POST-METAMORPHIC ALLOMETRY IN THE EARLIEST ACROTRETOID BRACHIOPODS FROM THE LOWER CAMBRIAN (SERIES 2) OF SOUTH CHINA, AND ITS IMPLICATIONS

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Abstract: The earliest growth of post-metamorphic (post-larval) shells in two species of Eohadrotreta is described from the Cambrian Shuijingtuo Formation of South China. Two different growth patterns can be observed by quantifying developmental variations in size and shape of successive stages of post-metamorphic shell growth (including the pedicle foramen forming stage, pedicle foramen enclosing stage and intertrough increasing stage) of Eohadrotreta zhenbaensis and Eohadrotreta zhujiahensis. The pedicle foramen is never enclosed within the metamorphic shell of E. zhenbaensis, while the enclosed pedicle foramen of E.? zhujiahensis is located directly outside the metamorphic shell after the pedicle foramen enclosing stage. A strongly allometric growth pattern of E. zhenbaensis is demonstrated by the early enclosure of the pedicle foramen; an accelerated lengthening of the ventral intertrough is associated with the development of a more complex dorsal median septum during the intertrough increasing stage. By contrast, E.? zhujiahensis demonstrates possible paedomorphic development by delayed enclosure of pedicle foramen and an associated decreased lengthening of ventral intertrough during the intertrough increasing stage. This ontogenetic developmental sequence represents the marginal accretionary formation and growth of the pedicle foramen, which resembles that of linguloid brachiopods. Furthermore, the developmental process of the pedicle foramen of Eohadrotreta seems to recapitulate the likely evolutionary transition from the Botsfordiidae, with open delthyrium, to the Acrotheloidea, with an enclosed foramen. This study provides a unique opportunity to obtain a complete understanding of the ontogenetic development of the earliest acrotetoids, and casts new light on the phylogeny of lingulate brachiopods.

Key words: ontogeny, allometry, acrotretoid brachiopods, Eohadrotreta, heterochrony, lower Cambrian.

Brachiopods first appeared during the early Cambrian (Stage 2), and rapidly became one of the most important components of Palaeozoic marine communities. The excellent fossil record of the group highlights their diversity, abundance and long evolutionary history (Sepkoski 1981; Holmer & Popov 1996; Bassett et al. 1999; Zhang et al. 2008; Zhang et al. 2016a). The acrotetoid brachiopods reached their maximum diversity significantly later than the linguloids, which dominated the earliest Cambrian brachiopod palaeocommunities (Bassett et al. 1999, 2002; Williams et al. 2000; Zhang et al. 2008; Ushatinskaya 2010). However, even from their relatively later Cambrian (Stage 4) divergence, they rapidly became abundant and attained a cosmopolitan distribution in rocks of mid-Cambrian to Ordovician age (Bassett et al. 1999; Holmer & Popov 2000; Ushatinskaya 2010). The rapid divergence and early representatives of the mostly micromorphic acrotetoids are still poorly understood (Holmer & Popov 2000; Topper et al. 2013) and require further study in order to improve our knowledge of ontogeny in different brachiopod clades during their long, rich history. Although the acrotetoids exhibit numerous important characters, like a columnar shell structure, a simplified muscle system, a pitted metamorphic shell (larval shell), a developed ventral apical process and an elevated dorsal median septum, it has so far been difficult to...
analyse their phylogenetic relationship with other groups within the Class Lingulata (Holmer & Popov 2000). Since the acrotretoids went extinct by the end of the Devonian period, their origin, earliest evolution and ontogeny are still poorly known, and can be examined only based on the fossil record. The main hypothesis on how acrotretoids attained their conical-tubular morphology of the ventral valve implies that they in effect are, 'rolled-up' linguloids, in which the posterior margin of a ventral linguloid valve formed the conical valve, the reduced ventral proparea partly formed the intertrough, and the acrotretoid pedicle foramen essentially formed from the linguloid pedicle groove (Popov 1992; Holmer & Popov 2000). However, this hypothesis needs further testing based on detailed ontogenetic studies.

Rudwick (1968) constructively proposed the main analytic methods for the study of ontogeny in fossils with accretionary growth. He concluded that descriptions of morphology should recognize the dynamic character of preserved structures as embodying a sequence of previous growth stages. Moreover, the varying body size and variable morphology during ontogeny is vital for understanding how heterochronic processes may relate to evolutionary change (Beecher 1891; Gould 1966; Rudwick 1968; Klingenberg 1998). The study of ontogeny offers the opportunity to observe varying morphology with increasing size and facilitates the recognition of divergence or convergence of characters during ontogenetic development (Baker & Carlson 2010; Baker & Logan 2011). Thus, detailed studies of ontogenetic development are needed in order to investigate the evolutionary and phylogenetic relationships of fossil brachiopods, and to understand the functional changes of different structures during different developmental stages. However, poorly preserved fossil material often limits the detailed ontogenetic studies, hindering our ability to identify major adaptive innovations from many taxa, especially stem groups (Balthasar 2004, Murdock et al. 2012). In that sense, the discovery of successive ontogenetic sequences is vital to study the dynamic structures, growth pattern, function changes and phylogeny of extinct brachiopods.

_Eohadrotreta zhenbaensis_ and _Eohadrotreta? zhujiahensis_ were first described by Li & Holmer (2004) from the Shuijingtuo and Guojia Formation of the Three Gorges area, South China, where the two species do not co-occur. Subsequently, _Eohadrotreta?_ has been recorded from early Cambrian strata in South China (Wang et al. 2010; Broce et al. 2014; Yang et al. 2015; Zhang et al. 2016b, c), the Himalayan region (Popov et al. 2015) and Australia (Betts et al. 2017). However, the detailed ontogeny of the two species was not studied by Li & Holmer (2004). A study of the earliest ontogeny and first developmental characters, shell secretion transitions, morphological and functional changes during the earliest developmental stage of both species is still in preparation and is outside the scope of this paper (ZLZ, L.E. Popov, LEH & ZFZ, unpub. data). The object of this study is to provide a detailed account of the later post-metamorphic ontogeny of _E. zhenbaensis_ and _E.? zhujiahensis_ from the Shuijingtuo Formation of the Three Gorges area, South China, which are some of the oldest known acrotretoid (Class Lingulata) brachiopods. The two species were first shown to co-occur in South China (Zhang et al. 2016b, c) and the differences in ontogenies described here may indicate that they represent two different genera, but this requires further study.

