

中国寄生蜂化石研究进展*

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摘 要 膜翅目的寄生蜂在生物防治和生态平衡中具有关键作用。自 2000 年以来, 中国在寄生蜂化石研究领域取得了显著进展。本文系统梳理了我国学者主导的寄生蜂化石分类学、系统发育及寄生行为演化等方面的研究成果: 东北地区中侏罗统九龙山组、上白垩统义县组地层以及缅甸琥珀中发现了大量保存完好的寄生蜂化石, 涵盖魔蜂科、旗腹蜂总科、细蜂总科等 18 个科, 且化石广泛分布于全球 18 个国家, 中国、哈萨克斯坦和缅甸的物种数量位居前列; 系统发育研究结合形态特征与基因数据, 揭示了长腹细蜂科、冠蜂科和旗腹蜂总科等类群的演化关系, 并提出了白垩纪物种多样性激增与被子植物兴起密切相关; 显微 CT 和三维重建技术助力解析墙冠褶翅蜂 *Tichostephanus longus* 和海妖肿腿蜂 *Sirenobethylus charybdis* 等灭绝类群特化结构, 为探寻寄生行为的起源与演化提供了直接证据。未来研究需进一步整合化石与现生类群数据, 深化对寄生蜂演化历史及其与生态系统互动的理解。

关键词 寄生蜂化石; 中生代; 分类学; 系统发育

Advances in research on Chinese parasitoid wasp fossils

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Abstract Parasitoid wasps play a vital role in biological pest control and thereby help maintain ecosystem equilibrium. Since 2000, significant progress has been made in research on Chinese parasitoid wasp fossils. This paper comprehensively reviews advances in taxonomy, phylogeny, and the evolution of parasitic behavior, gained from the study of parasitoid wasp fossils. Well-preserved fossils from the Middle Jurassic Jiulongshan Formation and Upper Cretaceous Yixian Formation in northeastern China, as well as Cretaceous amber deposits from Myanmar, have been classified into 18 families. Such fossils have been found in 18 countries, with China, Kazakhstan, and Myanmar having the highest species diversity. Phylogenetic analyses integrating morphological traits and molecular data have elucidated the evolutionary history of families such as the Peleciniidae, Stephanidae and Evanioidea, suggesting a correlation between the Cretaceous diversification of parasitoid wasps and the rise of angiosperms. Recent discoveries, enabled by micro-CT and 3D reconstruction, highlight extinct taxa like *Tichostephanus longus* and *Sirenobethylus charybdis*, providing direct evidence for the origin and adaptation of parasitic behaviors. Future studies should emphasize integrating information from fossils with data on extant taxa to unravel the evolutionary history of parasitoid wasps and their ecology.

Key words parasitoid wasp fossils; Mesozoic; taxonomy; phylogeny

寄生蜂主要隶属于膜翅目细腰亚目, 因其幼虫阶段主要寄生在其他节肢动物(如昆虫、蜘蛛)体内完成发育, 并最终导致宿主死亡而得名。寄

生蜂在控制害虫种群、维持生态系统平衡及农林业害虫生物防治中具有重要作用(时敏等, 2020)。现生的寄生蜂体型通常较小, 触角细长, 雌蜂具

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管状特化的产卵器，用于刺入宿主体内产卵，部分种类具有金属光泽或鲜艳颜色，包含 11 个总科，如姬蜂总科 Ichneumonidea、小蜂总科 Chalcidoidea、细蜂总科 Proctotrupoidea、旗腹蜂总科 Evanioidea、冠蜂总科 Stephanoidea 等。寄生蜂化石研究作为古生物学和昆虫学交叉研究的重要领域，不仅包含寄生蜂化石的发现与形态分类，而且为重要特征的演化事件和寄生蜂习性的起源与辐射提供重要理论支撑（任东等，2022）。值得关注的是，自 2000 年以来，我国寄生蜂分类学者先后参与了这些类群的研究工作。

1 2000 年来我国寄生蜂化石经典分类研究概况

我国东北地区的中侏罗统九龙山组 and 上白垩

统义县组地层具有许多保存完好的寄生蜂印模化石，根据这些标本的形态学特征，研究人员目前已发表 10 科 23 属，最具代表性的有细蜂总科的长腹细蜂 Pelecinidae、柄腹细蜂 Heloridae 和中细蜂 Mesoserphidae，旗腹蜂总科的现生科化石记录和化石科，古老的已灭绝类群魔蜂科 Ephialtitidae。除了印模化石，缅甸北部克钦邦的胡康河谷保存有晚白垩世早期丰富的三维立体琥珀化石标本，文献报道的化石类群也已超过 10 科，既有典型的生物防治寄生蜂姬蜂科和茧蜂科，又有目前仅在缅甸发现的特有类群缅甸蜂科。有幸的是，2000 年以来，我国寄生蜂分类工作者先后都参与了这些类群的研究工作，部分化石代表如图 1（A-K）。

1.1 寄生蜂化石研究简史

寄生蜂化石的研究历史长达百年之久。20 世



图 1 中国部分寄生蜂化石标本（任东等，2022）

Fig. 1 Parasitic fossil specimens from China (Ren et al., 2022)

A 和 G. 魔蜂科；B. 长腹细蜂科；C. 中细蜂科；D 和 F. 原举腹蜂科；E. 异背蜂科；

H. 卡拉达蜂科；I. 柄腹细蜂科；J. 旗腹蜂科；K. 拜萨德蜂科。比例尺：1 mm。

A and G. Ephialtitidae; B. Pelecinidae; C. Mesoserphidae; D and F. Praeaulacidae; E. Anomopterellidae;

