

贵州湄潭志留纪初期三叶虫动物群及其意义^{*}

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摘要 志留纪兰多维列世(Llandovery)鲁丹期(Rhuddanian)是奥陶纪末生物大灭绝后的残存期和复苏期。志留纪初期冈瓦纳大陆边缘壳相地层稀少, 多数地区为沉积间断或笔石相地层, 研究底栖壳相生物残存-复苏期的宏演化普遍缺乏理想材料, 而华南上扬子区贵州湄潭地区发育了志留纪早期的壳相地层, 即五里坡层(鲁丹阶中部)和牛场组(鲁丹阶上部), 为探索这一关键地史时期三叶虫动物群宏演化型式及其背景机制提供了依据。贵州湄潭岩坪剖面和高江剖面的五里坡层和牛场组共发现三叶虫 7 目 11 科 15 属(含亚属)17 种(含 1 新种、3 未定种), 根据其属级分类单元的时空分布规律, 将这些三叶虫识别为 5 种宏演化类型: 即减缩幸存型、扩增幸存型、复活幸存型、新生型和死支漫步型。不同类型的属级分类单元在大灭绝中具有不同的宏演化型式, 体现出其应对灾变而采取的不同生存策略。减缩幸存型和复活幸存型是大灭绝后生态系统复苏和再次辐射的主要源泉, 它们的发展在一定程度上影响着整个生态系统的宏演化进程; 新生型的出现则标志着大灭绝后环境的实质性改善, 三叶虫的全面复苏也随之到来。

关键词 三叶虫动物群 宏演化 五里坡层 牛场组 志留系兰多维列统鲁丹阶 贵州湄潭

1 前 言

地质历史时期的生物集群灭绝事件(mass extinction event)点断并改变了地球生态系统的宏演化进程, 使大量生物永远从地球上消失, 但也迎来了新的生命演化阶段(Boucot, 1983)。奥陶纪末的生物大灭绝事件是显生宙以来 5 次大规模生物集群灭绝事件之一(Raup and Sepkoski, 1982; Alroy *et al.*, 2008), 灭绝的量值位居第二。大灭绝后的残存期和复苏期是生物宏演化的重要阶段, 为后来的生态系统复苏和再辐射奠定了基础, 其中蕴含大量关于宏演化的重要信息。

三叶虫是“寒武纪演化动物群”的主要组成部分, 虽然其在奥陶纪被以腕足动物等滤食生物为主的“古生代演化动物群”逐步取代(Sepkoski, 1981), 但在海洋生态系统中仍然占有重要地位。奥陶纪生

物大幅辐射期间, 三叶虫的多样性也明显增加并出现一定规模的辐射(见 Adrain, 2013)。但好景不长, 奥陶纪末的大灭绝使三叶虫遭受重创, 属一级的灭绝率达到 70%(Brenchley *et al.*, 2001), 其中浮游类型、较深水底栖类型以及原虫营浮游生活的分子均遭受灭顶之灾(Briggs *et al.*, 1988; Chatterton and Speyer, 1989; Fortey, 1989), 代表寒武纪演化动物群的 Ibex 动物群全部灭绝, 而代表古生代演化动物群的 Whiterock 动物群的绝大多数分子都能够上延并成为志留纪三叶虫动物群的主要组分(Adrain *et al.*, 1998, 2004)。奥陶纪末的生物灭绝事件分为两幕, 分别与高纬度地区冈瓦纳大陆冰川的形成和消融紧密相关(Brenchley *et al.*, 2006)。赫南特期(Hirnantian)早中期, 冈瓦纳大陆冰川形成并迅速扩展, 海水温度大幅下降, 同时海平面也快速下降 50—100 m(戎嘉余, 1984; Brenchley *et al.*, 1994), 海洋底栖生态域的丧失以及海水性质的变化造成奥陶纪末第一幕生物集群灭绝事件(Berry and Bou-

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cot, 1973; Fortey, 1989; Zhang *et al.*, 2009; Finnegan *et al.*, 2012); 赫南特中期之后, 冈瓦纳大陆冰川快速消融, 海平面大幅度上升及海水性质的变化导致第二幕生物集群灭绝事件 (Brenchley *et al.*, 2001, 2006; Sheehan, 2001; Hammarlund *et al.*, 2012; Harper *et al.*, 2014)。大灭绝第二幕发生之后, 三叶虫进入残存阶段, 直到环境有所转好, 才开始复苏并逐步再次辐射。残存期和复苏期在生物宏演化历程中起到“承前启后”的作用, 对这些宏演化阶段的三叶虫动物群进行研究, 不仅有助于理解三叶虫动物群宏演化的基本型式, 还为深入研究大灭绝后三叶虫动物群的残存和复苏机制提供了线索和依据。

华南志留纪兰多维列世的地层广泛发育, 在扬子台地靠近古陆一侧的部分地点, 壳相化石和笔石在剖面中经常共同产出或交替出现, 是全世界开展奥陶纪末大灭绝后残存与复苏研究最理想的地区之一 (Rong and Chen, 1986; Chen and Rong, 1991; Rong *et al.*, 2002)。该时段的三叶虫材料前人已有过零星报道 (如张文堂等, 1964; 张文堂, 1974; 盛莘夫, 1982), 对其较大尺度的宏演化型式也进行了初

步探讨 (周志毅等, 2004)。本文以贵州湄潭岩坪剖面和高江剖面五里坡层和牛场组所产三叶虫化石为基础, 高精度地探讨它们的宏演化意义。

2 研究剖面

贵州湄潭地区的志留系在地层区划上属于扬子地层区黔北区的桐梓-遵义分区, 志留系仅发育兰多维列统, 地层序列自下而上包括龙马溪组 (个别地点其下部或近底部相变为壳相地层, 即五里坡层和牛场组)、石牛栏组 (下部桥沟段和上部石牛栏段) 和韩家店组 (贵州省区域地质矿产局, 1987; 戎嘉余等, 1990; 林宝玉等, 1998; Rong *et al.*, 2003)。

本文所研究的三叶虫化石主要采自岩坪和高江两条剖面的五里坡层和牛场组。这两条剖面均位于遵义市湄潭县的黄家坝镇 (插图 1), 其中岩坪剖面位于黄家坝镇西北方向约 5.7 km 处 (GPS: N 27°46'38.5", E 107°23'25.6"), 高江剖面位于黄家坝镇西南方向约 3.5 km 处 (GPS: N 27°42'32.4", E 107°23'22.6")。

