



缅甸北部克钦琥珀中的蜻蜓目化石*

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提要 近五年, 缅甸北部白垩纪中期克钦琥珀中相继发现了数百枚蜻蜓目化石, 包含现生蜻蜓目三个亚目类群, 目前已发表 16 科 29 属 35 种, 在所有已知琥珀记录中数量和多样性最高。克钦琥珀中的蜻蜓目以均翅亚目(豆娘)为主, 以 *Burmahemiphlebia zhangi* 最为常见, 不少现生豆娘的化石记录也首次在克钦琥珀中发现, 包括 Perilestidae, Platynemididae 和 Platystictidae 等。此外, 克钦琥珀中发现了一些中生代沉积岩中常见的蜻蜓目类群, 如 Araripegomphidae, Gomphaeschnidae 和 Stenophlebiidae 等, 指示克钦琥珀的时代可能为早白垩世晚期。这些发现为探讨蜻蜓目部分类群的起源、演化和揭示生物古地理提供了有力证据。

关键词 蜻蜓目 克钦琥珀 白垩纪 缅甸

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A REVIEW OF ODONATA IN MID-CRETACEOUS KACHIN AMBER OF NORTH MYANMAR

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Abstract In the past five years, abundant and diverse odonatans were described from mid-Cretaceous Kachin amber, including three extant suborders. The odonatans in Kachin amber are quite diversified with 35 species described and dominated by the damselfly *Burmahemiphlebia zhangi*. These odonatans contain some first fossil records of extant damselflies, i.e., Perilestidae, Platynemididae and Platystictidae. Some dragonflies previously only recorded in the Cretaceous sedimentary rocks, such as Araripegomphidae, Gomphaeschnidae and Stenophlebiidae, provide a late Early Cretaceous age for Kachin amber. The dragonflies in Kachin amber contribute to discussing the origin, evolution and palaeogeography of Odonata.

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1 前 言

蜻蜓目包括差翅亚目(俗称蜻蜓)、均翅亚目(俗称豆娘)和间翅亚目(俗称螳螂)。蜻蜓目化石在沉积地层中较常见,但在琥珀中非常稀少,仅零星记录在波罗的海、多米尼加、缅甸、法国、约旦、美国和黎巴嫩等地区的琥珀中(Bechly, 1996a, 1998, 2000, 2012; Fleck *et al.*, 2000; Bechly and Wichard, 2008; Lak *et al.*, 2009; Azar *et al.*, 2010; Nel *et al.*, 2010; Poinar *et al.*, 2010; Zheng *et al.*, 2018d)。蜻蜓体积较大,好盘旋于开阔区域,不易保存在琥珀中;豆娘尺寸相对较小,好停留在密林里,易于保存在琥珀中(Larsson, 1978; Bechly, 1998; Zheng *et al.*, 2016a)。近几年,本文作者于克钦琥珀中发现了约 300 枚蜻蜓目标本,涉及目前已发表的 35 种化石(表 1),但仍有不少新的属种有待发表。

现生蜻蜓目通常用于研究昆虫生态、行为和地理迁移等(van Tol and Müller, 2003; van Tol *et al.*, 2009; Suhling *et al.*, 2015)。因而,对于蜻蜓目化石的研究有助于恢复古生态(如: Zhang, 1999; Huang and Lin, 2001)、探讨古行为(如: Zheng *et al.*, 2017d)和揭示生物古地理和地层学意义(如: Zhang, 1999; Zhang *et al.*, 2010; Zheng *et al.*, 2015, 2016b, 2017e, 2017f, 2018g, 2018a, 2019a)。本文综述了克钦琥珀中的蜻蜓目,并探讨了上述相关意义。

2 研究材料和方法

缅甸琥珀主要产自北部克钦邦胡康河谷白垩纪中期地层(即克钦琥珀),此外有极少量琥珀产自中部提林地区白垩纪晚期地层(即提林琥珀)(Zheng *et al.*, 2018b)。本文中所涉及标本均产自北部克钦邦。SIMS U-Pb 同位素年代学证据表明克钦琥珀时代接近塞诺曼期最早期(earliest Cenomanian, 98.79 ± 0.62 Ma; Shi *et al.*, 2012)。克钦琥珀中的昆虫通常保存在黄色、棕红色琥珀中。