H. Karatavittidae; I. Heloridae; J. Evaniidae; K. Baissidae. Scale bars: 1 mm.

纪初期是寄生蜂化石研究的萌芽阶段。1903 年, Meunier 对产自西班牙晚侏罗-早白垩世的化石标本进行研究, 鉴定描述魔蜂科 1 新种 *Ephialtites jurassicus* (Meunier, 1903)。1917 年, Cockerell 研究缅甸晚白垩世的琥珀化石并报道举腹蜂科 1 新种 *Electrofoenus gracilipes* (Cockerell, 1917)。1938 年, Rohdendorf 描述了产自俄罗斯晚侏罗世的柄腹细蜂科 1 新种 *Protocyrtus jurassicus* (Rohdendorf, 1938)。随后, Rasnitsyn 在 1972-1999 年先后报道了产自中国和哈萨克斯坦中侏罗世旗腹蜂总科和魔蜂科 18 属近 70 种化石新物种, 包括原举腹蜂科具有特殊柄状腹部第一节的 *Evanigaster* 和 *Evanioops* 属 (Rasnitsyn, 1963, 1972, 1973, 1975, 1977, 1983a, 1983b, 1986a, 1986b, 1990a, 1990b, 1991, 1994, 1999)。Townes 于 1973 年对产自俄罗斯早白垩世的化石进行研究, 鉴定描述了姬蜂科早期物种代表, 包括 *Ampliocella*、*Catachora*、*Eubaeus* 和 *Tanychora* 属 (Townes, 1973)。20 世纪末, 我国老一辈古昆虫学者林启彬、洪有崇、张俊峰、任东等逐渐融入世界古昆虫研究热潮, 报道了中国的寄生蜂新物种 *Humiryssus leucus*、*Sinocephus haifanggouensis*、*Cephenopsis mirabilis*、*Sinephialtites glyptus*、*Manlaya flexuosa* (Lin, 1980; Hong, 1983; Zhang, 1986; Ren et al., 1995)。自此, 我国寄生蜂化石研究也成为世界寄生蜂研究的重要组成部分。2000 年至今, 我国寄生蜂化石研究进入快速发展时期, 研究的深度和广度也逐渐从经典物种分类向探讨系统演化和生态环境与特殊行为起源延伸。分类鉴定描述报道新属种类群广泛, 旗腹蜂总科、细蜂总科、姬蜂总科、冠蜂总科等现生属种非常丰富的类群在化石中均有报道 (Zhang et al., 2002a, 2002b; Álvarez-Parra and Huang, 2004; Zhang and Rasnitsyn, 2003, 2004; Zhang and Zhang, 2001; 张俊峰, 2005; Duan and Cheng, 2006; Engel, 2006, 2019; Engel and Grimaldi, 2004, 2006; Feng et al., 2010; Shih et al., 2010; Liu et al., 2011; Ding et al., 2013; Li et al., 2018a,b; Jouault et al., 2020a, 2020b, 2020c; Ge et al., 2023), 而魔蜂科作为细腰亚目寄生部古老的灭绝科已报道化石 29 属 77 种 (任东等, 2022), 中生代寄生

蜂主要化石名录, 如表 1 所示。此外, 科内部开展了基于形态特征矩阵的支序系统学研究或几何形态学聚类分析, 如长腹细蜂科开展支序系统学研究发现自然选择更偏向于体型较大的雌性个体, 它具备更强寻找寄主并产卵的能力, 而其前翅翅脉的“X”结构使整个翅的稳定性和飞行能力相应增加 (Shih et al., 2010)。对同时具有现生和化石属种的总科, 开展全证据支序系统学分析。如旗腹蜂总科选取 63 个物种的 81 个形态特征, 结合现生 12 个物种的基因序列 (CO I、16S 和 28S) 进行全证据支序系统学分析 (Li et al., 2018a)。2010 年以后, 以分类学和系统学研究结果为支撑, 讨论特征或习性的起源演化逐渐成为寄生蜂化石研究的重点。从早期提出蜂腰演化的 3 条路线到寄生行为相关化石标本的发现, 有了更多解释习性的演化证据。值得一提的是, 近 10 年缅甸琥珀标本的大量报道, 提供了岩石印模化石标本二维生物形态分类上无法提供的生物三维结构和内部细节, 对于研究生物演化过程中特定历史时期的形态、结构和行为意义重大, 如缅甸琥珀保存的寄生蜂产卵器上特殊的感受器可能揭示了一种独特的寄生定位方式, 腹部末端特化的“捕蝇器”可能与控制宿主活动密切相关 (Wang et al., 2024a; Wu et al., 2025)。

1.2 寄生蜂化石类群和区域分布

中生代寄生蜂化石物种分布类群非常广泛, 2000 年后我国分类工作者参与度高的类群超过 17 个科, 如图 2, 其中包含寄生蜂的原始类群魔蜂 (Rasnitsyn and Zhang 2010; Zhang et al., 2014; Li et al., 2016, 2019) 和冠蜂科 Stephanidae (Li et al., 2017b; Zhang et al., 2018a, 2018c; Jouault et al., 2020c, 2021; Ge et al., 2023), 占物种类群分布比例为 18%。细蜂总科中生代的灭绝类群中细蜂科 Mesoserphidae (Zhang and Zhang, 2000b; Shih et al., 2011; Li et al., 2017c)、现生子遗类群长腹细蜂科 Pelecinidae (Zhang and Rasnitsyn, 2006; Liu et al., 2009; Shih et al., 2009; Guo et al., 2016a, 2016b; Uchida, 2024; Wang et al., 2024b) 和柄腹细蜂科 Heloridae (Zhang, 1992; Shi et al., 2013, 2014;

Li *et al.*, 2017d), 占物种类群分布比例为 25%。旗腹蜂总科因其自近裔特征腹部着生在并胸腹节很高处而明显区别于其它类群, 在寄生蜂化石中物种非常丰富, 涉及 8 科 63 属 194 种(Rasnitsyn and Brother, 2007; Rasnitsyn and Zhang, 2007; Li *et al.*, 2013a, 2014a, 2014b, 2015, 2018a; Poinar, 2019; Turrisi and Ellenberger, 2019; Shih *et al.*, 2020; Jouault and Nel, 2021; Jouault *et al.*, 2022; Jouault, 2023; Jouault and Rosse-Guillevic, 2023; Jouault and Huang, 2024), 占物种类群分布比例超过 38%。姬蜂科作为现生生物防治害虫的主要寄生蜂类群, 在中生代物种也较为丰富, 占物种类群分布比例为 14%(Kopylov, 2010, 2011, 2012, 2018; Kopylov and Zhang, 2015; Li *et al.*, 2017a, 2022; Kopylov *et al.*, 2021)。而缅甸琥珀目前特有的寄生蜂类群缅甸蜂科 Myanmarinidae 由于研究时间较短, 仅占比 1%(Li *et al.*, 2018b; Zhang *et al.*, 2018b; Jouault *et al.*, 2020c)。

此外, 中生代寄生蜂化石物种的区域分布涉及范围也比较广, 目前化石物种在世界 18 个国家均有记录, 包括西班牙(Rasnitsyn and Ansoerge, 2000; Rasnitsyn and Martínez-Delclòs, 2000; Peñalver *et al.*, 2010; Pérez-de la Fuente *et al.*,