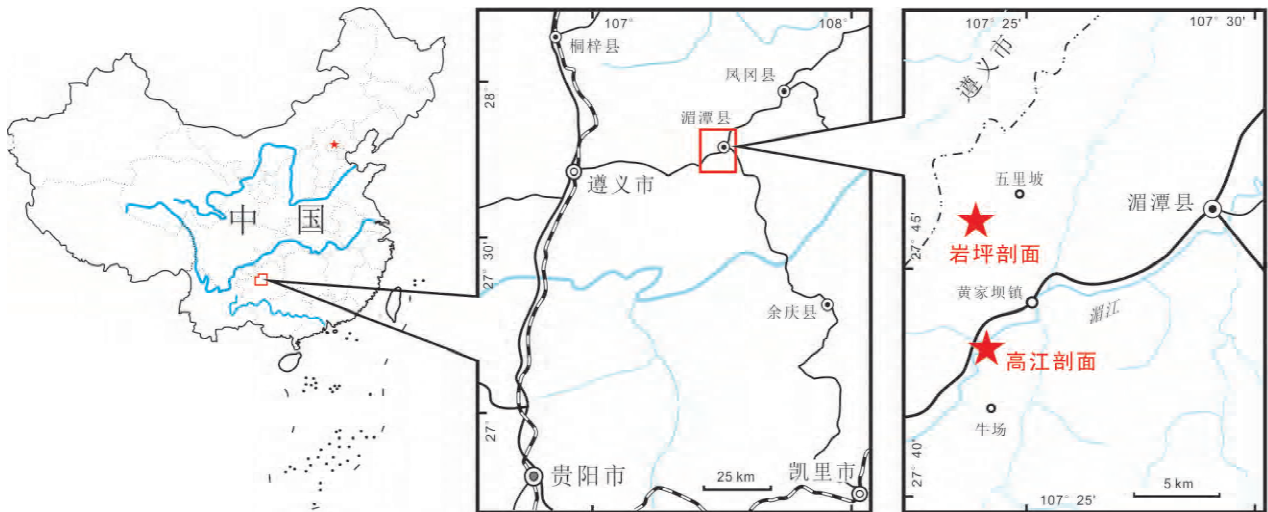


插图 1 研究剖面地理位置图 (据 Huang *et al.*, 2013)

Location map of the studied sections in Meitan, northern Guizhou (after Huang *et al.*, 2013).

五里坡层由戎嘉余 (1979) 创名, 命名剖面位于湄潭县官堰乡以西阎家寨五里坡山顶的苟连田附近, 标准地点的五里坡层可分为上下两部分: 上部为棕灰色泥质灰岩, 产腕足类和笔石化石, 与上覆龙马溪组整合接触, 厚 0.1—0.6 m; 下部为灰绿色页岩, 产丰富的腕足类化石, 与下伏临湘组平行不整合接触, 厚 0.15—0.2 m (戎嘉余、詹仁斌, 2004a)。其时代主要由上部地层所产笔石而确定, 笔石经陈旭院士鉴定属于 *Cystograptus vesiculosus* 带 (鲁丹阶中

部), 从而推知标准剖面五里坡层“可以与 *Parakidograptus acuminatus* 带上部对比, 或者可能进入 *C. vesiculosus* 带下部” (戎嘉余、詹仁斌, 2004a)。岩坪剖面距标准剖面直线距离仅 1 km, 这里的五里坡层厚 2.11 m, 岩性以两层灰岩夹一层碎屑岩为特征 (插图 2): 上部泥质灰岩产腕足类、三叶虫和苔藓虫; 中部泥岩产腕足类、三叶虫、腹足类和珊瑚; 下部砾屑灰岩, 含珊瑚和少量腕足类。高江剖面的五里坡层厚 0.8 m, 岩性也可分为三部分 (插图 3): 上部

泥晶灰岩,产少量腕足类和牙形类;中部粉砂质泥岩,产大量腕足类、三叶虫和珊瑚;下部细晶灰岩,产

少量珊瑚。岩坪剖面和高江剖面的五里坡层均与上覆牛场组和下伏上奥陶统临湘组呈平行不整合接触。

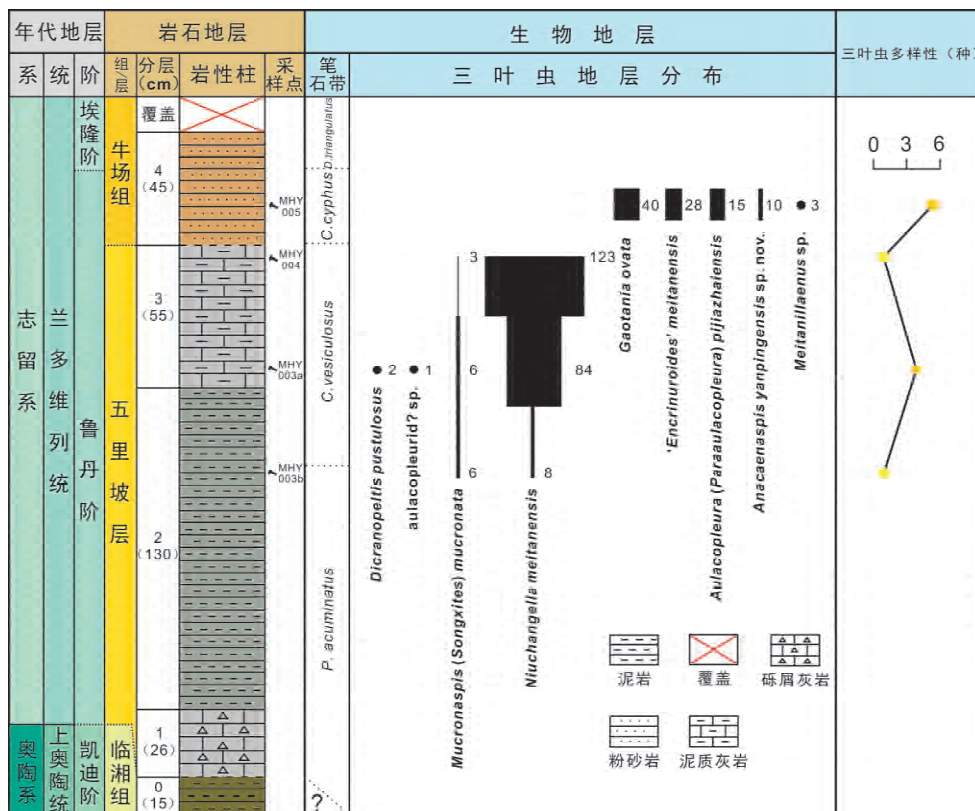


插图 2 贵州湄潭岩坪剖面志留系底部岩性柱状图及三叶虫化石的地层延限

Lithologic column and stratigraphic ranges of trilobites of the basal Silurian at Yanping, Meitan, northern Guizhou.

