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节肢动物吐卓虫咬痕化石在云南昆明附近寒武纪早期关山生物群的发现及意义*

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提要　本文报道了一块来自云南省昆明市附近寒武纪第二世第四期关山生物群具咬痕的双瓣壳节肢动物吐卓虫(*Tuzoia*)化石, 系吐卓虫咬痕化石在全球范围的首次发现。该发现证实作为主动捕食者的吐卓虫很可能被大型捕食者(如奇虾类或莱德利基虫类三叶虫等)捕食, 说明寒武纪早期的海洋生物群落已经具有高度复杂化的食物链, 为进一步了解吐卓虫的生态位及深入探讨寒武纪大爆发时期海洋生态系统食物网结构提供了新的信息。

关键词　吐卓虫　咬痕　关山生物群　寒武纪早期　食物网

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Occurrence of bite marks on *Tuzoia* (Arthropoda) from the early Cambrian Guanshan biota in Kunming, Yunnan

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Abstract　First fossil record of bite marks on the bivalved arthropod *Tuzoia* is reported from the Guanshan biota (Stage 4, Series 2, Cambrian) in Yunnan Province, South China. These bite marks, probably produced by predators such as radiodonts or redlichid trilobites, are interpreted as recovery of unsuccessful predatory attacks. The new discovery shows that *Tuzoia* were preyed upon by larger predators, indicating the existence of a complex food chain in the early Cambrian. This report provides new information in understanding the ecological niche of Tuzoid arthropods and the food web structure of the early Cambrian marine ecosystems.

Key words　*Tuzoia*, bite marks, Guanshan biota, early Cambrian, food webs

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1　前　言

吐卓虫(*Tuzoia*)是寒武纪海洋中一种常见的具有特征网状壳饰的双瓣壳节肢动物, 在北美、欧洲、澳大利亚、华南都有发现。吐卓虫最先由Walcott根据加拿大布尔吉斯页岩的壳体标本命名(Walcott, 1912), 但长期以来对其内部构造知之甚少(Vannier *et al*., 2007)。直到最近研究布尔吉斯型页岩保存软躯体结构的标本, 才对吐卓虫的软躯体结构有了初步了解。吐卓虫从前到后可分为头胸部、躯干和尾部。头部具有一对触角和分异的附肢; 躯干具有大约10对相同的腿肢, 尾部具一对尾扇(Izquierdo-López and Caron, 2022)。根据形态功能分析认为吐卓虫为近底游泳的节肢动物, 靠捕食其他动物或者食腐为生(Fatka and Herynk, 2016)。但吐卓虫是否被存在其他动物捕食的情况还没有确切证据, 对吐卓虫在寒武纪海洋生态系统中的生态位目前还缺乏共识。

云南寒武纪关山生物群作为典型的布尔吉斯页岩型动物群(朱茂炎, 2010), 保存了大量精美的多门类软躯体化石(罗惠麟等, 2008; 胡世学等, 2013; Hu *et al*., 2010; Liu *et al*., 2016)。吐卓虫是关山生物群的常见分子, 目前已经发现了6个种, 分别是*Tuzoia sinensis* (潘江, 1957; 罗惠麟等, 2006)、*Tuzoia tylodesa* (罗惠麟等, 2006)、*Tuzoia retifera* (Hu *et al*., 2010; Wu and Liu, 2022)、*Tuzoia multispinosa* (Zhao, 2015)、*Tuzoia* cf. *canadensis* (Wu and Liu, 2022)。其中中华吐卓虫(*Tuzoia sinensis* P'an)是关山生物群最常见的吐卓虫种类。从保存方式看, 大多数吐卓虫标本呈侧压方式保存, 仅能见到一侧的壳体, 仅少数标本呈背腹压蝴蝶状保存(Butterfly-type preservation), 左右两瓣壳均可在层面上见到。除少量标本保存了可能的眼睛外(Wu and Liu, 2022), 目前关山生物群吐卓虫还未发现其他的软躯体构造。

咬痕属于化石保存中畸形的一种。畸形大体上可分为愈合伤痕、发育畸形及病理畸形几大类(Owen, 1985; Babcock, 1993; Bicknell *et al*., 2018)。愈合伤痕来自动物遭受攻击或者蜕壳过程中造成的创伤。畸形生长可能是基因或者胚胎发育过程异常所造成。病理畸形则是源自疾病或寄生虫的影响。咬痕作为一种特别的愈合伤痕, 是动物之间捕食关系最直接的证据, 对古生态学研究具有特别的意义。

