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缅甸北部克钦白垩纪中期琥珀中的蜡蝉化石一新属新种: *Ayaimatum trilobatum* gen. et sp. nov. (半翅目: 蜡蝉总科: 拟蛛蜡蝉科)*

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提要 根据缅甸北部克钦地区产出的白垩纪中期琥珀中保存的蜡蝉, 建立了 1 新属 1 新种——三瓣残缺蜡蝉(*Ayaimatum trilobatum* gen. et sp. nov.), 该新属新种属于白垩纪的拟蛛蜡蝉科(Mimarachnidae)。本文对拟蛛蜡蝉科的属种记录进行了综述, 同时探讨了这一灭绝科属种的多样性和形态分异。

关键词 蜡蝉 缅甸琥珀 *Ayaimatum trilobatum* gen. et sp. nov. 分类学 形态学 生物古地理

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1 前言

蜡蝉亚目作为半翅目中最重要的一个类群, 目前已知有 33 个灭绝和现生科。该类群不仅种类繁多、分异度高, 而且有很长的演化历史, 其最早的化石记录可追溯至三叠纪, 且包含三个超科: Coleoscytoidea Martynov, 1935, Surijokocixioidea Shcherbakov, 2000 和 Fulgoroidea Latreille, 1807 (Szwedo, 2018)。蜡蝉通常为小型昆虫, 大部分身长 3—15 mm, 然而一些蜡蝉总科的属种身长可达 10 cm, 翼展可达 14.5 cm。蜡蝉的现生种类超过

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13 000 种，分布广泛，集中于热带和亚热带地区，部分属种科适应荒漠和寒冷苔原环境乃至北极圈，生物地理分布多样化(Bartlett *et al*., 2018)。形态学和分子生物学证据已证实了蜡蝉亚目和现生蜡蝉总科的单系关系，但现生蜡蝉总科中各科属间的关系并未得到清晰的确定(Bourgoin and Campbell, 2002; Urban and Cryan, 2007, 2009; Ceotto and Bourgoin, 2008; Ceotto *et al*., 2008; Urban *et al*., 2010; Cryan and Urban, 2012; Bartlett *et al*., 2014, 2018; Song *et al*., 2016, 2018)。目前，现生蜡蝉中的少数科，如 Achilidae Stål, 1866, Cixiidae Spinola, 1839, Dictyopharidae Spinola, 1839 和 Tropiduchidae Stål, 1866 有化石记录。在已灭绝的蜡蝉科中，白垩纪时期的蜡蝉科主要有 Dorytocidae Emeljanov and Shcherbakov, 2018, Jubisentidae Zhang, Ren and Yao, 2019, Lalacidae Hamilton, 1990, Mimarachnidae Shcherbakov, 2007, Neazoniidae Szwedo, 2007, Perforissidae Shcherbakov, 2007 和 Yetkhatidae Song, Szwedo and Bourgoin, 2019。

目前，Mimarachinidae 科化石仅发现于白垩纪(Szwedo, 2018)，广泛分布于北半球赤道及中高纬度地区，如俄罗斯西伯利亚巴依萨地区贝里阿斯期至巴列姆期(Berriasian–Barremian)地层(*Mimarachne mikhailovi* Shcherbakov, 2007, *Saltissus eskovi* Shcherbakov, 2007，约 125—113 Ma)，日本桑岛地区的早白垩世地层[*Nipponoridium matsuoi* (Fujiyama, 1978), 125—113 Ma]和西班牙东北部山地(*Mimamontsecia cretacea* Szwedo and Ansorge, 2015, *Chalicoridulum montsecensis* Szwedo and Ansorge, 2015, 129.4—125 Ma)等地。此外，蒙古、哈萨克斯坦和西伯利亚中、东部等地也有少数未描述标本(表 1)(Shcherbakov, 2007, 2017; Szwedo, 2008; Szwedo and Ansorge, 2015; Jiang *et al*., 2018; Zhang *et al*., 2018)。

表 1　Mimarachnidae 科已记述化石属种

Table 1　The described fossil genera and species of Mimarachnidae.

种名 (Species)	产地 (Locality)	时代 (Age)	层位 (Horizon)	参考文献 (Reference)
Mimarachne mikhailovi Shcherbakov, 2007	Baissa, Buryatia, Russian Federation	Berriasian–Barremian, ca. 145–125 Ma	Zaza Formation	Shcherbakov, 2007
Saltissus eskovi Shcherbakov, 2007	Baissa, Buryatia, Russian Federation	Berriasian–Barremian, ca. 145–125 Ma	Zaza Formation	Shcherbakov, 2007
Nipponoridium matusuoi (Fujiyama, 1978)	Kaseki-kabe, Japan	Aptian, 125–113 Ma	Kuwajima Formation	Fujiyama, 1978; Szwedo, 2008
Mimamontsecia cretacea Szwedo and Ansorge, 2015	La Cabrua outcrop, Sierra del Montsec, Spain	Barremian, 129.4–125 Ma	La Pedrera de Rubies Formation	Szwedo and Ansorge, 2015
Chalicoridulum montsecensis Szwedo and Ansorge, 2015	La Cabrua outcrop, Sierra del Montsec, Spain	Barremian, 129.4–125 Ma	La Pedrera de Rubies Formation	Szwedo and Ansorge, 2015
Burmissus raunoi Shcherbakov, 2017	Hukawng Valley, Kachin State, Myanmar	early Cenomanian, 98.8 Ma	burmite	Shcherbakov, 2017
Dachibangus trimaculatus Jiang, Szwedo and Wang B., 2018	Noije Bum, Hukawng Valley, Kachin State, Myanmar	early Cenomanian, 98.8 Ma	burmite	Jiang *et al*., 2018
Jaculistilus oligotrichus Zhang, Ren and Yao, 2018	Noije Bum, Hukawng Valley, Kachin State, Myanmar	early Cenomanian, 98.8 Ma	burmite	Zhang *et al*., 2018
Dachibangus formosus Fu, Szwedo, Azar and Huang, 2019	Noije Bum, Hukawng Valley, Kachin State, Myanmar	early Cenomanian 98.8 Ma	burmite	Fu *et al*., 2019
Mimaplax ekrypsan Jiang, Szwedo and Wang B., 2019	Noije Bum, Hukawng Valley, Kachin State, Myanmar	early Cenomanian, 98.8 Ma	burmite	Jiang *et al*., 2019
Ayaimatum trilobatum gen. et sp. nov.	Noije Bum, Hukawng Valley, Kachin State, Myanmar	early Cenomanian, 98.8 Ma	burmite	this work

Mimarachnidae 科的主要特征为具有简化的翅脉结构及纵脉间发育不规则网状小横脉，前胸背板和中胸背板均发育一对中脊线，后足胫节处端刺具刚毛，且成虫保存有若虫时期感觉窝残留构造等(Shcherbakov, 2007, 2017)。其中，个别属种具有特殊构造，如个体较大，头部伸长，或者是长于腹部的口器等(Shcherbakov, 2007, 2017; Jiang *et al*., 2018; Zhang *et al*., 2018)。

