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·研究论文·

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白垩纪缅甸琥珀中小型花蚤一新种(鞘翅目: 花蚤科)及对花蚤科的分类学修订*

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提要　根据产自缅甸北部白垩纪中期克钦琥珀中的一块小型花蚤化石标本, 建立 1 新种——小多刺花蚤(*Multispinus parvus* sp. nov.), 归于花蚤科(Mordellidae)。同时, 对缅甸琥珀中已发现的花蚤和泛花蚤进行了重新观察和研究, 重点分析了其形态学特征并认真考虑了相关分类学依据, 将短尾花蚤科(Apotomouridae)修订为花蚤科之下的短尾花蚤亚科(Mordellidae: Apotomourinae)。短尾花蚤中普遍存在的臀锥完全不发育, 不可作为区分于花蚤科的衍征。白垩纪中期琥珀中发现的花蚤化石类群体型均小, 这也许与白垩纪中期生态环境和栖息地被子植物花朵形态有关。

关键词　甲虫　花蚤科　缅甸琥珀　白垩纪　分类学　古生态

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A NEW SMALL-BODIED MORDELLID BEETLE (COLEOPTERA: MORDELLIDAE) FROM MID-CRETACEOUS BURMESE AMBER AND TAXONOMIC REVISION

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Abstract　A new small-bodied beetle, *Multispinus parvus* sp. nov., is described from the mid-Cretaceous Burmese amber and assigned to Mordellidae (Coleoptera: Tenebrionoidea). Based on a careful re-examination of the Mordellidae and mordellid-like beetles from the Burmese amber and analysis of their morphological characters, the family Apotomouridae is reduced herein to a subfamily of Mordellidae as Apotomourinae. The absence of a pygidium in Apotomourinae cannot be regarded as a synapomorphy. All known mordellids found in the mid-Cretaceous ambers are all small in size, which may be related to the mid-Cretaceous ecological environment and the early angiosperm flower morphology in their habitat.

SYSTEMATIC PALAEONTOLOGY

Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Superfamily Tenebrionoidea Latreille, 1802
Family Mordellidae Latreille, 1802
Subfamily Apotomourinae subfam. nov.
【Apotomouridae】Bao, 2018, Cretaceous Research, 91: 14–19

***Multispinus* Bao, 2018**
Type species　*Multispinus multispinosus* Bao, 2018
Emended diagnosis　Body small, length 1.2–2.5 mm, wedge-shaped; color from dark brown to black. Head strongly declined. Pygidium completely reduced. Fore- and middle legs obviously shorter than hind legs. Metafemora well developed, strongly enlarged. Comb-like setae widely preserved on the posterior metatibiae. Sclerotic spines preserved in the ventral metatibiae and metatarsi. Claws small, b-cleft.

***Multispinus parvus* sp. nov.**
urn:lsid:zoobank.org:act:8DCC3478-F601-47A7-A88A-8B920129A330
(Fig. 2)
Etymology　*parvus,* Latin, small.
Differential diagnosis　*Multispinus parvus* sp. nov. different from *Multispinus multispinosus* by: (1) body much smaller, (2) pronotum shape special, anterior rounded, posterior wide, with two bends; (3) 6 pairs of short spines preserved in ventral metatibiae.
Description　Holotype NIGP171284, body very small, length 1.21 mm, wedge-shape, widest in posterior pronotum, body slightly narrower anterior and posterior; laterally curved, C-shape. Body colour from dark brown to black, without patterns.

Head small, rounded triangular in frontal view; narrowest posterior, as wide as anterior pronotum; hypognathous. Eyes lateral, large, well-developed, shape oval, finely faceted, interfacial setae well developed. Antennae short, less than half body length; serrate-filiform. Clypeus distinct; maxillary palpi moderated with four palpomeres, apical palpomere expanded, securiform.

