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遗迹歧异度(ichnodisparity):另眼看寒武纪生命大爆发*

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提要　遗迹歧异度作为评估生物成因构造中形态轮廓变化的概念被引入,它揭示出造迹生物个体轮廓、运动系统和行为过程的主要创新。遗迹歧异度是基于形态结构设计的测量鉴别,而遗迹多样性是指遗迹分类的数量,即遗迹属或遗迹种的数量。本文统计前寒武纪-寒武纪之交(埃迪卡拉纪和寒武纪纽芬兰世、第二世)的88个遗迹属,并鉴定出40个形态结构设计类型,其中前寒武纪包含22个形态结构设计类型,遗迹多样性为32;寒武纪遗迹形态结构设计类型为38个,遗迹多样性为82。前寒武纪-寒武纪之交的遗迹化石资料显示,埃迪卡拉纪和寒武纪幸运期之交是遗迹多样性与遗迹歧异度的突变期,两者数量均显著增加。这表明造迹生物在数量上急剧增加,在形态类型上更加多样,造迹生物的个体轮廓、运动方式以及行为过程都渐趋复杂、多样,有力地支持了寒武纪生命大爆发事件。遗迹歧异度和遗迹多样性相结合,将会进一步增强遗迹学在演化古生物学中的重要性。

关键词　遗迹歧异度　遗迹多样性　形态结构　设计类型　演化古生物学　寒武纪

1　前　言

遗迹多样性的概念在遗迹学研究中已经有很长的研究历史,主要用来描述遗迹属或遗迹种的数量或分异度(Seilacher, 1974; Ekdale, 1985; Crimes, 1994; Bromley, 1996; Buatois *et al.*, 1998, 2005; Orr, 2001; Uchman, 2004)。遗迹学研究者很早就已认识到不能将遗迹多样性等同于生物多样性(Ekdale, 1985)。遗迹多样性本质上反映的是生物和不同基底(如:硬底、软底、壳底、木底等)的相互作用,只能代表遗迹属、遗迹种的数量(Buatois and Mángano, 2011)。Gould(1989)在《Wonderful Life》一书中引入歧异度(disparity,形态多样性)这一概念,并在随后的研究中进行了更详细的分析。随后,遗迹学者将遗迹歧异度(ichnodisparity)与遗迹多样性(ichnodiversity)进行比较研究,如Mángano和Buatois(2014)运用遗迹多样性和遗迹歧异度研究了埃迪卡拉纪-寒武纪之交生物演化和生物个体轮廓的变化;Buatois等(2016)利用遗迹歧异度和遗迹多样性分析了寒武纪生命大爆发和奥陶纪生物大辐射事件;Buatois和Mángano(2013)讨论了遗迹多样性和遗迹歧异度在实际应用中的重要意义和应注意的问题;Buatois等(2017)根据遗迹化石的形态结构,综合考虑其造迹生物的形态和行为习性,对遗迹化石形态结构设计类型进行了详细的划分和综述。遗迹歧异度和遗迹多样性相结合,对古生物学,尤其对研究后生生物起源、辐射以及大灭绝事件前后生物灭绝与复苏模式提供了新的思路和方法,能够进一步增强遗迹学在演化古生物学中的重要作用。

本文通过介绍遗迹歧异度的概念和分类,以及遗迹歧异度和遗迹多样性在前寒武纪-寒武纪之交的变化发展,为寒武纪生命大爆发提供了一个独特的证据,以此对遗迹歧异度研究方法在国内进行推广,希望尽快与国际接轨。

2　材料与方法

遗迹歧异度是衡量生物成因构造所包含的形态结构设计种类的参数,可反映因造迹生物身体结构、

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运动系统和行为习性不同而导致的遗迹化石形态的显著差异(Buatois and Mángano,2013)。遗迹歧异度较低表明生物在形态、个体轮廓和运动方式上都较单一;遗迹歧异度较高表明生物在形态上更加多样,个体轮廓、运动方式以及行为过程都更加多样化。

