



中国早白垩世脉翅目螳蛉科化石的新发现——孙氏逸仙蛉

师超凡^{1*}, 杨强², 任东³

1. 中山大学地球科学与工程学院, 广东省地质过程与矿产资源探查重点实验室, 珠海 519080;

2. 广州大学生命科学学院, 广州 510006;

3. 首都师范大学生命科学学院, 北京 100048

* 联系人, E-mail: shichf5@mail.sysu.edu.cn

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摘要 脉翅目螳蛉科昆虫化石记录较为丰富, 在中生代以绝灭亚科Mesomantispinae和Doratomantispinae的属种最多, 其中中螳蛉亚科Mesomantispinae分布时代更早, 集中于中侏罗世至早白垩世. 本文记述了采集自我国辽宁省北票市黄半吉沟下白垩统义县组地层的螳蛉科中螳蛉亚科一新属新种, 孙氏逸仙蛉*Yatsenia suni* gen. et sp. nov. 该新属种与同亚科其他属在前翅脉序和翅斑上具显著差异, 包括Sc与R1融合于近翅中部, CuP双分叉, 1A栉状分叉等特征, 揭示了白垩纪螳蛉更为丰富的形态与物种多样性.

关键词 化石, 昆虫, 螳蛉, 热河生物群, 中生代

螳蛉科Mantispidae是昆虫纲脉翅目中起源较早的一个现生科, 其典型特征为前胸延长, 前足特化为捕捉足^[1]. 螳蛉主要分为6个亚科, 即Mesomantispinae、Doratomantispinae、Symphrasinae、Drepanicinae、Calomantispinae和Mantispinae^[2-5]. 其中Mesomantispinae和Doratomantispinae为绝灭亚科, 其余4亚科为现生亚科. 螳蛉科现生属种相对丰富, 已报道400余种, 全球性分布^[6,7]. 螳蛉科的地质历史可以追溯至距今1亿8千万年前的早侏罗世. 最早的化石记录是采集自德国下侏罗统地层的*Liassochrysa stigmatica* Ansoerge and Schlüter, 1990, 模式标本是一个保存较为完整的前翅^[8,9]. 中侏罗世的螳蛉化石仅发现于我

国内蒙古道虎沟地区九龙山组1属1种——*Clavifemora rotundata* Jepson et al., 2013. 该种是目前发现的最早的保存有捕捉足的螳蛉. 这一时期的螳蛉捕捉足基节和股节均较粗壮, 股节腹面具有多排小刺, 未发现股节长刺^[10]. 晚侏罗世的螳蛉共报道4属5种, 均采集自哈萨克斯坦Karatau-Mikhailovkaz组地层^[11-15]. 其中*Promantispa* Panfilov, 1980的模式标本仅保存了一个前翅, 脉序较为简单. 其他3属*Karataumantispa*、*Longipronotum*、*Ovalofemora*均保存有捕捉足, 且脉序与*Clavifemora*较为相似. 早白垩世的螳蛉仍然集中在古北区, 已发表4属5种, 采集自我国辽宁义县组、俄罗斯Baissa组地层和朝鲜Sinuiju组地

层^[4,10,16]. 晚白垩世的螳蛉化石标本发现于哈萨克斯坦和缅甸琥珀中^[17-23]. 其中哈萨克斯坦的*Gerstaeckerella asiatica*正模标本仅保存了一个后翅, 根据其脉序特征暂将其归入现生属中, 是现生螳蛉属的最早期代表^[17]. 缅甸晚白垩世琥珀中发现大量螳蛉化石, 已报道成虫11属24种及部分幼虫标本, 其中包括现生亚科Symphrasinae的最早代表^[5,22]. 古近纪的螳蛉化石标本主要发现于德国、波罗的海、英国的始新世地层和法国的渐新世地层^[2,3,9,24-27]. 新近纪的螳蛉全部发现于新北区, 化石标本采集自多米尼加共和国和墨西哥琥珀中, 已描述2属3种^[28,29]. 新生代的螳蛉化石多归入现生亚科及现生属.