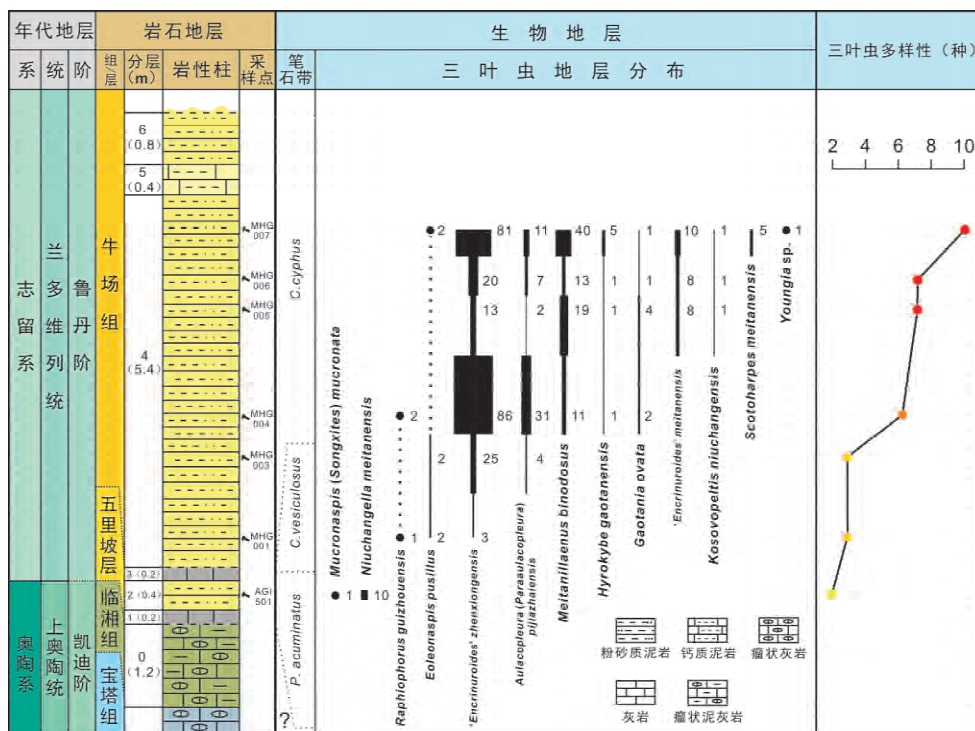


插图 3 贵州湄潭高江奥陶系-志留系界线剖面岩性柱状图及三叶虫化石的地层延限(改自 Wei and Zhan, 2017)

Lithologic column and stratigraphic ranges of trilobites across the Ordovician and Silurian boundary at Gaojiang, Meitan, northern Guizhou (modified from Wei and Zhan, 2017).

牛场组由戎嘉余、詹仁斌(2004b)创名,在建组之前,该段地层被作为龙马溪群的一部分(张文堂等,1964)。其命名地点在湄潭县牛场村高滩,岩性以棕黄色粉砂质泥岩和灰色泥岩为主,厚 38.5 m,与上覆石牛栏组整合接触,与下伏宝塔组之间为平行不整合接触(戎嘉余、詹仁斌,2004b)。标准剖面的牛场组时代大致与 *Coronograptus cyphus* 带—*Demirastrites triangulatus* 带相当(戎嘉余、詹仁斌,2004b)。岩坪剖面牛场组底部 14 cm (MHY005)厚的棕红色粉砂岩(插图 2)产三叶虫、腕足类和腹足类,考虑到其整体厚度与标准剖面厚度相近,推测其底部很可能也在 *C. cyphus* 带内(鲁丹阶上部)。高江剖面牛场组厚 6.6 m,岩性以土黄色粉砂质泥岩为主,向上钙质含量逐渐增加(插图 3),产丰富的三叶虫和腕足类,个别层位含少量笔石,经陈旭院士鉴定都属于 *C. cyphus* 带(Huang *et al.*, 2013; 王光旭, 2014; Wei and Zhan, 2017)。

3 三叶虫动物群

笔者主要对贵州湄潭岩坪剖面和高江剖面鲁丹阶五里坡层和牛场组的三叶虫进行研究,涉及到的标本共计 766 枚。经鉴定,包括 7 目 11 科 15 属(含亚属)17 种(其中 1 新种和 3 未定种)。

五里坡层的三叶虫包括 3 目 4 科 4 属(含亚属)4 种(含 1 未定种)($N = 244$): *Niuchangella* (Brachymetopidae 科)占 92.2% ($N = 225$), *Mucronaspis* (*Songxites*) (Dalmanitidae 科)占 6.6% ($N = 16$), *Dicranopeltis* (Lichidae 科)占 0.8% ($N = 2$), *aulacopleurid*? (Aulacopleuridae 科)占 0.4% ($N = 1$) ($N = \text{Number}$, 表示标本数量)(插图 4)。除以上 4 属外,张文堂等(1964)还报道过 *Eoleonaspis* (Odontopleuridae 科),但我们的野外发掘未采获该属标本。岩坪剖面和高江剖面的五里坡层均以 *Niuchangella* 占据绝对优势,而上奥陶统观音桥组(赫南特阶)常见的 *Mucronaspis* (*Songxites*) 相对较少,整个动物群以低分异度和 *Niuchangella* 的高丰度为特征,这一动物群也被周志毅等(2004)称为 *Niuchangella* 组合。五里坡层的三叶虫动物

群无一例外均为下伏地层的上延分子,包括 *Niuchangella*, *Mucronaspis* (*Songxites*), *Eoleonaspis* 和 *Dicranopeltis*, 这些三叶虫也发现于华南上奥陶统观音桥组(赫南特阶)及其同期地层中,显示出奥陶纪末大灭绝第二幕之后残存期的特征。值得一提的是,岩坪剖面五里坡层的三叶虫化石在地层中密集分布且多破碎,应是经过了一定距离的搬运才保存下来的;而高江剖面五里坡层的三叶虫有较多的完整或近完整的个体,珊瑚标本也保存完好,没有分选(王光旭, 2014),显示了原地或近原地埋藏的特征;距离相近的两个剖面却有不同埋藏特征,这可能与近岸地区复杂的沉积环境有关。

牛场组的三叶虫包括 6 目 8 科 11 属(含亚属)13 种(含 1 新种和 3 未定种)($N = 522$): ‘*Encrinuroides*’ (Encrinuridae 科)占 54.0% ($N = 282$), *Meitanillaenus* (Illaenidae 科)占 16.5% ($N = 86$), *Aulacopleura* (*Paraaulacopleura*) (Aulacopleuridae 科)占 13.4% ($N = 70$), *Gaotania* (Odontopleuridae 科)占 9.2% ($N = 48$), *Anacaenaspis* (Odontopleuridae 科)占 1.9% ($N = 10$), *Eoleonaspis* (Odontopleuridae 科)占 1.1% ($N = 6$), *Hyrokybe* (Cheiruridae 科)占 1.5% ($N = 8$), *Raphiophorus* (Raphiophoridae 科)占 0.6% ($N = 3$), *Scotoharpes* (Harpetidae 科)占 1.0% ($N = 5$), *Kosovopeltis* (Styginidae 科)占 0.6% ($N = 3$), *Youngia* (Cheiruridae 科)占 0.2% ($N = 1$)(插图 5)。在牛场组的标准剖面还报道过 *Dicranopeltis* 一属(戎嘉余、詹仁斌, 2004b),但我们的发掘没有获得该属标本。高江剖面的牛场组仅出露其下部,以 ‘*Encrinuroides*’ 为优势分子, *Meitanillaenus* 和 *Aulacopleura* (*Paraaulacopleura*) 为次要分子,自下而上三叶虫多样性逐渐增高,显示出奥陶纪末大灭绝第二幕之后复苏期的特征,这一动物群可称为 ‘*Encrinuroides*’ 组合(周志毅等, 2004 作为 *Encrinuroides* 组合)(Wei and Zhan, 2017)。岩坪剖面牛场组底部 14 cm (MHY005)产三叶虫 4 科 5 属,包括 *Gaotania*, ‘*Encrinuroides*’, *Aulacopleura* (*Paraaulacopleura*), *Anacaenaspis* 以及 *Meitanillaenus*, 其中 *Gaotania* 和 ‘*Encrinuroides*’ 为优势分子(Wei and Zhan, 待刊)。牛场组的三叶虫动物群,除新生分子

