GO LARGE OR GO CONICAL: ALLOMETRIC TRAJECTORY OF AN EARLY CAMBRIAN ACROTRETIDE BRACHIOPOD

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Abstract: Acrotretides are extinct micromorphic brachiopods that exhibited considerable morphological variation during their rapid evolution in the early Palaeozoic. The plano-conical shells of acrotretides are distinct in comparison to other brachiopod groups and despite their diversity and abundance in early Palaeozoic communities, their origins, early evolution, life history and phylogeny are poorly understood. Here, we employ advanced geometric morphometrics to quantitatively investigate ontogenetic variation and allometry in the ventral valve of the oldest known acrotretide species from the early Cambrian of South China. Our results identify substantial shape variation for Eohadrotreta zhenbaensis, along with a parabolic morphological trajectory through ontogeny, demonstrating a remarkable reversal to PC1 values equivalent to those obtained for juveniles, during later ontogenetic stages. The evolutionary novel body plan (diminutive and plano-conical) of Acrotretida was established gradually during two phases of allometry, formed initially during the final stage of the Cambrian evolutionary radiation from an ancestral low, equivalved lingulide body plan. The development of a conical shaped valve seems to have resulted in an overall smaller body size, when compared with non-conical forms. The heterochronic processes responsible for generating these ontogenetic modifications at different allometric phases may have facilitated the evolutionary diversification of acrotretide brachiopods during the early Palaeozoic.

Key words: geometric morphometrics, ontogenetic trajectory, micromorphic brachiopod, allometry, evolution, early Cambrian.

Brachiopods are one of the most important components of the early Cambrian Evolutionary Fauna (Sepkoski 1984). Despite their relatively simple bivalved body plan, they exhibit considerable variability in shell morphology, with a wide variety of shapes including circular, lingual, sub-circular, rostrate, cap-like and conical (Bassett et al. 1999; Budd & Jackson 2016; Topper et al. 2017; Zhang et al. 2018a, 2020a, 2021a). Markedly different from all other orders of the Brachiopoda are the micromorphic acrotretides, characterized by their very small size (millimetric scale) and unique plano-conical shell (Wright & McClean 1991; Holmer & Popov 2000; Topper et al. 2013). Acrotretide brachiopods were diverse and abundant in early Palaeozoic benthic marine communities and are readily retrieved as exquisitely preserved three-dimensional phosphatized shells using acid maceration techniques (Henderson & Dann 2010; Topper et al. 2013; Popov et al. 2015; Zhang et al. 2016a). The group originated relatively late (late Series 2, Cambrian), when compared with other major brachiopod groups, but diversified rapidly and dispersed across the globe through the mid-Cambrian and Ordovician. However, they then declined significantly during the end Ordovician mass extinction (Bassett et al. 1999; Holmer & Popov 2000; Ushatinskaya 2010), with only a few taxa surviving into the Silurian, and their final demise came in the Late Devonian (Holmer & Popov 2000). Despite being the most abundant brachiopod order in the latter half of the Cambrian (Ushatinskaya 2010), the origins, evolution, life history, ontogeny and phylogeny of acrotretides remain poorly resolved.

Allometry has long been an important focus in studies of evolution, development and growth, providing detailed
information about shape-size variation (Gould 1966; Klingenberg 1998, 2016). Dramatic variations in size, morphological disparity and differential trait growth during the life history of an organism may provide the phenotypic variation necessary for evolutionary selection (Alberch et al. 1979; Sheets & Zelditch 2013; Klingenberg 2016). Furthermore, allometric patterns are important in understanding how differential scaling of functional traits during growth impact organic resource acquisition in the surrounding environment (ecological efficiency), respond to and influence selective processes (Gould 1966; Klingenberg 2016; Simons et al. 2018). Thus, the study of size-correlated shape variation during ontogeny is crucial for understanding how ontogenetic disparity may relate to morphological and heritable adaptations. With the exception of a few studies (Zhang et al. 2018a; Claybourn et al. 2020; Zhang et al. 2020b), little attention has been paid to ontogenetic development in Cambrian animals and the potential importance of shape variation as an evolutionary driver in Cambrian communities has rarely been quantitatively assessed. One recent example is the work of Zhang et al. (2018a), which demonstrated that the post-metamorphic ventral valve of Eohadrotreta zhenbaensis exhibited allometric growth by rapidly increasing the posterior intertrough in relation to the overall growth of the length of the ventral valve.