文中化石拍照使用 Zeiss Stereo Discovery V16 显微成像系统和 Zen 软件。标本均存放在中国科学院南京地质古生物研究所古生物标本馆。蜻蜓目翅脉术语依据 Riek (1976)、Nel 等(1993)、Bechly (1996b)和 Lauriane 等(2018)。现生和化石蜻蜓目高级分类、科和属的特征,主要依据 Bechly (1996b, 2007)。蜻蜓目翅脉术语缩写如下(图 1): AA. 前臀脉; AL. 臀圈; Arc. 弓脉; Ax. 结前横脉; CuA. 前轴脉; T. 三角室; HT. 上三角室; IR. 插脉; MA. 中脉前支; MP. 中脉后支; Mspl. 中副脉; N. 翅结; 'O'. 斜脉; Pt. 翅痣; RA. 前径脉; RP. 后径脉; Rspl. 径副脉; ScP. 亚前缘脉后支; SdT. 亚三角室。

3 克钦琥珀中的蜻蜓目

克钦琥珀中的蜻蜓目包含现生蜻蜓目 3 个亚目类群,共计 16 科 29 属 35 种(表 1; 图 2)。其中,多样性以均翅亚目最高,差翅亚目次之,间翅亚目最低;而数量则是均翅亚目最高,间翅亚目次之,差翅亚目最低。

3.1 差翅亚目

克钦琥珀中的蜻蜓通常只有残翅保存,少量标本能保存较完整前翅或后翅。目前已发表克钦琥珀中差翅亚目化石 6 科 11 属 11 种,均属于灭绝科,包括 Araripegomphidae Bechly, 1996 (Zheng *et al.*, 2018a), Burmaeshnidae (Zheng *et al.*, 2017c; Huang *et al.*, 2017b, 2017c; Wei *et al.*, 2019), Burmagomphidae (Zheng *et al.*, 2018d), Gomphidae (Schädel and Bechly, 2016; Huang *et al.*, 2019a), Gomphaeschnidae (Zheng *et al.*, 2016a, 2019a)和 Paraburmagomphidae (Zheng *et al.*, 2018c)。

其中, Araripegomphidae 包含单一种 *Araripegomphus shai* (图 2-C; Zheng *et al.*, 2018a)。*Araripegomphus* 先前仅记录在巴西晚阿普特期—阿尔布期(late Aptian–Albian)克拉图组(Crato Formation)。该属在克钦琥珀的发现,表明克钦琥珀的时

表 1 克钦琥珀中的蜻蜓目化石名单
Table 1 List of Odonata in Kachin amber.