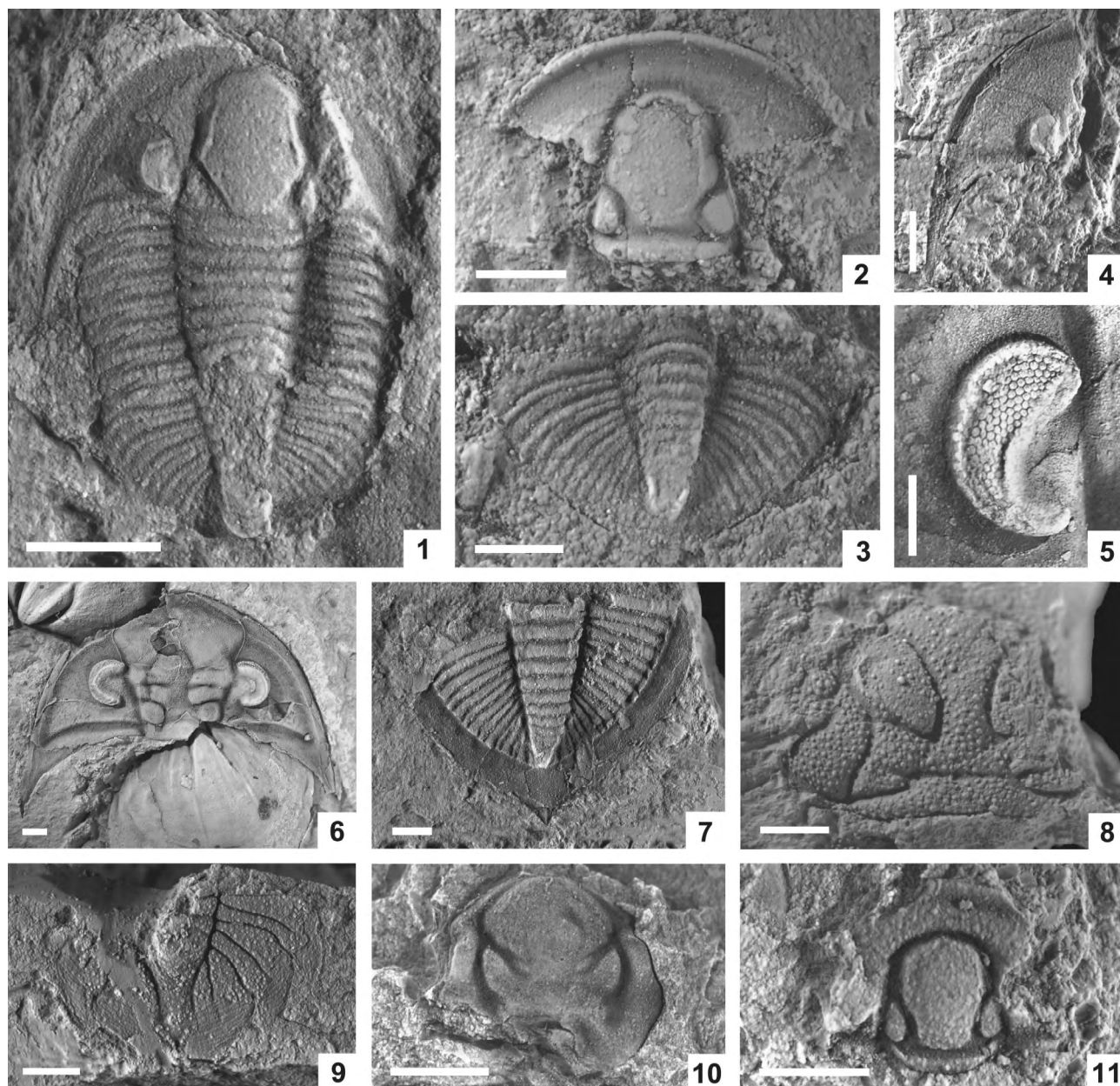


插图 4 贵州湄潭岩坪剖面和高江剖面五里坡层三叶虫

Trilobites from the Wulipo Bed at Yanping and Gaojiang sections, Meitan, Guizhou.

1—4. *Niuchangella meitanensis* Zhang, 1974, 1. 背壳 (dorsal shield), AGI501, NIGP166382; 2. 头盖 (cranidium), MHY003a, NIGP166383; 3. 尾部 (pygidium), MHY004, NIGP166384; 4. 活动颊和部分头盖 (librigena and incomplete cranidium), MHY003a, NIGP166385. 5—7. *Mucronaspis* (*Songxites*) *mucronata* (Brongniart, 1822), 5. 眼部 (eye), MHY003a, NIGP166386; 6. 头部 (cephalon), MHY003b, NIGP165301; 7. 尾部 (pygidium), MHY003b, NIGP165302. 8—10. *Dicranopeltis pustulosus* (Zhang, 1974), 8. 头盖 (cranidium), MHY004, NIGP166387; 9. 尾部 (pygidium), MHY003a, NIGP165303; 10. 唇瓣 (hypostome), MHY003a, NIGP166388. 11. aulacopleurid? sp.: 头盖 (cranidium), MHY003a, NIGP166389. 比例尺 2 mm (Scale bars equal 2 mm).

以外,还包括低纬度地区的迁入分子(如 *Raphiophorus*, *Youngia* 和 *Anacaenaspis*)和华南奥陶纪的上延分子[如 '*Encrinuroides*', *Aulacopleura* (*Paraaulacopleura*)和 *Scotoharpes*]. 高江剖面和

岩坪剖面牛场组的三叶虫头、胸、尾多分离,但保存完好,只有极个别较完整体的标本,指示了比较平静的浅水环境,这些壳相生物在埋藏之前没有经过长距离或破坏性的搬运(周志毅等, 2004)。