**MATERIAL AND METHOD**

Most of the specimens described here were collected from the Shuijingtuo Formation at the Aijiahe section, and some others from the Shuijingtuo Formation at the Wangjiaping section in the Three Gorges area of the Yangtze Platform, South China (Fig. 1A, B). At the Aijiahe section (30° 44′ 55.2″ N, 111° 03′ 58.5″ E), the Precambrian–Cambrian stratigraphic succession is particularly well exposed along the Yangtze River, comprising the Dengying Formation, Yanjiahe Formation, Shuijingtuo Formation, Shipai Formation and Shilongdong Formation in ascending order (Fig. 1C, D). The geological setting of the study areas was described in detail by Zhang et al. (2016b, c). To date, 75 complete conjunct valves, 2536 ventral and 2517 dorsal disarticulated valves of _E. zhenbaensis_, and 23 complete conjunct valves, 102 ventral and 115 dorsal disarticulated valves of _E.? zhujiahensis_ have been collected from the middle and upper part of the Shuijingtuo Formation (Fig. 1D). All specimens are deposited in the Early Life Institute, Northwest University (ELI), Xi’an, China.

The specimens from limestones were etched in a solution of 7% concentrated acetic acid, 63% water and 30% buffering solution formed after the dissolution of previous samples to avoid chemical damage, as proposed by Jeppsson et al. (1985). Scanning electron microscope (SEM) images of uncoated fossils were taken with a Philips Fei Quanta 400-PEG with 20 kV and 70–80 Pa at State Key Laboratory of Continental Dynamics, Northwest University, Xi’an. Some uncoated specimens were taken to Sweden and SEM imaging was carried out with a Zeiss Supra 35 VP field emission with 5 kV at the Evolutionary Biology Centre of Uppsala University.

A full morphometric analysis would be useful for the study of acrotretoid ontogeny. However, this is outside the scope of this paper, but it is part of a forthcoming morphometric study, based on more abundant mature specimens from different depositional environments that we are currently working on.
FIG. 1. Fossil localities, simplified geological map and early Cambrian stratigraphy of the Three Gorges area, South China. A, map showing the study area (box) on the northern Yangtze Platform. B, geographical map, showing the fossil localities in the Three Gorges area, Yichang, western Hubei province, China. C, geological map of Cambrian strata along the Huanglin anticline in the Three Gorges area, showing the Aijiahe and Wangjiaping sections (stars). D, stratigraphical column of the Lower Cambrian at the Aijiahe section, showing the stratigraphic horizon of acrotretoid *Eohadrotreta*. Colour online.
The umbo of both valves of all known acrotretoid brachiopods has a well-defined and most commonly pitted shell that is delineated by a distinctive interruption in growth (i.e. the ‘halo’ below) that has been most frequently referred to as the ‘larval shell’ (see, e.g. Holmer 1989; Williams & Holmer 1992; Holmer & Popov 2000). However, Ushatinskaya (2016) first recognized that the so-called ‘larval shells’ of some Siberian Cambrian acrotretoids preserve clear evidence of two pairs of distinctive lobes that are identical in size and position to setal lobes that are now well known from a wide range of organo-phosphatic linguliforms, craniiforms and rhyynchonelliforms (e.g. Williams et al. 1998; Popov et al. 2007; Balthasar 2009; Ghobadi Pour et al. 2011; Ushatinskaya 2016). The earliest ontogenies of the two species of *Eohadrotreta* discussed in this paper are still undergoing study (ZLZ, L.E. Popov, LEH & ZFZ, unpub. data), but following Popov et al. (2007, 2010) and Bassett & Popov (2017), the presence of these structures indicates that the previously termed acrotretoid ‘larval shell’ actually formed at the end of the acrotretoid metamorphosis, which involved the shedding of the larval setae (Lüter 2001), associated with a fundamental change in shell secretion and the development of adult marginal setae; this area is delineated by an interruption in growth marked by the halo, and we here suggest that the term ‘larval shell’ should be replaced by ‘metamorphic shell’ (Popov et al. 2009, 2012; Ghobadi Pour et al. 2011; Bassett & Popov 2017) in acrotretoid brachiopods.

The terms adopted in this paper are intended primarily to describe the stages in shell development and growth of post-metamorphic shell (post-larval shell) of acrotretoid brachiopod *Eohadrotreta* (Fig. 2) (see, e.g. Williams & Holmer 1992; Holmer & Popov 2000; Li & Holmer 2004). The area outwards from the metamorphic shell and halo is here referred as the ‘post-metamorphic shell’, characterized by the development of concentric growth lines or lamella (Fig. 2D). Such ornaments can be identified as ‘adult’ surface features to distinguish adult individuals of different taxa.

**RESULTS**

In living lingulid brachiopods, the major features of ontogenetic stages have already been well investigated (Yatsu 1902; Paine 1963; Chuang 1977). However, comparable detailed studies of the early ontogenies from fossil taxa are more problematic (e.g. Williams et al. 1998; Freeman & Lundelius 2005; Popov et al. 2007, 2009; Hints et al. 2013). The ontogeny of *Eohadrotreta zhenbaensis* can be best understood by the recognition of certain significant morphological transitions during the post-metamorphic increase of valve size, and these are more easily recognizable in the ventral valve (Figs 3–6). This ontogenetic development sequence is here empirically divided into the following three stages: (T1) the pedicle foramen forming stage (Figs 3A–D, 4A–I); (T2) the pedicle foramen enclosing stage (Figs 3E–G, 4J–L); and (T3) the intertrough increasing stage (Figs 3H–I, 4M–O), which are defined by the characteristic development of the ventral pedicle foramen and intertrough. The significant changes during the three ontogenetic developmental stages are described below. Measurements of the ventral and dorsal valves, which were made in most the complete specimens, are tabulated in Zhang et al. (2017, appendix S1, S2).

A comparable ontogenetic sequence of *Eohadrotreta zhujiahensis* is easily recognizable in the ventral valve during the post-metamorphic increase of valve size (Figs 7–10). The ontogeny of *E. zhujiahensis* can also be subdivided into the same three stages of ontogenetic development, including the pedicle foramen forming stage (T1) (Figs 7A–F, 8), the pedicle foramen enclosing stage (T2) (Fig. 7G, H) and the intertrough increasing stage (T3) (Figs 7I, 9A–G). Significantly, development variations in size and related shape can be clearly discriminated during the three ontogenetic developmental stages, described below. Measurements of the ventral and dorsal valves, which were made in most the complete specimens, are tabulated in Zhang et al. (2017, appendix S3, S4).