Building on this previous work (Zhang et al. 2018a), we use quantitative methods to investigate ontogenetic allometry and its relationship to evolutionary novelty (Gould 1966; Nelson 1978; Klingenberg 1998; Baker & Carlson 2010; Klingenberg 2016; Zhang et al. 2018a) in one of the first acrotretide brachiopods to have evolved during the early Cambrian. We also attempt to elucidate the degree to which allometric growth accounts for whole shape variation in E. zhenbaensis and offer explanations for the morphological changes observed during ontogeny.

Most studies of brachiopod ontogeny commonly focus on linear measurements of co-varied characters (mainly shell outline), but this does not allow identification of differential growth geometry for morphological structures using bivariate analysis (Huang & Harper 2013; Schreiber et al. 2014; Klingenberg 2016). Quantitative techniques can, however, provide an objective morphological foundation that allows for a comprehensive assessment of the ontogenetic significance of key character traits and also provides the necessary framework to assess the importance of heterochrony in evolutionary shape changes of an organism (Klingenberg 1998; Schreiber et al. 2014; Tallman 2016). It is not only possible to capture very subtle shape differences among specimens, but also effectively visualize the results of the statistical analysis as shape deformations using semilandmarks (Martinón-Torres et al. 2006; Mitteroecker & Gunz 2009; Boclaer & Schultheiß 2010; Zelditch et al. 2012; Gunz & Mitteroecker 2013; Chen et al. 2016; Wrozyna et al. 2016). Applying landmark and semilandmark-based geometric morphometrics to specimens of E. zhenbaensis, we establish the existence of a size-shape variation trend, that begins with juvenile individuals and ranges through to adults, that parallels the development of the unique conical shape of the acrotretide ventral valve. Combining geometric morphometric analysis with measurements for centroid size, as well as height data, we are able to clearly demonstrate that E. zhenbaensis exhibits allometric growth. These results help to better elucidate the condition under which evolutionary novelties may have arisen in the Brachiopoda and the specific environmental adaptations that have evolved in these ancestral diminutive organophosphatic brachiopods.

**MATERIAL AND METHOD**

*Brachiopod specimens*

The Cambrian Series 2 Shuijingtuo Formation mainly consists of black shales and intercalated thin bed limestones that crop out in the Three Gorges area of Hubei Province, located in South China. In this study, all acrotretide specimens were recovered by acetic acid (10%) leaching preparation of rock samples from thinly-bedded limestones collected in the middle part of the Shuijingtuo Formation, deposited in a transitional facies from deep basin to shallow platform (for geological setting, see: Broce et al. 2014; Zhang et al. 2016b).

*Eohadrotreta zhenbaensis* is ventribiconvex, subcircular to transversely oval in shape with a slightly straightened posterior margin. The ventral valve is the main focus of our morphometric analysis since it undergoes more drastic changes in shape during ontogeny than the dorsal valve, which changes very little through ontogeny (Zhang et al. 2018a; Claybourn et al. 2020). The great abundance of *E. zhenbaensis* from the Three Gorges area in South China allows the use of geometric morphometric analysis to quantify valve shape and test for allometric growth (Zelditch et al. 2012; Huang & Harper 2013; Jackson & Claybourn 2018). A total of 2084 specimens (1182 ventral valves, 900 dorsal valves and two conjoined valves) of *E. zhenbaensis* were obtained from one limestone sample collected at 14.5 m from the base of the Shuijingtuo Formation at Wangjiaping section (N 30°48'39.7", E 111°11'15.0") (Zhang et al. 2016b; Zhang 2018). The majority of these 2084 specimens were fragmentary or deformed, typical of fossil organophosphatic brachiopod shells, and were thus unsuitable for geometric morphometric analysis due to the absence of key landmarks.
From our total pool of specimens, we therefore only used mostly complete, undeformed and well-preserved ventral valves for morphological analysis and to obtain measurements of valve length (Fig. 1). A total of 158 specimens were deemed suitable for analysis. The size of the valves in our study ranges from 325 to 2379 µm in length, providing adequate sample size to assess allometry (Li & Holmer 2004; Huang & Harper 2013; Zhang et al. 2018a; Claybourn et al. 2020). Due to preservation issues, it was only possible to obtain height measurements from 141 specimens. An additional 27 complete ventral valves of *E. zhenbaensis* and 5 ventral valves of *Palaeotreta zhuijiaensis* (Zhang et al. 2020b), a taxon similar to *E. zhenbaensis*, were added to our dataset, sourced from other Shuijingtuo Formation sections at Aijiahe and Wangzishi (Zhang et al. 2016b). These were added to capture the full morphological variation of *E. zhenbaensis* from South China. All specimens were coated in gold and imaged using a scanning electron microscope (SEM) at either Northwest University (Fei Quanta 400- FEG SEM) or Macquarie University (JEOL JSM 7100F106 FESEM). All the images were taken in the same angle, perpendicular to the viewing plane. Following analysis, all specimens were deposited in the collections of the Early Life Institute, Northwest University, China (ELI) or Uppsala University (UU).

