古生物学报, 63(2): 171–182 (2024年6月)
Acta Palaeontologica Sinica, 63(2): 171–182 (June 2024)

·研究论文·

DOI: 10.19800/j.cnki.aps.2023052

寒武纪幸运期陕西宽川铺生物群疑难化石装饰玲珑球发育生物学*

刘 威[1,2] 项 楷[1,2] 殷宗军[2,3**]

1 造山带与地壳演化教育部重点实验室, 北京大学地球与空间科学学院, 北京 100871;
2 现代古生物学与地层学国家重点实验室, 中国科学院南京地质古生物研究所, 南京 210008;
3 中国科学院大学南京学院, 南京 211135

提要 作为磷酸盐化特异埋藏微体化石库, 寒武纪宽川铺生物群保存了大量软躯体动物胚胎和成体、藻类和多门类小壳化石, 为理解寒武纪大爆发初期的生物圈提供了重要的埋藏窗口。但前人的研究主要聚焦以橄榄蛋(*Olivooides*)为代表的刺细胞动物和以始祖动吻虫(*Eokinorhynchus*)等蠕虫为代表的蜕皮动物化石, 对化石库中大量疑难类群的探索尚有不足。本文报道了宽川铺生物群中一类新发现的疑难化石装饰玲珑球*Linglongsphaera ornata* n. gen. n. sp.。装饰玲珑球整体呈球状, 直径在544—1088 μm之间, 表面具瘤状突起装饰, 内部由平均直径24 μm的细胞组成。处于不同发育阶段的装饰玲珑球发育有8到180余个数量不等的腔室, 单个腔室的体积随着腔室数量的增长先增加而后减小, 分布的位置也从周缘直至布满整个内部, 最终腔室总体积占个体总体积的36%左右后保持稳定。根据现有证据, 笔者推测装饰玲珑球可能代表了一类已经灭绝的具有多细胞发育阶段的真核生物, 可能与某些多细胞藻类有较近的亲缘关系, 但具体的系统分类位置仍然不明。该研究为理解宽川铺生物群化石组合面貌和寒武纪大爆发初期生物圈的组成提供了新的线索。

关键词 装饰玲珑球 疑源类 寒武纪幸运期 宽川铺生物群 X射线显微断层成像

中文引用 刘威, 项楷, 殷宗军, 2024. 寒武纪幸运期陕西宽川铺生物群疑难化石装饰玲珑球发育生物学. 古生物学报, 63(2): 171–182. DOI: 10.19800/j.cnki.aps.2023052

英文引用 Liu Wei, Xiang Kai, Yin Zong-jun, 2024. Developmental biology of a problematic taxon, *Linglongsphaera ornata* n. gen. n. sp., from the Kuanchuanpu Biota (Fortunian, Cambrian), Shaanxi, China. Acta Palaeontologica Sinica, 63(2): 171–182. DOI: 10.19800/j.cnki.aps.2023052

Developmental biology of a problematic taxon, *Linglongsphaera ornata* n. gen. n. sp., from the Kuanchuanpu Biota (Fortunian, Cambrian), Shaanxi, China

LIU Wei[1, 2], XIANG Kai[1, 2], YIN Zong-jun[2, 3]

1 *Key Laboratory of Orogenic Belts and Crustal Evolution, Ministry of Education, and School of Earth and Space Sciences, Peking University, Beijing* 100871, *China*;
2 *State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing* 210008, *China*;
3 *Nanjing College, University of Chinese Academy of Sciences, Nanjing* 211135, *China*

Abstract The Kuanchuanpu Biota (535 Ma; Fortunian, Cambrian) represents an exceptionally phosphatized fossil

收稿日期: 2023-11-23; 改回日期: 2024-04-10; 录用日期: 2024-04-11

* 国家自然科学基金委优秀青年基金(42022010)、国家重点研发计划项目(2022YFF0800100)和中国科学院青年创新促进会优秀会员项目(Y2021083)联合资助。

** 通讯作者: 殷宗军, 研究员, e-mail: zjyin@nigpas.ac.cn

Lagerstätte, yielding abundant fossils of embryonic and adult soft-bodied animals, small shelly fossils, and algae. This biota serves as a crucial taphonomic window for unraveling the marine ecosystem during the very beginning of the Cambrian Explosion. However, previous studies have primarily focused on well-known groups such as the cnidarians represented by *Olivooides* and the ecdysozoans represented by scalidophorans (e.g., *Eokinorhynchus*), leaving numerous enigmatic taxa of this fossil assemblage uninvestigated. This study reports a newly discovered enigmatic fossil taxon, *Linglongsphaera ornata* n. gen. n. sp., from the Kuanchuanpu Biota. This taxon is characterized by a spherical body with its diameter ranging from 544 to 1088 μm. Its surface is ornamented with nodular projections, and its interior consists of cells with an average diameter of 24 μm. During different developmental stages, *Linglongsphaera ornata* exhibits a variable number of chambers ranging from 8 to over 180. The volume of an individual chamber increases at the beginning and then gradually decreases as the overall number of chambers increases. The chambers are distributed from the periphery to throughout the interior, with the total volume of chambers being stabilized at approximately 36% of the total volume of the organism body. Based on available evidence, we propose that *Linglongsphaera ornata* may represent an extinct multicellular eukaryote, with possible close affinity to multicellular algae. However, its precise classification and phylogenetic position remain uncertain. This discovery contributes to a more comprehensive understanding of the diverse and enigmatic taxa of the Kuanchuanpu Biota, and sheds light on the complex early Cambrian biosphere during the Cambrian Explosion.

Key words *Linglongsphaera ornata*, developmental biology, Cambrian Fortunian, Kuanchuanpu Biota, X-ray microtomography

SYSTEMATIC PALEONTOLOGY

Kingdom Eukaryota

Phylum, Class, Order, *et* Family Incertae sedis

Genus *Linglongsphaera* n. gen.

urn:lsid:zoobank.org:act:DA126062-9B6E-4A83-BF77-E95C8811780B

Etymology The generic name is combined from '*Linglong*', Chinese, a kind of traditional Chinese handicraft, which shares a resemblance with the fossils, and '*sphaera*', Latin, referring to the spherical shape of the fossils.

Type species *Linglongsphaera ornata* n. gen. n. sp.

Diagnosis Same as for the type species.

***Linglongsphaera ornata* n. gen. n. sp.**

urn:lsid:zoobank.org:act:92A9A1D2-B211-42C3-BE9D-AD57B7CFBC93

(Figs. 1–3)

Etymology The species epithet, '*ornata*', Latin, refers to the surface ornaments of the fossils.

Holotype Specimen NIGP 203476 is designated as the holotype (Fig. 3-D), and NIGP 203465 (Fig. 1-E) and NIGP 203471 (Fig. 2-C) are designated as the paratypes.

Diagnosis Spherical body with diameter ranging from 544 to 1088 μm (average 751 μm); intact surface decorated with nodular protrusions. Eight to 180 internal chambers slightly variable in size and morphology at different developmental stages. Space outside of the chambers occupied by thousands of small spherical structures with an average diameter of 24 μm.

Description Spherical body with diameter ranging from 544 to 1088 μm (average 751 μm); intact specimen surface decorated with nodular protrusions between 33 and 50 μm in diameter. Eight to over 180 internal chambers slightly variable in size and morphology at different developmental stages. Internal space outside of the chambers occupied by thousands of small spherical structures with an average diameter of 24 μm. Chambers of incomplete, naked specimens fully exposed, forming circular depressions resembling a traditional Chinese handicraft called "linglong ball" (Fig. 1). In early developmental stages, fewer chambers present and shallow or hemispherical depressions unevenly distributed on peripheral margin. Each chamber with only one large circular opening; some adjacent chambers connected (Fig. 2). In later stages, number of chambers increasing, with chambers gradually concentrating taking up a position at the core of the specimen. At this stage, chambers approximately spherical, and peripheral chambers connected to outside through 1 to 4 smaller circular openings, and some adjacent chambers connected via channels (Fig. 3).

Remarks The current species is similar in size, morphology, and surface ornamentation to the co-occurring *Archaeooides* (Qian, 1977; Pyle *et al*., 2006; Yin *et al*., 2018). However, the internal structures of *Archaeooides* significantly differ from those of *Linglongsphaera* (Yin *et al*., 2018). Bodies of *Archaeooides* possess thick cysts without developed openings and lack numerous internally partitioned chambers, suggesting that a close affinity between *Archaeooides* and *Linglongsphaera* is less likely.