亚目	科	属	种(标本数)	参考文献
Anisoptera	Gomphidae	<i>Burmalingenia</i>	<i>Burmalingenia imperfecta</i> (1)	Schädel and Bechly, 2016
		<i>Gunterbechlya</i>	<i>Gunterbechlya pumilio</i> (1)	Huang <i>et al.</i> , 2019a
Zygoptera	Gomphaeschnidae	<i>Cretogomphaeschnaoides</i>	<i>Cretogomphaeschnaoides jarzembowskiae</i> (1)	Zheng <i>et al.</i> , 2016a
		<i>Kachinaeschna</i>	<i>Kachinaeschna zhuoi</i> (2)	Zheng <i>et al.</i> , 2019a
		<i>Cretaeschna</i>	<i>Cretaeschna limi</i> (1)	Zheng <i>et al.</i> , 2017c
		<i>Burmaeschna</i>	<i>Burmaeschna azari</i> (1)	Huang <i>et al.</i> , 2017c
		<i>Angustaeschna</i>	<i>Angustaeschna magnifica</i> (1)	Huang <i>et al.</i> , 2017b
		<i>Proaeschna</i>	<i>Proaeschna zhangii</i> (1)	Wei <i>et al.</i> , 2019
		<i>Burmagomphides</i>	<i>Burmagomphides electronica</i> (1)	Zheng <i>et al.</i> , 2018d
		<i>Paraburmagomphides</i>	<i>Paraburmagomphides zhaoi</i> (1)	Zheng <i>et al.</i> , 2018c
		<i>Araripegomphus</i>	<i>Araripegomphus shai</i> (1)	Zheng <i>et al.</i> , 2018a
		<i>Palaeodisparoneura</i>	<i>Palaeodisparoneura burmanica</i> (1)	Poinar <i>et al.</i> , 2010
			<i>Palaeodisparoneura cretacea</i> (1)	Zheng <i>et al.</i> , 2017g
	Hemiptera		<i>Yijenplatycnemis</i>	<i>Yijenplatycnemis huangi</i> (9)
		<i>Cretadisparoneura</i>	<i>Cretadisparoneura hongii</i> (1)	Huang <i>et al.</i> , 2015
		<i>Burmahemiphlebia</i>	<i>Burmahemiphlebia zhangii</i> (157)	Zheng <i>et al.</i> , 2017h
			<i>Burmahemiphlebia hui</i> (1)	Zheng and Wang, 2019
		<i>Burmachysagriton</i>	<i>Burmachysagriton zhangii</i> (3)	Zheng <i>et al.</i> , 2016d
		<i>Palaeodysagriton</i>	<i>Palaeodysagriton cretacticus</i> (2)	Zheng <i>et al.</i> , 2017h
			<i>Palaeodysagriton youlini</i> (1)	Zheng <i>et al.</i> , 2017b
		<i>Electrodysagriton</i>	<i>Electrodysagriton limi</i> (5)	Zheng <i>et al.</i> , 2017a
		<i>Palaeoperilestes</i>	<i>Palaeoperilestes electronicus</i> (1)	Zheng <i>et al.</i> , 2016e
		<i>Mesosicta</i>	<i>Mesosicta electronica</i> (13)	Zheng <i>et al.</i> , 2016g
Coenagrionoidea		<i>Mesosicta burmatica</i> (12)	Huang <i>et al.</i> , 2015	
			<i>Mesosicta davidattenboronghi</i> (1)	Zheng <i>et al.</i> , 2019c
		<i>Burmacoenagrion</i>	<i>Burmacoenagrion pretiosus</i> (1)	Zheng <i>et al.</i> , 2019b
		<i>Burmachistigma</i>	<i>Burmachistigma cheni</i> (1)	Zheng <i>et al.</i> , 2019b
		<i>Electrocoenagrion</i>	<i>Electrocoenagrion elongatum</i> (1)	Zheng <i>et al.</i> , 2019b
			<i>Electrocoenagrion forficatum</i> (1)	Zheng <i>et al.</i> , 2019b
		<i>Burmagrion</i>	<i>Burmagrion marjannakoki</i> (2)	Möstel <i>et al.</i> , 2017
		<i>Paracoryphagrion</i>	<i>Paracoryphagrion deltoides</i> (1)	Zheng <i>et al.</i> , 2018e
		<i>Mesomegaloprepus</i>	<i>Mesomegaloprepus magnificus</i> (53)	Huang <i>et al.</i> , 2017a
		<i>Cretamegaloprepus</i>	<i>Cretamegaloprepus zhouuae</i> (1)	Zheng <i>et al.</i> , 2018f
Epitriptera		<i>Burmaphlebia</i>	Bechly and Poinar, 2013	
Stenophlebiptera		<i>Burmastenophlebia reiffi</i> (60)		
		<i>Burmastenophlebia flecki</i> (1)	Huang <i>et al.</i> , 2019b	

