ECOLOGY, BIOFACIES, BIOGEOGRAPHY AND SYSTEMATICS OF MICROMORPHIC LINGULATE BRACHIOPODS FROM THE ORDOVICIAN (DARIWILIAN–SANDBIAN) OF SOUTH-CENTRAL CHINA

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Abstract: Ordovician (Darriwilian to Sandbian) micromorph linguliform brachiopods are described from the Guniutan Formation at the Fenxiang section in Hubei province, and the Maocaopu and Cili sections in Hunan province of south-central China, situated on the Yangtze Platform. A total of 7560 specimens from 155 limestone samples (within the interval of Lenodus variabilis – Pygodus anserinus biozones) are assigned to 22 species, representing a low taxonomic diversity and low abundance fauna. The fauna is dominated by the Acrotretoidea, mainly species of the Torynelasmatidae, with Torynelasma the most abundant (more than 40% of total number of specimens), along with the Eoconulidae and Eoconulus (18% of total) representing the second most common forms. Species of the Ephippelasmatidae are also common (16% of total) diverse, and include representatives of Myotreta and Numericoma, as well as Ephippelasma, whereas species of the Scaphelasmatidae are somewhat less common (13% of total). All three investigated sections represent outer shelf environments, but the Maocaopu section is situated in a relatively deeper position, in proximity of the south-eastern outer margin of the Upper Yangtze Platform, close to its boundary with the Jiangnan Slope. A quantitative analysis of the relative abundance data was carried out in order to investigate the biofacies distribution of the micromorphic brachiopod communities across the Yangtze Platform, something that has not been attempted before with Palaeozoic linguliforms. Six lingulate microbrachiopod communities could be recognized in the sections. The major biofacies shift, which occurred in the Cili section in the upper part of the Microzarkodina ozarkodella Zone, at the time of the onset and initial rise of the Mid Darriwilian Carbon Isotope Excursion (MDICE) suggests that these biofacies may have been depth controlled.

Key words: Ordovician, Linguliformea, brachiopod, China, ecology, biogeography.

The Ordovician (Darriwilian to Sandbian) interval from the Lenodus variabilis to Pygodus anserinus biozones is one of the best known intervals in terms of the biogeographical distribution and abundance of lingulate microbrachiopod assemblages (see summaries in Popov et al. 2013; Holmer et al. 2016). However, there is only a single previous study of microbrachiopods from this interval in south-central China by Zhang (1995), which was restricted to the Guniutan Formation at the Cili section in Hunan, situated on the Yangtze Platform. The Darriwilian to Sandbian interval of the Ordovician of the Yangtze Platform is dominated by carbonates, which are very similar to the coeval ‘Orthoceratite limestone’ of Baltoscandia (e.g. Lindström et al. 1991; Zhang 1996). The main object of this study is to expand and update the study of this interval, which largely corresponds to the Guniutan Formation, in south-central China to also include and illustrate material mainly from the new Fenxiang section in Hubei province, as well as the Maocaopu section in Hunan (situated in a relatively deeper position), and to provide the first quantitative analysis of the biofacies distribution of the micromorphic brachiopod...
communities across the Upper Yangtze Platform (Figs 1–5). Unfortunately, the recorded changes cannot presently be tied directly to detailed environmental data on, for example, the detailed sea-level curves, which are largely lacking (but see Liu 2006; Su 2007). However, the chemostratigraphy is known from one of the investigated sections, and some of the recorded faunal changes can be correlated with the lower part of the Mid Darriwilian Carbon Isotope Excursion (MDICE; Schmitz et al. 2010; Fig. 3).

MATERIAL AND METHOD

All studied brachiopod specimens were obtained from the 155 limestone samples, originally collected (by Jian-Hua Zhang; Tables 1–3) for conodont and brachiopod extraction (Zhang 1995, 1998a, b) from the Fenxiang, Mao-caopu and Cili sections (Fig. 2; Tables 1–3; Holmer et al. 2017). The samples were processed in dilute acetic acid and the residues washed through a 125 mm screen (Zhang 1998a, p. 21). The new enlarged collection includes a total of 7560 specimens assigned to 22 different species (of which 12 are left in open nomenclature), building and expanding on an earlier collection (2440 specimens), which was restricted to the Cili section (Zhang 1995). With a few exceptions the specimens are preserved as disarticulated valves, and following common practice (e.g. Popov & Cocks 2006), the number of individuals \((n, n_i)\) is estimated as the sum of the number of articulated valves plus the number of either dorsal or ventral valves, whichever occurs more frequently. Specimens not identifiable down to the genus level have not been included into the analysis.

In general, the three studied sections are characterized by very low net deposition rates (e.g. Lindström et al. 1991); however, the recorded linguliform microbrachiopods are most commonly exceptionally well preserved, with little sign of breakage and including a considerable number of still-articulated complete shells that were most likely not transported very far. Whilst the samples may have been affected to various degrees by differences in preservation, it is likely that they may be considered to accurately represent the original composition of the microbrachiopod community. The unusually close sampling interval in the studied sections makes them well suited for the quantitative examination of the relative abundance data, which has never been attempted before for Palaeozoic linguliform brachiopod communities.

The data (Tables 1–3; Holmer et al. 2017) were analysed using the Simpson dominance \((\lambda)\), Buzas and Gibson’s evenness \((e^{H/S})\) and Margalef’s richness \((d)\) indices calculated using PAST v. 3 (Hammer et al. 2001). Simpson Dominance \((\lambda)\) is calculated as \(\lambda = \sum_{i}(n_i/n)\), where \(n\) is total number of individuals and \(n_i\) is total number of individuals of taxon \(i\). Buzas and Gibson’s evenness is calculated as \(e^{H/S}\), where \(H\) (Shannon index) is calculated as \(H = -\sum_{i} n_i \ln n_i\). Margalef’s richness index \((d)\) is calculated as \(d = (S - 1)/\ln n\), where \(S\) is number of species (Fig. 3).

The relative abundance data were further subjected to cluster analysis using the Morisita Similarity Index, which was chosen because outcomes are not strongly affected by variations in sample size. Six lingulate microbrachiopod communities (Fig. 3) have been recognized and for most of them similarity is less than 0.33. The only exception is for the Torynelasma sinensis and Scaphelasma–Torynelasma communities which show higher similarity, approaching 0.5. Each community is defined by its taxonomic composition and the relative abundance of the characteristic taxa, while it is named after a dominant species (Fig. 4).

These communities are also clearly recognized in the correspondence analysis (Fig. 5). The results of the correspondence analysis are to a significant extent defined by the cumulative effect of the low negative scores of both primary components characteristic for the most of the species. However, the results are in variously affected also by the occurrences and relative abundance of Torynelasma sinensis \((C_1 +0.9165; C_2 -0.3210)\) and Eoconulus cf. clivosus \((C_1 +0.2694; C_2 +0.9317)\). Scaphelasma mica \((C_1 +0.0256; C_2 +0.0166)\), which have low positive scores of both primary components as well as Numeridoma perplexa \((C_1 -0.064; C_2 +0.0375)\), which has a low positive score of the second component.

GEOLOGICAL OUTLINE

The three Ordovician sections investigated all are situated on the South China Palaeoplate, where they form outer shelf environments of the Yangtze Carbonate Platform (Fig. 1). The richly fossiliferous Ordovician brachiopod
FIG. 2. Stratigraphic columns of the Ordovician (Darriwilian–Sandbian) Fenxiang, Cili and Maocaopu sections, showing the sampled levels (modified after Zhang 1998a).
successions across the South China Palaeoplate have been intensively studied in numerous articles (see e.g. summaries in Zhan et al. 2005, 2011) and the Ordovician geology of this region has been summarized recently by Zhan & Jin (2007); a detailed description of the remarkable lithological and faunal similarities of the Darriwilian to Sandbian Yangtze Carbonate Platform successions with the coeval, so-called ‘Orthoceratite limestone’ of Baltoscandia was described by Lindström et al. (1991) and Zhang (1996, 1998a, b), and even more recently by Schmitz et al. (2010); a sea-level curve for the region was provided by Su (2007).

The Maocaopu section (Hunan) occupies a position in the proximity to the south-eastern outer margin of the Upper Yangtze Platform, close to its boundary with the Jiangnan Slope belt (Fig. 1), while the Fenxiang (Hubei)
and Cili (Hunan) sections are located at a relatively short distance from each other towards the interior of the platform. The general bed-by-bed lithofacies and conodont biostratigraphy as well as details of correlations of the Darrwilian to Sandbian interval at these three sections were described and discussed in detail by Zhang (1996, 1998a, b) and need not be repeated here. As noted by Zhang (1996, 1998a, b) the succession consists largely of the Darrwilian Guniutan Formation (bedded to nodular limestones), from which the majority of the investigated brachiopod-yielding samples were taken (Fig. 2). In all three sections the Guniutan Formation is underlain by the more nodular limestones of the Darrwilian Dawan Formation, from which only a few samples yielded microbrachiopods (Fig. 2; Tables 1–3). At the Cili and Maoacaopu sections the Guniutan Formation is overlain unconformably by the more pure, bedded and orthoconechrich limestones of the Darrwilian–Sandbian Datianba Formation (Figs 2, 3; Tables 1–2; see also Zhang 1996, 1998a, b; Schmitz et al. 2010). At the Fenxiang section,
FIG. 4. Results of the cluster analysis of relative abundance data (Morisita Similarity Index) for the micromorphic lingulate species from the Cili, Fenxiang, Maocaopu sections. Sample numbers are the same as shown on Figure 2 and Tables 1–3.
the Guniutan Formation is overlain by the shales and nodular limestones of the Darrwilian–Sandbian Miaopo Formation, which also yielded very scant material of microbrachiopods (Fig. 2; Table 3).

MICROMORPHIC LINGULATE ECOLOGY AND BIOFACIES

The six lingulate microbrachiopod communities discussed herein are summarized in Figures 3–5, Tables 1–3 and Holmer et al. (2017), and detailed below.

