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EDITED BY

Bertrand Lefebvre,
Université Claude Bernard Lyon 1, France

REVIEWED BY

Martin Vinther Sørensen,
University of Copenhagen, Denmark
Deng Wang,
Northwest University, China
Timothy Topper,
Swedish Museum of Natural History,
Sweden

*CORRESPONDENCE

Yunhuan Liu,
✉ yunhuanl@chd.edu.cn
Tiequan Shao,
✉ stotto@163.com

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Growth pattern of Fortunian scalidophoran sclerites

Jiachen Qin, Yunhuan Liu*, Tiequan Shao*, Mingjin Liu and Yanan Zhang

School of Earth Science and Resources, Chang'an University, Xi'an, China

Fortunian scalidophoran worms have shown high diversity, with 7 genera and species and 10 indeterminate forms. Current studies have mainly focused on morphology as well as early evolution, and studies on ontogeny have not been carried out due to the limited number of specimens. Here, we report new material of an Orsten-type preserved Indeterminate Form 3 from the Zhangjiagou section. Collected specimens of Indeterminate Form 3 with different annulus widths indicate the presence of several ontogenetic stages. We found newly formed sclerites on the annulus of Indeterminate Form 3 at different ontogenetic stages, suggesting that the sclerites of Indeterminate Form 3 become more numerous in addition to increasing in size during growth. The size of the large sclerites may also increase as the worms grow, however, their number may not change.

KEYWORDS

scalidophora, ontogeny, Fortunian stage, Zhangjiagou section, South China

1 Introduction

As the earliest unambiguous fossil record of ecdysozoans, scalidophorans showed high diversity during the early Cambrian Fortunian stage (~535 Ma), with 7 genera and species and 10 indeterminate forms (Liu et al., 2014a; 2019; Zhang et al., 2015; 2018; Shao et al., 2018a; 2020a; 2020b; Zhang, 2021; Qin et al., 2023). This is consistent with the hypothesis of molecular clock studies, which posits cycloneuralians may have originated in the Ediacaran and radiated during the early Cambrian period (Rota-Stabelli et al., 2013; dos Reis et al., 2016; Erwin, 2020).

These fossils have gone through three-dimensional phosphatization, i.e., Orsten-type preservation (Maas et al., 2006). Orsten-type fossils preserve the most primitive three-dimensional structures of organisms. This facilitates the reconstruction of body structures and means Orsten-type fossils are more conducive to the discussion of morphological functions, affinities, and paleoecology. In addition, the preservation of Orsten-types can preserve successive developmental stages of a species, thus facilitating the reconstruction of ontogeny (Maas et al., 2006). Contemporaneous cnidarians (*Olivoooides*, *Quadrapyrgites*, *Qinncyphus*, and *Hexaconularia*) have been found in a large number of fossils at different developmental stages, and more complete developmental sequences have been established on this basis (Dong et al., 2013; Han et al., 2013; Liu et al., 2014b; 2017; Steiner et al., 2014; Wang et al., 2017; Shao et al., 2018b; Zhang et al., 2023). In more recent strata, the developmental patterns of some paleoscolecid have also been discussed (Brock and Cooper, 1993; Müller and HinzSchallreuter, 1993; Zhang and Pratt, 1996; Duan and Dong, 2013; Xian et al., 2023).

In contrast to those, most Fortunian scalidophoran fossils are fragmented, and except for a little preserved introvert information, most of them only preserve the trunk part. The fossils of Fortunian scalidophorans are also relatively rare, and most of the species are only