Pronotum length 0.14 mm, widest at the base 0.44 mm, anterior rounded, posterior wide with two bends. Scutellum shield length 0.07 mm, width 0.09 mm, triangular. Elytra not exceed abdomen, length 1.12 mm, widest at anterior 0.42, surface almost smooth, with very fine setae; hind wing transparent, hided under elytra.

Metaepistena long, irregular rectangular, preserved with fine setae. Metacoxae enlarged formed metacoxal plate; trochanter oblique. Metafemora enlarged, numerous tiny spines preserved posterior. Metatibiae slim, long; comb-like setae preserved posterior. Tarsi form 5-5-4, slim. Metatibiae and metatarsi without any ridge. Ventral metatibiae preserved 6 pairs sclerotic tiny spines. Ventral metatarsus I preserved long and short fine spines; ventral metatarsus II-IV preserved short setae; comb-like setae preserved in each posterior metatarsus. Length metatarsi: 0.19 mm, 0.10 mm, 0.07 mm, 0.10 mm. Claw simple, b-cleft.

Abdomen with 1-5 five sterna, narrowed posteriorly, surface micro-rugose, length 0.11 mm, 0.08 mm, 0.07 mm, 0.05 mm, 0.15 mm, very fine setae preserved between sternites. Pygidium distinct, aedeagus partially exposed.

Key words　Beetle, Mordellidae, Burmese amber, Cretaceous, taxonomy, palaeoecology

1　前　言

花蚤科(Mordellidae)和短尾花蚤科(Apotomouridae)均为拟步甲总科(Tenebrionoidea)的基部类群(Hunt *et al*., 2007; McKenna and Farrell, 2009; Bao *et al*., 2018c)。花蚤, 俗称针尾甲虫, 绝大多数拥有完全发育的臀锥, 故此得名(Jackman and Lu, 2002); 花蚤科目前含三个亚科 Mordellinae, Ctenidiinae 和 Praemordellinae, 其中先花蚤亚科(Praemordellinae)仅含化石种(Bao *et al*., 2019b), 而前两个亚科现生种分布广泛。花蚤科的最早化石记录为侏罗纪中晚期道虎沟生物群中的侏罗五化甲 *Wuhua jurassica* Wang, 2011, 归于先花蚤亚科(Wang and Zhang, 2011)。该科在白垩纪缅甸琥珀

(Bao *et al*., 2019a)、西班牙琥珀(Peris and Ruzzier, 2013)和新泽西琥珀(Grimaldi and Engel, 2005)中均有发现, 新生代波罗的海琥珀中也有大量化石种发现(Odnosum and Perkovsky, 2010; Perkovsky and Odnosum, 2013; Bao *et al*., 2018b)。

短尾花蚤科与花蚤科、大花蚤科形态上具有高度相似之处, 显示出它们之间存在密切关系(Bao *et al*., 2018c)。但值得注意的是, 短尾花蚤的臀锥完全不发育, 使短尾花蚤在形态上与绝大多数花蚤科个体明显不同。而随着缅甸琥珀和其他产地中更多花蚤化石的发现, 短尾花蚤的先前分类暴露出一些问题, 对该类化石及其相近类群的形态学再分析和分类学修订越来越有必要。

在本次研究过程中, 笔者对现有泛花蚤类化石进行了再一次细致观察分析, 推敲各个形态特征的相对关系, 对已有短尾花蚤的分类进行了修订, 并讨论了其个体发生和生态学意义。