The Eurytreta ciliensis Community (samples SC77; MC90, MC 94-96), Pygodus anserinus Conodont Zone (average dominance 0.489 (min 0.324, max 0.455), average evenness 0.753 (min 0.596, max 0.883) average Margalef’s richness index 0.916 (min 0.519, max 1.291)). This association is dominated by Eurytreta ciliensis, which usually comprises more than 50% of the specimens in the samples from the Maocaopu section. In a single sample (SC77) from the Cili section, Eurytreta ciliensis is second in abundance (31.3%) to Ephippelasma minutum (45.8%). Although Eurytreta ciliensis is present sporadically in other communities, it occurs in small numbers in a single sample for each association (Tables 1–3; Holmer et al. 2017). Ephippelasma minutum is the only species that is confined to the Eurytreta ciliensis Community; however, it is also documented from a single locality in the Cili section but does not occur in the samples from the Maocaopu section. All other species occur in low frequencies. Between them only Eoconulus cf. clivosus and Numericoma spinosa occur at all three localities, while others (Myotreta...
| Fenxiang section | FC 20 | FC 22 | FC 23 | FC 24 | FC 25 | FC 26 | FC 27 | FC 28 | FC 30-1 | FC 34 | FC 39 | FC 41 | FC 44 | FC 46 | FC 49 | FC 50 | FC 51 | FC 53 | FC 55 | FC 57 | FC 58 |
|-----------------|------|------|------|------|------|------|------|------|--------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| \( Eoconulus \) cf. clivosus | D 3 2 2 2 5 4 3 2 5 25 34 5 6 8 2 9 8 11 | V 1 | | | | | | | | | | | | | | | | | | | | | |
| Biernatia cf. hohni | D 1 8 | 2 3 4 1 3 1 1 | V 2 1 | | | | | | | | | | | | | | | | | | | | |
| Numericoma spinosa | D 2 27 12 1 | V 2 1 17 13 | | | | | | | | | | | | | | | | | | | | |
| Numericoma perplexa | D 7 9 | 1 16 2 1 8 9 4 2 | V 5 2 | 3 8 | 13 17 3 2 2 1 | | | | | | | | | | | | | | | |
| Acanthambonia cf. delicata | D 3 4 | 2 | V 4 3 | 1 | | | | | | | | | | | | | | | | | | | |
| Cytronotreta sp | D 5 1 1 | 1 2 | V 1 | 1 | | | | | | | | | | | | | | | | | | | |
| Tornyelasma sinensis | D 2 1 | V 1 | 4 | | | | | | | | | | | | | | | | | | | |
| Scaphelasma mica | D 2 5 | 6 1 | V 1 | | | | | | | | | | | | | | | | | | | |
| Discinidae gen. et sp. | D 1 | 1 | V 1 | | | | | | | | | | | | | | | | | | | |
| Obolidae gen. et sp. | 3 | | | | | | | | | | | | | | | | | | | | | |
| Rowellella margarita | 2 2 2 | 1 1 | | | | | | | | | | | | | | | | | | | | |
| Indet. | | | | | | | | | | | | | | | | | | | | | | |
| Total | 2 1 2 7 1 51 3 55 36 40 3 7 4 13 66 40 14 3 27 47 13 2 17 11 14 | | | | | | | | | | | | | | | | | | | | | |
| Fenxiang section | FC 60 | FC 62 | FC 63 | FC 64 | FC 66 | FC 70 | FC 72 | FC 81 | FC 86 | FC 90 | FC 91 | FC 95 | FC 97 | FC 100 | FC 102 | FC 104 | FC 106 | FC 110-0 | FC 110-1 | FC 111 | Total |
|------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|---------|---------|-------|-------|
| Eoconulus cf. clivosus | D 6 | 27 | 1 | 38 | 4 | 2 | 11 | 1 | 3 | 229 | 254 |
| V 12 | 3 | 1 | 24 |
| C |
| Biernatia cf. hohni | D 1 | 2 | 3 | 229 | 254 |
| V 1 | 2 | 48 |
| C |
| Numericoma spinosa | D 2 | 1 | 6 | 1 | 45 | 90 |
| V 1 | 6 | 44 |
| C |
| Numericoma perplexa | D 2 | 1 | 6 | 1 | 1 | 1 | 70 | 142 |
| V 1 | 7 | 2 | 1 | 67 |
| C |
| Acanthambonia cf. delicata | D 9 | 1 | 2 | 9 | 19 |
| V |
| Cyrtonotreta sp. | D 8 | | 1 | 21 | 22 |
| V 1 |
| Torynelasma sinensis | D 1 | 1 | 1 | 1 | 7 | 15 |
| V 1 | 1 | 8 |
| Scaphelasma mica | D 2 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 26 | 28 |
| V |
| Discinidae gen. et sp. | D 5 | 1 | 1 | 2 | 11 | 15 |
| V 1 | 1 | 4 |
| Obolidae gen. et sp. | 11 | | | 16 | 16 |
| Rowellella margarita | 3 | 2 | 1 | 13 | 2 | 29 | 29 |
| Indet. | 3 |
| Total | 2 | 42 | 40 | 1 | 16 | 4 | 1 | 12 | 1 | 43 | 50 |

D, dorsal valves; V, ventral valves; C, complete articulated shells.
| Cili section | SC 15 | SC 16 | SC 19 | SC 20 | SC 28 | SC 31 | SC 33 | SC 34 | SC 35 | SC 36 | SC 37 | SC 38 | SC 41 | SC 42 | SC 43 | SC 44 | SC 45 | SC 46 | SC 47 | SC 48 | SC 49 | SC 50 | SC 51 | SC 52 | SC 53 |
|-------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Numericoma spinosa | D 1 2 2 | V 1 3 3 1 | C 1 | | | | | | | | | | | | | | | | | | | | | |
| Torynelasma sinensis | D 12 3 2 2 1 3 5 1 2 9 1 3 25 1 7 2 | V 19 4 2 1 1 16 6 6 3 10 6 2 10 1 1 3 | C 1 | | | | | | | | | | | | | | | | | | | | |
| Myotreta crassa | D 1 1 1 1 2 2 1 | V 1 2 1 | C 1 | | | | | | | | | | | | | | | | | | | | |
| Scaphelasma mica | D 1 2 1 6 2 4 6 8 1 1 4 2 18 2 2 3 2 | V 1 1 2 2 1 1 1 1 1 1 2 1 1 1 1 1 1 1 | C 3 1 1 4 | | | | | | | | | | | | | | | | | | | | |
| Scaphelasma afflata | D | V | C | | | | | | | | | | | | | | | | | | | | |
| Myotreta aff. dakcarlica | D 4 | V 2 78 15 2 | C | | | | | | | | | | | | | | | | | | | | |
| Sasyksoria abnormis | D | V 5 5 | | | | | | | | | | | | | | | | | | | | |
| Rowellella margarita | 1 | | | | | | | | | | | | | | | | | | | | | |
| Eurytreta ciliensis | D | V | | | | | | | | | | | | | | | | | | | | |
| Ephippelasma miutum | D | V | | | | | | | | | | | | | | | | | | | | |
| Rowellella distincta? | D | V | | | | | | | | | | | | | | | | | | | | |
| Eocconulus cf. clivosus | D 1 2 2 12 18 31 1 5 72 64 39 | V 4 33 7 2 85 6 170 86 20 71 | | | | | | | | | | | | | | | | | | | | |
| Obolidae gen. et sp. | 1 1 1 1 1 | | | | | | | | | | | | | | | | | | | | | |
| Numericoma perplexa | D | | | | | | | | | | | | | | | | | | | | | |
| Indet. | 1 | | | | | | | | | | | | | | | | | | | | | |
| Total | 1 3 4 4 34 21 30 36 15 9 45 104 85 42 1 7 4 57 19 7 281 35 182 97 26 78 | | | | | | | | | | | | | | | | | | | | | |
| Cili section               | SC 55 | SC 56 | SC 57 | SC 58 | SC 59 | SC 60 | SC 61 | SC 62 | SC 63 | SC 64 | SC 65 | SC 66 | SC 67 | SC 68 | SC 69 | SC 71 | SC 73 | SC 81 | SC 83 | SC 89 | SC 91 | SC 95 | Total |
|----------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| **Numericoma spinosa**     | D 1   |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       | 49  | 81   |
|                           | V 4   |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
|                           | C     |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| **Torynelasma sinensis**   | D 3   | 7    | 15    | 110   | 10    | 57    | 27    | 3     | 1     | 19    | 8     | 44    | 4     | 1     | 9     | 6     | 416   | 691   | 81   | 101  | 36   |       |       |       |
|                           | V 4   | 3    | 8     | 87    | 2     | 33    | 11    | 3     | 5     | 4     | 3     | 1     | 1     | 1     | 6     | 5     | 267   |       |       |       |       |       |       |
|                           | C     | 1    | 1     | 3     | 1     | 1     | 3     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 5     | 5     |       |       |       |
| **Myotreta crassa**        | D 16  | 2    | 10    | 22    | 4     | 2     | 2     | 3     | 1     | 1     | 1     | 1     | 3     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 8     | 153  | 222  |
|                           | V 9   | 6    | 1     | 13    | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1      | 6  |
|                           | C     | 2    |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| **Scaphelasma mica**       | D 36  | 8    | 29    | 2     | 1     | 2     | 6     | 4     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     |
|                           | V 1   | 2    | 2     | 6     | 8     | 4     | 2     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     |
|                           | C     | 4    | 5     | 2     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     |
| **Scaphelasma afflata**    | D 1   | 1    | 2     | 20    | 36    | 8     | 13    | 1     | 8     | 45    | 3     | 118   | 84    | 28    | 10    | 15    | 84    | 10    | 15    | 3     |       |       |       |
|                           | V 1   | 1    | 2     | 14    | 11    | 7     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     |
|                           | C     | 1    | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     |
| **Myotreta aff. dalearlica** | D 5  | 2    | 12    | 4     | 2     | 15    | 8     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     |
|                           | V 4   | 1    | 2     | 1     | 1     | 2     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     |
|                           | C     | 2    |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| **Sasyksoria abnormis**    | D     |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
|                           | V     |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| **Rowellella margarita**   |       | 24   |       | 3     |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| **Eurytreta cilliensis**   | D     |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
|                           | V     |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| **Ephippelasma miatum**    | D     |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
|                           | V     |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| **Rowellella distincta?**  | D     |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
|                           | V     |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| **Eoconulus cf. clivosus** | D 180 | 18   | 21    | 20    | 15    | 3     | 2     | 8     | 1     | 3     | 1     | 1     | 5     | 1     | 1     | 60    | 1     | 1072  | 1072  | 13   | 13   | 1     |
| Obolidae gen. et sp.      |       | 1    |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| **Numericoma perplexa**    | D     |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| Indet.                    |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| **Total**                 | 243   | 56   | 84    | 308   | 25    | 113   | 84    | 5     | 22    | 1     | 30    | 12    | 9     | 70    | 104   | 17    | 7     | 72    | 7     | 13    | 7     | 100   | 13    | 2629  |

