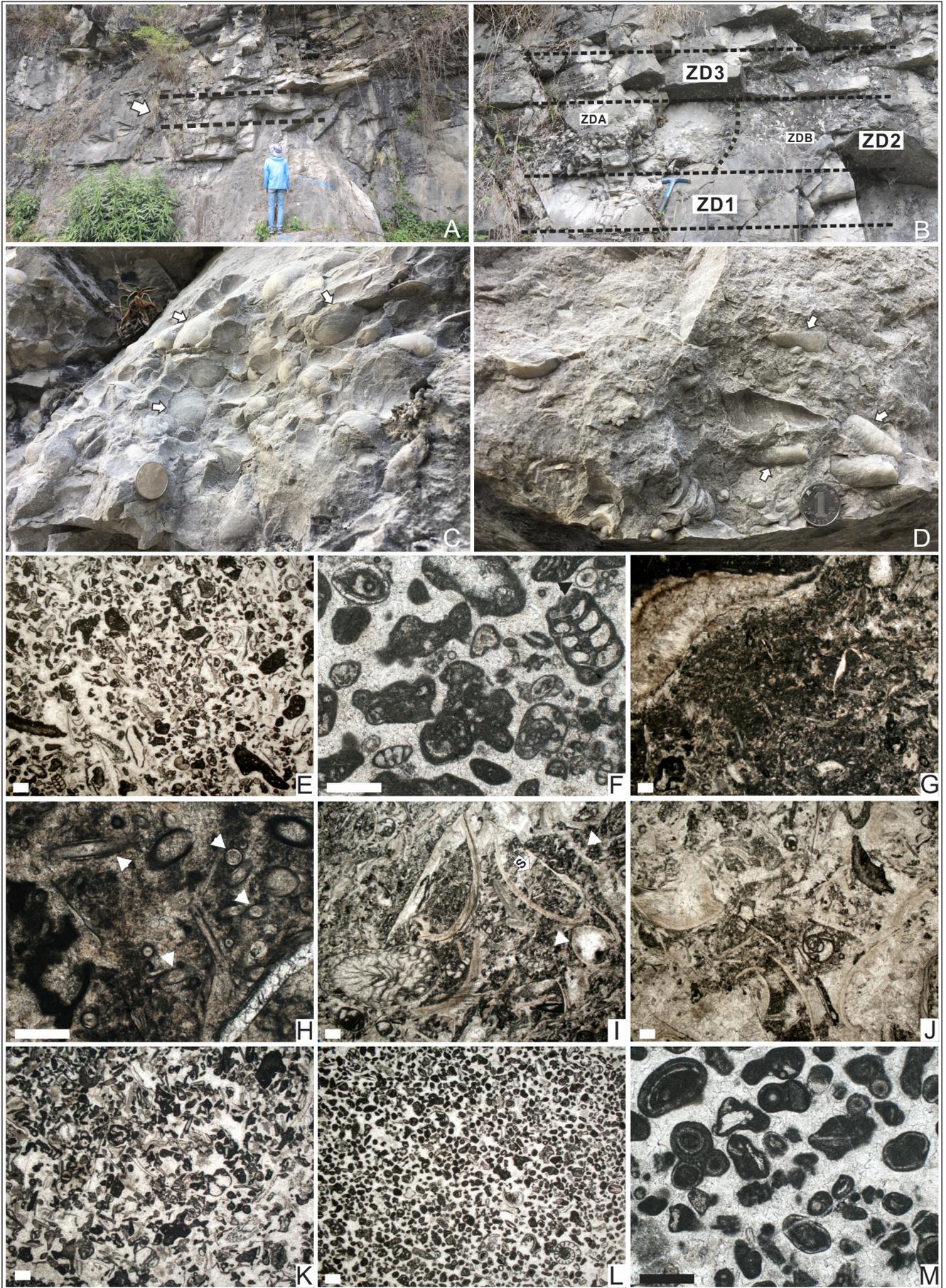
PRESERVATION OF THE COMMUNITY AND SEDIMENTARY ENVIRONMENT

A total of 2019 brachiopod specimens belonging to nine species of seven genera were found in sample ZDA and ZDB (Fig. 3, 4; Tab. 1): *Megachonetes zimmermanni* Paeckelmann, 1930, *Striatifera striata* (Fischer de Waldheim, 1837), *Echinoconchella elegans* McCoy, 1844, *Gigantoproductus schajenwanensis* Ozaki, 1939, *Gigantoproductus edelburgensis*, *Gigantoproductus moderatus* Schwetzow, 1922, *Fluctuaria undata* Defrance, 1826, *Cleiothyridina submabranacea* and *Weiningia ziyunensis* n. sp. All of them were previously recorded from the upper Lower Carboniferous in southern and western Guizhou except the new species (Wu et al. 1974; Yang 1978; Feng & Jiang 1978; GZGMRB 1987). Other macrofossils included corals, crinoid stems, ammonoids and gastropods. The microfossils were represented by foraminifers only. Although no conodonts were found, the shell bed can be dated to the Serpukhovian due to the large number of *Striatifera striata*, the index fossil of *Striatifera striata - Gigantoproductus edelburgensis* assemblage (GZGMRB 1987; Wu 1987). In the shell bed, more than 80% specimens of *Cleiothyridina* and *Weiningia* are preserved in articulated state and the opposite valves ratio is approximate to 1 (Tab. 2). Despite of *Echinoconchella*, *Gigantoproductus* and *Fluctuaria*, different sizes of conspecifics were also found. Most of them are preserved in life position without evidence to prove they were transported, strongly suggesting an in situ buried community.

Sample ZDA yields 1694 specimens in total. It is noteworthy that this sample can be clearly divided into a lower and an upper part. *Megachonetes*, *Striatifera*, *Gigantoproductus* and *Cleiothyridina* are restricted to the lower part (Fig. 5A), while the upper part is entirely instead of purely *Weiningia* (Fig. 5B). *Striatifera* individuals are generally preserved with their ventral valves downward and scattered on the substrate or lying on the dorsal valve of other individuals, providing the hard substrates for *Weiningia* and *Cleithyridina*. Some *Striatifera* bearing attached *Weiningia* display a sudden change of growth direction from horizontal to upward, making the anterior portion almost perpendicular to the posterior portion of the shell. Although *Weiningia* appears in both parts of the sample, the number of specimens in the upper one is much larger than that in the lower one. More than 70% of *Weiningia* are represented by articulate shells and most of them are preserved close to each other, with the ventral beaks in proximity to the dorsal valves of *Striatifera* or other shells of neighboring individuals (Fig. 2C). *Megachonetes* are preserved with either valves downward on the substrate. *Gigantoproductus* are preserved in the same way as *Striatifera,* with ventral valve downward, but no *Weiningia* attached on them.

Sample ZDB yields 325 specimens and all are randomly distributed within the sample. Most *Striatifera* are roughly parallel to the substrates with the ventral valves downward (Fig. 2D). Some are almost vertically oriented with the ventral beak downward or upward, probably resulting from current disturbance. *Cleithyridina* and *Megachonetes* are preserved in the same way as those in ZDA. Other productide species are preserved in original life position, i.e., they rested on the substrate with ventral valves downward. Compared with those in ZDA, specimens of *Weiningia* occurring in ZDB are all disarticulated single valves parallel to the substrate, suggesting that they correspond to dead shells from nearby clusters.