遗迹歧异度是基于遗迹形态结构设计的鉴别评估。遗迹多样性是指遗迹分类的数量(遗迹属或遗迹种的数量),是遗迹种类数量上的丰度,反映出生物数量上的多少。遗迹多样性和遗迹歧异度的变化有三种可能的关系:1)遗迹多样性与遗迹歧异度无关,即遗迹歧异度不随着遗迹多样化的增加或减少而变化(遗迹属、种在一定的形态结构设计中变化)。2)遗迹多样性与遗迹歧异度变化不一致。例如遗迹多样性的变化超过遗迹歧异度的变化。3)遗迹多样性与遗迹歧异度变化一致,即遗迹歧异度的变化随着遗迹多样性的增多而增多,随着遗迹多样性的减少而减少(Buatois *et al.*,2017)。

遗迹歧异度主要基于遗迹化石的形态特征来划分典型形态结构设计类型,考虑到各种不同的底质(如未固结沉积物、固结沉积物、壳体、骨质底质、木质底质等),可以将遗迹化石的形态结构设计类型进行如下划分(见插图1,2)。其中,"雕画迹"通常被认为是与沉积物-水界面连接的开放潜穴系统,后被沉积物填充(Seilacher,1977)。

本文统计了前寒武纪-寒武纪之交的30多篇文献(杨遵仪等,1981,1982;蒋志文等,1982;钱逸等,1984;林世敏等,1986;罗惠麟、张世山,1986;李日辉、杨式溥,1988;殷继成等,1989,1993;李大庆,1990;罗惠麟等,1990,1994;李日辉,1991;罗惠麟,1992;阎国顺等,1993;杨式溥,1994;齐永安、吴贤涛,1996;朱日祥等,2009;齐永安等,2012;唐烽等,2015;李妲等,2016;李晓波等,2016;Narbonne *et al.*,1987;Mángano and Buatois,2007,2014;Parcha and Pandey,2011;Tiwari *et al.*,2013;Birendra *et al.*,2014;Singh *et al.*,2014;Buatois *et al.*,2016),共统计出88个遗迹属,鉴定出40个遗迹形态结构设计类型,见表Ⅰ。其中前寒武纪遗迹形态结构设计类型为22个,遗迹属为32个;寒武纪遗迹形态结构设计类型为38个,遗迹属为82个。

3 前寒武纪-寒武纪之交的遗迹歧异度与遗迹多样性特征

前寒武纪-寒武纪之交遗迹化石资料显示出遗迹多样性与遗迹歧异度在埃迪卡拉纪和幸运阶之间均有一个突变,即遗迹多样性和遗迹歧异度的数量都大量增加(如插图3)。根据已知资料,埃迪卡拉纪共有22个遗迹形态结构设计类型和32个遗迹属;寒武纪幸运阶共有31个遗迹形态结构设计类型和58个遗迹属;第二阶共有34个遗迹形态结构设计类型和61个遗迹属;第三阶共有37个遗迹形态结构设计类型和73个遗迹属;第四阶共有38个遗迹形态结构设计类型和82个遗迹属。前寒武纪-寒武纪之交实体化石属的分异度研究指出(插图3,Na and Kiessling,2015),埃迪卡拉纪实体化石属的数量保持在较低水平,埃迪卡拉纪-寒武纪过渡时期实体化石属的数量开始逐步上升,寒武纪实体化石多样性在第三期达到一个显著的峰值。实体化石多样性的变化与遗迹化石多样性的变化相一致,都在埃迪卡拉纪-寒武纪过渡时期和寒武纪第三期有明显的上升,这表明生物体在数量上急剧增加;实体化石的多样性在一定程度上导致了遗迹化石的多样性,遗迹歧异度也进一步增加,表明生物在形态上更加多样,个体轮廓、运动方式以及行为过程都更加多样化。寒武纪幸运期出现了大量在埃迪卡拉纪所没有的遗迹形态结构设计类型,如三裂扁平拖迹、有波状横条和皱饰的拖迹、水平分支潜穴系统、复杂垂直蹼状构造、水平(单层)蹼状构造、单支蛇曲状雕画迹、放射状雕画迹等,表明进入寒武纪之后生物的运动方式和行为过程都更加复杂、多样。寒武纪早期幸运期遗迹歧异度和遗迹多样性的变化相对缓慢,但仍在不断增加。寒武纪第二期出现了更加复杂的结构设计类型,如螺旋(多层)蹼层构造和迷宫状、网格状潜穴系统;第三期出现垂直同心状充填潜穴和水平分支同心状充填潜穴等形态结构设计类型;第四期出现规则蛇曲状雕画迹。总的来看,从幸运期到第四期生物的运动方式和行为过程渐趋复杂。遗迹多样性在第二期和第三期之间有一个小的突变期,反映了生物体的数量和种类可能有较大变化。