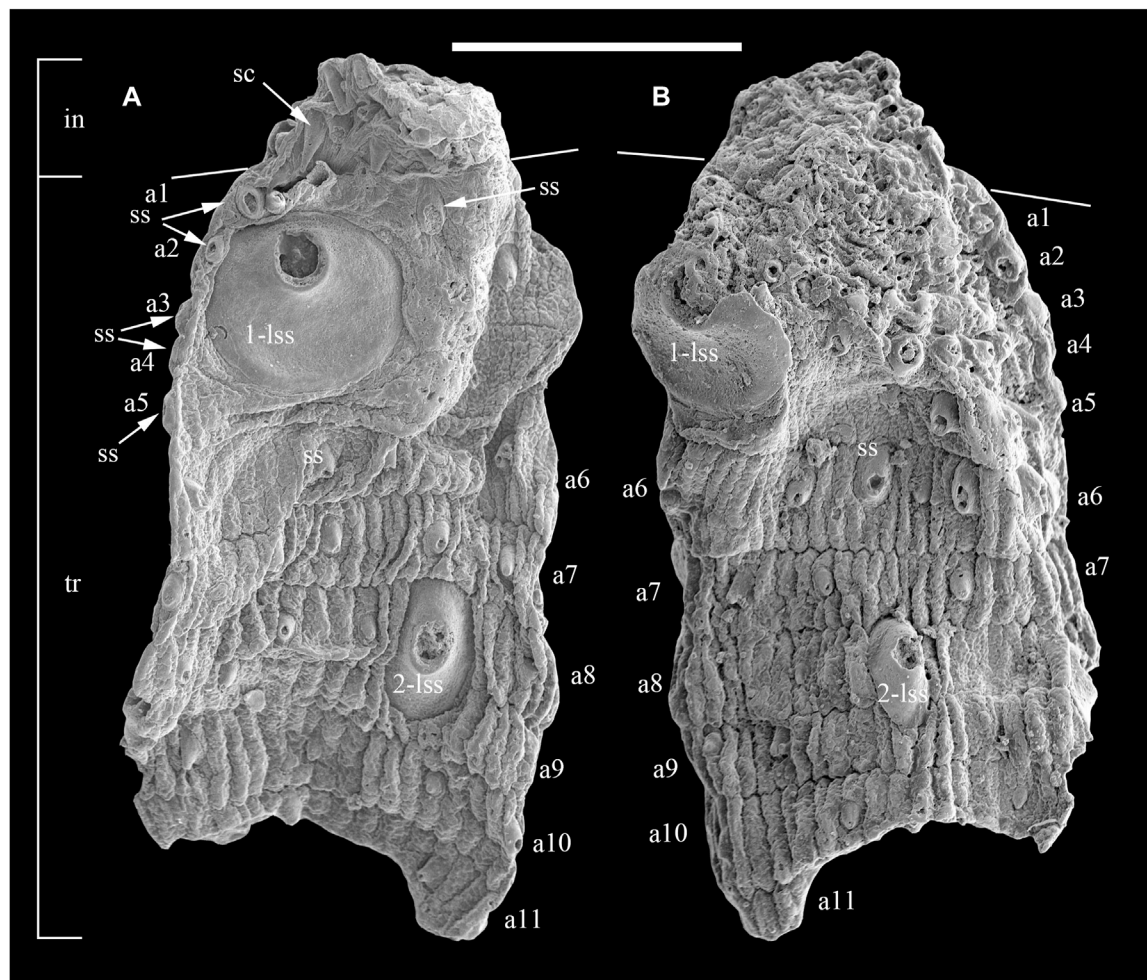


FIGURE 1

SEM images of Indeterminate Form 3 sensu Liu et al., 2019 from the Fortunian Zhangjiagou Section. (A and B) Two opposite sides of UMCU 23XX01. Abbreviations: in, introvert; tr, trunk; sc, scald; ss, spinose sclerite; 1-lss, first large spinose sclerite; 2-lss, second large spinose sclerite; (a1–a11), the 1st to 11th annuli. The scale bar represents 500 μm .

represented by a single specimen. Thus, the previous studies mainly focus on morphology, while a study of ontogenetic development has not been carried out.

Here, we describe a new specimen of Indeterminate Form 3 sensu Liu et al., 2019 (hereafter referred to as Form 3), which has narrower annuli and is probably at a younger developmental stage than the specimens already reported. This specimen also has a smaller number of sclerites and preserves some sclerites that are not yet fully developed. It is suggested that Form 3's armor will change as it grows, mainly by appearing larger and having more sclerites as it grows.

2 Material and methods

The studied specimens are now deposited at the University Museum of Chang'an University (UMCU), Xi'an, China. They were collected from the bottom of the Kuanchuanpu Formation in the Zhangjiagou section, Xijiang Country, Southern Shaanxi. This fossil-

rich horizon falls within the *Anabarites trisulcatus*–*Protohertzina anabarica* Assemblage Zone, with an estimated age of 531.8–536.4 Ma (Steiner et al., 2007; 2014), and belongs to the Fortunian Stage (Peng et al., 2020).

Rock samples were processed through standard acetic acid etching methods. Fossils were obtained from the undissolvable residues and picked out under a binocular microscope. Selected microfossils were mounted on stubs and coated with gold for observation under a Quanta 650 field-emission environmental scanning electron microscope at Chang'an University.