Composition charts reveal that *Striatifera striata* and *Weiningia ziyunensis* n. sp. are the dominant species of the community because the others only take up no more than 10% (Fig. 6A). *Weiningia ziyunensis* n. sp. is mainly restricted to ZDA, where it makes up more than 50% of the population whereas in ZDB it attains only 1% and all specimens are disarticulated valves. Compared with *Weiningia ziyunensis* n. sp.,

Fig. 3 - *Weiningia ziyunensis* n. sp., Ziyun County, Guizhou Province, southern China, Lower Carboniferous, Baizuo Formation, Serpukhovian. A) Paratypes PKUM 02-0840, ventral, dorsal, lateral, anterior and posterior views of small shells. B) Paratype PKUM 02-0841, ventral interarea of relatively large shell in dorsal view. C) Paratype PKUM 02-0842, dorsal interarea of relatively large shell in ventral view. D) Holotype PKUM 02-0843 with concentric growth lamellae, ventral, dorsal, lateral, anterior and posterior views. E) Paratype PKUM 02-0844, ventral, dorsal, lateral, anterior and posterior views of relatively large shell. F) Paratype PKUM 02-0845, ventral, dorsal and lateral views, and capillae microornament of large shell. G, J) Paratypes PKUM 02-0846, PKUM 02-0847, ventral and dorsal views of malformed shells. H) Paratype PKUM 02-0848, ventral, dorsal and lateral views of malformed shell. I) Paratype PKUM 02-0849, ventral, dorsal and anterior views of malformed shell. Scale bars represent 2 mm (F_4), 5 mm (B, C) and 10 mm (A, D-F_3, G-J).
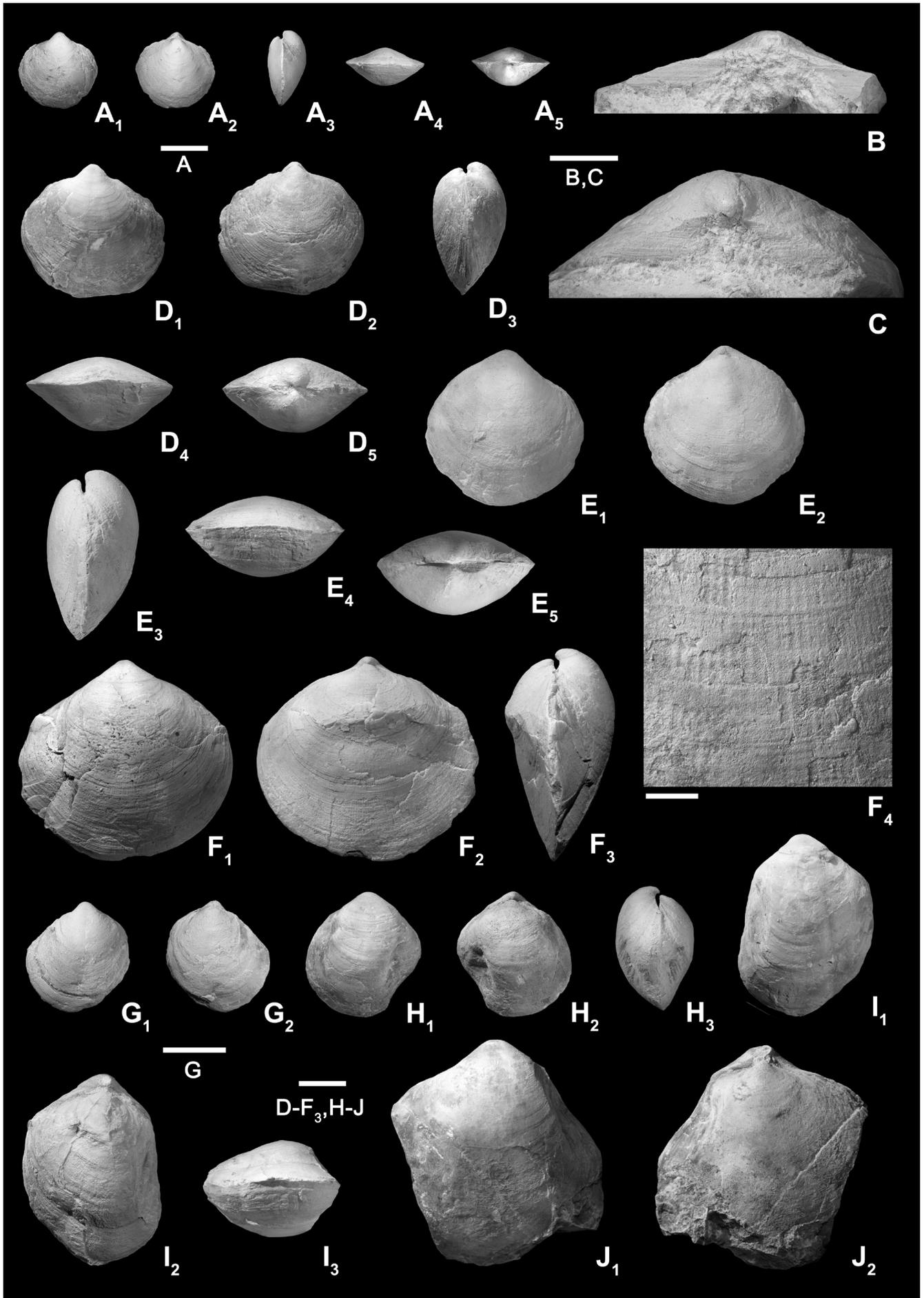
Striatifera striata is evenly distributed in both samples. It accounts for 43% in ZDA and nearly 90% in ZDB. Giving that *Striatifera striata* are confined in the lower part of ZDA, if *Weiningia ziyunensis* n. sp. is removed, *Striatifera striata* will occupy a large part of population as that in ZDB. Thus, it is reasonable to infer that the shell bed was dominated by evenly distributed *Striatifera striata* and other species before the settlement of *Weiningia ziyunensis* n. sp., which built the cluster on the framework of *Striatifera striata* thereafter. The absence of other species in the upper part of ZDA may result from the exclusive ecology of *Weiningia ziyunensis* n. sp. The dominance index (D, 0.46) is approximate to the median value as its minimal and maximal values are 0.11 and 1.00 respectively. Similarly, the equitability index (J, 0.40) is close to the medium value as well. Hence, both indexes indicate that the community is uneven, which is supported by vast different numbers between the dominant species and the others.

ZD1 is composed of bioclastic grainstone, which is featured by foraminifers, brachiopods, crinoids and calcareous algae, with the former two groups being the most dominant bioclasts (Fig. 2E). Brachiopod debris are mainly shell spines, which are probably exfoliated from productides (Fig. 2F). Spaces between the bioclasts are full of sparry calcite and few peloids. With the addition of poor sorting and roundness, ZD1 may represent a moderate to high energic environment. In ZD2 (the shell bed), four thin sections are processed inside ZDA and ZDB, and on their edges. Inside and on the edge of ZDA, the microfacies are composed of packstone with abundant weakly abraded brachiopods shells and productide spines (Fig. 2G-I). Other bioclasts include few corals and foraminifers. Spaces between bioclasts are filled with micrite grains. On the edge of ZDA, some brachiopods exhibit geopetal structures, which occur randomly within the shells (Fig. 2I). Some disarticulate shells are preserved in convex-down orientation on the bedding plane, suggesting that they were buried in-place. Microfacies of the other two thin sections are comprised of grainstone. Bioclasts inside ZDB are similar to those of the former two thin sections, with numerous weakly abraded brachiopod debris and some foraminifers (Fig. 2J). Yet less micrite grains and more sparry calcite are present among the bioclasts. It is worth noting that on the edge of ZDB, although bioclasts also take up a significant part of the total compo-

nents, brachiopod debris are rare and replaced with that of more foraminifers, crinoids and calcareous algae (Fig. 2K). Combining with the poor sorting and roundness, the microfacies within this site are very similar to those of ZD1. Based on these microfacies, this shell bed was deposited presumably in a shallow marine setting characterized by moderate to high energy. The varying amounts of micrite grains in different sites (inside ZDA and ZDB) indicate the influence of biotic barriers on sedimentation. That is, the flourishing and preserved in-place of *Striatifera striata* inside ZDB built a framework that blocked the current, resulting in deposition of fine sediments. Crowded *Weiningia ziyunensis* n. sp. forming dense clusters on many *Striatifera striata* in ZDA could further withstand the current and made more fine sediment deposit. As a result, more micrite grains appear inside ZDA than ZDB. Those shells inside or around the barriers would not experience prolonged transportation as well. On the other hand, the presence of *Gigantoproductus* and numerous *Striatifera* also indicate such environment. Ferguson (1978) investigated the paleoecology of *Gigantoproductus* in view of the morphology, feeding and growth pattern. He suggested that this genus probably lived in shallow and severe agitated water, where it could attain a large and constant supply of oxygen and food for its growth and reproduction (Wilson 1989; Nolan et al. 2017). The massive and weighty shell could stabilize its life position. Based on abundant associated benthic foraminifers and its restriction to grainstone rather than packstone or

