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LATE ORDOVICIAN BRACHIOPOD *RONGATRYPA XICHUANENSIS* FROM XICHUAN, HENAN PROVINCE, CENTRAL CHINA

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Keywords: atrypide; *Rongatrypa xichuanensis* (Xu, 1996); allometric growth; Paleoecology; South China palaeoplate.

Abstract. The atrypide brachiopod *Rongatrypa* Popov & Cocks, 2014 is one of the early members of the subfamily Clintonellinae. This genus was previously known only from the Kazakh terranes. Here, we reassign a species to the genus, *Rongatrypa xichuanensis* (Xu, 1996), from the Shiyanhe Formation (Katian, Upper Ordovician) of Xichuan, Henan Province, central China. A wide range of shell sizes was found and measured to investigate the ontogeny of the species, and several specimens were selected for serial sectioning to examine the internal morphology. The linear regression results of natural logarithms of length vs. width and depth vs. width revealed an allometric growth pattern, perhaps influenced by the development of the lophophore. *Rongatrypa xichuanensis* inhabited a shallow marine oxygenated environment in the South China palaeoplate near the palaeo-equator. The distribution of *Rongatrypa* across South China and Kazakh terranes reflects the proximity of these blocks in the Late Ordovician.

Introduction

Rongatrypa Popov & Cocks, 2014 is an early representative of the subfamily Clintonellinae. This genus has thus far only been described from the Katian (the Upper Ordovician) of the Chingiz-Tarbagatai terrane (Popov & Cocks 2014), the Chu-Ili terrane (Popov et al. 2000), and the Selety terrane (Nikitin et al. 2003) in Kazakhstan, central Asia.

Here, we describe a species, *Rongatrypa xichuanensis* (Xu, 1996), from the Katian (Upper Ordovician) of Xichuan, Henan Province, which is the first report of this genus in China. This species has been previously described as different atrypide and rhynchonellide genera (see Systematic Palaeontology), but it is here reassigned to *Rongatrypa* based on its dorsi-biconvex and subpentagonal outline, uniplicate anterior commissure, dorsal median septum, and the presence of jugal processes rather than a jugum in adult shells.

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A large collection of *Rongatrypa xichuanensis* was made from two sections in the study area. The large quantity of shells and the wide variety of their sizes in the collection make it well-suited for the study of the ontogeny of this species. There has been little published regarding early atrypide ontogeny (although, see Sproat & Zhan in press), and much remains unknown about how shell shape changes through development in this group.

The aims of this paper are to provide a systematic description of the brachiopod *Rongatrypa xichuanensis*, to demonstrate the allometric growth within a population of this species, and to investigate its palaeoecological and palaeogeographical implications.

