



*Halkieria*系统进化及其化石分类学研究进展*

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提要 *Halkieria*是寒武纪一类躯体上披有骨质鳞片的疑难后生动物, 前后各有一个大壳板, 两侧对称, 其钙质骨片在软躯体上排列形成几条规律的纵向带。半个世纪以来, 学术界对*Halkieria*生物系统确切位置的讨论以及*Halkieriidae*不同属种亲缘关系的探索从未停止。本文总结了*Halkieria*化石在骨片属种分类、古地理和地层分布、生物系统分类学的研究进展, 对当前的生物系统分类归纳出以下几种观点: 1) *Halkieria*为腕足动物的祖先, 并与托莫特壳类有一定的亲缘关系; 2) *Halkieria*与*Wiwaxia*等骨片化石具有单源性, 组成一种新的分类单元*Halwaxiidae*, 属于软体动物干群或腕足动物和环节动物的干群; 3) *Halkieria*为软体动物有刺亚门干群, 与无板纲、多板纲更为亲近; 4) *Halkieria*为环节动物的祖先。目前, 虽然多数人根据*Halkieria*与现生多板纲的骨片排列一致将*Halkieria*归属软体动物有刺亚门的干群, 但近年来世界各地新化石材料的陆续发现及壳体发育研究使得*Halkieria*的系统分类位置出现新的争议。通过对化石分类学的系统厘定和生物分类研究进展的总结梳理, 本文进一步讨论了*Halkieria*对小壳化石的分类、骨片系重建及冠轮动物各门类的起源和谱系演化关系等方面的重要意义, 并提出当前*Halkieria*研究存在的问题及今后工作重点。

关键词 *Halkieria* 寒武纪 生物亲缘关系 冠轮动物

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Phylogeny and taxonomy of *Halkieria*: progress and prospects

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Abstract *Halkieria* is a problematic Cambrian metazoan with mineralized sclerites covering its body. It possesses a large shell plate on both anterior and posterior parts of the body. The arrangement of its calcareous sclerites is bilaterally symmetric, forming several regular longitudinal bands on the body. For over half a century, the biological affinities of *Halkieria* or *halkieriids* have been contentious. This paper summarizes the research progress of *Halkieria* fossils in aspects of taxonomy, palaeogeographical distribution, and stratigraphic range, and reviews the following viewpoints regarding its biological affinities: 1) *Halkieria* is a stem group brachiopod, and has a close relationship with tommotiids; 2) *Halkieria* and *Wiwaxia* are monogenic, forming a monophyletic lineage, *Halwaxiidae*, which belongs to

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a stem group mollusk or brachiopod and annelid; 3) *Halkieria* is a stem group of the Aculifera that includes the Polyplacophora and the Aplacophora; and 4) *Halkieria* is the ancestor of annelids. Of these hypotheses, it is currently widely accepted that *Halkieria* is a stem group aculiferan because of the close comparability of scleritome construction between *Halkieria* and chitons. However, this hypothesis has been challenged by new fossil materials discovered around the globe and the ontogenetic studies of these animals. Through review of its taxonomy and summary of research progress on its biological affinities, this paper discusses the significance of *Halkieria* in the taxonomy of small shell fossils (SSFs), reconstruction of scleritome, and origin and evolution of the lophotrochozoans. And we further point out the limitations of current studies of *Halkieria* and highlight the research emphasis in the future.

Key words *Halkieria*, Cambrian, biological affinities, lophotrochozoans

1 前 言

“寒武纪大爆发”事件开启了地球动物多样化演化的序章(Zhuravlev and Wood, 2018)。此事件中, 包括halkieriids在内的许多仍有争议的小型骨骼化石大量涌现, 它们通常个体微小(以毫米-厘米计量), 常呈磷酸盐化离散形态保存, 与特异埋藏化石库完整骨片系化石保存形成鲜明对比, 统称为“小壳化石(small shelly fossils)” (Matthews and Missarzhevsky, 1975)。其中, halkieriids (即哈氏虫科Family Halkieriidae Poulsen, 1967)特征明显、数量庞大, 包括了*Halkieria*骨片、*Sinosachites*骨片等一些常见骨片, 在寒武纪早期小壳化石生物群中占据着重要的地位(Bengtson and Conway Morris, 1984; Conway Morris and Peel, 1995)。

完整骨片系化石*Halkieria evangelista* Conway Morris and Peel, 1995在格陵兰岛寒武系第三阶Sirius Passet Lagerstätte特异埋藏化石库被首次发现(Conway Morris and Peel, 1990)。这是一种大约8 cm长的蠕形动物, 身体背部覆盖着成百上千个规律排列的鳞甲状骨片, 前后端各有一个壳板(图2-A)。特异埋藏化石库中完整标本的发现, 将单个壳体与大量不同类型的孤立骨片化石联系在一起, 为小壳化石离散骨片的重塑(骨片系重建)提供了重要启示(李国祥, 2004)。但是, 不同研究者对*Halkieria*的系统分类位置争议颇大: 认为可能属于软体动物(钱逸, 1999; Bergström, 1989; Runnegar, 1996; Scheltens and Ivanov, 2002; Lindberg and Haszprunar, 2004; Vendrasco *et al.*, 2004; Vinther and Nielsen, 2005; Caron *et al.*, 2006; Sigwart and Sutton, 2007; Parkhaev, 2008; Todt *et al.*, 2008; Paps *et al.*, 2009; Paterson *et al.*, 2009; Parkhaev, 2017;

Harper *et al.*, 2019)、腕足动物(赵鑫, 2010; Poulsen, 1967; Bengtson, 1985; Conway Morris and Peel, 1995; Holmer *et al.*, 2002; Ushatinskaya, 2002; Williams and Holmer, 2002; Cohen *et al.*, 2003; Li and Xiao, 2004; Conway Morris, 2006; Skovsted *et al.*, 2015; Sun *et al.*, 2018)、环节动物(Jell, 1981; Conway Morris and Caron, 2007)、节肢动物(殷继成等, 1980; 何廷贵, 1981; Kono *et al.*, 2021)、或冠轮动物超门中未定动物门类(Conway Morris and Caron, 2007; Butterfield, 2008; Kouchinsky *et al.*, 2012; Harper *et al.*, 2017; Zhao *et al.*, 2017; Hammarlund *et al.*, 2019)。实体化石证据和分子钟的研究表明, 冠轮动物中的各门类分化于前寒武纪晚期至寒武纪早期, 与*Halkieria*骨片化石的产出年代相近(Giribet, 2003, 2008)。因此, 对*Halkieria*系统分类位置的研究无论对小壳化石的分类、骨片系重建, 还是对冠轮动物乃至两侧对称动物的各门类的起源和谱系演化关系都具有重要的意义(张晓川、姚锦仙, 2011; Conway Morris and Caron, 2007; Butterfield, 2008; Porter, 2008)。

基于此, 本文将系统介绍*Halkieria*的骨片种属分类、古地理和地层分布、生物系统分类学研究进展及其存在的问题, 详细探讨确立*Halkieria*分类位置的几个关键因素, 并为未来的研究重心提供参考性意见。

2 骨片种属分类研究进展

Poulsen (1967)在丹麦Gronne Skifre组地层最早发现*Halkieria*骨片, 并建立*Halkieria*属及其两个种(Bengtson, 1985)。而Meshkova (1969)将西伯利亚地区Tommotian阶发现的类似骨片化石建立了

新属 *Sachites*。此后,大量 *Sachites* 骨片化石在西伯利亚地区和华南地区寒武系早期地层中被发现(钱逸, 1977; 殷继成等, 1980; 何廷贵, 1981; 罗惠麟等, 1982; 段承华, 1984; Meshkova, 1974), 为骨片化石的系统分类研究提供了充分的化石材料。但研究中也存在一些问题: 1) *Sachites* 属与 *Halkieria* 属特征相似, 属级划分界限模糊; 2) *Sachites* 属的形态种仅在中国地区就已命名接近40种, 数量很多, 种一级别的鉴定较为困难; 3) 一些形态种的化石图版少, 图像模糊, 加大了对骨片鉴定的难度。

对这些问题的解决, 经历了两个阶段。第一阶段是 Bengtson 和 Conway Morris (1984) 将丹麦地区的 *Halkieria* 骨片与西伯利亚地区的 *Sachites* 骨片进行详细对比和分析, 认为 *Sachites* 应该是 *Halkieria* 晚出现同义名, 但考虑到 *Sachites* 属的模式种骨片背面无纵脊, 也无侧翼结构, 加之产出层位低于 *Halkieria* 属, 因而最终保留了 *Sachites* 属; 但除了 *Sachites* 属的模式种外, 建议将中国地区和西伯利亚地区描述的 *Sachites* 属的其他种全都归入 *Halkieria* 属(Bengtson and Conway Morris, 1984)。第二阶段则是对软躯体化石 *Halkieria evangelista* 的研究, 开始出现“骨片系(scleritome)”的概念(Conway Morris and Peel, 1995), 即同一生物出现不同类型骨片的形态组合。骨片系的重建, 就是对具多骨片动物骨骼面貌的恢复, 在进行骨片化石系统分类研究中需要综合分析产地、层位、时代以及化石形态特征、组合类型等多方面的信息(Bengtson *et al.*, 1990)。基于以上原则, 一些形态种被陆续修订为同物异名(见表1; Bengtson, 1985; Qian and Bengtson, 1989; Conway Morris and Chapman, 1997; Parkhaev and Demidenko, 2010)。

目前, *Halkieria* 属有效的形态种有33种, 本文总结出这些种的产地、层位、围岩类型、化石大小和化石拉丁名等信息(见表2, 表3)。另外, 以 *Halkieria* 属为代表的 *Halkieriidae* 科自建立以来, 属级划分方案不断被修正(殷继成等, 1980; 何廷贵, 1981; 钱逸, 1999; 岳昭, 2004; Bengtson, 1985; Qian and Bengtson, 1989; Conway Morris, 1994; Porter, 2004; Conway Morris and Caron, 2007; Parkhaev and Demidenko, 2010; Zhao *et al.*, 2017)。