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Fig. 4 - Other brachiopod species from the shell bed of the Baizuo Formation. A) *Cleiothyridina submabranacea*, PKUM 02-0851, ventral, dorsal, lateral and anterior views. B) *Echinoconchella elegans*, PKUM 02-0852, ventral, lateral and posterior views. C, D) *Megachonetes zimmermanni*, PKUM 02-0853 and PKUM 02-0854, ventral views. E) *Fluctuaria undata*, PKUM 02-0855, ventral and lateral views. F-H) *Gigantoproductus moderatus*, PKUM 02-0856, PKUM 02-0857 and PKUM 02-0858, ventral (F_1, G_1, H_1), lateral (F_2, G_2, H_2), anterior (F_3, H_3) and posterior views (F_4, G_3, H_4). I) *Gigantoproductus schajenwanensis*, PKUM 02-0859, ventral, lateral and posterior views. J) *Gigantoproductus edelburgensis*, PKUM 02-0860, ventral, lateral, anterior and posterior views. K-Q) *Striatifera striata*, PKUM 02-0861 - PKUM 02-0867, ventral (K, P, Q), dorsal (L) and lateral (M-O) views. Note the different locations of geniculate points on ventral valves (M-O) and asymmetric forms showing sideward growth direction (P, Q). Scale bars represent 5 mm (C) and 10 mm (A, B, D-Q).
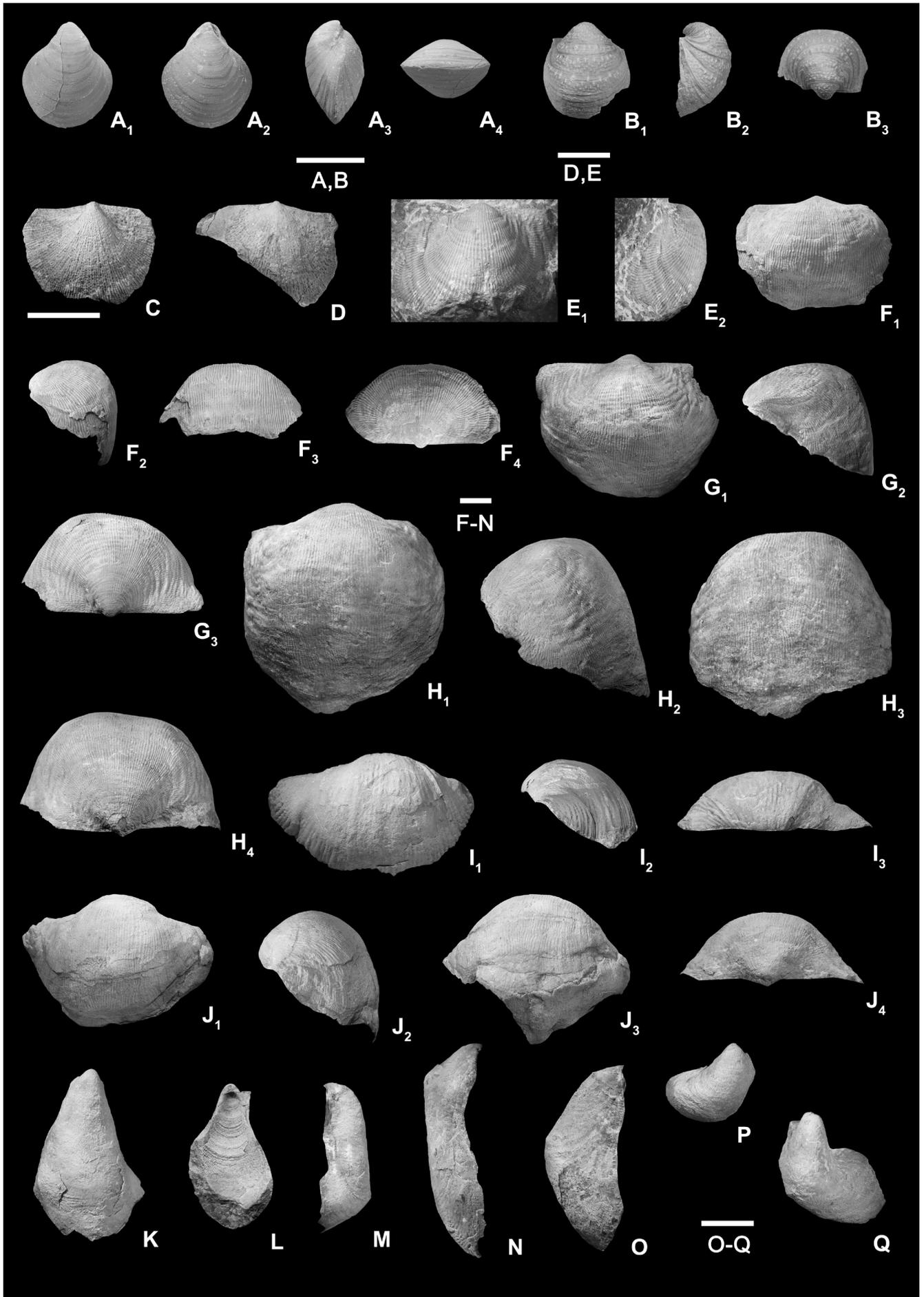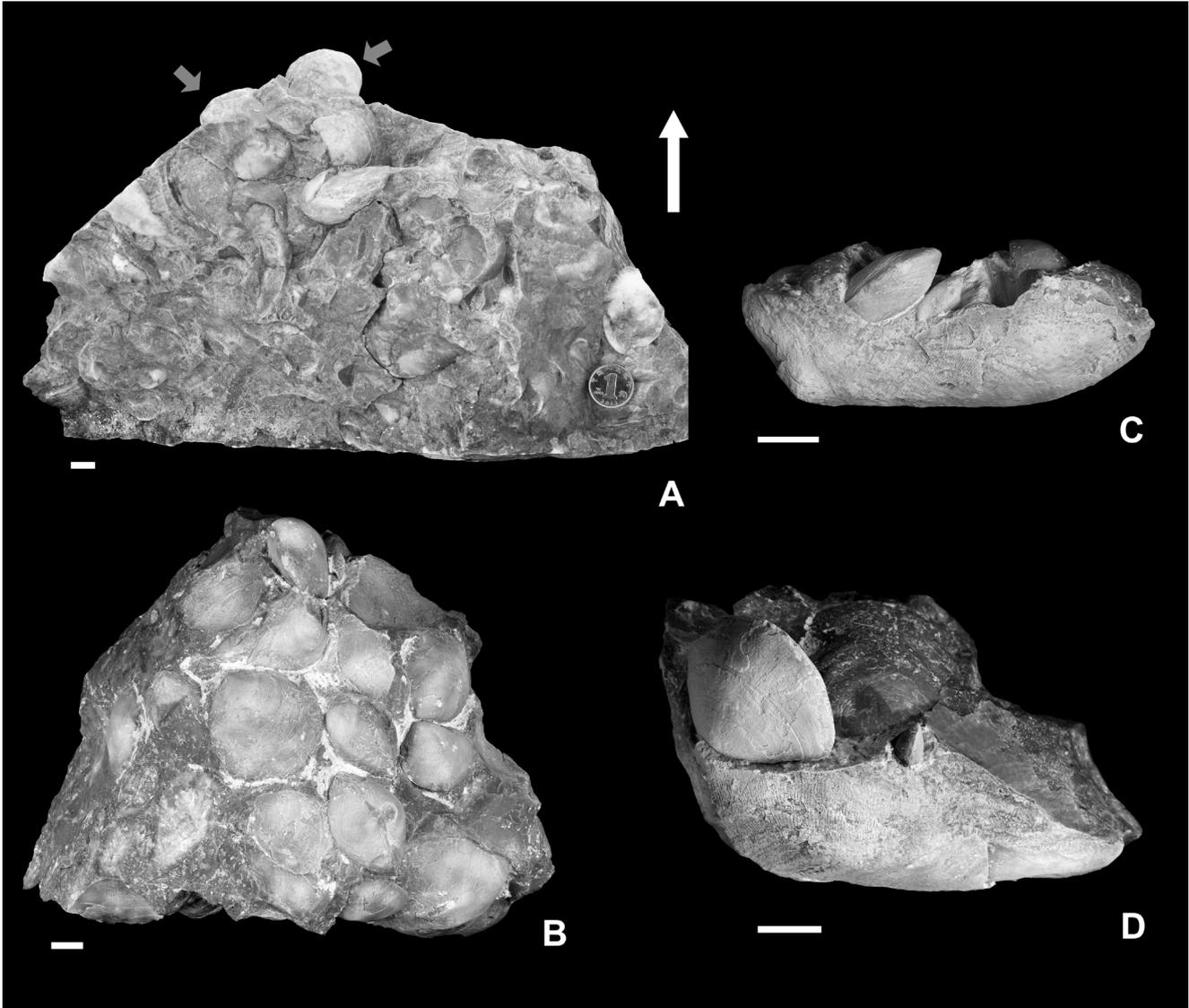
Fig. 5 - Some rock specimens from the shell bed of the Baizuo Formation. A) The lower part of ZDA. Many *Striatifera striata* are at the bottom and some *Weiningia ziyunensis* n. sp. are at the top (grey arrows). White arrow indicates vertically upward direction to bedding plane. B) The upper part of ZDA. Note the close preservation of many *Weiningia ziyunensis* n. sp. and the absence of other species. C, D) Original life position of *Weiningia ziyunensis* n. sp., showing their attachment to the dorsal valves of *Striatifera striata* with posterior portion downward. Scale bars represent 10 mm long.