D, dorsal valves; V, ventral valves; C, complete articulated shells.
| Maocaopu section | MC 2 | MC 4 | MC 6 | MC 7 | MC 17 | MC 19 | MC 22 | MC 24 | MC 26 | MC 28 | MC 30 | MC 31 | MC 33 | MC 35 | MC 36 | MC 38 | MC 39 | MC 42 | MC 44 | MC 45 | MC 46 | MC 50 | MC 51 | MC 53 | MC 54 | MC 56 | MC 57 | MC 59 | MC 60 | MC 62 |
|------------------|------|------|------|------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Myotreta crassa  | D    | 3    | 62   | 54   | 13    | 5     | 7     | 1     | 1     | 2     | 1     | 1     | 1     | 2     | 1     | 3     | 1     | 2     | 1     | 1     | 2     | 1     | 2     | 2     | 2     | 2     | 2     | 2     | 2     | 2     | 2     |
| Eoconulus cf. clivosus | V    | 2    | 45   | 93   | 33    | 6     | 1     | 6     | 12    | 2     | 1     | 1     | 3     | 1     | 1     | 5     | 1     | 2     | 1     | 1     | 2     | 1     | 2     | 2     | 2     | 2     | 2     | 2     | 2     | 2     |
| Torynelasma sinensis | V    | 3    | 4    | 2    | 12    | 2     | 6     | 29    | 9     | 14    | 3     | 4     | 5     | 1     | 16    | 1     | 26    | 1     | 2     | 1     | 10    | 1     | 2     | 1     | 1     | 1     | 1     | 1     | 1     |
| Scaphelasma afflata | C    | 1    | 2    | 1    | 12    | 2     | 6     | 29    | 9     | 14    | 3     | 4     | 5     | 1     | 16    | 1     | 26    | 1     | 2     | 1     | 10    | 1     | 2     | 1     | 1     | 1     | 1     | 1     | 1     |
| Eocaphelasma sp. | D    | 105  | 1    | 6    | 21    | 12    | 9     | 144   | 56    | 29    | 3     | 68    | 16    | 8     | 171   | 13    | 5     | 12    | 25    | 29    | 40    | 2     | 25    | 5     | 16    | 2     | 1     | 2     | 1     |
| Eurytreta ciliensis | V    | 78   | 1    | 2    | 4     | 1     | 12    | 2     | 6     | 29    | 9     | 14    | 3     | 4     | 5     | 1     | 16    | 1     | 26    | 1     | 2     | 1     | 10    | 1     | 2     | 1     | 1     | 1     | 1     |
| Numericoma spinosa | C    | 1    | 2    | 4     | 1     | 12    | 2     | 6     | 29    | 9     | 14    | 3     | 4     | 5     | 1     | 16    | 1     | 26    | 1     | 2     | 1     | 10    | 1     | 2     | 1     | 1     | 1     | 1     |
| Obolidae gen. et sp. |      | 4    | 1    | 2    | 4     | 1     | 1    | 2    | 6     | 29    | 9     | 14    | 3     | 4     | 5     | 1     | 16    | 1     | 26    | 1     | 2     | 1     | 10    | 1     | 2     | 1     | 1     | 1     | 1     |
| Undiferina sp. | D    | 2    | 1    | 1    | 1    | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     |
| Discinidae gen. et sp. |      | 1    | 2    | 4     | 1     | 12    | 2     | 6     | 29    | 9     | 14    | 3     | 4     | 5     | 1     | 16    | 1     | 26    | 1     | 2     | 1     | 10    | 1     | 2     | 1     | 1     | 1     | 1     |
| Nushbiella sp. | D    | 2    | 1    | 1    | 1    | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     |
| Biernatia cf. holmi |      | 1    | 2    | 4     | 1     | 12    | 2     | 6     | 29    | 9     | 14    | 3     | 4     | 5     | 1     | 16    | 1     | 26    | 1     | 2     | 1     | 10    | 1     | 2     | 1     | 1     | 1     | 1     |
| Indet. |       | 1    | 2    | 4     | 1     | 12    | 2     | 6     | 29    | 9     | 14    | 3     | 4     | 5     | 1     | 16    | 1     | 26    | 1     | 2     | 1     | 10    | 1     | 2     | 1     | 1     | 1     | 1     |
| Total |       | 5    | 697  | 1    | 1    | 1    | 6    | 47    | 12    | 9    | 9    | 366   | 291   | 97    | 14    | 147   | 28    | 14    | 369   | 64    | 8    | 63    | 62    | 64    | 104   | 2    | 7    | 69    | 9    | 70    | 4    |
| TABLE 3. (Continued) |
|-----------------------|
| Maocao pu section     | MC63 | MC64 | MC65 | MC68 | MC69 | MC71 | MC72 | MC73 | MC74 | MC75 | MC77 | MC78 | MC81 | MC82 | MC83 | MC85 | MC86 | MC87 | MC88 | MC89 | MC90 | MC91 | MC92 | MC93 | MC94 | MC95 | MC96 | MC97 | MC98 | MC99 | MCT0 | MCT1 | MCT2 | MCT3 | MCT4 | MCT5 | MCT6 | MCT7 | MCT8 | MCT9 | MCT10 | MCT11 | MCT12 | MCT13 | MCT14 | MCT15 | MCT16 | MCT17 | MCT18 | MCT19 | MCT20 | MCT21 | MCT22 | MCT23 | MCT24 | MCT25 | MCT26 | MCT27 | MCT28 | MCT29 | MCT30 |
| Myotreta crassa       | D    | 1    |   3 | 3    | 1    | 1    | 156  | 392  |
| V                     | 1    | 1    | 8  | 9    | 1    | 1    | 225  |
| C                     | 1    | 1    | 1  | 1    |     |     | 11   |
| Eoconulus cf. diurus | D    | 77   | 7  | 5    | 7    | 1    | 1    | 2    | 18   |
| V                     | 6    | 5    | 1  | 2    | 4    | 3    | 9    | 2    | 18   |
| C                     | 1    | 1    | 1  | 1    | 1    |     |     |     |     |
| Torynelasma sinensis  | D    | 12   | 6  | 24   | 12   | 24   | 5    | 3    | 11   | 9    | 11   | 5    | 11   | 5    | 8    | 65   | 32   | 118  | 6    | 1    | 2    | 1303  | 2349  |
| V                     | 9    | 3    | 23 | 5    | 25   | 2    | 4    | 3    | 2    | 4    | 2    | 3    | 7    | 36   | 42   | 68   | 3    | 1    |     |     | 1029  |
| C                     | 2    | 1    | 1  | 1    | 1    | 1    | 1    |
| Scaphelasma afflata   | D    | 3    | 2  | 1    | 7    | 3    | 2    | 5    | 105  | 19   | 1    | 3    | 3    | 1    | 1    |     |     |     |     | 271   | 446   |
| V                     | 1    | 5    | 1  | 2    | 1    | 4    | 4    | 4    | 4    | 4    | 4    | 9    |     |     |     |     |     |     |     | 160   |
| C                     | 6    | 1    | 2  | 1    | 1    | 1    |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 15    |
| Eoconulas sp.         | D    | 59   | 150|
| V                     | 88   |
| C                     | 3    |
| Euryreta cilicenosis  | D    | 1    | 39 | 3    | 1    | 2    | 4    | 7    | 1    | 1    |     |     |     |     |     |     |     |     |     |     | 60    | 115   |
| V                     | 2    | 4    | 32 | 3    | 1    | 2    | 4    | 3    | 4    |     |     |     |     |     |     |     |     |     |     | 55    |
| C                     |     | 0    |
| Numeronoma spinosa    | D    | 21   | 3  | 1    | 1    | 23   |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 49    | 92    |
| V                     | 25   | 1    | 1  | 3    | 10   |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 40    |
| C                     |     | 3    | 3  |
| Obolidae gen. et sp.  |     | 4    | 4  |
| Undiferina sp.        |     | 5    | 5  |
| Discinidae gen. et sp.|     | 1    | 2  |
| Nushbella sp.         |     | 4    | 4  |
| Biernatia cf. holmi    |     | 2    | 2  |
| Indet.                |     | 1    | 2  |
| Total                 | 21   | 10   | 136 | 32   | 6    | 59  | 10   | 29   | 14   | 7    | 15   |
|                      |     | 21   | 24  | 126  | 139  | 390 | 40   | 8    | 84   | 22   | 4    | 4    | 10   | 16   | 11   | 37   | 4    |
|                      |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     | 1    |     |     |     |     |     | 3920  |

D, dorsal valves; V, ventral valves; C, complete articulated shells.
crassa, Rowellella distincta?, Scaphelasma afflata, Scaphelasma mica and Torynelasma sinensis) are documented from one or two localities (Tables 1–3; Holmer et al. 2017).

In the cluster analysis (Morisita Similarity Index) the Eurytreta ciliensis Community is placed rather distantly (Fig. 4) from the other micromorphic lingulate brachiopod communities. In the correspondence analysis (Fig. 5) it shows slightly negative to moderately positive scores of component 1 and moderately negative scores of component 2, while the area occupied by slightly negative component 2 scores overlaps slightly with the Torynelasma–Scaphelasma and Numericoma perplexa communities.

The Numericoma perplexa Community (samples FC29, FC 30–1, FC49, FC50, FC62, FC66), Lenodus antivariabilis and Lenodus variabilis conodont zones (average dominance 0.358 (min 0.194, max 0.781), average evenness 0.771 (min 0.335, max 0.860), average Margalef’s richness index 1.276 (min 0.481, max 1.747)). None of the nine taxa documented in the Numericoma perplexa Community are confined exclusively to this community and only two species (Numericoma perplexa and Eoconulus cf. clivosus) occur in all samples (Tables 1–3; Holmer et al. 2017). Biernatia cf. holmi, Cyrtotretta sp., Rowellella margarita and Scaphelasma mica are also common, but usually occur in low frequencies. Numericoma perplexa is also represented in the Eoconulus–Torynelasma Community, but confined almost exclusively to the Fenxiang section in its distribution. Acanthambonia cf. delicata and Torynelasma sinensis each occur in a single locality and are not considered to be characteristic of the community (Table 1–3; Holmer et al. 2017). In the cluster analysis (Morisita Similarity Index) the Eurytreta ciliensis Community shows the closest similarity (< 0.3) to the Eoconulus–Torynelasma Association (Fig. 4), while in the correspondence analysis (Fig. 5) it shows low to moderately positive scores of component 1, which is defined by the relative abundance of Eoconulus cf. clivosus (C1 +0.2694) and low negative scores of component 2, probably, defined by the cumulative input of minor components of the association. The area occupied by scores obtained for the sample from the Eoconulus–Torynelasma Community is adjacent to the Eoconulus–Torynelasma Community and slightly overlaps with the area of the Eurytreta ciliensis Community. The latter is characterized by more negative scores of component 2 (Fig. 5).

The Numericoma spinosa Community (samples FC26, FC28, FS81, FC110–1, MC97, SC68), Lenodus antivariabilis, Lenodus variabilis, Pygodus serra and Pygodus anserinus conodont zones (average dominance 0.547 (min 0.302, max 0.929), average evenness 0.743 (min 0.586, max 0.986), average Margalef’s richness index 0.822 (min 0.258, max 1.470)). In generic composition this association shows no significant difference from the Numericoma perplexa Community (Tables 1–3; Holmer et al. 2017), but it is characterized by the distinct predominance of Numericoma spinosa, which constitutes 42–97% of the total number of individuals in the samples. Other species occur as minor components of the assemblage, and their taxonomic composition varies greatly from one sample to another one (Tables 1–3; Holmer et al. 2017). In the cluster analysis (Morisita Similarity Index), the Numericoma spinosa Community appears as the most distant in relation to all other lingulate brachiopod communities (similarity > 0.15). In the correspondence analysis (Fig. 5), it shows low positive scores of component 1, and the highest negative scores of component 2 and is distantly from all other communities.

The Scaphelasma–Torynelasma Community (samples SC34, SC59, MC4, MC56, MC84, MC 87, MC88, MC91), Microzarkodina hartae, Microzarkodina ozarkodella and Pygodus anserinus zones (average dominance 0.458 (min 0.349, max 0.688), average evenness 0.700 (min 0.302, max 0.999), average Margalef’s richness index 0.866 (min 0.329, max 1.243)). This is a low to medium diversity association, which is characterized by the predominance of Scaphelasma mica (25–75%) and Torynelasma sinensis (7–52%). These are the only two species occurring in all samples referred to the association. Among other species, only Eoconulus cf. clivosus is relatively common, but occurs in low frequencies (Tables 1–3; Holmer et al. 2017). Biernatia cf. holmi, Nushbiella sp. and Discinidae gen. et sp. are represented by a few individuals from a single locality. Somewhat unusual is the spike of abundance of Eoscahelasma? sp. (21.7%) in sample MC4. Otherwise this species is unknown from all other analysed samples. In the cluster analysis (Morisita Similarity Index) the Numericoma spinosa Community appears in a single third order cluster with the Torynelasma spinosa Community, with similarity slightly exceeding 0.5 (Fig. 4). In the correspondence analysis (Fig. 5) it shows negative scores of component 1 and low positive to moderately negative scores of component 2, which are slightly overlapping with the Eurytreta ciliensis Community.

The Eoconulus cf. clivosus Community (samples FC39, FC41, FC44, FC57, FC58, FC63, FC87, MC46, MC60, MC65, MC73, MC84, SC29, SC31, SC33, SC37, SC38, SC41, SC45, SC46, SC48, SC49, SC50, SC51, SC52, SC53, SC55, SC56, SC57, SC63), Lenodus antivariabilis – Eoplacognathus succinctus zones (average dominance 0.565 (min 0.254, max 0.931), average evenness 0.671 (min 0.303, max 0.999), average Margalef’s richness index 0.723 (min 0.271, max 1.384)). Among the 14 species documented in the Eoconulus cf. clivosus Community only Eoconulus cf. clivosus invariably occurs in all samples (Tables 1–3; Holmer et al. 2017). Torynelasma sinensis is
the second most common species; however, it is not represented in the samples from the Fenxiang section, while in the Maocaopu section its relative abundance in individual samples is up to 47%. *Scaphelasma mica* is common in the samples from the Maocaopu and Cili sections, but in the Fenxiang section it is documented in only two samples. *Biernatta cf. holmi* and *Numericoma perpexa* are present in the samples from the Fenxiang section, but absent in other sections. However, the species richness in the samples from the Fenxiang section is usually lower. *Acanthambonia cf. delicata* and *Cyrtontotreta* sp. are represented only by a few individuals in one sample from the Fenxiang section and are not documented in the samples of the *Eoconulus cf. clivosus* Community in the two other sections. *Myotreta crassa*, *Numericoma spinosa*, *Rowellella margarita*, *Scaphelasma afflata* and *Discinidae gen. et sp.* do not occur in the samples from Fenxiang. In the cluster analysis (Morisita Similarity Index), the samples of the *Torynelasma sinensis* Community slightly with high conical shells, including the Ephippelasmatidae, exceeding 0.5; although there is no clear differentiation between samples from the Maocaopu and Cili sections (Fig. 4). In the correspondence analysis (Fig. 5) the samples of the *Torynelasma sinensis* Community form a compact group with negative scores for component 1 and slightly negative to moderately positive scores for component 2. The area occupied by these samples is closely spaced, but it does not overlap with the area occupied by samples of the *Scaphelasma–Torynelasma* Community.

**Biodiversity Patterns and Life Strategies of Micromorphic Linguliforms**

The life strategies of Early Palaeozoic linguliform microbrachiopods and the palaeoecology of acrotretide-dominated brachiopod associations have been discussed repeatedly in a number publications, where it was also noticed that linguliform microbrachiopod associations often occur in hexactinellide sponge-dominated environments (e.g. Popov et al. 1994; Bassett et al. 1999; Mergl 2002; Holmer et al. 2005; Percival et al. 2016). Nevertheless, direct evidence for biotic relationships between linguliform microbrachiopods and other benthic organisms, such as sponges, are extremely rare, and most of the direct evidence for a secondary tiering life strategy of micromorphic acrotretide brachiopods comes from the Cambrian Chengjiang Fauna (Wang et al. 2012) and the Burgess Shale (Topper et al. 2015). The only documented post-Cambrian cases include the lingulide *Paterula*, which has been found in significant numbers attached to the oscular margin of sponges (Lenz 1993, erroneously referred to as *Craniopt*) and a few records of the cementing *Eoconulus* preserved attached to hard substrates (Holmer et al. 2000, Hansen & Holmer 2011). More indirect evidence is provided by the occurrence of dense concentration of the acrotretide shells (including many complete articulated specimens) of *Ottenbyella* within dense accumulation of sponge spicule aggregates (Holmer et al. 2005, fig. 3.1–8). While *Paterula* itself is not represented in the studied Dariwilian microbrachiopod fauna of South China (only a single specimen of the enigmatic related *Diencobolas* is present), it includes *Eurytreta*, which is an acrotretide that is most likely closely related to *Ottenbyella* and probably was adopted to a similar life habit. It is also well established, that *Eurytreta*-dominated microbrachiopod biofacies are frequently associated with dysoxic environments (Popov & Holmer 1994).