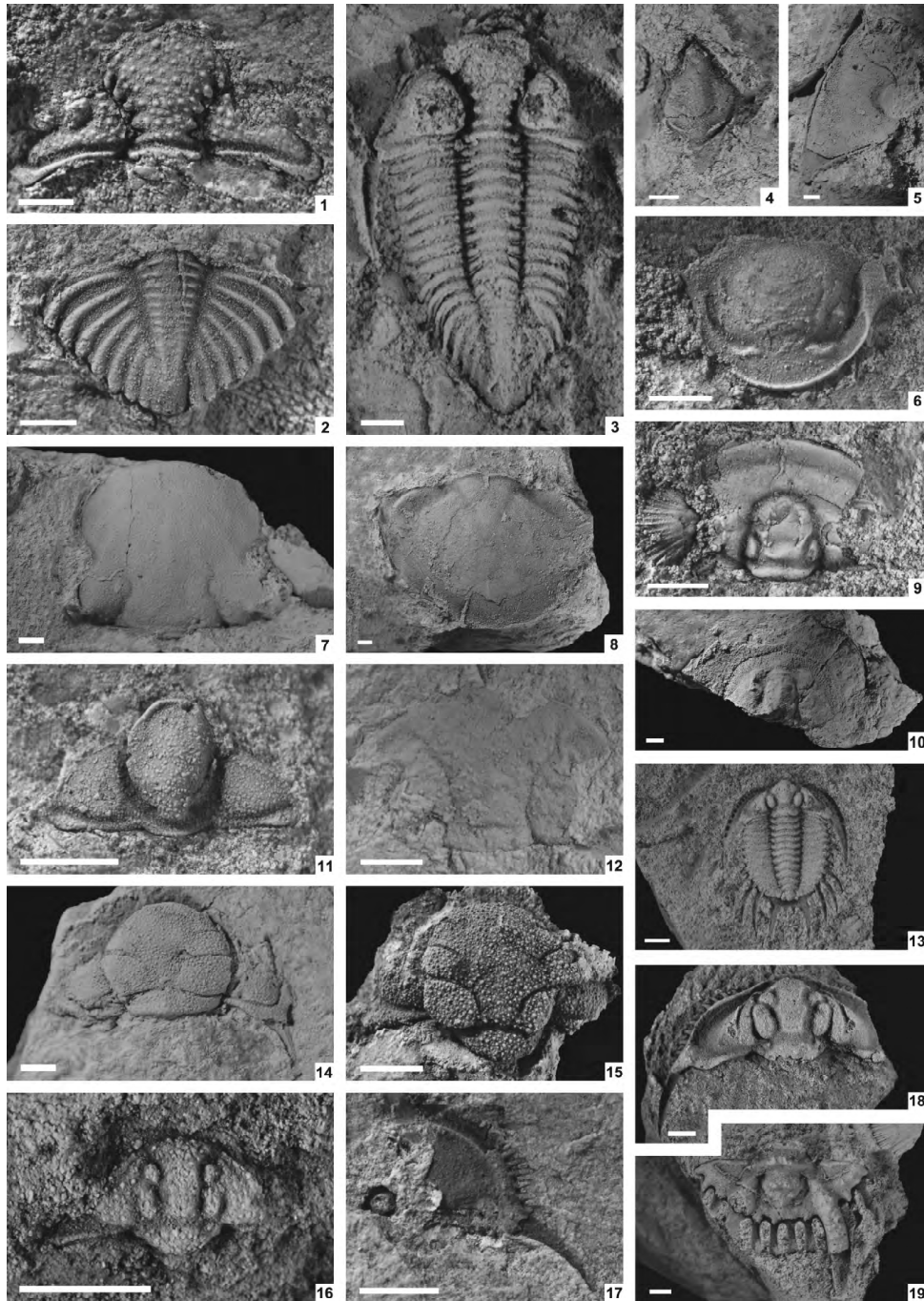


插图 5 贵州湄潭岩坪剖面和高江剖面牛场组三叶虫

Trilobites from the Niuchang Formation at Yanping and Gaojiang sections, Meitan, Guizhou.

1, 2, 4. '*Encrinuroides*' *zhenxiongensis* (Sheng, 1964), 1. 头盖 (cranidium), MHG004, NIGP166390; 2. 尾部 (pygidium), MHG006, NIGP166391; 4. 唇瓣 (hypostome), MHG006, NIGP166392. 3. '*Encrinuroides*' *meitanensis* (Zhang, 1974), 背壳 (dorsal shield), MHY005, NIGP166393. 5—8. *Meitanillaenus binodosus* Zhang, 1974, 5. 活动颊, MHG007, NIGP166394; 6. 唇瓣 (hypostome), MHG004, NIGP166395; 7. 头盖 (cranidium), MHG005, NIGP166396; 8. 尾部, MHG005, NIGP166397. 9. *Aulacopleura* (*Paraaulacopleura*) *pijiashaiensis* (Zhang, 1974), 头盖 (cranidium), MHG004, NIGP166398. 10. *Scotoharpes meitanensis* Yin and Li, 1978, 不完整头部 (incomplete cephalon), MHG007, NIGP166399. 11. *Raphiophorus guizhouensis* Zhang, 1974, 头盖 (cranidium), MHG004, NIGP166400. 12. *Kosovopeltis niuchangensis* (Zhang, 1974), 头盖 (cranidium), MHG004, NIGP166401. 13. *Gaotania ovata* Zhang, 1974, 背壳 (dorsal shield), MHY005, NIGP166402. 14. *Hyrokybe gaotianensis* (Zhang, 1974), 头盖 (cranidium), MHG005, NIGP166403. 15. *Youngia* sp., 头盖 (cranidium), MHG007, NIGP166404. 16, 17. *Eoleonaspis pusillus* (Zhang, 1974), 16. 头盖 (cranidium), MHG007, NIGP166405; 17. 活动颊 (librigena), MHG003, NIGP166406. 18, 19. *Anacaenaspis yanpingensis* Wei and Zhan, 待刊 (in press), 18. 头部 (cephalon), MHY005, NIGP166409; 19. 尾部 (pygidium), MHY005, NIGP166410. 比例尺 2 mm (Scale bars equal 2 mm)

4 宏演化意义

生物大灭绝后的残存期和复苏期是生物宏演化的重要阶段,蕴含有许多重要的宏演化信息,是“承前启后”的重要时期(戎嘉余等,1996)。许多学者高度关注大灭绝后残存期和复苏期的生物类型,对它们进行划分并深入分析其在重大事件前-中-后的具体表现型式,以进一步探索它们的宏演化意义(如Kauffman and Harries,1996;戎嘉余等,1996;戎嘉余、詹仁斌,1999,2006;戎嘉余、方宗杰,2004;黄冰,2008),但是,世界范围内多以型式探讨为主,实例研究很少。诚然,对残存期和复苏期的化石类群进行宏演化划分,详细研究它们的时空分布规律(插图6),有助于我们理解宏演化的基本型式和意义,探讨大灭绝后生物残存和复苏的机制。

4.1 减缩幸存型(Declining survivors)

即在大灭绝期间或之后恶化环境尚未改善时,居群大规模减缩、数量骤减、分布局限的属(戎嘉余、詹仁斌,2006)。本文研究的三叶虫 *Raphiophorus*, *Niuchangella* 和 *Dicranopeltis* 属于这种类型。