2 地质背景和材料

本次研究材料为缅甸硬琥珀(“burmite”, 又称克钦琥珀), 产自缅甸北部克钦邦胡康河谷达奈镇附近[Zheng 等(2018)报道了缅甸中部新发现琥珀矿址(“提林琥珀”), 埋藏年代距今约 72 Ma, 埋藏环境和琥珀性质与本文所讨论的材料不同], 保存于中国科学院南京地质古生物研究所。关于缅甸琥珀的最早文字记录可见《汉纪》(公元 205 年—265 年)(张一骋等, 2017), 最早的疑似缅甸琥珀实物标本出土于江西南昌海昏侯墓(约公元前 59 年)(Yang *et al*., 2017)。千百年来, 缅甸琥珀在当地经济、医疗和艺术等方面扮演了重要角色。缅甸琥珀埋藏于白垩纪复理石沉积单元中, 含灰绿色至蓝绿色的细粒沉积岩, 具有细小的火山碎屑(Shi *et al*., 2012)。根据 U-Pb 锆石测年分析, 缅甸琥珀的埋藏年代为晚白垩世早塞诺曼期(Cenomanian), 距今约 99 Ma (Shi *et al*., 2012)。然而, 琥珀表面的磨圆程度和内含物中的海洋生物, 表明琥珀被埋入围岩基质前有一系列再作用过程, 从而揭示了缅甸琥珀的实际年代可能更老(Bao *et al*., 2018a)。

3 研究方法

研究所用琥珀标本在中国科学院南京地质古生物研究所琥珀实验室进行处理并拍照。切割和打磨使用德国产 Buehler ISOMET 系列设备, 显微摄影应用配备了高清相机的蔡司体式显微镜(Zeiss Stereo Discovery AXIO Zoom V16), 图片叠加应用软件 Helicon Focus, 文中所用地图由软件 R studio-2017 及其地图软件包生成, 后期图像处理运用软件 Adobe Photoshop CS4。

文中所用术语和名称遵循相关文献(见 Bouchard *et al*., 2005, 2011; 刘名, 2007)。本研究描述的标本已经在 ZooBank 中注册, 具有唯一 ZooBank 登记码(LSID urn:lsid:zoobank.org:pub:AD5E35A2-7F2D-4ACB-BD86-D27D9BD1918D)。新建种的 LSID 编号将在系统古生物学部分体现。

4 系统古生物学

昆虫纲 Insecta Linnaeus, 1758

鞘翅目 Coleoptera Linnaeus, 1758

拟步甲总科 Tenebrionoidea Latreille, 1802

花蚤科 Mordellidae Latreille, 1802

短尾花蚤亚科(新亚科) Apotomourinae subfam. nov.

2018 Apotomouridae, Bao, Cretaceous Research, 91: 14－19.

亚科特征(修订) 虫体小, 楔形。身体前部可伸缩, 身体常呈 C 型; 鞘翅短; 臀椎完全消失; 腹部 5 节, 1 至 4 节末端(两腹节交界处)有一列刚毛; 跗节 5-5-4 型。触角短, 不超过体长一半, 11 节, 丝状。下颚须 4 节, 末节膨大。后足发育完全, 基节特化为基节板, 股节粗壮, 胫节和跗节附有硬化短刺。头部、前胸背板、鞘翅、腹节和腿的表面均有细短刚毛。爪小, 简单, 二裂。

多刺花蚤属 *Multispinus* Bao, 2018

模式种 多刺花蚤 *Multispinus multispinosus* Bao, 2018

属征(修订) 虫体小, 体长 1.2—2.5 mm; 流线型; 深棕色至黑色。头极向后下收缩。臀锥完全

不发育。前足和中足明显比后足短，纤细。后足股节强烈膨大，胫节末端有梳状端距；胫节和跗节内侧有硬化刺(刚毛)；爪二裂。

小多刺花蚤(新种)　*Multispinus parvus* sp. nov.

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(图 1)