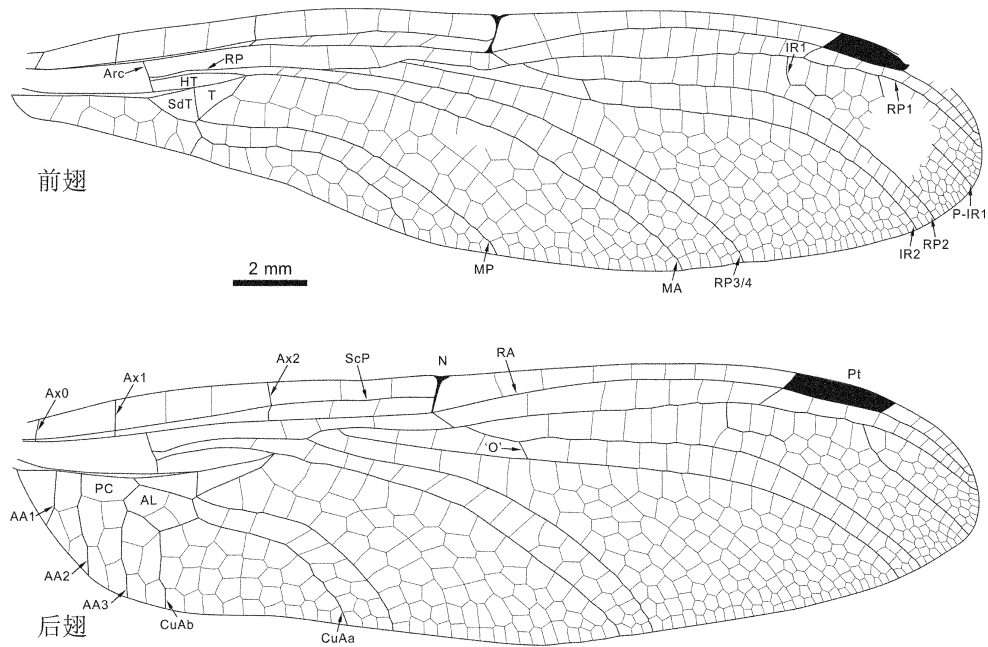


图 1 蜻蜓翅脉术语说明(以 *Burmagomphides electronica* 为例)。缩写含义见正文。

Fig. 1 Line drawing of *Burmagomphides electronica* showing wing venations of dragonfly. Abbreviations are explained in the text.

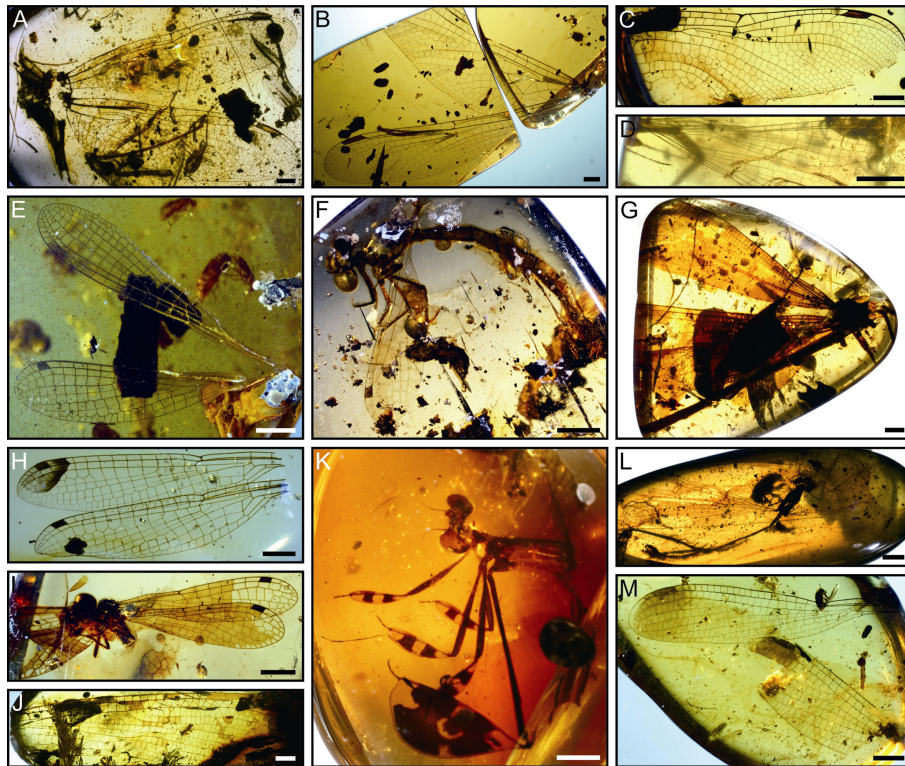


图 2 克钦琥珀中代表性蜻蜓目化石

Fig. 2 Typical odonatans from Kachin amber.