通过对这些不同方案的厘定(见表4), 本文认为 *Halkieriidae* 科包含以下9个有效属: *Sachites* 属、*Halkieria* 属、*Sinosachites* 属、*Oikozetetes* 属、*Ocruranus* 属、*Orthrozancus* 属、*Eohalobia* 属、*Hippopharangites* 属、*Australohalkieria* 属。其中, *Ocruranus* 属和 *Eohalobia* 属是寒武系幸运阶到第四阶发现的单个壳体(Peel and Skovsted, 2005; Yang *et al.*, 2014; Peel, 2021; Yang and Steiner, 2021), 其分类位置一直存在争议(刘第壖, 1979; Qian and Bengtson, 1989; Bengtson, 1992; Siegmund, 1997), 近年来的研究认为, *Ocruranus* 和 *Eohalobia* 属于软体动物干群或软体动物多板纲的干群(Conway Morris and Caron, 2007; Vendrasco *et al.*, 2009), 是 *Halkieriidae* 科动物躯体上的壳体(Parkhaev and Demidenko, 2010)。*Oikozetetes* 属最初仅在加拿大苗岭统布尔吉斯页岩中发现壳体(Conway Morris, 1994), 后来在澳大利亚南部地区的寒武系第三阶 *Pararaia bunyeroensis* 三叶虫组合带中发现了与其壳体伴生的骨片(Paterson *et al.*, 2009; Jacquet *et al.*, 2014)。*Hippopharangites* 属、*Thambetolepis* 属、*Australohalkieria* 属均是骨片属, 后两者仅在澳大利亚出现, *Hippopharangites* 属的骨片背面无纵脊, 与西伯利亚的 *Sachites* 属相似(Bengtson *et al.*, 1990; Gravestock *et al.*, 2001; Betts *et al.*, 2016), *Thambetolepis* 属因为和 *Sinosachites* 属具有相似的中央沟、侧翼下的侧沟结构(图2-J), 发现的层位较为接近, 被认为是 *Sinosachites* 属的晚出同义名(岳昭, 2004; Jell, 1981; Vinther, 2009), *Australohalkieria* 属在寒武系乌溜阶 *Ptychagnostus gibbus* 三叶虫带被发现(Porter, 2004; Jacquet *et al.*, 2016), 骨片特征明显, 具有中空结构(图2-H, 2-I)。*Orthrozancus* 属是在加拿大苗岭统布尔吉斯页岩、中国云南澄江生物群发现的具软躯体保存的化石, 是一类拥有单个壳体的多骨片动物(Conway Morris and Caron, 2007; Zhao *et al.*, 2017)。*Sachites* 属、*Sinosachites* 属与 *Halkieria* 属在华南地区分布最为密集, 同为纽芬兰统小壳化石组合的重要化石, 长期以来被研究人员置于 *Halkieriidae* 科中(罗惠麟等, 1982; 钱逸, 1999; Li *et al.*, 2007; Parkhaev and Demidenko, 2010)。

表 1 *Halkieria*属同物异名和有效种名修订
Table 1 Lists of synonyms and valid species of *Halkieria*

同物异名 (Synonymy)	有效种名 (Valid species)
<i>Halkieria angulosus</i> Xiao, 1992 <i>Halkieria densistriatus</i> Xiao, 1992 <i>Halkieria glossoides</i> Gao, 1985 <i>Halkieria grossus</i> Xiao, 1992 <i>Halkieria liratus</i> Xiao, 1985 <i>Halkieria pennatifidus</i> Xiao, 1992 <i>Halkieria platytanius</i> Xiao, 1989 <i>Halkieria plumsus</i> Xiao, 1989 <i>Halkieria sepaloideus</i> Xiao, 1992 <i>Halkieria sibiriformis</i> Xiao, 1992	<i>Halkieria mira</i> Qian, 1984
<i>Halkieria asymmetrica</i> Mostler, 1980	<i>Halkieria lata</i> Mostler, 1980
<i>Halkieria hastatus</i> He, 1980	<i>Sinosachites flabelliformis</i> He, 1980
<i>Halkieria latus</i> Qian, 1984	<i>Halkieria elongus</i> Qian, 1984
<i>Halkieria pressus</i> Qian, 1984	<i>Halkieria uncostatus</i> Qian, 1984
<i>Halkieria symmetrica</i> Poulsen, 1967	<i>Halkieria obliqua</i> Poulsen, 1967

3 古地理分布与地层分布

3.1 骨片古地理分布

*Halkieria*软躯体化石目前只在格陵兰岛Sirius Passet Lagerstätte 特异埋藏化石库中被发现(Conway Morris and Peel, 1990),但其离散骨片以磷酸盐化小壳化石的形式在全球寒武系地层却有极为广泛的分布(图1,表2): 丹麦(Poulsen, 1967; Bengtson, 1985)、英国(Brasier, 1984; Conway Morris *et al.*, 1998)、南极(Wrona, 1989, 2004)、加拿大(钱逸, 1999; Landing *et al.*, 1989)、美国(Landing and Bartowski, 1996; Landing *et al.*, 2002)、德国(Elicki, 1998)、蒙古国(Khomentovsky and Gibsher, 1996; Esakova and Zhegallo, 1996; Maloof *et al.*, 2010)、哈萨克斯坦(Missarzhevsky and Mambetov, 1981)、巴基斯坦(Mostler, 1980)、澳大利亚(Bengtson *et al.*, 1990; Gravestock *et al.*, 2001; Porter, 2004; Betts *et al.*, 2016)、西伯利亚(Meshkova, 1969, 1974; Bengtson and Conway Morris, 1984; Maloof *et al.*, 2010; Kouchinsky *et al.*, 2015; Zhu *et al.*, 2017)以及中国(图1,表3)。其中,在中国发现于华北地区(潘兵, 2019)、新疆塔里木地区(钱建新、肖兵, 1984; 王务严等, 1985; 肖兵、段承华, 1992; Conway Morris and Chapman, 1997)、川北陕南地区(丁莲芳等, 1992; Stenier *et al.*, 2004; Yang *et al.*, 2015)、湖北神农架地区(钱逸、张师本,

1983; 段承华, 1984; 那琳、李国祥, 2011), 尤其在中国西南地区分布最为广泛: 川西地区(钱逸, 1977; 殷继成等, 1980; 何廷贵, 1981; Yang and Steiner, 2021)、贵州中西部(钱逸、尹恭正, 1984; 罗惠麟等, 1988)、云南东部地区(蒋志文, 1980; 罗惠麟等, 1982; 赵鑫, 2010; Qian and Bengtson, 1989; Parkhaev and Demidenko, 2010; Yang *et al.*, 2014; Kono *et al.*, 2021)。

3.2 层位特征对比

综合考虑层位、骨片形态和古地理分布特点, 本文主要讨论 *Halkieria* 属与 *Sachites* 属、*Sionosachites*属、*Orthrozanclus*属、*Oikozetetes*属、*Hippopharangites*属(图2, 3)。

从层位上看, *Halkieria*地层分布主要在寒武系第二阶, 少量分布于幸运阶和第二统地层(张志飞、陈飞扬, 2017; 潘兵, 2019; Conway Morris and Peel, 1995; Conway Morris and Chapman, 1997; Maloof *et al.*, 2010; Bowyer *et al.*, 2022); *Sachites*暂只见于华南、西伯利亚和格陵兰岛地区, 分布于纽芬兰统*Anabarites trisulcatus*——*Protohertzina anabacica*小壳化石组合带到*Watsonella crosbyi*小壳化石组合带(殷继成等, 1980; Meshkova, 1969, 1974; Skovsted, 2006; Li *et al.*, 2007; Maloof *et al.*, 2010); *Sinosachites*层位较高, 大致分布于第二阶顶部到第三阶中部地层(岳昭, 2004; Vinther, 2009;

表 2 国外地区 *Halkieria* 属分布特征
Table 2 Distribution of *Halkieria* outside China

地区	主要层位	围岩特征	化石大小	化石拉丁名
英国、德国、丹麦(Poulsen, 1967; Bengtson, 1985)	寒武系组芬兰统第二阶顶部、第二统第三阶底部 (下寒武统, Tommotian—Atdabanian阶)	磷质粉砂岩、 泥质粉砂岩	长2-4 mm, 宽0.5-1.5 mm	<i>Halkieria evangelista</i> Conway Morris and Peel, 1995 <i>Halkieria obliqua</i> Poulsen, 1967
美国、加拿大(Landing <i>et al.</i> , 1989; Landing and Bartowski, 1996)	寒武系组芬兰统幸运阶上部、第二阶 (下寒武统, NemaKit-Daldynian—Tommotian阶)	泥岩、灰岩	长1 mm左右	<i>Halkieria fordi</i> Landing, 1991 <i>Halkieria stoneri</i> Landing, 1989
西伯利亚、蒙古国、哈萨克斯坦(Meshkova, 1969, 1974; Esakova and Zhegallo, 1996; Khomentovsky and Gibsher, 1996)	寒武系组芬兰统幸运阶上部、第二阶 (下寒武统, NemaKit-Daldynian—Tommotian阶)	含磷白云岩、 灰岩	大部分长1 mm, 最长可达5 mm	<i>Halkieria amorpha</i> Meshkova, 1974 <i>Halkieria costulatus</i> Meshkova, 1974 <i>Halkieria curvata</i> Mambetov, 1981 <i>Halkieria deplanatiformis</i> Mambetov, 1981 <i>Halkieria longus</i> Qian, 1977 <i>Halkieria operculus</i> Qian, 1982 <i>Halkieria projecta</i> Bokova, 1985 <i>Halkieria sacciformis</i> Meshkova, 1969 <i>Halkieria terastios</i> Qian, 1979 <i>Halkieria trianguliformis</i> Mambetov, 1981 <i>Halkieria costulatus</i> Meshkova, 1974
巴基斯坦 (Mostler, 1980)	寒武系组芬兰统第二阶 (下寒武统, Tommotian阶)	含磷灰岩	长0.5-1 mm	<i>Halkieria directus</i> Mostler, 1980 <i>Halkieria hexagona</i> Mostler, 1980 <i>Halkieria lata</i> Mostler, 1980 <i>Halkieria longispinosa</i> Mostler, 1980 <i>Halkieria sacciformis</i> Meshkova, 1969 <i>Halkieria solida</i> Mostler, 1980 <i>Halkieria ventriosus</i> Mostler, 1980 <i>Halkieria zapfei</i> Mostler, 1980
澳大利亚、南极 (Bengtson <i>et al.</i> , 1990; Gravesstock <i>et al.</i> , 2001; Betts <i>et al.</i> , 2016)	寒武系组芬兰统第二阶顶部、第二统第三阶底部 (下寒武统, Tommotian—Atdabanian阶)	粉砂岩、灰岩	长0.3-1.5 mm, 宽0.25-0.6 mm	<i>Halkieria parva</i> Conway Morris, 1990