Locality and horizon Hexi section, Xixiang County, Shaanxi Province, China; Kuanchuanpu Formation (Fortunian, Cambrian). All the specimens examined in this study are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, Jiangsu Province, China.

1 前 言

寒武纪大爆发作为地质历史上最引人瞩目的生物演化事件之一, 诞生了包括从简单的海绵动物到复杂的脊索动物等几乎全部现生动物门类, 和至少6种难以归类到现生任何一个动物门的类群(张兴亮和舒德干, 2014; 朱茂炎等, 2019)。在寒武纪大爆发之后的整个显生宙, 基本上没有新的门一级的动物出现, 动物界各门类躯体构型的演化高度保守, 奠定了其后5亿多年的演化基本框架。关于寒武纪大爆发的详细过程前人提出了幕式演化模型: 埃迪卡拉纪早期的隐形阶段、埃迪卡拉纪晚期的序幕阶段、寒武纪纽芬兰世大爆发第一幕、寒武纪第二世到苗岭世的大爆发第二幕(朱茂炎等, 2019)。其中寒武纪纽芬兰世的大爆发第一幕爆发的生物多样性很高, 成为了显生宙的起点。宽川铺生物群正是寒武纪纽芬兰世具有代表性的特异埋藏化石记录, 除了保存有多门类小壳化石外, 还产出大量三维磷酸盐化保存的软躯体微型动物及其胚胎化石(Bengtson and Yue, 1997; Han *et al*., 2010, 2013; Dong *et al*., 2013, 2016; Liu *et al*., 2014, 2022; Steiner *et al*., 2014; Zhang *et al*., 2015; Duan *et al*., 2017; Wang *et al*., 2020)。与埃迪卡拉纪瓮安生物群多保存早期卵裂期胚胎状化石不同, 宽川铺生物群多保存发育晚期阶段的标本(Donoghue *et al*., 2015; Bottjer *et al*., 2020), 这为探讨早期动物个体发育过程、动物躯体构型的演化过程以及实证检验动物起源和早期演化相关的理论模型提供了绝无仅有的埋藏窗口。以往对宽川铺生物群的研究主要聚焦软躯体动物化石, 尤其是动物胚胎和有吻刺动物(Bengtson and Yue, 1997; Dong *et al*., 2013; Han *et al*., 2013, 2017; Duan *et al*., 2017)。但是, 宽川铺生物群中还保存有许多复杂的疑难真核生物(Liu *et al*., 2023), 相比之下它们受关注的程度较低。研究宽川铺生物群中除后生动物之外的复杂真核生物化石, 不仅对了解其生物多样性及生态具有重要意义, 而且对理解寒武纪大爆发初期生物圈复杂程度和真核生物的演化提供新的启示。因此, 本文重点研究了在宽川铺生物群中新发现的一类具有表面装饰和内部结构的球形化石, 利用高分辨率X射线显微断层成像技术(简称显微CT, Micro-CT)重建了它的三维结构, 并在此基础上讨论了它的发育序列和可能的亲缘关系。

2 地质背景、研究材料和研究方法

宽川铺生物群产自寒武系底部宽川铺组, 广泛分布于扬子地台北缘—西北缘。其经典产出地点有陕西省汉中市宁强县宽川铺乡石钟沟剖面、陕西省汉中市西乡县大河镇窝坝河村张家沟剖面、四川省广元市南江县新立乡九岭村剖面。宽川铺生物群包含多门类小壳、刺细胞动物(含胚胎化石)、蜕皮动物等, 其组合面貌属于三叉阿纳巴管—原牙形赫兹刺组合带(*Anabarites trisulcatus–Protohertzina anabarica* Assemblage Zone), 时代应为寒武纪纽芬兰世幸运期(Steiner *et al*., 2014; Yin *et al*., 2018)。Peng等人认为该小壳化石组合带的年龄大约为532—537 Ma (Peng *et al*., 2020), Steiner等给出的估计年龄为535 Ma (Steiner *et al*., 2014)。

本文研究的化石材料来自陕西省西乡县大河镇窝坝河村张家沟剖面, 前人也称之为河西剖面(赵多多等, 2021; Steiner *et al*., 2014)。该剖面宽川铺组厚约22 m, 其岩性主要为块状磷质碎屑灰岩、细晶灰岩和白云质灰岩。其中磷质生物碎屑灰岩为宽川铺生物群的核心产出层位(Yin *et al*., 2018)。

磷酸盐化的化石赋存于块状磷质碎屑灰岩中, 可以使用冰醋酸溶液处理后将化石从围岩中分离。酸处理获得的重要标本使用场发射扫描电子显微镜(TESCAN Maia3)进行观察。为研究化石内部结构, 笔者采用X射线显微断层成像技术(吴素萍等, 2018)重建了103枚标本的三维结构。扫描使用的设备是Zeiss Xradia 620 Versa。为获得高衬度的图像, X射线管工作电压设定为50—80 kV, 对应的功率为4—10 W。扫描过程中使用了4倍光学镜头, 获得的体像素大小为0.707—1.35 μm。初筛标本内部结构时每次扫描采集了401张X射线投影图。针对内部结构保存较好的标本, 为保证高分辨率下图像仍然具有高信噪比, 每一次扫描采集3201张X射线投影图。根据标本内部对X射线的吸收程度不同, 而将每张投影图的曝光时间设定为1—8.7 s。部分

标本的图像采用了基于深度学习的Zeiss Deepre-con AI重构技术, 获得了更高衬度和更高分辨率的图像堆栈。扫描过程中选用了LE1或者LE2型X射线滤镜以避免图像中出现射线硬化伪影。所有标本的体数据均采用VGstudio Max (2023.2版本)处理, 统计分析中涉及的所有测量数据包括标本或结构的直径、体积等均在该软件中测量获得。

本研究涉及的所有实验分析工作, 包括酸处理、扫描电镜成像和显微CT扫描, 均在中国科学院南京地质古生物研究所实验技术中心完成。

3 系统古生物学

本研究共收集了三百余枚标本, 对其中103枚进行了高分辨率X射线断层扫描, 重构了它们的三维结构, 并将其命名为装饰玲珑球*Linglong-sphaera ornata* n. gen. n. sp.。

真核生物界 Kingdom Eukaryota

门纲目科未定 Phylum, Class, Order, *et* Family Incertae sedis

玲珑球属 Genus *Linglongsphaera* n. gen.

urn:lsid:zoobank.org:act:DA126062-9B6E-4A83-BF77-E95C8811780B

词源 “*Linglong*”, 中文“玲珑球”, 为中国一种传统工艺品, 该种与其外形相似; “*sphaera*”, 拉丁文, 示标本的球形形态。

模式种 *Linglongsphaera ornata* n. gen. n. sp.

属征 球状化石, 直径544—1088 μm; 完整标本表面具瘤状突起装饰; 标本内部发育8到180余个腔室, 不同发育阶段标本的腔室在尺寸和形态上略有不同; 腔室之外的部分由成千上万小球结构组成, 小球平均直径24 μm。

装饰玲珑球(新种) *Linglongsphaera ornata* n. gen. n. sp.

urn:lsid:zoobank.org:act:92A9A1D2-B211-42C3-BE9D-AD57B7CFBC93

(图1—3)

词源 “*ornata*”, 拉丁文“具装饰的”, 示新种表面的瘤状突起装饰。

模式标本 正模标本NIGP203476 (图3-D); 副模标本NIGP203465 (图1-E)、NIGP203471 (图2-C)。

特征 同属征。

描述 玲珑球的形状一般为椭球形到球形(图1—3), 部分标本由于在埋藏过程中遭受挤压呈现次生软变形结构(图2-D1, 3-C1, 3-D1)或破损(图1)。玲珑球的直径范围为544—1088 μm, 平均直径为751 μm (标准差=130, 标本数n =103), 统计结果显示标本直径服从正态分布(图5-A, Kolmogo-rov-Smirnov检验, p =0.54898)。