wackestone. Qiao & Shen (2015) also inferred that *Gigantoproductus* inhabited shallow environment with relatively high current energy. Like modern oysters, *Striatifera* usually is found living in high density using their spines on the ears and flanks to cement to one another (Muir-Wood & Cooper 1960), forming a relatively robust framework on the substrate. This life mode is suitable for a high energetic environment, which could help them resist the water movement (Watkins 1974).

ZD3 is composed of grainstone with abundant ooids (Fig. 2L, M). Bioclasts contain a few of foraminifers and gastropods without brachiopod debris, even the spines. The well sorting and good roundness of ooids reflect a turbulent current condition (Flügel 2010; Sang & Ma 2012), which is unsuitable for settlement of epifauna.

PALEOECOLOGY OF *WEININGIA ZIYUNENSIS* N. SP.

Numerous specimens of *Weiningia ziyunensis* n. sp. have been measured for paleoecological and population dynamic investigations. A total of 666, 605 and 552 measurements were obtained repre-

senting the length, width and thickness respectively. From the dimension data, shell length is constantly equal to the width, and nearly twice as large as the thickness, indicating that the three-dimension of *Weiningia ziyunensis* n. sp. were equally increased from juvenile to senior. The delthyrium and notothyrium, although hidden between umbones, are open and relatively large (Fig. 3B, C), suggesting a corresponding sized pedicle may have emerged. Among pediculate brachiopods, pedicles can be divided into several types for special functions. Some species, such as Megathyrididae and Kraussinidae, use pedicles to tether to hard substrates and lead a sedentary life (Richardson 1997). *Magadina cumingi*, equipped with a motile pedicle, can stretch and shrink it to elevate the shells above soft sediments (Richardson 1981). The pedicle of lingulids, although develop from different sources and organs compared with articulate members, assists in burrowing (Thayer & Steele-Petrović 1975; Emig 1997). Considering the great thickened posterior part of shell substance and limited life space within the cluster (Fig. 8), the pedicle of *Weiningia ziyunensis* n. sp. may serve as a motionless attachment device. The heavy posterior shell would sink down and anchor on the substrates, leaving the anterior part suspend to attain food particles. Those preserved in original life position with ventral beaks close to *Striatifera* also demonstrate this life mode (Fig. 5C, D). Strong dental teeth and sockets provided a robust articulation for the large individuals to withstand the current (Fig. 8). Large ctenophoridium, as a muscle attachment site, may reflect the strong diductors, which can keep the shell open when carrying the weight of other clustered neighboring individuals. Furthermore, *Weiningia ziyunensis* n. sp. may only colonize on the firm substrates because most specimens are preserved attaching to the adjacent shells. None are found living directly on the soft substrate away from the cluster. Such life mode was similar to that of *W. haikawai* Yanagida & Matsusue, 1995, whose thickened posterior valve may also stabilize the shell at the growing position, but the latter species could partly bury its umbo in the sediment without attaching to hard substrate (Yanagida & Matsusue 1990).

The size-frequency distribution of *Weiningia ziyunensis* n. sp. represents a right skewed type, with the smallest and largest lengths of 3 mm and 62 mm respectively (Fig. 6C). More than 75% of individuals concentrate in the small to medium sizes from 5 mm to 35 mm, where the numbers distribute evenly without a prominent peak. Those longer than 35 mm decrease gradually in number toward larger size, and the smallest and largest sizes only occupy a small part (3%). It is noteworthy that the right skewed distribution is common in many recent and fossil brachiopod populations (e.g. Curry 1982; Collins 1991; Li 1996; Lü & Ma 2017). High proportion of juvenile in some modern articulate brachiopod populations is partly attributed to brooding recruitment (Thayer 1977; Doherty 1979; Noble & Logan 1981; Witman & Cooper 1983; Brey et al. 1995; Baumgarten et al. 2014), which can result in bimodal or polymodal distributions if they possess more than one breeding season. Such recruitment strategy can maintain the population size as a high proportion of young will possibly survive. The planktonic stage of larvae will also be shortened, making many of them settle nearby or on the parents, eventually resulting in clusters and patchy distributions (Webb et al. 1976; Brey et al. 1995; Peck et al. 1995; Kowalewski 1996; Kowalewski et al. 2002; Baumgarten et al. 2014). Since the fossil population is the product of time-averaging, it is difficult to observe directly whether a fossil brachiopod species had brooding behavior. Other evidences should be added into consideration.

The survivorship curve of *Weiningia ziyunensis* n. sp. is concave (Fig. 6E), with relatively high mortalities in the small and medium sizes (0-50 mm) while low mortalities in the large ones (50-62 mm). Together with the size-frequency distribution and the percentages of malformed individuals within each size class (Fig. 6C, D), the ontogeny of *Weiningia ziyunensis* n. sp. is presumably divided into juvenile (0-30 mm), adult (30-50 mm) and senile (50-62 mm) stages. High juvenile mortality is common in modern invertebrates and usually happens in the turbid environment characterized by muddy bottom and quiet water (Richards & Bambach 1975; Flessa & Bray 1977; Bitner 2002). Considering that ZDA yields more micrite grains than ZDB due to the suppression of current, more unconsolidated sediments such as organic detritus and fecal pellets, probably deposited at ZDA as well. In this case, the juvenile individuals were constantly threatened by burial and their lophophores would be easily fouled by fine sediments, resulting in high mortality.