2012)、中国(Hong and Wang, 1990; Zhang and Zhang, 2000a; Zhang *et al.*, 2007; Zhang and Rasnitsyn, 2008; Li *et al.*, 2013b, 2022, 2024; Li and Shih, 2015; Wang *et al.*, 2015; Zheng and Chen, 2017)、蒙古(Rasnitsyn, 2008; Kopylov, 2009)、哈萨克斯坦(Kozlov, 1968; Rasnitsyn, 1972)、缅甸(Engel *et al.*, 2013a, 2013b; Jennings *et al.*, 2013; Engel and Wang, 2016; Engel, 2017; Rasnitsyn and Öhm-Kühnle, 2018; Jouault, 2021; Rosse-Guillevic and Jouault, 2023; Jouault and Nel, 2024; Yang *et al.*, 2024; Ge *et al.*, 2025)、俄罗斯(Rasnitsyn, 1975)、美国(Basibuyuk *et al.*, 2000; Engel, 2013)、英国(Rasnitsyn *et al.*, 1998)、博茨瓦纳(Kopylov *et al.*, 2010)、黎巴嫩(Basibuyuk *et al.*, 2002; Deans, 2004)、澳大利亚(Jell and Duncan, 1986; Oberprieler *et al.*, 2012)、约旦(Kaddumi, 2007)、德国(Zessin, 1981, 1985; Rasnitsyn *et al.*, 2003)、巴西(Rasnitsyn, 1999)、朝鲜(Jon *et al.*, 2019; Won and So, 2022; Ri *et al.*, 2023)、印度(Rasnitsyn, 2008)、吉尔吉斯斯坦(Rasnitsyn, 1975) 和加拿大(McKellar *et al.*, 2013), 其中分布物种数量位居前 6 的国家依次是中国、哈萨克斯坦、缅甸、俄罗斯、蒙古和西班牙。

表 1 中生代寄生蜂化石昆虫名录
Table 1 List of Mesozoic fossil species of parasitica

科 Family	种 Species	产地 Distribution	年代 Period
Andreneliidae	<i>Andrenelia pinnata</i> Rasnitsyn and Martínez-Delclòs, 2000	西班牙 Spain	K ₁
Anomopterellidae	<i>Anomopterella ampla</i> Li <i>et al.</i> , 2013	中国 China	J ₂
	<i>Anomopterella brachystelis</i> Li <i>et al.</i> , 2013	中国 China	J ₂
	<i>Anomopterella brevis</i> Li <i>et al.</i> , 2014	中国 China	J ₂
	<i>Anomopterella coalita</i> Li <i>et al.</i> , 2013	中国 China	J ₂
	<i>Anomopterella divergens</i> Li <i>et al.</i> , 2013	中国 China	J ₂
	<i>Anomopterella gobi</i> Rasnitsyn, 2008	蒙古 Mongolia	J ₃
	<i>Anomopterella huangi</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Anomopterella mirabilis</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₂
	<i>Anomopterella ovalis</i> Li <i>et al.</i> , 2013	中国 China	J ₂
	<i>Anomopterella pygmaea</i> Li <i>et al.</i> , 2014	中国 China	J ₂
	<i>Choristopterella stenocera</i> Li <i>et al.</i> , 2013	中国 China	J ₂
	<i>Synaphopterella patula</i> Li <i>et al.</i> , 2013	中国 China	J ₂
Aulacidae	<i>Archeofoenus engeli</i> Turrisi and Ellenberger, 2019	缅甸 Myanmar	K ₂
	<i>Archeofoenus tartaricus</i> Engel, 2017	缅甸 Myanmar	K ₂
	<i>Electrofoenia jehani</i> Jouault <i>et al.</i> , 2020	缅甸 Myanmar	K ₂
	<i>Electrofoenops cockerelli</i> Turrisi and Ellenberger, 2019	缅甸 Myanmar	K ₂
	<i>Electrofoenops diminuta</i> Engel, 2017	缅甸 Myanmar	K ₂
	<i>Electrofoenops exaltatus</i> Li <i>et al.</i> , 2021	缅甸 Myanmar	K ₂

续表 1 (Table 1 continued)

科 Family	种 Species	产地 Distribution	年代 Period
Aulacidae	<i>Electrofoenops rasnitsyni</i> Turrisi and Ellenberger, 2019	缅甸 Myanmar	K ₂
	<i>Electrofoenus gracilipes</i> Cockerell, 1917	缅甸 Myanmar	K ₂
	<i>Exilaulacus advenus</i> Li et al., 2021	缅甸 Myanmar	K ₂
	<i>Exilaulacus eximius</i> Li et al., 2021	缅甸 Myanmar	K ₂
	<i>Exilaulacus latus</i> Li et al., 2018	缅甸 Myanmar	K ₂
	<i>Exilaulacus loculatus</i> Li et al., 2018	缅甸 Myanmar	K ₂
	<i>Hyptiogastrites electrinus</i> Cockerell, 1917	缅甸 Myanmar	K ₂
	<i>Paleoaulacus minutus</i> Jouault and Nel, 2021	缅甸 Myanmar	K ₂
Baissidae	<i>Aulacopsis laiyangensis</i> Hong and Wang, 1990	中国 China	K ₁
	<i>Baissa anomala</i> Rasnitsyn, 1975	俄罗斯 Russia	K ₁
	<i>Baissa magna</i> Rasnitsyn, 1991	俄罗斯 Russia	K ₁
	<i>Baissa mongolica</i> Rasnitsyn, 1991	俄罗斯 Russia	K ₁
	<i>Electrobaissa omega</i> Engel, 2013	新泽西 New Jersey	K ₂
	<i>Heterobaissa apetiola</i> Li et al., 2018	中国 China	K ₁
	<i>Humiryssus cancellatus</i> Zhang and Rasnitsyn, 2004	中国 China	K ₁
	<i>Humiryssus leucus</i> Lin, 1980	中国 China	K ₁
	<i>Humiryssus oculatissimus</i> Rasnitsyn and Jarzembowski, 1998	英国 Britain	K ₁
	<i>Humiryssus specialis</i> Zhang and Rasnitsyn, 2004	中国 China	K ₁
	<i>Humiryssus vulgatus</i> Zhang and Rasnitsyn, 2004	中国 China	K ₁
	<i>Manlaya anglica</i> Rasnitsyn and Jarzembowski, 1998	英国 Britain	K ₁
	<i>Manlaya ansorgei</i> Rasnitsyn and Martínez-Delclòs, 2000	西班牙 Spain	K ₁
	<i>Manlaya capelensis</i> Rasnitsyn and Jarzembowski, 1998	英国 Britain	K ₁
	<i>Manlaya caudata</i> Rasnitsyn, 1986	蒙古 Mongolia	K ₁
	<i>Manlaya corrugata</i> Rasnitsyn, 1986	蒙古 Mongolia	K ₁
	<i>Manlaya flexuosa</i> Ren et al., 1995	中国 China	K ₁
	<i>Manlaya ghidarina</i> Rasnitsyn, 1990	俄罗斯 Russia	K ₁
	<i>Manlaya gurbanica</i> Rasnitsyn, 1986	蒙古 Mongolia	K ₁
	<i>Manlaya lacabrua</i> Rasnitsyn and Ansorge, 2000	西班牙 Spain	K ₁
	<i>Manlaya laevinota</i> Rasnitsyn, 1986	蒙古 Mongolia	K ₁
	<i>Manlaya magna</i> Li et al., 2019	中国 China	K ₁
	<i>Manlaya minima</i> Álvarez-Parra and Huang, 2024	中国 China	K ₁
	<i>Manlaya mongolica</i> Rasnitsyn, 1980	蒙古 Mongolia	K ₁
	<i>Manlaya obscura</i> Rasnitsyn, 1986	蒙古 Mongolia	K ₁
	<i>Manlaya ockleyensis</i> Rasnitsyn and Jarzembowski, 1998	英国 Britain	K ₁
	<i>Manlaya pachyura</i> Rasnitsyn, 1990	俄罗斯 Russia	K ₁
	<i>Manlaya pallida</i> Rasnitsyn, 1986	蒙古 Mongolia	K ₁
	<i>Manlaya pinguis</i> Rasnitsyn, 1986	蒙古 Mongolia	K ₁
	<i>Manlaya proba</i> Li et al., 2019	中国 China	K ₁
	<i>Manlaya ultima</i> Li et al., 2019	中国 China	K ₁
	<i>Manlaya ventricosa</i> Rasnitsyn, 1986	蒙古 Mongolia	K ₁
	<i>Mesepipolaea nanligezhuangica</i> Zhang and Rasnitsyn, 2004	中国 China	K ₁
	<i>Mesepipolaea parva</i> Li et al., 2019	中国 China	K ₁
	<i>Tillywhimia colorata</i> Rasnitsyn and Jarzembowski, 1998	英国 Britain	K ₁
	<i>Tillywhimia spectra</i> Rasnitsyn and Jarzembowski, 1998	英国 Britain	K ₁