注: “主要层位”括号为原文出现层位, 对应于国际寒武系地层划分参考 Peng *et al.*, 2020。

Note: The “main stratigraphic position” in parentheses is the stratigraphic position in the original text, which corresponds to the international Cambrian stratigraphic division, see Peng *et al.*, 2020.

表 3 国内地区 *Halkieria* 属分布特征
Table 3 Distribution of *Halkieria* in China

地区	主要层位	围岩特征	化石大小	化石拉丁名
贵州中西部 (钱逸、尹恭正, 1984)	寒武系纽芬兰统幸运阶上部、第二阶底部 (下寒武统梅树村阶灯影组戈仲伍段)	含磷白云岩、磷块岩	长1 mm以内, 宽约0.3 mm	<i>Halkieria bisulcate</i> Qian, 1984; <i>Halkieria elongus</i> Qian, 1984; <i>Halkieria equilateralis</i> Qian, 1984; <i>Halkieria maidipingensis</i> Qian, 1977; <i>Halkieria mira</i> Qian, 1984; <i>Halkieria operculus</i> Qian, 1982; <i>Halkieria uncostatus</i> Qian, 1984; <i>Halkieria amorphe</i> Meshkova, 1974; <i>Halkieria costulatus</i> Meshkova, 1974; <i>Halkieria longus</i> Qian, 1977; <i>Halkieria maidipingensis</i> Qian, 1977; <i>Halkieria operculus</i> Qian, 1982; <i>Halkieria phylloideus</i> He, 1981; <i>Halkieria praeinguis</i> Jiang, 1982; <i>Halkieria sacciformis</i> Meshkova, 1969; <i>Halkieria sthenobasis</i> Jiang, 1982; <i>Halkieria undulata</i> Wang, 1994; <i>Halkieria wangi</i> Demidenko, 2010;
云南东部(罗惠麟等, 1982; Parkhaev and Demidenko, 2010; Yang <i>et al.</i> , 2014)	寒武系纽芬兰统幸运阶上部、第二阶、第二统第三阶底部(下寒武统梅树村阶中道村段、右岩头段、大海段)	白云质磷块岩、白云岩、灰岩	长0.3–1.5 mm, 宽0.2–0.6 mm	<i>Halkieria alatus</i> Duan, 1984; <i>Halkieria desquamatus</i> Duan, 1984; <i>Halkieria foliiformis</i> Duan, 1984; <i>Halkieria mina</i> Qian, 1979; <i>Halkieria sacciformis</i> Meshkova, 1969; <i>Halkieria terastios</i> Qian, 1979 <i>Halkieria amorphe</i> Meshkova, 1974 <i>Halkieria maidipingensis</i> Qian, 1977 <i>Halkieria mira</i> Qian, 1984 <i>Halkieria sacciformis</i> Meshkova, 1969
湖北神农架地区(钱逸、张师本, 1983; 段承华, 1984)	寒武系纽芬兰统第二阶、第二统第三阶 (下寒武统灯影组底部、灯影组西蒿坪段)	白云岩、磷块岩	长0.5–2 mm不等	<i>Halkieria alatus</i> Duan, 1984; <i>Halkieria desquamatus</i> Duan, 1984; <i>Halkieria foliiformis</i> Duan, 1984; <i>Halkieria mina</i> Qian, 1979; <i>Halkieria sacciformis</i> Meshkova, 1969; <i>Halkieria terastios</i> Qian, 1979 <i>Halkieria amorphe</i> Meshkova, 1974 <i>Halkieria maidipingensis</i> Qian, 1977 <i>Halkieria mira</i> Qian, 1984 <i>Halkieria sacciformis</i> Meshkova, 1969
新疆塔里木地区(钱建新、肖兵, 1984; Conway Morris and Chapman, 1997)	寒武系纽芬兰统第二阶顶部、第二统第三阶底部 (下寒武统玉尔吐斯组)	含磷白云岩、含磷白云质灰岩	多数长1 mm以内, 宽0.2–0.5 mm	<i>Halkieria alatus</i> Duan, 1984; <i>Halkieria desquamatus</i> Duan, 1984; <i>Halkieria foliiformis</i> Duan, 1984; <i>Halkieria mina</i> Qian, 1979; <i>Halkieria sacciformis</i> Meshkova, 1969; <i>Halkieria terastios</i> Qian, 1979 <i>Halkieria amorphe</i> Meshkova, 1974 <i>Halkieria maidipingensis</i> Qian, 1977 <i>Halkieria mira</i> Qian, 1984 <i>Halkieria sacciformis</i> Meshkova, 1969
陕西南部、四川北部地区(丁莲芳等, 1992; Steiner <i>et al.</i> , 2004; Yang <i>et al.</i> , 2015)	寒武系纽芬兰统第二阶、第二统第三阶 (寒武系宽川铺组、水井沱组)	砂质灰岩、含磷白云岩	长0.5–1 mm, 宽0.5 mm以内	<i>Halkieria alatus</i> Duan, 1984; <i>Halkieria desquamatus</i> Duan, 1984; <i>Halkieria foliiformis</i> Duan, 1984; <i>Halkieria mina</i> Qian, 1979; <i>Halkieria sacciformis</i> Meshkova, 1969; <i>Halkieria terastios</i> Qian, 1979 <i>Halkieria amorphe</i> Meshkova, 1974 <i>Halkieria maidipingensis</i> Qian, 1977 <i>Halkieria mira</i> Qian, 1984 <i>Halkieria sacciformis</i> Meshkova, 1969
四川西部、南部地区 (殷维成等, 1980; 何廷贵, 1981; 胡强等, 2022; Yang and Steiner, 2021)	寒武系纽芬兰统幸运阶上部、第二阶底部 (下寒武统梅树村阶麦地坪组)	含磷白云岩、 磷质泥晶灰岩	长0.3–1.2 mm, 宽0.6 mm以内	<i>Halkieria alatus</i> Duan, 1984; <i>Halkieria desquamatus</i> Duan, 1984; <i>Halkieria foliiformis</i> Duan, 1984; <i>Halkieria mina</i> Qian, 1979; <i>Halkieria sacciformis</i> Meshkova, 1969; <i>Halkieria terastios</i> Qian, 1979 <i>Halkieria amorphe</i> Meshkova, 1974 <i>Halkieria maidipingensis</i> Qian, 1977 <i>Halkieria mira</i> Qian, 1984 <i>Halkieria sacciformis</i> Meshkova, 1969
山西南部、安徽、河南地区 (潘兵, 2019)	寒武系第二统第三阶顶部、第四阶底部 (寒武系第二统猴家山组、辛集组)	砂质白云岩、 含磷含砾粉砂岩	长1 mm以内, 宽0.2 mm左右	<i>Halkieria alatus</i> Duan, 1984; <i>Halkieria desquamatus</i> Duan, 1984; <i>Halkieria foliiformis</i> Duan, 1984; <i>Halkieria mina</i> Qian, 1979; <i>Halkieria sacciformis</i> Meshkova, 1969; <i>Halkieria terastios</i> Qian, 1979 <i>Halkieria amorphe</i> Meshkova, 1974 <i>Halkieria maidipingensis</i> Qian, 1977 <i>Halkieria mira</i> Qian, 1984 <i>Halkieria sacciformis</i> Meshkova, 1969

注: “主要层位”括号内为原文出现层位, 对应于国际寒武系地层划分参考朱茂炎等, 2019, 2021。

Note: The “main stratigraphic position” in parentheses is the stratigraphic position in the original text, which corresponds to the international Cambrian stratigraphic division, see Zhu *et al.*, 2019, 2021.