Crowding in dense clusters is another important factor in elevating the juvenile mortality (Richards & Bambach 1975; Yang & Li 1989; Cate & Ev-
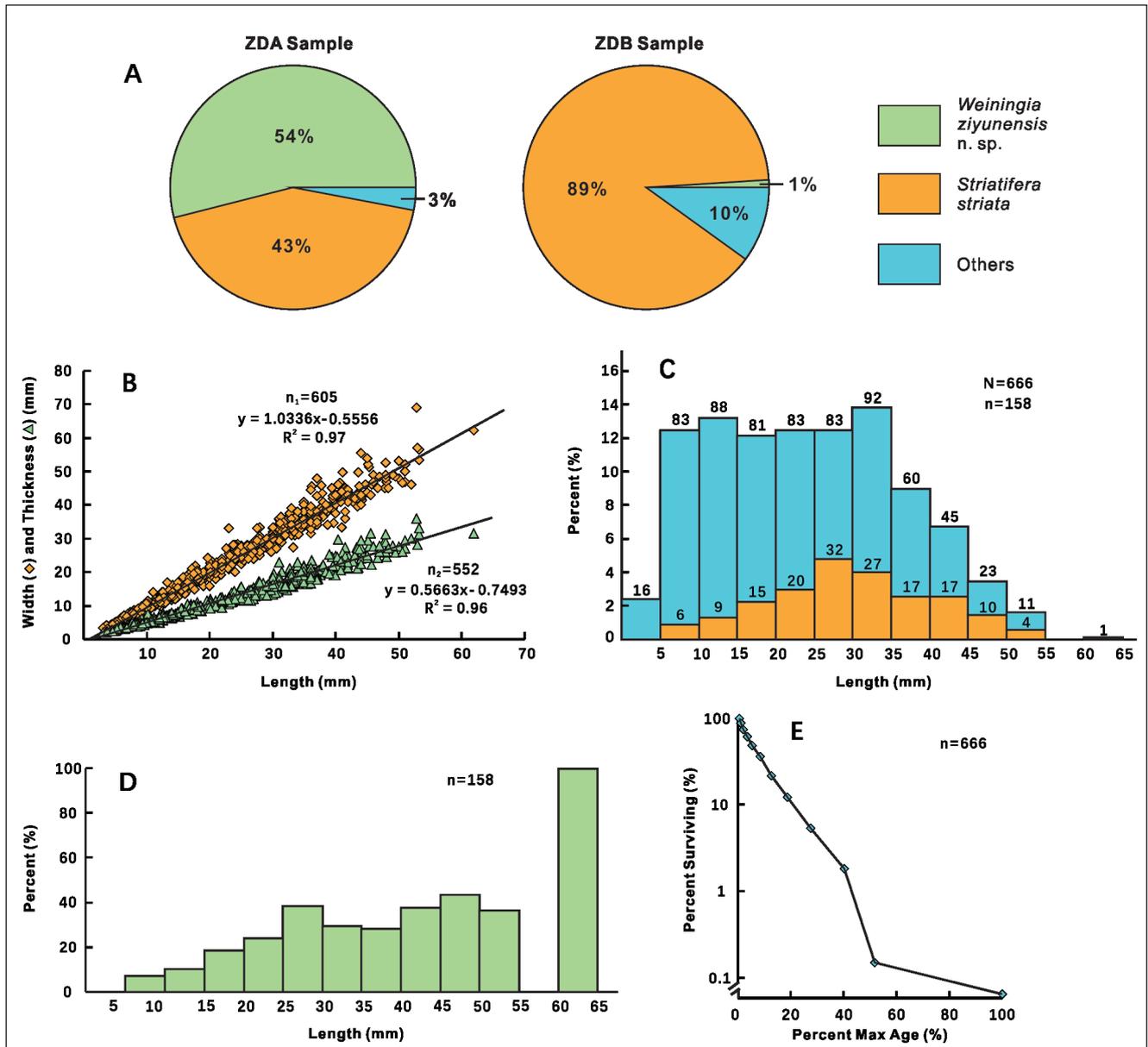
Fig. 6 - Statistical data of the shell bed. A) Composition of *Weiningia ziyunensis* n. sp., *Striatifera striata* and others species in ZDA and ZDB. B) Bivariate plots of shell width (diamond) and thickness (triangle) to length of *Weiningia ziyunensis* n. sp. C) Size-frequency (blue bars) and malformation (yellow bars) distribution of *Weiningia ziyunensis* n. sp. Numbers above the bars represent the amounts of specimens in each size class of size-frequency and malformation distribution respectively. Note that the only one specimen in the size 60-65 mm is malformed. A total of 158 malformed individuals among 666 specimens was analyzed. D) Percentages of malformed individuals among the total specimens within each size class. Note that 100% in the size 60-65 mm is attributed to the only one malformed specimen. E) Survivorship curve of *Weiningia ziyunensis* n. sp.

ans 1992). In ZDA, 158 of 666 measured specimens display evident growth malformation, suggesting that *Weiningia ziyunensis* n. sp. adapted to crowded life. With the exception of those smaller than 5 mm, malformation occurs in all size classes (Fig. 6C, D). The distribution curve of malformed specimens represents a bell shape type, with the peak located at size 25-30 mm (Fig. 6C). It is not surprising that the percentages of malformed specimens increase in each size class between 5 mm and 30 mm, as the larger specimens are more exposed to the pressure of adjacent shells (Fig. 6D). In shells longer than 30 mm the percentage of malformed specimens stays at a more or less stable level of around 40%, with the exception of size range 60-65 mm represented by only a single specimen. On the other hand, most malformation are located at either near the beak or lateral slopes (Fig. 3G-J). The high mortality among

juvenile while less malformed individuals may indicate that not the pressure from adjacent shells, but rather limited attachment opportunity possibly resulted in considerable numbers of dead individuals. Starvation is another consequence of crowded life mode. The water pumped by one individual may contain less food particles, as it may already be filtered by neighboring larger individuals. Like *Calloria inconspicua* Sowerby, 1846 and *Notosaria nigricans* Sowerby, 1846, the small *Weiningia ziyunensis* n. sp. which are often found between the larger ones, would need more energy to obtain adequate food (Peck et al. 1997). The high mortality at juvenile stage may indicate that *Weiningia ziyunensis* n. sp. possessed brooding behavior. This recruitment strategy ensured that many larvae could quickly attach to the nearby substrates once they left the parent (Williams et al. 1997), forming patchy clusters on the substrates. However, many juvenile individuals failed to grow up due to the unfavorable turbid environment and limited life space.

The adult mortality remains as constantly high as the juvenile one. In this stage, Density of individuals may be the major threat to the population. In addition to the adverse impact of limited living space, they would suffer more pressure from the adjacent individuals due to larger size. This could cause not only external distortion of shell (Fig. 3H, I), but also interfere with disposition of the lophophore interiorly, which eventually lead to low feeding and cleaning efficiency. The constant mortality as well as the approximate proportions of malformed individuals in this stage, as suggested by Richards & Bambach (1975), probably reflects a fixed proportion of the dead population for each increment of time. At the length of 50 mm, the senile mortality decreased (Fig. 6E), which may be associated with the ability of larger individuals to cope with a turbid environment and withstand the pressure from adjacent shells. They were large enough to avoid being buried by the accumulating sediments. Their ciliary systems were also more able to clean the threatening particles from the lophophore and mantle chamber.