Some micromorphic acrotretides, like *Pomeraniotreptes* (Ephippelasmatidae), occur also in radiolarian cherts (Tolmacheva et al. 2004) and clearly were able to spread from the shelf to the abyssal depths. For these acrotretides...
Biernatidae (e.g. *Biernatia*, *Opiscomidion*), and possibly the Torynelasmatidae, a life association with sponges appears to be likely also in these cases.

*Eoconulus* is one of a few linguliforms that show evidence of an attached and encrusting life habit and it is widely represented in the investigated microbrachiopod associations. The shape of the encrusting surfaces of some ventral valves of *Eoconulus* (e.g. Popov et al. 1994, pl. 6, figs 8, 9) suggest attachment to cylindrical objects, probably, sponge spicules. Holmer et al. (2000, fig. 5Z–CC) illustrated a ventral valve of *Eoconulus* that was attached to a shell fragment and even more convincing direct evidence was illustrated by Hansen & Holmer (2011, pl. 21, figs 11–13), where a ventral valve of *Eoconulus* is preserved attached to a cylindrical organism. It is likely that *Eoconulus* was also adapted to some kind of epibenthic habit, or attached to hard objects in small accumulations of bioclasts or spiculite aggregates, presumably in areas with low sedimentation rates. Moreover, it is likely that brachiopods of the Scaphelasmatidae (e.g. *Eostaphelasmatia* and *Scaphelasma*), which are phylogenetically closely related to the Eoconulidae (Popov & Holmer 1994), adopted a similar habit. A similar life strategy can be considered also for aberrant sphonotretidines such as *Acanthambonia* (Bassett et al. 1999) and *Nushbiella* (Perckval et al. 2016), which occur as minor components in the linguliform microbrachiopod associations and suggest that these microbrachiopods may also have lived as secondary tiering organisms attached to other benthic organisms.

The characters of distribution of the microbrachiopod biofacies through the Darriwilian succession suggest that, within the interval from *Lenodus variabilis* to the lower part of the *Microzarkodina ozarkodella* conodont zones, the Fenxiang and Cili sections were located mainly within the area mainly occupied by both the *Eoconulus cf. clivosus* and *Torynelasma sinensis* communities, while the Maocaup section, within the interval from the *Yangtzeplacognathus crassus* Zone to the lower part of the *Microzarkodina ozarkodella* Zone, was within the area inhabited by the *Torynelasma sinensis* Community. A significant biofacies shift occurred in the upper part of the *Microzarkodina ozarkodella* Zone, when the *Torynelasma sinensis* Community replaced the *Eoconulus cf. clivosus* Community in the Cili section and here it retained its dominance through the *Eoplacognathus suciius* Zone. The transitional interval from the Darriwilian to Sandbian (*Pygodus anserinus* Zone) in the Cili and Maocaup sections is characterized by frequent biofacies shifts, probably, reflecting unstable environment at that time.

Data on the biofacies changes in the lower part of the Darriwilian succession, corresponding to the *Lenodus antivariabilis* and *Lenodus variabilis* conodont zones, are available only for the Fenxiang section. While there is a significant biofacies shift in the lower part of the *Lenodus antivariabilis* Zone, the main part of the observed succession in Fenxiang displays a dominance of the *Eoconulus cf. clivosus* Community with three short term disruptions caused by three successive invasions of the *Numericoma perplexa* Community within the *Lenodus variabilis* Zone and by the recurrence of the *Numericoma spinosa* Community in the uppermost part of this zone.

The fauna in sample FC26 (at the base of the *Lenodus antivariabilis* Zone) represents a pioneering stage of the *Numericoma spinosa* Community. The nominal species in this sample constitutes almost 82% of the number of individuals in the assemblages, whereas two other associated species, including *Biernatia cf. holmi* and *Eoconulus cf. clivosus* occur in low frequencies. In sample FC28, the species richness increases up to six, yet *Numericoma spinosa* comprises 42% of the total number of individuals (Fig. 3, Table 1). The succeeding *Numericoma perplexa* Community (sample FC29, FC30) is mainly defined by the replacement of the dominant *Numericoma* species and the appearance of *Scaphelasma micus* while almost all other minor components of the assemblage remain unchanged; although *Cyrtonotreta* sp. and *Eoconulus cf. clivosus* are extremely rare or absent in the samples of the *Numericoma spinosa* Community; they are relatively common in the *Numericoma perplexa* Community (Table 1). There is a steady increase in evenness values and substantial decrease in the dominance values from sample FC26 to sample FC30 (Fig. 5).

The appearance of the *Eoconulus cf. clivosus* Community in samples FC39, FC41 coincides with decrease of diversity (Table 1; Fig. 3) and general increase in dominance values from samples FC30 to FC44, while the evenness values drop sharply, shortly after the transition but then show minor fluctuations (Fig. 3). The decrease in richness down to 2–4 species is mainly due to significant decline of the acroretidines of the *Ephippelasmatidae*, while *Torynelasma* is completely absent in the samples from the Fenxiang section. Only *Numericoma perplexa* remains a relatively common minor component in the *Eoconulus cf. clivosus* Community. Remarkably, the increase in relative abundance of *Numericoma perplexa* up to c. 30–35% in samples FC39 and FC41, is associated with increase in abundance of *Biernatia cf. holmi* (13.5–20%). The return of the *Numericoma perplexa* Community coincides with increase of richness up to 5–7 genera, decrease in dominance and a substantial decrease in the relative abundance of *Eoconulus cf. clivosus*. A brief recurrence of the *Numericoma spinosa* Community is apparent in the uppermost part of the *Lenodus variabilis* Zone. While *Numericoma spinosa* behaves often as opportunistic species and its occurrence may indicate increased environmental stress, inadequate sampling within this interval makes further discussion speculative.
The available data on the linguliform microbrachiopod biofacies changes through the mid and late Darriwilian (Yangtzeplacognathus crassus – Pygodus anserinus zones) are based on the samples obtained from the Cili and Maocaopu sections. Both sections contain a distinct hiatus covering significant part of Eoplacognathus succicus and Pygodus serra zones (Zhang 1995, 1998a, b). The nature of this non-depositional interval is uncertain; however, no significant biofacies changes is indicated in biofacies replacement on either side of the hiatus, thus it was probably not directly related to the sizeable sea-level fluctuations or subaerial exposure of the area. Remarkably, similar gaps were documented within the same stratigraphical interval also in Baltoscandia, in particular in the Gullhögen Quarry (e.g. Holmer 1989). While detailed data on the sea-level curves for these two sections are not available (but see Su 2007), the lower part of the Mid Darriwilian Carbon Isotope Excursion (MDICE) with the onset occurring at the middle part of the Microzarkodina ozarkodella Zone was documented by Schmitz et al. (2010) for the Maocaopu section and also for the Puxi River section near Fenxiang situated in relative proximity of Cili. This event has distinct correlation with biofacies changes as it will be discussed below.

In the Cili section the Eoconulus cf. clivosus Community prevails for most of the Yangtzeplacognathus crassus, Microzarkodina hagetiana and Microzarkodina ozarkodella zones. The only significant short term shift occurred above the base of Microzarkodina hagetiana Zone (samples SC34, SC36) when successive colonization of the Torynelasma sinensis and Scaphelasma–Torynelasma communities had occurred. There is also no significant change in biodiversity, except the upper half of the Microzarkodina hagetiana Zone when species richness approach the maximum values and significant decline in dominance levels had occurred (Fig. 3). It was followed by gradual, but steady raise in values of Margalef’s richness index from 0.577 (sample SC50) to 1.169 (sample SC57). The observed patterns suggest that during most of that time the Eoconulus cf. clivosus Community was close to the equilibrium condition.

The major biofacies shift in Cili section is documented in the upper part of the Microzarkodina ozarkodella Zone, when Torynelasma sinensis Community becomes firmly established in the area (Figs 3, 5). There was a single brief recurrence of the Eoconulus cf. clivosus Community, which occurred somewhat below the non-deposition interval. A brief appearance of the Numericoma spinosa Community above the non-depositional interval at the uppermost part of the Pygodus serra Zone may signify an unstable environment, while invasion of the Eurytreta ciliensis Community into the Pygodus anserinus Zone was probably related to the proliferation of dysaerobic environments evident at that time.

The biodiversity pattern revealed in the Maocaopu section was remarkably different. While the Torynelasma sinensis Community can be considered to represent background linguliform microbrachiopod biofacies from Yangtzeplacognathus crassus to Microzarkodina ozarkodella zones, there are five short term Eoconulus cf. clivosus Community and two Scaphelasma–Torynelasma Community excursions within the upper part of the Microzarkodina hagetiana and Microzarkodina ozarkodella zones (Figs 3, 5). These excursions usually coincided with decrease in values of dominance and evenness, and slight increase in species richness (Table 3). The unusual feature of the Eoconulus cf. clivosus Biofacies in the Maocaopu section is the relative abundance of Torynelasma sinensis (25–47%), which is not observed in the samples of the Eoconulus cf. clivosus Community in the Fenxiang and Cili sections. The most likely explanation is that both communities coexisted at that time in the area, while there was no competition for ecospace between their nominal species because they occupied different niches. If so, during the invasions of the Eoconulus cf. clivosus Community, the habitats occupied by the Torynelasma sinensis Community were practically unaffected. Occasional invasions of the Scaphelasma–Torynelasma Community below non-deposition interval in the Maocaopu section require little attention because of the small size of the samples (Table 3). A major shift occurs during the Pygodus anserinus Zone, when Scaphelasma–Torynelasma and Eurytreta ciliensis communities became firmly established in the Maocaopu area. By analogy with Cili it is likely that the arrivals of the Eurytreta ciliensis Community may be related to the proliferation of dysaerobic environments, which became a common feature of the Yangtze Platform during the Sandbian time (Munnecke et al. 2010).

**DISCUSSION**

All three studied Darriwilian sections represent outer shelf environments. The monotonous condensed succession of the of relatively pure, reddish to light grey, bedded to nodular limestones with numerous discontinuity surfaces characteristic of the Guniutan Formation makes it difficult to provide independent evidence for environmental factors which controlled the distribution of the linguliform microbrachiopod biofacies and detailed sedimentological studies are needed, which were out of scope of the present paper. Nevertheless, the biofacies shift, which occurred in the Cili section in the upper part of the Microzarkodina ozarkodella Zone, at the time of the onset and initial raise of the MDICE (Schmitz et al. 2010) suggests that these biofacies were depth controlled. In Baltoscandia the onset of MDICE coincides
closely with the Helskjer Drowning (see Nielsen 2004), but detailed sea-level curves for the studied Chinese sections are not presently available. A similar and probably synchronous sea level rise is also reported in the mid Darriwilian (Lenodus pseudoplanus Zone) of the Alborz terrane in Iran (Ghobadi Pour et al. 2011, fig. 2, Unit L21), where it coincides with the invasion of the Echinospaerites echinoderm biofacies and Saucrorthis brachiopod fauna (Popov et al. 2016). In North African and Arabian sectors of Gondwana major flooding (‘fomosa event’ of Paris et al. 2007) occurred about the same time (Videt et al. 2010; Ghavidel-Syooki et al. 2014). Another significant, but short term biofacies shift occurred in the Cili section in the lowermost part of the Microzarkodina hagetiana Zone. It can be correlated with the ‘Basal Llanvirn’ Drowning Event (Nielsen 2004), which was discussed in more detail by Rasmussen et al. (2009).