A. *Burmagomphides electronica*, Burmagomphidae 科; B. *Kachinaeshna zhuoi*, Gomphaeschnidae 科; C. *Araripegomphus shai*, Araripegomphidae 科; D. *Mesosticta burmatica*, Platystictidae 科; E. *Mesosticta davidattenboroughi*, Platystictidae 科; F. *Burmahemiphlebia zhangi*, Hemiphlebiidae 科; G. *Mesomegaloprepus magnificus*, Mesomegaloprepidae 科; H. *Electrodysagrion lini*, Dysagrionidae 科; I. *Burmadyagrion zhangi*, Dysagrionidae 科; J. *Paracoryphagrion deltoides*, Pseudostigmatoidea 科; K. *Yijenplatynemis huangi*, Platynemididae 科; L. *Burmacoenagrion preciosus*, Coenagrionoidea 科; M. *Electrocoenagrion elongatum*, Coenagrionoidea 科。比例尺(Scale bars) = 2 mm。

代可能为阿普特期晚期。Burmaeshnidae 是缅甸琥珀中特有的科, 与现生科 Telephlebiidae 亲缘较近, 包含 4 属 4 种: *Cretaeshna lini*, *Burmaeshna azari*, *Angustaeshna magnifica* 和 *Proaeshna zhangii* (Zheng *et al.*, 2017c; Huang *et al.*, 2017b, 2017c; Wei *et al.*, 2019)。Burmagomphidae 和 Paraburmagomphidae 均归属于 Gomphoidea 超科下的 Oligophlebiata 支系。Burmagomphidae 的模式种是记录自克钦琥珀的 *Burmagomphides electronica* (图 2-A)。Burmagomphides 随后在阿根廷始新世地层中被发现 (Petrulevičius, 2017)。Paraburmagomphidae 包含 *Paraburmagomphides zhaoui* (Zheng *et al.*, 2018c), 而 Gomphaeschnidae 包含 *Cretagomphaeschnaoides jarzembowskiae* 和 *Kachinaeshna zhuoi* (图 2-B) (Zheng *et al.*, 2016a, 2019a)。Gomphaeschnaoidinae 先前仅记录在早白垩世地层, 且主要发现在克拉图组, 同样反映克钦琥珀的时代可能为早白垩世晚期。

3.2 间翅亚目

琥珀中的间翅亚目保存极少, 仅在克钦琥珀中有记录。克钦琥珀中目前发表间翅亚目化石 2 科 2 属 2 种, 包括 Burmaphlebiidae 科和 Stenophlebiidae 科 (Bechly and Poinar, 2013; Huang *et al.*, 2019b)。Burmaphlebiidae 科包含单一种 *Burmaphlebia reifi*, 在克钦琥珀中发现数量较多。*Burmaphlebia* 翅膀尺寸较小 (单个翅膀长 11—13 mm), 后翅具有明显凸出的臀角 (该特征常见于中生代蜻蜓化石)。此外, 另一枚蜻蜓化石, *Burmastenophlebia flecki* 是琥珀中 Stenophlebiidae 科的首次记录 (Huang *et al.*, 2019b)。该科化石在中生代地层广泛分布, 最老层位记录是在哈萨克斯坦上侏罗统卡拉巴斯套组 (Karabastau Formation), 最年轻记录是在法国西部的塞诺曼期早期地层 (Nel *et al.*, 2015)。Stenophlebiidae 科在我国见于辽宁北票黄半吉沟和内蒙古宁城柳条沟义县组尖山沟层 (Aptian 期最早期; Nel and Huang, 2015; Zheng *et al.*, 2016c, 2016f) 以及甘肃玉门早峡沟中沟组上部 (早 Albian 期; Zheng *et al.*, 2018g)。克钦琥珀中该科化石的发现表明克钦琥珀的时代可能不超过塞诺曼期早期。