DEVELOPMENT OF THE SHELL BED

Based on the paleoecological consideration of *Weiningia ziyunensis* n. sp. and the preservation of all brachiopod species, the development of the shell bed corresponded essentially to the settlement process of *Weiningia ziyunensis* n. sp., which could be divided into three stages, namely before, during and after the settlement. Before the arrival of *Weiningia ziyunensis* n. sp., the shell bed was dominated by *Striatifera striata*, *Gigantoproductus moderatus*, *Megachonetes zimmermanni* and other species present in ZDB (Fig. 7A). These free-lying or spine-supported species suggest the community was founded on soft carbonate mud substratum of sea floor in a shallow marine setting (Ferguson 1978; Qiao & Shen 2015). Initially, *Striatifera striata* widely colonized the substrates as it can adapt to soft bottom and probably live in high density similarly like *Weiningia ziyunensis* n. sp. Watkins (1974) reported a *Striatifera* coquina from the Upper Mississippian in California, where closely packed and preserved in-place large individuals provided attachment places for many small ones. Similar biostromes were discovered by the same author in which numerous *Striatifera* displayed asymmetrical forms as a result of crowding (Watkins 1999). By cementing to each other, *Striatifera* could build a robust framework. Their large shells would baffle the current and provided local shelters for the young and other organisms (Watkins 1974). Although cemented specimens are not observed in ZDA and ZDB, large *Striatifera striata* are preserved close to each other and many resting upon one another in a convex valve downward orientation. Small individuals (shell length shorter than 10 mm) are common and account for nearly 50% of this species. Most of them are located between the large ones, indicating that they may cement to each other previously. As for other members, *Megachonetes zimmermanni* may live attached with a small pedicle in early growth stages. Thereafter the pedicle was probably lost and they rested on the sea bottom with dorsal valve uppermost (Muir-Wood 1962). Spines on the hinge margin served as balance equipment. *Echinoconchella elegans*, supported by dense fine prostrate spines on both valves, rested on the substrate with ventral valve downward and the anterior margin obliquely upward (Muir-Wood & Cooper 1960). Three *Gigantoproductus* species rested on the substrate with the ventral umbo downward and the trail obliquely upward. Their massive pedicle umbo maintained the position and the large ears prevented the shell from sinking in the soft substrate (Muir-Wood & Cooper 1960; Ferguson 1978). *Fluctuaria undata* also rested on the substrate with
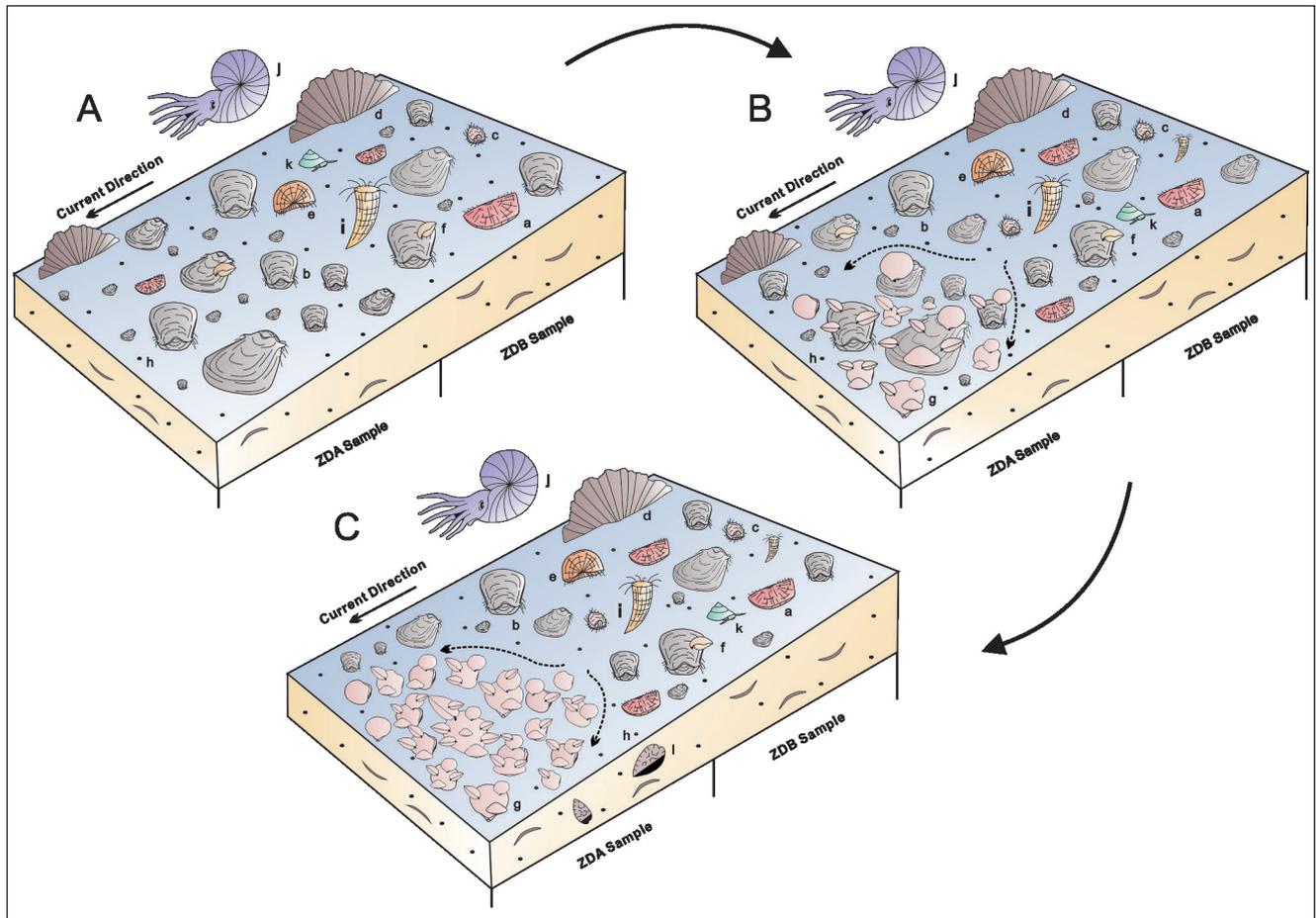
Fig. 7 - Development of the shell bed. A) Before the arrival of *Weiningia ziyunensis* n. sp. B) Formation of the lower part of cluster. C) Formation of the upper of cluster. Dashed lines in B, C represent spilt currents resulting from blocking by the cluster. Letter a-l represent *Megachonetes, Striatifera, Echinoconchella, Gigantoproductus, Fluctuaria, Cleiothyridina, Weiningia*, foraminifera, coral, ammonoid, gastropod and geopetal structure.

the trails obliquely upward (Muir-Wood & Cooper 1960). Crowded productide shells resting on the sea bottom supplied a suitable attachment site for many other pediculate brachiopods such as *Cleiothyridina submabranacea*.

The first colonists of *Weiningia ziyunensis* n. sp. would have a random choice on the dispersed firm substrates. It is unlikely that they could survive exposing themselves to the moderately to high current energy in early stages without weighty shells. They colonized on the dorsal valves of alive *Striatifera striata* and shell fragments on the sea floor, where the current was relatively weak around the barrier formed by neighboring large individuals (Brookfield 1973). Once *W. ziyunensis* n. sp. became mature, the heavy posterior part of shells helped them against the current and maintain life positions. In conjunction with large *Striatifera striata*, the barrier became stronger and blocked the current, resulting in deposition of suspended food (Fig. 7B). Quiet life spaces

behind the barrier were created as well. The assumed brooding behavior drove *Weiningia ziyunensis* n. sp. to produce many descendants nearby, which quickly occupied the suitable substrates and the interspace between large shells. Some descendants may be transported to the other places by current where they would follow the settlement process of the elders. However, a significant amount of those settling near the parents died of the limited firm substrates. Their shells became the seats of attachment. When these descendants grew up, the biotic barrier became bigger and further blocked the current to bring more food and create more life spaces. In consequence the base of the cluster formed. On the other hand, the dense population had negative effects on *Weiningia ziyunensis* n. sp. and *Striatifera striata*, such as growth malformation. In the lower part of ZDA, some *Striatifera striata* show sudden changes of growth direction from horizontal to upward, making the anterior portion nearly perpendicular to the posterior

portion of the shell. The geniculate points are variable and locate at beak (Fig. 4N), mid-length (Fig. 4O) and the anterior part (Fig. 4M). Some specimens display changes of growth direction from straight to curving (Fig. 4P, Q). Deposition of fecal pellets and other small particles could also foul the lophophore or bury small individuals.