During the mid Darriwilian, it is likely that the Torynelasma sinensis Community occupied the outer margin of the Upper the Yangtze Platform, while the Scaphelasma—Torynelasma Community occurred nearby, probably in the transitional area towards the Jiangnan Slope. The Numericoma perplexa Community was located inshore and its area did not overlap with the areas inhabited by the Torynelasma communities, while the space dividing these stenotopic communities was inhabited by the low diversity Eoconulus cf. clivosus Community. Eoconulus cf. clivosus itself may have been a generalist, which probably also benefited from an environment rich in small bio- clasts, and characterized by extremely low sedimentation rate and negligible mud supply. Remarkably, it is almost absent in the Numericoma spinosa Community and very uncommon in the samples of the Torynelasma sinensis Community from the Yangtzeplacognathus crassus Zone and the lower part of the Microzarkodina hagetiana Zone (Holmer et al. 2017, table 6; samples MC19-MC39), but constantly present in the upper samples in medium frequencies. A distinct shift from Numericoma to Eoconulus biofacies in the middle part of the Lenodus antivariabilis Zone of the Fenxiang section (samples FC26–FC30) may reflect a sea level rise in the early Darriwilian, which is also reported by Wu et al. (2014, fig. 8) for the Dingxiang section, but not discussed in detail. No significant flooding events were reported for that stratigraphical interval in Baltoscandia by Nielsen (2004). It may represent the first in a sequence of recurrent invasions of the Numericoma perplexa Community in the Fenxiang section; the Eoconulus cf. clivosus and Scaphelasma—Torynelasma communities in the Maocaopu section show some similarity to the biodiversity pattern documented for the lower to middle Darriwilian of the East Baltic by Rasmussen et al. (2009) and could be assigned to the environmental changes caused by the 400 kyr eccentricity cycle, but this requires support from detailed sedimentological studies.

**BIOGEOGRAPHY AND AFFINITIES**

This study of the Ordovician (Darriwilian to Sandbian) micromorphic linguliform brachiopods from South China builds on previous work by Zhang (1995), which has been expanded across the carbonate succession on the Yangtze Platform. It can now be compared in detail to the better known and closely similar faunas from the so-called ‘Orthoceratite limestone’ of Baltoscandia (Gorjan sky 1969; Holmer 1989) as well as other micromorphic faunas that have been recorded, including those from the eastern (Alabama) and western (Nevada) Laurentia margins (Cooper 1956; Krause & Rowell 1975; Hansen & Holmer 2011), New Zealand (Percival et al. 2009), Australia (Percival 1978; Percival et al. 1999, 2016), Bohemia (Mergl 2002), Avalonia, Britain (Sutton et al. 1999, 2000), Alborz, Iran (Popov et al. 2008) as well as a number of Kazakhstani terranes (Popov 2000; Nikitina et al. 2006). Remarkably, nearly all listed occurrences correspond more or less to the distribution of conodonts of the so-called Atlantic Province (e.g. Zhang 1998b), which makes it possible to obtain a rather precise correlation supported in some cases also by the occurrences of graptolites.

The major characteristic of the recorded Chinese Darriwilian to Sandbian micrombrachiopod fauna within the interval of the Lenodus variabilis – Pygodus anserinus biozones, is a low taxonomic diversity and abundance of ephippelasmatids belonging to the genera Myotreta, Numericoma and Ephippelasma. Other characteristic genera include Scaphelasma (Scaphelasmatidae), Torynelasma (Torynelasmatidae) and Eoconulus (Eoconulidae). All of these genera, with the exception of Myotreta, are cosmopolitan and present in all the known faunas of that age, except for the early Darriwilian Kurchilik Formation of central Kazakhstan, where torynelasmatids are represented by the endemic Issedonia. Another remarkable feature of the Chinese fauna is the lack of lingulids, such as Elliptoglossa and Paterula, as well as a near absence of the family Acrotretidae (e.g. Acrotreta, Conotreta, Cyrtotreta and Spondylotre). which is otherwise rather characteristic of the contemporaneous faunas across the Baltic, Laurentia and Kazakhstani terranes. The remarkable abundance of the acrotretid Myotreta has only been recorded from Baltic, and this accentuates the close similarity to the contemporaneous Baltic fauna, something which is also supported by the occurrence of a number of common species such as Numericoma perplexa, N. spinosa, Acanthambonia cf. delicata and Scaphelasma mica. Another characteristic Baltic genus is Biennatta, and the
biernatids are restricted to Baltica during the Floian to early Darriwilian and widespread only from the late Darriwilian (*Pygodus serra – Pygodus anserinus* biozones) when they emerge in the South China, Australian, New Zealand, Laurentian and Kazakhstanian terranes and are also represented by two endemic genera in Avalonia (Sutton et al. 1999).

The *Pygodus anserinus* Biozone was also a time of remarkable changes in the lingulate microbrachiopod assemblages of South China. The generic diversity of the assemblage is nearly doubled and genera such as *Eurytretia, Ephippelasma, Biernatia, Undiferina, Acanthambonia* and *Nushbiella* make their first appearance, but genera of the family Acrotretidae remain very rare.

The predominance of the ephippelasmatids, torynelasmatids, scaphelasmatids and eocomulids in the Darriwilian to Sandbian micromorphic brachiopod fauna of South China could be explained by its geographical location in temperate latitudes in relative proximity of island arcs and small crustal terranes filling the oceanic space between the eastern margin of Baltica and East Gondwana. Available records (Popov & Holmer 1994) suggest that these island arc sets may represent locations where these families originally evolved and diversified during the middle and late Cambrian. However, the Darriwilian to Sandbian brachiopod faunas of South China remained less diverse as compared to contemporaneous faunas of the Kazakhstanian terranes; moreover, they lack several torynelasmatid and ephippelasmatid genera (e.g. *Issedonia, Polylasma, Velsipeptum, Lurgiticoma*) as well as the micromorphic lingulides *Paterula* and *Elliptoglossa*. A possible explanation is that the South China plate was situated at somewhat higher latitudes in the Middle Ordovician.

The palaeogeographical principal component analysis of the Darriwilian–Sandbian linguliform faunas by Holmer et al. (2016) showed that the Darriwilian linguliform faunas of South China are clearly differentiated from other peri-Gondwana faunas (Sutton et al. 1999, 2000; Mergl 2002; Popov et al. 2008) but are connected also to the Darriwilian fauna from New Zealand (Percival et al. 2009).

**SYSTEMATIC PALAEONTOLOGY**

All illustrated specimens from the investigated three sections on the Yangtze Platform are deposited in the Nanjing Institute of Geology and Palaeontology and in the Early Life Institute and Department of Geology, Northwest University, Xi’an, China.

Class LINGULATA Gorjansky & Popov, 1985
Order LINGULIDA Waagen, 1885
Superfamily LINGULOIDEA Menke, 1828
Family OBOLIDAE King, 1846
Obolidae gen. et sp.

Figure 6O

**Material.** 33 fragmentary valves.

**Remarks.** Species of the Obolidae are usually common and widely distributed in the Ordovician. However, the investigated Chinese faunas are very unusual in yielding only a very few possible fragmentary specimens; they are not possible to identify further. Zhang (1995) only illustrated a fragmentary specimen that was referred to *Linugelleta* sp.

**Occurrence in China.** Ordovician: Guniutan and Datianba formations, Cili section; Guniutan Formation, Fenxiang and Maozaopu sections (Tables 1–3).

**Family ZHANATELLIDAE** Koneva, 1986

**Genus ROWELLELLA** Wright, 1963

**Type species.** By original designation *Rowellella minuta* Wright, 1963; Ordovician, Katian, Portrane Limestone, Ireland.

**FIG. 6.** A–F, *Rowellella margarita* Krause & Rowell, Guniutan Formation, Fenxiang section (A–F sample FC17.76/110), and Cili section (D, E, sample SC57); A, ELI-BO2017-1, possible ventral valve interior, showing visceral field with deep muscle scars; B, ELI-BO2017-2, possible dorsal valve interior, showing visceral field with raised rim; C, oblique lateral view of A; D, ELI-BO2017-3, oblique lateral view of E, external view of D; F, ELI-BO2017-4, valve exterior. G–K, *Rowellella distincta* Bednarczyk & Biernat, Cili section (sample SC77); G, ELI-BO2017-5, valve exterior; H, oblique lateral view of G; I, enlargement of H, showing ornament of concentric rugae; J, enlargement of I; K, detail of shell ornamentation, enlargement of J. L–N, *Diencobolus* sp., Dawan Formation, Cili section (sample SC20); L, ELI-BO2017-6, external view of dorsal valve; M, enlargement of L, with detail of umbo; N, oblique lateral view of L. O, Obolidae gen. et sp., Guniutan Formation, Fenxiang section (sample FC30-1); ELI-BO2017-77, partly exfoliated ventral interior. P, *Cytontotrema* sp., ELI-BO2017-78, Guniutan Formation, Fenxiang section (sample FC30-1); fragment of dorsal interior, showing the pseudointerarea. Scale bars represent: 500 μm (A–H); 100 μm (I); 50 μm (J, M); 5 μm (K); 200 μm (L, N, O–P).
Remarks. Rowellella remains a very poorly known genus and close taxonomic discrimination is difficult due to the mostly fragmentary preservation and limited number of preserved characters, where it is usually problematic even to distinguish between ventral and dorsal valves. The two species described by Zhang (1995) were considered to be Rowellella margarita by Holmer et al. (2016, p. 35), but re-examination of the Chinese material of Rowellella distincta reveals differences and they are here considered to be separate species. As noted by Tapanila & Holmer (2006), the pitted micro-ornamentation (typical of the Zhanatellidae) that is found on the juvenile and/or the mature shell in most known Rowellella (e.g. Holmer 1989, p. 77) is sometimes missing and it has been recorded on neither Argentinian (Holmer et al. 2016) nor Chinese material, possibly due to poor preservation.

Rowellella margarita Krause & Rowell, 1975
Figure 6A–F

1975 Rowellella margarita sp. nov.; Krause & Rowell, p. 24, pl. 3, figs 8–15.
1995 Rowellella aff. margarita Krause & Rowell; Zhang, p. 158, pl. 1, figs 5–6.
2016 Rowellella margarita Krause & Rowell; Holmer et al., p. 35, fig. 3J–N.

Material. 57 indeterminate fragmentary valves.

Remarks. The posterior part of all available specimens is broken and the pseudointerareas are not preserved. However, the elongate suboval outline of the shell and the distinctive, deeply impressed visceral areas of both valves are identical to the types from Nevada. In particular one possible more complete dorsal valve has a visceral area with a distinctive oval shape with a raised rim; the moderately lamellose ornamentation is also closely similar in the Nevanadan and Chinese material. As noted by Krause & Rowell (1975), the muscle scars in Rowellella are also very difficult to interpret. One possible more complete ventral valve has muscle scars that appear to be considerably more deeply impressed in the single available ventral valve from China as compared with the Nevanadan and Argentinian material.

Occurrence in China. Ordovician: Guniutan Formation, Cili and Fenxiang sections (Tables 1, 2).

Rowellella distincta? Bednarczyk & Biernat, 1978
Figure 6G–K

1975 Rowellella distincta Bednarczyk & Biernat; Zhang, p. 158, pl. 1, figs 2–4.

Material. 9 fragmentary indeterminate valves.

Remarks. Only the anterior part of the strongly thickened shell is preserved in the material, but they clearly have a more strongly lamellose ornamentation, with ridge-like growth lamellae, as compared with Rowellella margarita and fine irregularly distributed superposed fila, which are lacking in Rowellella distincta?. The strongly thickened and lamellose shell is similar to the Polish type material of Rowellella distincta Bednarczyk & Biernat (1978, figs 1–2) from the basal mid-Ordovician of Poland. Similar material has also been recorded from the lower part of Klabava Formation of Bohemia (Mergl 1996, 2002) and the Tremadoc Lashkarak Formation (Baltoniodus navis Biozone) of Alborz, Iran (Popov et al. 2008).

Occurrence in China. Ordovician: Datianba Formation, Cili section (Table 2).

Family PATERULIDAE Cooper, 1956

Genus DIENCOBOLUS Holmer et al., 2001

Type species. Diencobolus simplex Holmer et al., 2001; Cambrian, Guzhangian, Glyptagnostus solidotus Biozone, Malyi Karatau Range, Kazakhstan.

Diencobolus sp.
Figure 6L–N

Material. 1 dorsal valve.

Remarks. This is the youngest record of Diencobolus, which has previously only been recorded from the late Cambrian (Guzhangian) to the Early Ordovician, Floian (Ghobadi Pour et al. 2011) of Poland, Kyrgyzstan and Iran (Holmer & Popov 2007, p. 2549). It is also the first record from China.