**Geometric morphometric analysis**

SEM images of each specimen were used to digitalize landmarks, with digitization performed using TpsDig2 v2.25 (Rohlf 2016a). Due to the simple morphology of the ventral valve of *Eohadrotreta*, we apply a combination of landmarks and semilandmarks or sliding landmarks, for analysing homologous point locations, together with curves measured on a sample of organisms (Zelditch et al. 2012; Gunz & Mitteroecker 2013; Mitteroecker et al. 2013). The position of landmarks and semilandmarks (Zelditch et al. 2012) were chosen so as to cover as many taxonomically significant morphological traits as possible, with a focus placed on the shape variation of the ventral valve. The rationale for this choice is that the key characteristics used to assess the taxonomy and phylogeny of acrotretides are best captured by assessing the overall shape of the ventral valve, including the outline of the pedicle foramen, the relative position of the pedicle foramen to the posterior margin of the valve (the posterior vector of the pseudointerarea, landmarks 1–3) and the length and gradient of the pseudointerarea (landmark 4), as indicated by the position of the pedicle foramen when supplemented by height data (Fig. 2A; Table 1). These four landmarks can be unambiguously defined on all the specimens.

The outline of the ventral valve and pedicle foramen of *Eohadrotreta* are smooth curves, which are difficult to represent using landmarks. This is because the positions of points along the curves cannot be homologized across different specimens. Semilandmarks make it possible to quantify two dimensional homologous curves, and to analyse them together with traditional landmarks, providing a richer description of shape in very broad animal taxa (Bookstein 1997; Adams et al. 2004; Martinón-Torres et al. 2006; Mitteroecker & Gunz 2009; Boclaer & Schultheiss 2010; Zelditch et al. 2012; Gunz & Mitteroecker 2013; Chen et al. 2016; Rohlf 2016a; Wrozyna et al. 2016; Mitteroecker et al. 2020). In order to present a more accurate and complete outline of the ventral valve, additional semilandmarks were chosen to characterize curves where no homologous point could be defined with the necessary precision (Bookstein 1997; Gunz & Mitteroecker 2013). Following the semilandmark measurement protocol of Gunz & Mitteroecke (2013), semilandmarks are used here to represent homologous curves as sets of points, establishing a geometric homology between corresponding semilandmarks across all samples. To define the position of semilandmarks, curves were first constructed along both the pedicle foramen margin and shell margin in a counter-clockwise direction using the TpsDio2 v2.25 (Rohlf 2016a). Then, using TpsUtil v1.70 (Rohlf 2016b), these densely defined semilandmarks were allowed to slide along the curves by optimizing the position of the semilandmarks with respect to the average shape of the entire sample (average of the Procrustes shape coordinates) to remove the effects of the arbitrary spacing (Gunz & Mitteroecker 2013). The start and end of each curve are delineated by landmarks 1–4. The final result is 11 equidistant semilandmarks (5–15) along the outline of pedicle foramen and 23 equidistant semilandmarks (16–38) on the outline of valve margin (Fig. 2A; Table 1). After sliding, landmarks and semilandmarks were treated identically in subsequent statistical analyses (Bookstein 1997; Mitteroecker & Gunz 2009; Zelditch et al. 2012; Gunz & Mitteroecker 2013; Chen et al. 2016).

Once compiled, each set of raw landmark coordinates was converted to Procrustes shape coordinates through generalized orthogonal least-squares Procrustes superimposition (GPA) computed using TpsRelw v1.65 (Rohlf 2016c) (Fig. 2B). Generalized Procrustes analysis calculates the average or ‘consensus’ landmark configuration, which then serves as a reference point for the superimposition of all specimens (Chen et al. 2016). All landmarks were centred, scaled and rotated by minimizing Procrustes distances between individual specimens and the average or reference shape configuration, following the method used by Zelditch et al. (2012) and Rohlf (2016c). Due to the scaling step that is a component of Procrustes
FIG. 1. Cambrian Series 2 acrotretide brachiopods used in geometric morphometric study, showing shape and size variations of ventral valves of *Eohadrotreta zhenbaensis* from one fossil assemblage with size ranges from 300 to 2200 µm. A, ELI AA07; B, ELI AA96; C, ELI AA08; D, ELI AA09; E, ELI AA29; F, ELI AA41; G, ELI AA119; H, ELI AA91; I, ELI AA95; J, ELI AA128; K, ELI AA81; L, ELI AA63; M, ELI AB01; N, ELI AA82; O, ELI 6R98; P, ELI AA42; Q, ELI AA89; R, ELI AB08. Scale bars represent: 200 µm (A–F); 500 µm (G–J); 1000 µm (K–N); 2000 µm (O–R).