表 4 *Halkieriidae*科的属级分类比较
Table 4 Classification of *Halkieriidae* at genus levels

参考文献 (References)	划分依据 (Basis of classification)	提出的 <i>Halkieriidae</i> 科的属级分类方案 (Proposed classification of the <i>Halkieriidae</i> at genus levels)
Poulsen (1967)	<i>Halkieria</i> 骨片与软舌螺形态相似	首次建立Family <i>Halkieriidae</i> Poulsen, 1967; <i>Halkieria</i> Poulsen, 1967
何廷贵(1981)	骨片侧翼结构与节肢动物 三叶虫的相似性	<i>Sachites</i> Meshkova, 1969; <i>Sinosachites</i> He, 1980; <i>Dictyosachites</i> He, 1981; <i>Microsachites</i> He, 1981
Bengtson (1985)	文石质骨片, 背面均有明显纵脊, 基部较小, 腹 面光滑或有较浅的横纹, 侧翼结构可有可无	<i>Sachites</i> Meshkova, 1969; <i>Halkieria</i> Poulsen, 1967; <i>Sinosachites</i> He, 1980; <i>Dictyosachites</i> He, 1981; <i>Microsachites</i> He, 1981; <i>Thambetolepis</i> Jell, 1981; <i>Tianzhushania</i> Qian, 1979; <i>Acrosquama</i> Qian, 1984
Bengtson等 (1990)	<i>Sachites</i> 、 <i>Dictyosachites</i> 、 <i>Tianzhushania</i> 、 <i>Acrosquama</i> 均为 <i>Halkieria</i> 的晚出同义名	<i>Halkieria</i> Poulsen, 1967; <i>Sinosachites</i> He, 1980; <i>Microsachites</i> He, 1981; <i>Thambetolepis</i> Jell, 1981
Conway Morris and Peel (1995)	<i>Oikozetetes</i> 的两种形态壳体可能代表了 <i>Halkieriidae</i> 动物的前后壳, 且 <i>Microsachites</i> 为 <i>Halkieria</i> 的晚出同义名	<i>Halkieria</i> Poulsen, 1967; <i>Sinosachites</i> He, 1980; <i>Thambetolepis</i> Jell, 1981; <i>Oikozetetes</i> Conway Morris, 1994
钱逸(1999)	<i>Sachites</i> 的模式种骨片背面无纵脊, 且 化石层位较低, 故保留 <i>Sachites</i> 属	<i>Sachites</i> Meshkova, 1969; <i>Halkieria</i> Poulsen, 1967; <i>Sinosachites</i> He, 1980; <i>Thambetolepis</i> Jell, 1981
岳昭(2004)	<i>Thambetolepis</i> 和 <i>Sinosachites</i> 具有相似的中央沟、 侧翼下的侧沟结构, 且发现的层位较为接近	认为 <i>Thambetolepis</i> 应全部归入 <i>Sinosachites</i>
Porter (2004)	<i>Australohalkieria</i> 骨片较细长, 部分扭曲, 腹面 有横纹, 并具有明显的基部结构, 符合 <i>Halkieriidae</i> 科的特征描述	增加 <i>Australohalkieria</i> Porter, 2004
Conway Morris和 Caron (2007)	披有鳞甲状骨片的后生动物, 且拥有三个骨片 类型区域	<i>Halkieria</i> Poulsen, 1967; <i>Sinosachites</i> He, 1980; <i>Thambetolepis</i> Jell, 1981; <i>Ocruranus</i> Liu, 1979; <i>Eohalobia</i> Jiang, 1982; <i>Wiwaxia</i> Walcott, 1911; <i>Australohalkieria</i> Porter, 2004
Parkhaev和 Demidenko (2010)	<i>Ocruranus</i> 、 <i>Eohalobia</i> 、 <i>Oikozetetes</i> 可能代表了 <i>Halkieriidae</i> 科动物的壳体, <i>Hippopharangites</i> 背 面无纵脊, 但有瘤状装饰, 存在基部结构	<i>Sachites</i> Meshkova, 1969; <i>Halkieria</i> Poulsen, 1967; <i>Sinosachites</i> He, 1980; <i>Thambetolepis</i> Jell, 1981; <i>Ocruranus</i> Liu, 1979; <i>Eohalobia</i> Jiang, 1982; <i>Hippopharangites</i> Bengtson, 1990; <i>Oikozetetes</i> Conway Morris, 1994
Zhao等(2017)	<i>Orthrozanclus</i> 骨片排列与 <i>Halkieria</i> 一致	增加 <i>Orthrozanclus</i> Conway Morris, 2007
本文	两侧对称的后生动物, 骨片呈长板状、长扇状、 长椭圆状或三角状、桨状, 两个壳体均有较微弱 的边缘同心生长线	<i>Sachites</i> Meshkova, 1969; <i>Halkieria</i> Poulsen, 1967; <i>Sinosachites</i> He, 1980; <i>Ocruranus</i> Liu, 1979; <i>Eohalobia</i> Jiang, 1982; <i>Hippopharangites</i> Bengtson, 1990; <i>Oikozetetes</i> Conway Morris, 1994; <i>Australohalkieria</i> Porter, 2004; <i>Orthrozanclus</i> Conway Morris, 2007

Maloof *et al.*, 2010), 目前是华南纽芬兰统小壳化石组合带*Sinosachites flabelliformis*——*Tannuolina zhangwentangi*的标志性化石(朱茂炎等, 2019); *Orthrozanclus*在华南扬子地台发现的层位低于加拿大苗岭统Burgess Shale层位, 最早出现在寒武系第三阶底部的澄江生物群中(Conway Morris and Caron, 2007; Zhao *et al.*, 2017); *Oikozetetes*在第三阶、第四阶均有发现, 暂只见于澳大利亚地区和北美地区; *Hippopharangites*化石层位跨度较大, 从第二阶到第四阶均有分布(潘兵, 2019; Bengtson *et al.*, 1990; Gravestock *et al.*, 2001; Betts *et al.*, 2016;

Peel, 2021)。
从属种形态演替上看, 幸运阶出现了*Sachites*和*Halkieria*两个属(图2-B–2-E), 到第二阶顶部出现*Sinosachites*, 骨片化石特征由刺形、剑形演化为带侧翼的三角形、扇形, 背面中脊隆起(图2-F, 2-J), 腹面开始出现针管状结构, 基部变宽(何廷贵, 1981)。寒武系第三阶只存在少量*Sinosachites*分布于澳大利亚地区(Jell, 1981; Vinther, 2009), 但*Halkieria*分布区域扩大到格陵兰岛和中国湖北、塔里木地区(段承华, 1984; Conway and Peel, 1990; Conway Morris and Chapman, 1997), 第三阶出现的

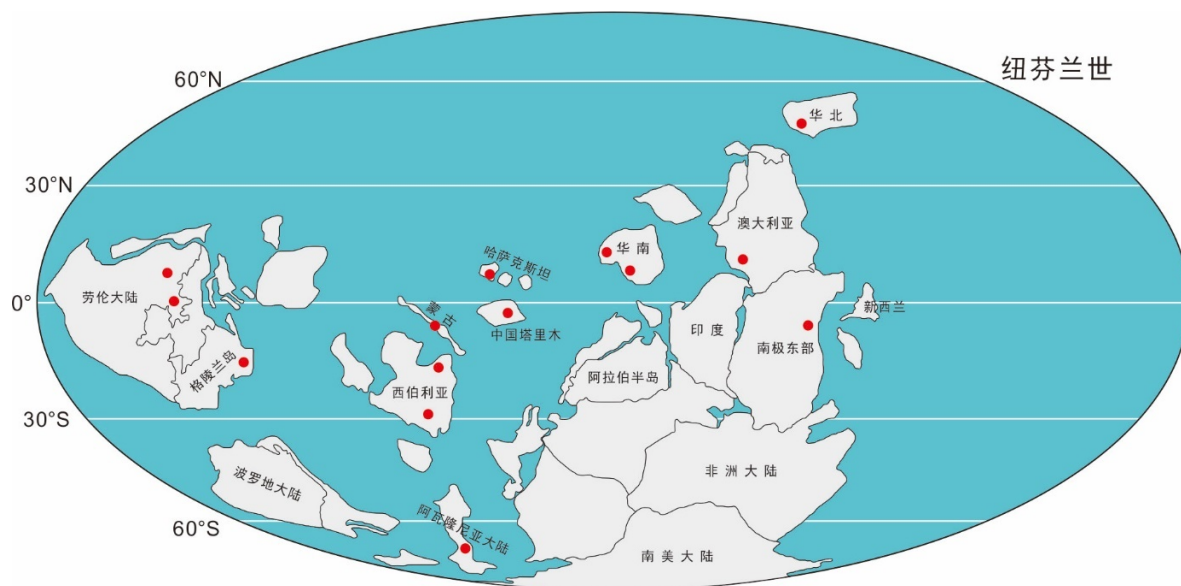


图 1 *Halkieria*在寒武纪纽芬兰世古地理分布(修改自Torsvik and Cocks, 2013; Yang *et al.*, 2015)

Fig. 1 Palaeogeographical distribution of *Halkieria* during the Terreneuvian of Cambrian (modified from Torsvik and Cocks, 2013; Yang *et al.*, 2015)

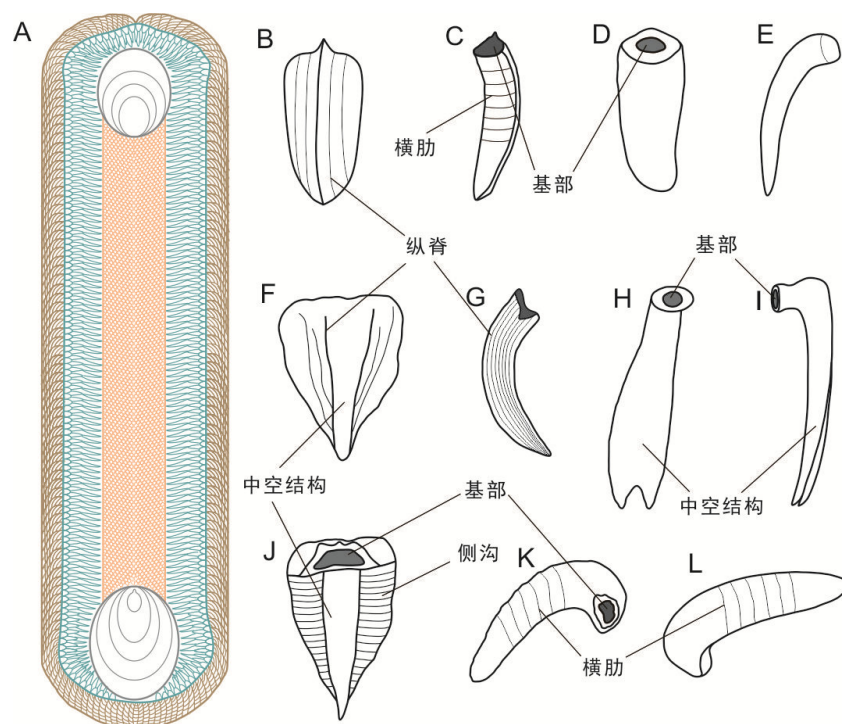


图 2 Halkieriidae科的部分骨片属化石简图

Fig. 2 Schematic drawings of some sclerites of the Halkieriidae

A. *Halkieria evangelista*复原图, 修改自(张晓川、姚锦仙, 2011; Conway Morris and Peel, 1990; Zhao *et al.*, 2017); B–C. 为*Halkieria*骨片简图: B. 背视图, C. 腹视图; D–E. *Sachites*骨片简图: D. 腹视图, E. 侧视图; F–J. *Sinosachites*骨片简图: F. 背视图, J. 腹视图; G. *Oikozetetes*骨片简图; H–I. *Australohalkieria*骨片简图, 修改自(Porter, 2004): H. 腹视图, I. 侧视图; K–L. *Hippopharangites*骨片简图: K. 侧视图, L. 背视图。