2 材料和方法

研究材料来源于缅甸胡康河谷白垩纪琥珀矿区(北纬 26°21'33.41", 东经 96°43'11.88")(Kania *et al*., 2015, fig. 1; Thu and Zaw, 2017)。缅甸琥珀的开采已有几百年的历史，而该地区也是缅甸最主要的琥珀矿藏地区(Helm, 1892, 1893; Noetling, 1892; Laufer, 1907; So, 2013)。缅甸琥珀也是白垩纪琥珀中内含物最为丰富的琥珀，保存了大量的植物、无脊椎和脊椎动物化石，为研究白垩纪中期现代动物区系的发展形成提供了重要的依据(Szwedo and Nel, 2015; Ross, 2019)。放射性测年结果显示缅甸琥珀的沉积年龄约为 98.8 ± 0.62 Ma (Shi *et al*., 2012)，也有学者根据琥珀中再沉积的证据认为琥珀的形成年龄还要更早一些(Ross *et al*., 2010; Rasnitsyn *et al*., 2016; Grimaldi and Ross, 2017; Smith and Ross, 2018; Zheng *et al*., 2018)。

缅甸琥珀的化学组成和内含物显示其植物来源可能为龙脑香科、南洋杉科或柏科植物(Poinar *et al*., 2007; Ross *et al*., 2010; Grimaldi and Ross, 2017)。琥珀产区位于西缅陆块，其与当时位于热带地区的滇缅陆块于 80 Ma 左右相撞(Heine and Müller, 2005; Seton *et al*., 2012; Metcalfe, 2013; Broly *et al*., 2015)。孢粉化石的研究表明白垩纪时期琥珀沉积地区为温暖湿润气候和热带植物群落覆盖地区(Cruickshank and Ko, 2003)。

琥珀产出的沉积地层主要为碎屑沉积，含薄层灰岩和大量的煤炭层。海相化石如菊石、腹足类和双壳类化石以及微体化石包括沟鞭藻等的记录显示琥珀产出层位的沉积环境为近岸滨海环境，与三角洲邻近，并因此推测琥珀产区当时可能位于海岛或列岛环境中(Xing *et al*., 2018a, 2018b; Jiang *et al*., 2018; Rasnitsyn and Öhm-Kühnle, 2018; Yu *et al*., 2019)。

样品的观察和拍摄工作在中国科学院南京地质与古生物研究所进行，其中样品的观察使用尼康 SMZ1000 和蔡司 AxioZoomV.16 体视显微镜。线条图的绘制使用尼康 SMZ1000 体视显微镜及配置的绘图臂，照片的拍摄使用蔡司 AxioZoomV.16 体视显微镜及配置的 Axiocam 512 图像采集系统，并使用 HeliconFocus 6.7.1 图像软件将图像进行叠加以获得立体图像。另外，使用紫外线 UV 灯(395 nm)用于观察和拍摄琥珀标本内部的裂纹和流纹。

标本(标本号: JSSNU 2019005)目前保存于江苏第二师范学院。

形态学术语主要参考 Kramer (1950) 与 Anufriev 和 Emeljanov (1988)。翅脉结构参考半翅目翅脉基本划分方案(Nel *et al*., 2012; Bourgoin *et al*., 2015)。中文术语的使用参考彩万志等(2011)和周尧等(1985)。翅脉缩写如下: A_1. 第二臀脉; A_2. 第二臀脉支脉; CuA. 前肘脉; CuP. 后肘脉; MP. 后中脉; Pcu. 第一臀脉; R. 径脉; RA. 前径脉; RP. 后径脉; ScP. 亚前缘脉; *cua-cup*. 中肘横脉; C1. 径室; C3. 中室; C5. 肘室。

3 系统古生物学

昆虫纲 Class Insecta Linnaeus, 1758

半翅目 Order Hemiptera Linnaeus, 1758

蜡蝉亚目 Suborder Fulgoroidea Evans, 1946

蜡蝉总科 Superfamily Fulgoroidea Latreille, 1807

拟蛛蜡蝉科 Family Mimarachnidae Shcherbakov, 2007

残缺蜡蝉属(新属) Genus *Ayaimatum* gen. nov. Jiang and Szwedo

urn:lsid:zoobank.org:act:EB31B47F-65EC-4057-A02B-BB96FD7007D3

模式种 *Ayaimatum trilobatum* gen. et sp. nov.

词源 属名源于缅甸北部克钦语(Jingpho),

"ayai mat"意为"残缺的"，参考模式标本的保存状况。

比较讨论 新属的翅脉结构与 Mimarachnidae 科的另一属 *Burmissus* Shcherbakov, 2017 较为相似，但是新属的头顶形状与其有明显的差别，复眼的前缘低于头顶高度中线位置(在 *Burmissus* 属中，复眼前缘明显超过了头顶高度中线)；头顶前端未见中侧脊三角区(trigon)(在 *Burmissus* 属中可见)；中胸背板明显凸起，中脊凸起(*Burmissus* 属的中胸背板较平)；中胸小盾片扁平(*Burmissus* 属中胸盾片凸起)；ScP+R+MP+(CuA)脉主干在 MP 脉从其分离前的部分与 ScP+R 脉等长[*Burmissus* 属中 ScP+R+MP+(CuA) 脉主干明显短于 ScP+R 脉]；CuA 脉分支点位于 Pcu 脉和 A_1 脉的交汇点基侧(*Burmissus* 属 CuA 脉分支点位于交汇点端侧)。

属征 头部加复眼的宽度是前胸背板的一半。头顶的长度是宽度的 0.7 倍。头顶前缘呈三角状，侧缘弯曲状，后边缘向内凹；前部和侧部边缘都呈凸起状。头顶明显呈凹陷状；没有中脊线；头顶前部呈五角形，后部加宽，两侧外扩至复眼边缘。头顶前端未见 trigon。侧视可见头顶和额之间的夹角约 30º。额长度为宽度的 1.6 倍，最宽处位于触角基部，可见中脊线，中脊线在单眼前侧消失，侧边缘呈脊状。额中下部可见单眼。额唇基缝呈弓形。后唇基凸起，可见中脊和侧缘脊，侧缘脊向前唇基处汇聚，前唇基具不明显的中脊，其基部插入后唇基的端部。

复眼鼓起，其下可见单眼。触角窝凸起，柄节近圆柱形，长宽比 2∶1，梗节近圆椎形，端部较宽，可见少许斑状感觉器，鞭节基部为球状，鞭节为刚毛状，长度与复眼长度相近。

前胸背板近六角形，宽度是长度的 3.8 倍左右；前缘外凸，在一对复眼间区域微向外伸出；侧前缘脊状，向后外扩；侧后缘平直，后缘呈拱形向内凹。前胸背板中骨片微突起，可见两条明显突起的中脊，中脊伸达前缘和后缘且后方向外扩；骨片侧部分界不明显；前胸背板两侧向下倾斜，与眼后区分界不明显，侧边缘呈尖脊状，侧背板强烈弯曲至近水平。

中胸背板呈菱形，宽度大于长度，向上突起；可见两条突起的中脊，中脊后端向外扩，发育两条侧脊，侧脊后端向外扩且伸达中胸背板的后缘；中胸背板侧部向下倾。中胸小盾片扁平，与中胸背板通过下陷分隔。后胸背板呈矩形。