镜下挑样的过程中最容易识别裸露的装饰玲珑球。它们表面可见数量不等的圆形凹坑(图1, 2), 显著区别于宽川铺生物群中已报道过的多种球状化石, 包括胚胎阶段的橄榄蛋(*Olivooides*)、古球蛋(*Archaeooides*)、假球蛋(*Pseuooides*)和胚胎阶段的四方塔形壳(*Quadrapyrgites*)等(赵多多等, 2021; Han *et al*., 2013; Steiner *et al*., 2014; Dong *et al*., 2016; Wang *et al*., 2017)。保存完整的玲珑球标本表面具有一层带有瘤状突起装饰的包膜(图2-B1, 2-C1, 2-C4, 3-B1, 3-C1, 3-C4), 包膜表面可以观察到数量不等的小孔(图3)。瘤状突起较为扁平, 直径为33—50 μm。显微CT数据显示, 小孔内部是球形腔室(图3), 与裸露的玲珑球表面观察到的凹坑一致。尽管由于埋藏和成岩过程改造的影响, 大部分玲珑球标本带装饰的外包膜没有保存(96枚未保存), 但仍然可以在7枚标本中观察到明显的瘤状突起。

显微CT数据揭示, 整个标本内部在腔室之外充满了小球结构(图2), 不同标本中小球直径范围基本在17—35 μm, 平均24 μm。小球保存的形式多样, 部分小球内部保存为空腔(图1-B2, 2-A3, 2-A4, 2-C3, 2-C5, 3-D3, 3-D8), 而另一些则充填了矿物, 充填的矿物密度较基质密度高则偏亮色(图2-A3, 2-B3, 2-C3, 3-A3, 3-E3)或较基质密度低则偏暗色(图2-C5, 3-A3, 3-D3, 3-D8)。保存较好的小球边缘保存了一层暗色膜状结构(图2-C5绿色箭头所示), 是典型的生物学特征。而部分小球暗色膜边缘保存为一层亮色磷酸钙镀层(coating)或者内衬(lining)(图2-A4, 2-C5, 3-D08)。

标本内部发育腔室是玲珑球最典型的特征。根据腔室的形态及分布规律可将标本划分为早期和晚期两个不同的发育阶段(表1)。早期阶段腔室数量较少, 通常为8—14个, 腔室总体积占标本总体

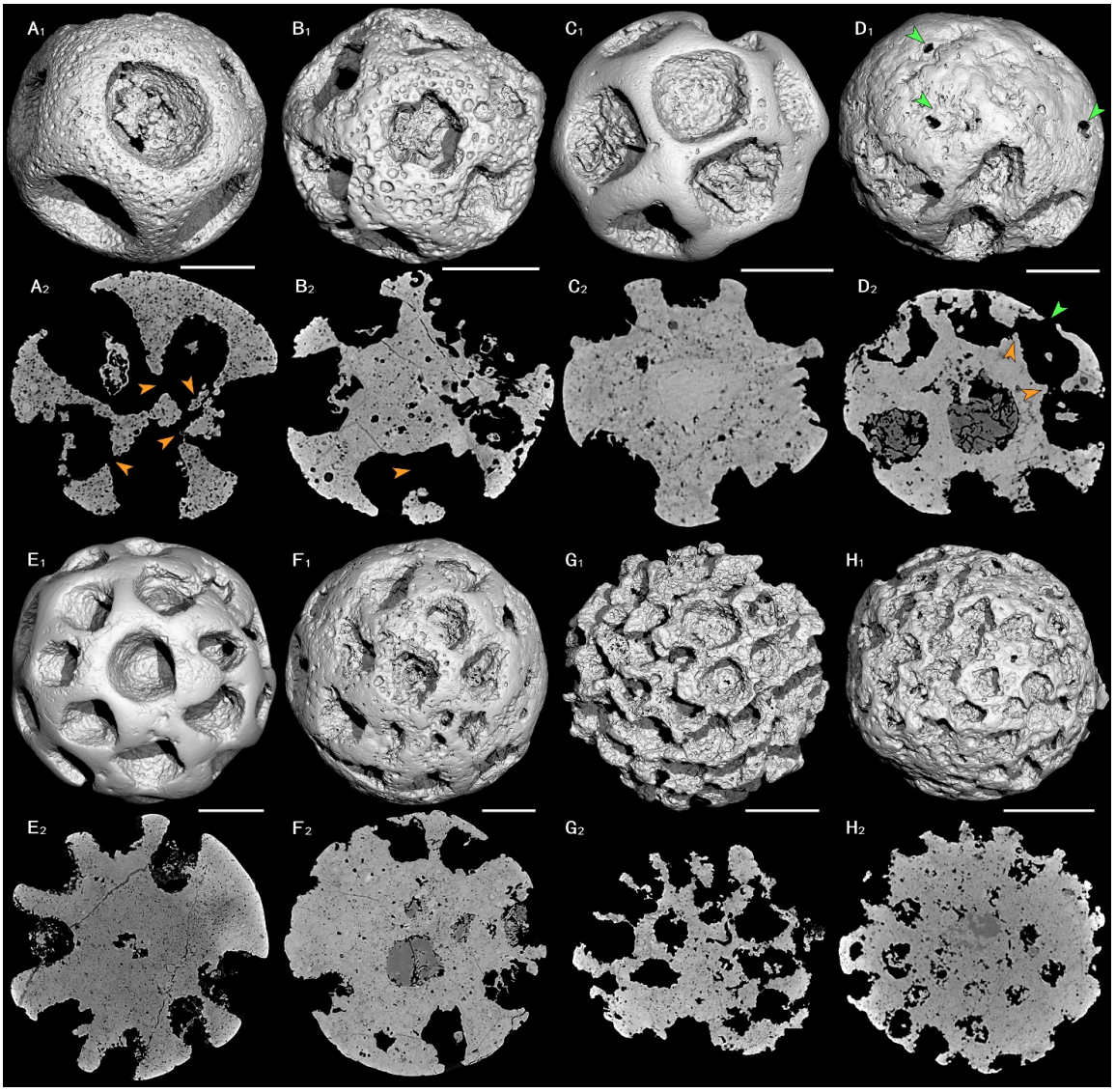

图 1　寒武纪宽川铺生物群装饰玲珑球(*Linglongsphaera ornata*)标本

Fig. 1　*Linglongsphaera ornata* from the early Cambrian Kuanchuanpu Biota

A1–**H1**. 显微 CT 等值渲染图, 显示裸露标本发育有不同数量的腔室, A–H 标本中腔室数量分别为 10、16、21、26、34、39、130、186。D1 标本保存了部分外包膜, 部分腔室被包膜遮盖, 保存了完整的圆孔状出口(绿色箭头); **A2**–**H2**. 分别为 A1–H1 的虚拟切面图, 显示标本内部结构特征, 其中 A2、B2 中腔室分布在标本周缘, 核心部位不具腔室; **C2**–**H2**. 其核心部位也发育有腔室, D2 中绿色箭头指示部分腔室的孔状出口, 橙色箭头指示部分腔室之间的通道。A 的标本号为 NIGP203461; B 为 NIGP203462; C 为 NIGP203463; D 为 NIGP203464; E 为 NIGP203465 (副模标本); F 为 NIGP203466; G 为 NIGP203467; H 为 NIGP203468。比例尺为 200 μm。

A1–**H1**. Micro-CT isosurface rendering showing specimens with varying numbers of chambers. The numbers of chambers in specimens A–H are 10, 16, 21, 26, 34, 39, 130, and 186, respectively. Specimen D1 preserves a partial envelope, with some chambers covered by the envelope, and exhibits circular pore-like openings (indicated by green arrows). **A2**–**H2**. Virtual cross-sectional images corresponding to A1–H1, revealing internal structures. In A2 and B2, chambers are distributed at the periphery, while no chambers are at the center. The centers of specimens **C2**–**H2** are occupied by chambers, with the green arrow in D2 indicating a pore-like opening, and the orange arrows indicating channels between some chambers. Specimen numbers: A, NIGP203461; B, NIGP203462; C, NIGP203463; D, NIGP203464; E, NIGP203465 (paratype); F, NIGP203466; G, NIGP203467; H, NIGP203468. Scale bars: 200 μm.