Occurrence in China. Ordovician: Dawan Formation, Cili section (Table 2).

Superfamily DISCINOIDEA Gray, 1840

Family DISCINIDAE Gray, 1840

Discinidae gen. et sp.

Material. 11 dorsal and 4 ventral valves in addition to 2 indeterminate fragments.

Remarks. Species of the Discinidae are usually common and widely distributed in the Ordovician. However, the investigated Chinese faunas are unusual in yielding only a very few fragmentary specimens; they are not possible to identify further.
Occurrence in China. Ordovician: Guniutan Formation, Fenxiang and Maocaopu sections (Tables 2, 3).

Order SIPHONOTRETIDA Kuhn, 1949
Superfamily SIPHONOTRETOIDAE Kutorga, 1848
Family SIPHONOTRETIDAE Kutorga, 1848

Genus NUSHBIELLA Popov in Kolobova & Popov, 1986

Type species. Multispinula dubia Popov, 1977, Ordovician, Darriwilian–Sandbian, Bestamak Limestone, Chingiz range, Kazakhstan.

Nushbiella? sp. Figure 7

Material. 2 dorsal valves.

Description. Dorsal valve gently convex with maximum height about one quarter valve length from the umbo, transverse suboval in outline. Dorsal pseudointerarea vestigial, with narrow median groove. Shallow sulcus originating in the umbonal area, fading anteriorly. Ornament of concentric rugellae and superimposed irregular radial ribs bearing hollow spines of about equal sizes. Dorsal interior lacking diagnostic features.

Remarks. The available material consists only of dorsal valves of Nushbiella? sp. and thus the presence of an internal pedicle tube in the ventral valve cannot be confirmed. However, the characteristic combination of radial and concentric ornament strongly suggests that they belong to this genus. They are rather similar to Nushbiella lillianae Holmer, 1989 from the Ordovician, Darriwilian–Sandbian (lower Dalby and Ryd limestones) of Sweden, but differ in having weaker concentric ornamentation and finer, more sparsely spaced spines.

Occurrence in China. Ordovician: Guniutan Formation, Maocaopu section (Table 3).

Genus ACANTHAMBONIA Cooper, 1956

Type species. Acanthambonia minutissima Cooper, 1956; Ordovician, Darriwilian–Sandbian, Pygodus anserinus Biozone, Pratt Ferry Limestone, Alabama, USA.

Acanthambonia cf. delicata Holmer, 1989 Figure 8

Material. 9 dorsal and 10 ventral valves.

FIG. 7. Nushbiella? sp., Guniutan Formation, Maocaopu section (sample MC87). A, ELI-BO2017-7, dorsal exterior, showing well developed spine-bearing lamellae. B, ELI-BO2017-8, dorsal exterior. C, ELI-BO2017-9, dorsal exterior. D–E, ELI-BO2017-10; D, dorsal exterior; E, detail of the larval shell. F, ELI-BO2017-11, dorsal interior, note the low median ridge. Scale bars represent: 200 µm (A–D, F); 100 µm (E).
Remarks. The Chinese specimens are comparable with *Acanthambonia delicata* Holmer, 1989 from the Darriwilian of Dalarna, Sweden in having a relatively low and broad, crescent-shaped ventral pseudointerarea, a short external and internal pedicle tube tapered anteriorly and sparse evenly spaced hollow spines on the shell surface. The small number of poorly preserved specimens makes closer taxonomic discrimination difficult.

Occurrence in China. Ordovician: Guniutan Formation, Fenxiang section (Table 1).

Order ACROTRETIDA Kuhn, 1949
Superfamily ACROTRETOIDEA Schuchert, 1893
Family ACROTRETIDAE Schuchert, 1893
Genus EURYTRETA Rowell, 1966

Type species. *Acrotreta curvata* Walcott, 1902; Ordovician, Tremadocian, Pogonip Limestone, Eureka district, Nevada, USA.

*Eurytreta ciliensis* (Zhang, 1995)

Figure 9

1995 *Hisingerella ciliensis* Zhang, p. 159, 166, pl. 1, figs 7–11.

*Holotype.* NIGP 2049, dorsal valve, Ordovician, Darriwilian–Sandbian, *Pygodus anserinus* Zone, Datianba Formation (sample Sc77), Cili section, Hunan Province, China.

Material. 67 dorsal and 72 ventral valves.

Description. Shell rounded, transversely oval, 90–95% as long as wide; ventral valve invariably fragmented, but high conical with maximum height at the umbo; deltoid pseudointerarea apsacine poorly defined laterally and slightly curved posteriory in the umbonal region; profile of anterior and lateral slopes of the valve gently convex; pedicle foramen placed within larval shell, lacking external pedicle tube; dorsal valve very gently convex with narrow subtriangular pseudointerarea occupying about 40% of the maximum valve width, divided by shallow median groove occupying more than half of its width; ventral interior with long elongate subtriangular apical process anterior to internal foramen; dorsal interior with low median ridge extending anteriorly about 70% of maximum sagittal valve length, buttressed posteriorly; dorsal cardinal muscle scars, large, strongly impressed, elongate suboval in outline diverging anteriorly, bordered by strong bounding ridges.

Remarks. Originally this species was referred to *Hisingerella*, however it possesses a well-developed elongate subtriangular apical process and low dorsal median ridge instead of having a blade-like triangular septum as seen in species of *Hisingerella* (e.g. Holmer & Popov 2000, p. 112). The morphology of the median ridge and ventral

**Fig. 8.** *Acanthambonia cf. delicata* Holmer, Guniutan Formation, Fenxiang section (A–C, sample FC28; D, E, sample FC29). A, ELI-BO2017-12, ventral exterior. B, detail of pustular ornamentation of A. C, ELI-BO2017-13, dorsal exterior. D, ELI-BO2017-14, ventral interior, showing the pustular ornament. E, ELI-BO2017-15, posterior view of dorsal valve, showing flexure lines of the pseudointerarea. Scale bars represent: 200 μm (A, C–E); 50 μm (B).
valve is also closely similar to species of *Eurytreta*. The most current information on this taxonomically difficult genus was summarized by Popov & Holmer (1994, p. 95), Holmer et al. (2001, p. 88), and Hansen & Holmer (2011, p. 53). The closest of the known species is *Eurytreta minor* Biernat, 1973 (see also Popov & Holmer 1994; Holmer & Biernat 2002), from the Tremadoc of Poland and Kazakhstan (Holmer et al. 2001) which is characterized by a closely similar external shape; both species have a procline subconical ventral valve, narrow triangular dorsal interarea and low median ridge transforming into a very low triangular median septum in the gerontic specimens. However, *Eurytreta ciliensis* can be distinguished from that species in having a well-developed, subtriangular apical process typical of the most species of the genus, large elongated dorsal cardiac muscle scars and completely lacking an external pedicle tube.

**Occurrence in China.** Ordovician: Gunuiutan Formation, Cili and Maocaopu sections; Datianba Formation, Maocaopu section (Tables 2, 3).
Genus CYRTONOTRETA Holmer, 1989

Type species. Conotreta depressa Cooper, 1956; Ordovician, Darriwilian–Sandbian, Pygodus anserinus Biozone, Pratt Ferry Limestone, Alabama, USA.

Cyrtonotreta sp. Figure 6P

Material. 21 dorsal and 1 ventral valves.

Remarks. The Chinese specimens have a characteristic well-defined dorsal pseudointerarea and most likely represent Cyrtonotreta. The small number of poorly preserved specimens makes closer taxonomic discrimination difficult.

Occurrence in China. Ordovician: Guniutan Formation, Fenxiang section (Table 1).

Family TORYNELASMATIDAE Rowell, 1965

Genus TORYNELASMA Cooper, 1956

Type species. Torynelasma toryniferum Cooper, 1956; Ordovician, Darriwilian–Sandbian, Pygodus anserinus Biozone, Pratt Ferry Limestone, Alabama, USA.

Torynelasma sinensis Zhang, 1995 Figure 10

1995 Torynelasma sinensis Zhang, p. 159, 166, pl. 2, figs 5–8.

Holotype. NIGP 2042, dorsal valve, Ordovician, Microzarkodina ozarkodella Subzone, Guniutan Formation (sample Sc60), Cili section, Hunan Province, South China.

Material. 1726 dorsal and 1304 ventral valves, and 25 complete articulated shells.

Description. Shell transversely suboval, about 80–85% as long as wide; ventral valve conical about 80% as high as wide with highest point slightly anterior to the pedicle foramen; profile of anterior and lateral slopes evenly convex; deltoid pseudointerarea procline to catacline, planar, undivided; dorsal valve very gently convex with maximum height at the umbonal area; dorsal pseudointerarea straight, about 60% as wide as the valve; median plate very weakly defined; ventral interior with very short internal pedicle tube and almost rudimentary apical process; dorsal interior with high surmounting plate, buttressed posteriorly; platform slightly concave in lateral and transverse profile, gradually widening distally; cardinal muscle scars large, elongate suboval extending to mid-valve.

Measurements. See Zhang (1995, p. 159).

Remarks. Torynelasma sinensis is by far the most abundant species (more than 40% of the total number of specimens) in the investigated sections. As noted by Zhang (1995), Torynelasma sinensis is closely similar in most important characters to the much less common Torynelasma suecicum Holmer, 1989, from the Darriwilian Ryd Limestone of Västergötland, Sweden. The Chinese species differs from the Swedish, in having the following characters: (1) a high conical shell with height of valve up to 80% of maximum valve width (as compared with less than half the width); (2) a more straight and less recurved lateral profile of the ventral umbonal area (as compared with a recurved and depressed profile); (3) a very rudimentary apical process, which forms an indistinct thickening anterior to the internal pedicle tube (as compared with a very strong and forked ridge-like apical process); and (4) an unusually robust, and strongly developed, raised dorsal median buttress (as compared with a low dorsal median buttress). As noted by Holmer (1989, p. 109) the detailed morphology of the ventral valve of the type species Torynelasma toryniferum Cooper, is poorly understood, but the American species has a higher and considerably longer dorsal median septum, with a convex anterior profile (Holmer & Popov 2000, fig 66.1). The Darriwilian Torynelasma papillosum Krause & Rowell, 1975, from Meiklejohn Peak, Nevada (USA) has a distinctive flattened dorsal valve and papillose ornamentations that are lacking from both the Swedish and Chinese species; whilst the Darriwilian Torynelasma takakaea Percival in Percival et al., 2009, from Thompson Creek, New Zealand has the highest ventral valve known within the genus. The Chinese species also differs from the Darriwilian Torynelasma zhetysuicum Popov et al. in Nikitin et al., 2006 from Kazakhstan, mainly in having a folded anterior margin of the dorsal median septum, which is much higher and has a more widely triangular upper surmounting plate as that of Torynelasma sinensis.

Occurrence in China. Ordovician: Dawan and Guniutan formations, Fenxiang section; Guniutan and Datianba formations, Cili and Maocaopu sections (Tables 1–3).

Genus SASYKSORIA Popov & Holmer, 1994

Type species. Sasyksoria rugosa Popov & Holmer, 1994; Ordovician, Floian–Dapingian, Olenty Formation, Sasyksor Lake, Kazakhstan.

Sasyksoria abnormis (Zhang, 1995) Figure 11A–F

1995 Torynelasma? abnormis Zhang, p. 160, 167, pl. 2, figs 1–4.
**FIG. 10.** *Torynelasma sinensis* Zhang, Guniutan Formation, Fenxiang section (C–D, H–I, sample FC30-1), and Datianba Formation, Maocaopu section (A, B, E–G, J, sample MC4). A, ELI-BO2017-20, lateral view of conjoined shell valves. B, ELI-BO2017-21, lateral view of ventral exterior. C, ELI-BO2017-22, posterior view of ventral exterior. D, ELI-BO2017-23, larval shell of ventral valve, showing the boundary of the post-larval shell. E, ELI-BO2017-24, ventral interior, showing the pedicle foramen. F, G, ELI-BO2017-25; F, dorsal interior, showing well developed surmounting plate; G, lateral view. H–I, ELI-BO2017-26; H, enlargement of pseudointerarea; I, dorsal interior. J, ELI-BO2017-27, detail of pitting on dorsal larval shell. Scale bars represent: 500 μm (A–C, E–G, I); 50 μm (D, J); 200 μm (H).
**Holotype.** NIGP 2045, dorsal valve, Ordovician, Microzarkodina hagetiana Subzone, Guniutan Formation (sample SC36), Cili section, Hunan Province, South China.