A. reconstruction of *Halkieria evangelista*, modified from Conway Morris and Peel, 1990; Zhang and Yao, 2011; Zhao *et al.*, 2017; B, C. a sclerite of *Halkieria*: B. dorsal view, C. ventral view; D–E. a sclerite of *Sachites*: D. ventral view, E. lateral view; F–J. a sclerite of *Sinosachites*: F. dorsal view, J. ventral view; G. a sclerite of *Oikozetetes*; H–I. a sclerite of *Australohalkieria*, modified from Porter, 2004: H. ventral view, I. lateral view; K–L. a sclerite of *Hippopharangites*: K. lateral view, L. dorsal view.

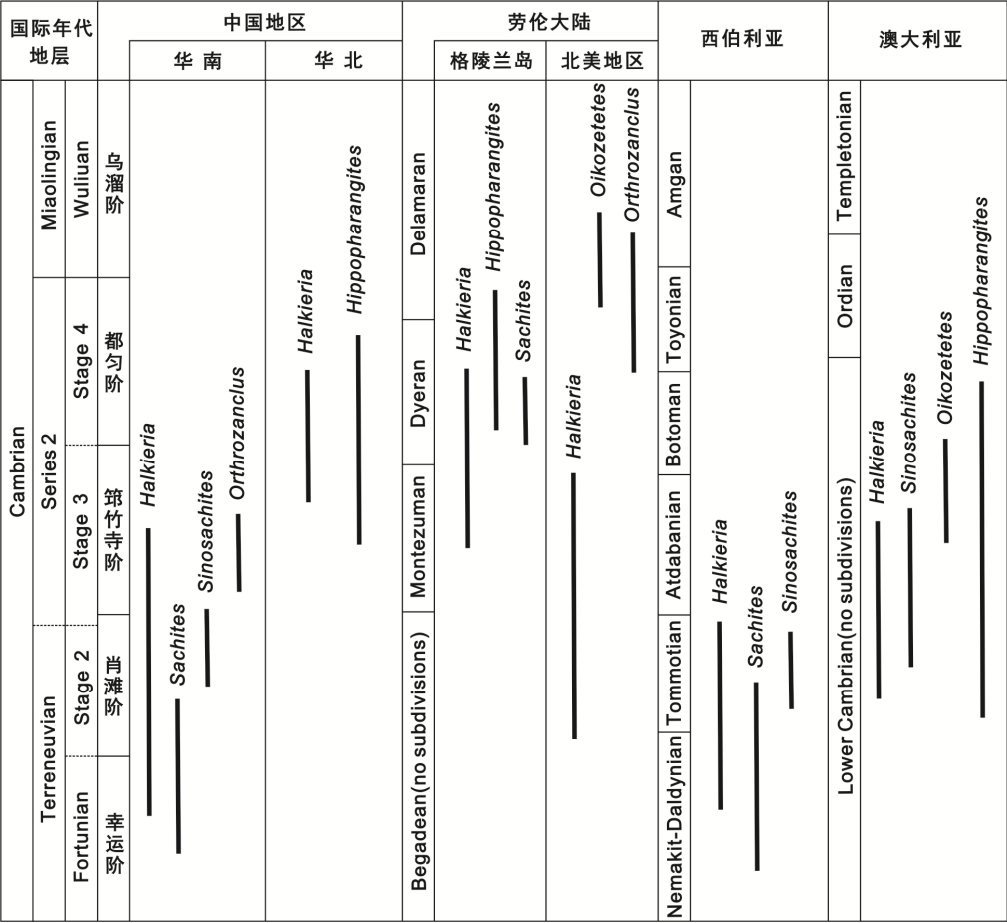


图3 *Halkieriidae*科的部分骨片属全球层位对比图
Fig. 3 Global stratigraphic distribution of some genera of *Halkieriidae*

*Hippopharangites*和*Oikozetetes*骨片显示(Bengtson *et al.*, 1990; Paterson *et al.*, 2009; Jacquet *et al.*, 2014), 骨片背部鳞甲状的纵脊已经变浅甚至消失(图2-G), 云南澄江动物群发现的*Orthrozanclus*表明, 部分骨片进化为长刺形(Zhao *et al.*, 2017)。第四阶*Hippopharangites*分布区域进一步扩大到中国华北、澳大利亚和格陵兰岛地区(潘兵, 2019; Bengtson *et al.*, 1990; Peel, 2021), 骨片逐渐变细, 背部略有褶皱(图2-K, 2-L), *Orthrozanclus*骨片排列紧密, 软躯体从长直状演化为椭圆形(Conway Morris and Caron, 2007)。未在第四阶发现*Oikozetetes*骨片, 只有其独立壳体(Conway Morris, 1994)。综上, *halkieriids*骨片整体演化趋势为由薄片状到细长管状, 背部纵脊由深变浅, 骨片中空结构、腹面侧翼和基部的发育体现了骨片演化结构越来越复杂(图2)。

从化石古地理分布的地区差异上看, *Halkieria*在不同地区的骨片形态差异较大。同一生物个体不同部位骨片的差异仅表现在骨片类型和大小不同, 同类骨片中骨片形态差异较小, 大多为长宽比例不同, 其余特征均相同。而*Halkieria*的地方性差异表现在骨片背部纹饰、基部形状和大小、骨片扭曲程度等特征上, 骨片形态差异较大, 是种一级别划分和对比的重要依据。例如, 保存于寒武系第二阶地层中的*Halkieria*的特征: 华南地区骨片类型狭长或呈囊状, 背部纹饰明显, 尾端尖细(钱逸, 1977, 1999; 殷继成等, 1980; Parkhaev and Demidenko, 2010; Yang *et al.*, 2014; Yang *et al.*, 2015; Yang and Steiner, 2021); 塔里木、哈萨克斯坦、巴基斯坦地区呈长扇形、三角形或弯月形, 基部较大且口端略平, 骨片向背部弯曲明显(钱建新、肖兵, 1984; 王务严等, 1985; 肖兵、段承华,

1992; Mostler, 1980; Missarzhevsky and Mambetov, 1981; Conway Morris and Chapman, 1997); 蒙古国、西伯利亚地区骨片类型呈掌形、剑形, 基部较大且延伸, 骨片轻微扭曲 (Meshkova, 1969; Bengtson and Conway Morris, 1984; Esakova and Zhegallo, 1996; Kouchinsky *et al.*, 2015; Zhu *et al.*, 2017); 华北地区骨片类型呈叶状, 左右不对称, 具有显著的环形生长纹 (潘兵, 2019)。这些差异展现了 *Halkieria* 具有明显的地方性色彩, 再结合 *Halkieria* 骨片化石在不同岩性中都有发现 (表2, 3), 表明该类生物适应于寒武纪早期的多种生态环境, 具有广泛的环境耐受性 (Conway Morris *et al.*, 1998)。

4 系统生物学研究进展

4.1 *Halkieria* 系统分类位置的不同观点

半个世纪以来, *Halkieria* 的系统分类研究一直备受关注, 虽然已取得很多进展, 但仍然存在较大争议, 主要有以下几个观点。

1) *Halkieria* 是腕足动物的祖先

Halkieria 最初被描述为软舌螺一大类 (Poulsen, 1967)。之后, Conway Morris 发现 *Halkieria* 的壳体较为特殊, 与软体动物的各类外壳存在很大差异, 其后侧壳板却与腕足动物的壳体有相似性, 由此他否认了 *Halkieria* 与 Chitons 的亲缘关系, 认为 *Halkieria* 更接近腕足动物 (Conway Morris and Peel, 1995; Conway Morris, 2006)。Nielsen 根据腕足动物 *Neocrania* 幼虫生长过程中的折叠和反转现象, 支持腕足动物祖先为具有类似蠕虫类躯体构型的后生动物 (Nielsen, 1991), 符合 *Halkieria* 软躯体的体态特征。随着研究的深入, 不断有学者把 *Halkieria* 置于腕足动物的起源中。详细的骨片超微结构和形态学数据等证据, 支持了一种演化模式, 即腕足动物躯体折叠起源假说: *Halkieria* 躯体发生折叠; 前壳、后壳加速生长分别成为腕足动物的背壳、腹壳, 尤其是前壳, 发育到口部前方以达到腹侧边缘, 从而为内脏团提供更大空间; 重组肌肉系统来协调腔室之间的控制; 躯体表面的骨片分泌减少来提供腕足动物附着器官 (肉茎) 的生长; *Halkieria* 骨片的基底构造表明其支撑着前部的一对肌肉和后部的生殖腺囊 (Holmer, 2001; Holmer *et*