FIG. 2. Definition (A) and superimposition through Procrustes analysis (B) of landmarks (yellow squares) and semilandmarks (red circles).
superimposition, the shape coordinates do not provide any information on overall specimen size, while information about the size of ventral valve is represented by the centroid size of the landmark configurations (Mitteroecker & Gunz 2009). To visualize the transformation in shape and to provide shape variables that can be used in subsequent multivariate analyses, thin plate splines (TPS) were generated (Gunz & Mitteroecker 2013). Principal component analysis (PCA) was subsequently applied to explore the overall diversity of within-sample shape variation using software package TpsRelw v1.65 (Macleod 2010; Rohlf 2016c).

### Allometric analysis

To determine how much shape variation is correlated with size difference in all 158 specimens, a multivariate regression analysis was conducted between all shape components and centroid size using TpsRegr v1.49 (Rohlf 2016d). The multivariate regressions involve permutation tests on the correlations with 10 000 replicates (Chen et al. 2016). The relationship between shape and centroid size was assessed using multiple linear regression, focusing on the first two principal components generated during PCA analysis and performed using PAST v3.25 (Hammer et al. 2001). The first two principal components were chosen because they represent the majority of shape variation (90.04%). The morphospace was then constructed by augmenting the shape by centroid size as an additional independent variable to estimate the ontogenetic trajectory of the fossil population across different age stages (Mitteroecker et al. 2013; Chen et al. 2016). As valve height or length is considered to be a good proxy for size, and previously used for variation in growth parameters related to the holoperipheral shell of *Eohadrotreta* (Klingenberg 1998; Zhang et al. 2016a), linear regression of shape versus height was also undertaken. The population allometry is effectively visualized and compared using a series of deformation grids in the geometry of original specimens (Mitteroecker & Gunz 2009; Gunz & Mitteroecker 2013; Mitteroecker et al. 2013, 2020).

### RESULTS

Size varies considerably across the measured *E. zhenbaensis* specimens, with length ranging from 325 to 2379 μm and height ranging from 80 to 1083 μm (Fig. 3). The distribution of valve lengths is right-skewed (Fig. 3A), typical of populations with high juvenile mortality rates living in the quiet-water environments (Shapiro–Wilk test: W = 0.852, p = 2.82 × 10⁻⁹; Skewness G1 = 1.155) (Paine 1969; Richards & Bambach 1975; Broce et al. 2014; Waller & Svensson 2017; Zhang 2018). Valve width and length increase in direct proportion to one another during ontogenetic development, while valve height increases proportionally faster than length during ontogeny, with a slope of 1.23 (Fig. 3B).

Shape variation for ventral valves of *Eohadrotreta* is illustrated using thin plate splines, allowing for comparison of analytical results with actual specimens in morphospace (Fig. 4; Mitteroecker et al. 2013; Chen et al. 2016; Simons et al. 2018). We identified considerable intraspecific variation in *E. zhenbaensis*, but there is some clustering of valve shapes of similar size (Fig. 4). Specimens of *E. zhenbaensis* from other localities fall within the total range of shape variation for the assemblage from the Wangjiaping section (Fig. S1). In total, 72 principal component values for the 158 specimens analysed were obtained from PCA (Zhang et al. 2021b, appendix S2). The first three principal components (PCs) account for 92.84% of the total shape variation (Table 2). PC1 accounts for the majority of total shape variance (76.01%) and relates predominantly to the position and shape of the pedicle foramen in relation to the posterior margin as demonstrated by the transformed TPS (Fig. 4). Lower values on PC1 represent a closer position of the pedicle foramen to the posterior margin resulting in a relatively steeply inclined pseudointerarea and a longitudinally compressed posterior. Higher values on PC1, by contrast, correspond to the relatively distant position of the pedicle foramen from the posterior margin, a more laterally compressed posterior and a pseudointerarea with a relatively decreased inclination. PC2 accounts for 14.03% of the total shape variation. Lower valves on PC2 reflect a constriction of the pseudointerarea (in terms of width) and a relative decrease in size of the pedicle foramen compared to the entire valve, with higher values showing an expansion of the pseudointerarea (in terms of