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中螳蛉亚科Mesomantispinae是螳蛉科中仅发现于中侏罗世至早白垩世的绝灭亚科,已报道7属9种,采集自我国中侏罗世、哈萨克斯坦晚侏罗世、我国和俄罗斯早白垩世的多个地层^[4,10,12-15,30](表1)。中螳蛉亚科代表了螳蛉科中捕捉足的早期演化特征,表现为基节延长与增粗、股节加粗与股节刺的发育,而现生螳蛉中较为常见的股节主刺在中螳蛉亚科中未发现。中螳蛉亚科的脉序也与其他化石属种,特别是现生螳蛉具有较大差异,前翅多具有肩迴脉,前缘域基部宽,前缘横脉多分叉,Sc与R1末端融合,CuA栉状分叉,支脉众多。本文基于采集自我国早白垩世义县组热河生物群中的螳蛉化石标本描述中螳蛉亚科一新属新种——孙氏逸仙蛉*Yatsenia suni* gen. et sp. nov.,新属种在前后翅脉序、翅斑等特征异于该亚科其他属种。

本文所述化石标本采集自我国辽宁省北票市炒米店乡黄半吉沟村,含化石地层归入义县组,下白垩统巴雷姆阶至阿普特阶,距今约126.5~113.2亿年^[31-34]。本文中模式标本馆藏于首都师范大学昆虫演化与环境变迁重点实验室。

本研究使用Zeiss Discovery V20体视显微镜检视标本,使用显微镜附载绘

图臂进行标本线条图绘制、显微镜附载Axiocam 506彩色数码相机进行标本拍摄;借助Adobe Illustrator CS6和Adobe Photoshop CS6等软件完成标本最终线条图绘制工作。

翅脉的命名术语参考Lambkin (1986)的命名系统^[2,31]。翅脉简称:1A~3A,第1~3臀脉;C,前缘脉;Cu,肘脉;CuA,前肘脉;CuP,后肘脉;M,中脉;MA,前中脉;MP,后中脉;R,径脉;R1,第1径脉;Rs,径分脉;Sc,亚前缘脉。

昆虫纲Class Insecta Linnaeus, 1758^[35]

脉翅目Order Neuroptera Linnaeus, 1758^[35]

螳蛉科Family Mantispidae Leach, 1815^[36]

中螳蛉亚科Subfamily Mesomantispinae Makarkin, 1996^[4]

逸仙蛉属*Yatsenia* gen. nov.

模式种:孙氏逸仙蛉*Yatsenia suni* gen. et sp. nov.

属征:前足股节较粗壮,翅具条带状翅斑,几乎整个翅缘都具有缘饰,前翅Sc与R1在距翅端约五分之二翅长处融合,前缘横脉多重分叉,亚前缘域具两条横脉,3条r1-rs横脉,MP分叉早于MA从Rs分出处,CuA栉状分叉,CuP双分叉,后翅

CuA长,平行于翅后缘,栉状分叉。

词源:属名与种名献给中国民主革命先驱孙中山先生,纪念先生创办中山大学一百周年。

孙氏逸仙蛉*Yatsenia suni* gen. et sp. nov.

模式标本:标本号CNU-NEU-LB2011019(图1)。

产地与地层:中国辽宁省北票市炒米店乡黄半吉沟村。义县组,早白垩世。

种征:同属征。

描述:复眼较大,触角念珠状,上颚粗壮、对称。前胸无明显延长,前胸和中胸背板具显著的刻点。前足基节延长且膨大,股节粗大,腹脊具一系列短刺。

前翅长12.0 mm,宽5.3 mm。前、后翅卵圆形,翅前缘中部浅凹,末端略尖。翅面具条带状翅斑。整个翅缘具缘饰。前翅前缘域基部加宽,向端部逐渐变窄。前缘横脉均分叉,多为多重分叉。Sc与R1在距翅端约2/5翅长处融合。亚前缘域与R1、Rs脉间距近等宽。亚前缘域的基半部具2支sc-r1横脉,近基部一支位于R1与Rs分离之前。Sc+R1在翅顶点之前汇入翅缘,距翅端约十分之一翅长。3支r1-rs横脉,2支位于Sc与R1融合前,最基部一支位于MA从Rs主干脉分出前,第2支位于近翅中部,第3支位于Sc+R1中部。