The specimens were measured using the ruler tool in Adobe Photoshop CS5, and the annuli with less deformation were mainly selected for the measurement.

3 Systematic paleontology

Ecdysozoa Aguilardo et al., 1997.

Cycloneuralia Ahlrichs, 1995.

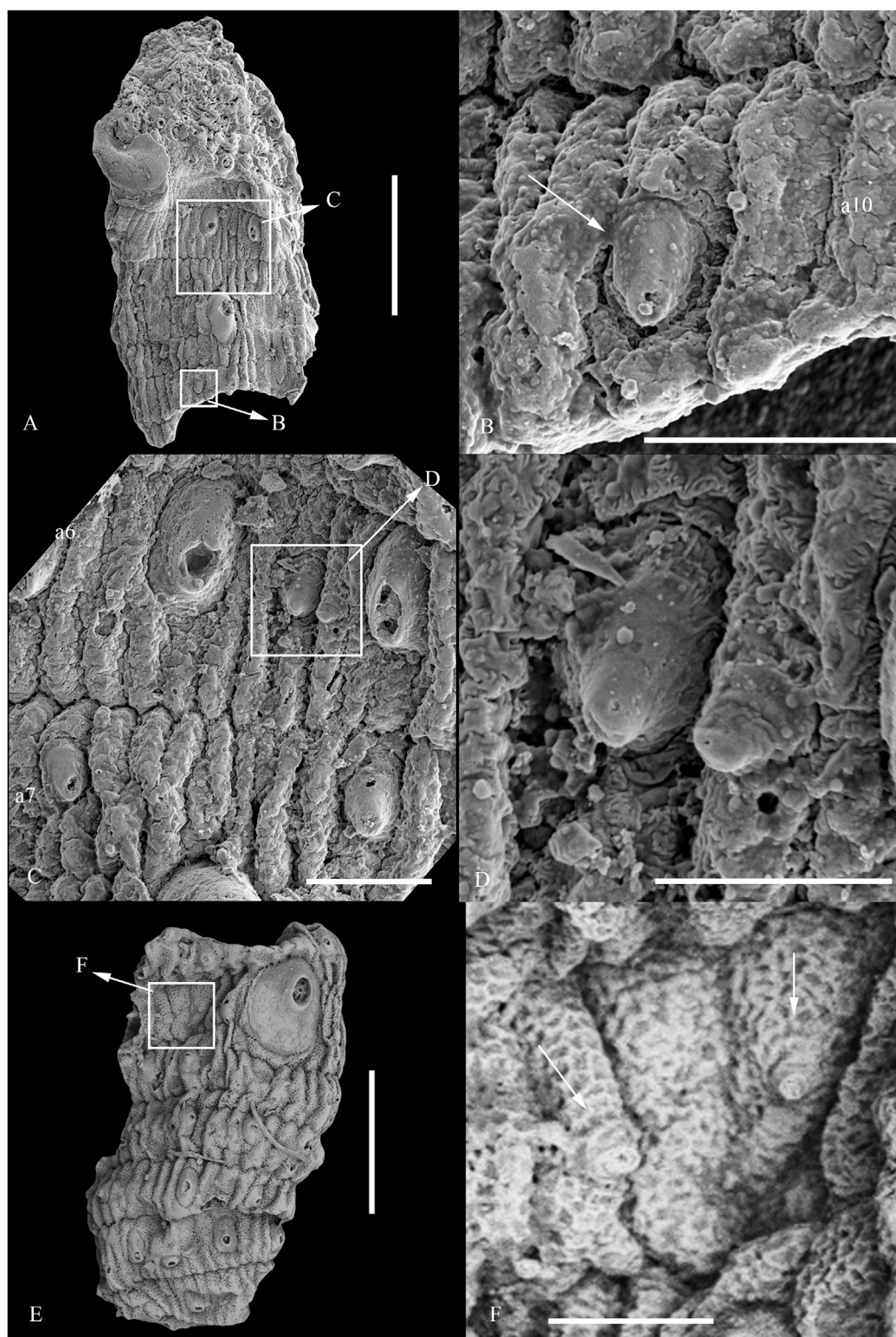


FIGURE 2 Newly formed sclerites of Indeterminate Form 3 *sensu* Liu et al., 2019. (A–D) UMCU 23XX01; (E–F) UMCU 22XX02; (B–C) close-up of A; (D) close-up of C; (F) close-up of (E). The scale bars represent 500 µm (A and E), 100 µm (B, C, and (F), and 50 µm (D).