Raphiophorus 最早见于中高纬度的捷克波希米亚地区,时间为中奥陶世达瑞威尔期(Darriwilian)晚期(Horný and Bastl,1970),多生活在较深水水域。奥陶纪末大灭绝前该属多分布在捷克(Vaněk,1995)、瑞典(Angelin,1854)和威尔士(Price and Magor,1984)等地;奥陶纪末大灭绝期间(赫南特期),该属仅发现一个种,且限于波兰分布(Temple,1965;Owen,1986),与 *Hirnantia* 伴生,可能指示了相对浅水的底域环境。当环境转好时(志留纪兰多维列世早、中期之交),*Raphiophorus* 开始向中国华南(张文堂,1974;王齐政,1989)、塔里木(张太荣,1981)和澳大利亚新南威尔士(Edgecombe and Sherwin,2001)等低纬度地区较深水水域扩散,而这一扩散很可能与洋流有关。温洛克世(Wenlock)—普里道利世(Pridoli),该属广泛分布于英国(Thomas,1978)、美国阿肯色州(Holloway,1980)、波兰(见 Thomas,1978)、澳大利亚维多利亚(Sandford,2000)、阿尔及利亚(Alberti,1980)、摩洛哥(Alberti,1970)和意大利撒丁岛(Kříž and Serpagli,1993)等地。

Niuchangella 是短眉虫类已知最早的属,首先

出现在冈瓦纳高纬度地区晚奥陶世桑比期(Sandbian)晚期—凯迪期(Katian)早期(Pereira *et al.*, 2015)。大灭绝前,*Niuchangella* 主要分布于华南(周志强等,2016)、西班牙(Owens and Hamman, 1990)、葡萄牙(Thadeu,1947;Pereira *et al.*, 2015)和乌兹别克斯坦(Kolobova,1978),在华南扬子区上奥陶统宝塔组出现于深水一侧(周志强等,2000)。赫南特期该属仅分布在华南板块和中天山—北山地块(戎嘉余等,2003),与 *Mucronaspis* (*Songxites*) 伴生,浅水和深水环境均有分布,至志留纪兰多维列世鲁丹中期,仅分布在华南上扬子区浅水底域。温洛克世 *Niuchangella* 向阿凡隆尼亚板块(如威尔士、英格兰,Owens and Thomas,1975)和劳伦板块(如美国纽约州,Adrain and Tetreault,2005)迁移扩散,形成较深水的 *Niuchangella*-*Cornuproetus* 相(见 Thomas,1979,作为 *Radnor*-*Cornuproetus* 相)。罗德洛世(Ludlow)时 *Niuchangella* 仅见于澳大利亚新南威尔士(Sun,1990)。在奥陶纪末大灭绝前后,该属的种在形态上有一定的差异,究其原因,可能是在恶劣的环境下,个别种改变生态策略,形态也发生相应变化,从而在大灭绝事件中得以幸存并在之后的生态系统残存、复苏和再辐射过程中得到进一步发展。

Dicranopeltis 首现于华南板块的桑比晚期(见周志强等,2016),晚奥陶世主要分布在华南(孙振华,1984)、北羌塘—思茅(李善姬、肖兴铭,1984)、中天山—北山(周志毅、周志强,1982)、挪威(Owen,1981)、瑞典(Owens,1973)、爱尔兰(Dean,1974)、哈萨克斯坦(Apollonov,1974)和西班牙(Owens and Hamman,1990)等地。奥陶纪末(赫南特期)大灭绝期间,只见于华南(张文堂,1974)、挪威奥斯特陆和哈萨克斯坦(见 Owen,1986)等地。志留纪时主要分布在美国、英国、加拿大和捷克等地(见 Thomas and Holloway,1988),华南仅发现一个种。

4.2 扩增幸存型(Increasing survivors)

即在大灭绝期间或之后恶化环境尚未改善时,居群规模非但未减缩,反而扩大、数量增多、分布更广的分类单元(戎嘉余、詹仁斌,2006)。*Eoleonaspis* 属于这种类型。

Eoleonaspis 最早出现在捷克波希米亚地区晚奥陶世桑比期(Šnajdr,1984),凯迪期向低纬度地区拓展,但均分布在冈瓦纳大陆边缘,如华南、捷克和

缅甸(见 Ramsköld and Chatterton, 1991), 大灭绝期间(赫南特期) *Eoleonaspis* 向阿凡隆尼亚板块和波罗的板块等中低纬度地区扩散, 广泛分布于华南(张文堂, 1974)、柴达木—祁连地区(曲新国, 1986)、缅甸(Reed, 1915)、哈萨克斯坦(Apollonov *et al.*,

1980)、威尔士(Cocks and Price, 1975)、瑞典(Troedson, 1918)、新西兰?(Cocks and Cooper, 2004)和阿根廷?(Halpern *et al.*, 2014), 两幕大灭绝后该属的子遗分子散落在华南(本文)、缅甸和英国等地(Ramsköld and Chatterton, 1991)。

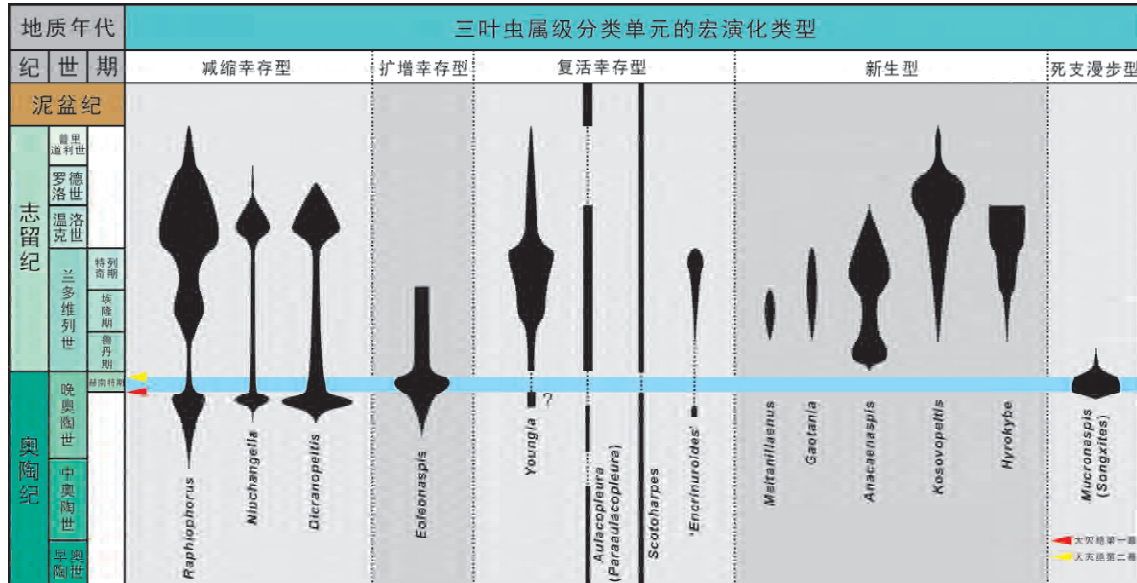


插图 6 三叶虫属级分类单元的宏演化类型及各属的时空分布

Macroevolutionary types of trilobites across the Ordovician-Silurian boundary.