词源　*parvus*，拉丁语，意为“小”。

正模　NIGP171284，雄性，保存完整，头部上方和口器处各有一气泡。

种征　虫体极小。触角短，不超过体长 1/2，各节长度类似。前胸背板前缘与侧缘形成半圆，后缘宽二弯状。颈极短，不可见。胫节内侧有六对硬质小刺，呈 V 型。

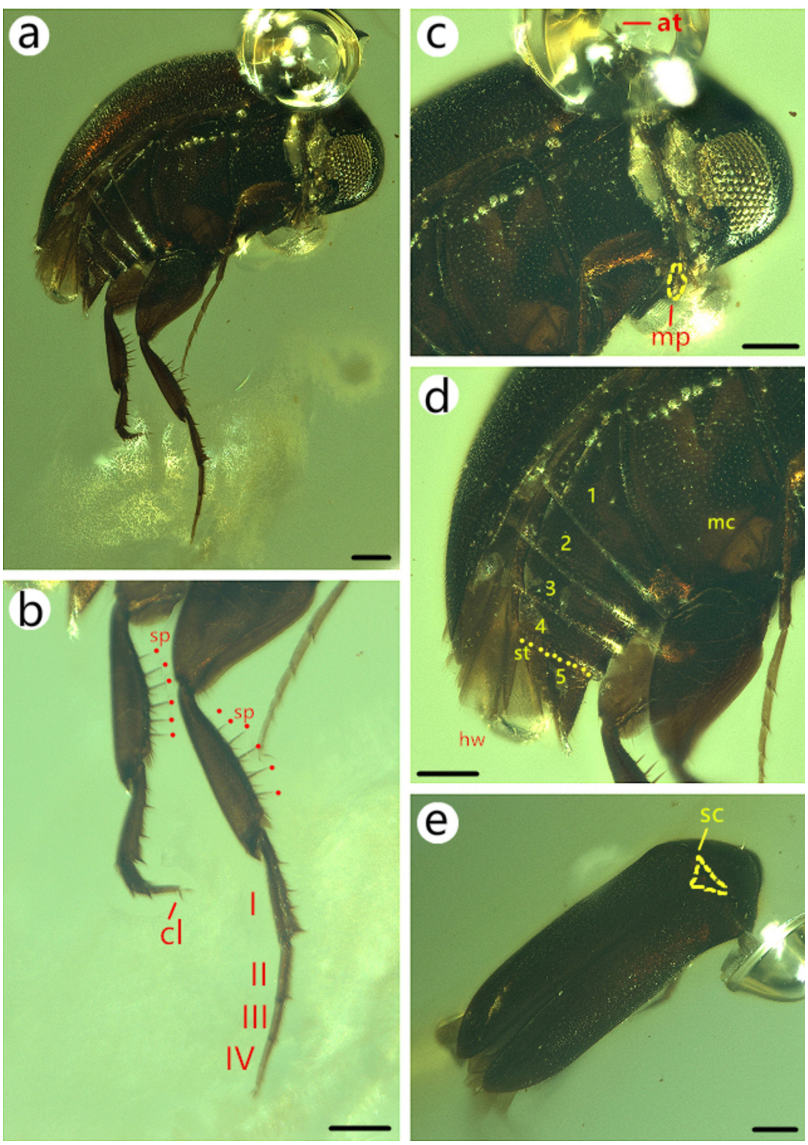

图 1　小多刺花蚤(新种)

Fig. 1　*Multispinus parvus* sp. nov.

a. 全身侧面观; b. 后足细节, I—IV 代表第 1 至第 4 跗节，红点标示胫节内侧的六对刺; c. 身体前部(头和胸部)细节; d. 后胸和腹部细节, 1—5 代表第 1 至第 5 腹节，黄点标示第 4 和第 5 腹节之间的一排细刚毛; e. 全身背面观。缩略语: at. 触角; cl. 爪; hw. 后翅; mc. 后基节板; mp. 下颚须; sc. 中胸小盾片; sp. 胫节内侧的刺; st. 刚毛。比例尺 = 0.1 mm。

a. lateral view; b. details of hind legs, I–IV represent 1st to 4th metatarsomeres, metatibiae spines pointed by red dots; c. details of head and thorax; d. details of metathorax and abdomen, 1–5 represent 1st to 5th sternites, a row of fine setae between 4th and 5th sternites pointed by yellow dots; e. dorsal view. Abbreviations: at. antennae; cl. claw; hw. hind wings; mc. metacoxal plate; mp. maxillary palp; sc. scutellum; sp. spines on metatibiae; st. setae. Scale bars = 0.1 mm.