实体化石的保存对环境有较高的要求,海洋环境特别是海洋化学对生物骨骼矿化有一定的影响,是实体化石能否保存的一个重要因素。遗迹化石不受海洋化学环境的影响。前寒武纪-寒武纪之交的遗迹化石记录比实体化石记录更连续,反映出生物特别是软体生物与沉积底质之间的相互作用。可以看出,遗迹化石是寒武纪生命大爆发期间评估生物多样性和生态系统结构的重要指标(Mángano and Buatois,2014)。

插图 1　遗迹化石的形态结构设计类型-1(据 Buatois *et al.*，2017 修改)

Classification of architectural designs of trace fossils-1 (Modified from Buatois *et al.*, 2017)

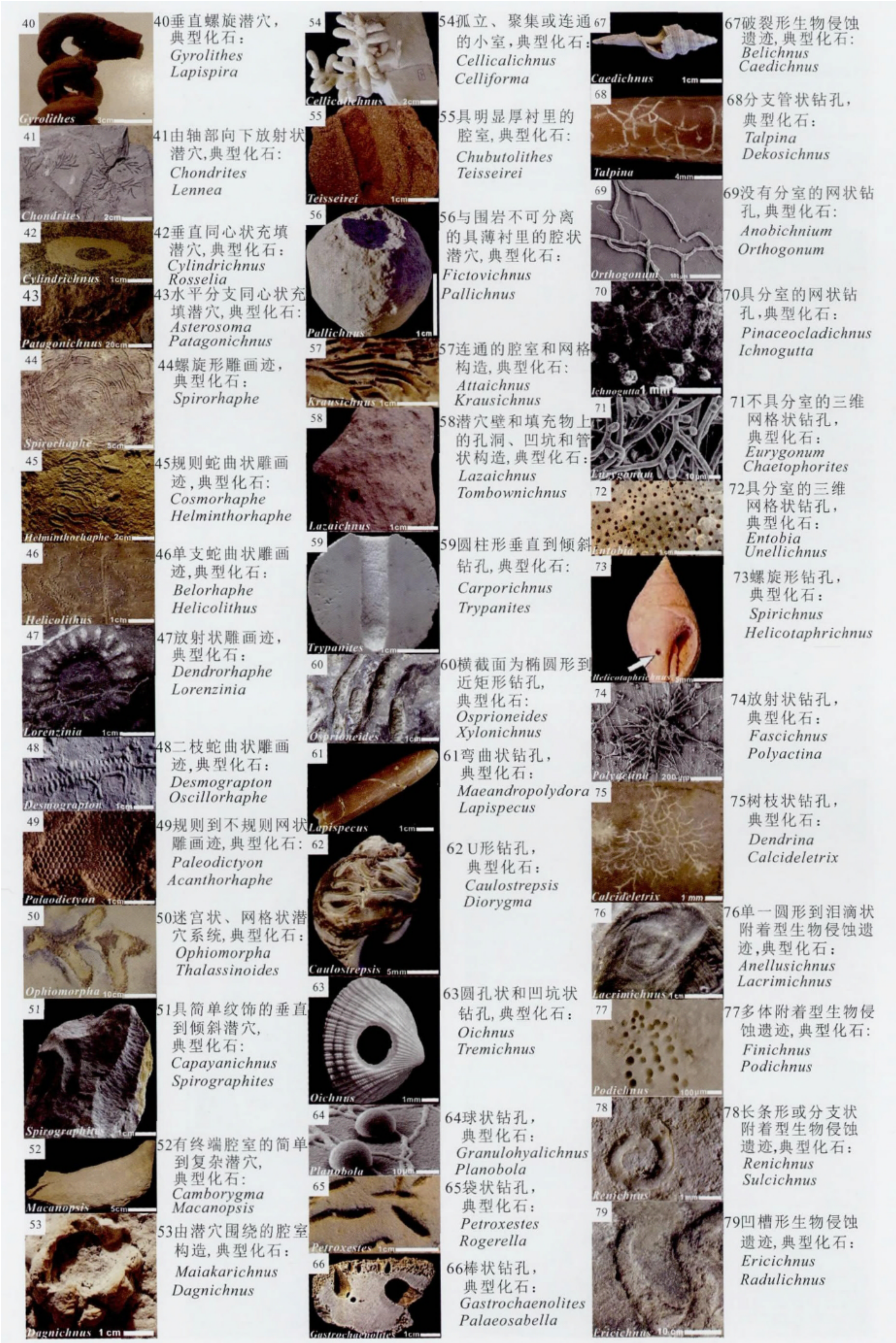

插图 2 遗迹化石的形态结构设计类型-2(据 Buatois *et al*.,2017 修改)