续表 1 (Table 1 continued)

科 Family	种 Species	产地 Distribution	年代 Period
Evaniidae	<i>Botsvania cretacea</i> Rasnitsyn and Brothers, 2007	博茨瓦纳 Botswana	K ₂
	<i>Burmaevania aequalis</i> Shih et al., 2020	缅甸 Myanmar	K ₂
	<i>Burmaevania brevis</i> Shih et al., 2020	缅甸 Myanmar	K ₂
	<i>Cretevania alcalai</i> Peñalver et al., 2010	西班牙 Spain	K ₂
	<i>Cretevania alonsoi</i> Peñalver et al., 2010	西班牙 Spain	K ₂
	<i>Cretevania bechlyi</i> Jennings et al., 2013	缅甸 Myanmar	K ₂
	<i>Cretevania concordia</i> Rasnitsyn and Jarzembowski, 1998	英国 Britain	K ₁
	<i>Cretevania cyrtocerca</i> Deans, 2004	黎巴嫩 Lebanon	K ₁
	<i>Cretevania exquisita</i> Zhang et al., 2007	中国 China	K ₁
	<i>Cretevania extincta</i> Kaddumi, 2007	约旦 Jordan	K ₁
	<i>Cretevania kachinensis</i> Rosse-Guillevic and Jouault, 2023	缅甸 Myanmar	K ₂
	<i>Cretevania major</i> Rasnitsyn, 1975	俄罗斯 Russia	K ₂
	<i>Cretevania meridionalis</i> Rasnitsyn, 1991	蒙古 Mongolia	K ₁
	<i>Cretevania minor</i> Rasnitsyn, 1975	俄罗斯 Russia	K ₂
	<i>Cretevania minuta</i> Rasnitsyn, 1975	俄罗斯 Russia	K ₂
	<i>Cretevania mitis</i> Li et al., 2014	中国 China	K ₁
	<i>Cretevania montoyai</i> Peñalver et al., 2010	西班牙 Spain	K ₂
	<i>Cretevania pristina</i> Zhang and Zhang, 2000	中国 China	K ₁
	<i>Cretevania rubusensis</i> Peñalver et al., 2010	西班牙 Spain	K ₂
	<i>Cretevania soplensis</i> Pérez-de la Fuente et al., 2012	西班牙 Spain	K ₁
	<i>Cretevania tenuis</i> Li et al., 2018	缅甸 Myanmar	K ₂
	<i>Cretevania venae</i> Zhang et al., 2007	中国 China	K ₁
	<i>Curtevania enervia</i> Li et al., 2018	缅甸 Myanmar	K ₂
	<i>Grimaldivania ackermani</i> Basibuyuk et al., 2000	美国 America	K ₂
	<i>Grimaldivania mckimorum</i> Engel, 2006	美国 America	K ₂
	<i>Iberoevania nova</i> Li et al., 2024	缅甸 Myanmar	K ₂
	<i>Iberoevania roblesi</i> Peñalver et al., 2010	西班牙 Spain	K ₂
	<i>Lebanevania azari</i> Basibuyuk and Rasnitsyn, 2002	黎巴嫩 Lebanon	K ₁
	<i>Newjersevania brevis</i> Li et al., 2018	缅甸 Myanmar	K ₂
	<i>Newjersevania casei</i> Basibuyuk et al., 2000	美国 America	K ₂
	<i>Newjersevania longa</i> Li et al., 2018	缅甸 Myanmar	K ₂
	<i>Newjersevania nascimbenei</i> Basibuyuk et al., 2000	美国 America	K ₂
	<i>Newjersevania rasnitsyni</i> Shih et al., 2020	缅甸 Myanmar	K ₂
	<i>Praevania sculpturata</i> Rasnitsyn, 1991	蒙古 Mongolia	K ₂
	<i>Protoparevania lourothi</i> Deans, 2004	黎巴嫩 Lebanon	K ₁
	<i>Sinuevania mira</i> Li et al., 2018	缅甸 Myanmar	K ₂
	<i>Sinuevania pouilloni</i> Jouault and Nel, 2024	缅甸 Myanmar	K ₂
	<i>Sorellevania deansi</i> Engel, 2006	缅甸 Myanmar	K ₂
	<i>Sorellevania guillami</i> Jouault, 2023	缅甸 Myanmar	K ₂
	<i>Sorellevania rara</i> Li et al., 2024	缅甸 Myanmar	K ₂
Gasteruptiidae	<i>Hypselogastrion simplex</i> Engel and Wang, 2016	缅甸 Myanmar	K ₂
	<i>Kotujellites crucis</i> Rasnitsyn, 1975	俄罗斯 Russia	K ₂
	<i>Kotujisca kholbotensis</i> Rasnitsyn, 1991	蒙古 Mongolia	K ₁
	<i>Tichostephanus hui</i> Engel, 2019	缅甸 Myanmar	K ₂