### TABLE 1. Definition of landmarks and semilandmarks.

| Landmark | Description |
|----------|-------------|
| 1        | Left juncture point of metamorphic shell and proparea |
| 2        | Right juncture point of metamorphic shell and proparea |
| 3        | Proximal point of intertrough |
| 4        | Distal point of intertrough |
| 5–9      | Sliders between landmarks 1 and 2, along the margin of pedicle foramen |
| 10–12    | Sliders between landmarks 2 and 3, along the margin of pedicle foramen |
| 13–15    | Sliders between landmarks 3 and 1, along the margin of pedicle foramen |
| 16–38    | Sliders from landmark 4, along the margin of valve |

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width) and a relatively larger pedicle foramen (Fig. 4). PC3 accounts for only 2.8% of total shape variation and predominantly corresponds to the maximum width and length of the entire valve, changing the outline from circular to slightly sub-circular with growth (Fig. 4). It indicates that the valve marginal landmarks (16–38) have relatively little contribution to the whole shape variations (Zhang et al. 2021b, appendix S3), which is further confirmed by the isometric growth of valve length and width (Fig. 3B).

Multivariate regression of overall shape vs ventral valve size (using centroid size as a proxy for valve size) indicates a significant relationship between shape and size (Wilks’ lambda test: $\Lambda_{\text{Wilks}} = 0.437$, $p < 0.0001$, percentage unexplained: 54.8%; generalized Goodall $F$-test: $F = 132.115$, $p < 0.0001$; Zhang et al. 2021b, appendix S4). Shape changes along PC1 and PC2 are closely related to differences in shell size (Figs 5, 6). Smaller individuals, in terms of length and height (taken here as representing younger specimens;
Paine 1969) have predominantly negative PC1 and positive PC2 values, while larger specimens display positive PC1 and negative PC2 values, with the largest, most mature specimens negative on both PC1 and PC2. Multiple linear regression of PC1 versus centroid size indicates that shape change is a function of size ($r^2 = 0.34$, $p < 0.0001$; Fig. 5). A similar multiple linear regression of PC1 versus height also indicates a relationship between shape and height ($r^2 = 0.31$, $p < 0.0001$; Fig. 6; Zhang et al. 2021b, appendix S5). Shape variations are visually illustrated by fossil specimens, allowing for comparison with biological features in morphospace (Fig. 6).

The parabolic curve illustrated in Figure 5 suggests a two phase allometric trajectory for *E. zhenbaensis*, with a reversal to PC1 values equivalent to those obtained for juveniles during later ontogenetic stages. Juvenile specimens of *Eohadrotreta* possess a relative short intertrough and a pedicle foramen positioned closer to the posterior margin (Figs 1A–E, 7H–K). Juvenile specimens with these features are typically up to 0.7 mm in length and only 0.21 mm in height (mean L/H ratio of 2.90) giving a low,
cap shape appearance (Fig. 7H–K). As specimens increase in length and height and PC1 values become positive, specimens dramatically develop a longer intertrough and the position of the pedicle foramen begins to move away from the posterior margin (Fig. 1F–K). The anterior movement of the pedicle foramen from the posterior margin creates a pseudointerarea with a relatively lower gradient (procline; Fig. 7N) (compared to more matured specimens). At the peak of this parabolic curve, specimens are approximately 1.5 mm in length and 0.41 mm in height (mean L/H ratio of 2.50) and appear as a

**TABLE 2.** Singular values (SV) and percentages of variance for the first five PCs from principal component analysis for ventral valve of *Eohadrotreta zhenbaensis*.

| PC | SV       | %     | Cum   |
|----|----------|-------|-------|
| 1  | 0.94763  | 76.01 | 76.01%|
| 2  | 0.40719  | 14.03 | 90.04%|
| 3  | 0.18176  | 2.80  | 92.84%|
| 4  | 0.16532  | 2.31  | 95.15%|
| 5  | 0.11245  | 1.07  | 96.22%|

**FIG. 5.** Ontogenetic trajectory of the fossil assemblage of *Eohadrotreta zhenbaensis* from the Shuijingtuo Formation at Wangjiaping section, demonstrated by the multiple linear regression of shape with centroid size. All thin plate splines correspond to the shapes of specimens in morphospace. Valve length is indicated by different colours.