4.3 复活幸存型(Lazarus survivors)

即在大灭绝期间或之后恶化环境持续时, 虽未灭绝, 但居群规模和数量大幅减少, 至今没有发现其化石记录, 但在其后的复苏期特别是再次辐射期重新出现在化石记录中, 这样的类群即复活幸存型。严格地说, 它就是减缩幸存型的一个极端情况(Rong *et al.*, 2006; 戎嘉余、詹仁斌, 2006)。本文研究的三叶虫 *Youngia*, *Aulacopleura* (*Paraaulacopleura*), *Scotoharpes* 和 ‘*Encrinuroides*’ 就属于这种类型。

志留纪早期 *Youngia* 就已经在劳伦板块、波罗的板块和华南板块大量出现, 见于华南[鲁丹晚期, Wei and Zhan, 2017; 特列奇期(Telychian), 伍鸿基和 Lane, 见陈旭、戎嘉余, 1996]、苏格兰[埃隆期(Aeronian)早期, Howells, 1982; 特列奇期, 见 Lane, 1971]、格陵兰(埃隆中期, Lane, 1979, 时代意见据 Holloway and Lane, 2012)、瑞典中南部(埃隆期, Ramsköld, 1994)、澳大利亚昆士兰(特列奇期, Holloway, 1994)、加拿大(特列奇期, Chatterton and Perry, 1984)和英格兰(兰多维列世, Lane, 1971); 温洛克世主要见于加拿大(Chatterton and Perry, 1984; Adrain, 1998); 罗德洛世—普里道利

世, 该属分布于中亚地区(见 Weber, 1932; Ivanova *et al.*, 2009)。目前已知晚奥陶世仅有一个种 *Youngia ? tuberculata* (Warburg) 报道于英国(见 Thomas *et al.*, 1984)。奥陶纪末大灭绝期间, 各地均未发现 *Youngia*, 大灭绝后不久(鲁丹期), *Youngia* 作为“复活分子”再次出现在化石记录中(Owen, 1986; Robertson *et al.*, 1991), 并于兰多维列世中晚期出现高度分化, 发育有多个种。

奥陶纪末大灭绝前, *Aulacopleura* (*Paraaulacopleura*) 仅见于华南早—中奥陶世(卢衍豪, 1975)和苏格兰晚奥陶世(Příbyl, 1947)地层中; 大灭绝期间(赫南特期)各地均未发现该属分子; 志留纪兰多维列世, 该属再次出现并逐渐分化、辐射。常见于深水贫氧环境(Fortey, 1979; Thomas and Lane, 1984), 同时也取代了大灭绝前油栉虫类(olenid)深水三叶虫所在的生态位(Fortey and Owens, 1975)。从早奥陶世至中泥盆世该属的形态结构一直保持基本稳定, 与晚奥陶世一些特化分子相比, *Aulacopleura* 稳定的表征反映了其对环境变化有更强的适应能力(卢衍豪, 1975)。华南就是最好的例证: 鲁丹期—埃隆早期(残存期—复苏期) *Aulacopleura* 在近岸较浅水环境中富集, 而埃隆中晚期(辐射期)环境更加

适宜,三叶虫多样性也逐渐增高,浅水生态位饱和,这时 *Aulacopleura* 则向远岸较深水迁移,足以体现其较宽的生态幅度以及对较深水环境的适应性。

Scotoharpes 是源于早奥陶世的长命分子,在空间上几乎全球分布,时间上从早奥陶世至中泥盆世都有其踪迹,但在大灭绝期间(赫南特期)却未见其化石记录。大灭绝后的兰多维列世,该属作为“复活分子”再次出现(Owen, 1986; Robertson *et al.*, 1991)。*Scotoharpes* 是区内志留纪三叶虫动物群的一员,但分布零星,丰度和分异度从未出现过发展的状态(周志毅等, 2004)。

‘*Encrinuroides*’是典型的地方性分子。大灭绝前(凯迪中期),该属分布在华南板块(盛莘夫, 1964; 尹恭正、李善姬, 1978; 孙振华, 1984; 周志毅等, 2014),但丰度较低。大灭绝期间(赫南特期)未见其踪迹。大灭绝后的鲁丹期—埃隆早期,该属作为“复活分子”再次出现并占据优势,在特列奇期辐射演化,衍生出多个属种,是华南志留纪三叶虫动物群的典型分子,也是王冠虫类三叶虫的祖先类群(Zhang, 1983; Edgecombe *et al.*, 1988)。

4.4 新生型(New arrivals)

即在残存期(少数)或复苏期(多数)首次出现的分子(戎嘉余等, 1996)。本文研究的三叶虫 *Anacaenaspis*, *Meitanillaenus*, *Kosovopeltis*, *Hyrokybe* 和 *Gaotania* 都属于这种类型。其中 *Meitanillaenus* 和 *Gaotania* 是新生土著分子,而 *Anacaenaspis*, *Kosovopeltis* 和 *Hyrokybe* 属于新生广布分子。

Meitanillaenus 的延限从鲁丹晚期到埃隆期,目前仅发现于华南板块;*Gaotania* 最早出现在华南板块(鲁丹晚期),在区内可持续生活到特列奇期,区外仅在澳大利亚昆士兰的特列奇期有一个种报道(Holloway, 1994)。以上两属均在大灭绝后的复苏期开始出现,是典型的华南新生土著分子。

Anacaenaspis 首先见于兰多维列世鲁丹早期的加拿大安迪考斯第岛(Anticosti Island)(Chatterton and Ludvigsen, 2004)以及麦肯锡山(Mackenzie Mountains)(Chatterton and Perry, 1983),整个兰多维列世该属主要分布在劳伦板块;华南板块(鲁丹晚期, Wei and Zhan, 待刊)与澳大利亚板块(特列奇期, Holloway and Sandford, 1993)仅有零星分布;温洛克世则主要见于波罗的板块。对于华南板块,该属既是复苏期的新生分子也是从劳伦板块而来的迁入分子。

Kosovopeltis 是典型的志留纪三叶虫,与奥陶纪的 *Eokosovopeltis* 可能存在系统发育关系(Příbyl and Vaněk, 1971)。目前已知最早的 *Kosovopeltis* 就是见于华南的 *K. niuchangensis*, 时代为兰多维列世鲁丹晚期,除此以外,该属还在我国埃隆期和特列奇期有报道(张文堂, 1974; 伍鸿基, 1977)。奥陶纪末大灭绝后, *Kosovopeltis* 首先出现在低纬度地区,如华南黔北(鲁丹期—特列奇期)、威尔士(埃隆末期, Curtis and Lane, 1997)、澳大利亚昆士兰(特列奇期, Holloway, 1994)、加拿大魁北克(特列奇期, Chatterton and Ludvigsen, 2004);温洛克世该属主要分布在美国和英格兰(见 Holloway and Lane, 2012);罗德洛世—早泥盆世该属主要分布在澳大利亚、捷克、摩洛哥、哈萨克斯坦、土耳其、北非和日本等地(见 Holloway and Lane, 2012),罗德洛世时 *Kosovopeltis* 种的多样性达到顶峰。