3.3 均翅亚目

克钦琥珀中均翅亚目的数量和多样性最高, 保存也较好。目前发表均翅亚目化石 8 科 16 属 22 种, 涉及以下科 Coenagrionoidea (Möstel *et al.*, 2017; Zheng *et al.*, 2019b), Dysagrionidae (Zheng *et al.*, 2016d, 2017h, 2017a, 2017b), Hemiphlebiidae (Zheng *et al.*, 2017h; Zheng and Wang, 2019), Mesomegaloprepidae (Huang *et al.*, 2017a; Zheng *et al.*, 2018f), Paracoryphagrionida (Zheng *et al.*, 2018e), Perilestidae (Zheng *et al.*, 2016e), Platycnemididae (Poinar *et al.*, 2010; Huang *et al.*, 2015; Zheng *et al.*, 2017d, 2017g) 和 Platystictidae (Huang *et al.*, 2015; Zheng *et al.*, 2016g, 2019c)。克钦琥珀中的均翅亚目化石以 Hemiphlebiidae 为主, 占据所有蜻蜓目比例近 70.2%, 其次为 Mesomegaloprepidae (24.6%), Platystictidae (11.5%), Platycnemididae (5.2%) 和 Dysagrionidae (4.8%)。

现生 Platystictidae 科豆娘俗称森林豆娘或阴影豆娘, 常栖息在溪流边的树枝上。该科有 4 亚科 8 属约 250 个现生种, 包括分布于南美中部和北部的 Palaemnematinae 亚科和东南亚的 Platystictinae, Protostictinae 和 Sinostictinae 亚科 (van Tol *et al.*, 2009; Dijkstra *et al.*, 2014; Schorr and Paulson, 2015; Suhling *et al.*, 2015)。根据克钦琥珀中的该科化石建立了亚科 Mesostictinae, 包含 1 属 3 种: *Mesosticta burmatica*, *M. electronica* 和 *M. davidattenboroughi* (图 2-D, 2-E; Huang *et al.*, 2015; Zheng *et al.*, 2016g, 2019c)。Platystictidae 在克钦琥珀中比较常见, 该科先前认为起源于北半球晚白垩世地层 (van Tol and Müller, 2003; van Tol *et al.*, 2009), 但并无化石记录, *Mesosticta* 的发现将 Platystictidae 的起源追溯到至少白垩纪中期。

现生 Hemiphlebiidae 科豆娘包含单一种 *Hemiphlebia mirabilis*, 仅分布在澳大利亚维多利亚地区的沼泽地带 (Cordero-Rivera, 2016, 2017)。Hemiphlebiidae 的盘室通常在前翅开放而在后翅封闭。然而, 最近对现生 Hemiphlebiidae 的统计发现盘室的开放情况也存在变动: 一些 *H. mirabilis* 的盘室在前后翅均封闭, 一些则在后翅也发现封闭的盘室 (Cordero-Rivera, 2017)。Hemiphlebiidae 化石记录较多, 目前已报道 8 属, 记录于英国、约旦、巴

西、法国、以色列、美国和缅甸晚侏罗世至早白垩世沉积地层和琥珀中 (Zheng *et al.*, 2017h; Zheng and Wang, 2019)。克钦琥珀中该科化石包含 1 属 2 种: *Burmahemiphlebia zhangii* (图 2-F) 和 *B. hui* (Zheng *et al.*, 2017h; Zheng and Wang, 2019)。*B. zhangii* 是克钦琥珀中最常见的蜻蜓目化石, 据不完全统计已发现约 157 枚。此外, *B. zhangii* 可能具有群居行为, 本文作者曾在 1 枚琥珀标本中发现 5 枚完整个体。

现生 Perilestidae 科豆娘通常称作断翅, 具有短的翅膀(长 20—25 mm)和长而纤细的、彩色环带状的腹部(长 40—56 mm)(Williamson and Williamson, 1924; Haber and Wagner, 2014)。该科类群较小, 仅包含 2 属(*Perilestes* 和 *Perissolestes*)19 种 (Dijkstra *et al.*, 2011, 2014; Schorr and Paulson, 2015; Machado, 2015)。克钦琥珀中的 *Palaeoperilestes electronicus* 是该科首次化石记录, 将该科的起源追溯到至少白垩纪中期。