Classification of architectural designs of trace fossils-2(Modified from Buatois *et al*., 2017)

表Ⅰ　前寒武纪-寒武纪之交识别出的形态结构设计类型

Architectural designs during the Precambrian-Cambrian transition

形态结构设计类型	代表性遗迹属
1 简单水平拖迹	*Cochlichnus*$_{12}$, *Gordia*$_{12}$, *Helminthopsis*$_{12}$, *Helminthoidichnites*$_{12}$, *Lumbricaria*$_{2}$
2 三裂扁平拖迹	*Curvolithus*$_{12}$
4 有波状横条和皱饰的拖迹	*Climactichnites*$_{4}$, *Paraspongeliomorpha*$_{2}$
5 有成对凹槽的二裂拖迹	*Cruziana*$_{2}$, *Didymaulichnus*$_{12}$, *Subphyllochorda*$_{3}$
6 足辙迹和抓痕	*Allocotichnus*$_{2}$, *Dimorphichnus*$_{2}$, *Diplichnites*$_{2}$, *Merostomichnites*$_{2}$, *Monomorphichnus*$_{2}$, *Oniscoidichnus*$_{4}$, *Protichnites*$_{2}$, *Tasmanadia*$_{2}$
8 两侧对称的短抓痕和潜穴	*Rusophycus*$_{2}$
10 被动充填水平潜穴	*Palaeophycus*$_{12}$
11 简单主动充填(大量的)水平到倾斜潜穴	*Nenoxites*$_{1}$, *Planolites*$_{12}$, *Torrowangea*$_{14}$
12 简单主动充填(月牙形的)水平到倾斜潜穴	*Scoyenia*$_{5}$, *Beaconites*$_{5}$, *Taenidium*$_{4}$
14 复杂主动充填水平潜穴	*Neonireites*$_{2}$, *Nereites*$_{2}$, *Psammichnites*$_{2}$, *Scolicia*$_{12}$
16 水平分支潜穴系统	*Multina*$_{2}$
17 水平到垂直分支的水平潜穴	*Arthrophycus*$_{12}$, *Phycodes*$_{12}$, *Streptichnus*$_{4}$, *Treptichnus*$_{12}$
18 表层覆盖分支潜穴	*Oldhamia*$_{12}$
19 放射状到莲座状潜穴	*Cavaulichnus*$_{12}$, *Monocraterion*$_{2}$, *Volkichnium*$_{2}$
21 连续突起的水平潜穴	*Hormosiroidea*$_{14}$
22 简单垂向蹼纹的水平潜穴	*Halopoa*$_{5}$, *Teichichnus*$_{12}$, *Trichophycus*$_{2}$
23 水平螺旋形潜穴	*Multilaqueichnus*$_{2}$, *Taphrhelminthopsis*$_{12}$
25 复杂垂直蹼状构造的潜穴	*Dictyodora*$_{4}$, *Daedalus*$_{4}$, *Gyrochorte*$_{2}$, *Syringomorpha*$_{2}$
26 水平蹼状构造的潜穴	*Plagiogmus*$_{2}$, *Rhizocorallium*$_{2}$
27 螺旋蹼状构造的潜穴	*Qipanshanichnus*$_{4}$, *Spirophyton*$_{3}$, *Zoophycos*$_{5}$
30 孤立和连续的卵状到杏仁状潜穴	*Lockeia*$_{2}$
31 五角星状印痕和潜穴	*Asteriacites*$_{12}$
33 哑铃状和箭状潜穴	*Bifungites*$_{2}$
34 垂直塞子状潜穴	*Astropolichnus*$_{12}$, *Bergaueria*$_{12}$, *Conichnus*$_{2}$, *Conostichus*$_{5}$
35 垂直无分支潜穴	*Laevicyclus*$_{5}$, *Skolithos*$_{12}$, *Stipsellus*$_{4}$
36 垂直单个 U 形和 Y 形潜穴	*Arenicolites*$_{12}$, *Diplocraterion*$_{12}$
40 垂直螺旋潜穴	*Gyrolithes*$_{12}$
41 有轴或向下放射状探管束的潜穴	*Chondrites*$_{12}$, *Lennea*$_{5}$, *Trichichnus*$_{2}$
42 垂直同心充填潜穴	*Cylindrichnus*$_{4}$, *Rosselia*$_{5}$
43 水平分支同心充填潜穴	*Asterosoma*$_{4}$
45 有引导的蛇曲雕画迹	*Helminthorhaphe*$_{5}$
47 放射状雕画迹	*Glockerichnus*$_{4}$, *Lorenzinia*$_{2}$
48 二枝蛇曲雕画迹	*Paleomeandron*$_{2}$
49 规则到不规则网状雕画迹	*Paleodictyon*$_{12}$, *Protopaleodictyon*$_{2}$, *Megagrapton*$_{1}$
50 迷网格构造潜穴	*Spongeliomorpha*$_{3}$, *Thalassinoides*$_{4}$
57 互结腔室和网格构造	*Squamodictyon*$_{1}$
59 圆柱形垂直到倾斜钻孔	*Trypanites*$_{2}$
63 圆孔和凹形钻孔	*Oichnus*$_{12}$
67 破裂形生物侵蚀遗迹	*Mandibulichnus*$_{2}$
79 凹槽生物侵蚀遗迹	*Radulichnus*$_{1}$