积比例为10%—30% (图4-C), 腔室形态为较浅的凹坑状或半球状(图2-A1–2-D1), 不均匀分布在标本外周缘(图2, 4-B)。在非裸露的标本中, 腔室仅一个较大圆形出口(图2), 少数相邻的腔室之间有通道连通(图2-A2–2-D2)。晚期发育阶段的标本腔室数量增多, 最多可多达186个(图4-B), 且腔室的位置也从只占据标本周缘的状态逐渐转变为占据标本中心位置(图3, 4-B)。最晚期阶段腔室总体积约

表 1 玲珑球不同发育阶段特征

Table 1 Features of *Linglongsphaera ornata* at different developmental stages

特征	早期阶段	晚期阶段
腔室数量	<15	15—186
腔室位置	仅分布在表面	腔室增多, 且出现内部腔室
腔室分布	不均匀	较为均匀
腔室形态	浅坑状、半球状、袋状	腔室形态多为不规则的近球形
腔室总体积占比	10%—30%	30%—45%
单个腔室体积占比	0.34%—1.2%	1.8%—0.18% (随腔室数增加而降低)
单个腔室的出口数量	1	1—4
出口形态	较大的圆形	较小的圆孔
连通率	仅少部分腔室之间连通	腔室连通率高, 最终所有腔室之间均连通
表面球状突起	有	有
内部小球	有	有

占标本总体积36%(图4-C), 较早期阶段有所升高, 但单个腔室的体积随着数量的增多而逐渐减小(图3-A2–3-E2, 4-D)。晚期阶段的腔室近似球形, 外围腔室发育1到4个较小的圆孔通道与外界连通(图3绿色箭头所示), 部分相邻腔室也保持连通状态(图3橙色箭头所示)。

统计分析显示, 在单个标本中腔室体积的大小满足正态分布(图4-D)。腔室体积的离散系数, 即标本中腔室体积的标准差与平均值之比(该参数能够反映同一个标本中腔室体积之间的离散程度)在不同标本中基本保持在一个较窄的区间(1.2—1.65, 图4-D), 这表明在同一个标本中所有腔室的体积相似, 且偏差程度在不同标本中也相似。离散系数在不同标本中维持在稳定的区间, 不仅能够证明各个标本中的腔室体积没有经历严重的埋藏改造, 还表明玲珑球同一个标本中所有腔室的体积没有出现显著的大小分化。

综上所述, 基于以下特征可将这些标本划分为同一属种: (1)相同的表面装饰(图2, 3); (2)相同的内部小球特征(图2, 3); (3)相同的标本直径区间, 在直径分布直方图上没有出现多个峰(图5-A); (4)都发育有腔室, 其中部分标本同时保存了暴露的腔室和完整的腔室(图1-D1, 1-D2)。腔室特征存在过渡, 包括腔室数量、分布、形态、体积、占比、开口、连通性等; (5)单个标本中囊腔体积的离散系数在这两个阶段中保持一致。

讨论 与同期出现的古球蛋属*Archaeooides* (钱逸, 1977)具有相似的尺寸、形态和表面装饰(Pyle *et al*., 2006; Yin *et al*., 2018)。不过古球蛋的内部结构和本文材料有显著区别, 前者的厚壁囊胞并不发育开口, 内部也不发育众多分隔的小腔室(Yin *et al*., 2018)。因此已有证据表明古球蛋属和玲珑球属之间不太可能有较近的亲缘关系。

产地层位 陕西省西乡县大河镇河西窝坝河村张家沟剖面, 寒武系宽川铺组。

4 玲珑球的发育过程和亲缘关系讨论

装饰玲珑球为一类具有瘤状突起装饰的球状化石, 内部保存了大量球状细胞, 发育有数量不等的凹坑状至近球形腔室。尽管具相似瘤状突起装饰的球状化石在埃迪卡拉纪瓮安生物群(Xiao *et al*., 2014)和寒武纪宽川铺生物群及其同期地层中(Pyle *et al*., 2006; Yin *et al*., 2018)均有发现, 但已经报道的这些球状化石内部均不发育大量具有多个开口的腔室。由此可见玲珑球的装饰可能是趋同演化的结果。这种因适应同样的生活环境而趋同演化出相似的装饰, 在埃迪卡拉纪瓮安生物群的疑源类中十分常见(Yin *et al*., 2020), 因此很难根据表面装饰特征来确定玲珑球的亲缘关系。

玲珑球内部的小球的矿化模式多样, 内部保存为空腔或充填磷灰石矿物。需要指出的是, 很多小球的边缘由一层暗色呈膜状结构的环带圈闭而成(图2-C5)。这种厚度均一的膜状结构的灰度值在显微CT数据呈暗色, 意味着它对X射线吸收较弱, 是典型的生物学结构被磷酸盐化后的特征, 显著

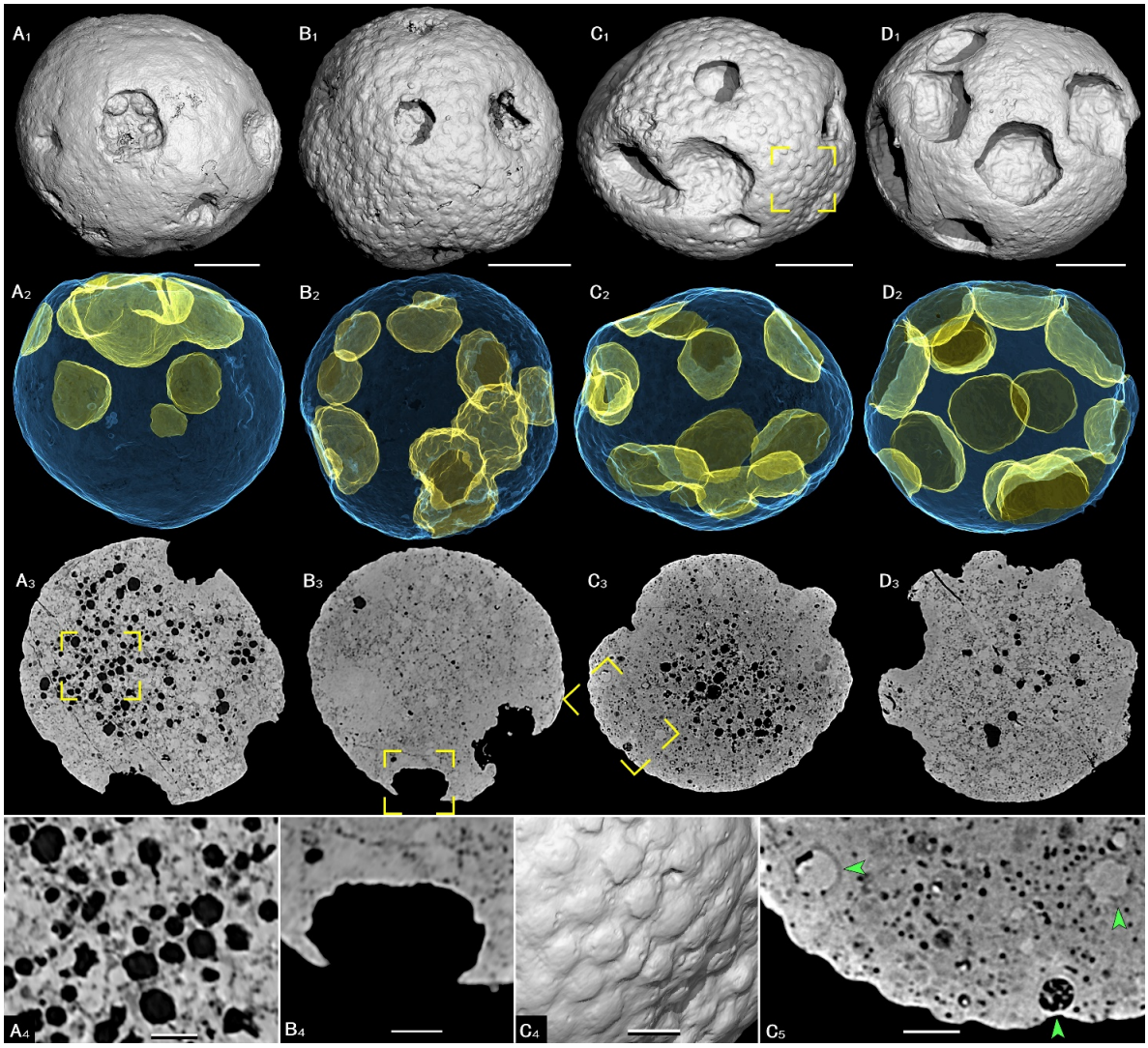

图 2　寒武纪宽川铺生物群装饰玲珑球(*Linglongsphaera ornata*)早期发育阶段标本

Fig. 2　*Linglongsphaera ornata* at early developmental stages from the early Cambrian Kuanchuanpu Biota