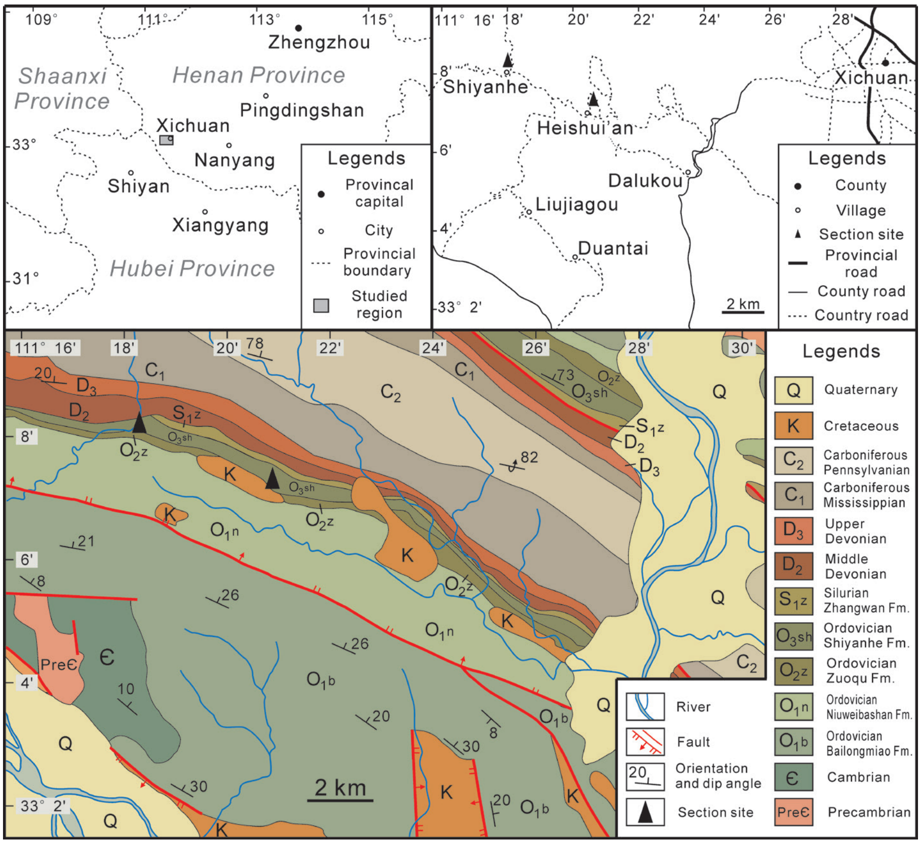

Fig. 1 - Simplified geographical and geological maps of central China and the study area in southwestern Henan, modified from Zhang et al. (2019) and Henan Provincial Bureau of Geology (1966).

Geological setting

The study area is located north of Shiyanhe Village in Xichuan County, southwestern Henan Province, central China (Fig. 1). The two sections examined in this study (the Shiyanhe and Heishui'an sections) are located at N33°07'37.02", E111°18'33.6" and N33°07'06.6", E111°20'07.8" respectively. Loose individuals of *Rongatrypa xichuanensis* were collected from the upper Shiyanhe Formation at both sections. Shiyanhe Formation in this region mainly contains a series of grey thick-bedded bioclastic grainstones with yellow siltstone intercalations, yielding abundant fossils of brachiopods, corals, trilobites, bryozoans, conodonts.

The study area is located to the east of the Qinling Mountains, and paleogeographically was part of a shallow water platform on the north margin of South China palaeoplate in the Late Ordovician (Xu 1996b; Ma et al. 2009; Dong et al. 2011; Rong et al. 2015; Jing et al. 2017). Conodonts from this formation belong to the *Oulodus ulrichi*, *Oulodus robustus*, *Aphelognathus grandis* and *Aphelognathus divergens* biozones, indicating a Katian age (Ka2–Ka4) (Jing et al. 2017).

Materials and methods

The collection consists of 190 shells from the upper Shiyanhe Formation at Shiyanhe Section and 212 shells from the upper Shiyanhe Formation at Heishui'an section. Brachiopod shells were collected randomly, ensuring that the collection was not biased by shell size, for example. Most of the brachiopod shells, in general, have undamaged outlines, but shell interiors are commonly obscured by recrystallization.

Nine shells in different growth stages (5.36–20.00 mm in shell width) were selected and photographed under an optical microscope (Zeiss Microsystems SYCOP 3). Two conjoined valves were selected for transverse serial sectioning to investigate the internal structures. The distance between two adjacent serial sections is between 0.05 mm and 0.50 mm and an acetate peel is made for each section. Each peel is observed and photographed under microscope, and used to reconstruct the internal structures.

Shell length, width, and depth of complete shells were measured by digital callipers. Basic summary statistics were calculated for each set of measurements for all measured specimens (Tabs. 1, 2). Natural logarithms of measured data were calculated and imported into software PAST (version 3.20, Hammer et al. 2001) and bivariate plots of natural logarithms of length vs. width and natural logarithms of depth vs. width were produced. Linear regression using the reduced major axis (RMA) method was applied to plot a trend through each dataset. A dataset converted to natural logarithms should produce a linear trend if the data are related based on the power law (see below).

Repositories and institutional abbreviations

Nine specimens in different growth stages and serial grinding replications of two shells made by cellulose acetate peel examined in this study are deposited in Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. Catalogue numbers are NIGP 169681–169690.