**Eohadrotreta zhenbaensis**

*Eohadrotreta zhujiahensis* has a ventribiconvex and subcircular to transversely oval shell, with a rounded to straightened posterior margin (Figs 3–6; Zhang et al. 2017, appendix S1, S2). The ventral pseudointerarea varies from almost catacline to procline, divided by a narrow elongate intertrough (about 116 µm long). The length of ventral valve is about 710 µm, varying from 361 µm to 1689 µm. The ventral valve is widely conical, on average 84% as long as wide and 30% as high as long. The pedicle foramen is oval, about 67 µm long and 65 µm wide. The apical process forms a tongue-shaped mound with a depression in the middle, and it occupies on average 27% of the maximum shell length. The ventral cardinal muscle scars are pronounced, occupying about 18% of the shell length and 54% of the shell width. The dorsal valve is relatively flat in lateral view, on average 85% as long as wide and 16% as high as long. The dorsal pseudointerarea remains orthocline throughout ontogeny. The median septum is well developed, extending beyond mid-valve, to about 64% of the valve length. The dorsal cardinal muscle scars are pronounced, occupying about 26% of the valve...
length, and 54% of the valve width. A more detailed description of the ontogeny is given below.

Eohadrotreta? zhujiahensis

The general morphology of *E.? zhujiahensis* is very similar to that of *E. zhenbaensis*, but as shown below they are characterized by significant differences in ontogeny (Figs 7–10; Zhang et al. 2017, appendix S3, S4). The ventral pseudointerarea of *E.? zhujiahensis* is almost catacline, divided by a slightly wider but short intertrough (about 51 µm long). The average length of ventral valve is 715 µm, with variations from 360 µm to 1617 µm. The ventral valve is cap-like, on average 83% as long as wide and 28% as high as long. The metamorphic shell is clearly elevated above the shell surface. The comparatively large pedicle foramen is about 92 µm long and 84 µm wide, with an average length–width ratio of 109%. The tongue-like apical process encircles the pedicle foramen, occupying on average 30% of valve length. The ventral cardinal muscle scars are weakly developed, occupying about 15% of shell length and 61% of shell width. The dorsal valve is about 82% as long as wide and 17% as high as long. The dorsal pseudointerarea remains orthocline throughout ontogeny. The median septum is weakly developed, extending posterior to mid-valve to about 25% of the valve length. The dorsal cardinal muscle scars are well developed, occupying about 22% of valve length and 51% of valve width. The very similar outline and general statistic data between *E.? zhujiahensis* and *E. zhenbaensis* may hide the essentially different growth patterns. However, significant variations can be clearly discriminated between them during different ontogenetic developmental stages described below.

**Pedicle foramen forming stage (T1)**

Eohadrotreta zhenbaensis. The metamorphic ventral valve is not perforated by a foramen; instead the posteromedian ventral margin is indented by a pedicle notch. This represents an incipient pedicle opening that takes the shape from the unrestricted notch between the ventral and
The ontogenetic development sequence of *Eohadrotreta zhenbaensis* from the Cambrian (Series 2) Shuijingtuo Formation in the Three Gorges area, South China. A–D, conjunct valves demonstrating the pedicle foramen forming stage (T1) with opening pedicle foramen, posterior view; A, ELI-AJH-S05-N023; B, ELI-AJH-8-2-1-AD2-013; C, ELI-AJH-8-2-1-AD2-011; D, ELI-AJH-8-2-1-ac2-1-106. E–G, conjunct valves demonstrating the pedicle foramen enclosing stage (T2) with enclosing pedicle foramen, posterior view; E, ELI-AJH-8-3-1-013, F, ELI-AJH-8-2-1-AE003; G, ELI-AJH-8-2-3-AC009. H–I, conjunct and ventral valves demonstrating the intertrough increasing stage (T3) with elongate ventral intertrough; H, ELI-AJH-S05-N001, posterior view of conjunct valves; I, ELI-AJH-S05-L025, posterior lateral view of ventral valve. Scale bar represents 200 μm.
FIG. 4. Morphology of different ontogenetic developmental stages of conjunct valves of *Eohadrotreta zhenbaensis* from the Cambrian (Series 2) Shuijingtuo Formation in the Three Gorges area, South China. A–C, ELI-AJH-S05-N023, very small specimen with U-shape pedicle foramen at the beginning of stage T1; A, dorsal; B, oblique posterior; C, lateral view. D–F, ELI-AJH-8-2-1-AD2-019, the pedicle foramen is almost enclosing at the end of stage T1; D, posterior; E, dorsal; F, ventral view, showing the halo (ha), metamorphic shell (ms) and post-metamorphic shell (ps). G–I, ELI-AJH-8-2-1-AF010, pedicle foramen is already closed at the end of stage T1; G, posterior; H, lateral; I, ventral view. J–L, ELI-AJH-8-2-3-AC010, conjunct valves with increasing ventral intertrough at the end of stage T2; J, lateral; K, dorsal; L, oblique posterior view. M–O, ELI-AJH-8-2-3-AD2-008, conjunct valves with elongate intertrough during stage T3; M, oblique dorsal; N, lateral; O, posterior lateral view. Scale bars represent 100 μm (A–I); 200 μm (J–O).
dorsal valves at valve lengths less than 450 μm (Fig. 3A–D). The outline of ventral valve is subcircular, on average 87% as long as wide, with maximum width posterior to mid-length. The shell is almost flat with slight convexity at shell lengths less than 380 μm, and about 16% as high as long (Figs 3A, 4A–C). As the valve continues to grow, its shape changes to be gently convex, on average 21% as high as long, while the umbo of ventral valve becomes slightly raised (Figs 3C–D, 4D–F). The pedicle foramen varies from an unrestricted notch to a more teardrop-shape, with variable lengths from 25 μm to 83 μm, and about 79% as long as wide; the inclination of the foramen to the pseudointerarea is almost vertical at this growth stage (Fig. 3A–D). The intertrough is not developed in most specimens, while a very short intertrough is rarely observed at the formation of an enclosed pedicle opening at the end of this stage (Fig. 4G–I). The cardinal muscle scars and apical process are vestigial.

At this stage, the dorsal valve is flat in lateral view, about 16% as height as long (Fig. 6A–D). The maximum height of the shell is posterior to mid-valve. The outline of the dorsal valve is subcircular, about 87% as long as wide. The average length is 399 μm, with variations from 346 μm to 448 μm. The pseudointerarea is narrow and shallow, occupying on average 43% of valve width. The median septum is very low and extends posterior to mid-valve (Fig. 6D), occupying about 40% of valve length. The cardinal muscle scars and median buttress are slightly developed (Fig. 6B).