The equation for the regression is $y = (-2.204 \times 10^{-9})x^2 + (1.73 \times 10^{-8})x - 0.272$ with $r^2 = 0.34$, $F = 39.05$, and $p < 0.0001$.
relatively low conical shape (Figs 1L, 7L–O). The subsequent phase of growth results in the pedicle foramen moving back towards the posterior margin and this results in a relatively steeply inclined pseudointerarea and a rising conical shape (mean L/H ratio of 2.27) (Figs 1M–R, 7P–R).

Multiple linear regression of PC2 versus centroid size indicates a significant relationship between shape and size ($r^2 = 0.7$, $p < 0.0001$) (Fig. 5). There is a decrease in pseudointerarea width with a relatively smaller pedicle foramen during the entire allometric development trajectory. Juveniles have a relatively larger pedicle foramen and a wider pseudointerarea, while adult specimens have a relatively small pedicle foramen and narrower pseudointerarea (Figs 5, 6).

**DISCUSSION**

Shape-size variation and morphological adaptations in Eohadrotreta zhenbaensis

Deciphering the size variation of morphological traits during growth is crucial for constraining the factors that influence shape variation in fossils. Here, geometric morphometric analysis of *E. zhenbaensis* identifies significant
FIG. 7. Lateral view of ventral valves of Cambrian Series 2 Lingulata brachiopods. A–D, Lingulida brachiopods with relatively flat shape from the Shuijingtuo Formation: A, Botsfordia (Botsfordiidae), ELI S05 CB12; B, Eoobolus (Eoobolidae), ELI XYB S4-3 AU11; C, Palaeobolus (Obolidae), ELI S4-2 BN06; D, Lingulellotreta (Lingulellotretidae), ELI S5-4 CI02. E–F, Acrotretida brachiopods with low conical shape from the Shuijingtuo Formation: E, Palaeotreta shannanensis, ELI S4-3 AU02; F, Palaeotreta zhuihaensis, ELI S05 M24. G, Acrotretida with conical shape from middle Cambrian calcareous sandstone of Limön, Sweden: Vandalotreta sp., UU CL10. H–R, Eohadrotreta zhuetensis from the Shuijingtuo Formation, showing ontogenetic development of low-cap like shape juvenile to low conical valve and to rising conical adult: H–I, ELI 8-2-1 AE05; J–K, ELI 8-2-3 AC25; L–M, ELI WJP DR04; N–O, ELI WJP DR06; P, ELI WJP DR08; Q–R, ELI WJP DR09. Scale bars represent: 200 μm (A, B, E–G, H–M); 500 μm (C, D, N–R).
morphological variations within a single assemblage (Figs 4–6). It reveals that shape variations of ventral valves are predominantly due to the allometry of *E. zhenbaensis*, as the influence of size is separated from shape (Lleonart et al. 2000).

A previous study demonstrated three ontogenetic stages in the ontogenetic sequence of *E. zhenbaensis*, the pedicle foramen forming stage, the pedicle foramen enclosing stage and the intertrough increasing stage (developmental stage T3) (Zhang et al. 2018a). We observe two allometric phases that result in a reversal of PC1 values for adult specimens of *E. zhenbaensis* at later ontogenetic stages (Figs 5, 6). This can be correlated with the late T3 developmental stage described in Zhang et al. (2018a). The first allometric phase results in the length of the valve increasing (length = 1.5 mm) but the height of the valve remains relatively stable and low (height = 0.41 mm) at approximately 27% of length on average (Figs 3, 5). Specimens in this first phase also develop a longer intertrough as the position of the pedicle foramen moves away from the posterior margin. It is during the second allometric growth phase, that we observe a dramatic extension in height, as the height increases rapidly to 1.1 mm, now representing 44% of length on average (Figs 3, 5). The pedicle foramen also begins to move back towards the posterior margin resulting in a steeply inclined pseudointerarea and the conical shape, characteristic of acrotretides is formed.

The question remains however, why do we see such a dramatic ontogenetic change in *E. zhenbaensis*? In some modern calcareous brachiopods, ontogenetic changes may represent the onset of sexual maturity (Paine 1969; Peck et al. 1987). However, it is typically the rate of growth, rather than specific changes in morphology that varies with the onset of sexual maturity, as resources are redirected from increasing body size to gametogenesis and reproduction (Curry 1982; Buening & Carlson 1992). Consequently, it is likely that the ontogenetic shift observed in *E. zhenbaensis* is not a consequence of reaching sexual maturity. Rather the results presented here align with previous evidence that the morphology (size and shape) of *Eohadrotreta* may have evolved both as an adaptation to the demands of a sessile life mode and to allow the exploitation of particular niches (Fig. 8).