Systematic palaeontology

Order **Atrypida** Rzhonsnitskaya, 1960
Suborder **Atrypidina** Rzhonsnitskaya, 1960
Superfamily Atrypoidea Gill, 1871
Family Atrypinidae McEwan, 1939
Subfamily Clintonellinae Poulsen, 1943
Genus *Rongatrypa* Popov & Cocks, 2014

Rongatrypa xichuanensis (Xu, 1996)

Figs. 2, 1-39; 3

1991 *Nalivkinia zhaohuajingensis* Fu, 1982 - Liu et al., pp. 176, 219, pl. 10, figs. 10–14, 16, 17.
1991 *Kritorhynchia gr*acilis Rong & Yang, 1981 - Liu et al., pp. 175, 219, pl. 10, figs. 18–21.
1993 *Nalivkinia* (*Anabaria*) *zhaohuajingensis* Fu, 1982 - Zeng et al., p. 383, pl. 2, figs.8–9.
1993 *Nalivkinia* (*Anabaria*) sp. 1 - Zeng et al., p. 383, pl. 2, fig. 11.
1993 *Rostricellulla* sp. 4 - Zeng et al., p. 383, pl. 2, fig. 12.
1993 *Paraplectatrypa* sp. 1 - Zeng et al., p. 383, pl. 3, figs. 5, 6.
1996a *Nalivkinia* (*Anabaria*) *xichuanensis* Xu, 1996 - Xu pp. 561–563, figs. 8–10, pl. 4, fig. 9; pl. 5, figs. 12, 13; pl. 6, figs. 1–10.

Material: A total of 402 conjoined valves.

Occurrence: Upper Shiyanhe Formation (Katian, Upper Ordovician), Shiyanhe Village and Heishui'an Village, Xichuan City, Henan Province, central China.

Description. Shell dorsi-biconvex to convexo-plane, subpentagonal to elliptical in outline. Anterior commissure rectimarginate or uniplicate. Ventral valve lateral profile convex to plane, with maximum height at 1/6 to 1/2 of length of the shell from posterior. Ventral beak small, erect. Delthyrium open, triangular. Ventral median sulcus variably developed in larger-sized shells, measuring 1/5 to 1/2 of valve width, originating at 2/5 to 7/10 from ventral beak. Dorsal valve convex, with maximum height at about half shell. Dorsal median fold variably developed originating at mid-valve anteriorly in larger-sized shells. Ornament of 35–40 simple rounded ribs separated by narrow interspaces, including 5–10 ribs in ventral sulcus and up to 12 ribs on dorsal fold if present. Fine concentric growth lamellae without growth interruptions.

Ventral interior with strong teeth. Short, divergent dental plates extending to 1/5 length. Base of delthyrial cavity occupied by pedicle callist. Weekly impressed, triangular ventral muscle bounding scar from beak extending to 1/3 length. Dorsal valve with a median septum supporting simplex cruralium, becoming more rounded around 1/4 length. Cardinal process absent or thin and ridge-like if present. Hinge plates discrete. Crura divergent. Jugal processes short, extending anteriorly, and closely to each other with no jugum developed. Spiralia dorso-medially directed with four to nine whorls.

Ontogenetic variation. There is a great variation of *Rongatrypa xichuanensis* through its ontogeny. Shell sizes vary a lot in different growth stages (i.e. width varying from 4.58 mm to 21.00 mm in this collection) (Tabs. 1, 2). Juvenile shells normally have a biconvex outline with a nearly rectimarginate anterior commissure, whereas larger shells are more convexo-plane with a well-defined dorsal fold and a U-shaped ventral sulcus. The average ratio of length vs. width is 1.10 in juvenile shells, but decreases to 0.83 in mature shells. Ventral beak tends to

	L	W	D	L/W	T/W	T/L
Mean	11.17	12.31	6.51	0.92	0.52	0.57
Median	11.00	12.20	6.18	0.92	0.53	0.57
SD	3.21	4.06	2.43	0.09	0.06	0.08
Min	4.95	5.30	2.28	0.72	0.37	0.37
Max	19.23	21.00	11.66	1.27	0.70	0.81

Tab. 1 - Dimensions of conjoined valves of *Rongatrypa xichuanensis* from the Upper Ordovician Shiyanhe Formation of Shiyanhe Section, Xichuan, Henan Province (N=190). Abbreviations for measured values are as follows: L=length, W=width, D=depth, SD=standard deviation.