Eohadrotreta? zhuijahensis. The metamorphic ventral valve is never perforated by a foramen, but the incipient pedicle opening is formed by the unrestricted notch between ventral and dorsal valves at valve lengths less than 650 μm (Fig. 7A–F). The ventral outline is slightly different from that of *E. zhenbaensis*, in being transversely oval, on average 84% as long as wide (Fig. 8). The ventral valve is gently convex when the shell is quite small (less than 400 μm in length) (Fig. 7A, B), while the ventral umbo becomes slightly raised when the shell grows bigger (Figs 7C–E, 8G–O). The umbo is prominently raised above the shell surface (Figs 7F, 8J–O), marking the elevated metamorphic shell when the shell length exceeds 500 μm (Fig. 8J, N). The larger pedicle opening invariably forms a notch, varying in lengths from 31 μm to 115 μm, and about 95% as long as wide (Fig. 8). The inclination of the pedicle foramen to the pseudointerarea is the same as that of *E. zhenbaensis*, but remains unchanged during the entire ontogeny development (Fig. 7A–F). The interior cardinal muscle scars and apical process are vestigial (Fig. 9I). The intertrough is not developed in any of the specimens at this stage. It is important to note that the boundary delineating the pedicle foramen from the metamorphic shell is gradually developed at the end of this stage (Fig. 8M–O).

During this stage, the general shape of dorsal valve and dorsal pseudointerarea are quite similar to that of *E. zhenbaensis* (Fig. 10A–E). However, the metamorphic shell is slightly raised above the shell surface when valve increases in size (Fig. 10B–D). The average valve length is 487 μm, about 81% of valve width. The dorsal median septum is very weakly developed and extends less, and the cardinal muscle scars and median buttress are weakly developed (Fig. 10E).

**Fig. 5.** Morphology of different ontogenetic developmental stages of ventral and dorsal valves of *Eohadrotreta zhenbaensis* from the Cambrian (Series 2) Shuijingtou Formation in the Three Gorges area, South China. A, ELI-AJH-S05-EL22, internal surface of ventral valve at stage T2, showing the poorly developed apical process (tailed arrow) and *vascula lateralia* (double-headed arrows). B, ELI-WJP-7-AB089, external view of a very large ventral valve at the end of stage T3. C, ELI-WJP-7-AB009, lateral view of a very large ventral valve at the end of stage T3. D, ELI-WJP-7-AH008, very elongate ventral intertrough at the end of stage T3. E, ELI-WJP-7-AH006, internal view of the elongate ventral intertrough, noting the pedicle foramen (f) marked by a tailed arrow. F, ELI-WJP-7-AH011, ventral valve at stage T3. G–H, ELI-AJH-8-2-3-AC008, internal view of ventral valve at stage T3; G, internal view of apical process (tailed arrow), cardinal muscle scars by arrows and *vascula lateralia* by double-headed arrows; H, oblique posterior view showing apical process (tailed arrow) and *vascula lateralia* (double-headed arrows). I, ELI-AJH-S05-E006, enlarged apical process of ventral valve at stage T3. J, ELI-AJH-S05-1026, internal surface of dorsal valve at stage T3, noting the *vascula lateralia* (double-headed arrows), two bifurcated limbs of median septum (tailed arrows) and the swelling median septum terminal (arrow). K, ELI-AJH-8-2-3-AC020, internal surface of a large dorsal valve at the end of stage T3, showing two bifurcated limbs of median septum (tailed arrows) and swelling median septum terminal (arrow). L, ELI-WJP-7-AB121, internal surface of a very large dorsal valve at the end of stage T3, showing the swelling median septum terminal (arrow). M, ELI-AJH-S05-1005, enlarged median septum, showing two bifurcated limbs of median septum (tailed arrows) and swelling median septum terminal (arrow). N, enlarged median septum of K, showing two bifurcates limbs of median septum by tailed arrows. O, ELI-8-3-1-012a, detailed cardinal muscle scars and pseudointerarea of dorsal valve at stage T3. P, ELI-WJP-7-AH009, longitudinal section of dorsal median buttress at stage T3. Scale bars represent 200 μm (A, D–I, K, M, O); 1 mm (B, L); 500 μm (C, F, J); 100 μm (E, P); 50 μm (N).
lengths from 450 µm to maximum 750 µm, whilst the intertrough of the ventral pseudointerarea is still not well defined (Fig. 3E, F) or relatively short, about 57 µm long (Fig. 3G). The outline of ventral valve becomes transversely oval, on average 84% as long as wide. The umbo of ventral valve is elevated, resulting in a shallow cap shape of the ventral valve, on average 27% as high as long (Figs 3G, 4J–L). The shape of the pedicle foramen changes from teardrop-shape to subcircular at around 28–89 µm in length and 36–93 µm in width, with the average length–width ratio about 102% (Fig. 3E–G). More importantly, the pedicle foramen is not enclosed within the metamorphic shell during the remaining growth of the shell (Fig. 5B); the pseudointerarea is divided by a narrow and shallow intertrough, and changes from catacline (Fig. 3E, F) to procline (Figs 3G, 4J–L) as the valve gradually increases in size. The intertrough starts to develop surface growth lines, while the proparea is not distinguishable. The thin intertrough is about 78% as long as wide, occupying 10% of shell length. On the internal surface, the apical process is increasingly well developed (Fig. 5A). The paired cardinal muscle scars are developed, on average occupying 17% of valve length and 54% of valve width.

The dorsal valve is relatively flat, compared to the ventral valve. The height of the dorsal valve is on average 88 µm, occupying about 16% of valve length. The average dorsal valve length is 587 µm, and about 85% as long as wide. The median buttress and the cardinal process are well developed on the internal surface (Fig. 6E). The low median septum is on average 316 µm long and extends anterior to mid-valve, occupying about 53% valve length.