Scalidophora [Lemburg, 1995](#).
 Indeterminate Form 3 *sensu* [Liu et al., 2019](#).
 (Figure 1Figure 2; Figure 3A–H)

2018 Form B [Zhang et al., Fig. 5.4](#).
 2019 Indeterminate Forms 3 [Liu et al., Fig 9D](#).
 2023 Indeterminate Form 3 [Qin et al., Figures 1–3](#).

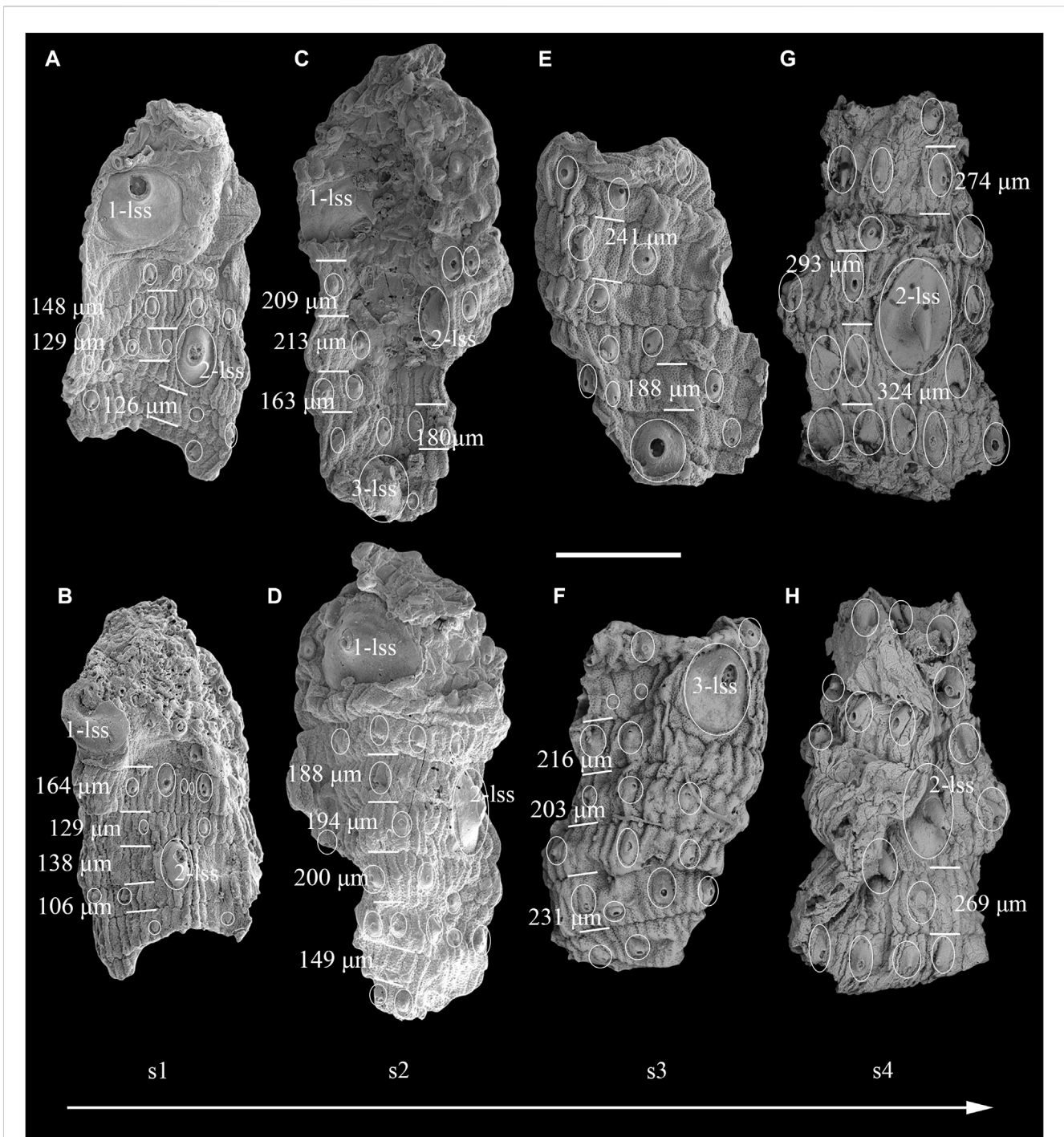


FIGURE 3

The possible developmental sequence of Indeterminate Form 3 *sensu* Liu et al., 2019. (A,B) UMCU 23XX01; (C,D) UMCU 22XX01; (E,F) UMCU 22XX02; (G,H) UMCU 16CHD0409-004. (C, D, E, and F) as cited in Qin et al., 2023; (G and H) as cited in Liu et al., 2019. The outlines of sclerites are marked by circles. Abbreviations: 1-lss, first large spinose sclerite; 2-lss, second large spinose sclerite; 3-lss, third large spinose sclerite; (s1–s4), developmental stages 1–4. The scale bar represents 500 μm.

3.1 Material

UMCU 23XX01 (Figure 1; Figure 2A–D; Figure 3A,B), UMCU 22XX01 (Figures 3C,D), UMCU 22XX02 (Figures 2E,F; Figure 3E,F), UMCU 16CHD0409-004 (Figures 3G,H).

3.2 Description

UMCU 23XX01 has two parts; the anterior part is the introvert and the posterior part is the trunk. The introvert has long, spine-link, internally hollow scalds. The trunk has 11 annuli with spinose sclerites, each with an enlarged base and a spine. The spinose

sclerites on the same annulus vary in size and are randomly and sparsely distributed. A pair of rounded large spinose sclerites are located at the anterior part of the trunk, and a pair of large oval spinose sclerites are located on the eighth and ninth annuli.

UMCU 22XX01 is described in Qin et al., 2023; UMCU 16CHD0409-004 is described in Liu et al., 2019. The description of UMCU 22XX02 follows Qin et al., 2023, with only minor revisions to the sclerites. Two small sclerites appear on its second annulus (Figure 3B in Qin et al., 2023; Figures 2E,F); they seem to be newly formed.

3.3 Occurrence

Kuanchuanpu Formation (Fortunian Stage), Zhangjiagou section, Xixiang County, Shaanxi Province, South China; *Anabarites trisulcatus-Protohertzina anabarica* Assemblage zone.

3.4 Comparison