	L	W	D	L/W	T/W	T/L
Mean	11.10	12.18	6.65	0.92	0.54	0.59
Median	11.49	12.32	6.70	0.91	0.54	0.59
SD	2.35	2.84	1.86	0.08	0.06	0.08
Min	4.48	4.58	2.26	0.73	0.40	0.40
Max	17.23	18.12	11.52	1.15	0.75	0.82

Tab. 2 - Dimensions of conjoined valves of *Rongatrypa xichuanensis* from the Upper Ordovician Shiyanhe Formation of Heishui'an Section, Xichuan, Henan Province (N=212). Abbreviations the same as for Tab. 1.

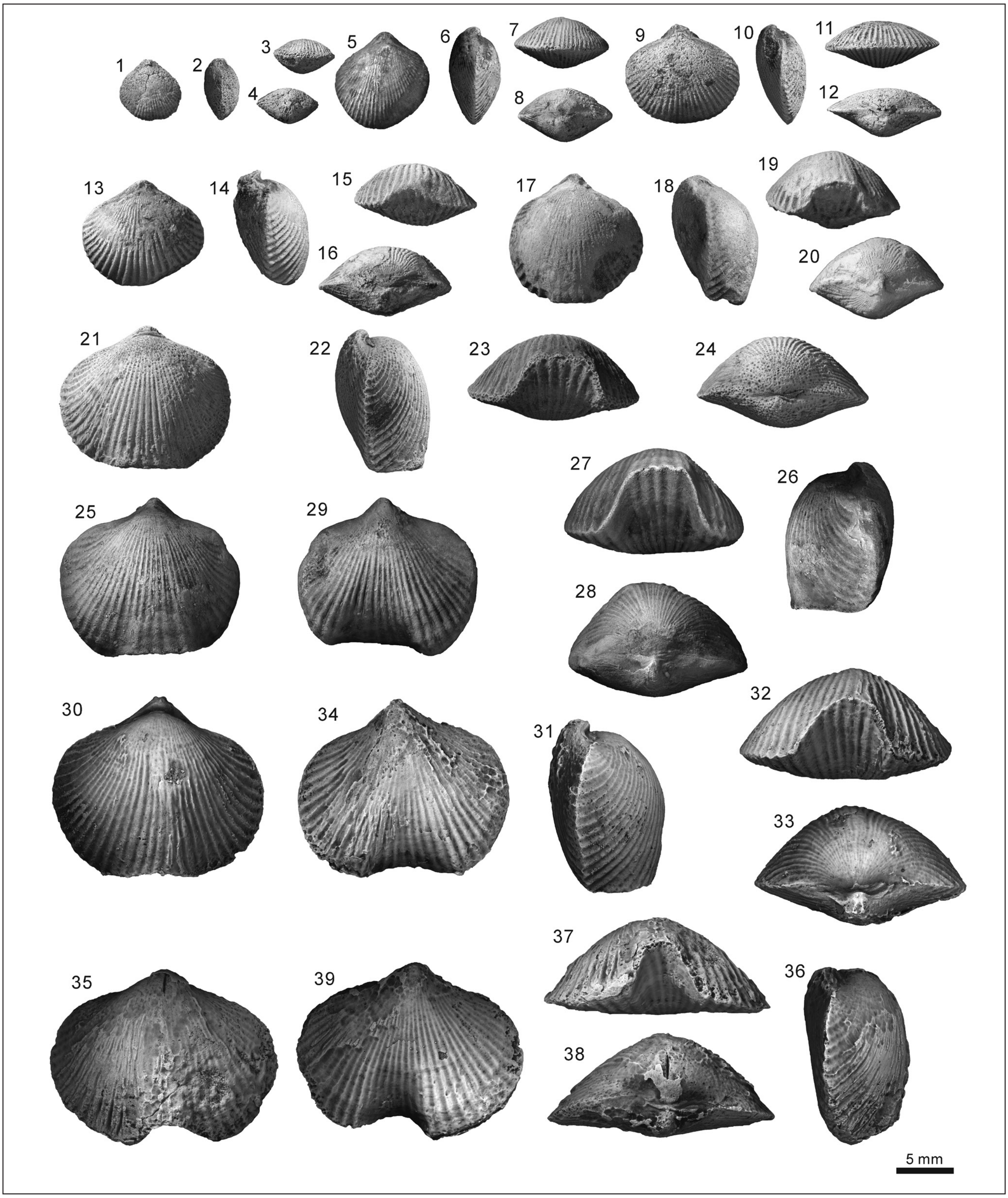

Fig. 2 - Variation in the size of *Rongatrypa xichuanensis* from the Upper Ordovician Shiyanhe Formation of Xichuan, Henan Province. 1–4) NIGP 169681; 5–8) NIGP 169682; 9–12) NIGP 169683; 13–16) NIGP 169684; 17–20) NIGP 169685; 21–24) NIGP 169686; 25–29) NIGP 169687; 30–34) NIGP 169688; 35–39) NIGP 169689. (1, 5, 9, 13, 17, 21, 25, 