**FIG. 6.** Morphology of different ontogenetic developmental stages of dorsal valve of *Eohadrotreta zhenbaensis* from the Cambrian (Series 2) Shuijingtuo Formation in the Three Gorges area, South China. A–D, ELI-AJH-8-2-1-AE011, small valve at the end of stage T1; A, external; B, internal; C, lateral; D, lateral internal view. E, ELI-AJH-8-2-1-AE017, internal surface at stage T2. F, ELI-AJH-8-3-1-001e, internal surface at stage T3. Scale bar represents 200 µm.
The ontogenetic development sequence of *Eohadrotreta zhuijahensis* from the Cambrian (Series 2) Shuijingtuo Formation in the Three Gorges area, South China. A–F, conjunct and ventral valves demonstrating the pedicle foramen forming stage (T1) with opening pedicle foramen; A, ELI-AJH-8-2-1-ac2-004, posterior view of a very small specimen with U-shape pedicle foramen; B, ELI-AJH-8-2-1-ac003, external view of ventral valve; C, ELI-AJH-8-2-1-AD2-014, posterior view; D, ELI-AJH-8-1-2-AF012, posterior view; E, ELI-AJH-8-3-1-026t, oblique posterior view of ventral valve; F, ELI-AJH-8-2-1-AE008, the pedicle foramen is almost enclosed at the end of stage T1. G–H, ventral valves demonstrating the pedicle foramen enclosing stage (T2) with enclosing pedicle foramen, posterior view; G, ELI-AJH-S05-M024; H, ELI-AJH-8-2-2-AF22-012. I, ELI-AJH-S05-K033, ventral valve demonstrating the intertrough increasing stage (T3) with short but wide ventral intertrough and pedicle foramen outside the metamorphic shell. Scale bar represents 200 μm.
FIG. 8. Morphology of pedicle foramen forming stage (T1) of conjunct and ventral valves of *Eohadrotreta zhujahensis* from the Cambrian (Series 2) Shuijingtuo Formation in the Three Gorges area, South China. A–C, ELI-AJH-AD2-014, conjunct valves with U-shape pedicle opening at the beginning of stage T1; A, ventral; B, oblique posterior; C, lateral view. D–F, ELI-AJH-8-1-2-AF012, pedicle opening increasing; D, lateral; E, dorsal; F, ventral view. G–I, ELI-AJH-8-2-3-AC018, pedicle opening increasing; G, posterior; H, posterior lateral; I, ventral view. J–L, ELI-AJH-8-2-3-AD2-007, conjunct valves with elevated ventral metamorphic shell; J, lateral; K, oblique posterior; L, poster view. M–O, ELI-AJH-S05-AG007, ventral valve with elongate pedicle foramen outside of the metamorphic shell at the end of stage T1; M; lateral; N, posterior lateral; O, lateral view. Scale bars represent 100 μm (A–L); 200 μm (M–O).
The dorsal pseudointerarea, occupying on average 39% of the shell width, is orthocline during the whole life time. The median groove is shallow and narrow, occupying on average 41% of the pseudointerarea width.

Eohadrotreta zhujiahensis. The broad cap-shape of ventral valve of E.? zhujiahensis is very similar to that of E. zhenbaensis. However, the enclosure of the pedicle foramen becomes delayed at valve lengths from 650 μm up to a maximum 850 μm, while the intertrough of the ventral pseudointerarea is relatively short (Fig. 7G, H). The shape of the pedicle foramen changes from an unrestricted notch to oval at around 64–142 μm in length, and 65-100 μm in width. The pedicle foramen elongates rapidly during this
developmental stage, with a length–width ratio of about 118%. The most important difference between the ontogenies of *E.? zhujiahensis* and *E. zhenbaensis* is that the enclosing pedicle foramen is invariably located outside of the metamorphic shell in the former (Fig. 7G, H). Moreover, the pseudointerarea is invariably catacline, divided by a short but wide intertrough (Fig. 7G, H) throughout ontogeny. The intertrough has a surface ornamentation of fila, while the proparea is not distinguishable from that of *E. zhenbaensis*. The wider intertrough is about 40% as long as wide, occupying about 9% of valve length. On the internal surface, the apical process and cardinal muscle scars become increasingly developed. However, they are not as well developed as in *E. zhenbaensis*.

The shape of the dorsal valve does not change much during this developmental stage, with an average length

FIG. 10. Morphology of different ontogenetic developmental stages of dorsal valve of *Eohadrotreta zhujiahensis* from the Cambrian (Series 2) Shuijingtuo Formation in the Three Gorges area, South China. A, ELI-AJH-8-2-1-ac2-t04, very small valve at the beginning of stage T1. B, ELI-AJH-S05-K051, external surface at stage T1. C, ELI-AJH-S05-K055, external surface with gently elevated metamorphic shell at stage T1. D–E, ELI-AJH-8-2-1-AE001, dorsal valve at the end of stage T1; D, posterior; E, internal view. F, ELI-AJH-S05-K053, internal surface at the beginning of stage T2, showing developed cardinal muscle scars and vestigial median septum. Scale bar represents 200 μm.
of about 785 μm (Fig. 10F). The cardinal process can be seen but is not strongly developed. However, the median septum is lower and shorter than that of *E. zhenbaensis*, just occupying about 31% valve length. There is no obvious difference in the dorsal pseudointerarea from that of *E. zhenbaensis* through ontogeny.

**Intertrough increasing stage (T3)**

*Eohadrotreta* _zhenbaensis_. Both valves continue increasing in size; all of the morphological characters gradually become more pronounced, and tend to be fully developed at valve lengths from 750 μm to 1700 μm. The outline of the ventral valve remains transversely oval. However, the shape of the ventral valve changes from cap-like to wider conical (Figs 3H–I, 4M–O) and eventually to tubular conical at valve lengths larger than 1400 μm (Fig. 5B–D). The umbo of the ventral valve is greatly elevated as the maximum height of the valve, resulting in a conical ventral valve, about 40% as high as long (Figs 3H, 4M–O). The shape of pedicle foramen changes from subcircular to elliptical and varies in length from 67 μm to 146 μm, and in width from 58 μm to 105 μm (Figs 3I, 5B, D). The pseudointerarea remains procline during the remaining ontogeny (Figs 3I, 4N, 5C). The intertrough, dividing the pseudointerarea (Fig. 4M–O), is still narrow (about 149 μm in width), but it can extend as long as 665 μm and becomes gently deep on the biggest specimens (Fig. 5D). The length–width ratio of the intertrough is on average 149%, varying from 44% to 270%. As growth continues, the intertrough length occupies as much as 73% of the valve height. However, the proparea of the pseudointerarea remains vestigial throughout ontogeny. Internally, the apical process is developed as a wide triangular platform that encircles the pedicle foramen posteriorly (Fig. 5G). The terminal portion of the median septum forms a triangular platform-like swelling (Fig. 5K–M). The dorsal *vascula lateralia* are well developed, emerging from between the cardinal muscle scars and median buttress (Fig. 5J). There are no important morphological changes in the dorsal pseudointerarea.

*Eohadrotreta? zhuijahensis*. The ventral valve continues increasing in size, and all the morphological characters gradually become significantly more pronounced and are fully developed at valve lengths from 850 μm to 1617 μm during this stage. However, the outline of ventral valves remains transversely oval as *E. zhenbaensis*. The ventral valve is still cap-like with a gently elevated umbo (Figs 7I, 9D–G), about 33% as high as long. The shape of the elongate pedicle foramen changes from oval to elongate elliptical at variable lengths from 86 μm to 181 μm, and about 125% as long as wide. The enclosing pedicle foramen is located directly outside of the metamorphic shell during this whole stage (Figs 7I, 9E–G), and the pseudointerarea remains catacline throughout ontogeny (Figs 7I, 9A–D). The intertrough, remains short (about 113 μm in width), while it can extend as wide as 590 μm and becomes quite pronounced on larger specimens (Figs 7I, 9E–F). The length–width ratio of the intertrough is on average 38% with variations from 8% to 56%. However, the proparea of the pseudointerarea remains vestigial during the entire ontogeny. The ventral internal structures are invariably not as well developed as in *E. zhenbaensis*. However, the apical process, cardinal muscle scars and short *vascula lateralia* are quite similar to those of *E. zhenbaensis* (Fig. 9H, I, L).