节肢动物化石上的咬痕主要发现于三叶虫(程美蓉等, 2019; Rudkin, 1979; Babcock, 1993, 2003, 2007; Pratt, 1998; Nedin, 1999; Jago and Haines, 2002; Ou *et al*., 2009; Fatka and Herynk, 2016; Pates *et al*., 2017; Bicknell and Paterson, 2018), 以W形、V形及U形为主, 位置可见于头鞍、胸节和尾部(Babcock, 1993, 2003; Nedin, 1999)。另外在纳罗虫(Zhang and Erwin, 2007: 图41)、鲨(Bicknell *et al*., 2018)等节肢动物的化石上也发现有咬痕, 但吐卓虫化石的咬痕一直未见报道。关山生物群内的咬痕化石此前仅发现于三叶虫满苏氏莱德利基虫类(*Redlichia mansui*) (胡世学等, 2013)。

2　研究材料与方法

本文所描述的吐卓虫咬痕标本系作者之一的董存治在野外发现。化石材料产于昆明附近的高楼房乌龙箐组下部的小古油栉虫(*Palaeolenus*)带底部黄绿色泥岩之中。化石保存完好, 呈棕红色, 与黄色围岩有明显区别。化石系在野外顺层面劈开泥岩获得, 后在室内在显微镜下修理露出全貌。化石照相系用CANON佳能Mark II相机配备EF 100 mm f/2.8 L IS USM微距镜头在自然光下拍摄, 局部细节放大在ZEISS Smartzoom 5及显微镜下完成。图片处理及图版编排利用Adobe Photoshop CS3完成。本文中具咬痕的吐卓虫标本(编号NIGP 201899)及莱德利基虫唇瓣标本(编号NIG P203981、NIGP 203982)保存在中国科学院南京地质古生物研究所。

3　描　述

该枚吐卓虫标本前后长7 cm, 高8 cm (图1-A, 2)。同一块标本上还可见满苏氏莱德利基虫(*Redlichia mansui*)及少量节肢动物碎片。吐卓虫双壳展开呈背腹压蝴蝶状保存。壳表面网纹状装饰发育, 呈不规则的多边形(4—7边形), 以5—6边形为主。网眼直径2—6 mm, 以4—6 mm居多。壳中部