After the formation of the lower part of cluster, *Weiningia ziyunensis* n. sp. gradually established its upper part and spread around and upward by attaching to each other (Fig. 7C). Their descendants continually occupied the life space between the large individuals. Dead shells fell nearby and provided substrates for others. No other species appears in this part even *Striatifera striata*, probably because they could no longer tolerate the more turbid environment created by the growing cluster. A similar example was suggested by Richards & Bambach (1975) about the biotic baffle formed by *Holtedahlina* cluster that created a turbid environment in the same way as *Weiningia ziyunensis* n. sp., which caused high juvenile mortalities of *Hebertella*, *Rhynchotrema* and *Platystrophia* that lived in the cluster.

The development of the cluster indicates that *Weiningia ziyunensis* n. sp. gradually adapted to a moderate to high energetic environment by living in high density. Although this life strategy resulted in turbid environment and malformation, it brought more food and generated more suitable life spaces. The cluster was also an ideal shelter for reproduction because it could provide a defensive advantage against many swimming fish and invertebrates, such as ammonoids and gastropods (Dodd & Stanton 1981). Furthermore, it is interesting to realize that the asymmetrical shell form of *W. haikawai* and *W. areatus* Aleksandrov, 1973 may result from the crowded life mode (Aleksandrov & Solomina 1973; Yanagida & Matsusue 1995) and different species of *Weiningia* from various regions possibly had the similar life strategy.

SYSTEMATIC PALEONTOLOGY

Order **Spiriferida** Waagen, 1883
Suborder **Spiriferidina** Waagen, 1883
Superfamily Martinioidea Waagen, 1883
Family Martiniidae Waagen, 1883
Subfamily Martiniinae Waagen, 1883
Genus *Weiningia* Jin & Liao, 1974
Type species - *Weiningia transversa* Jin & Liao, 1974

Weiningia ziyunensis n. sp.
Fig. 3, A-J

Etymology: Geographic name, after Ziyun County (southern China), from which the present species originates.

Holotype: Complete articulated shell PKUM 02-0843 (Fig. 3D).

Paratypes: Complete articulated shells PKUM 02-0840, PKUM 02-0844 - PKUM 02-0849 (Fig. 3A, E-J); disarticulated shells PKUM 02-0841, PKUM 02-0842 (Fig. 3B, C); serial sectioned shell PKUM 02-0850 (Fig. 8); all from the type locality.

Type locality: Ziyun County, south of Guizhou Province, southern China.

Type horizon: Baizuo Formation, Serpukhovian, Lower Carboniferous.

Material: More than 500 complete specimens.

Diagnosis: Outline circular to subcircular; ventral sulcus absent or weakly developed; dorsal fold absent; hinge line very short; ventral and dorsal interareas moderately developed but hidden between umbones; dorsal interior with long crura which can extend almost to the anterior margin.

Description. Shell medium- to large-sized, ventribiconvex, outline circular to subcircular; shell length approximately equal to maximum width and twice as long as thickness (Fig. 3A, D-F), maximum length up to 62 mm, maximum width at mid-length; hinge line much shorter than maximum width; ventral and dorsal interareas hidden between umbones and can only be seen in disarticulate valves (Fig. 3B, C); cardinal extremities and anterior margin rounded, anterior commissure rectimarginate or weakly uniplicate.

Ventral umbo moderately swollen; ventral beak slightly incurved, interarea concave and moderate, orthocline to slightly apsacline; delthyrium open; ventral sulcus absent in most specimens, if present, weakly developed, shallow and narrow, originating at mid-length and gradually widen but not deepen toward anterior commissure. Dorsal valve circular to subcircular, with the greatest convexity at mid-length; umbonal region inflated; dorsal beak small, close to the ventral one, not incurved; interarea flat, lower than ventral one, orthocline; notothyrium open; dorsal fold absent.

Interior of ventral valve with large hinge teeth and weak dental flanges; dental plates, median septum or myophragm absent; muscle area unknown.

Dorsal cardinalia simple, with large ventrally projected ctenophoridium and large dental sockets; inner socket ridges extend to the valve floor; median septum absent, but low and narrow median ridge (possibly myophragm), bisecting the muscle area and located anteriorly to dental sockets, grad-
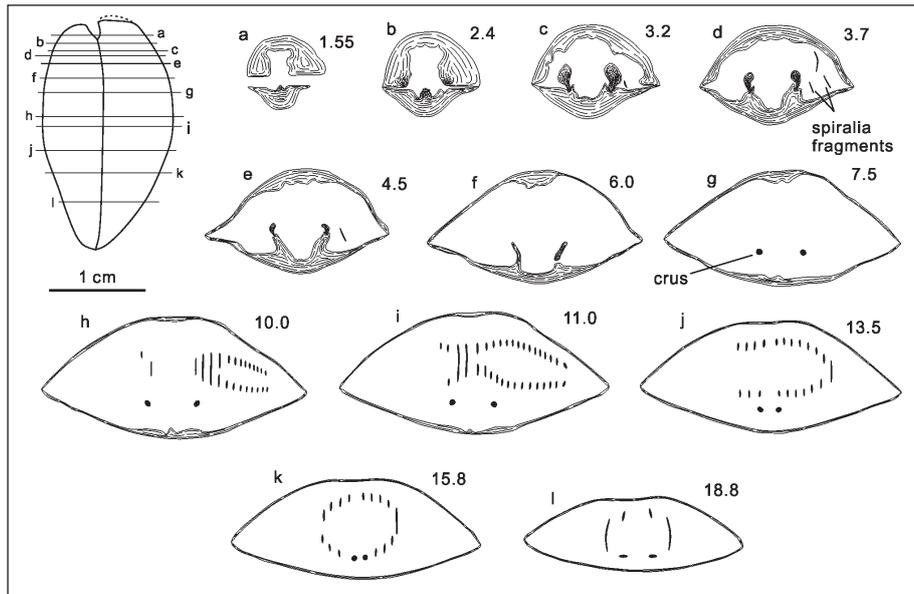
Fig. 8 - Transverse serial sections of *Weiningia ziyunensis* n. sp., PKUM 02-0850. Distances measured in millimeters from the tip of the broken ventral beak.

ually lowering forward, usually extending up to 1/5 of the shell length; crural plates absent; crus long, originating from inner socket ridges and almost extending to anterior margin. Spiralia located at the anterior half of shell, filling the mantle cavity. Spiral cones directed to the cardinal extremities, usually contain 10 to 14 whorls. No jugum or other jugal structure is present. Shell substance greatly thickened posteriorly compared with the anterior region of both valves.

Shell surface smooth except dense and even growth lamellae. Microornament absent in most specimens due to exfoliation or destruction of outer shell layer. In some well-preserved specimens, capillae can be clearly observed (Fig. 3F$_4$).

Remarks. The present species is easily regarded as an athyrididine at the first glance on its external morphology: circular to subcircular shell outline, very short hinge line due to interareas hidden between umbones, growth lamellae on shell surface, and absence of sulcus and fold. However, it can be certainly distinguished from athyrididine by capillae microornament and the loss of pedicle foramen exteriorly, the absence of cardinal plate and the totally different brachidium interiorly (Alvarez & Rong 2002). Instead, the typical spiriferide brachidium, which is characterized by posterolaterally directed spiralia without any jugal structure, undoubtfully identify it as spiriferid.