翅基片较大，中线脊状。

前翅膜质，长度为宽度的 3.3 倍。前缘基部呈弓型弯曲，后呈平直状，顶角和肛角浑圆，缝缘平直。在翅基部，ScP+R+MP+(CuA)脉主干平直，等长于 ScP+R 脉主干。ScP+R 脉主干在 1/4 翅长处分支；ScP+RA 脉不分支，略弯曲状，与前缘近平行，与翅边缘相交于顶角处；RP 脉不分支，与 ScP+RA 脉近平行，与翅边缘的交点比 ScP+RA 脉末端更靠近翅端。MP 脉从 ScP+R+MP+(CuA)脉主干分离的部位在 *cua-cup* 脉基侧，MP 脉在基部平直，其后略弯曲，分支点与 Pcu+A_1 脉和缝缘的交点处于同一垂直位置，终止于翅端缘。CuA 脉基部被 *cua-cup* 脉截断，靠近基部近平直，在 Pcu 和 A_1 脉汇合点基侧分叉，支脉 CuA_1 基部与 MP 脉近平行，后呈弯曲状，与翅边缘交汇于肛角处，支脉 CuA_2 基部弯曲且靠近爪缝和 CuP 脉，后稍远离爪缝且呈弯曲状。爪缝和 CuP 脉近翅基部分平直，近翅端部分弯曲，与翅缘相交于约 3/4 翅长处。Pcu 脉和 A_1 脉交汇于 1/2 翅长处，Pcu+A_1 脉端部强烈弯曲，与缝缘相交于约 0.7 翅长处。基室未完全发育，在 CuA 脉基部没有发育闭合脉而由 *cua-cup* 取代。前缘室(costal cell)较宽，为 C1(径室)宽度的两倍，C3(中室)长度超过了 C5(肘室)长度的一半。纵脉间可见由无序的小横脉构成的多边形网状脉络。

后翅膜质，前缘基部强烈弯曲，后转平直，稍弯曲于顶角处，外缘弓形弯曲，轭缘平直。ScP+R+MP+CuA 脉主干很短，ScP+R 脉主干平直，与前缘平行且与之非常靠近，分为 ScP+RA 脉和 RP 脉，后两者不分支。MP 脉主干近翅基部分出，不分支。CuA 脉主干起始点早于 MP 脉，平直，分支点早于 ScP+R 脉分支点。CuP 脉主干弯曲，CuP 脉与 CuA_2 脉末端之间的距离小于 CuA 支脉末端之间的距离。A_1 脉弯曲状，A_2 脉在臀区长度 1/2 处

分为两支，三者端部未保存，但是推测均延伸至翅缘；A_{2a} 脉弯曲且平行于 A_1 脉，A_{2b} 脉平行于翅缘。纵脉间可见无序的小横脉构成的多边形网状脉络，这些脉络在臀区加厚。

三瓣残缺蜡蝉(新属新种) *Ayaimatum trilobatum* gen. et sp. nov. Jiang and Szwedo

urn:lsid:zoobank.org:act:84E593AC-FD2A-41EA-89B0-8BCC5AE93F61

(图 1—4)

词源 种名意为“三瓣式的”，参考头顶的形态特征。

材料 正模，标本号：JSSNU-2019005，蜡蝉的腹部和足部均缺失，保存部分为头部、前翅、后翅。标本保存于江苏第二师范学院。

特征 新种为该新属目前发现的唯一种，部分特征见属征。额部表面多疣状，头顶侧后缘突起至与复眼齐平。前胸背板和中胸背板布满了残留的感觉陷。前翅长度为宽度的 3.3 倍，C1 室长为 C3 室的两倍。后翅 CuA 脉两分支端点的距离比 CuP 脉和 CuA_2 脉端点间的距离宽。

描述 虫体保存部分长 20.32 mm，宽 11.26 mm。头部加复眼宽度为 2.95 mm。头顶长 1.26 mm，最宽处 2.15 mm，后缘处宽约 1.84 mm。额长 2.16 mm，最宽处位于触角部位，宽约 1.43 mm。后唇基长 1.89 mm，额唇基缝处宽 1.39 mm。前唇基长 1.53 mm。前胸背板长 1.47 mm，宽 5.68 mm。中胸背板长 3.47 mm，宽 5.16 mm。翅基片宽 1.26 mm，长 0.79 mm。前翅长 15.4 mm，宽 4.68 mm。前缘室宽 1.05 mm; C1 室长 10.05 mm，宽 0.53 mm; C3 室长 4.95 mm，宽 1.03 mm；C5 室长 7.53 mm，宽 1.05 mm。后翅长 12.95 mm，宽 5.42 mm; C1 室长 3.79 mm, C5 室长 3.47 mm。

产地层位 缅甸北部克钦胡康河谷 Noije Bum 山; Cenomanian 阶。

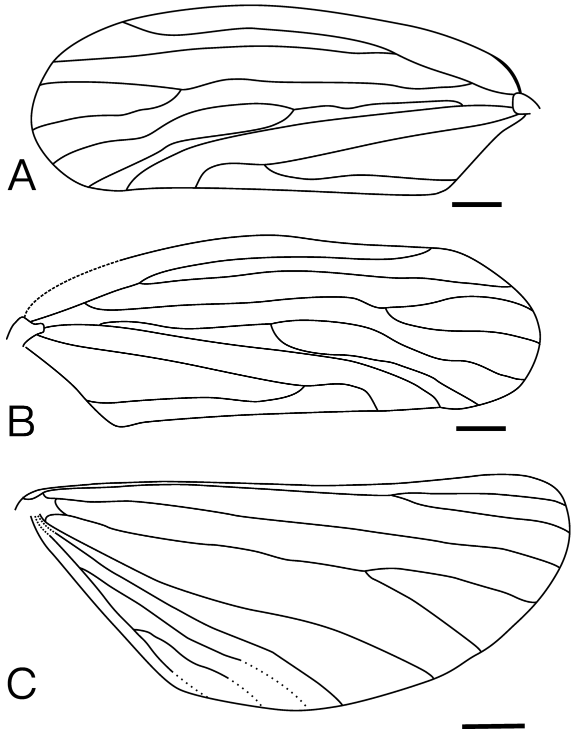

图 1 三瓣残缺蜡蝉(新属新种)正模标本线条图

Fig. 1 Line drawing of the holotype of *Ayaimatum trilobatum* gen. et sp. nov.

A. 左前翅脉序; B. 右前翅脉序; C. 右后翅脉序。比例尺: 1 mm。

A. venation pattern of left tegmen; B. venation pattern of right tegmen; C. venation pattern of right hind wing. Scale bars = 1 mm.