A1–**D1**. 显微CT表面渲染图, 显示标本发育有不同数量的腔室, A–D标本中腔室数量分别为8、9、12、14。注意B1和C1保存了带瘤状装饰的包膜; **A2**–**D2**分别为A1-D1的透明渲染图, 显示标本的轮廓(蓝色)和腔室(黄色); **A3**–**D3**分别为A1–D1的切面图, 显示标本内部的小球和外缘的腔室; **A4**、**B4**、**C4**、**C5**分别为A3、B3、C3、C1中方框位置的局部放大, 其中A4和B4分别展示呈空腔形式保存的小球和腔室, C4展示标本表面的丘状突起结构, C5展示多种形式保存的小球, 绿色箭头指示小球的膜状结构。A的标本号为NIGP203469; B为NIGP203470; C为NIGP203471 (paratype); D为NIGP203472。比例尺: A1–D1、A2–D2、A3–D3为200 μm; A4、B4、C4、C5为40 μm。

A1–**D1**. Micro-CT isosurface rendering showing specimens with different numbers of chambers. The chamber numbers in specimens A–D are 8, 9, 12, and 14, respectively. Note that B1 and C1 preserve envelopes with nodular decorations. **A2**–**D2**. Transparent rendering corresponding to A1–D1, displaying the specimens' outlines (blue) and chambers (yellow). **A3**–**D3**. Virtual cross-sectional images corresponding to A1–D1, revealing internal spheres and peripheral chambers. **A4**, **B4**, **C4**, **C5**. Enlargements of boxed areas in A3, B3, C3, C1, where A4 and B4 showcase spheres and chambers preserved in a hollow form, C4 displays detailed nodular ornaments on the specimen surface, and C5 exhibits spheres with different preservation forms, with the green arrows indicating the membrane-like structures of the spheres. Specimen numbers: A, NIGP203469; B, NIGP203470; C, NIGP203471 (paratype); D, NIGP203472. Scale bars for A1–D1, A2–D2, A3–D3: 200 μm; A4, B4, C4, C5: 40 μm.

区别于有紧密堆积矿物组成的亮色镀层(coating)或内衬(lining) (图2-C5)。它们往往在暗色膜状结构的内侧或者外侧发育, 属于典型的成岩作用伪像。由于有膜状生物学结构, 因此本文排除气泡和脂滴等解释(气泡和脂滴均无生物膜包裹)。小球的这种矿化模式与埃迪卡拉纪瓮安生物群中大量的磷酸盐化胚胎状化石中的细胞结构矿化模式相类似(Bottjer *et al*., 2020; Landon *et al*., 2019; Yin *et al*., 2022), 宽川铺生物群中不少微体化石也保留了类似的细胞结构(Yue and Bengtson, 1999)。根据小球

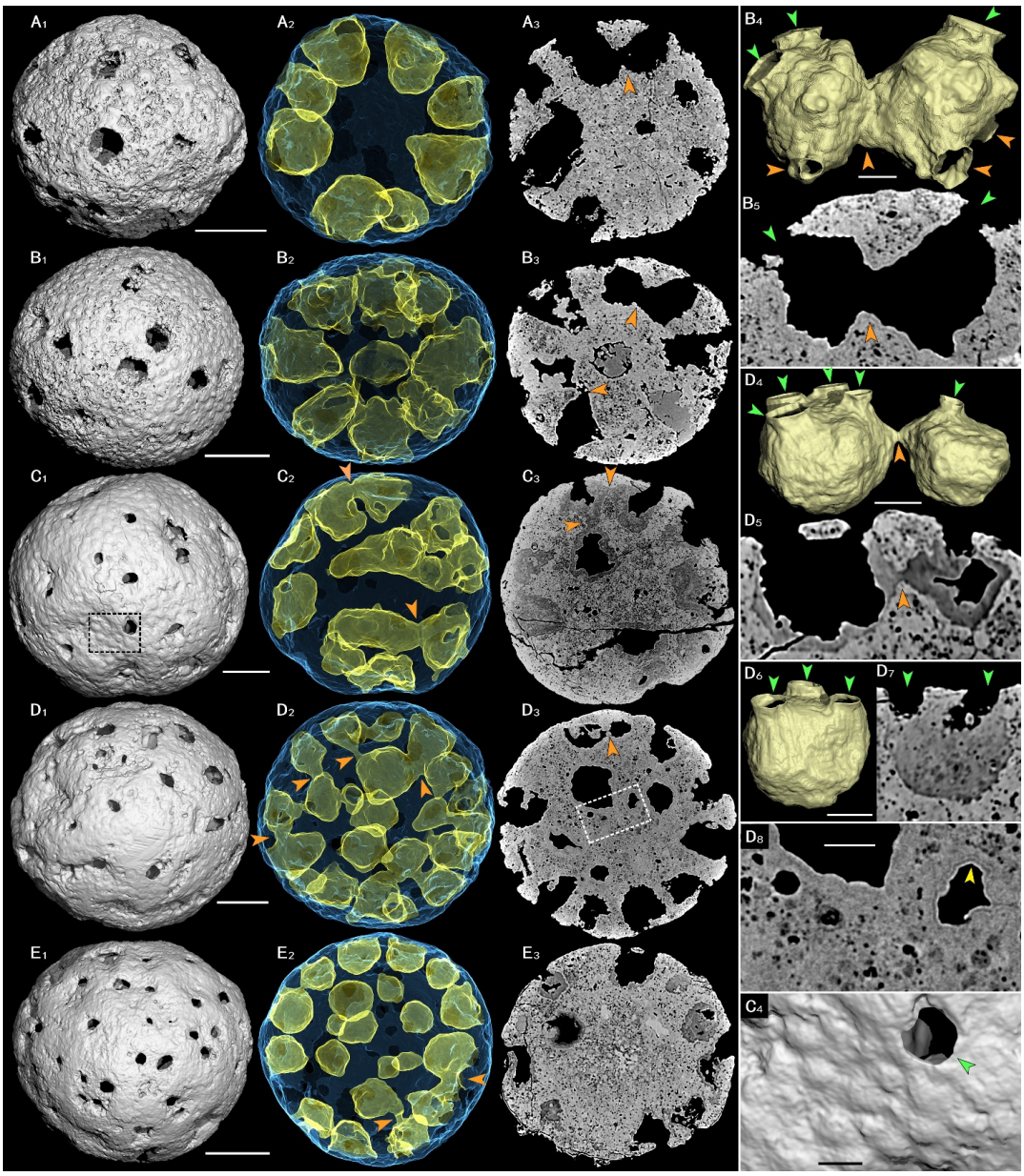

图 3 寒武纪宽川铺生物群装饰玲珑球(*Linglongsphaera ornata*)晚期发育阶段标本

Fig. 3 *Linglongsphaera ornata* at late developmental stages from the early Cambrian Kuanchuanpu Biota

A1–**E1**. 表面渲染图, 显示标本发育有不同数量的腔室和较为完整的包膜, A–D标本中腔室数量分别为15、21、37、65、71。B1和C1的外包膜保存了丘状突起装饰; **A2**–**E2**. 分别为A1–E1的透明渲染图, 显示标本轮廓(蓝色)和部分在腔室(黄色), 展示腔室数量增多并出现在标本的核部; **A3**–**E3**. 分别为A1-E1的切面图, 显示小球和的腔室; **B4**, **B5**. 分别为标本B中两个腔室及其对应切面, 展示腔室的开口和连通部位; **D4**–**D7**为标本D中的腔室及其对应切面, 展示开口和连通部位; **D8**为D3局部放大, 展示小球和腔室内壁的矿物内衬(黄色箭头); **C4**为C1局部放大, 展示腔室开口和标本表面丘状突起。绿色箭头示腔室开口, 橙色箭头指示腔室连通处。A的标本号为NIGP203473; B为 NIGP203474; C为NIGP203475; D为NIGP203476 (正模标本); E为NIGP203477。比例尺: A1–D1、A2–D2、A3–D3为200 μm; A4、B4、C4、C5为50 μm。

A1–**E1**. Micro-CT isosurface rendering showing specimens with different numbers of chambers and relatively complete envelopes. The chamber numbers in specimens A–D are 15, 21, 37, 65, and 71, respectively. The envelopes of B1 and C1 preserve nodular ornaments. **A2**–**E2**. Transparent renderings corresponding to A1–E1, displaying the specimens' outlines (blue) and some chambers (yellow), showing an increase in chamber numbers. **A3**–**E3**. Virtual cross-section images corresponding to A1–E1, revealing spheres and chambers. **B4**, **B5**. Two chambers in specimen B and their corresponding cross-sections, showing the openings and connection channel of the two chambers. **D4**–**D7**. Chambers in specimen D and their corresponding cross-sections, displaying openings and connection channels between them. **D8**. Enlargement of D3, showing spheres and mineral lining on the inner wall of the chambers (indicated by yellow arrow). **C4**. Enlargement of C1, showing chamber openings and nodular ornaments on the specimen surface. The green arrow indicates chamber openings, and the orange arrow indicates chamber connection channels. Specimen numbers: A, NIGP203473; B, NIGP203474; C, NIGP203475; D, NIGP203476 (holotype); E, NIGP203477. Scale bars for A1–D1, A2–D2, A3–D3: 200 μm; A4, B4, C4, C5: 50 μm.