During the first allometric phase, the valve length increases rapidly (Figs 1A–K, 7H–O), which may reflect the need for juveniles emerging from the benthic sediment–water interface to rapidly take advantage of less stagnant waters to obtain food and oxygen (Fig. 8). This is a feature observed in many extant juvenile brachiopods (Chuang 1997; Baker & Carlson 2010). The second allometric growth phase consists of a notable increase in height and the growth of a well-developed, flattened pseudointerarea (Figs 1M–O, 3B, 6, 7P–R). It is most likely that this is related to stabilization of the brachiopod on the substrate, as the wide, flattened pseudointerarea would provide an ideal surface for the brachiopod to rest directly on the substrate (Fig. 8). As the lophophore of acrotretides is attached to the dorsal valve, resting on the steeply inclined pseudointerarea of the ventral valve would have also created a high angle to the substrate surface, lifting the lophophore off the sediment–water interface and minimizing sedimentary disturbances (Fig. 8; see Henderson & Dann 2010, fig. 12). This orientation has long been thought to have been the life position of acrotretides, with the plano-conical body plan additionally interpreted as minimizing the current drag (Wright & McClean 1991; Peck 1996; Baker & Carlson 2010; Henderson & Dann 2010; Wang et al. 2012; Popov et al. 2015; Zhang et al. 2018a) and it has even been suggested that the eddies generated off the margin of the ventral valve may have enhanced water flow over the lophophore (Henderson & Dann 2010). However, detailed studies investigating the fluid dynamics associated with a conical shell have not been undertaken to confirm these theories.

The diminutive size of the Acrotretida has often been used to separate the group from the other brachiopod orders (Holmer & Popov 2000). The implications of possessing a millimetric-sized shell however, are rarely discussed (Popov 1992; Holmer & Popov 2000; Henderson & Dann 2010; Zhang et al. 2018b). Whilst acrotretides are rarely preserved in life position, specimens from the Burgess Shale (Bengtson & Collins 2015; Topper et al. 2015) and Chengjiang Lagerstätten (Wang et al. 2012; Hu et al. 2018) have provided some understanding of their palaeoecology, showing that individuals are capable of attaching to a variety of substrates including sponges and chancelloroids (Mergl 2002; Holmer et al. 2005), algae (Wang et al. 2012) or pterobranchs (Hu et al. 2018). While the majority of Cambrian brachiopod species from these communities occupy low tiering positions (within 50 mm of the sediment–water interface), acrotretide species are one of the few taxa that are classified as medium tierers, attaching to substrates that place them above 50 mm from the sediment–water interface (Wang et al. 2012; Topper et al. 2015). Based on available evidence, it is conceivable that their minute body size allowed acrotretides to occupy a higher tiering level above the seabed, exploiting a niche that larger and heavier shelled brachiopods could not inhabit. The possibility of reaching higher, secondary tiering positions may have proved immensely advantageous allowing the group to flourish and dominate some assemblages in the Cambrian.

**Evolution of the acrotretide plano-conical body plan**

Understanding modifications of size and shape in organisms has been crucial in understanding the development of
novel body plans in organisms (Gould 1966; Klingenberg 1998, 2016; Tomasových et al. 2008; Simons et al. 2018). The evolution of the novel body plan of acrotretide brachiopods has long been a conundrum, since the conical shape of the ventral valve is unlike that found in nearly all other extinct and extant brachiopods (Popov 1992; Holmer & Popov 2000; Henderson & Dann 2010; Zhang et al. 2018b). By analysing patterns of dynamic shape variation during ontogeny in one of the oldest acrotretide taxa, it is possible to identify a more complete set of character traits that may be associated with the evolution of the conical ventral valve in many acrotretide lineages.