续表 1 (Table 1 continued)

科 Family	种 Species	产地 Distribution	年代 Period
Gasteruptiidae	<i>Tichostephanus longus</i> Wang et al., 2024	缅甸 Myanmar	K ₂
	<i>Tichostephanus kachinensis</i> Wang et al., 2024	缅甸 Myanmar	K ₂
Othniodellithidae	<i>Othniodellitha mantichora</i> Engel and Wang, 2016	缅甸 Myanmar	K ₂
	<i>Xenodellitha preta</i> Engel, 2017	缅甸 Myanmar	K ₂
	<i>Keratodellitha anubis</i> Jouault et al., 2022	缅甸 Myanmar	K ₂
	<i>Keratodellitha basilisci</i> Jouault et al., 2022	缅甸 Myanmar	K ₂
	<i>Keratodellitha kirin</i> Jouault et al., 2022	缅甸 Myanmar	K ₂
Praeaulacidae	<i>Archaulacus probus</i> Li et al., 2014	中国 China	J ₂
	<i>Archeogastrinus kachinensis</i> Jouault and Rosse-Guillevic, 2023	缅甸 Myanmar	K ₂
	<i>Aulacogastrinus ater</i> Rasnitsyn, 1983	哈萨克斯坦 Kazakhstan	J ₃
	<i>Aulacogastrinus hebeiensis</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Aulacogastrinus insculptus</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Aulacogastrinus longaciculatus</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Azygdellitha nova</i> Yang et al., 2024	缅甸 Myanmar	K ₂
	<i>Eosaulacus giganteus</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Eosaulacus granulatus</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Evanigaster petiolatus</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Evaniops rostratus</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Gulgonga beattiei</i> Oberprieler et al., 2012	澳大利亚 Australia	J ₃
	<i>Habraulacus zhaoi</i> Li et al., 2015	缅甸 Myanmar	K ₂
	<i>Habraulacus splendidus</i> Jouault and Huang, 2024	缅甸 Myanmar	K ₂
	<i>Hadraulacus perrarus</i> Li et al., 2023	缅甸 Myanmar	K ₂
	<i>Paleosyncrasis hongii</i> Poinar, 2019	缅甸 Myanmar	K ₂
	<i>Praeaulacinus crassipes</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacinus minor</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacinus parvus</i> Rasnitsyn, 1973	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacinus medius</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacites minimus</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacites nigripes</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacites pachygaster</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacites subniger</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacon caudatus</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacon coniventer</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacon elongatus</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacon tenuis</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacon elegantulus</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Praeaulacon ningchengensis</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Praeaulacon grossus</i> Li et al., 2022	中国 China	J ₂
	<i>Praeaulacops lucidus</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacus subrhombeus</i> Li et al., 2014	中国 China	J ₂
	<i>Praeaulacus tenellus</i> Li et al., 2014	中国 China	J ₂
	<i>Praeaulacus afflatus</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Praeaulacus byssinus</i> Wang et al., 2015	中国 China	J ₂
	<i>Praeaulacus cephalotus</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃

续表 1 (Table 1 continued)

科 Family	种 Species	产地 Distribution	年代 Period
Praeaulacidae	<i>Praeaulacus cubocephalus</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacus daohugouensis</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Praeaulacus elegans</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacus exquisitus</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Praeaulacus leptogaster</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacus obscurus</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacus obtutus</i> Li et al., 2014	中国 China	J ₂
	<i>Praeaulacus orientalis</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Praeaulacus patiens</i> Rasnitsyn, 2008	蒙古 Mongolia	J ₃
	<i>Praeaulacus ramosus</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praeaulacus rectus</i> Li et al., 2018	中国 China	J ₂
	<i>Praeaulacus robustus</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Praeaulacus scabratus</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Praeaulacus sculptus</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Praeaulacus sharteg</i> Rasnitsyn, 2008	中国 China	J ₂
	<i>Praeaulacus ventricosus</i> Rasnitsyn, 1972	哈萨克斯坦 Kazakhstan	J ₃
	<i>Praegastrinus edithae</i> Jouault and Nel, 2024	缅甸 Myanmar	K ₂
	<i>Sinaulacogastrinus eucallus</i> Zhang and Rasnitsyn, 2008	中国 China	J ₂
	<i>Mesevania swinhoei</i> Basibuyuk et al., 2000	缅甸 Myanmar	K ₂
	<i>Cretocleistogaster vitimica</i> Rasnitsyn, 1975	俄罗斯 Russia	K ₂
	<i>Cretocleistogaster undurgensis</i> Rasnitsyn, 1975	俄罗斯 Russia	K ₂
	<i>Cretocleistogaster hyperura</i> Rasnitsyn, 1990	俄罗斯 Russia	K ₂
	<i>Miniwestratia minima</i> Rasnitsyn, 1990	蒙古 Mongolia	J ₃
	<i>Nanowestratia parvula</i> Rasnitsyn, 1990	俄罗斯 Russia	K ₂
	<i>Sinowestratia communicata</i> Zhang and Zhang, 2000	中国 China	J ₂
	<i>Westratia nana</i> Jell and Duncan, 1986	澳大利亚 Australia	J ₃
	<i>Westratia caudata</i> Rasnitsyn, 1990	俄罗斯 Russia	K ₂
	<i>Westratia curtipes</i> Rasnitsyn, 1990	俄罗斯 Russia	K ₂
	<i>Westratia femorata</i> Rasnitsyn, 1990	蒙古 Mongolia	J ₃
	<i>Westratia gobiensis</i> Rasnitsyn, 1990	蒙古 Mongolia	J ₃
	<i>Westratia pachygaster</i> Rasnitsyn, 1990	蒙古 Mongolia	J ₃
	<i>Westratia pentadecamera</i> Rasnitsyn, 1990	蒙古 Mongolia	J ₃
	<i>Westratia striata</i> Rasnitsyn, 1990	俄罗斯 Russia	K ₂
	<i>Nevania robusta</i> Zhang and Rasnitsyn, 2007	中国 China	J ₂
	<i>Nevania deviata</i> Li et al., 2022	中国 China	J ₂
	<i>Nevania exquisita</i> Zhang and Rasnitsyn, 2007	中国 China	J ₂
	<i>Nevania malleata</i> Zhang and Rasnitsyn, 2007	中国 China	J ₂
	<i>Nevania ferocula</i> Zhang and Rasnitsyn, 2007	中国 China	J ₂
	<i>Nevania retenta</i> Zhang and Rasnitsyn, 2007	中国 China	J ₂
	<i>Nevania delicata</i> Zhang and Rasnitsyn, 2007	中国 China	J ₂
	<i>Nevania karatau</i> Zhang and Rasnitsyn, 2008	哈萨克斯坦 Kazakhstan	J ₃
	<i>Nevania perbella</i> Li et al., 2014	中国 China	J ₂
	<i>Nevania aspectabilis</i> Li et al., 2014	中国 China	J ₂
	<i>Eonevania robusta</i> Rasnitsyn and Zhang, 2010	中国 China	J ₂