表1 螳蛉科中螳蛉亚科化石记录表

Table 1 Fossil records of Mantispinae

属种名	分布	地层	年龄(Ma) ^[30]
<i>Clavifemora rotundata</i> Jepson et al. 2013 ^[10]	中国	中侏罗统巴通阶至卡洛夫阶九龙山组	168.2~165.3
<i>Karataumantispia carnaria</i> (Khrmov 2013) ^[12,13]	哈萨克斯坦	上侏罗统牛津阶至提塘阶 Karatau-Mikhailovkaz组	161.5~149.2
<i>Longipronotum benmaddoxi</i> Jepson et al. 2018 ^[14,15]	哈萨克斯坦	上侏罗统牛津阶至提塘阶 Karatau-Mikhailovkaz组	161.5~149.2
<i>Ovalofemora abbottae</i> Jepson et al. 2018 ^[14]	哈萨克斯坦	上侏罗统牛津阶至提塘阶 Karatau-Mikhailovkaz组	161.5~149.2
<i>Ovalofemora monstrosa</i> (Khrmov, 2013) ^[12,14]	哈萨克斯坦	上侏罗统牛津阶至提塘阶 Karatau-Mikhailovkaz组	161.5~149.2
<i>Mesomantispia sibirica</i> Makarkin 1996 ^[4]	俄罗斯	下白垩统瓦兰今阶至阿普特阶Baissa组	137.7~121.4
<i>Archaeodrepanicus acutus</i> Jepson et al. 2013 ^[10]	中国	下白垩统巴雷姆阶至阿普特阶义县组	126.5~113.2
<i>Archaeodrepanicus nudsi</i> Jepson et al. 2013 ^[10]	中国	下白垩统巴雷姆阶至阿普特阶义县组	126.5~113.2
<i>Sinomesomantispia microdentata</i> Jepson et al. 2013 ^[10]	中国	下白垩统巴雷姆阶至阿普特阶义县组	126.5~113.2
<i>Yatsenia suni</i> gen. et sp. nov.	中国	下白垩统巴雷姆阶至阿普特阶义县组	126.5~113.2

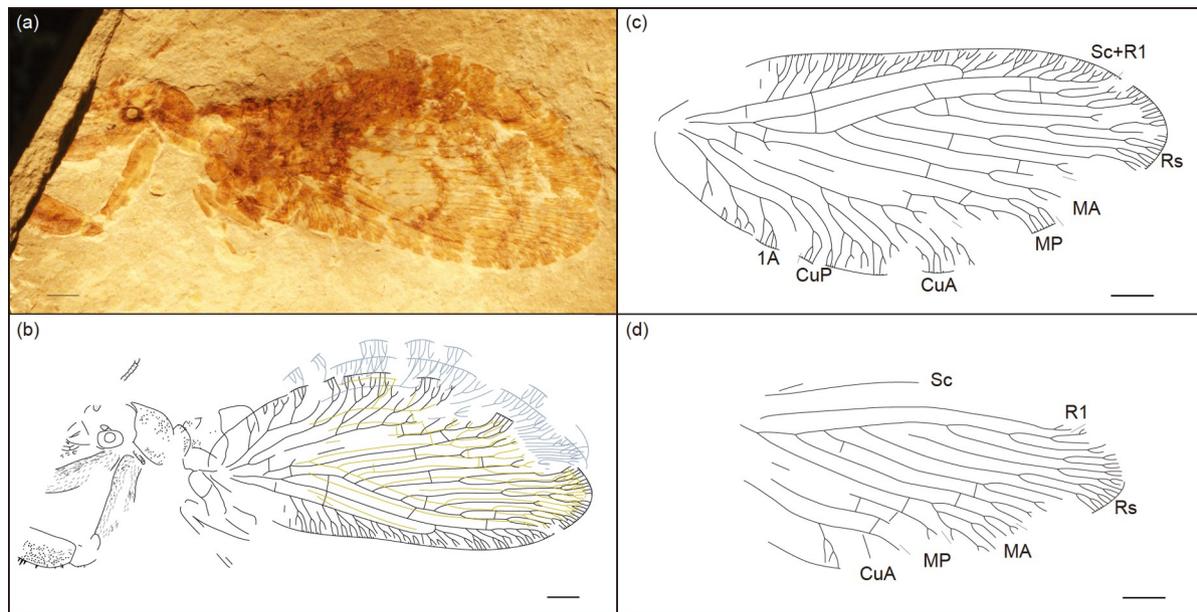


图1 孙氏逸仙蛉 *Yatsenia suni* gen. et sp. nov. 模式标本CNU-NEU-LB2011019. (a) 化石标本照片; (b) 化石标本特征线条图; (c) 左前翅脉序线条图; (d) 左后翅脉序线条图. 比例尺 = 1 mm

Figure 1 *Yatsenia suni* gen. et sp. nov. Holotype CNU-NEU-LB2011019. (a) Habitus photograph; (b) habitus line drawing; (c) line drawing of left forewing; (d) line drawing of left hind wing. Scale bar = 1 mm.