描述 正模标本 NIGP171284, 体型极小, 体长 1.21 mm, 楔形, 身体最宽处位于前胸背板基部; 身体前端与末端均有不同程度的收缩, 流线型。侧面观, 身体卷曲, 呈 C 型。虫体颜色于琥珀中呈深棕至黑色, 无花斑。

头小, 正面观呈倒三角形, 基部最窄, 与前胸背板前缘同宽, 下口式。额区窄, 后头宽, 表面附有短刚毛。复眼一对, 侧置, 大, 完全发育, 具边框, 微多面型小眼面, 椭圆形, 边缘有刚毛, 于后头处不相接。触角短, 不及身长 1/2, 丝状。上唇突出; 下颚须末节膨大, 斧状。

前胸背板长 0.14 mm, 宽(基部最宽处)0.44 mm, 侧缘及前缘组合呈半圆状, 后缘宽二弯状。中胸小盾片长 0.07 mm, 宽 0.09 mm, 倒三角形。鞘翅一对, 不长于腹部, 长 1.12 mm, 宽(前部最宽处)0.42 mm, 表面近光滑, 有刻点及极短刚毛; 后翅透明, 膜质, 藏于鞘翅下。

足三对, 分别着生于前胸、中胸和后胸, 跗节 5-5-4 型。后胸前侧片窄, 不等四边形, 表面有小粒及极短刚毛; 后胸腹板宽阔, 表面有小粒及极短刚毛。后足基节特化为基节板, 膨大; 转节突出; 股节强烈膨大, 末端与胫节连接处有若干小刺; 胫节细长, 内侧弓型弯曲, 末端略扩大, 具端距, 数量多, 呈梳状; 跗节细长, 端部具爪, 无齿, 二裂。后足胫节与跗节表面无脊; 胫节内侧有六对硬质小刺, 呈 V 型; 跗节第一节内侧有长短两种小刺, 交互排布; 跗节第二节至第四节仅有短刺(或短刚毛); 每节跗节末端具有硬化端距。四节跗节长度依次为: 0.19 mm, 0.10 mm, 0.07 mm, 0.10 mm。

腹部 1—5 节可见腹板, 长度依次为: 0.11 mm, 0.08 mm, 0.07 mm, 0.05 mm, 0.15 mm, 腹板间有稀疏短刚毛一列, 腹板表面附有小粒及极短刚毛; 臀锥完全不发育。阳茎部分伸出。

种间差异 新种小多刺花蚤 *Multispinus parvus* sp. nov.与多刺花蚤 *Multispinus multispinosus* 相比: 1)虫体明显小; 2)前胸背板形状特殊, 侧缘及前缘组合呈半圆状, 后缘宽二弯状; 3)胫节内侧仅有六对硬质小刺, 呈 V 型。