There are few observed changes in the dorsal valve. The dorsal valve is quite flat, forming a lid on the cap-shaped ventral valve. The average length is 1060 μm. All of the internal structures are less developed as compared to those of *E. zhenbaensis*. The median septum is still relatively short, occupying 27% of valve length. However, unlike *E. zhenbaensis* the median septum lacks signs of bifurcation or swelling and the *vascula lateralia* are vestigial. The pseudointerarea and developed cardinal muscle scars are quite similar to those of *E. zhenbaensis* and there are no other recognizable scars.

**DISCUSSION**

_Different ontogenetic growth patterns of E. zhenbaensis and E.? zhuijahensis_

It is commonly difficult to distinguish *E. zhenbaensis* from *E.? zhuijahensis*, because of the similarities in morphology. However, the variations in morphology and
structures at certain developmental stages in the ontogeny are significantly different between the two species (Figs 4, 5, 8, 9). The changes in shape with increasing size are measured during the ontogenetic development sequence, which enables a more complete understanding of the dynamic growth characters (Figs 11–13). The division of the ontogenetic development sequence into three stages (T1–3) can be used to illustrate the most significant changes that are related to the formation of the ventral pedicle foramen and intertrough.

The correlation of ventral valve length:width is a useful index when dealing with all the measured data of *E. zhenbaensis* (Fig. 11A). However, several discrete variations are quite obvious during different ontogenetic developmental stages. The pedicle foramen is open at stage T1 and gradually enclosed during the later stages T2, but never enclosed within the ventral metamorphic shell (Figs 3, 4). During stage T2, the ventral intertrough starts developing gradually with the enclosure of pedicle foramen (Fig. 3E–G), and it is more rapidly developed during stage T3 (Figs 3H–I, 11B). The increasing growth of the ventral intertrough length is identified as an important event in acrotretoid brachiopod ontogeny, and results in both the elevation of the ventral valve (Figs 3I, 4M–O, 5B–F) and the formation of the conical shape of the ventral valve of *E. zhenbaensis* (Figs 3, 5C). The length of the ventral intertrough is smaller than its width during most part of stage T2, while it markedly exceeds the intertrough width during stage T3, which is clearly demonstrated by the exponential curve of the length:width ratio of the ventral intertrough in Fig. 11D. Because of the more rapid development of the intertrough length as compared with the valve length, the orientation of the ventral pseudointerearae gradually changes from catacline (Fig. 4A–I) to procline (Fig. 4J–O). Moreover, the ventral apical process is more developed at stage T3 (Fig. 5G–I). However, the variations in the dorsal valve are weak during the three ontogenetic stages as compared to that observed in the ventral valve (Fig. 13A, B; for details bearing on ontogeny of dorsal valve see Zhang et al. 2017, appendix S2). The most significant modifications are identified as the variable characteristic of the dorsal median septum at stage T3 (Fig. 5J–N). The extension and divergence of the well developed median septum (Fig. 5I, M), the development of paired anterior central muscle scars along the bifurcated limbs (Fig. 5K, N), and the swelling of terminal median septum as a triangular platform (Fig. 5K–M) are correlated with the rapid development of the ventral intertrough length during stage T3 (Fig. 5C, D).

Similarly, the correlation of valve length:width is very useful when dealing with all the measurements from the ventral valve of *E.? zhujiahensis* (Fig. 12A). Several discrete variations are also observed during the different ontogenetic developmental stages. However, the growth pattern is clearly distinguished from that of *E. zhenbaensis*. The pedicle foramen has a delayed enclosing, and is open at stage T1 when the valve length is less than 650 μm (Figs 7A–F, 8). However, the pedicle foramen is located directly outside the ventral metamorphic shell of *E.? zhujiahensis* after the end of stage T1 (Figs 7G–I, 8K–O). During stage T2, the ventral intertrough starts developing slowly with the enclosure of pedicle foramen (Fig. 7G, H), and it develops more slowly during stage T3 (Figs 7I, 12B). The growth rate of the ventral intertrough is decreased, resulting in a slower elevation of the ventral valve (Figs 7, 12B) and the formation of the cap-like shape of ventral valve of *E.? zhujiahensis* (Figs 7, 8). The length of the ventral intertrough is smaller than the width during all the three developmental stages, which clearly demonstrates the slowed growth of intertrough length forming a parabola-shaped curve in the length:width ratio in Fig. 12D. Furthermore, the slow development of the intertrough length keeps the ventral pseudointerearae catacline (Fig. 7). The wider pedicle foramen (about 84 μm in width) of *E.? zhujiahensis* may be correlated with the relatively rapid development of the intertrough width (Fig. 9E, K). However, the interior characters of *E.? zhujiahensis* are not so well developed as in *E. zhenbaensis* (Fig. 9B, H–J). Furthermore, no significant modification is identified as a variable characteristic on the dorsal valve of *E.? zhujiahensis* during stage T3 (Fig. 13C, D; for details bearing on ontogeny of dorsal valve see Zhang et al. 2017, appendix S4).

The allometric growth pattern that can be obtained from the ontogenetic sequence of *E. zhenbaensis*, is characterized by the rapid growth of the length of the ventral intertrough and correlated with the increased complexity of the dorsal median septum (Figs 3, 5). This kind of growth pattern results in that the ventral valve of *E. zhenbaensis* gradually changes into a conical shape with

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**FIG. 11.** Bivariate plots of ventral valve of *Eohadrotreta zhenbaensis* from the Cambrian (Series 2) Shuijingtuo Formation in the Three Gorges area, South China, demonstrating the three ontogenetic developmental stages, differentiated by colour. A, plots of valve length:width ratio (L/W), valve height:width ratio (H/L), and pedicle foramen length – valve length (L_f/L). B, plots of ventral intertrough length – valve height ratio (L_f/H), length at maximum width – valve length ratio (L_m/L), and intertrough length – valve length ratio (L_i/L). C, pedicle foramen length – width ratio (L_f/W). D, ventral intertrough length – width ratio (L_i/W), demonstrating an exponential curve. The dashed line represents equal length and width (L/W = 1).
an elongate intertrough (Fig. 3). By contrast, the paedomorphic development of *E.? zhujiahensis* is characterized by slow growth of the length of the ventral intertrough and the delayed enclosing of the pedicle foramen at valve lengths of about 650 μm during stage T1 (Figs 7, 9), while the maximum length is just about 450 μm of *E. zhenbaensis* when the pedicle foramen is enclosed. More importantly, the pedicle foramen is gradually separated from the metamorphic shell of *E.? zhujiahensis*, corresponding to the enclosing process of the pedicle foramen during stages T2 and T3. Furthermore, the average length of the ventral intertrough of *E. zhenbaensis* is three times longer than that of *E.? zhujiahensis*. This kind of paedomorphic growth pattern makes the ventral valve of *E.? zhujiahensis* gradually change into a cap-like shape with a short intertrough (Fig. 7). However, no prominent morphological changes are recognized on the external surface of both dorsal valves of *E. zhenbaensis* and *E.? zhujiahensis*. As the ontogenetic change in shape may accompany change in mode of life (Gould 1966; Raup & Stanley 1971; Tomásovyč et al. 2008), such different growth patterns observed in the two acrotretoid species *E. zhenbaensis* and *E.? zhujiahensis* may correspond to subtle changes in mode of life during the gradual cumulative change in size. The life strategies of Early Palaeozoic linguliform microbrachiopods and the palaeoecology of acrotretide brachiopods have been discussed repeatedly in a number of publications. But the lack of soft-tissue preservation makes it hard to understand the life habit of acrotretids at present (Popov & Holmer 1994; Holmer & Popov 2000; Holmer et al. 2005, 2017; Wang et al. 2012).