**Material.** 10 dorsal and 5 ventral valves.

**Description.** Shell transversely suboval, about 70–80% as long as wide; ventral valve conical about 60–70% as high as wide with highest point slightly anterior to the pedicle foramen; anterior and lateral ventral slopes evenly convex in cross section; deltoid pseudointerarea procline to catacline, planar, undivided; dorsal valve evenly convex with straight pseudointerarea, occupying about 70% of maximum valve width; ventral interior with internal pedicle tube supported anteriorly by ridge-like apical process; dorsal interior with high triangular septum, with highest point about mid-valve, buttressed posteriorly; dorsal septum with strong upper septal rod and occasionally with spines along anterior slope; dorsal cardinal muscle scars elongate suboval, occupying up to half of maximum valve length.

**Measurements.** See Zhang (1995, p. 160).

**Remarks.** This species was referred conditionally to Torynelasma by Zhang (1995), but the lack of a surmounting platform on the dorsal septum, which is typical of Torynelasma, has led to the re-assignation to Sasyksoria. This is only the second known species of the genus, and it differs from Sasyksoria rugosa Popov & Holmer, 1994, from the Ordovician (Floian–Dapingian) Olenty Formation of north-central Kazakhstan in having a smooth shell that lacks the growth lamellae of the type species and, unlike the Kazakh species, the ventral pseudointerarea is undivided, whereas there is a distinct interridge in the type species; moreover Sasyksoria abnormis has a septal rod and occasional spines on the dorsal triangular median septum, whereas the septum of Sasyksoria rugosa is simple and triangular. There is a distinct similarity between Chinese species and the dorsal valves described by Biernat (1973, pl. 7, fig. 1 and pl. 8, fig. 1) under the name Paratreta similis from the Darriwilian of north-eastern Poland. However, the ventral valve attributed to the Polish species and chosen as holotype possesses a distinct external pedicle tube that has never been recorded in torynelasmatids. It is likely that Paratreta similis may represent an amalgam of two different acrotretid taxa belonging to different families and therefore precise taxonomic distribution of dorsal valves of Paratreta similis remains uncertain (see also Holmer & Popov 2000, p. 236), Biernat & Harper (1999, p. 85) and Percival et al. (2011, p. 490) questioned the affinity of Sasyksoria with the Torynelasmatidae due to the lack of a surmounting platform on the dorsal median septum; however, the characteristic shape of the ventral valve and very wide dorsal pseudointerarea still warrants keeping Sasyksoria within this family. Moreover, it was argued by Percival et al. (2011) that the lamellose

**FIG. 11.** Sasyksoria abnormis (Zhang), Guniutan Formation, Cili section (A–D, F, sample SC27; E, sample SC36). A, B, ELI-BO2017-28; A, lateral view of ventral exterior; B, posterior view of ventral exterior. C, D, ELI-BO2017-29; C, dorsal exterior; D, lateral view of dorsal interior, showing the high median septum. E, F, ELI-BO2017-30; E, dorsal interior; F, anteriorly lateral view of dorsal interior. All scale bars represent 200 μm.
Measurements. See Zhang (1995, p. 163).

tum bearing single strong upper septal rod.

cardinal muscle field and a high, blade-like triangular median sep-
margin of internal foramen; dorsal interior with weakly impressed
rior with small ridge-like apical process bifurcating near anterior
curved in cross section and with fine concentric fila; ventral inte-
shell with up to eight regularly spaced strong growth lamellae,
pseudointerarea low, with wide, lens-like median grove; postlarval
convex recurved umbonal area, weakly sulcate anteriorly; dorsal
valve flat with
tral umbo close to marginal; pedicle foramen relatively small, sub-
defined laterally, but divided by broad, shallow intertrough; ven-
with slightly procline to almost catacline pseudointerarea, poorly
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Occurrence in China. Ordovician: Guniutan Formation, Cili sec-
tion (Table 2).

Family SCAPHELASMATIDAE Rowell, 1965

Genus SCAPHELASMA Cooper, 1956

Type species. Scaphelasma septatum Cooper, 1956; Ordovician, Darriwilian–Sandbian, Pygodus anserinus Bio-
zone, Pratt Ferry Limestone, Alabama, USA.

Scaphelasma afflata Zhang, 1995

Figure 12

1995 Scaphelasma afflata Zhang, p. 163, 168, pl. 5, figs 1–6.

2006 Scaphelasma afflata Zhang; Popov et al. in Nikitina
et al., p. 170, fig. 20.1:3–5.

Holotype. NIGP 2074, dorsal valve, Ordovician, Yangtzeplacognathus protoramosus Zone, Datanba Formation (sample Sc69),
Cili section, Hunan Province, South China.

Material. 352 dorsal and 205 ventral valves, and 18 complete articulated shells.

Description. Shell strongly transverse suboval about 70–75% as
long as wide; ventral valve conical about 20–40% as high as wide,
with slightly procline to almost catacline pseudointerarea, poorly
defined laterally, but divided by broad, shallow intertrough; vent-
ral umbo close to marginal; pedicle foramen relatively small, sub-
circular touching border of larval shell; dorsal valve flat with
convex recurved umbonal area, weakly sulcate anteriorly; dorsal
pseudointerarea low, with wide, lens-like median grove; postlarval
shell with up to eight regularly spaced strong growth lamellae,
curved in cross section and with fine concentric fila; ventral inte-
rior with small ridge-like apical process bifurcating near anterior
margin of internal foramen; dorsal interior with weakly impressed
cardinal muscle field and a high, blade-like triangular median seps-
tum bearing single strong upper septal rod.

Measurements. See Zhang (1995, p. 163).

Remarks. This species has recently been described from
the Darriwilian of Kazakhstan by Nikitina et al. (2006),
who also provided a detailed comparative discussion.

Percival et al. (2009, p. 627) most recently compared the
known Ordovician members including Scaphelasma afflata,
with Scaphelasma paturauensis from the Darriwilian of
Thompson Creek, New Zealand (see also Hansen & Hol-
mer 2011, Holmer et al. 2016; Percival et al. 2016). As
noted by Nikitina et al. (2006), the strongly lamellose
Scaphelasma afflata is most similar to Scaphelasma rugosum
Gorjansky (Holmer, 1989) from the mid-Darriwilian of
Baltoscandia, and Scaphelasma lamellosum Krause & Row-
ell, 1975 from the Darriwilian of Meiklejohn Peak, Nevada
(USA), but the Chinese species differs from both species in
having a more transverse shell outline, and a smaller pedi-

cle foramen that only touches the posterior border of the
larval shell; Scaphelasma afflata also has a much strongly
developed and almost plate-like upper septal rod.

Occurrence in China. Ordovician: Guniutan and Datianba for-

cations, Cili and Maocaopu sections (Tables 2, 3).

Scaphelasma mica Popov, 1975.

Figure 13

1975 Scaphelasma mica Popov, p. 39, pl. 5, figs 21–30.

1989 Scaphelasma mica Popov; Holmer, p. 139, figs 36, 47f,
90d–n, 100, 101h–k, 103a–e, 104 (full synonymy).

1995 Scaphelasma hunanensis Zhang, pp 163, 167, pl. 4,
figs 6–10.

Holotype. CNIGR 28/10696, complete shell; Ordovician, Sand-
bian (Nemagraptus gracilis Biozone), lower Bestamak Formation,
Chingiz Range, Kazakhstan.

Material. 179 dorsal and 51 ventral valves and 25 complete
articulated shells.

Description. See Holmer (1989, p. 139).

Remarks. Comparison with the well-known Darriwilian–
Sandbian Baltic and Kazakhstanian specimens of Scaphe-
lasma mica (see Holmer 1989, p. 139) shows that Chinese
specimens described under the name Scaphelasma hunanen-
sis are well within the limits of observed variations in shell
morphology, including general shell shape, and height and
morphology of the dorsal median septum. Holmer (1989)
provided a detailed comparative discussion of the closely
related species known at the time and Percival et al. (2009,
p. 627) more recently included a comparative discussion of
the known Ordovician members, including Scaphelasma
mica, with Scaphelasma paturauensis from the Darriwilian of
Thompson Creek, New Zealand (see also Hansen & Holmer
2011, Holmer et al. 2016; Percival et al. 2016). Scaphelasma
cf. mica has also been described from the Darriwilian, Fac-
tory Cove Member, Newfoundland (Robson & Pratt 2001).
Occurrence in China. Ordovician: Guniutan Formation, Fenxiang section; Dawan, Guniutan and Datianba formations, Cili section (Tables 1, 2).

Genus EOSCAPHELASMA Koneva et al. in Koneva et al., 1990

Type species. Eoscaphelasma satpakensis Koneva et al. in Koneva et al. 1990; upper Cambrian, Furongian, Kujandy Formation, Kazakhstan.

Material. 59 dorsal and 88 ventral valves, and 3 complete articulated shells.

Description. Shell transversely suboval about 60–70% as long as wide; ventral valve extremely low conical about 10–20% as high...
as wide with extremely poorly defined, procline pseudointerarea, poorly defined laterally, but divided by broad, shallow poorly defined intertrough; pedicle foramen relatively small, marginally placed within border of larval shell; dorsal valve strongly flattened with slightly convex recurved umbonal area, weakly sulcate anteriorly; dorsal pseudointerarea vestigial, low, with wide, extremely poorly defined median groove; postlarval shell with up to four regularly spaced marginal growth lamellae, and with fine concentric fila; ventral interior lacking well defined characters, only with very slight indication central low apical process; dorsal interior lacking well defined characters.

**Remarks.** *Eosphantasma?* sp. differs from the known species of the genus (see e.g. Popov & Holmer 1994, p. 129) in having a marginal pedicle foramen inside the larval shell. It is not closely comparable with any known species apart from an unnamed problematic scaphelasmid described by Percival *et al.* (2011, p. 490) from the Darriwilian of New Zealand. The species from New Zealand also has a very low conical shell with the pedicle foramen that does not cut across the larval shell. However, the foramen in the Chinese species is marginal and the lamellose ornamentation is less well developed. As noted by Percival *et al.* (2009, 2011, 2016) the species of the Scaphelasmatidae (including the Chinese scaphelasmid material, including *Eosphantasma?* sp.) commonly have a characteristic microstructure with ‘radial rods and slots’. This is a variety of the camerate acrotretoid shell structure as defined by Holmer (1989, p. 31; see also Williams
Holmer (1992); Ushatinskaya (1996, fig. 1) further redefined the type of camerate shell structure exhibited by many species of the Scaphelasmatidae as septate. Holmer (1989, p. 47) noted that although this type of structure is found in many species of the Scaphelasmatidae, it has also been illustrated from other taxa (cf. e.g. Poulsen 1971, fig. 4; Williams & Holmer 1992, pl. 2, fig. 2); the septate form clearly grades into the columnar type of shell structure in some specimens (Holmer 1989, fig. 36) and the detailed taxonomic distribution of this shell structure needs to be further investigated.

Occurrence in China. Ordovician: Dawan Formation, Maocaopu section (Table 3).
Family **EPHIPPELASMATIDAE** Rowell, 1965

Genus **EPHIPPELASMA** Cooper, 1956

*Type species.* *Ephippelasma minutum* Cooper, 1956; Ordovician, Darriwilian–Sandbian, *Pygodus anserinus* Biozone, Pratt Ferry Limestone, Alabama, USA.

**Ephippelasma minutum** Cooper, 1956

**Figure 15**

1956 *Ephippelasma minutum* Cooper, p. 261, pl. 17A, figs 1–14.
1989 *Ephippelasma minutum* Cooper; Holmer, p. 131, pl. 13, figs 6–7, pl. 15, figs 1–5.
1995 *Ephippelasma minutum* Cooper; Zhang, p. 160, pl. 2, figs 9–11, pl. 3, fig. 1.
2000 *Ephippelasma minutum* Cooper; Holmer & Popov, fig. 68.3a–e.

**Holotype.** USNM 116821a, complete articulated shell, Ordovician, Darriwilian–Sandbian, *Pygodus anserinus* Biozone, Pratt Ferry Formation, Alabama, USA.

**Material.** 15 dorsal and 22 ventral valves.

**Remarks.** The rare Chinese material of *Ephippelasma minutum* appears to differ slightly from the American type material (Holmer & Popov 2000, fig. 68.1a–h) mainly in that the ventral valve is somewhat less conical. Moreover, the dorsal median septum appears to be somewhat higher and extends closer to the anterior margin as compared with the type material. However, the differences are not considered to be large enough to warrant the naming of a new species. As noted by Holmer et al. (2016), it is most similar to the coeval *Ephippelasma intutum* Popov, 1975 from the Darriwilian of Kazakhstan. More recently Engelbreten (in Percival et al. 2016, p. 475) described closely similar material of *Ephippelasma cf. minutum* from the mid-Katian of New South Wales, Australia.