Rs具有7支支脉, Rs支脉间分布着不规则排列的横脉, 第2支脉在中段前开始双分叉, 其余支脉近末端双分叉, 并在近翅缘处多次分叉. MA在翅基部三分之一处自Rs主干脉分出, MP在R1与Rs分离后、MA分出前双分叉, 在MP分叉前一支横脉连接Rs与MP, 在翅中部一支横脉连接MA与MP前支脉. MP1双分叉, MP2栉状分叉. 2支mp-cua横脉, 基部一支位于MP双分叉前、CuA与CuP分离后, 端部一支位于翅中部. CuA与CuP在近翅基部分离. CuA自距翅基部约1/3翅长处开始栉状分叉, 具五支支脉, 支脉在近翅缘处多重分叉. CuA与CuP之间无横脉. CuP双分叉, 分叉位置早于CuA, 支脉末端多分叉. 1A较长, 栉状分叉, 具四支支脉, 支脉末端多重分叉.

后翅前缘域较窄, 亚前缘域与R1、Rs脉间距近等宽. Rs具八支支脉, 横脉少, 支脉近末端双分叉. MP支脉近末端分叉. CuA长, 平行于翅后缘, 栉状分叉.

新属逸仙蛉属 *Yatsenia* gen. nov. 基于以下特征归入中螳蛉亚科: (1) 未延长的前胸; (2) 翅缘具缘饰; (3) 前缘域基部宽, 向末端逐渐变窄; (4) Sc与R1融

合(或被解释为由横脉相连接^[14]); (5) 翅痣不显著; (6) MP分叉晚于Rs分出处(或被解释为M分叉晚于RP分出处^[14]); (7) CuA栉状分叉. 中螳蛉亚科已报道中侏罗世1属 *Clavifemora*, 晚侏罗世3属 *Karataumantispa*、*Longipronotum*、*Ovalofemora*, 早白垩世3属 *Archaeodrepanicus*、*Sinomesomantispa*、*Mesomantispa*(表1).

新属与 *Karataumantispa* 相比, 有如下特征: 前足股节未严重膨大, 前翅Rs具7支支脉, CuA栉状分叉, CuP双分叉, 支脉少; 而 *Clavifemora* 前翅Rs支脉超过10支, CuA主支双分叉, CuP支脉多(基于检视模式标本)^[10]. 新属区别于 *Karataumantispa* 有如下特征: 前翅基部具亚前缘横脉、r1-rs横脉, rs-mp早于MP双分叉处, MP2近翅末端分叉, 无cua-cup横脉; 而 *Karataumantispa* 前翅基部无亚前缘横脉、r1-rs横脉, rs-mp晚于MP分叉处(原文命名为1r-m晚于MA与MP分离处), MP2于近翅基部双分叉(原文中同源翅脉命名为MP), 具多支cua-cup横脉^[12,13]. 新属区别于 *Longipronotum* 有如下特征: 前翅Sc与R1融合处较 *Longipronotum* 更近翅中部, CuA与CuP分离早于