al., 2002; Ushatinskaya, 2002; Williams and Holmer, 2002; Cohen *et al.*, 2003)。

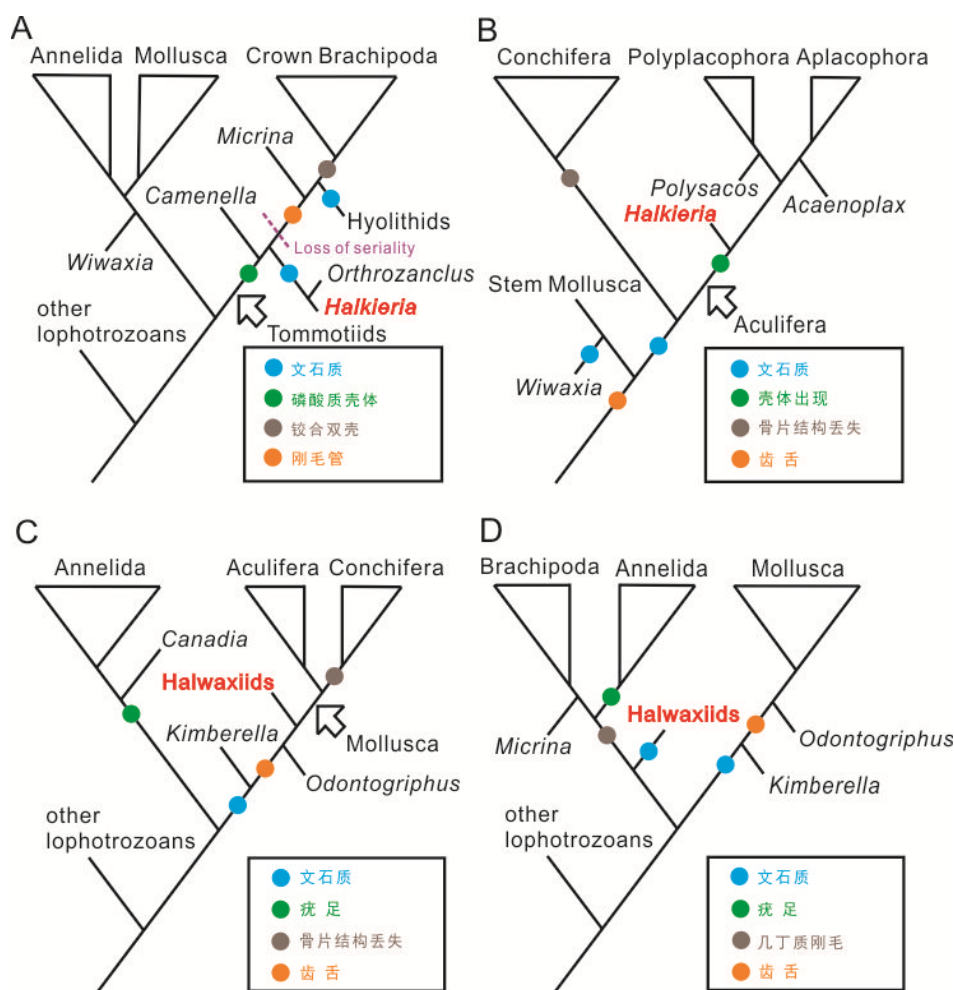
近年来, 有关 *Halkieria* 与腕足动物关系的研究尚在继续 (Skovsted *et al.*, 2015; Sun *et al.*, 2018; Smith, 2020; Johnston and Streng, 2021), 新发现的长形黎镰虫 *Orthrozanclus elongata* 骨片排列和身体构造更接近于 *Halkieria*, 同样拥有三种类型骨片形成的纵向区域, 从外到内分别对应于 *Halkieria* 的剑形 (siculates)、刀形 (cultrates) 和掌形骨片 (palmates)。但是 *Orthrozanclus elongata* 与 *Wiwaxia corrugata* 背部间隔交错的骨片排列并不相同, 该类化石的发现一定程度上否认了 *Halkieria* 与 *Wiwaxia* 的亲缘关系, 挑战了 *halwaxiids* 分类单元的合理性 (Zhao *et al.*, 2017)。同时, 基于 *Orthrozanclus elongata* 和托莫特壳类 *tommotiids* 的 *Dailyatia* 属复原结构的相似性, *Orthrozanclus elongata* 成为了拉近 *halkieriids* 与托莫特壳类 *tommotiids* 系统分类位置的有力证据 (图4-A)。

Johnston 和 Streng (2021) 提出腕足动物骨片融合理论, 即钙质腕足动物的两个壳体经过发育和融合而形成较合双壳。腕足动物壳体成分最初可能为钙质矿物, 其中 *Halkieria* 骨片成分为有机文石矿物, 磷质腕足动物是托莫特壳类 *tommotiids* 经过几次独立地进化而来的 (Johnston and Streng, 2021)。

2) *Halkieria* 是软体动物的干群, 与 *Wiwaxia* 具有同源性

早期研究中, Bengtson 和 Conway Morris (1984) 发现了与 *Wiwaxia* 具有高度相似的 *Halkieria* 骨片化石。Bengtson (1984) 虽然将二者详细比较, 但最后他并没有将二者确定归为某一门类, 只是提到了与软体动物的亲缘关系, 这也为后来的“同源性”观点做出了铺垫。

Caron 等 (2006) 对来自苗岭统布尔吉斯页岩中的 *Odontogriphus* 进行研究, 对其进行了结构上的复原后发现: 该类动物具有齿舌结构, 具有身体扁平、柔软的特征, 可能为 *Halkieria* 的近亲。而软体动物的祖先被推测为一种爬行的、身体不分节的两侧对称动物 (Valentine, 2004), 符合 *Halkieria*、*Odontogriphus* 的身体构造, 故他支持将 *Halkieria* 和 *Odontogriphus* 都置于软体动物干群。

图4 *Halkieria*在不同分类系统树中的位置示意图Fig. 4 Positions of *Halkieria* in different phylogenetic trees

A由Skovsted (2015)、Zhao (2017)、Sun (2018)研究人员主要支持的观点: *Halkieria*为腕足动物的干群; B由钱逸(1999)、Vinther和Nielsen (2005)、Parkhaev(2008)等研究人员主要支持的观点: *Halkieria*为软体动物有刺亚门的干群; C由Caron等(2006)、Conway Morris和Caron (2007)、Sigwart和Sutton (2007)等研究人员主要支持的观点: *Halkieria*为软体动物的干群; D由Conway Morris和Caron (2007)提出的副观点: *Halkieria*为腕足动物与环节动物的干群。

A. Mainly supported by Skovsted *et al.*, 2015, Zhao *et al.*, 2017, Sun *et al.*, 2018: *Halkieria* is a stem group of brachiopods; B. Mainly supported by Qian, 1999, Vinther and Nielsen, 2005, Parkhaev, 2008: *Halkieria* is a stem group of Aculifera; C. Mainly supported Caron *et al.*, 2006, Conway Morris and Caron, 2007, Sigwart and Sutton, 2007: *Halkieria* is a stem group of mollusks; D. Sub-view supported by Conway Morris and Caron, 2007: *Halkieria* is a stem group of annelids and brachiopods.

Conway Morris 和 Caron (2007) 在研究 *Orthrozanclus reburrus* 时发现, 其具有与 *Halkieria* 相似的前壳, 但也有 *Wiwaxia* 背部的密集长直骨片, 因此将 *Orthrozanclus reburrus* 分类位置放在 *Halkieria* 与 *Wiwaxia* 的中间, 并将这三者和 *Siphonochites* 等其他一些疑难离散骨片和壳体并入一个新的单元 *halwaxiids*。研究指出 *Halkieria* 与现生软体动物骨片生长模式不符 (Conway Morris and Caron, 2007), 因而他们更倾向于支持

Halkieria 为软体动物的干群 (图4-C), 并得到了后来研究的支持 (Sigwart and Sutton, 2007; Shigeno *et al.*, 2010)。

另外, 来自志留纪的一个新种 *Kulindroplax perissokomos*, 其背部上覆盖的7个背瓣并非联结的 (Sutton *et al.*, 2012), 该类化石与 *Phthipodochiton thraivensis*、*Acaenoplax hayae* 的发现支持了软体动物门双神经亚门 (Aculifera) 这个独立分支的存在 (Sutton *et al.*, 2001, 2004; Sigwart and Sutton, 2007;

Sutton and Sigwart, 2012)。而*Halkieria evangelista*是完整联结的软躯体化石,两个背壳与*Oikozetetes*、*Ocruranus*、*Eohalobia*是同源的(Conway Morris, 1994; Parkhaev and Demidenko, 2010; Jacquet *et al.*, 2014),其钙质成分很难维持与腕足动物磷质化石之间的系统发育关系(Balthasar *et al.*, 2009),因此*Halkieria*被认为是软体动物的干群(Conway Morris and Caron, 2007; Vinther *et al.*, 2008; Paterson *et al.*, 2009; Sutton *et al.*, 2012)。

3) *Halkieria*是软体动物有刺亚门的干群,与多板纲、无板纲亲近

多板纲和无板纲组成了软体动物有刺亚门(Aculifera),也叫双神经亚门(Vinther, 2015)。其分泌的碳酸钙质外骨骼类型包含骨刺、骨针、骨片,而多板纲动物部分透镜状骨骼甚至可接收光信号,发挥“眼睛”的功能,与有壳亚门(Conchifera)的壳体明显不同(Giribet *et al.*, 2006; Sigwart *et al.*, 2014; Li *et al.*, 2015; Checa *et al.*, 2017)。Dzik (1987)曾复原过halkieriids的身体结构,并认为其与环节动物存在明显差异(Dzik, 1987; Bergström, 1989)。尽管如此,他还是最终得出结论:*Halkieria*可能是环节动物或软体动物,若是后者,则应与多板纲或无板纲存在密切联系。