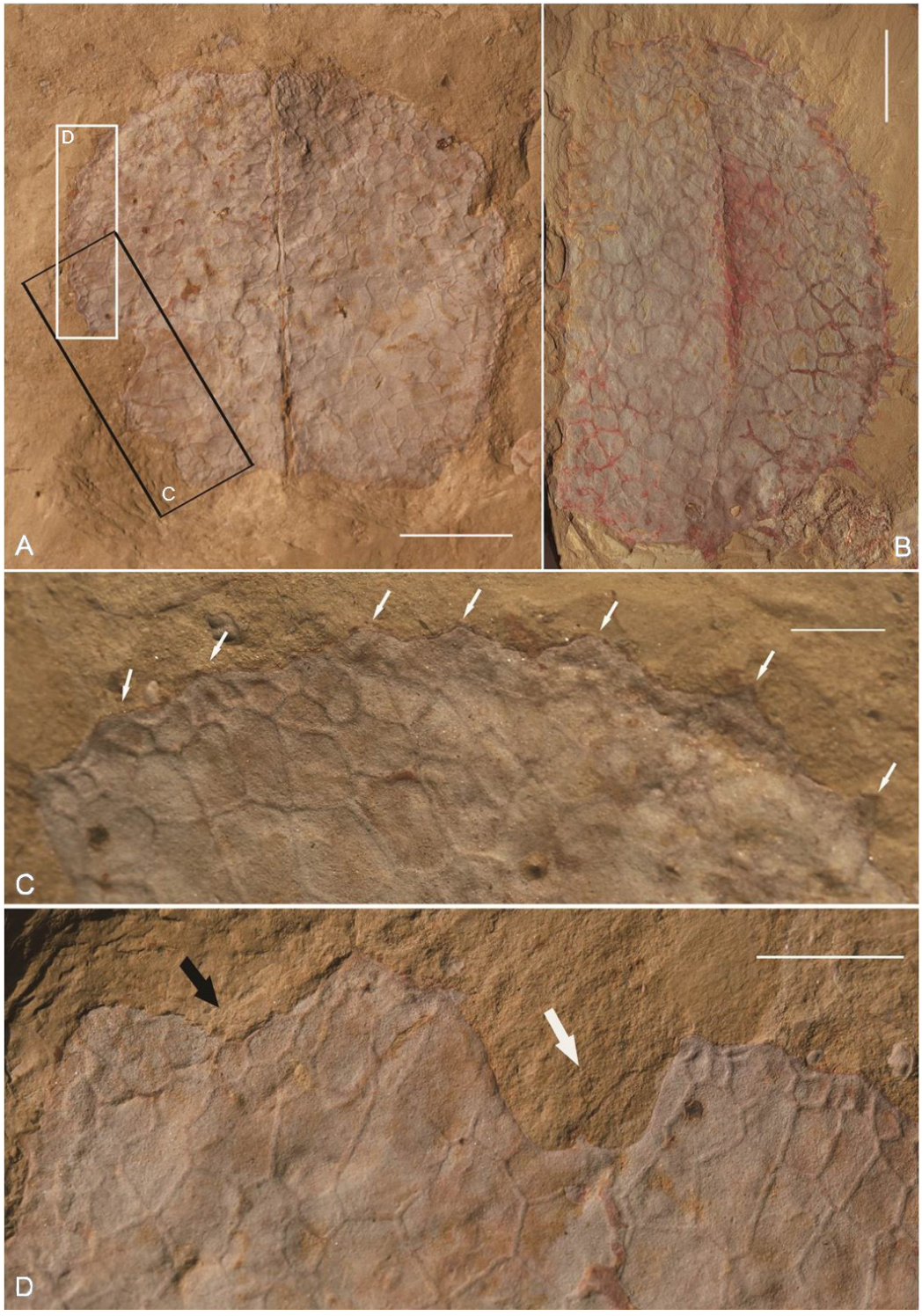

图 1 关山生物群吐卓虫化石

Fig. 1 Bite marks on *Tuzoia* from the Guanshan biota (NIGP 201899)

A. 具咬痕的标本 NIGP 201899 全貌。**B**. 侧压保存的完整中华吐卓虫化石(Kgx-4-246)。**C** 为 A 中白色方框的放大，显示左前侧脊上保存的侧脊刺(白色箭头)。D 为 A 中黑色方框的放大，显示左壳后部的两处咬痕(箭头所示)。A、B 中比例尺为 2 mm, C、D 中均为 1 mm。

A. Overview of the specimen (NIGP 201899) with bite marks. **B**. A laterally preserved, complete specimen of *Tuzoia sinensis* (Kgx-4-246). **C**. Enlargement of white rectangular area in A, showing spines along the lateral ridge. **D**. Enlargement of black rectangular area in A, showing the two bite marks at the posterior part of the left carapace. Scale bars = 2 mm in A and B and 1 mm in C and D.