1sc-r1, 横脉多, 1A栉状分叉, 支脉多, 翅面具条带状斑纹; 而 *Longipronotum* 前翅CuA与CuP分离晚于1sc-r1, 横脉少, 1A双分叉(原文中命名为AA1), 翅斑为斑点状^[14,15]. 新属区别于 *Ovalofemora* 有如下特征: 前翅Sc与R1融合处较 *Ovalofemora* 更近翅中部, 前翅基部横脉多, MP分叉早于MA由Rs分出处, 条带状翅斑; 而 *Ovalofemora* 前翅基部横脉少, MP分叉晚于MA由Rs分出处(原文中命名为M分叉晚于RP第一支脉分出处), 翅斑为斑点状^[12,14]. 新属区别于 *Archaeodrepanicus* 有如下特征: 前翅脉脉不完整, CuA支脉少, 仅5支, CuP双分叉; 而 *Archaeodrepanicus* 前翅具一系列阶脉, CuA支脉多, 具7~9支支脉, CuP栉状分叉^[10]. 新属区别于 *Sinomesomantispa* 有如下特征: 前翅Sc与R1融合处较 *Sinomesomantispa* 更近翅中部, 前缘域中后部较 *Sinomesomantispa* 宽, Rs支脉少, 翅中后部2条带状翅斑; 而 *Sinomesomantispa* 前翅前缘域中部窄于亚前缘域, Rs支脉多, 具独特的不规则带状翅斑(基于检视模式标本)^[10]. 新属区别于 *Mesomantispa* 如下特征: 前翅横脉显著少于 *Mesomantispa*, CuA、CuP支脉

间无横脉, CuP双分叉, 1A主干脉近平行于翅后缘, 支脉近末端分叉; 而 *Mesomantispa* 前翅CuA、CuP支脉间横脉多, CuP栉状分叉, 具四支支脉, 1A支脉分叉深^[4]。

新属逸仙蛉属 *Yatsenia* gen. nov. 是我国中生代地层中发现的螳蛉科第4属。截至目前, 我国发现的螳蛉科化石属占全球已报道化石属的1/7, 全球已报道中螳蛉亚科化石属近一半^[14,23]。我国中生代陆相地层发育, 特别是在燕辽地区(北京-冀北-辽西-内蒙古东南部)形成了侏罗-白垩系沉积盆地, 富含多样的陆生生物化石, 主要包括中侏罗世的燕辽生物群和早白垩世的热河生物群^[32]。这一段地史时期是脉翅目昆虫科级分化的重要时期^[1], 出现了多个仅在中生代存在的绝灭科, 如丽蛉科、线蛉科、丽翼蛉科等^[37-39]; 此外, 绝大多数现生科在这一时期起源, 如草蛉科、蚁蛉科、细蛉科

等^[40-42]。上述类群也在我国的燕辽生物群和热河生物群中大量发现, 同时, 燕辽地区也成为了多个脉翅目科级分类单元的起源中心^[30,32]。螳蛉科自早侏罗世在地层中首现以来, 以中螳蛉亚科为代表的化石属种在中侏罗世-早白垩世的燕辽及周边国家地区的地层中大量出现, 代表了其在早期演化历史中的第一次辐射事件, 表现为捕捉足的发育、前后翅脉序的多样化等特征。基于系统发育树的演化速率估算显示, 在这一时期, 螳蛉科整体形态、前足结构与前翅脉序特征均表现出一个快速演化期, 但是其快速演化的具体时期在3个形态分区略有差异^[43]。这一时期螳蛉科的支系数也迅速积累, 表现为物种多样化与形态多样化的同步辐射, 是螳蛉科起源与早期演化阶段的特征之一。该阶段的快速辐射演化可能归因于此前三叠纪末大灭绝事件, 由此空出大量生态位; 在侏

罗纪伊始, 随着陆地生态系统的复苏, 为螳蛉科物种及其形态的快速多样化创造了条件^[43-45]。以中螳蛉为代表的中侏罗世-早白垩世螳蛉捕捉足形态较为相似, 以基节延长增粗、股节膨大并附着成排短刺为特征^[10,12-15], 是螳蛉捕捉足演化的初始阶段。中螳蛉亚科的捕捉足形态在几何形态分析中聚集为一簇, 祖先状态重建结果也验证了该类捕捉足为螳蛉捕捉足演化的原始状态, 功能形态分析则揭示了其功能性状指数在螳蛉捕捉足演化历史中处于平均水平, 即在捕食过程中其自身承受应力、施加于猎物的力、捕食距离均表现为较好的状态, 但未发生功能上的极度特化, 而在演化后期, 捕捉足的功能性状发生了多方向的特化^[43]。至晚白垩世和新生代, 螳蛉科经历了多次支系多样化、形态与功能复杂化以及低级阶元的灭绝事件, 逐渐形成了现代的四亚科和遍布全球的丰富属种^[2,6,30,43]。

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Summary for “中国早白垩世脉翅目螳蛉科化石的新发现——孙氏逸仙蛉”