The main part of the trunk of these specimens is very similar, upon which similarly shaped sclerites are randomly and sparsely distributed. Both UMCU 23XX01 and UMCU 22XX01 have two pairs of large sclerites, and the first pair of large sclerites are both found in the anterior part of the trunk, and the second pair of large sclerites are both found in the middle of the trunk. This suggests that these specimens are from the same species, and the position of the large sclerites on the trunk may be fixed. There are at least five large sclerites (lss, Figure 1; Figure 3) on the trunk, in order from anterior to posterior: the first pair of large sclerites (1-lss), the second pair of large sclerites (2-lss), and the third large single sclerite (3-lss). Comparisons of Form 3 with other worms can be found in Liu et al., 2019 and Qin et al., 2023 and will not be repeated here.

Because the position of the large sclerites on the trunk may be fixed, when using UMCU 22XX01 as a reference, UMCU 23XX01 may represent the first two-thirds of it. UMCU 16CHD0409-004 has a pair of oval large spinose sclerites that may represent the middle part of UMCU 22XX01. The large rounded sclerites in UMCU 22XX02 may not correspond to the first large paired sclerites in UMCU 23XX01 and UMCU 22XX01: 1) the large sclerites in UMCU 22XX02 are not paired (also possibly due to incomplete preservation); 2) the first large paired sclerites in UMCU 22XX01 are next to triangular sclerites rather than oval sclerites as in UMCU 22XX02. Therefore, the large sclerite in UMCU 22XX02 may correspond to the single large sclerite located at the posterior part of the trunk in UMCU 22XX01.

3.5 Remarks

It is generally accepted that the annulus widens as the worm grows, both in extant scaldiphorans (Neuhauser, 1995) and in paleoscolecid, which are considered to be early scaldiphorans (cycloneuralians) (Brock and Cooper, 1993; Müller and HinzSchallreuter, 1993; Zhang and Pratt, 1996; Duan and Dong, 2013; Xian et al., 2023), so we divided these four specimens into four developmental stages according to the width of the annulus

(Table 1; Figure 3s1-s4). According to these specimens, the size of the sclerites also gradually increases with growth (Table 1).