**Occurrence in China.** Ordovician: Datianba Formation, Cili section (Table 2).

Genus **MYOTRETA** Gorjansky, 1969

*Type species.* *Myotreta crassa* Gorjansky, 1969; Ordovician, lower Darriwilian, Kunda Regional Stage, Pechory Core, Pskov, Russia.

**Myotreta crassa** Gorjansky, 1969

**Figure 16**

1969 *Myotreta crassa* Gorjansky, p. 67, pl. 11, figs 10–27.
1973 *Myotreta crassa* Gorjansky; Biernat, p. 81, pl. 13, figs 1–9, pl. 14, figs 6–7, pl. 15, figs 1–5.
1995 *Myotreta crassa* Gorjansky; Zhang, p. 160, pl. 2, figs 9–11, pl. 3, fig. 1.
2000 *Myotreta crassa* Gorjansky; Holmer & Popov, fig. 68.3a–e.

**Holotype.** CNIGR 155/9960, dorsal valve, Ordovician, Kunda Regional Stage, Obukhovo Formation, depth 479.1 m, Pechory Core, Pskov, Russia.

**Material.** 217 dorsal and 261 ventral valves, and 15 complete articulated shells.

**Description.** Shell transversely suboval, 89% as long as wide; ventral valve strongly apsaconical 89% as high as wide with well-defined intertrough and short external pedicle tube; dorsal valve with large, slightly raised cardinal muscle scars and with triangular, weakly folded median septum, extending to mid-valve, and bearing up to two septal rods.

**Measurements.** See Zhang (1995, p. 160).

**Remarks.** The specimens from the Guniutan Formation are closely similar to *Myotreta crassa* Gorjansky from the Obukhovo Formation of the Pskov District (Holmer & Popov 2000, fig. 68.3a–e) in external morphology and size of the shell, as well as in the characters of the weakly folded dorsal median septum with two septal rods; they were regarded as conspecific by Zhang (1995), which is followed here.

**Occurrence in China.** Ordovician: Dawan and Guniutan formations, Cili section; Guniutan and Datianba formations, Mao-caopu section (Tables 2, 3).

**Myotreta aff. dalecarlica** Holmer, 1989

**Figure 17**

1995 *Myotreta aff. dalecarlica* Holmer; Zhang, p. 161, pl. 3, figs 3–6.

**Material.** 118 dorsal and 84 ventral valves, and 3 complete articulated shells.

**Description.** Shell with transverse suboval commissural outline 85% as long as wide; ventral valve low catacline to procline 45% as high as wide, lacking well-defined intertrough; dorsal valve
with large, slightly raised cardinal muscle scars and with triangular, simple low median septum.

**Measurements.** See Zhang (1995, p. 161).

**Remarks.** Myotreta aff. dalecarlica differs from *Myotreta crassa* mainly in being much less conical, and the ventral valve being catacline to procline and lacking both a well-defined intertrench and an external pedicle tube. Moreover, the dorsal median septum is low and simple and lacks well defined septal rods. The bifurcating ventral median septum that is present in *Myotreta dalecarlica* Holmer (1989, fig. 80j) is not observed and following Zhang (1995) the comparatively rare and less widely distributed species is kept in open nomenclature. *Myotreta aff. dalecarlica* is the only species that is restricted to the Guniutan Formation, Cili section.

**Occurrence in China.** Ordovician: Guniutan Formation, Cili section (Table 2).

**Genus NUMERICOMA Popov in Nazarov & Popov, 1980**

**Type species.** *Numericoma ornata* Popov in Nazarov & Popov, 1980; Ordovician, Darriwilian, Karakan Formation, northern Betpak-Dala, Kazakhstan.

**Numericoma spinosa** (Biernat, 1973)

**Figures 18, 19**

1973 *Ephippelasma spinosum* Biernat, p. 96, pl. 23, pl. 24, fig. 9, pls 25–26, text-figs 10, 19a, 35.

1995 *Numericoma spinosa* (Biernat); Zhang: p. 161, pl. 3, figs 8–11 (full synonymy).

**Holotype.** PAN Bp.XV/12z, ventral valve; Ordovician, Darriwilian, borehole Ketrzyn IG-1, depth 1595.5 m, north-eastern Poland.

**Material.** 143 dorsal and 115 ventral valves, and 5 complete articulated shells.

**Description.** Shell transversely suboval, 85–95% as long as wide; ventral valve strongly apsaconical, up to 100% as high as wide, lacking well defined intertrench; dorsal valve with large, slightly raised cardinal muscle scars and with triangular, strongly folded median septum, bilaterally symmetrical, and extending beyond mid-valve, and bearing numerous septal rods.

**Measurements.** See Zhang (1995, p. 161).

**Remarks.** Holmer (1989, p. 127) provided detailed discussion of variable morphology, ontogeny and affinities.
of this species from the Darriwilian of Baltoscandia. The specimens from the Guniutan and Datianba formations fit well within wide limits of morphological variability of the Baltoscandian specimens and were regarded as conspecific by Zhang (1995), which is followed here.

Occurrence in China. Ordovician: Guniutan and Datianba formations, Maocaopu and Cili sections; Dawan and Guniutan formations, Fenxiang section (Tables 1–3).
Material. 119 dorsal and 107 ventral valves and 8 complete articulated shells.

Description. Shell transversely suboval, 70–80% as long as wide; ventral valve strongly apsaconical, up to almost 100% as high as wide, divided by intertrough, with snout-like exterior pedicle tube; dorsal valve with large, slightly raised cardinal muscle scars and with triangular, strongly folded median septum, invariably strongly asymmetrical, and extending beyond mid-valve, and bearing several septal rods.

Measurements. See Zhang (1995, p. 161).

Remarks. Holmer (1989, p. 127) provided detailed discussion of variable morphology, ontogeny and affinities of this species from the Darriwilian of Baltoscandia. The
specimens from the Guniutan Formation fall well within wide limits of morphological variability of the Swedish material and they were regarded as conspecific by Zhang (1995), which is followed here.

Occurrence in China. Ordovician: Guniutan formation, Fenxiang section (Table 1).

Family BIERNATIDAE Holmer, 1989

Genus BIERNATIA Holmer, 1989

Type species. Torynelasma minor rossicum Gorjansky, 1969; Ordovician, lower Darriwilian, Kunda Regional Stage, Pechory Core, Pskov, Russia.

**FIG. 18.** *Numericoma spinosa* (Biernat), Dawan Formation, Fenxiang section (sample FC26). A, ELI-BO2017-54, oblique lateral view of conjoined shell valves. B, ELI-BO2017-55, ventral exterior. C, D, F, ELI-BO2017-56; C, lateral view of dorsal interior; D, anterior view showing the bilaterally symmetrical median septum; F, dorsal interior. E, ELI-BO2017-57, dorsal exterior. G, ELI-BO2017-58, lateral view of ventral exterior. All scale bars represent 200 $\mu$m.
**Biernatia cf. holmi** Holmer, 1989

**Figure 21**

**Material.** 27 dorsal and 48 ventral valves, and 1 complete articulated shell.

**Remarks.** This rare species is mostly represented by fragmented material and a single well preserved complete shell. Although similar to *Biernatia holmi* Holmer, 1989, from the Darriwilian of Sweden, the dorsal median septum cannot be observed in detail in any of the available specimens, which therefore remain in open nomenclature.

**Occurrence in China.** Ordovician: Guniutan Formation, Fenxiang section (Table 1).
**FIG. 20.** *Numericoma perplexa* Holmer, Guniutan Formation, Fenxiang (A, B, G, sample FC50; C, F, sample FC41; D sample FC98; H, I, sample FC30-1). A, B, G, ELI-BO2017-63 4FC-08; A, ventral exterior; B, larval shell; G, lateral view. C, ELI-BO2017-64, lateral view of conjoined shell valves, showing the high median septum of dorsal valve. D, E, ELI-BO2017-65; D, dorsal interior; E, oblique lateral view. F, ELI-BO2017-66, dorsal interior, showing the symmetrical median septum with complex 90° loop. H, I, ELI-BO2017-67; H, dorsal exterior; I, larval shell pitting. Scale bars represent: 200 μm (A, C–H); 50 μm (B); 20 μm (I).
Family EOCONULIDAE Cooper, 1956

Genus EOCONULUS Cooper, 1956

Type species. *Eoconulus rectangulatus* Cooper, 1956; Ordovician, Darriwillian–Sandbian, *Pygodus anserinus* Biozone, Pratt Ferry Limestone, Alabama, USA.

*Eoconulus* cf. *clivosus* Popov, 1975

1989 *Eoconulus* cf. *clivosus* Popov; Holmer, p. 148, figs 38a–b, 39a–h, 105 g–l, 110a–h, 111.

1995 *Eoconulus cuboides* Zhang, p. 164, pl. 5, fig. 7–12.

1995 *Eoconulus* sp. Zhang, p. 164, pl. 5, fig. 13.

2006 *Eoconulus* cf. *clivosus* Popov; Popov *et al.* in Nikitin *et al*., p. 172, figs 18.8–11, 20.2. (full synonymy).

Material. 1568 dorsal and 105 ventral valves and 1 complete articulated shell.

Description. Shell of varying outline, rectangular to close to circular; ventral valve strongly thickened, 60–69% as high as wide, with flattened to irregularly shaped attachment scar; ventral interior usually with well-developed raised apical process; both valves with...
strongly developed, raised cardinal muscle scars; dorsal valve with subcentral umbo and convex outline of slopes of valve, usually somewhat less than half as high as wide.

**Measurements.** See Zhang (1995, p. 34).

**Remarks.** Species of *Eoconulus* are taxonomically very difficult since the outline, shape and many other characters are strongly variable and depend on the shape of the substrate to which the ventral valve was attached. Direct evidence for this has been described by Holmer et al. (2000, fig. 5Z-CC) and Hansen & Holmer (2011, pl. 21, figs 11–13). Comparison with the widely distributed Darriwilian *Eoconulus cf. clivosus* (see Holmer 1989; Nikitina *et al.* 2006) shows that the Chinese specimens described under the name *Eoconulus cuboides* as well as *Eoconulus sp.* are within the wide limits of observed variations in shell morphology of *Eoconulus cf. clivosus*. Holmer (1989, p. 148) and Nikitina *et al.* (2006, p. 172) provided a detailed comparison with the closest known Darriwilian species, *Eoconulus antelopensis* Krause & Rowell, 1975, from the Meiklejohn Peak, Nevada, USA. *Eoconulus puteus* Engelbreten *et al.*., 2016, from the Katian of New South Wales, Australia, is also somewhat similar to *Eoconulus cf. clivosus*, but the Australian species has a much lower ventral valve.

**FIG. 22.** *Eoconulus cf. clivosus* Popov, Guniutan Formation, Fenxiang (A–C, sample FC63; E, G, sample FC30-1; F, sample FC44) and Maoaopu (D, sample MC83; H, sample MC46) sections. A, ELI-BO2017-70, ventral exterior, showing the attachment scar. B, ELI-BO2017-71, ventral interior. C, ELI-BO2017-72, ventral interior. D–G, ELI-BO2017-73; D, dorsal exterior; E, lateral view; F, dorsal exterior, showing the larval shell; G, larval fila ornamentation. H, ELI-BO2017-74, dorsal interior. I, ELI-BO2017-75, dorsal interior. Scale bars represent: 200 μm (A–F, H, I); 50 μm (G).
Occurrence in China. Ordovician: Dawan and Guniutan formations, Fenxiang section; Guniutan and Datianba formations, Cili and Maocaopu sections (Tables 1–3).

Genus UNDIFERINA Cooper, 1956

Type species. Undiferina rugosa Cooper, 1956; Ordovician, Darriwilian–Sandbian, Pygodus anserinus Biozone, Pratt Ferry Limestone, Alabama, USA.

Undiferina sp.

Figure 23

Material. 5 dorsal valves.

Remarks. The five dorsal valves have a rugose ornamentation and shape that indicates that they belong to Undiferina, which is a common genus in the Darriwilian–Sandbian interval globally, but it is not possible to identify them further.

Occurrence. Ordovician: Guniutan Formation, Maocaopu section (Table 3).

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Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.1n4f7

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