Furthermore, the only in situ occurrences of Cambrian acrotretoids come from the celebrated Chengjiang and Burgess Shale faunas, where they are invariably found as a secondary tiering organism, most commonly attached to sponges or sponge-like organisms (Wang et al. 2012; Topper et al. 2015a, b). Therefore, the conical ventral valve appears to be related to the secondary tiering life habits sitting like little ‘bells’ on sponges and other filtering benthos (Wang et al. 2012; Topper et al. 2015a, b). Compared to *E.? zhujiahensis*, the tubular conical ventral valve and the dorsal internal structures of *E. zhenbaensis* are more complex, with an elongate and bifurcating median septum, triangular platform-like swelling of the terminal portion of the median septum, and the development of a pair of anterior lateral muscle scars (Fig. 5J–N). The elevation of the ventral valve and related developed structures of the dorsal median septum probably provided more support for the lophophore. The muscular system would have provided more capable lophophore protractors, retractor and elevators, suggesting a different life strategy from that of *E.? zhujiahensis* (Williams et al. 2000).

**Development of the pedicle foramen**

The shapes and sizes of the ventral pedicle foramina of *E. zhenbaensis* and *E.? zhujiahensis* are comparable. Both pedicle foramina change from the simplest type (incipient pedicle opening) to a complex type (enclosed pedicle foramen). However, two different developmental processes of pedicle foramina are observed corresponding to the respective growth patterns of *E. zhenbaensis* and *E.? zhujiahensis*. The change in relative growth rates result in a gradual transition of the shape and position of the pedicle foramina within the two species.

The incipient pedicle foramen of *E. zhenbaensis* is open between the ventral and dorsal valves, crossing the margin of the metamorphic shell during stage T1 when the valve length is less than 450 μm (Figs 3A–D, 14A) and gradually becomes enclosed during the subsequent stage T2 (Figs 3E–G, 14B). It is not enclosed within the ventral metamorphic shell at any ontogenetic stage. During stage T1, the incipient pedicle foramen is very small, with an average length of 52 μm and width of 65 μm. Furthermore, the inclination of the pedicle foramen to the pseudointerarea is vertical, which reveals that the pedicle foramen is already developed during early ontogeny. The shape of pedicle foramen changes from an unrestricted notch to subcircular during stage T1 (Fig. 3A–D) and eventually becomes elliptical with an average length–width ratio of 118% during stage T3 (Figs 3I, 14C). The length of the pedicle foramen is less than its width during stage T1 and most of stage T2, eventually exceeding the pedicle foramen width during stage T3, as demonstrated in Figure 11C. However, the increase in size of the pedicle foramen ceases at the end of stage T3 (Fig. 11A). The pronounced arch-shaped notch at the posterior margin of ventral metamorphic shell indicates resorption of some shell material in order to accommodate the pedicle foramen formation of *E. zhujiahensis*.

**FIG. 12.** Bivariate plots of ventral valve of *Eohadrotreta? zhujiahensis* from the Cambrian (Series 2) Shuijingtuo Formation in the Three Gorges area, South China, demonstrating the three ontogenetic developmental stages, differentiated by colour. A, plots of valve length–width ratio (L/W), valve height – length ratio (H/L), and pedicle foramen length – valve length ratio (L_f/L). B, plots of ventral intertrough length – valve height ratio (L_i/H), length at maximum width – valve length ratio (L_m/L), and intertrough length – valve length ratio (L_i/L). C, plots of the pedicle foramen length – width ratio (L_f/W). D, plots of the ventral intertrough length – width ratio (L_i/W), demonstrating a parabolic curve. The dashed line represents equal length and width (L/W = 1).
E. zhenbaensis (Fig. 3), which has also been observed from numerous other Cambrian lingulate brachiopods including the Zhanatellidae (Holmer & Popov 2000) and the lingulid Eoobolus (Balthasar 2009). The decrease of the metamorphic shell length–width ratio from ontogenetic developmental stage T2 to T3 indicates continuous resorption of the metamorphic shell (Zhang et al. 2017, appendix S1).

The pedicle foramen of E.? zhujiahensis continues opening between the ventral and dorsal valves during stage T1 when the valve length is less than 650 μm (Figs 7A–F, 14D) and is gradually enclosed during the later stage T2 (Figs 7G–H, 14E). However, it is clearly located outside the ventral metamorphic shell after the end of stage T1 (Figs 7G–I, 8J–O) and this is considered to be a significantly diagnostic character of acrotretoid brachiopods (Mei 1993; Holmer & Popov 2000; Topper et al. 2013). The pedicle foramen of E.? zhujiahensis is larger, observed from the smallest specimen (360 μm in length) with an average length of 30 μm and width of 60 μm. Similarly, the inclination of the pedicle foramen to the ventral pseudointerarea also reveals that the pedicle foramen is already developed during early ontogeny. The shape of the pedicle foramen changes from an unrestricted notch at stage T1 (Figs 8, 14D) eventually becoming elongate-elliptical when the length–width ratio is around 125%, during stage T3 (Figs 7I, 14F). The length of pedicle foramen increases greatly during stage T1 with a larger width of about 74 μm, and completely exceeds the pedicle foramen width during stages T2 and T3, as demonstrated in Figure 12C. However, the increase in size of the pedicle foramen ceases at the end of stage T3 (Fig. 12A). The shell material resorption is demonstrated by the pronounced arch-shaped indentation at the
posterior margin of the ventral metamorphic shell (Fig. 7). The decrease in metamorphic shell length–width ratio from stage T2 to T3 is much larger in *E. zhenbaensis* than in *E.? zhujiahensis* (Zhang et al. 2017, appendix S1, S3). A possible interpretation is that the amount of resorption of the metamorphic shell during the development of the pedicle foramen of *E.? zhujiahensis* is much less than that of *E. zhenbaensis*, resulting in the clear separation of the pedicle foramen from the metamorphic shell of *E.? zhujiahensis* during the ontogenetic developmental stages T2 and T3.