续表 1 (Table 1 continued)

科 Family	种 Species	产地 Distribution	年代 Period
Praeaulacidae	<i>Rasnitsevania ferox</i> Jouault <i>et al.</i> , 2020	缅甸 Myanmar	K ₂
Aptenoperissidae	<i>Aptenoperissus amabilis</i> Zhang <i>et al.</i> , 2018	缅甸 Myanmar	K ₂
	<i>Aptenoperissus burmanicus</i> Rasnitsyn and Poinar, 2017	缅甸 Myanmar	K ₂
	<i>Aptenoperissus delicatus</i> Zhang <i>et al.</i> , 2018	缅甸 Myanmar	K ₂
	<i>Aptenoperissus etius</i> Rasnitsyn <i>et al.</i> , 2018	缅甸 Myanmar	K ₂
	<i>Aptenoperissus formosus</i> Zhang and Rasnitsyn, 2018	缅甸 Myanmar	K ₂
	<i>Aptenoperissus magnifemoris</i> Rasnitsyn <i>et al.</i> , 2018	缅甸 Myanmar	K ₂
	<i>Aptenoperissus pusillus</i> <i>et al.</i> , 2018	缅甸 Myanmar	K ₂
	<i>Aptenoperissus zonalis</i> Zhang <i>et al.</i> , 2018	缅甸 Myanmar	K ₂
Ephialtitidae	<i>Acephialtitia colossa</i> Li <i>et al.</i> , 2015	中国 China	K ₁
	<i>Altephialtites altaicus</i> Rasnitsyn, 2008	蒙古 Mongolia	J ₃
	<i>Asiephialtites lini</i> Rasnitsyn and Zhang, 2010	中国 China	K ₁
	<i>Brigittepterus brauckmanni</i> Rasnitsyn <i>et al.</i> , 2003	德国 Germany	J ₁
	<i>Cephenopsis mirabilis</i> Hong, 1983	中国 China	K ₁
	<i>Cratephialtites koiurus</i> Rasnitsyn, 1990	巴西 Brazil	K ₁
	<i>Crephanogaster femorata</i> Rasnitsyn, 1990	俄罗斯 Russia	K ₁
	<i>Crephanogaster rara</i> Zhang <i>et al.</i> , 2002	中国 China	K ₁
	<i>Ephialtites jurassicus</i> Meunier, 1903	西班牙 Spain	K ₁
	<i>Karataus daohugouensis</i> Zhang <i>et al.</i> , 2014	中国 China	J ₂
	<i>Karataus strenuus</i> Zhang <i>et al.</i> , 2014	中国 China	J ₂
	<i>Karataus vigoratus</i> Zhang <i>et al.</i> , 2014	中国 China	J ₂
	<i>Karataus exilis</i> Zhang <i>et al.</i> , 2014	中国 China	J ₂
	<i>Karataus orientalis</i> Zhang <i>et al.</i> , 2014	中国 China	J ₂
	<i>Karataus hispanicus</i> Rasnitsyn and Martínez-Delclòs, 2000	西班牙 Spain	K ₁
	<i>Karataus pedalis</i> Rasnitsyn, 1977	哈萨克斯坦 Kazakhstan	J ₃
	<i>Karataus ryonsangensis</i> Won and So, 2022	朝鲜 North Korea	K ₁
	<i>Karataviola leptogastra</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Karataviola micrura</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Kotaphialtites frankmortoni</i> Rasnitsyn, 2008	印度 India	J ₁
	<i>Leptephalitites angustus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Leptephalitites caudatus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Leptephalitites euryarthrus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Leptephalitites gigas</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Leptephalitites linearis</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Leptephalitites minor</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Leptephalitites pallidus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Leptephalitites picturatus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Leptephalitites stephanocephalus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Leptephalitites tenuicornis</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Liadobracona raduhna</i> Zessin, 1981	德国 Germany	J ₁
	<i>Mesephialtites paurocerus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Microphialtites minor</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Montsecephialtites zherikhini</i> Rasnitsyn and Martínez-Delclòs, 2000	西班牙 Spain	K ₁
	<i>Parephialtites reductus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃

续表 1 (Table 1 continued)

科 Family	种 Species	产地 Distribution	年代 Period
Ephialtitidae	<i>Praeproapocritus vulgates</i> Rasnitsyn and Zhang, 2010	中国 China	J ₂
	<i>Praeproapocritus flexus</i> Li et al., 2013	中国 China	J ₂
	<i>Proapocritus atropus</i> Rasnitsyn and Zhang, 2010	中国 China	J ₂
	<i>Proapocritus bialatus</i> Li et al., 2015	中国 China	J ₂
	<i>Proapocritus densipediculus</i> Rasnitsyn and Zhang, 2010	中国 China	J ₂
	<i>Proapocritus elegans</i> Rasnitsyn and Zhang, 2010	中国 China	J ₂
	<i>Proapocritus formosus</i> Rasnitsyn and Zhang, 2010	中国 China	J ₂
	<i>Proapocritus longatennatus</i> Rasnitsyn and Zhang, 2010	中国 China	J ₂
	<i>Proapocritus sculptus</i> Rasnitsyn and Zhang, 2010	中国 China	J ₂
	<i>Proapocritus praecursor</i> Rasnitsyn 1975	吉尔吉斯斯坦 Kyrgyzstan	J ₁
	<i>Proapocritus parallelus</i> Li et al., 2013	中国 China	J ₂
	<i>Proepialtitia acanthi</i> Li et al., 2015	中国 China	J ₂
	<i>Proepialtitia tenuata</i> Li et al., 2015	中国 China	J ₂
	<i>Sessiliventer macrurus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Sessiliventer oppositus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Sessiliventer rostratus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Sessiliventer symphytus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Sessiliventer temporalis</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Sinephialtites glyptus</i> Zhang, 1986	中国 China	J ₂
	<i>Sinocephus haifanggouensis</i> Hong, 1983	中国 China	J ₂
	<i>Stephanogaster pristinus</i> Rasnitsyn, 1975	中国 China	J ₂
	<i>Stephanogaster brachyura</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Stephanogaster integra</i> Li et al., 2019	中国 China	J ₂
	<i>Stephanogaster longipalpa</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Stephanogaster magna</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Stephanogaster ningchengensis</i> Ding et al., 2013	中国 China	J ₂
	<i>Stephanogaster similis</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Stephanogaster pyriformis</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Stephanogaster rasnitsyni</i> Ding and Zhang, 2016	中国 China	J ₂
	<i>Symphyogaster cylindrica</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Symphytopterus graciler</i> Wang et al., 2015	中国 China	J ₂
	<i>Symphytopterus dubius</i> Rasnitsyn, 1963	哈萨克斯坦 Kazakhstan	J ₃
	<i>Symphytopterus liasinus</i> Zessin, 1985	德国 Germany	J ₁
	<i>Symphytopterus ater</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Symphytopterus clavicornis</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Symphytopterus geniculatus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Symphytopterus macrophthalmus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Symphytopterus minutus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Symphytopterus nigricornis</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Symphytopterus nigridorsatus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Symphytopterus nigripes</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Symphytopterus obliquus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Symphytopterus oculatus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Symphytopterus pallicornis</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃

续表 1 (Table 1 continued)

科 Family	种 Species	产地 Distribution	年代 Period
Ephialtitidae	<i>Symphyocterus pallipes</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Symphyocterus robustus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Thiopterus lampei</i> Rasnitsyn et al., 2003	德国 Germany	J ₁
	<i>Tuphephialtites zherikhini</i> Zhang et al., 2002	中国 China	K ₁
	<i>Trigonalopterus brachycerus</i> Rasnitsyn, 1975	哈萨克斯坦 Kazakhstan	J ₃
	<i>Archaeohelorus hoi</i> Shih et al., 2011	中国 China	J ₂
Heloridae	<i>Archaeohelorus polyneurus</i> Shi et al., 2014	中国 China	J ₂
	<i>Archaeohelorus tensus</i> Shi et al., 2014	中国 China	J ₂
	<i>Bellohelorus fortis</i> Li et al., 2017	中国 China	K ₂
	<i>Conohelorus stenocerus</i> Rasnitsyn, 1990	俄罗斯 Russia	K ₁
	<i>Laiyanghelorus erymnus</i> Zhang, 1992	中国 China	K ₁
	<i>Liaoropronia leonine</i> Zhang and Zhang, 2001	中国 China	K ₁
	<i>Liaoropronia regia</i> Zhang and Zhang, 2001	中国 China	K ₁
	<i>Obconohelorus obconicus</i> Rasnitsyn, 1990	俄罗斯 Russia	K ₁
	<i>Novhelorus macilentus</i> Li et al., 2017	中国 China	K ₁
	<i>Novhelorus saltatrix</i> Shi et al., 2013; Li et al., 2017	中国 China	K ₁
	<i>Protocyrtus jurassicus</i> Rohdendorf, 1938	俄罗斯 Russia	J ₃
	<i>Protocyrtus turgensis</i> Rasnitsyn, 1990	俄罗斯 Russia	K ₁
	<i>Protocyrtus mongolicus</i> Li et al., 2017	蒙古 Mongolia	K ₁
	<i>Protocyrtus parilis</i> Li et al., 2017	中国 China	K ₁
	<i>Sinohelorus elegans</i> Shi et al., 2013	中国 China	K ₁
	<i>Spherogaster coronata</i> Zhang and Zhang, 2001	中国 China	K ₁
	<i>Spherogaster beipiaoensis</i> Shi et al., 2013; Li et al., 2017	中国 China	K ₁
	<i>Sinuijuhelorus baektoensis</i> Jon et al., 2019	朝鲜 North Korea	K ₁
	<i>Paekthohelorus sinuijuensis</i> Ri et al., 2023	朝鲜 North Korea	K ₁
	<i>Agapia sukatchevae</i> Kopylov, 2012	俄罗斯 Russia	K ₂
Ichneumonidae	<i>Agapteron popovi</i> Kopylov, 2012	俄罗斯 Russia	K ₂
	<i>Albertocryptus dossenius</i> McKellar et al., 2013	加拿大 Canada	K ₂
	<i>Ampllicella abbreviata</i> Li et al., 2019	中国 China	K ₁
	<i>Ampllicella bashkuyevi</i> Kopylov, 2011	俄罗斯 Russia	K ₁
	<i>Ampllicella beipiaoensis</i> Zhang and Rasnitsyn, 2003; Kopylov, 2010	中国 China	K ₁
	<i>Ampllicella exquisita</i> Zhang and Rasnitsyn, 2003; Kopylov, 2010	中国 China	K ₁
	<i>Ampllicella exquisitissima</i> Kopylov and Zhang, 2015	中国 China	K ₁
	<i>Ampllicella flagellata</i> Kopylov and Zhang, 2015	中国 China	K ₁
	<i>Ampllicella mininae</i> Kopylov, 2011	俄罗斯 Russia	K ₁
	<i>Ampllicella minor</i> Kopylov, 2018	俄罗斯 Russia	K ₁
	<i>Ampllicella sessilis</i> Townes, 1973	俄罗斯 Russia	K ₁
	<i>Ampllicella shcherbakovi</i> Kopylov, 2011	俄罗斯 Russia	K ₁
	<i>Ampllicella spinata</i> Zhang and Rasnitsyn, 2003; Kopylov, 2010	中国 China	K ₁
	<i>Ampllicella townesi</i> Kopylov and Zhang, 2015	中国 China	K ₁
	<i>Angitia nigra</i> Kopylov and Zhang, 2015	中国 China	K ₁
	<i>Armanopimpla zherikhini</i> Kopylov, 2010	俄罗斯 Russia	K ₂
	<i>Caloichneumon perrarus</i> Li et al., 2017	缅甸 Myanmar	K ₂
	<i>Catachora minor</i> Townes, 1973	俄罗斯 Russia	K ₂

续表 1 (Table 1 continued)