30, 35) dorsal views of conjoined valves; (2, 6, 10, 14, 18, 22, 26, 31, 36) lateral views of conjoined valves; (3, 7, 11, 15, 19, 23, 27, 32, 37) anterior views of conjoined valves; (4, 8, 12, 16, 20, 24, 28, 33, 38) posterior views of conjoined valves; (29, 34, 39) ventral views of conjoined valves.

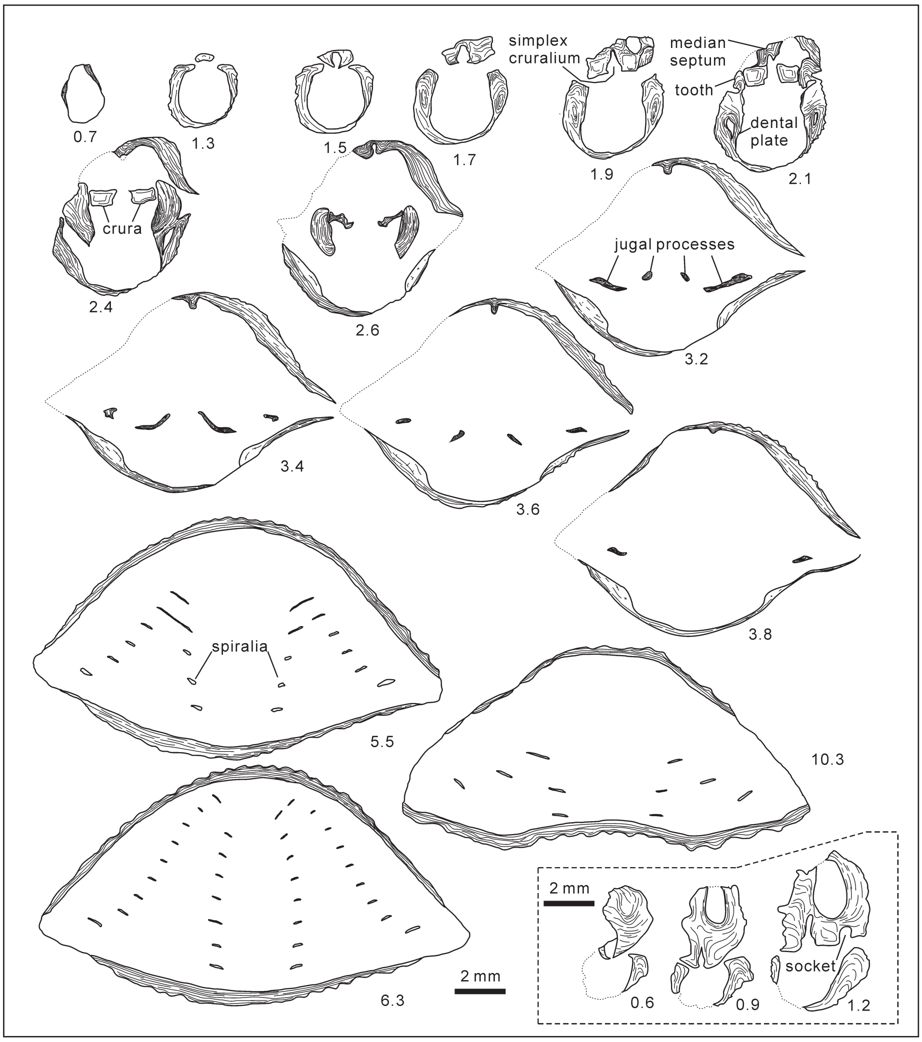

Fig. 3 - Sketches of internal structures of brachiopod *Rongatrypa xichuanensis* from the Upper Ordovician Shiyanhe Formation of Xichuan, Henan Province. Numbers below sketches indicate the distance of each section away from the posterior end of the shell. Three sketches surrounded by dashed lines are presented based on another specimen of the same species from the same bedding. Catalogue number of cellulose acetate peels is NIGP 169690.