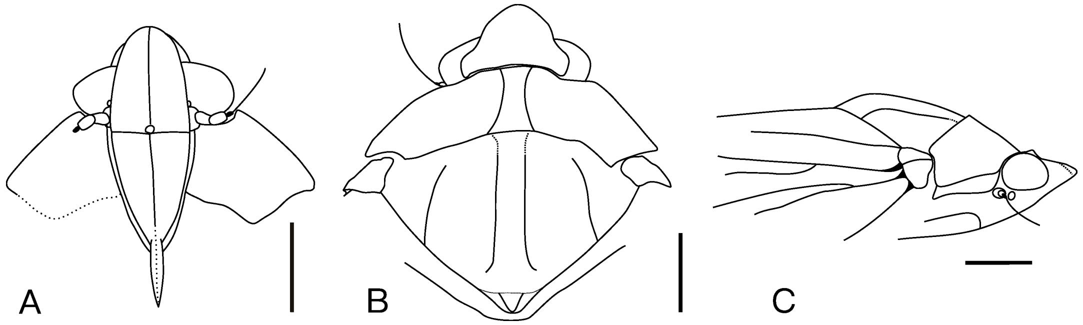

图 2 三瓣残缺蜡蝉(新属新种)正模标本线条图

Fig. 2 Line drawing of the holotype of *Ayaimatum trilobatum* gen. et sp. nov.

A. 头部腹视; B. 头部，前胸背板和中胸背板背视; C. 标本侧视。比例尺: 1 mm。

A. head and pronotum in ventral view; B. head capsule, pronotum and mesonotum in dorsal view; C. inclusion in lateral view. Scale bars = 1 mm.

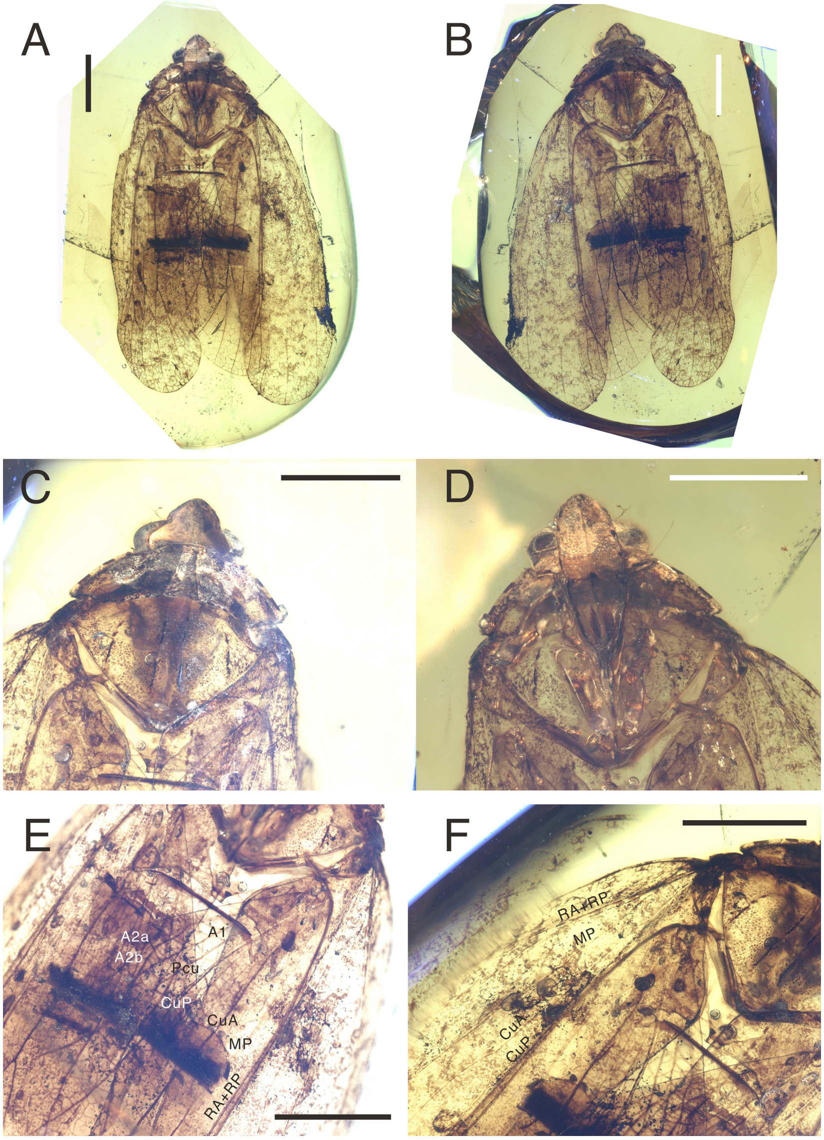

图 3　三瓣残缺蜡蝉(新属新种)正模标本光学图像。缩写含义见正文。

Fig. 3　Photographs of *Ayaimatum trilobatum* gen. et sp. nov., holotype. Abbreviations are explained in the text.

A. 标本腹视; B. 标本背视; C. 头部、前胸背板和中胸背板背视; D. 头部腹视; E. 后翅部分，腹视; F. 左前翅部分，背视。比例尺: 2 mm。

A. ventral view of the preserved body; B. dorsal view of the preserved body; C. dorsal view of head capsule, pronotum and mesonotum; D. ventral view of the face; E. part of hind wing in ventral view; F. part of left tegmen in dorsal view. Scale bars = 2 mm.

4　讨　论

此次研究的新属新种为 Mimarachnidae 科的第 6 个来自缅甸琥珀的新种，使我们对 Mimarachnidae 科化石的属种多样性和形态学特征有了进一步的认识。Mimarachnidae 科最早的化石记录是西班牙巴列姆期(Barremian)地层发现的 *Mimamontsecia* Szwedo and Ansorge, 2015 属和 *Chalicoridulum* Szwedo and Ansorge, 2015 属，其中本文新属与 *Mimamontsecia* 属在大小上较为接近，但是二者翅脉结构不同。在俄罗斯巴依萨地区阿普第期(Aptian)地层中产出的 *Mimarachne* Shcherbakov, 2007 属和 *Saltissus* Shcherbakov, 2007 属，与新属在大小、翅脉颜色和结构上都存在区别(Shcherbakov, 2007)。*Nipponoridium* Szwedo, 2008 属产出于日本桑岛阿普第期地层，该属只保存了后翅的一部分，与新属的后翅差别主要是其 CuA