Coenagrionoidea 超科包含了约 3/5 的现生豆娘, 超过 1800 种。该超科包含 3 个科: Isostictidae, Platycnemididae 和 Coenagrionidae (Dijkstra *et al.*, 2014)。该超科化石常见于波罗的海、多米尼加和墨西哥琥珀以及美国、德国、法国和巴西等中-新生代沉积地层中 (Carle and Wighton, 1990; Nel and Paicheler, 1993; Poinar, 1996; Jarzembowski *et al.*, 1998; Nel and Jarzembowski, 1999; Bechly, 2000, 2012; Ross *et al.*, 2016)。Coenagrionoidea 在克钦琥珀中较为多样, 以 Platycnemididae 和 Burmacoenagrionidae 为代表, 包含 7 属 9 种 (Poinar *et al.*, 2010; Huang *et al.*, 2015; Möstel *et al.*, 2017; Zheng *et al.*, 2017d, 2017g, 2019b)。现生 Platycnemididae 科包含约 400 种, 广泛分布在旧大陆 (Dijkstra *et al.*, 2014; Schorr and Paulson, 2015; Theischinger *et al.*, 2015)。Platycnemididae 在克钦琥珀中多样性较高, 包含 1 亚科 3 属 4 种: *Cretadisparoneura hongii*, *Palaeodisparoneura burmanica*, *P. cretatica* 和 *Yijenplatycnemis huangii* (Poinar *et al.*, 2010; Huang *et al.*, 2015; Zheng *et al.*, 2017d, 2017g)。这其中, *Y. huangii* (图 2-K) 具有极度膨大、豆荚状的跗节, 用于驱避其它捕食者和吸引雌性, 而增加成功交配的机会, 这也是蜻蜓目首次求偶行为

化石间接证据。Burmacoenagrionidae 在克钦琥珀中较为多样, 包含 4 属 5 种: *Burmacoenagrion pretiosus*, *Burmachistigma cheni*, *Electrocoenagrion elongatum*, *Electrocoenagrion forficatum* 和 *Burmagrion marjanmakoki* (图 2-L, 2-M; Zheng *et al.*, 2019b)。但是 Burmacoenagrionidae 在 Coenagrionoidea 中的分类位置仍有待解决。

现生 Pseudostigmatoidea 超科包含 Coryphagrionidae 科和 Pseudostigmatidae 科 (Bechly, 2007; Dijkstra *et al.*, 2014)。其中, Coryphagrionidae 包含单一一种 *Coryphagrion grandis*, 分布在肯尼亚和坦桑尼亚零星的沿海森林处 (Clausnitzer, 2010)。而 Pseudostigmatidae 包含现代最大的豆娘 *Megaloprepus caerulatus*, 其翅展超过 19 cm (Ingley *et al.*, 2012; Dijkstra *et al.*, 2014)。*Paracoryphagrion deltoides* (图 2-J; Zheng *et al.*, 2018e) 单翅长度约 30 mm, 它被归并到 Pseudostigmatoidea 基于以下特征: CuA 脉细长、轻微锯齿形, 与后翅边缘平行, 并拥有大量 *C. grandis* 所拥有的三角形翅室。

Dysagrionidae 属于灭绝科, 与现生 Thaumatoeurinae 科可能是姊妹类群 (Bechly, 2007), 但前者目前被认为是一个独立的科 (Garrouste and Nel, 2015)。Dysagrionidae 包含 3 亚科 10 属, 最老的层位记录是我国山东下白垩统莱阳组的 *Congqingia* (Zhang, 1992)。此外, 该科化石在北美、丹麦、德国、英国和俄罗斯的新生代地层, 以及克钦和波罗的海琥珀中有报道 (Zheng *et al.*, 2017h)。克钦琥珀中该科化石多样性较高, 包含 3 属 3 种: *Burmadyagrion zhangii*, *Palaeodyagrion cretacicus* 和 *Electrodyagrion lini* (图 2-H, 2-I)。Dysagrionidae 拥有多样的方形盘室, 有助于探讨蜻蜓目盘室的演变 (Rust *et al.*, 2008; Zheng *et al.*, 2016d, 2017f)。

4 结 论

克钦琥珀中蜻蜓目多样性和丰度均非常高, 其数量已超过其它所有琥珀中的蜻蜓目化石, 为蜻蜓目的系统分类研究、起源和演化、生物古地理以及行为学研究均提供了很好的素材。目前已报道了近 35 种蜻蜓目化石, 但仍有不少属种有待

发表。此外, 克钦琥珀中也发现了多个种类的蜻蜓目幼虫标本, 目前尚未有文章发表, 未来关于蜻蜓目幼虫的研究工作仍需加强。

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