奥陶纪末大灭绝后, *Hyrokybe* 在华南上扬子近岸浅水区域首次出现(鲁丹晚期),埃隆期初步辐射,区内一直持续到特列奇期。此外,在区外(如劳伦板块和波罗的板块) *Hyrokybe* 在兰多维列世晚期至温洛克世的地层中多有报道(见 Lane and Owens, 1982; Ramsköld, 1983; Chatterton and Perry, 1984; Adrain, 1998)。

4.5 死支漫步型(Dead Clade Walking)

即在大灭绝过程中遭受重创,之后很短时间内消亡的类型(Jablonski, 2002; 黄冰等, 2014)。本文研究的 *Mucronaspis* (*Songxites*) 即属于死支漫步型。

Mucronaspis (*Songxites*) 在晚奥陶世赫南特期广泛分布于欧洲、亚洲和北美洲(Zhou *et al.*, 2011),而在志留纪兰多维列世鲁丹期仅见于华南(本文; Zhang *et al.*, 2007),并很快消失。*Mucronaspis* (*Songxites*) 在我国以及东亚从未在赫南特期以前的地层中发现过(Zhou and Dean, 1989 作为 *Dalmanitina*),它的出现及其宏演化与赫南特期全球环境变凉有关。

4.6 对华南奥陶纪末大灭绝后幸存型三叶虫的认识

减缩幸存型分子(如 *Raphiophorus*, *Niuchangella* 和 *Dicranopeltis*) 在灾难发生时只是相关动物群的配角,其居群规模、个体数量和分布范围都无法和当时的全球广布分子(如 *Mucronaspis*, *Brong-*

niartell/*Platycoryphe* 和 *Eoleonaspis*) 相比。“减缩”不仅是幸存分子穿过大灭绝的一种表现型式,还是生物应对灾变而采取的一种生存策略,其短暂的“休眠”已为种系的延续而蓄势。也正是采取了这样的潜伏策略,使其保存了能量,赢得了更多的生存机会(Rong *et al.*, 2006; 戎嘉余、詹仁斌, 2006)。减缩幸存型分子在灾变环境下有很强的生态忍耐度或较宽的生态幅度,奥陶纪末大灭绝事件使深水及较深水类型的三叶虫动物群遭受灭顶之灾,极少数在较深水域生活的三叶虫(如 *Raphiophorus*)和具较宽生态幅度的三叶虫(如 *Niuchangella* 和 *Dicranopeltis*)在大灭绝期间迁往浅水水域幸存下来,至大灭绝后环境逐渐好转,这类分子逐渐扩大居群规模和分布范围,甚至再次占据较深水生态位(如 *Raphiophorus* 和 *Niuchangella*)。

扩增幸存型分子在奥陶纪末大灭绝两幕之间占据优势地位,对灾变环境有更好的适应性,属于特定环境下的机遇分子。华南板块赫南特期的三叶虫大部分是从高纬度地区迁入的外来分子(如 *Eoleonaspis*),这些类群能够适应全球变冷的环境而幸存下来,第一幕大灭绝多数属的消失也为其提供了广阔的缺少竞争的生存空间,使其在大灭绝两幕之间广泛分布。到志留纪早期,它们仅作为志留纪动物群的一些“陪衬分子”零星分布,未见大的发展。

复活幸存型可以分为两类:其一,在很早就已经起源;其二,在大灭绝前不久起源。前者多具有稳定的表征,反映了其对环境变化有更强的适应能力(如 *Aulacopleura* 和 *Scotoharpes*),它们复出后在局部地区可能富集,但在整个志留纪三叶虫动物群中处于次要地位;后者在大灭绝前丰度和分异度均较低,而在大灭绝后的残存期或复苏期逐渐兴起,并于辐射期演化出大量后裔类群(如‘*Encrinuroides*’),在整个志留纪三叶虫动物群中常占据主导地位。

志留纪初期处于赤道附近的华南板块,奥陶纪末大灭绝之后可能是海洋底栖生态群落的避难所之一(Rong *et al.*, 2013; Li *et al.*, 2015; Botting *et al.*, 2017),本文报道的幸存型三叶虫全部都是奥陶纪的上延分子,且包含有多种宏演化类型,进一步证明了华南是志留纪三叶虫动物群的主要源泉之一,华南在三叶虫古生代演化动物群起源与演化过程中具有特殊且重要的地位。

5 结 语

贵州湄潭岩坪剖面和高江剖面的五里坡层(志留系兰多维列统鲁丹阶中部)和牛场组(鲁丹阶上部)所产三叶虫 7 目 11 科 15 属(含亚属)17 种(其中 1 新种和 3 未定种),分别显示出奥陶纪末大灭绝第二幕之后三叶虫残存期和复苏期的特征。对三叶虫动物群进行属级分类单元分析,识别出 5 种不同的宏演化类型:减缩幸存型(3 属)、扩增幸存型(1 属)、复活幸存型(4 属)、新生型(5 属)和死支漫步型(1 属)。不同宏演化类型的属级分类单元在大灭绝中具有不同的表现型式,体现出其应对灾变而采取不同的生存策略。减缩幸存型和复活幸存型是大灭绝之后生物复苏及再辐射的主要源泉,它们在一定程度上影响了整个生态系统演化的进程。死支漫步型分子是大灭绝后残存期的产物。扩增幸存型在未来的演化过程中长期处于从属地位。而新生型的出现,不仅丰富了动物群面貌,还标志着大灭绝之后环境的实质性改善,显示了三叶虫复苏期的到来。

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TRILOBITE FAUNA FROM THE LOWERMOST SILURIAN OF MEITAN, GUIZHOU AND ITS IMPLICATIONS

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Abstract

The Rhuddanian (Llandovery, Silurian) includes the survival and recovery intervals respectively after the end-Ordovician mass extinction. The marine environment during the earliest Silurian was dominated by deeper-water, commonly anoxic conditions and sustained transgression, so shelly facies of this time interval are rarely known in the Gondwana and peri-Gondwana regions. However, in the upper Yangtze region of South China paleoplate, some shelly facies are well-developed (e. g. the Wulipo Bed and the Niuchang Formation). The trilobite fauna documented in this paper provides a unique window for investigating trilobite macroevolution in South China during the Late Ordovician and early Silurian. Trilobite fossils were collected from

the Wulipo Bed (middle Rhuddanian) and the Niuchang Formation (upper Rhuddanian) at Yanping and Gaojiang sections of Huangjiaba town, Meitan County, northern Guizhou, including 17 species of 15 genera (subgenera), 11 families and 7 orders, amongst which five macroevolutionary types could be recognized, i. e. the declining survivors, the increasing survivors, the Lazarus survivors, the new arrivals and the Dead Clade Walking (DCW). Different types of trilobites have different kinds of survival strategies facing the crisis. Declining survivors and Lazarus survivors are major source of biological evolution after the mass extinction, to a certain extent, they influence the process of the biological evolution of the entire ecosystem. New arrivals mark the improvement of the environment after the mass extinction and the beginning of the trilobite recovery interval.