become more strongly curved towards the dorsal valve through its ontogeny. Spiralia grow up from four whorls to up to nine with a gradual change from a truncated conical shape to a high steeple-like shape.

Remarks. *Rongatrypa xichuanensis* differs from *Rongatrypa rudis* (Rukavishnikova, 1956) in having a larger shell size, more convexo-plane outline, in the dorsal fold and ventral sulcus originating at approximate mid-length, and by the presence of a lower median ridge in dorsal cavity. *Rongatrypa zvontsovi* (Nikitin et al., 2003) has a smaller shell in comparison to *R. xichuanensis*, it is more biconvex and more elliptical in outline, and it has less than 30 ribs that are stronger. In comparison with *Rongatrypa instabilis* Popov & Cocks, 2014, *R. xichuanensis* has less numerous ribs (usually not exceeding 39 in number) and a weaker impressed triangular ventral muscle bounding scar. *Rongatrypa*? *sigangensis* (Xu, 1996) (from the same formation of Shiyanhe Section, Henan, central China – Xu 1996a) has a rectimarginate anterior commissure and rounded outline in mature shells, with less than 35 coarser radial costae and fewer spiralia whorls.

There are several reasons why *Rongatrypa xichuanensis* was previously regarded as belonging to other genera. The large degree of variation in shell size and shape at different growth stages (Fig. 2) creates the illusion of multiple genera in the systematic identification of smaller collections, but there is a clear, continuous gradational trend when a large collection of shells is analysed. The occurrence of dorsal median septum, as in *Rongatrypa,* was once regarded to have first evolved in the Silurian (Copper 2002), and the shell shape of *Rongatrypa* is very similar to the Silurian atrypide genus *Nalivkinia* Bublichenko, 1927, leading earlier works to assign this species to the Silurian genus. The poor preservation of many of the internal structures is critical to taxonomic assignment and recrystallization of the mantle cavities may also lead to some confusion.

Allometric Growth

Allometry refers to the differential growth rates of different body parts of an individual through its ontogeny (Gould 1966). Allometry in fossil brachiopods was first reported by Parkinson (1952) by comparing the relative growth rates of shell length, width, and depth for interpreting the outer morphological change of the shell in three dimensions through its ontogeny. This method has since been used in various brachiopod fossils in different periods for allometric study (e.g. Parkinson 1954, 1969; Westermann 1964; Liljeroth et al. 2017).

The relative growth rates of two measured quantities of one organism (i.e. shell length vs. shell width and shell depth vs. shell width of brachiopod *Rongatrypa xichuanensis*) can be expressed as a power law equation (Gould 1966):

$y=ax^k$ (Formula 1)

where x and y are two measured quantities of the shell, k is the scaling exponent of the law. A 'k' value of 1 indicates isometry, meaning the growth rates of two dimensions are equal. Any other value indicates allometry (Gould 1966).

The power law (Formula 1) can be transformed by natural logarithms on both sides:

$\ln y=k\ln x+\ln a$ (Formula 2)

where natural logarithms of measured qualities (i.e. ln$x$ and ln$y$) can be directly substituted into the formula for the linear regression, simplifying computing process and getting the linear regression trends on plots. The slope rate k has the same meaning as that in Formula 1.

The trends in plots of the natural logarithms of shell length vs. width and natural logarithms of shell depth vs. width of *Rongatrypa xichuanensis* match the linear regression equation (Formula 2), with r square values of 0.9190 and 0.8889 respectively (Fig. 4). The k values equalled to 0.8741 (0.8489–0.8998, 95% bootstrapped confidence intervals, N=1999) (Fig. 4, a) and 1.1494 (1.1110–1.1859, 95% bootstrapped confidence intervals, N=1999) (Fig. 4, b) respectively.