Although, the majority of acrotretide taxa possess a similar, homologous basic body plan (Ushatinskaya 2010; Zhang 2018; Zhang et al. 2020b), characterized by their conical ventral valve, our study of *E. zhenbaensis* demonstrates that a conical ventral valve is formed through two successive phases of the entire ontogeny of the species. Juvenile specimens of *E. zhenbaensis* instead exhibit a low-cap shape ventral valve with a relatively short pseudointerarea (Fig. 7H–K), a morphology that most closely resembles the shape of sympatric lingulides (Fig. 7A–C). The similarity in morphology between juvenile acrotretides and lingulides adds weight to the theory that the diminutive and conical shaped ventral valve found in acrotretides is likely to have been derived from an early Cambrian lingulide-like low equivalved form (Fig. 7A–D). This hypothesis, known as the ‘rolled-up’ lingulide hypothesis (Popov 1992; Holmer & Popov 2000; Zhang et al. 2020b) suggests that a raised ventral lingulide valve is the source of the conical valve, with the reduced ventral propareas partly forming the acrotretide intertrough, the acrotretide enclosed pedicle foramen modified from the lingulide pedicle groove, and the advanced median septum derived from lingulide median ridge (Popov 1992; Holmer & Popov 2000; Zhang et al. 2018a).

During the early Cambrian, the cosmopolitan members of the brachiopod Order Acrotretida, such as *Vandatreta*, *Linnarssonia*, *Prototreta*, *Palaeontreta* and *Hadrotreta* all possessed a similar diminutive plano-conical shape similar to *Eohadrotreta* (Fig. 7G; Ushatinskaya 2010; Zhang 2018; Zhang et al. 2020b). The development of this conical shape together with the adaptive fitness of acrotretides across the early Palaeozoic strengthens the evidence for a similar, homologous basic body plan across the Acrotretida, which was rapidly derived from a common ancestor through different heterochronic pathways in different taxa (Fig. 7E–G, R).

The potential relationship between acrotretides and lingulides is further indicated by additional plesiomorphic characteristics such as the micro-pitted surface of the metamorphic shell, and larval metamorphosis after the free-swimming stage, and the columnar shell structures that are shared between early Cambrian acrotretides and the oldest known lingulides (Popov et al. 2015; Zhang et al. 2018b, 2020a, 2021a). The addition of our results adds another line of evidence indicating that the novel conical acrotretide shape is derived from a lingulide ancestor during the Cambrian evolutionary radiation (Bassett et al. 1999; Mergl 2002; Popov et al. 2015).

**CONCLUSION**

Our results demonstrate that there is significant shape variation in the acrotretide *E. zhenbaensis* from the Cambrian Series 2 Shuijingtuo Formation. Furthermore, there
is a strong relationship between shape and size in acrotretides, with juvenile specimens exhibiting higher variability in shape. During the juvenile stage, the pedicle foramen is located close to the valve posterior margin, with a steeply inclined pseudointerarea, a longitudinally compressed posterior and a relatively larger pedicle foramen. As the valve grows larger, the pedicle foramen moves away from the posterior margin, the posterior of the valve becomes more lateral and the inclination of the pseudointerarea is decreased. However, as maximum size increases, the pedicle foramen returns to a position closer to the posterior margin, with a constriction of the posterior and increasingly inclined pseudointerarea.

This ontogenetic trajectory reveals how what is initially a low-cap shape changes into a conical shape gradually during a two phase allometry. This has significant implications for the taxonomy, adaptation and evolution of early Cambrian acrotretides. Increasing the height of the ventral valve, rather than growing longer or wider, helped to stabilize the acrotretides on the substrate and their minute size proved a successful adaptive strategy for exploiting higher secondary tiering levels that larger brachiopod taxa could not attain. Our results indicate that acrotretides are likely to have been derived from an early Cambrian lingulide-like ancestry, with their unique morphology developed through the transformation of the raised apical posteriorly during the final stage of Cambrian explosion. The innovative shape and later modified epizoic lifestyle may account for the dominance of many acrotretide assemblages in the latter half of the Cambrian, continuing through to the Ordovician biodiversification event.

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Author contributions. ZLZ, ZFZ and GAB conceived the project. ZFZ, FYC and ZLZ collected the fossils. YLC, LCS and ZLZ analysed the data, ZLZ and TPT wrote the paper with input from the other authors. All authors read and approved the final manuscript.

DATA ARCHIVING STATEMENT

Data for this study, including details of shape variation, GPA and PCA data, landmark details and multivariate regression data are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.jzpc86d8

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article (https://doi.org/10.1111/pala.12568):

**Figure S1.** Shape variation in the ventral valve of *Eohadrotreta zhenubaensis* from the Cambrian Series 2 Shuijingtuo Formation at the Wanhjiaping section of South China, as well as *E. zhenubaensis* and *P. zhuijiangensis* from the Shuijingtuo Formation at Aijiahe and Wangzishi sections of South China for comparison, with an indication of characteristic thin plate splines. All thin plate splines correspond to the shapes of 190 specimens in morphospace. Data point colour indicates valve length.

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