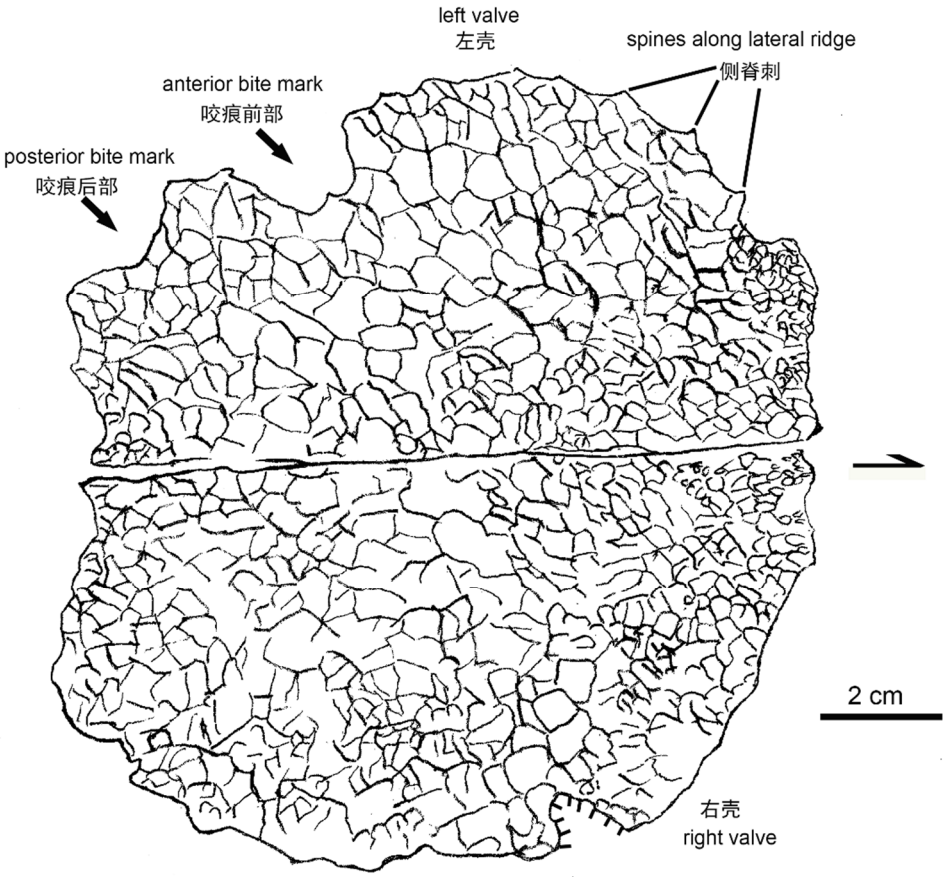

图 2　具咬痕的吐卓虫化石(NIGP 201899)解释图

Fig. 2　Interpretive drawing of the *Tuzoia* specimen (NIGP 201899) with bite marks

的网眼较大, 接近前后两端的网眼较小。铰合线较直, 前背角约为90°, 后背角稍大, 约为110°, 前、后铰突呈短小的三角形。后腹缘较前腹缘明显膨出。根据与关山生物群吐卓虫标本的对比来看, 该个体的外缘应该是侧脊, 左右两壳的外缘没有显露。左壳前部可见数个侧脊刺。侧脊刺基部较宽, 约0.5 mm, 刺尖高约0.1 mm (图1-C)。

标本右壳相对完整, 未见明显的缺失。左壳前部至腹中部边缘完整, 但在后部外缘可见前后两处缺口(图1-A、1-D)。前部缺口呈深“U”形, 左右近对称, 底部宽约6 mm, 顶部宽约5 mm, 深度5.5 mm。底部中央略有凸起而呈桃心形。该缺口边缘表面光滑(图1-D)。后部缺口呈浅“V”形, 顶部宽约5 mm, 深3 mm。该缺口边缘表面呈锯齿状起伏。外缘未见破损, 明显区别于化石采集过程中劈开岩石导致的破损。

关山生物群目前已报道的吐卓虫之中, *Tuzoia sinensis*、*Tuzoia retifera*、*Tuzoia multispinosa*、*Tuzoia* cf. *canadensis* (Wu and Liu, 2022)壳表面都具有网格状纹饰。与其他种不同, *Tuzoia tylodesa*壳表面仅发育瘤状的装饰, 缺乏网格状纹饰。故当前标本可以排除是*Tuzoia tylodesa*的可能性。与另外几个壳表面具网格状纹饰的吐卓虫相比, 当前标本在个体大小、前后背角及网纹的形态等特征与中华吐卓虫(*Tuzoia sinensis* P'an)较为接近(图1-B), 但由于腹边缘刺这一最重要的鉴定特征之一没有观察到, 故当前的标本仅鉴定到属, 暂不能定种。

4　讨　论

当前标本左壳后侧腹部边缘的W形缺口外缘未见破损, 明显区别于化石采集过程中常见的劈开泥岩时人为引起的破损。缺口外缘具有窄而加厚的边缘, 与前后壳体完整部分的边缘一致。这一现

象与多数三叶虫及鲎类节肢动物化石上的咬痕较为类似(程美蓉等, 2019; Rudkin, 1979; Babcock, 1993; Pratt, 1998; Nedin, 1999; Jago and Haines, 2002; Fatka *et al*., 2015; Pates *et al*., 2017; Bicknell and Paterson, 2018;)。故本文认为这一缺失部分属于吐卓虫遭受攻击后的愈合痕迹。这是吐卓虫咬痕化石在全球的首次发现。当前标本上的两处咬痕, 前部较深, 边缘较光滑; 后部较浅, 边缘略呈锯齿状。两处咬痕的轮廓差别较大, 因此很可能代表不同类型的捕食者的前后两次攻击。该个体得以幸存的原因可能是遭受攻击的部位位于躯体后部。根据最近的研究, 吐卓虫躯体后部的软体组织主要集中在靠近绞合线的中轴(Izquierdo-López and Caron, 2022)部位, 故而很可能受到伤害的主要是壳体, 壳内的软体组织未遭受致命性的伤害。