随着*Halkieria evangelista*软躯体在格陵兰岛被报道,人们发现*Halkieria*比起*Wiwaxia*多了一前一后两个大壳板(Conway Morris and Peel, 1990)。钱逸(1999)对比了*Halkieria*与*Wiwaxia*在骨片矿化程度、数目和排列位置的差异,认为二者差异较大,更重要的是有无帽贝状的壳板是最为本质的,仅仅这一区别就已经表明二者在解剖学和生物学特征上超过纲一级的范围,使得其他相似性不过是一种趋同现象。他提出,*Halkieria*可能是介于软体动物无板纲、多板纲之间潜在有纲一级的新类别(图4-B),得到了众多研究人员的支持(Scheltema and Ivanov, 2002; Lindberg *et al.*, 2004; Vinther and Nielsen, 2005; Parkhaev, 2008; Ponder and Lindberg, 2008; Parkhaev and Demidenko, 2010; Vinther, 2014; Parkhaev, 2017)。

Vinther和Nielsen (2005)总结了*Halkieria*与软体动物的亲缘关系的证据:(1)壳体数目:不管是现

生多板纲还是化石种多板纲动物,都是由背部均匀排列的壳板(通常为8个)和身体边缘针状、鳞状的骨刺所构成(Pojeta *et al.*, 2003)。但是新发现的石炭纪多板纲动物*Polysacos*却有17个壳板,并分为两列,一前一后由两个大壳板进行固定(Vendrasco *et al.*, 2004; Vinther *et al.*, 2012),这表明了壳板数目与演化的阶段相关,只拥有两个壳板的*Halkieria*也可以是多板纲演化初期的形态。(2)壳体 and 骨片成分:有研究发现,多板纲的壳板和周围鳞片的成分为文石矿物(Scheltema, 1988),与*Halkieria*的骨片成分非常相似。(3)骨片排列方式:部分无板纲动物具有密集的钙质针状覆盖,同时还具有背瓣结构(与壳类似),比如志留纪的*Acaenoplax hayae* (Steiner and Salvini-Plawen, 2001; Sutton *et al.*, 2001, 2004),该类软体动物的针状覆被与*Halkieria*的刀形骨片在排列上几乎相同。

Zhang (2014)将*Halkieria*与多板纲动物*Ischnochiton hakodadensis*作了骨骼微观结构上的比较,并得出结论:*Halkieria*与多板纲的壳体有一定的相似之处,包括相同的钙质成分和表面明显的环形纹饰,但是基于现生多板纲与*Halkieria*化石的壳体数目相差甚远,*Halkieria*的壳不太可能是多板纲冠群的壳;从*I. hakodadensis*和*Halkieria*壳体周边的骨片整体排列方式和微观结构上看,支持*Halkieria*为软体动物冠群的双神经亚门干群的观点。

Vinther (2017)描述了奥陶纪的一个新种*Calvapilosa kroegeri*,该化石保存完整,显示出规律排列的骨片和前端一个壳板,骨片是未矿化的。系统发育分析和贝壳、齿舌等证据表明,*C. kroegeri*更接近双神经亚门的干群,由此Vinther提出一种新的猜想:软体动物的祖先形态往往被推测为是无壳体的蠕虫状(Salvini-Plawen and Steiner, 1996; Valentine, 2004),但双神经亚门很可能是从一种存在未矿化骨片和单个钙质壳体的形态发育而来的,这类单壳状生物一方面通过具有两个壳体的过渡形态(例如*Halkieria*),发育成八个壳体的多板类冠群;另一方面,通过壳体脱落,发育成无板类。因此,*C. kroegeri*化石的研究被认为是*Halkieria*与双神经亚门干群亲缘关系的有力证据

(Vinther *et al.*, 2017; Wanninger and Wollesen, 2019; Peel, 2020; Thomas *et al.*, 2020)。

4) *Halkieria*是环节动物的祖先

1981年, 研究人员Jell在南澳大利亚发现了新属 *Thambetolepis* (后被证实为 *Sinosachites* 属, 与 *Halkieria* 同科), 该骨片化石以两侧翼变宽的特征引发关注, 侧翼腹部显示密集的小管。他认为, 骨片的侧翼变宽是为容纳不断延伸的软躯体, 骨片或其相邻区域可能代表了促进环节动物呼吸的器官, 因为该结构极大增加了身体直接接触海水的表面积。另一方面, 骨片侧翼结构也有可能连接到消化系统, 成为消化和吸收的区域(Jell, 1981), 因其与海洋中环节动物的基本特征相当, Jell 暂将 *halkieriids* 一大类置于环节动物门。

Conway Morris 和 Caron (2007) 提出 *halwaxiids* 单系演化假说, 描述了该类 *halwaxiids* 的单元特征为拥有三个骨片类型区域的带壳后生动物, *Halkieria* 的两个壳脱落形成单个壳体的 *Orthrozancus*, 最后壳体完全脱落演化为 *Wiwaxia*, 通过对该分支系统发育的研究, 他们认为 *halwaxiids* 可能是环节动物和腕足动物的共同祖先(图4-D)。

对于软体动物观点中的齿舌争议, Butterfield (2008) 表示 *Halkieria* 有无齿舌结构还是未知, 就算有摄食器官也不能单纯与软体动物比较, 还应与环节动物多毛类进行对比, *Halkieria* 的亲缘关系表现在整个冠轮动物超门中。随后的研究也表明, *halwaxiids* 与环节动物在骨片分泌方式、身体构型方面有许多相似之处(Zhang *et al.*, 2015), 但考虑到软体动物与环节动物早期分化的相似性, 仍不能将其准确归于某一门类中。

5) 讨论

Halkieria 的高级分类位置是探索该生物起源和演化的关键问题, 目前 *Halkieria* 与软体动物的亲缘关系受到普遍认可 (Vinther and Nielsen, 2005; Vinther *et al.*, 2017; Wanninger and Wollesen, 2019; Murdock, 2020; Pang *et al.*, 2022), 但 *halkieriids* 新化石的研究和发现使得 *Halkieria* 的系统发育位置仍存争议 (Zhao *et al.*, 2017; Sun *et al.*, 2018; Han *et al.*, 2019; Peel, 2020; Smith, 2020; Johnston and Streng, 2021; Kimmig *et al.*, 2021; Kono *et al.*, 2021)。

首先, *Halkieria* 软躯体化石没有发现确切的齿舌结构, 且软体动物各纲之间谱系演化关系不明确, 尤其是多板纲和无板纲两个分类单元的分子数据仍是模糊的 (Passamaneck *et al.*, 2004; Caron *et al.*, 2006; Todt *et al.*, 2008; Smith *et al.*, 2011)。*Halkieria* 与软体动物现生多板纲的研究 (Vinther and Nielsen, 2005), 也因骨片排列的不恰当比较和现生多板纲的同源性而缺乏说服力 (Conway Morris and Caron, 2007)。因此, *Halkieria* 与软体动物的关系, 还需要对其他双神经亚门物种进行更多的微观结构研究和比较, 以帮助揭示更多软体动物系统发育的全貌 (Zhang and Yao, 2014)。

其次, *Halkieria* 腕足动物躯体折叠起源假说观点被推翻, 因为腕足动物 *Neocrania* 幼虫的系统发育未发生躯体折叠 (Altenburger *et al.*, 2013), 且重新复原后的 *Micrina* 的壳体并非 *Halkieria* 形态似的一前一后排列, 而是半封闭式的铰合, 不再适合作为 *Halkieria* 与腕足动物发育的中间过渡体 (Holmer *et al.*, 2008, 2011)。

Halkieria 壳体与腕足动物壳体具有同源性 (Conway Morris and Peel, 1995; Cohen *et al.*, 2003; Williams and Carlson, 2007), *halkieriids* 骨片排列和托莫特壳类 *Daliyatia* 相似性得到证实 (Skovsted *et al.*, 2015; Zhao *et al.*, 2017)。有关 *Halkieria* 钙质化石与托莫特壳类、腕足类磷质化石成分不符的观点, 可以得到解释: 腕足动物存在钙质成分化石, 说明该类动物已经发生过生物矿物的转变 (Balthasar, 2008; Skovsted, 2016), 因而化石成分的不符, 不能作为反对 *Halkieria* 与腕足动物的亲缘关系的证据 (Zhao *et al.*, 2017)。早期钙质腕足动物的双壳经过融合发育形成铰合双壳 (Johnston and Streng, 2021), 符合 *Halkieria* 身体构型, 为 *halkieriids* 与腕足动物的亲缘关系的研究提供了支持。

4.2 *Halkieria*与寒武系其他疑难化石的关系

1) *Halkieria*与 *Wiwaxia*

Wiwaxia 最初被认为与 *Halkieria* 有密切关系 (Bengtson and Conway Morris, 1984), 但在后来的研究中, 这种关系似乎越来越弱 (钱逸, 1999; Conway Morris and Peel, 1990; Butterfield, 2006,

2008), 以至于不断加入新的属种(又或者说是新的证据)来保持 *halwaxiids* 单元(Conway Morris and Caron, 2007; Shigeno *et al.*, 2010)。与 *Halkieria* 相似的是, *Wiwaxia* 的发现层位和地理分布都与 *Halkieria* 大致相同(Zhao *et al.*, 2015; Smith *et al.*, 2016; Slater *et al.*, 2017)。这种相似性还体现在生物亲缘关系上, *Wiwaxia* 也是经历了“软体动物—环节动物—冠轮动物”亲缘相关性的曲折研究(张晓川等, 2009; Conway Morris, 1985; Butterfield, 1990; Scheltema and Ivanov, 2002; Eibye-Jacobsen, 2004; Scheltema and Schander, 2006; Smith, 2012, 2014; Scheltema, 2014; Schieman *et al.*, 2017)。