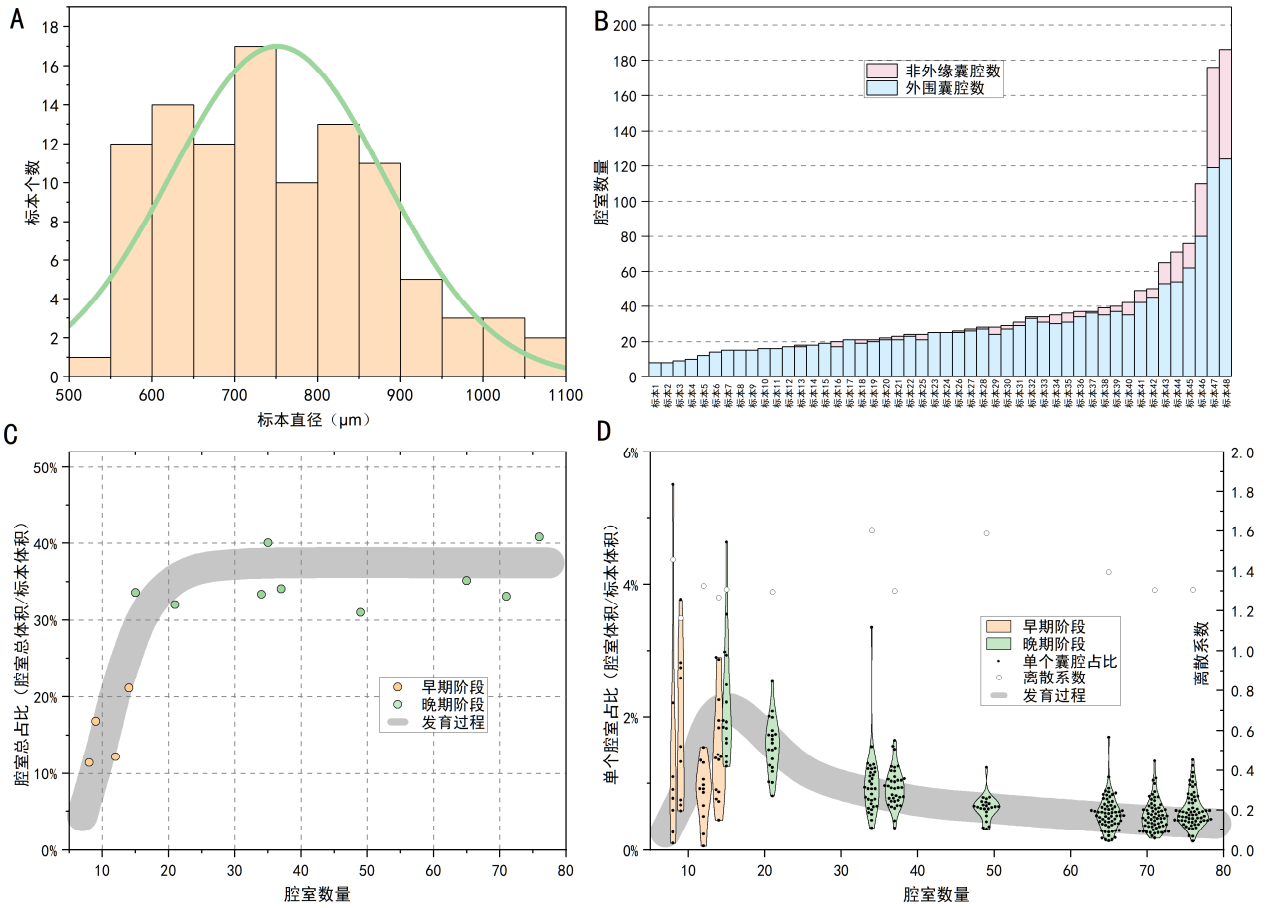

图 4　玲珑球统计分析图

Fig. 4　Statistic of *Linglongsphaera ornata*

A. 标本直径分布直方图及拟合正态分布曲线; **B**. 柱状图显示不同标本中腔室的数量; **C**. 散点图显示腔室总体积与腔室数量的关系; **D**. 小提琴图和散点图, 显示单个腔室体积与腔室数量的关系。

A. Histogram and fitted normal distribution curve of diameter distribution; **B**. Bar chart illustrating the number of chambers in different specimens; **C**. Scatter plot depicting the relationship between total chamber volume and the number of chambers; **D**. Violin plot and scatter plot demonstrating the relationship between individual chamber volume and the number of chambers.

的形态、尺寸和保存特征, 笔者将其解释为细胞结构。因此玲珑球不仅有复杂的装饰包膜, 而且有多细胞结构。由于保存有细胞结构的标本中, 所有细胞的尺寸和形态都比较一致, 因此可以排除玲珑球有细胞分化的可能。

目前收集到的玲珑球标本直径没有明显变化(图4-A), 且内部细胞大小没有发生明显变化, 但是腔室数量、大小、形态等有所不同。基于目前收集到的玲珑球标本的三维结构特征, 笔者构建了一个相对连续的发育序列(图5): 玲珑球首先由边缘开始形成少量浅坑状初始腔室, 后腔室体积增大为近球状, 腔室总体积增大到一定阈值后保持不变(图4-C), 但是单个腔室体积减小(图3-A–3-E, 4-D)。整个发育过程中腔室数量逐渐增多, 单个腔室的体积先增大后减小(图4-D)。

假设上述关于发育过程的解释是正确的, 那么腔室在形成之前标本应该是充满细胞的实心状态, 由一层具有瘤状装饰的囊壁包裹。那腔室是如何发育产生的呢? 考虑到细胞尺寸没有发生变化, 且每个腔室均发育了向标本外的开口, 笔者推测腔室可能是玲珑球通过向体外释放细胞而逐渐形成的。这也一定程度上解释了在早期阶段腔室均分布在个体周缘的特征。在发育的晚期阶段, 标本的最核心部位也出现了腔室, 这些部位的细胞很可能是通过腔室之间的连接通道经过外周腔室最终释放到环境中。释放到体外的细胞很可能具有类似

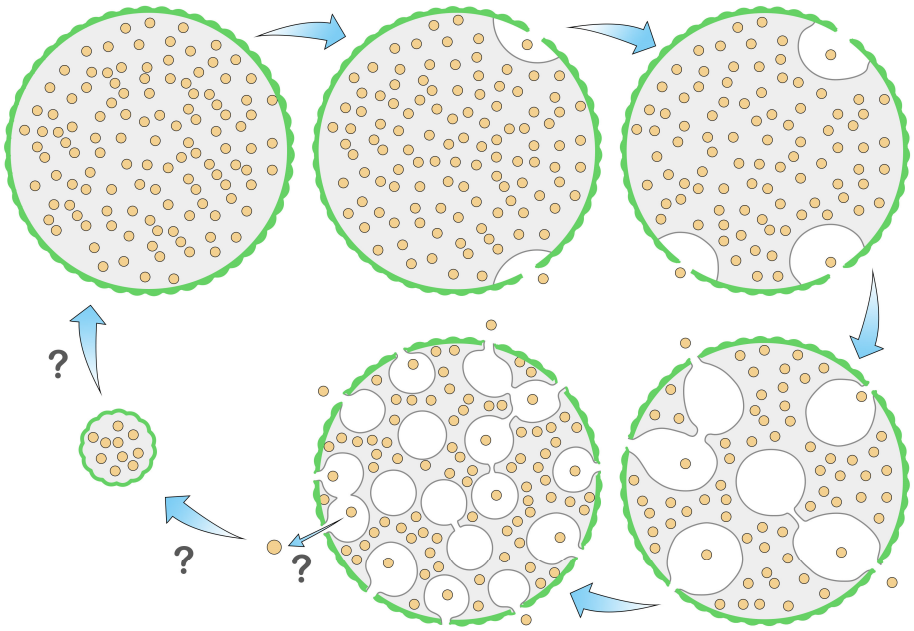

图 5 玲珑球的生命周期模式图

Fig. 5 Putative life cycle of *Linglongsphaera ornata*

藻类的繁殖孢子的功能，是玲珑球进行快速繁殖的方式。当然，这种推测的可信度还需要更多证据做支撑。需要特别提及的是，尽管在数百个玲珑球标本中尚未观察到显著的细胞凋亡的证据，笔者目前还无法排除腔室的发育是通过细胞凋亡的方式而实现。