**Phylogenetic implications**

The position of the characteristic pedicle foramen is considered to be one of the most taxonomically important characters of the acrotretoid brachiopods (Mei 1993; Holmer & Popov 2000; Popov et al. 2009; Topper et al. 2013). However, it is also important to study how the foramen changes during ontogenetic development. The pedicle foramen of *E. zhenbaensis* is not enclosed within the post-metamorphic shell during any part of the ontogenetic development (Fig. 14A–C), which is typical for all the Cambrian Series 2 (Early Cambrian) acrotretoid brachiopods (i.e. *Linnarssonia*, *Prototreta* (or *Homotreta*), *Hadrotreta* and *Vandalotreta*; Holmer & Popov 2000; Popov et al. 2009; Ushatinskaya 2010; Topper et al. 2013; Popov et al. 2015). By contrast, the pedicle foramen of *E.? zhujiahensis* starts separating from the metamorphic shell at the end of stage T1 (Fig. 8J–M). As growth continues, it is clearly located outside the metamorphic shell (Fig. 14D–F). This unique position of the pedicle foramen has only been observed in the Cambrian Series 2

**FIG. 14.** Schematic reconstruction of *Eohadrotreta zhenbaensis* and *Eohadrotreta? zhujiahensis*, showing variations in relative size and shape by accumulated changes during the three ontogenetic developmental stages. A–C, *E. zhenbaensis*; A, pedicle foramen forming stage; B, pedicle foramen enclosing stage; C, intertrough increasing stage. D–F, *E.? zhujiahensis*; D, pedicle foramen forming stage; E, pedicle foramen enclosing stage; F, intertrough increasing stage. Scale bars represent 100 μm (A, B, D, E); 500 μm (C, F).
acrotretoid E.? zhujiahensis. This indicates that the type of pedicle foramen that is typical for acrotretoid brachiopods first developed at the beginning of Cambrian when they made their first appearance. A similar feature can be observed in the Lower Ordovician Eoconulidae Otariella (= Otariconulus), illustrated by Popov & Holmer (1994), in which the pedicle foramen is also partly outside the metamorphic shell. It is worth noting that the only other examples of a pedicle foramen that is enclosed within the metamorphic shell, are not known until the mid-Cambrian Series 3 as demonstrated by Amictocracens, Angulotreta, Aphelotreta, Araktina, Neotreta, Stilpnotreta and Treptotreta (Popov & Holmer 1994; Holmer & Popov 2000; Topper et al. 2013; Popov et al. 2015) and all the Late Cambrian members of the Ephippelasmatidae (Holmer & Popov 2000). However, variations in the position of pedicle foramina during ontogenetic developmental stages have not been studied sufficiently in most acrotretoid brachiopods. Thus, further detailed studies of ontogeny of the pedicle foramen are needed in order to get a better understanding of the phylogeny of acrotretoids and their relation to other brachiopods (Beecher 1891; Li & Holmer 2004; Zhang et al. 2016b).

During the early part of stage T1, the incipient pedicle foramina of E. zhenbaensis and E.? zhujiahensis are short and open between the ventral and dorsal valves (Fig. 14A, D); this represents the simplest type of pedicle opening in shells with a posterior gaping of the valves (Beecher 1891). Such simple pedicle foramina are compare well with those of linguloid brachiopods, including the living Lingula (Chuang 1971) and Cambrian (Series 2) juvenile specimens of Palaeobolus and Eoobolus (Li & Holmer 2004; Zhang et al. 2016b, figs 9J, 10B). As growth continues, the size of initial pedicle foramen of Eohadrotreta increases, but remains open by sub-peripheral shell secretion. The pseudointerarea is poorly developed and vertical to the valve floor, which may represent the process of elevation. The pseudointerarea of the pedicle foramen are needed in order to get a better understanding of the phylogeny of acrotretoids and their relation to other brachiopods (Beecher 1891; Li & Holmer 2004; Zhang et al. 2016b).

The allometric growth of E. zhenbaensis is demonstrated by the early enclosure of the pedicle foramen at about 450 μm in length, the accelerated growth of ventral intertrough length and the accommodated complexity of dorsal median septum at the intertrough increasing stage (Fig. 14A–C). By contrast, the paedomorphosis of E.? zhujiahensis is demonstrated by the delayed enclosure of pedicle foramen at about 650 μm in length (Fig. 14D) and slowed growth of the ventral intertrough length after the pedicle foramen enclosing stage (Fig. 14E, F). Thus, the variable characters during the ontogenetic developmental stages between the two species may be induced by the heterochronic processes of accretionary shell growth and ventral pseudointerarea (Fig. 14). The heterochronic processes indicated by different growth patterns of E. zhenbaensis and E.? zhujiahensis, suggest that the divergence within the genus Eohadrotreta happened at the beginning of Cambrian, and was followed by subsequent adaptive radiation towards morphologies required for optimal adaptation to various ecological niches (Baker & Logan 2011). This adaptive radiation coincides with a considerable increase in morphological diversity, particularly among acrotretoids at the transition from the Cambrian Stage 4 to Stage 5 and the subsequent Ordovician radiation of acrotretoids (Basset et al. 1999, 2002; Popov et al. 2015). The morphological
variations of Eohadrotreta during ontogenetic development may be one kind of phenotypic evolution attributed to mechanical requirements of size increase (Huxley 1958; Gould 1966; Tomášových et al. 2008; Baker & Logan 2011; Vaux et al. 2016). It is also interesting to note the variations in abundance between the two species; the valves of E. zhenbaensis are ten times more common than those of E. zhujiahensis, which may indicate that E. zhenbaensis were better adapted to the relatively shallow shoal carbonate environment of the Cambrian (Series 2) Shujiangtuo Formation. The more elevated ventral cardinal muscles and more developed dorsal median septum may adaptively accommodate the rapid growth of ventral intertrough and the conical shape of ventral valve (Figs 5B–M, 14A–C). It is possible that the successful growth pattern of E. zhenbaensis may have been retained by later acrotretoids during the great Ordovician radiation. Further study on the relationship between variations in shape and the different living environment of acrotretoids will cast new light on the ecophenotypic adaptations in shape and the different living environment of the Lower Cambrian bivalved problematic fossil M. muralensis Walcott, 1913. Lethaia, 37 (4), 381–400.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.823ff
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