Wiwaxia 与环节动物多毛类 *Canadia spinosa* 具有高度相似的骨片显微特征(Butterfield, 1990), 且 *Wiwaxia* 的齿舌结构符合环节动物多毛类的齿舌构造特征(Butterfield, 2006, 2008), 因此 Butterfield 认为 *Wiwaxia* 属于环节动物。澄江动物群寒武系第三阶发现的 *Wiwaxia papilio* 系统发育显示, *Wiwaxia* 可能为软体动物和环节动物的共同祖先(Zhang *et al.*, 2015)。目前, 谱系演化关系和众多系统发育学证据显示了 *Wiwaxia* 与软体动物的亲缘关系, *Wiwaxia* 属于软体动物的观点仍占主导(Yang *et al.*, 2014; Vinther *et al.*, 2017)。

2) *Halkieria* 与 *Siphogonuchitids*、*Chancelloriids*

最初的具腔骨片 *Coeloscleritophora* 一名是由 Bengtson 和 Missarzhevsky (1981) 提出来的, 主要由哈氏壳类 *halkieriids*、棱管壳类 *siphogonuchitids* 和开腔骨类 *chancelloriids* 组成该类群。其分类依据是这些动物以复合的外骨骼为特征, 单个骨片都有一个显著的腔室和一个较小的基孔(钱逸, 1999; Bengtson and Missarzhevsky, 1981)。但寒武系地层底部大多都是相似的离散骨片, 对其展开的分类研究相对较难, 需要参考大量生物种类之间的谱系关系和种群内部表型变异。显然, 他们所认为“骨片为彼此联结的环形外硬壳”的观点很难得到广泛认可(Conway Morris and Peel, 1990)。

从骨片整体形态上看, 三者的区别非常显著, 但 Porter (2004, 2008) 的一些研究尝试为具腔骨片这个分类单元提供支持。具腔骨片都有着含有有机质的薄壁, 其表面覆盖着一层躯体走向的文石纤维,

这在所有寒武系骨片里是这个类群所独有的, 表明了哈氏壳类 *halkieriids*、棱管壳类 *siphogonuchitids* 与开腔骨类 *chancelloriids* 的骨片都是同源的(Porter, 2008)。

目前, 棱管壳 *siphogonuchitids* 被认为是软体动物的干群(Conway Morris and Caron, 2007; Vinther *et al.*, 2017)。而开腔骨 *chancelloriids* 因为其骨针的细微构造与现代海绵体的一种胶原蛋白成分的纤维结构相似, 最初被认为与海绵动物密切相关(Butterfield and Nicholas, 1996)。但是随后的研究表明, 普通海绵纲的硅质根刺是实心的, 而开腔骨显示出中空结构, 内部充满软组织, 并且硅质骨针也明显不同于开腔骨的文石质成分(Janussen *et al.*, 2002), 再结合开腔骨顶部骨针和体部骨针的生长模式不符合 *halkieriids* 骨片, 因此开腔骨类仍是分类位置不明确的类群(Cong *et al.*, 2018; Yun *et al.*, 2021)。具腔骨片 *Coeloscleritophora* 现今被认为是并系群(Bengtson and Collins, 2015), 即拥有共同祖先的小部分类群。

3) *Halkieria* 与 *Micrina*、*Mickwitzia*

Micrina、*Mickwitzia* 是托莫特类 *tommotiids* 的两个属, 一直被认为是 *tommotiids* 与腕足动物之间关系的纽带(Ushatinskaya, 2002; Holmer *et al.*, 2008; Skovsted *et al.*, 2009b; Butler *et al.*, 2015)。早期的研究认为, *Micrina* 壳体与 *Halkieria* 壳体具有同源性, *Halkieria* 在依次经历了 *Micrina*、*Mickwitzia* 的壳体形态发育之后, 成为现生腕足动物双瓣壳的模样(腕足动物躯体折叠起源假说), 也从自由移动的海生底栖动物变为了营固着生活的海生底栖动物(Holmer *et al.*, 2002; Williams and Holmer, 2002; Cohen *et al.*, 2003; Williams and Carlson, 2007)。

但是, 与 *Micrina* 同科的 *Tannuolina* 化石显示, 骨片由左右旋排列的帽状和叠瓦状的鞍形骨片构成, 与 *Halkieria* 骨片的纵向带排列相差较大(Li and Xiao, 2004)。Li 和 Xiao 推测 *Micrina* 与 *Halkieria* 壳体并非同源, 其相似性只是趋同现象, 并提出 *Micrina* 与 *Tannuolina* 可能代表着磷质腕足动物舌形贝类(*linguliformeans*)的干群, 而 *Halkieria* 则是钙质腕足动物的祖先(Li and Xiao, 2004)。

随着对 *Micrina* 的进一步研究, 其与 *Halkieria*

的关系出现转折。新发现的 tommotiids 化石 *Eccentrotheca* 具有双壳较合的特征 (Skovsted *et al.*, 2008), 在此基础上, Holmer 等 (2008) 对 *Micrina* 进行重新复原, 否定了他此前提出的 *Micrina* 具有 *Halkieria* 似的前后壳排列, 并将其恢复为半封闭式的较合排列, 认为 *Micrina* 可能为腕足动物早期进化的过渡类群 (Holmer *et al.*, 2008; Skovsted *et al.*, 2008, 2009a, 2011)。加之 *Micrina* 与 *Mickwitzia* 壳体表面布满了管状刚毛结构 (setigerous tubes), 以 *Micrina*、*Mickwitzia* 为代表的 tommotiids 与腕足动物的亲缘关系得到支持 (Holmer *et al.*, 2002; Ushatinskaya, 2002; Skovsted *et al.*, 2014; Harper *et al.*, 2017)。因此腕足动物躯体折叠起源假说被推翻, 腕足动物的托莫特壳化石起源假说正式形成 (张志飞等, 2016; Holmer *et al.*, 2008, 2011; Devaere *et al.*, 2014; Larsson *et al.*, 2014; Murdock *et al.*, 2014; Butler *et al.*, 2015; Steiner *et al.*, 2021)。

5 *Halkieria*系统分类的研究方向与展望

迄今为止, 对 *Halkieria* 骨片的研究已经长达半个世纪。在这期间, 人们对 *Halkieria* 的认识不断深入, 但很难将其毫无争议地置于任一动物门类中。主要由于这些原因: 1) 早期化石记录不完备, 且大部分是身体结构中的骨质残片以小壳化石形式被保存下来, 特异埋藏化石库中保存完整躯体形态的化石少之又少; 2) 对大量离散骨片的分类混乱, 分类单元出现重复; 3) *Halkieria* 骨片区域性明显, 不同地区形态差异较大, 种属间差异与种内不同骨片类型的差异研究难度大; 4) 冠轮动物不同门类及内部谱系演化关系复杂, 目前解析度不高, 加之冠轮动物系统发生和谱系演化的时间节点尚不确定, 无法与 *Halkieria* 产出时代相对应。

因此, 加强 *Halkieria* 骨片等疑难化石的研究, 还有待于更多学科交叉和新技术、新方法的引用; 同时更为系统深入地研究, 也需要更多更好的化石材料的发现。从意义上看, 对 *Halkieria* 系统进化的探索, 即是对所有离散骨片进行的综合研究。本文认为, 确立 *Halkieria* 的系统分类位置或与其他动物类别的亲缘关系, 在以下方面还需要作进一

步的思考:

1) 骨片或壳体表面超微结构。众多研究人员对 halkieriids 骨片的壳壁微细结构进行过研究 (Bengtson and Conway Morris, 1984; Conway Morris and Peel, 1990, 1995; Cohen *et al.*, 2003; Porter, 2004, 2008; Vinther and Nielsen, 2005; Chen *et al.*, 2015)。Bengtson (1984) 和 Porter (2008) 根据 halkieriids 与棱管壳 siphonochitids、开腔骨类 cancelloriids 的相似壳壁微细构造, 支持将它们放在同一个类别 (腔骨类)。Vinther (2005) 认为软体动物多板纲、无板纲动物的针状边缘或钙质体表覆被和 halkieriids 的骨片表面超微结构从排列、成分上都非常相似。但是, Conway Morris (1995) 与 Cohen (2003) 观点一致, 认为 *Halkieria* 壳体的形态结构与腕足动物十分相似。值得一提的是, 寒武纪冠轮动物各分支的干群类型相对原始, 各个类群之间的相似性很高 (Zhang *et al.*, 2015)。因而, 需要通过对早期冠轮动物骨质微结构的研究, 尤其是软体动物多板纲、无板纲的表面超微结构, 总结其形态多样性的特点, 为进一步确定 *Halkieria* 系统分类提供生物矿化方面的新证据。

2) 早期冠轮动物系统发生和谱系演化的研究。上述有关 *Halkieria* 分类观点已经论述详尽, 对冠轮动物系统发育学的研究缺乏一个普遍认可的观点, 这使得 *Halkieria* 乃至更多离散骨片的生物亲缘关系问题尚未解决。近几年的一些研究将 *Halkieria* 的系统发育范围缩小到腕足动物和软体动物附近 (Vinther, 2015; Vinther *et al.*, 2017; Zhao *et al.*, 2017)。但是, halkieriids 类型骨片的区域差异性、壳体与骨片的同源性、古海洋中的生态位以及在寒武纪的迅速辐射与灭绝模式等问题还没有相应的解释。早期的大部分研究局限于形态恢复和显微结构方面, 也缺乏关键生物学解剖信息的支撑 (张志飞等, 2016)。因此, 对于像 *Halkieria* 一样同时拥有壳体和多骨片的后生动物, 不仅需要探究其骨片和壳体的起源, 同时还需要更多的化石证据和对关键生物学信息的解析来分析冠轮动物的演化。

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