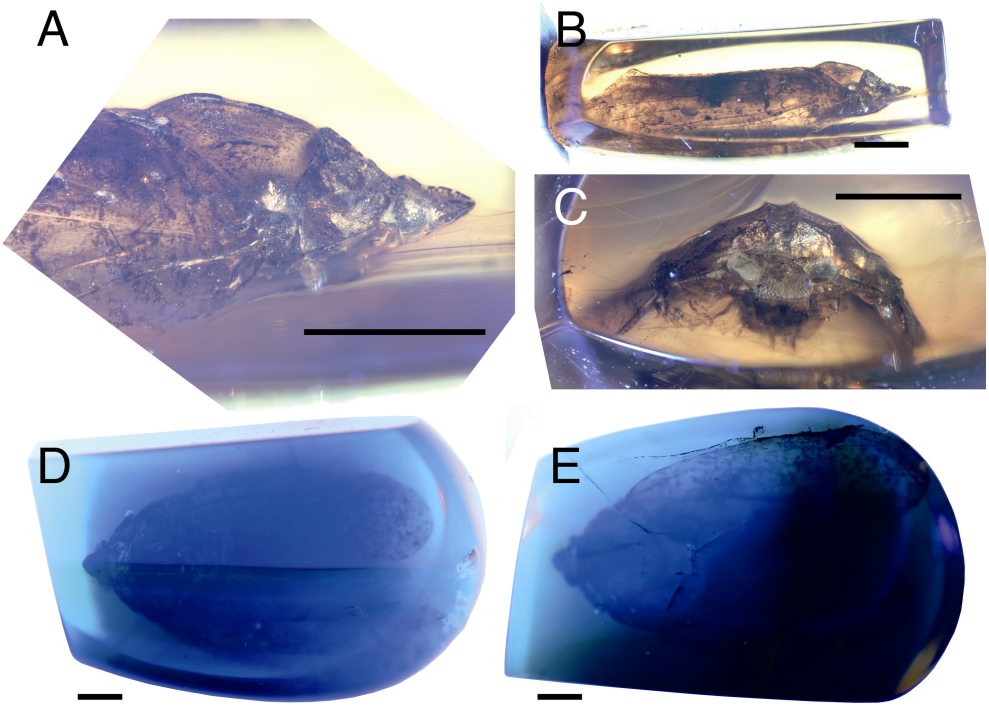

图4 三瓣残缺蜡蝉(新属新种)正模标本光学图像

Fig. 4 Photographs of *Ayaimatum trilobatum* gen. et sp. nov., holotype.

A. 头部、前胸背板、中胸背板和右前翅侧视; B. 标本侧视; C. 标本前视; D. 紫外线灯(395 nm)下标本背视; E. 紫外线灯(395 nm)下标本腹视。比例尺: 2 mm。

A. lateral view of head, pronotum, mesonotum and right tegmen; B. lateral view of the preserved portion of the body; C. front view of the inclusion; D. dorsal view of inclusion in the amber piece under UV light (395 nm); E. ventral view of inclusion in the amber piece under UV light (395 nm). Scale bars = 2 mm.

脉有三个分支。其他 Mimarachnidae 科的属则均来自缅甸琥珀, 包括 *Burmissus* Shcherbakov, 2017, *Dachibangus* Jiang, Szwedo and Wang, 2018, *Jaculistilus* Zhang, Ren and Yao, 2018 和 *Mimaplax* Jiang, Szwedo and Wang, 2019。新属在个体大小, 翅脉结构及个体形态等多个方面都与上述 4 属存在明显区别。其中, 新属与 *Burmissus* Shcherbakov, 2017 存在一定相似性, 但是在前翅 ScP+R 脉的长度和 CuA 脉的分支位置, 以及头顶前缘结构等重要特征上二者存在明显区别。此外, 新属的后翅 CuA 脉分支脉间的距离和 Pcu 脉和 CuP 脉间的距离明显宽于 CuA_2 脉和 CuP 脉之间的距离, *Burmissus* 属中上述距离则较接近(Shcherbakov, 2017)。新属向上高高突起的前胸背板和中胸背板以及突出的脊线也与 Mimarachnidae 科其他属区别明显。

缅甸琥珀中保存的 Mimarachnidae 科属种分化明显, 其属种和形态的多样性很可能也代表了不同的生态策略。新属在形态特征上以扁平的头部和凸起的中胸为特征, 与其他半翅目类群存在一定相似性, 如叶蝉 Cicadellidae Latreille, 1825 科的 Ledrinae Fairmaire, 1855 和 Tartessinae Distant, 1908 亚科中的一些代表属种。在缅甸琥珀中也发现了这些 Ledrinae 亚科的属种(Chen *et al.*, 2019), 这一属种在巴西的阿普第期地层中也有发现(Hamilton, 1990), 现生的 Ledrinae 亚科的属种主要栖息于双子叶树木和灌木中(Jones, 2009)。为适应在树干栖息而进化的扁平化形态特征目前已有报道出现在 *Mimaplax* 属中, 而本文中的新属也呈现一定的伪装形态(Szwedo and Stroiński, 2017; Jiang *et al.*, 2019)。Shcherbakov (2017) 认为, *Burmissus* 属较为细长的喙表明该属栖息于树干上并穿透厚而粗糙的树皮进食。在现生的 *Stomaphis* 属蚜虫中, 同样也有栖息于落叶乔木树干的现象, 其上颚和下颚刺必须深深插入树皮中进食(Brożek *et al.*, 2015)。Depa 等(2014)观察认为, 这种蚜虫需要花费数分钟的时间才能将下唇和刺从树皮中收

回。因此对于它们来说迅速地逃离捕食者的抓捕是不太可能的。在本文的新属标本中，喙并没有保存下来，但是从其他 Mimarachnidae 科属种的形态结构推测，新属应该也具有伸长的喙部结构，因此也可能更趋向于定栖。新属前翅不均匀的深色斑点也很可能与逃避捕食有关，有利于隐藏在树干和粗枝上。这为我们研究 Mimarachnidae 科属种的多样性和形态特异性提供了新的证据，也为重建缅甸琥珀生物群所处的古环境和古气候提供了一定的证据。

致谢　评审专家提出宝贵修改意见，特此致谢。

AYAIMATUM TRILOBATUM GEN. ET SP. NOV. OF MIMARACHNIDAE (HEMIPTERA: FULGOROMORPHA) FROM MID-CRETACEOUS AMBER OF KACHIN (NORTHERN MYANMAR)

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Abstract　A new genus and species, *Ayaimatum trilobatum* gen. et sp. nov. Jiang and Szwedo, is described based on a planthopper preserved in mid-Cretaceous amber from Kachin State, northern Myanmar, and assigned to the Cretaceous planthopper family Mimarachnidae. A short overview of fossil record of the Mimarachnidae is given. The taxonomic diversity and morphological disparity of this extinct group is briefly discussed.

Key words　Planthopper, Burmese amber, *Ayaimatum trilobatum* gen. et sp. nov., taxonomy, morphology, palaeobiogeography

1　INTRODUCTION

Fulgoromorpha (planthoppers) is a suborder of the Hemiptera, constituting a large group of phytophagous insects known in the fossil record since the Permian. It covers three superfamilies: two extinct superfamilies—Permian Coleoscytoidea Martynov, 1935, Permian and Triassic Surijokocixioidea Shcherbakov, 2000, and Fulgoroidea Latreille, 1807, known in the fossil record since the Jurassic (Szwedo, 2018). Planthoppers are generally small insects, in vast majority varying in size from 3 mm to 15 mm, nevertheless, some species of the family Fulgoridae have a body length of about 10 cm and a wingspread of about 14.5 cm. The recent families comprise some 13 000 species, distributed worldwide, but mainly in the tropical and subtropical zones, with some species adapted to the deserts and dry areas or cold tundra environments even north of the Arctic Circle. Interactions with their host plants play a major role in distributional and ecological patterns of planthoppers. Therefore, biogeographical diversity is unequal for all the families, with some restricted to a few zoogeographical regions (Bartlett *et al*., 2018). Monophylies of the Fulgoromorpha and recent Fulgoroidea are attested by morphological and by molecular evidence as well (Bourgoin and Campbell, 2002; Urban and Cryan, 2007; Bartlett *et al*., 2014, 2018). Family relationships of recent Fulgoroidea are not fully resolved, neither by morphological nor by molecular evidences. It must be mentioned that only a few families have been shown to be monophyletic (Urban and Cryan, 2007, 2009; Ceotto and Bourgoin, 2008;

Ceotto *et al*., 2008; Urban *et al*., 2010; Cryan and Urban, 2012; Song *et al*., 2016, 2018) and very probably all these hypotheses should be modified in the future. The inference of fossil families on the shape of the phylogenetic tree of Fulgoroidea is still a subject of discussions. Among the recent families, Achilidae Stål, 1866, Cixiidae Spinola, 1839 and Dictyopharidae Spinola, 1839 enter the fossil record, and probably also Tropiduchidae Stål, 1866. The following extinct planthoppers families are known to be present in the Cretaceous Period including Dorytocidae Emeljanov and Shcherbakov, 2018, Jubisentidae Zhang, Ren and Yao, 2019, Lalacidae Hamilton, 1990, Mimarachnidae Shcherbakov, 2007, Neazoniidae Szwedo, 2007, Perforissidae Shcherbakov, 2007, and Yetkhatidae Song, Szwedo and Bourgoin, 2019.