Yatsenia suni gen. et sp. nov., a new genus and species of Mantispidae (Insecta, Neuroptera) from the Early Cretaceous of China

Chaofan Shi^{1*}, Qiang Yang² & Dong Ren³

¹ School of Earth Sciences and Engineering, Guangdong Provincial Key Laboratory of Geological Processes and Mineral Resources, Sun Yat-sen University, Zhuhai 519080, China;

² School of Life Sciences, Guangzhou University, Guangzhou 510006, China;

³ College of Life Sciences, Capital Normal University, Beijing 100048, China

* Corresponding author, E-mail: shichf5@mail.sysu.edu.cn

Mantispidae (mantid lacewings) are a family of Neuroptera with ample fossil records extended back to the Early Jurassic. Mantid lacewings are characterized by their elongated prothoraces and raptorial forelegs. The family are divided into six subfamilies, i.e., Mesomantispinae, Doratomantispinae, Symphrasinae, Drepanicinae, Calomantispinae, and Mantispinae. Among them, Mesomantispinae and Doratomantispinae are extinct and only found in the Mesozoic, accounting for the majority of fossil mantispid genera and species, while the other four subfamilies have extant representatives, totally including more than 400 species. The extant mantid lacewings are distributed worldwide except the Antarctic. The fossil mantid lacewings have been found in multiple strata from the Jurassic to the Neogene. The oldest mantispid, *Liassochrysa stigmatica* Ansoerge and Schlüter, 1990, was collected from the Lower Jurassic in Germany, but only preserved with one forewing. *Clavifemora rotundata* Jepson et al., 2013, from the Middle Jurassic of China, is the earliest mantispid preserved with raptorial forelegs, which possessed stout forecoxae and forefemora, rows of short spines on the ventral of forefemora. Most genera from the Jurassic to the Early Cretaceous were assigned to Mesomantispinae. In the Late Cretaceous, 24 species of 11 genera have been described from the Burmese ambers, many of which belong to the Doratomantispinae. In the Cenozoic, most fossil mantid lacewings were assigned to the extant subfamilies and genera.

Mesomantispinae, as the earliest subfamily, have been found in strata from the Middle Jurassic to the Early Cretaceous in China, Russia and Kazakhstan. The raptorial forelegs of this subfamily presented the primitive stage of their evolutionary history, distinguished with elongated and stout forecoxae, stout forefemora with developed spines. But the major long femoral spine, which is commonly present in the extant mantid lacewings, was absent in the Mesomantispinae. The subfamily are also distinct in their forewing venation, i.e., recurrent humeral veinlet present, the basal costal area broad, costal crossveins mostly forked, Sc and R1 fused distally, CuA pectinately forked. In this study, we describe one new genus and new species of Mesomantispinae, *Yatsenia suni* gen. et sp. nov., from the Lower Cretaceous Yixian Formation at Huangbanjigou village, Liaoning Province, China. The new genus and species exhibits distinct forewing venation and wing markings, including Sc and R1 fused near forewing midway, CuP dichotomously forked, 1A pectinately forked, which is distinguished from the previously reported genera of the subfamily. The new finding indicates the morphologic disparity and species diversity of the Cretaceous mantid lacewings.

Eight genera and ten species from the Mesozoic have been described and assigned to Mesomantispinae up to now, including the new genus and species, which represented the first evolutionary radiation of the family. According to the evolutionary rates based on phylogenetic tree, the family was in a phase of rapid changing of integrated morphology, foreleg structure and forewing venation during this geochronological interval. Meanwhile, the lineage number increased quickly, which indicates the synchronous accumulation of morphologic disparity and species diversity in Mantispidae during their early evolution history. This is plausibly relevant to the preceding mass extinction event at the end of the Triassic, which resulted in abundant vacant ecological niches. During the Jurassic, as the terrestrial ecosystem was recovering, it facilitated the rapid evolution of the mantid lacewings. The foreleg morphology of Mesomantispinae were testified as the primary state of their foreleg evolution. Functional morphology analyses revealed that their predatory functionalities were among the average levels of all mantid lacewings. Henceforth, the raptorial forelegs diversified into multiple specialized morphologies with their functional properties strengthened in various ways.

fossil, insect, mantid lacewing, Jehol Biota, Mesozoic

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