尽管通过释放成熟生殖细胞的方式产生规则分布的腔室在机制上可行，不过在个体发育过程中，腔室数量增多时，单个腔室的体积会缩小。这种现象很难单纯通过生殖细胞释放而产生。因此笔者推测，在生殖细胞释放的同时，玲珑球内部的细胞会在某种调控机制下进行有序迁移和重组。所有标本中的细胞均呈球形且相互之间不共壁，这一特征支持了这种解释。目前构建的玲珑球发育序列中(图5)是否已包含玲珑球的最终成体阶段，基于现有的数据很难得出确切的结论。但在没有新标本发现的情况下，笔者倾向于认为腔室数量达接近200个的标本已经是或者接近最终发育阶段。

需要指出的是，重建的玲珑球发育序列(图5)只包括了有腔室的发育阶段，完整的个体发育过程和生活周期尚不完整，仍缺乏很多的信息，比如释放的生殖细胞长大后如何分泌具有装饰的外包膜并启动细胞分裂？其细胞分裂是否遵循体积不增长的分裂模式(即个体在细胞分裂过程中总体积不变，细胞数量增长，单个细胞体积减小)等等？这些未知信息需要未来发现更多发育阶段的标本后方能等到答案。

综上所述，玲珑球具有带装饰的外包膜和多细胞结构，且通过细胞迁移和释放生殖细胞而发育了复杂的腔室结构。这些特征表明玲珑球是一种具有多细胞发育阶段的真核生物。然而其在真核生物树上确凿的系统发生位置仍不能确定。现生的多细胞真核生物包括多细胞藻类、有胚植物、一些真菌和后生动物(Lane and Archibald, 2008; Adl *et al*., 2012; Katz, 2012)。其中有胚植物和真菌无论是形态、解剖结构还是发育过程，均与玲珑球存在巨大的差异，且有胚植物的起源远晚于寒武纪，因此玲珑球与真菌和有胚植物的亲缘关系较远。与后生动物相比，玲珑球缺乏组织和器官分化特征，甚至没有空间上的细胞分化，因此不可能是后生动物，尽管玲珑球的复杂性与动物总界中的某些单细胞类群的复杂性可以类比(Yin *et al*., 2019, 2022)。真核藻类(包括具绿藻和红藻)具有较高的多样性和漫长的演化史(Lee, 2018)，且绿藻和红藻等真核藻类在距今10亿年的拉伸纪就出现了复杂的多细胞化(Butterfield *et al*., 2009; Tang *et al*., 2020)。考虑

到很多藻类, 尤其是绿藻不仅发育带装饰的囊壁, 有多细胞的发育阶段, 还通过释放孢子的方式完成生殖, 给玲珑球的亲缘关系解释提供了潜在的类比对象。

5 结 论

本文报道了寒武纪幸运期宽川铺生物群中一类新发现的疑源类化石装饰玲珑球(*Linglongsphaera ornata* n. gen. n. sp.)。笔者采用高分辨率显微CT技术重建了其三维结构, 发现它们具有带装饰的外包膜和多细胞结构, 是内部发育有复杂腔室的球状生物。结合体数据统计分析, 笔者重构了玲珑球的发育阶段。玲珑球很可能通过生殖细胞释放和迁移重组形成内部腔室, 并完成个体快速繁殖。基于已经获得的数据, 笔者推测玲珑球是一种已经灭绝的有多细胞阶段的真核生物, 与后生动物、有胚植物或真菌的亲缘关系较远, 而可能与真核藻类的亲缘关系更近。当然, 目前的数据也不排除玲珑球是动物总界中一类已经灭绝的单细胞类群。不过它们在真核生命树上的具体位置仍然不明, 有待未来新标本的发现和研究。

玲珑球作为寒武纪宽川铺生物群中新发现的多细胞真核生物, 不仅为理解宽川铺生物群的化石组合面貌提供了新的数据, 同时也为理解寒武纪大爆发初期海洋生物圈的规模和复杂程度提供了新的信息。这项发现本身也暗示宽川铺生物群作为特异埋藏化石库, 它记录寒武纪初期生物多样性的潜力超过前人预估, 值得未来投入更多研究资源。

致谢 感谢中国科学院南京地质古生物研究所李国祥研究员和匿名评审专家提出的宝贵修改建议。中国科学院南京地质古生物研究所实验技术中心吴素萍帮助完成CT数据的初筛和扫描, 特此致谢。

参考文献 (References)

钱逸, 1977. 华中西南区早寒武世梅树村阶的软舌螺纲及其它化石. 古生物学报, 116: 255–275.

吴素萍, 殷宗军, 孙玮辰, 赵多多, 吴若琳, 2018. 三维 X 射线显微技术与小型微体化石高分辨率无损成像. 古生物学报, 57: 157–167.

张兴亮, 舒德干, 2014. 寒武纪大爆发的因果关系. 中国科学: 地球科学, 44: 1155–1170.

赵多多, 殷宗军, 陈均远, 李国祥, 2021. 寒武纪早期四方塔型壳属的胚胎发育及其系统学意义. 古生物学报, 60: 124–137.

朱茂炎, 赵方臣, 殷宗军, 曾晗, 李国祥, 2019. 中国的寒武纪大爆发研究: 进展与展望. 中国科学: 地球科学, 49: 1455–1490.

Adl S M, Simpson A G B, Lane C E, Lukeš J, Bass D, Bowser S S, Brown M W, Burki F, Dunthorn M, Hampl V, Heiss A, Hoppenrath M, Lara E, le Gall L, Lynn D H, McManus H, Mitchell E A D, Mozley-Stanridge S E, Parfrey L W, Pawlowski J, Rueckert S, Shadwick L, Schoch C L, Smirnov A, Spiegel F W, 2012. The revised classification of eukaryotes. Journal of Eukaryotic Microbiology, 59: 429–514. DOI: 10.1111/j.1550-7408.2012.00644.x

Bengtson S, Yue Zhao, 1997. Fossilized metazoan embryos from the earliest Cambrian. Science, 277: 1645–1648. DOI: 10.1126/science.277.5332.1645

Bottjer D J, Yin Zong-jun, Zhao Fang-chen, Zhu Mao-yan, 2020. Comparative taphonomy and phylogenetic signal of phosphatized Weng'an and Kuanchuanpu Biotas. Precambrian Research, 349: 105408. DOI: 10.1016/j.precamres.2019.105408

Butterfield N J, 2008. Modes of pre-Ediacaran multicellularity. Precambrian Research, 173: 201–211. DOI: 10.1016/j.precamres.2009.01.008

Dong Xi-ping, Cunningham J A, Bengtson S, Thomas C W, Liu Jian-bo, Stampanoni M, Donoghue P C J, 2013. Embryos, polyps and medusae of the Early Cambrian scyphozoan *Olivooides*. Proceedings of the Royal Society B: Biological Sciences, 280: 20130071. DOI: 10.1098/rspb.2013.0071

Dong Xi-ping, Vargas K, Cunningham J A, Zhang Hua-qiao, Liu Teng, Chen Fang, Liu Jian-bo, Bengtson S, Donoghue P C J, 2016. Developmental biology of the early Cambrian cnidarian *Olivooides*. Palaeontology, 59: 387–407. DOI: 10.1111/pala.12231

Donoghue P C J, Cunningham J A, Dong Xi-ping, Bengtson S, 2015. Embryology in deep time. Evolutionary Developmental Biology of Invertebrates 1. Vienna: Springer. 45–63. DOI: 10.1007/978-3-7091-1862-7_3

Duan Bai-chuan, Dong Xi-ping, Porras L, Vargas K, Cunningham J A, Donoghue P C J, 2017. The early Cambrian fossil embryo *Pseudooidesis* a direct-developing cnidarian, not an early ecdysozoan. Proceedings of the Royal Society B: Biological Sciences, 284: 20172188. DOI: 10.1098/rspb.2017.2188

Han Jian, Kubota S, Li Guo-xiang, Yao Xiao-yong, Yang Xiao-guang, Shu De-gan, Li Yong, Kinoshita S, Sasaki O, Komiya T, Yan Gang, 2013. Early Cambrian pentamerous cubozoan embryos from South China. PLoS One, 8: e70741. DOI: 10.1371/journal.pone.0070741