4 Discussion

Among the previously reported Fortunian armored scaldiphorans, most of them have similar morphology and size to the sclerites within the same annulus, such as *Zhongpingscolex* (Shao et al., 2020a), *Shanscolex* (Liu et al., 2019), and *Dahescolex* (Shao et al., 2020b), Forms 1-3 and 5-6 (Liu et al., 2019; Qin et al., 2023).

UMCU 23XX01 was identified as Form 3, but its sclerites within the same annulus are clearly different in size, and some of the sclerites appear to be recently formed and are only one-fifth the size of other sclerites in the same annulus (Figure 2D). We re-examined the material previously attributed to Form 3 and also found two small sclerites in UMCU 22XX02 (Figures 2E,F). Compared to UMCU 23XX01, UMCU 22XX02 is at a more advanced developmental stage, and newly formed sclerites were found in worms at different developmental stages, possibly suggesting that the sclerites of worms not only become larger in size during development but also increase in number.

UMCU 23XX01 (Figure 3s1, Figure 1; Figure 2A-D; Figure 3A,B) has a low number of sclerites (about 4-5 sclerites on one annulus on average) and a high percentage of newly formed sclerites (if the sclerite in the middle of the a6 in UMCU 23XX01 (Figure 1B; Figure 2C) is considered as normal size, all other sclerites of the same type in UMCU 23XX01 are may be newly or recently formed, they are morphologically similar and differ only in size). At this stage, the number of newly formed sclerites is high, indicating a peak in sclerite development and that the sclerites are developing faster. In addition, there are smaller sclerites on almost every annulus of UMCU 23XX01, which means that the increase in sclerites may occur simultaneously throughout the trunk of the worm. The number and size of sclerites are greater in UMCU 22XX02 (Figure 3s3, Figures 2E,F and Figure 3E,F); there are only two newly formed sclerites at this stage, and the number of newly formed sclerites is reduced, indicating that the sclerite development is slowed down at this time. The high number of sclerites in UMCU 16CHD0409-004 (Figure 3s4, Figures 3G,H) (about six sclerites on one annulus on average: this specimen is partially folded and there should be a higher number of sclerites) did not reveal newly formed sclerites, indicating that the number of sclerites may not be increasing at this stage. However, because these fossils are fragmented, we cannot be sure whether newly formed sclerites are still present in the unpreserved parts of these fossils so it is also possible that the number of sclerites continues to increase. Whether or not the number of sclerites increases after Figure 3s4, the worms may continue to grow and the size of the sclerites may increase accordingly.

The common sclerites develop within a single annulus; the large sclerite is more unusual in that it can span 2-3 annuli. The size of large sclerites may also increase as the worms grow (Table 1), however, based on the specimens at hand, their numbers may not change (Figure 3).

The growth of the worm is accompanied by periodic molting, with the annulus widening as the worm grows. However, it is not

TABLE 1 Measurements.

Collected number	Annulus		Sclerites		First large paired sclerites (1-Iss)		second large paired sclerites (2-Iss)		Large single sclerite (3-Iss)	
	L (μm)	L (μm)	W (μm)	L (μm)	W (μm)	L (μm)	W (μm)	L (μm)	W (μm)	
UMCU 23XX01	106-164	23-105	11-58	326	279	233	140			
UMCU 22XX01	149-213	100	60	385	420	330	140	285	150	
UMCU 22XX02	188-241	104	70					344	266	
UMCU 16CHD0409-004	269-324	200	95			460	280			

clear whether sclerites increase and grow simultaneously with worm growth or whether an increase in sclerites requires more frequent molting. Therefore, the rate of increase in the number of sclerites does not represent the growth rate of the worms, and there may be no correlation between them.

5 Conclusion

We have reported new material of Indeterminate Form 3 *sensu* Liu et al., 2019 from the Fortunian Zhangjiagou section, southern Shannxi, South China. Based on the material at hand, we established a possible partial developmental sequence of Indeterminate Form 3 *sensu* Liu et al., 2019, which illustrates that during its growth, in addition to the size of the sclerites increasing, the number of sclerites also increases. Large sclerites only increase in size with growth but not in number.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding authors.

Author contributions

JQ coordinated the field work, preparation and curation of fossils, wrote the manuscript, and processed the images. YL edited the manuscript. ML, TS, and YZ assisted in collecting the rock samples in the field. All authors contributed to the article and approved the submitted version.

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