注:表中下标 1. 埃迪卡拉纪具有的遗迹属,2. 从寒武纪幸运期开始出现的遗迹属,3. 从寒武纪第二期开始出现的遗迹属,4. 从寒武纪第三期开始出现的遗迹属,5. 从寒武纪第四期开始出现的遗迹属,12. 从埃迪卡拉纪延续到寒武纪幸运期的遗迹属,14. 埃迪卡拉纪具有,寒武纪第三期重新出现的遗迹属。

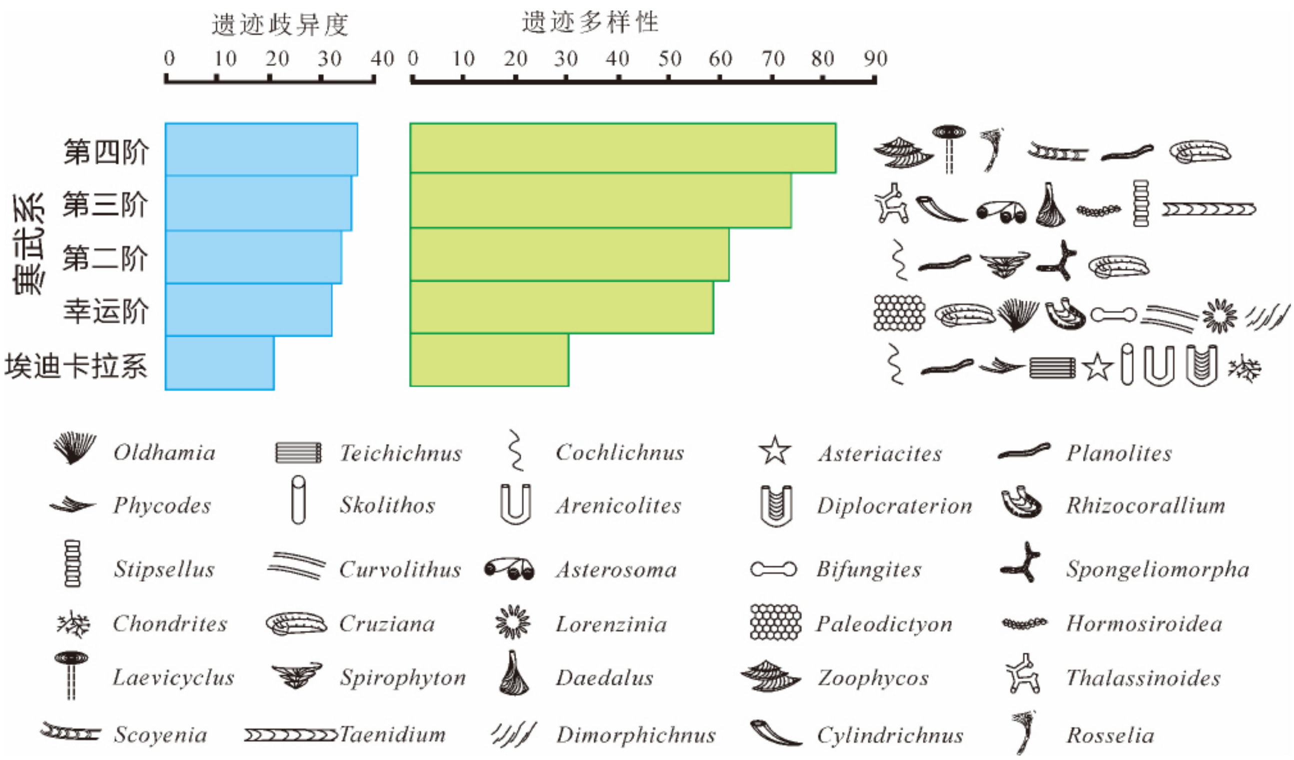

插图 3 前寒武纪-寒武纪遗迹差异与遗迹多样性变化示意图(实体化石数据来源于文献 Na 和 Kiesling,2015;主要遗迹行为差异数据来源于文献 Mángano 和 Buatois,2014)

Summary diagram of ichnodisparity and ichnodiversity changes during the Precambrian-Cambrian transition(Data of body fossils from Na and Kiessling,2015;Data of main behavioural innovations from Mángano and Buatois,2014)

4 结 论

遗迹歧异度依据遗迹化石的形态结构设计来进行鉴别划分,它反映出造迹生物个体轮廓、运动系统和行为习性的主要差异。遗迹歧异度能够记录造迹生物形态轮廓的变化,更好地反映出生物与基底的相互作用。造迹生物很小的行为变异可能会导致较高的遗迹多样性,而遗迹歧异度则会保持不变或较低水平。本文搜集的前寒武纪-寒武纪之交遗迹化石资料表明,在埃迪卡拉系和寒武系幸运阶之交遗迹多样性显著增加、遗迹歧异度也有较大增长,进入寒武纪后遗迹化石形态结构设计数量增多且渐趋复杂,表明生物的数量和种类逐步增加且运动方式和行为策略更加复杂多样。遗迹化石在前寒武纪-寒武纪之交具有连续分布的特点,与实体化石资料相结合,能够更好地为寒武纪生命大爆发提供有力的数据支撑。遗迹歧异度与遗迹多样性相结合并与重大地质事件相联系,能够反映出生物行为演化对重大地质事件的响应,为生物大灭绝和生物大辐射提供遗迹学方面的信息。遗迹歧异度这一概念为我们研究遗迹化石提供了新的思路。遗迹学研究者应该把遗迹歧异度作为新的分析工具和研究手段,并与遗迹多样性相结合,进一步增强遗迹学在演化古生物学中的重要作用。

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ICHNODISPARITY: ANOTHER VIEW OF CAMBRIAN EXPLOSION

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Key words Ichnodisparity, ichnodiversity, architectural design, evolutionary paleontology, Cambrian

Abstract

Ichnodisparity has been recently introduced as a concept to assess the variability of morphologic plans, revealing major innovations in body plan, locomotive system and behavior patterns. Ichnodisparity is evaluated based on the identification of categories of architectural design, whereas ichnodiversity is measured in terms of the number of ichnotaxa (i. e. ichnogenera and/or ichnospecies). This study summarizes ninety ichnogenera and identifies forty architectural designs during the Precambrian-Cambrian transition (Ediacaran, Terreneuvian, Epoch 2). There are 22 architectural designs and 32 ichnogenera found in the Ediacaran, and 38 architectural designs and 84 ichnogenera for the Terreneuvian and Epoch 2 of Cambrian. Trace fossil data of the Precambrian-Cambrian transition reveals that ichnodisparity and ichnodiversity both expanded during this period. The significant increase in ichnodisparity and ichnodiversity in the Precambrian-Cambrian transition, reveals that the variety and numbers, body plans, locomotive modes and the complexity of behavior processes of organisms have increased dramatically in the Cambrian, which effectively support the Cambrian explosion event from the ichnological evidences. Combining the studies of ichnodisparity and ichnodiversity will further enhance the significance of ichnology in the study of evolutionary paleontology.