The results indicate a negative growth rate of shell length compared with shell width and a positive growth rate of shell depth compared with shell width. Differential growth rates of the shell length and width in outline can be visualized by the shape change in different sized shells, which gradually develops from a circular shape in juvenile shells to a subpentagonal or elliptical shape in larger shells (Fig. 2). This change in shell shape over ontogeny indicates allometric growth.

In this study, the allometric growth trends could have been caused by spiralium development. Small-sized shells typically have less than four whorls while large-sized shells have up to nine. The shape of the spiralia also changes from a flattened cone to a high-spired shape. Here we conjecture that the adjustment of the mantle cavity surrounding the spiralia to accommodate the change in size and shape of the spiralia may reflect in the change of the external shape of the shell.

Palaeoecological and palaeogeographical implications

The Shiyanhe Formation yields a variety of invertebrates including brachiopods, corals, cephalopods, bivalves, crinoids, gastropods, and trilobites. The tabulate coral *Agetolite*s is abundant in the upper part of the formation and it is interpreted to be buried in situ, indicating a shallow (euphotic zone), well-oxygenated, warm marine environment (Deng 1987; Liu et al. 1991). Other brachiopods, like *Altaethyrella,* are also found in the same horizon, indicating a shallow marine setting (Zhan & Li 1998; Sproat & Zhan 2018). These findings indicate that *Rongatrypa xichuanensis* inhabited a relatively shallow water marine environment in the photic zone with normal salinity.

The brachiopods from the Shiyanhe Formation in the study area are similar to those from the Xiazhen and Sanqushan formations in the JCY area of eastern China (Jiangshan, Changshan and Yushan counties in the border region of Zhejiang and Jiangxi provinces), both assemblages including *Mimella*?, *Sowerbyella*, *Triplesia*, *Altaethyrella*, and the atrypide brachiopods. These are the only two regions known to yield a Upper Ordovician shallow water brachiopod fauna on the South China palaeoplate.

Rongatrypa has still not been found in the JCY area though the detailed fossil collecting has been conducted since 1990s, perhaps due to different paleoenvironments. A sequence of dark grey thick-bedded argillaceous limestone with calcareous mudstone interbeds of the Xiazhen Formation (Katian, Upper Ordovician) in the JCY area reflects