Mimarachnidae is a family of planthoppers (Hemiptera: Fulgoromorpha: Fulgoroidea) known exclusively from the fossil record of the Cretaceous (Szwedo, 2018). The family was widespread from the equatorial to high latitude regions in the northern hemisphere in the Cretaceous Period. The known fossil sites bearing Mimarachnidae are: Aptian deposits in Baissa (Buriatiya, Russia), Aptian Kaseki-kabe locality in Kuwajima (Shiramine-mura, Japan), Barremian deposits from Sierra del Montsec (north-eastern Spain), Cenomanian Burmese amber and some undescribed specimens known from localities like Turga (Aptian, central Siberia), Bon Tsagaan (Aptian, Mongolia) or Khetana (Turonian, East Siberia), Kzyl-Zhar Hill (Turonian, Kazakhstan) (Table 1; Shcherbakov, 2007, 2017; Szwedo, 2008; Szwedo and Ansorge, 2015; Jiang *et al*., 2018; Zhang *et al*., 2018).

Mimarachnidae is characteristic of simplified venation pattern with meshwork of irregular veinlets on both wings, double carination in median line of pronotum and mesonotum, setigerous metatibial pecten and hind leg armature, and retention of nymphal sensory pits in adults (Shcherbakov, 2007, 2017). Some taxa possess peculiar morphological characters like giant size, elongated head, and a rostrum that exceeds the length of the body (Shcherbakov, 2007, 2017; Jiang *et al*., 2018; Zhang *et al*., 2018).

Here we present another representative of this family from the mid-Cretaceous burmite, representing a new genus and species.

2 MATERIAL AND METHODS

The studied specimen is a piece of amber from the Cretaceous deposits in the Hukawng Valley of Myanmar. The mining area is located at Noije Bum, near Bum, close to Tanai Village (26°21'33.41"N, 96°43'11.88" E; palaeocoordinates 12.4° N, 93.8° E) (Kania *et al*., 2015, fig. 1; Thu and Zaw, 2017), which is the main source of amber in the country. This fossil resin is frequently referred as Burmese amber or burmite (Helm, 1892, 1893; Noetling, 1892) and has been mined for centuries (Laufer, 1907; So, 2013). It is the most productive source of Cretaceous amber inclusions, preserving enormous diversity of plants, invertebrates and vertebrates (Ross, 2019), giving new insights into the very important period of formation of modern faunistic complexes at mid-Cretaceous biotic re-organisation times (Szwedo and Nel, 2015). Radiometric dating performed with zircons in the matrix associated with amber has provided an estimated age of the deposit at 98.8 ± 0.62 Ma (Shi *et al*., 2012). A slightly older age was then postulated (Albian by Ross *et al*., 2010, late Albian by Zheng *et al*., 2018; Albian-Cenomanian boundary by Rasnitsyn *et al*., 2016), due to the fact that the amber shows evidence of redeposition (Grimaldi and Ross, 2017; Smith and Ross, 2018).

The botanical affiliation of this resin remains unclear. The chemical composition and botanical inclusions found in this amber suggest that the potential botanical source of the resin is among the Araucariaceae (Poinar *et al*., 2007) or the Dipterocarpaceae (Ross *et al*., 2010), but Cupressaceae gymnosperms, very likely *Metasequoia* or related taxa, were also suggested as the trees exuding the resin at time of burmite formation (Grimaldi and Ross, 2017).

The amber locality lies within the West Burma terrane (Broly *et al*., 2015), which finally collided with the Eurasian marginal Sibumasu terrane at around 80 Ma (Heine and Müller, 2005; Seton *et al*., 2012). The Sibumasu terrane, which might be the nearest land mass of the burmite deposit locality, was placed in the climatic tropical zone (Metcalfe, 2013). Palynological study suggested a humid warm temperate climate (Cruickshank and Ko, 2003), indicating placement of the amber origination area in the equatorial floristic realm of the Cretaceous.

Sediments where amber is found are variety of clastic sedimentary rocks, with thin limestone beds and abundant coaly and carbonaceous material. Amber is found within a narrow horizon in the fine clastic facies. The records of macrofossils like ammonites, gastropods and bivalve and the microfauna including dinoflagellates, suggest that the depositional environment for amber was a nearshore marine setting, close to deltas (Xing *et al*., 2018a; Yu *et al*., 2019). This suggests that at least part of the amberiferous area was an island or archipelago environment at time of resin formation and deposition (Jiang *et al*., 2018; Rasnitsyn and Öhm-Kühnle, 2018; Xing *et al*., 2018b).

Observations were performed using stereomicroscopes Nikon SMZ1000 and Zeiss AxioZoomV.16 in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. Drawings were prepared with use of camera lucida attached to Nikon SMZ1000, microphotographs were taken with a digital camera Axiocam 512 color attached to Zeiss AxioZoomV.16 stereoscopic microscope under control of Zen software package. Photomicrographic composites of more than 50 individual focal planes were digitally stacked and obtained using the software HeliconFocus 6.7.1 for a better illustration of 3D structures. Because of the amber thickness, some of the samples were placed in a sugary liquid to improve their light transmission and remove optical distortions. Flow lines and internal cracks within the amber were observed in greater detail using UV light (395 nm). Photographs and drawings were adjusted and composed into plates using CorelDraw X8 and CorelPhoto-Paint X8 packages.

The specimen (No. JSSNU 2019005) is housed in the Zoological collection, Jiangsu Second Normal University, Nanjing, China.

The morphological nomenclature is adopted according to Kramer (1950) and Anufriev and Emeljanov (1988). The wing venation used in this paper is based on the general scheme for the Hemiptera (Nel *et al*., 2012; Bourgoin *et al*., 2015). Chinese terms used in morphology and wing venation descriptions refer to works of Zhou *et al*. (1985) and Cai *et al*. (2011). Abbreviations: A_1. second anal vein; A_2. branch of A_1; CuA. cubitus anterior; CuP. cubitus posterior; MP. media posterior; Pcu. first anal vein; R. radius; RA. radius anterior; RP. radius posterior; ScP. subcosta posterior; *cua*-*cup*. transverse veinlet connecting media posterior and cubitus anterior; C1. area delimited by forking of RA and RP; C3. area between first fork of stem MP; C5. area delimited by the first fork of stem CuA.