In the original description of *Weiningia* by Jin & Liao (1974), this genus is diagnosed by small to large shell size; subcircular to elongate outline and ventribiconvex in profile; ventral interarea high with open delthyrium, but dorsal interarea absent; ventral sulcus narrow, low and indistinct and shell surface with growth lamellae only; ventral interior with strong teeth and large muscle field and dorsal interior with a large cardinal process. Due to the presence of a high ventral interarea and limited information about its internal structures, this genus is considered as a problematic genus in terms of its taxonomic position at order level (Shen et al. 2017). However, after examining the holotype of the type species *W. transversa* Jin & Liao, 1974, we found this specimen is somewhat crushed and has a broken lateral slope (Fig. 9A, B). The dorsal valve shifts anteriorly and leans to the left relative to the ventral one (Fig. 9E, H, J, K), which made a false appearance that the specimen looks to have a high ventral interarea and lack the dorsal interarea. The original appearance of it should have a low dorsal interarea as well as a moderate to high ventral one that are completely and partly hidden between umbones respectively (Fig. 9I). Similar interareas appear in *W. areatus* described by Aleksandrov in Aleksandrov & Solomina (1973) under the previous name of *Elenchus*. This species has a moderate ventral interarea and a low dorsal one, both of which are hidden between umbones (Aleksandrov & Solomina 1973, pl. 29, fig 5c). Besides, it is also worth noting that the interareas in *W. sugimurai* Yanagida & Matsusue (1995, pl. 5, fig. 1) and *W. haikawai* Yanagida & Matsusue (1995, pl. 5, fig. 2,3; pl.6, fig. 3) from the upper part of the Lower Carboniferous Akiyoshi Limestone Group in Japan are not hidden between umbones probably because the anacline dorsal interarea together

Fig. 9 - The holotype of *Weiningia transversa* Jin & Liao, 1974, NIGP 22450. A-G) Ventral, dorsal, lateral (C, D), oblique lateral (E), anterior and posterior views. One of the lateral slopes is broken in both valves showing the thickened posterior part of shell (C). The dorsal valve shifts anteriorly relative to the ventral one (E). H) Explanatory drawing of E showing the shifting between both valves. I) Explanatory drawing showing the original lateral view of the specimen. The dorsal and part of the ventral interareas are actually hidden between umbones. J, K) Enlargement of the ventral interarea and its explanatory drawing showing that the dorsal valve also leans to the left side, resulting in well exposure of the ventral interarea. Scale bars represent 10 mm.
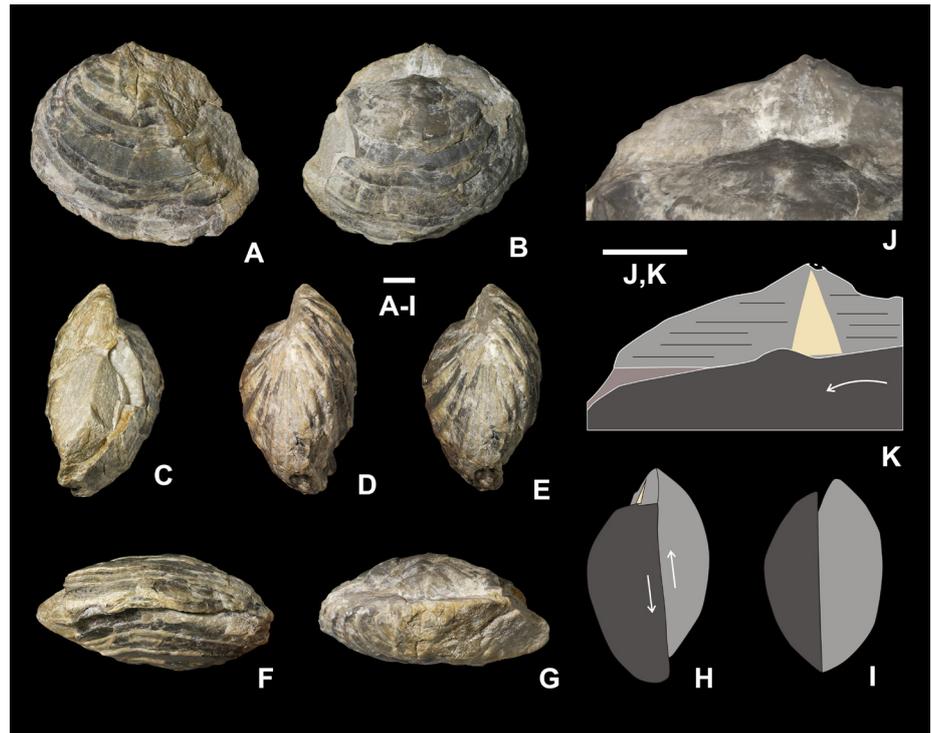
with the concave and apsacline ventral one makes the interareas more distinct, whereas the combination of orthocline dorsal interarea with straight or rarely concave ventral one in *W. transversa* and *W. areatus* results in the hidden interareas. Hence, *Weiningia* possesses a moderate to high ventral interarea and a low dorsal one, and both of them are variably exposed. The thickened posterior part of shell may also be another character of this genus because it is commonly present in *W. transversa* (Fig. 9C), *W. areatus* (Aleksandrov & Solomina 1973, fig. 35), *W. sugimurai* and *W. haikawai* (Yanagida & Matsusue 1995, fig. 2, 4). Based on the circular to subcircular outline, hidden interareas which are similar to those of *W. areatus*, thickened posterior part of shell, growth lamellae on shell surface, strong dental teeth and a large cardinal process interiorly, the present species is identified as *Weiningia*. The taxonomic position issue of *Weiningia* which has so far been pending between spiriferoids and orthoids due to the absence of spiriferoid brachidium can thus be solved (Shen et al. 2017).

In addition to the difference of interareas which are larger and partly hidden in the type species while smaller and complete hidden in the present species, *W. transversa* differs from *W. ziyunensis* n. sp. by the suberect and acuminate ventral beak, transversally elliptical outline and strong, step-like growth lamellae. *W. areatus* is distinguishable from

the present species by having an elongate shell form and pointed ventral beak. *W. subrugosa*, described by Li (1987) from Luocheng Formation in southern China, differs from *W. ziyunensis* n. sp. by having a transversally elliptical outline and strong concentric rugae. *W. haikawai* is distinguishable from the present species by the asymmetrical form, much curved ventral beak and variably developed sulcus on the dorsal valve. As for *W. sugimurai*, it differs from *W. ziyunensis* n. sp. by the transversally elliptical outline and distinct ventral interarea.

Occurrence. Serpukhovian (Early Carboniferous), Guizhou Province, southern China.

CONCLUSION

The preservation of more than 80% complete and articulated shells, and poor size sorting of conspecifics indicate that the shell bed from the Baizuo Formation represents an in situ buried brachiopod community, which deposited on a normal shallow marine muddy substrate characterized by moderate to high energy. A total of nine species belonging to seven genera forms this community. Among them, a new species, *Weiningia ziyunensis* n. sp., is described. Morphology and preservation analysis suggest that this pediculate species colonized only on the firm substrates, including living and dead shells (*Stria-*

tifera striata and conspecifics), and used the heavy posterior shell to stabilize the life position. Population dynamics of *Weiningia ziyunensis* n. sp. is derived from size-frequency distribution and survivorship curve. Large number of juvenile shells accompanied by high mortality reflects that many juvenile individuals suffered from the limited life space and turbid environment generated by dense clusters, while the same mortality rate at adult stage is mainly the result of more pressure from neighbors, which caused shell malformation and eventually low feeding and cleaning efficiency. The low senior mortality is attributed to the ability of larger individuals to cope with a turbid environment and withstand the crowded population.

Abundance of these species shows great difference in this community. *Striatifera striata* and *Weiningia ziyunensis* n. sp. take up nearly or more than 90% of the population while the others make up only a very small part. The restricted distribution in clusters of *Weiningia ziyunensis* n. sp. and the even distribution of *Striatifera striata* indicate that the abundance of these two species may be explained by their similar life strategies that were governed by different morphological adaptations. The free-living *Striatifera striata*, living close to each other cementing probably with spines, gradually spread on the soft sea floor. On the other hand, *Weiningia ziyunensis* n. sp. formed patchy clusters attached to *Striatifera striata* or other shell fragments and was adapted to crowded life and to resist the current.

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