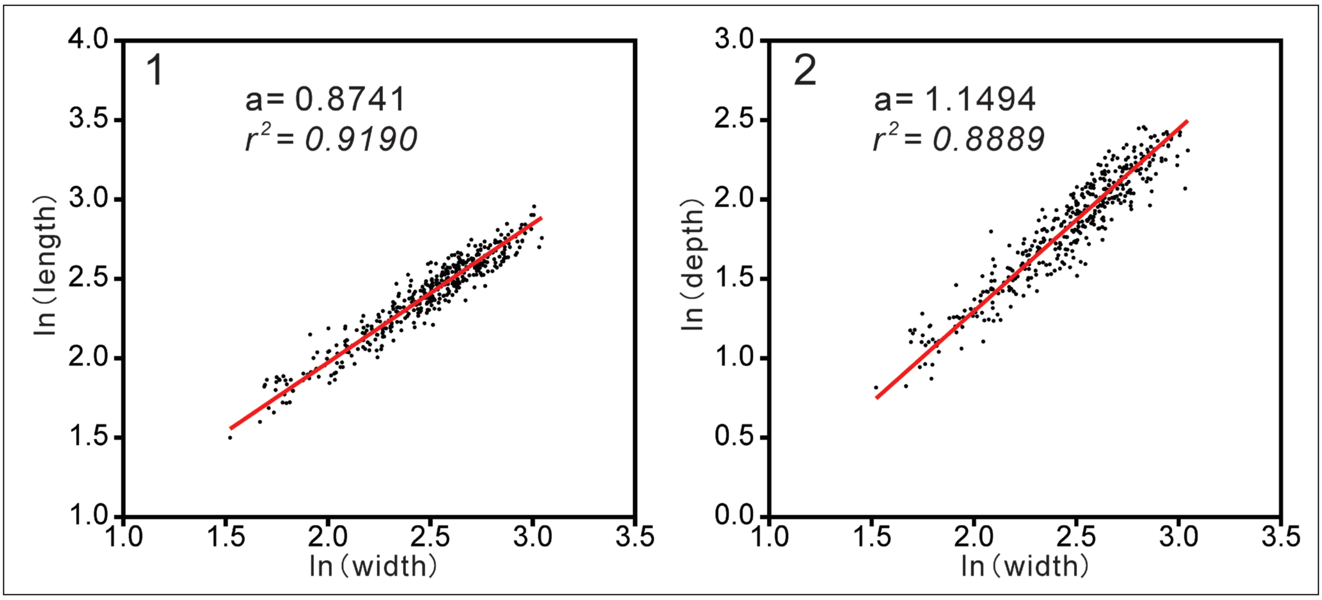

Fig. 4 - Bivariate plots of the natural logs of: 1) length vs. width, and 2) depth vs. width in measured shells of *Rongatrypa xichuanensis* from the Upper Ordovician Shiyanhe Formation of Xichuan, Henan province. R square valve of 0.9190 and 0.8889, k value of 0.8741 (0.8489–0.8998, 95% bootstrapped confidence intervals, N=1999) and 1.1494 (1.1110–1.1859, 95% bootstrapped confidence intervals, N=1999) in 1 and **2** respectively. Plot 2 is modified from Zhang et al. (2019).

a relative anaerobic environment compared with lithofacies in the study region, that may have prevented *Rongatrypa* from establishing in the JCY area.

The brachiopod *Rongatrypa* has thus far only been found in three of the Kazakh terranes: *Rongatrypa parudis* from the Chu-Ili terrane, *Rongatrypa zvontsovi* from the Selety terrane, *Rongatrypa instabilis* form the Chingiz-Tarbagatai terrane (Rukavishnikova 1956; Klenina 1984; Popov et al. 2000; Nikitin et al. 2003; Popov et al. 2014). This new occurrence of *Rongatrypa* expands its distribution to the South China paleoplate, supporting the conclusions of previous studies that show a close faunal relationship between Kazakh terranes and South China during the Late Ordovician (e.g. Zhan & Cocks 1998; Nikitin et al. 2006; Popov & Cocks 2014, 2017; Rong et al. 2014).

The brachiopod faunas of South China, North China, Tarim, and Kazakh terranes formed a Katian low-latitude province (Harper et al. 2013). However, opinions on the accurate locations of these landmasses have not reached a general consensus (e.g. Percival et al. 2011; Popov et al. 2009; Sohrabi & Jin 2013; Torsvik & Cocks 2017) due to a lack of geological data (especially palaeomagnetic data).

Popov & Cocks (2017) reconstructed the palaeogeography of the plates that now comprises China and Central Asia based on palaeontological data. The four landmasses on which *Rongatrypa* has been found all plot subequatorially (Selety terrane and Chingiz-Tarbagatai terrane at 10–20 degrees north latitude; Chu-Ili terrane and South China palaeoplate at 10–20 degrees south latitude), but they may have been in the path of cool ocean currents (Popov & Cocks 2017). *Rongatrypa* has not yet been found in North China and Tarim palaeoplates thus far, which were thought to have been affected by warm currents and closer to the palaeo-equator in the Late Ordovician (Popov & Cocks 2017). The discovery of *Rongatrypa* in Xichuan on the northern margin of South China palaeoplate provides additional evidence that the South China palaeoplate may have been influenced by cool currents during the Katian of the Late Ordovician (Jin et al. 2018).

Conclusions

The atrypide brachiopod *Rongatrypa xichuanensis* from the Shiyanhe Formation (Katian, Upper Ordovician) of Xichuan, Henan Province, central China is one of the early members of the Clintonellinae with dorsi-biconvex and subpentagonal outline, uniplicate anterior commissure, and a dorsal median septum. Bivariate plots of natural logarithms of the shell length, width, and depth indicate the allometric growth pattern in three dimensions perhaps related to the development of the spiralia.

Rongatrypa xichuanensis inhabited a shallow marine oxygenated environment in the photic zone with normal salinity, similar to other previously reported species from Kazakh terranes. The genus *Rongatrypa* has only been found on three Kazakh terranes and South China thus far, supporting a close affinity between these landmasses during the Late Ordovician.

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