3 SYSTEMATIC PALAEONTOLOGY

Class Insecta Linnaeus, 1758
Order Hemiptera Linnaeus, 1758
Suborder Fulgoromorpha Evans, 1946
Superfamily Fulgoroidea Latreille, 1807
Family Mimarachnidae Shcherbakov, 2007
Genus *Ayaimatum* gen. nov. Jiang and Szwedo
urn:lsid:zoobank.org:act:EB31B47F-65EC-4057-A02B-BB96FD7007D3

Type species *Ayaimatum trilobatum* gen. et sp. nov. Jiang and Szwedo; by present designation and monotypy.

Etymology Generic name is derived from Jingpho language spoken in northern Myanmar—“ayai mat”—meaning “to be broken”, and refers to the preservation of the inclusion. Gender: neuter.

Diagnosis Differs from *Burmissus* Shcherbakov, 2017 by shape of vertex, with anterior margin of compound eyes not exceeding half of head length (anterior margin of compound eyes distinctly exceeding half of head length on the middle in *Burmissus*); head with trigons not visible from above (trigons visible from above in *Burmissus*); distinctly convex mesonotum with strongly elevated median carinae (mesonotum less convex in *Burmissus*); mesoscutellum flat (mesoscutellum raised in *Burmissus*); section of common stem ScP+R+MP+(CuA) before separation of MP about as long as stem

ScP+R (common stem ScP+R+MP+(CuA) distinctly shorter than stem ScP+R in *Burmissus*); stem CuA forked basad of claval veins Pcu and A_1 junction (stem CuA forked apicad of claval veins junction in *Burmissus*).

Description Head with compound eyes about as wide as half of pronotum width. Vertex about 0.7 long as its maximum width. Anterior margin of vertex triangular, lateral margins sinuous, distinctly diverging posteriad, posterior margin concave; anterior and lateral margins of vertex elevated. Disc of vertex distinctly concave; no median carina on disc; anterior portion of vertex pentagonal, posterior portion widened, forming two lateral expanded areas extending on compound eyes. Trigons not visible in dorsal view. In lateral view, angle between vertex and frons about 30°. Frons about 1.6 times as long in mid line as wide, widest at level of antennae, median carina present, faint before reaching median ocellus, lateral margins carinate. Median ocellus present. Frontoclypeal suture slightly arcuate. Postclypeus convex, with median and lateral carinae, lateral carinae converging to anteclypeus, anteclypeus with faint median carina, base of anteclypeus slightly incised in lower part of postclypeus.

Compound eyes bulging, subocular expansions present. Lateral ocelli present, a little below compound eyes, closer to base of antenna than to anterior margin of head capsule. Antennal fovea elevated, scapus subcylindrical, about twice as long as wide, pedicel subconical, widened apicad, covered with a few sensory plaque organs, base of flagellum bulbous, flagellum bristle-like, about as long as compound eye.

Pronotum subhexagonal, arched anteriorly, about 3.8 times as wide as long in mid line, anterior margin convex, slightly protruding between compound eyes, anterolateral margins carinate, diverging posteriad, posterolateral margins straight, posterior margin distinctly arcuate, concave. Disc of pronotum slightly elevated, with two distinct, elevated, diverging posteriad median carinae, reaching anterior and posterior margins; disc weakly delimited laterally, sides of pronotum declivous, postocular field weakly delimited, lateral margin sharply carinate, paranota strongly bent, subhorizontal.

Mesonotum transversely diamond-shaped, wider than long in middle, disc of vertex convex, with two strongly elevated median carinae, slightly diverging posteriad and two lateral carinae, diverging posteriad, reaching posterior margin of mesonotum, lateral portions sloping downwards. Mesoscutellum flat, separated from mesoscutum by depression. Metascutellum rectangular.

Tegulae large, subquadrate, with median carnation.

Tegmen membranous, about 3.3 times as long as wide. Costal margin widely arcuately curved at base, then straight, anteroapical angle widely rounded, apex rounded, posteroapical angle rounded, tornus short, slightly arcuate, claval margin straight. Veins of costal complex fused from base; stem ScP+R+MP+(CuA) straight, about as long as common stem ScP+R. Stem ScP+R forked at basal ¼ of tegmen length, branch ScP+RA single, slightly arcuate, subparallel to costal margin, reaching margin at anterorapical angle, branch RP single, nearly parallel to ScP+RA reaching margin more apically than branch ScP+RA. Stem MP separating from common stem ScP+R+MP+(CuA) more basal than *cua-cup* connection, straight at base then slightly curved, forked at level of claval veins Pcu+A_1 connection to claval margin, terminals reaching margin at apex. Stem CuA with base completely intercepted by basal *cua-cup* veinlet, straight from base, forked basad of claval veins Pcu and A_1 junction, branch CuA_1 basally subparallel to distal section of stem MP, then more wavily curved, reaching margin at level of posteroapical angle, branch CuA_2 curved at base, close to claval suture and CuP, then slightly diverging from claval suture, sinuate, reaching margin at level of tornus. Claval suture and CuP straight at proximal section, more arcuate in distal section, reaching margin at apical ¾ of tegmen length. Claval veins Pcu and A_1 fused at about half of tegmen length, their common portion strongly arcuate distally, reaching claval margin at about 0.7 of tegmen length. Basal cell not developed-basal section of CuA closing basal cell reduced, intercepted by basal veinlet *cua-cup*. Costal cell wide, more than twice as wide as cell C1. Cell C3 longer than half of cell C5. Areas between longitudinal cells filled with meshwork of veinlets, forming irregular polygonal cells.

Hind wing membranous, costal margin strongly curved at base, then straight to level of nodus, then weakly curved to anteroapical angle, posterior margin arcuate, jugal margin straight. Stem ScP+R+MP+CuA very short, stem ScP+R straight, parallel and very close to costal margin, forked at level of nodus, ScP+RA reaching margin slightly basad of apex, RP reaching margin at apex. Stem MP separated at very base of hind wing, single, reaching margin slightly basal of apex. Stem CuA separated at very base, straight, forked slightly basad of stem ScP+R fork. Stem CuP sinuous, distance between tip of CuP and tip of CuA_2 smaller than distance between branches of CuA. Stem Pcu weakly sinuous, more curved in distal section, distance between tip of Pcu and tip of CuP wider than distance between branches of CuA. Vein A_1 slightly arcuate, vein A_2 forked at about half of anal field length, their apical sections probably reach the margin of hind wing. Branch A_2 forked, terminal A_{2a} curved and parallel to branch A_1, branch A_{2b} parallel to the margin. A meshwork of veinlets between longitudinal veins present, forming irregular, polygonal cells, those veinlets slightly thicker on anal field.

Age and distribution Mid-Cretaceous; Kachin State, northern Myanmar.

Ayaimatum trilobatum gen. et sp. nov. Jiang and Szwedo

urn:lsid:zoobank.org:act:84E593AC-FD2A-41EA-89B0-8BCC5AE93F61
(Figs. 1–4)

Etymology Specific epithet is derived from trilobate shape of the vertex.

Material Holotype. Specimen number JSSNU 2019005 housed in the Zoological collection, Jiangsu Second Normal University, Nanjing, China. Sex unknown. Inclusion in mid-Cretaceous Burmese amber, with only anterior portion of body, tegmina, hind wings and rostrum preserved, legs and abdomen missing.