产地与层位 缅甸联邦共和国克钦邦达奈镇, 缅甸硬琥珀原矿; 上白垩统塞诺曼阶底部(～99 Ma)。

5 讨 论

5.1 分类学修订

短尾花蚤由科(Apotomouridae)修订为花蚤科下的亚科(Mordellidae: Apotomourinae), 现包括 2 属 3 种, 均发现于白垩纪缅甸琥珀。短尾花蚤亚科的鉴定特征大部分吻合花蚤科的特征, 如: 身体蜷缩、楔形; 触角短; 鞘翅不超过腹节; 后足发达; 后足基节特化为基节板。该亚科明显异于绝大多数花蚤的特征为: 臀锥完全不发育; 身体多附属结构, 如刚毛, 刺等。臀锥完全不发育亦可见于侏罗纪先花蚤亚科(Mordellidae: Praemordellinae)(Bao *et al*., 2019b), 于白垩纪西班牙琥珀中发现的 *Mediumiuga sinespinis* Peris, 2013 表现为臀锥极不完全发育 (Peris and Ruzzier, 2013), 于缅甸琥珀中发现的 *Primaevomordellida burmitina* Bao, 2019 则与绝大多数现生花蚤一样臀锥非常发育 (Bao *et al*., 2019a)。这表明花蚤科内不同种类的臀锥发育程度呈极大多样性, 故此特征非科间鉴定衍征。现生花蚤各属种间, 后足胫节和跗节上的脊结构呈现多样性, 如端脊、亚端脊、侧脊、背脊(Jackman and Lu, 2002)。短尾花蚤亚科各属种均不具此特征, 但具有较发达的刺或刚毛附属结构, 而 *M. sinespinis* 兼具刚毛和脊, 故 *M. sinespinis* 可能为短尾花蚤亚科与其他花蚤的中间过渡种, 足的附属结构为短尾花蚤亚科衍征。一般来说, 甲虫胸部及其基节结构特征具有重要的分类学意义(Beutel and Friedrich, 2005), 如后基节特化为基节板为花蚤科区别于其他相邻分支(大花蚤科, 芫菁科等)的重要特征(Hsiao *et al*., 2017)。此特征在短尾花蚤亚科表现清晰, 故很难将短尾花蚤独立建新科。

分子系统发生学分析表明, 花蚤和大花蚤存在姐妹群关系(Mordellidae + Ripiphoridae)(Kergoat *et al*., 2014), 但 Falin (2003)指出大花蚤科的单系缺乏有力支持。短尾花蚤亚科作为花蚤科中的原始化石类群, 与先花蚤亚科一样, 具有许多原始大花蚤的特征。这也说明了拟步总科(Tenebrionoidea)的基部类群分类仍模糊, 尚需进一步研究。

5. 2　个体发生学和古生态学

现生花蚤科个体大小范围 1.5—15 mm (Jackman and Lu, 2002)。小多刺花蚤 *Multispinus parvus* 体长 1.2 mm, 属于花蚤科中体型最小的类群之一。相比其他缅甸琥珀中的花蚤类群(*Multispinus multispinosus*, 2.2—2.5 mm; *Apotomoura fortiscrura*, 1.5—1.7 mm; *Primaevomordellida burmitina*, 2.9—3.0 mm), 小多刺花蚤体型也明显小。事实上, 迄今白垩纪琥珀中发现的花蚤体型均小, 未见体长超过 5 mm 的个体。与此相比, 先花蚤亚科各属种体型明显大, 体长约 10 mm。但身体形态上, 先花蚤亚科与其他花蚤明显不同, 表现为: 后足细长, 不膨大; 身体平展, 不强烈蜷曲。这可能揭示了先花蚤亚科与其他花蚤取食策略和生态环境的不同(Wang *et al*., 2013; Bao *et al*., 2018c)。短尾花蚤与现生绝大多数花蚤一样, 具有发达的后足和蜷曲的体型, 据此推测其可能具有相似的飞行、跳跃动作(黄迪颖、杨俊, 1999) 和花冠取食行为(Franciscolo, 1957)。白垩纪中期被子植物出现并快速辐射, 从而影响陆生昆虫等同样快速协同进化与辐射, 是陆地生命进化中生物学上最重要的时期之一(Dilcher, 2000; Benton, 2010)。缅甸琥珀中发现的被子植物花朵均不具有大型花冠, 不形成花序, 多数呈小型、简单五瓣花状(Poinar, 2017; Liu *et al*., 2018), 这与访花花蚤类甲虫的小体型吻合。由此设想, 白垩纪被子植物与访花昆虫类群可能存在协同进化, 相互影响。

6　结　论

白垩纪中期缅甸琥珀中发现花蚤科一新种, 命名为小多刺花蚤 *Multispinus parvus* sp. nov.。短尾花蚤科被重新修订为花蚤科下的亚科——短尾花蚤亚科。白垩纪中期被子植物处于快速发展期, 花朵结构不甚发达, 或许可从协同进化角度解释这一时期花蚤类甲虫的普遍小型化现象。

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