吐卓虫曾被一些学者认为是主动捕食者, 能捕食三叶虫等动物(Fatka *et al*., 2015)。咬痕在吐卓虫化石上的发现, 说明吐卓虫本身又被更高一级的动物所捕食。关山生物群内吐卓虫潜在的捕食者首推奇虾类。奇虾类是公认的寒武纪海洋中的霸主, 位于食物链顶端。目前关山生物群已经报道的奇虾类(或射齿目)主要是单独保存的前附肢及少数口器化石(Zeng *et al*., 2018), 尚未发现完整的奇虾类化石。奇虾类在关山生物群中共发现5种, 即抱怪虫科的昆明关山虾(*Guanshancaris kunmingensis*)、奇虾科的多节拟奇虾(*Paranomocaris multisegmentalis*)和简单拟奇虾(*P. simplex*)、拟背脱虾未定种*Parapeytoia* sp.及另外一个未定名的筛虾科分子(tamisiocaridid) (Hu *et al*., 2010; Wang *et al*., 2013; Jiao *et al*., 2021; Zhang *et al*., 2023)。最近对关山生物群奇虾类的研究认为多节拟奇虾(*Paranomalocaris multisegmentalis*)是用大附肢捕食(raptorial predation) (Jiao *et al*., 2021); 昆明关山虾可能为壳食性(durophagous predator), 以腕足等为食(Zhang *et al*., 2023); 简单拟奇虾及另外一个未定名的筛虾科分子可能是底泥筛食者(sweep feeding)或者滤食者(filter feeding), 用大附肢在泥质海底翻找食物(Jiao *et al*., 2021)。吐卓虫作为游泳性能较强的生物, 不太可能是简单拟奇虾这类底泥筛食者或滤食者的猎物。故就奇虾类而言, 关山生物群内吐卓虫最可能的捕食者是昆明关山虾(*Guanshancaris kunmingensis*)和多节拟奇虾(*Paranomocaris multisegmentalis*)。

奇虾类之外, 一些大型三叶虫也可能捕食吐卓虫。目前为止关山生物群内已报道的三叶虫共有6属15种(罗惠麟等, 2008; 胡世学等, 2013)。其中个体较大且与吐卓虫共生的有莱德利基虫属的三个种, 即满苏氏莱德利基虫(*Redlichia mansui*)、诺脱林莱德利基虫(*Redlichia noetlingi*)和云南莱德利基虫(*Redlichia yunnanensis*)。Fortey和Owens (1999)根据形态功能学研究认为莱德利基虫类三叶虫是捕食者。Bicknell等(2022)对澳大利亚寒武纪鹌鹑湾生物群(Emu Bay biota)三叶虫的研究也认为*Redlichia rex*是凶猛的捕食者, 可以捕食其他体型较小的莱德利基虫同类。从个体大小及化石共生的角度看, 关山生物群中能够捕食吐卓虫的可能是莱德利基虫类, 尤其是云南莱德利基虫。云南莱德利基虫是关山生物群体型最大的三叶虫, 其体长可达15 cm (罗惠麟等, 2008)。值得指出的是当前标本前部咬痕的轮廓与三叶虫的唇瓣(也称口板)较为相似, 可能暗示该处咬痕系由三叶虫捕食所造成。此前的研究已经明确关山生物群内的莱德利基虫均具有较大的唇瓣, 唇瓣与腹边缘板相连, 后侧缘具有1—2对口板刺(罗惠麟等, 2018) (图3), 符合捕食类三叶虫唇瓣的条件(Fortey and Owens, 1999)。虽然体型巨大的云南莱德利基虫唇瓣轮廓跟伤口在细节上仍有一些细微差异, 但综合以上分析, 我们认为关山生物群体型巨大的云南莱德利基虫最有可能捕食吐卓虫。值得一提的是, 该伤口是否经过几次蜕壳而使伤口边缘变得更加圆滑, 尚未可知。但后部伤口边缘粗糙且略呈锯齿状, 显然未经过蜕皮。因此极有可能, 前部伤口受伤时间可能早于后部伤口。

已有的化石记录表明, 三叶虫伤口在身体左右两侧都是不对称的(程美蓉等, 2019; Babcock, 1993; Jago and Haines, 2002; Fatka *et al*., 2015; Bicknell and Paterson, 2018)。而吐卓虫这枚标本咬痕仅见于左侧, 显然捕食者只是从吐卓虫的一侧发动攻击。在遭受两次攻击时, 吐卓虫都未将两壳合拢以御敌, 暗示捕食者也未从腹侧发动攻击。另