Diagnosis As for genus as it is the only included species. Additionally: disc of frons verrucose, posterolateral margins of vertex elevated at level of compound eyes. Pronotum and mesonotum densely and evenly punctate by remains of sensory pits. Tegmen about 3.3 times as long as wide, cell C1 more than twice as long as cell C3. Hind wing with distance between terminals of CuA at margin wider than distance between apices of MP and CuA_1.

Description Measurements: preserved part of the body with tegmina 20.32 mm long, 11.26 mm wide. Head with compound eyes 2.95 mm wide. Vertex 1.26 mm long at mid line, 2.15 mm wide at widest point, 1.84 mm wide at posterior margin. Frons 2.16 mm long in mid line, 1.43 mm wide at widest point at level of antennae. Postclypeus 1.89 mm long in mid line, 1.39 mm wide at frontoclypeal suture. Anteclypeus 1.53 mm long in mid line. Pronotum 1.47 mm long at mid line, 5.68 mm wide. Mesonotum 3.47 mm long at mid line, 5.16 mm wide. Tegula 1.26 mm wide, 0.79 mm long. Tegmen 15.4 mm long, 4.68 mm wide at the level of tornus; costal cell 1.05 mm wide; cell C1 10.05 mm long, 0.53 mm wide; cell C3 4.95 mm long, 1.03 mm wide; cell C5 7.53 mm long 1.05 mm wide. Hind wing 12.95 mm long, 5.42 mm wide in the level of nodus; cell C1 3.79 mm long; cell C5 3.47 mm long. Coloration indistinct, some irregular patches of darker areas preserved.

Horizon and occurrence Cenomanian; Noije Bum Hill, Hukawng Valley, Kachin State, northern Myanmar.

4 DISCUSSION

The new genus and species described above enriches the known taxonomic diversity and morphological disparity of the family Mimarachnidae. It is the sixth species known from amber from Kachin, which makes this locality the richest in terms of taxa of this family known. The oldest fossils of Mimarachnidae are *Mimamontsecia* Szwedo and Ansorge, 2015 and *Chalicoridulum* Szwedo and Ansorge, 2015, reported from La Cabrua outcrop, Sierra del Montsec, Spain, which is dated as Barremian. The genus *Ayaimatum* gen. nov. is similar in size to *Mimamontsecia*, but differs in features of tegmen venation. In this respect it is more similar to *Chalicoridulum*, however these similarities could be artificial due to very simplified patterns presented by tegmina of Mimarachnidae. From Aptian (125–113 Ma) genera *Mimarachne* Shcherbakov, 2007 and *Saltissus* Shcherbakov, 2007, described from Baissa, *Ayaimatum* gen. nov. differs in size, coloration and venation pattern of tegmina (Shcherbakov, 2007). *Nipponoridium* Szwedo, 2008 from the Aptian of Shiramine, Japan is represented by only a partly preserved hind wing (Szwedo, 2008), differing from *Ayaimatum* gen. nov. by additional branching of CuA_2. The distance between apex of MP and CuA_1 in *Mimarachne* is wider than that between apices of CuA (Shcherbakov, 2007). From other genera known from inclusions in burmite, i.e. *Dachibangus* Jiang, Szwedo and Wang, 2018, *Jaculistilus* Zhang, Ren and Yao, 2019 and *Mimaplax* Jiang, Szwedo and Wang, 2019 (Jiang *et al*., 2018, 2019; Zhang *et al*., 2019), the new genus differs by size, details of morphological structures of body and venation. *Ayaimatum* gen. nov. is slightly similar to *Burmissus* Shcherbakov, 2017 in venation pattern of tegmen, but differs in longer stem of ScP+R and earlier branching of CuA (Shcherbakov, 2017). In those features the new genus resembles the pattern observed in *Mimaplax*. *Ayaimatum* gen. nov. differs from *Burmissus* and *Mimplax* by structure of the head, with trigons small, merely visible in ventral view and not visible in dorsal view, while in both of the above-mentioned genera, the trigons are visible in dorsal view. The new genus differs also from *Burmissus* in features of the hind wing, with distance between branches of CuA and between CuP and Pcu wider than that between CuA_2 and CuP, while in *Burmissus* these distances are more even (Shcherbakov, 2017). The new genus *Ayaimatum* gen. nov. is different from all other genera known from burmite and compression/impression fossils by its elevated pronotum and mesonotum with cristate carinae, forming declivous slope in lateral view.

Regarding the taxonomic diversity and morphological disparity the Mimarachnidae at the time of formation of Burmese amber were represented by the very differentiated taxa, probably presenting also various ecological strategies. *Ayaimatum* gen. nov. in its morphological features with flattened head and elevated mesonotum, superficially resembles some other hemipteran groups, e.g. representatives of subfamilies Ledrinae Fairmaire, 1855 (some Ledrini Fairmaire, 1855 and Rubrini Jones, 2009) and Tartessinae Distant, 1908 (the tribe Stenocotini Kirkaldy, 1906) of the family Cicadellidae Latreille, 1825 (Cicadomorpha Evans, 1946: Cicadelloidea Latreille, 1825). Representatives of extinct Ledrinae tribe Paracarsonini Hamilton, 1990 were recently found as inclusions in Burmese amber (Chen *et al*., 2019), the group known also from the Aptian Crato Formation of Brazil (Hamilton, 1990). Modern Ledrinae are feeding on dicotyledonous trees and shrubs (Jones, 2009). Cryptic behaviour and flatinidisation syndrome (Szwedo and Stroiński, 2017) on tree trunks is proposed as explanation of body and wing form in *Mimaplax* (Jiang *et al*., 2019). Body shape of *Ayaimatum* gen. nov. seems to be also cryptic. Shcherbakov (2017) suggested that the extremely long and slender rostrum of *Burmissus* extending apices of folded tegmina, suggesting this genus feeding on trees with thick and rough bark. Recent aphids of the genus *Stomaphis* feed on tree trunks of deciduous trees, so their maxillary and mandibulary stylets must always penetrate deeply into phloem through a thick layer of the cortex, and these aphids present exceptional mechanism of labium shortening (Brożek *et al*., 2015). A report by Depa *et al*. (2014) suggested that the retraction of a labium part from body and the retraction of the stylets from plant tissues in those aphids may take several minutes. Thus, a rapid escape and refuge from predators seems hardly possible. Rostrum in *Ayaimatum* gen. nov. is not preserved, but judging from other mimarachnids from burmite (e.g. *Jaculistilus*), long rostrum is plausible also in this taxon. With such elongated mouthparts these planthoppers were very probably more sedentary. Patchy darker markings on the tegmina could also be explained as part of the anti-predatory mechanisms. These features of *Ayaimatum* gen. nov. indicate these planthoppers probably hiding on the bark of the tree trunks or thick branches of gymnosperm trees constituting Burmese amber forests to avoid the predatory attentions. The finding described above gives additional insight to systematics, diversity and disparity of Mimarachnidae. It gives also some new thoughts to the reconstruction of palaeoenvironments and palaeobiota of amber producing forests of the area of West Burma block during the mid-Cretaceous.

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