Han Jian, Kubota S, Uchida H O, Stanley G D, Yao Xiao-yong, Shu De-gan, Li Yong, Yasui K, 2010. Tiny sea *Anemone* from the lower Cambrian of China. PLoS One, 5: e13276. DOI: 10.1371/journal.pone.0013276

Han Jian, Li Guo-xiang, Wang Xing, Yang Xiao-guang, Guo Jun-feng, Sasaki O, Komiya T, 2017. *Olivooides*-like tube aperture in Early Cambrian Carinachitids (Medusozoa, Cnidaria). Journal of Pa-

leontology, 92: 3–13. DOI: 10.1017/jpa.2017.10

Katz L A, 2012. Origin and diversification of eukaryotes. Annual Review of Microbiology, 66: 411–427. DOI: 10.1146 /annurev-micro-090110-102808

Landon E N U, Liu Peng-ju, Yin Zong-jun, Sun Wei-chen, Shang Xiao-dong, Donoghue P C J, 2019. Cellular preservation of excysting developmental stages of new eukaryotes from the early Ediacaran Weng'an Biota. Palaeoworld, 28: 461–468. DOI: 10.1016/j.palwor.2019.05.005

Lane C E, Archibald J M, 2008. The eukaryotic tree of life: endosymbiosis takes its TOL. Trends in Ecology & Evolution, 23: 268–275. DOI: 10.1016/j.tree.2008.02.004

Lee R E, 2018. Phycology. Cambridge: Cambridge University Press. DOI: 10.1017/9781316407219

Liu Wei, Yin Zong-jun, Pan Bing, Shen Bing, Dong Lin, Li Guo-xiang, 2023. Germ-soma differentiation and reproduction in a new species of early Cambrian acritarch. Palaeontology, 66: e12687. DOI: 10.1111/pala.12687

Liu Yun-huan, Xiao Shu-hai, Shao Tie-quan, Broce J, Zhang Hua-qiao, 2014. The oldest known priapulid-like scalidophoran animal and its implications for the early evolution of cycloneuralians and ecdysozoans. Evolution & Development, 16: 155–165. DOI: 10.1111/ede.12076

Liu Yun-huan, Carlisle E, Zhang Hua-qiao, Yang Ben, Steiner M, Shao Tie-quan, Duan Bai-chuan, Marone F, Xiao Shu-hai, Donoghue P C J, 2022. *Saccorhytus* is an early ecdysozoan and not the earliest deuterostome. Nature, 609: 541–546. DOI: 10.1038/s41586-022-05107-z

Peng Shan-chi, Babcock L, Cooper R, 2012. The Cambrian Period. *In*: Gradstein F M, Ogg J G, Schmitz M D, Ogg G M (eds.), The Geologic Time Scale 2020. Amsterdam: Elsevier BV. 437–488. DOI: 10.1016/B978-0-444-59425-9.00019-6

Pyle L J, Narbonne G M, Nowlan G S, Xiao Shu-hai, James N P, 2006. Early Cambrian metazoan eggs, embryos, and phosphatic microfossils from northwestern Canada. Journal of Paleontology, 80: 811–825. DOI: 10.1666/0022-3360(2006)80[811: ecmeea]2.0.co;2

Qian Yi, 1977. Hyolitha and some problematica from the Lower Cambrian Meishucunian Stage in central and southwestern China. Acta Palaeontologica Sinica, 16: 255–275 (in Chinese with English abstract). DOI: 10.19800/j.cnki.aps.1977.02.007

Steiner M, Qian Yi, Li Guo-xiang, Hagadorn J W, Zhu Mao-yan, 2014. The developmental cycles of early Cambrian Olivooidae fam. nov. (? Cycloneuralia) from the Yangtze Platform (China). Palaeogeography, Palaeoclimatology, Palaeoecology, 398: 97–124. DOI: 10.1016/j.palaeo.2013.08.016

Tang Qing, Pang Ke, Yuan Xun-lai, Xiao Shu-hai, 2020. A one-billion-year-old multicellular chlorophyte. Nature Ecology & Evolution, 4: 543–549. DOI: 10.1038/s41559-020-1122-9

Wang Xing, Han Jian, Vannier J, Ou Qiang, Yang Xiao-guang, Uesugi K, Sasaki O, Komiya T, 2017. Anatomy and affinities of a new 535-million-year-old medusozoan from the Kuanchuanpu Formation, South China. Palaeontology, 60: 853–867. DOI: 10.1111/pala.12320

Wang Xing, Vannier J, Yang Xiao-guang, Kubota S, Ou Qiang, Yao Xiao-yong, Uesugi K, Sasaki O, Komiya T, Han Jian, 2020. An intermediate type of medusa from the early Cambrian Kuanchuanpu Formation, South China. Palaeontology, 63: 775–789. DOI: 10.1111/pala.12483

Wang Xing, Vannier J, Yang Xiao-guang, Leclère L, Ou Qiang, Song Xi-kun, Komiya T, Han Jian, 2022. Muscle systems and motility of early animals highlighted by cnidarians from the basal Cambrian. eLife, 11: 74716. DOI: 10.7554/elife.74716

Wu Su-ping, Yin Zong-jun, Sun Wei-chen, Zhao Duo-duo, Wu Ruo-lin, 2018. High-resolution tomography of millimeter-to centimeter-sized fossils using three-dimensional X-ray microscopy. Acta Palaeontologica Sinica, 57: 157–167 (in Chinese with English abstract). DOI: 10.19800/j.cnki.aps.2018.02.002

Xiao Shu-hai, Zhou Chuan-ming, Liu Peng-ju, Wang Dan, Yuan Xun-lai, 2014. Phosphatized acanthomorphic acritarchs and related microfossils from the Ediacaran Doushantuo Formation at Weng'an (South China) and their implications for biostratigraphic correlation. Journal of Paleontology, 88: 1–67. DOI: 10.1666/12-157r

Yin Zong-jun, Sun Wei-chen, Reitner J, Zhu Mao-yan, 2022. New holozoans with cellular resolution from the early Ediacaran Weng'an Biota, SW China. Journal of the Geological Society, 179: jgs2021-061. DOI: 10.1144/jgs2021-061

Yin Zong-jun, Vargas K, Cunningham J, Bengtson S, Zhu Mao-yan, Marone F, Donoghue P, 2019. The early Ediacaran caveasphaera foreshadows the evolutionary origin of animal-like embryology. Current Biology, 29: 4307–4314.e2. DOI: 10.1016/j.cub.2019.10.057

Yin Zong-jun, Zhao Duo-duo, Pan Bing, Zhao Fang-chen, Zeng Han, Li Guo-xiang, Bottjer D J, Zhu Mao-yan, 2018. Early Cambrian animal diapause embryos revealed by X-ray tomography. Geology, 46: 387–390. DOI: 10.1130/g40081.1

Yue Zhao, Bengtson S, 1999. Embryonic and post-embryonic development of the Early Cambrian cnidarian *Olivooides*. Lethaia, 32: 181–195. DOI: 10.1111/j.1502-3931.1999.tb00538.x

Zhang Hua-qiao, Xiao Shu-hai, Liu Yun-huan, Yuan Xun-lai, Wan Bin, Muscente A D, Shao Tie-quan, Gong Hao, Cao Guo-hua, 2015. Armored kinorhynch-like scalidophoran animals from the early Cambrian. Scientific Reports, 5: 16521. DOI: 10.1038/srep16521

Zhang Xing-liang, Shu De-gan, 2014.Causes and consequences of the Cambrian explosion. Scientia Sinica: Terrae, 44: 1155–1170 (in Chinese). DOI: 10.1360/zd-2014-44-6-1155

Zhao Duo-duo, Yin Zong-jun, Chen Jun-yuan, Li Guo-xiang, 2021. The embryonic development of the early Cambrian Quadrapyrgites and its phylogenetic implication. Acta Palaeontologica Sinica, 60: 124–137 (in Chinese with English abstract). DOI: 10.19800/j.cnki.aps.2020058

Zhu Mao-yan, Zhao Fang-chen, Yin Zong-jun, Zeng Han, Li Guo-xiang, 2019. The Cambrian explosion: Advances and perspectives from China. Science China Earth Sciences, 49: 1455–1490 (in Chinese). DOI: 10.1007/s11430-019-9508-4

(责任客座主编: 杨兴莲)