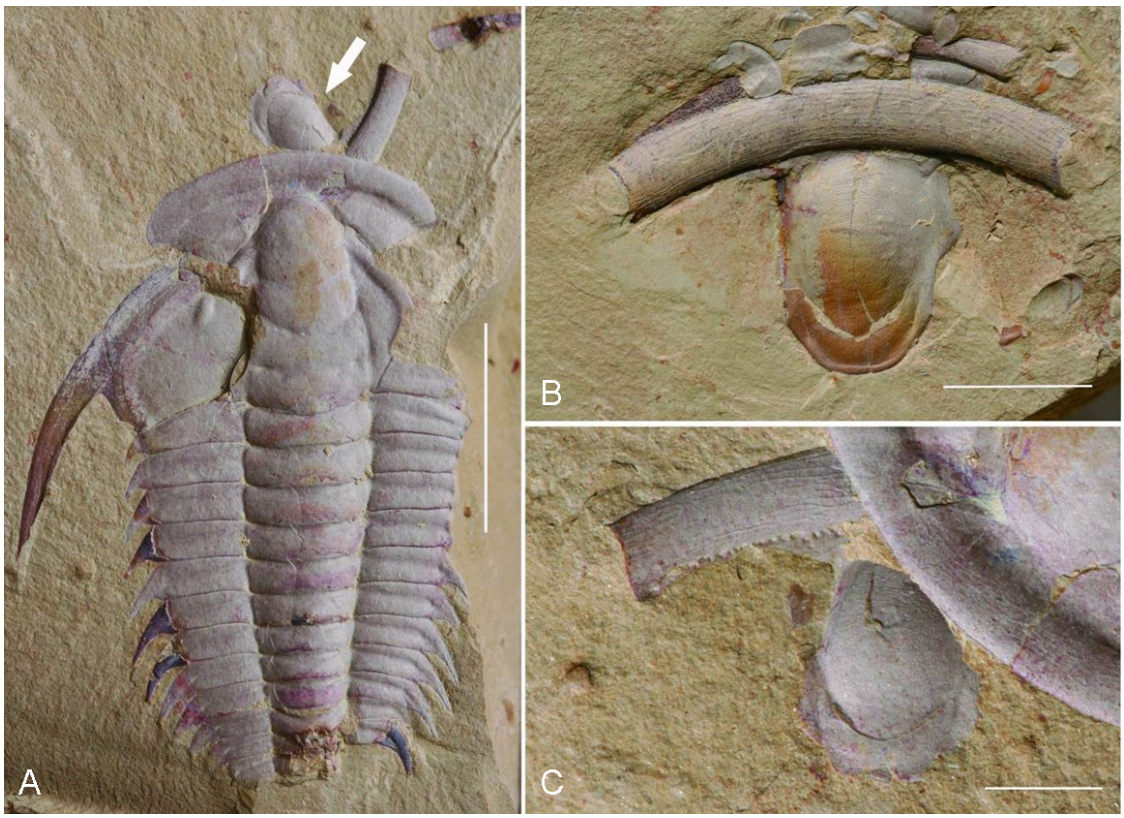

图 3　关山生物群三叶虫莱德利基虫及其唇瓣

Fig. 3　Trilobite *Redlichia* and associated hypostomes from the Guanshan biota

A. 满苏氏莱德利基虫及唇瓣(白色箭头) (NIGP 203982); **B**, 单独保存的满苏氏莱德利基虫唇瓣及腹边缘板(NIGP 203981)。比例尺均为 10 mm。**C**. 图A中唇瓣的放大(白色箭头所示)。

A. *Redlichia mansui* with a disarticulated hypostome (NIGP 203982). **B**. A hypostome of *Redlichia mansui* attached to the doublure (NIGP 203981). **C**. Enlargement of the hypostome in A (indicated by the white arrow). All scale bars equal 10 mm.

外, 近同一时期的双瓣壳节肢动物等刺虫(*Isoxys*)等壳体边缘具有显著的环边, 意味着可以将两个壳瓣紧密封闭起来。而吐卓虫在生活状态时左右两壳有可能不能完全关闭, 背部绞合线活动范围可能有限。

5　结　论

关山生物群吐卓虫咬痕化石的发现, 证实吐卓虫很可能被大型捕食者如奇虾类或大型莱德利基虫类等捕食, 说明寒武纪早期的海洋生物群落已经具有高度复杂化的食物链, 为探讨寒武纪大爆发时期海洋生态系统食物网提供了新的信息。

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