科 Genus	种 Species	产地 Distribution	年代 Period
Ichneumonidae	<i>Dischysma maculata</i> Kopylov, 2009	蒙古 Mongolia	K ₁
	<i>Dischysma ramulata</i> Kopylov, 2009	蒙古 Mongolia	K ₁
	<i>Dischysma similis</i> Kopylov, 2009	蒙古 Mongolia	K ₁
	<i>Eubaeus abdominalis</i> Kopylov, 2012	俄罗斯 Russia	K ₂
	<i>Eubaeus leiponeura</i> Townes, 1973	俄罗斯 Russia	K ₂
	<i>Heteroichneumon rasnitsyni</i> Kopylov et al., 2021	缅甸 Myanmar	K ₂
	<i>Heteropimpla megista</i> Li et al., 2019	缅甸 Myanmar	K ₂
	<i>Heteropimpla pulverulenta</i> Kopylov et al., 2021	缅甸 Myanmar	K ₂
	<i>Khasurtella buriatica</i> Kopylov, 2011	俄罗斯 Russia	K ₁
	<i>Khasurtella Sinensis</i> Kopylov and Zhang, 2015	中国 China	K ₁
	<i>Khasurtella Zhangi</i> Kopylov and Zhang, 2015	中国 China	K ₁
	<i>Labenopimpla kasparyani</i> Kopylov, 2010	俄罗斯 Russia	K ₂
	<i>Labenopimpla orapa</i> Kopylov et al., 2010	博茨瓦纳 Botswana	K ₂
	<i>Labenopimpla rasnitsyni</i> Kopylov, 2010	俄罗斯 Russia	K ₂
	<i>Megachora sibirica</i> Kopylov, 2010	俄罗斯 Russia	K ₁
	<i>Micropimpla lucida</i> Kopylov, 2010	俄罗斯 Russia	K ₂
	<i>Micropimpla obscura</i> Kopylov, 2010	俄罗斯 Russia	K ₂
	<i>Novichneumon longus</i> Li et al., 2017	缅甸 Myanmar	K ₂
	<i>Palaeoichneumon danu</i> Kopylov, 2009	蒙古 Mongolia	K ₁
	<i>Palaeoichneumon freja</i> Kopylov, 2009	俄罗斯 Russia	K ₁
	<i>Palaeoichneumon micron</i> Kopylov, 2009	俄罗斯 Russia	K ₁
	<i>Palaeoichneumon mirabilis</i> Kopylov, 2009	俄罗斯 Russia	K ₁
	<i>Palaeoichneumon ornatus</i> Kopylov, 2009	蒙古 Mongolia	K ₁
	<i>Palaeoichneumon tenebrosus</i> Kopylov, 2009	蒙古 Mongolia	K ₁
	<i>Palaeoichneumon townesi</i> Kopylov, 2009	蒙古 Mongolia	K ₁
	<i>Paratanychora mongoliensis</i> Zhang and Rasnitsyn, 2003	蒙古 Mongolia	K ₁
	<i>Pareubaeus incertus</i> McKellar et al., 2013	加拿大 Canada	K ₂
	<i>Pareubaeus rasnitsyni</i> McKellar et al., 2013	加拿大 Canada	K ₂
	<i>Polychorella magica</i> Zhang, 1985	中国 China	K ¹
	<i>Ramulimonstrum intermedium</i> Kopylov, 2010	俄罗斯 Russia	K ₂
	<i>Rasnichneumon alexandri</i> Kopylov et al., 2021	缅甸 Myanmar	K ₂
	<i>Rasnichneumon gracilis</i> Kopylov et al., 2021	缅甸 Myanmar	K ₂
	<i>Rogichneumon braconidicus</i> Kopylov et al., 2021	缅甸 Myanmar	K ₂
	<i>Rudimentifera mora</i> Kopylov, 2009	蒙古 Mongolia	K ₁
	<i>Rudimentifera suspecta</i> Kopylov, 2009	俄罗斯 Russia	K ₁
	<i>Rugopimpla angusticella</i> Kopylov, 2010	俄罗斯 Russia	K ₂
	<i>Rugopimpla botswana</i> Kopylov et al., 2010	博茨瓦纳 Botswana	K ₂
	<i>Rugopimpla fallax</i> Kopylov, 2010	俄罗斯 Russia	K ₂
	<i>Rugopimpla macra</i> Kopylov, 2010	俄罗斯 Russia	K ₂
	<i>Rugopimpla matrona</i> Kopylov, 2010	俄罗斯 Russia	K ₂
	<i>Rugopimpla vulgaris</i> Kopylov, 2010	俄罗斯 Russia	K ₂
	<i>Sinochora distorta</i> Kopylov and Zhang, 2015	中国 China	K ₁
	<i>Tanychora liaoningensis</i> Kopylov and Zhang, 2015	中国 China	K ₁
	<i>Tanychora loki</i> Kopylov, 2010	蒙古 Mongolia	K ₁

续表 1 (Table 1 continued)

科 Family	种 Species	产地 Distribution	年代 Period
Ichneumonidae	<i>Tanychora petiolata</i> Townes, 1973	俄罗斯 Russia	K ₁
	<i>Tanychora rasnitsyni</i> Kopylov and Zhang, 2015	中国 China	K ₁
	<i>Tanychorella dubia</i> Zhang and Rasnitsyn, 2003	中国 China	K ₁
	<i>Tanychorella parvula</i> Rasnitsyn, 1975	俄罗斯 Russia	K ₁
	<i>Tryphopimpla xoridoptera</i> Kopylov, 2010	俄罗斯 Russia	K ₂
	<i>Urotryphon baikurensis</i> Kopylov, 2012	俄罗斯 Russia	K ₂
	<i>Urotryphon pusillus</i> Townes, 1973	俄罗斯 Russia	K ₂
	<i>Myanmarina kachin</i> Zhang and Rasnitsyn, 2018	缅甸 Myanmar	K ₂
Myanmarinidae	<i>Myanmarina lahu</i> Zhang and Rasnitsyn, 2018	缅甸 Myanmar	K ₂
	<i>Myanmarina lisu</i> Zhang and Rasnitsyn, 2018	缅甸 Myanmar	K ₂
	<i>Myanmarina jeannineae</i> Li <i>et al.</i> , 2018	缅甸 Myanmar	K ₂
	<i>Myanmarina sidorchukae</i> Jouault <i>et al.</i> , 2020	缅甸 Myanmar	K ₂
	<i>Cretephialtites pedrerae</i> Rasnitsyn and Ansoerge, 2000	西班牙 Spain	K ₁
Ohlhoffiidae	<i>Myanmephialtites bashkuevi</i> Jouault <i>et al.</i> , 2021	缅甸 Myanmar	K ₂
	<i>Ohlhoffia robusta</i> Jouault <i>et al.</i> , 2021	缅甸 Myanmar	K ₂
	<i>Abropelecinus annulatus</i> Feng <i>et al.</i> , 2010	中国 China	K ₁
Pelecinidae	<i>Abropelecinus tythus</i> Guo <i>et al.</i> , 2016	缅甸 Myanmar	K ₂
	<i>Abropelecinus rasnitsyni</i> Wang <i>et al.</i> , 2024	缅甸 Myanmar	K ₂
	<i>Abropelecinus rectus</i> Wang <i>et al.</i> , 2024	缅甸 Myanmar	K ₂
	<i>Allopelecinus terpnus</i> Zhang and Rasnitsyn, 2006	中国 China	K ₁
	<i>Allopelecinus ruoyae</i> Wang <i>et al.</i> , 2024	缅甸 Myanmar	K ₂
	<i>Ampluspelecinus robustus</i> Uchida, 2024	缅甸 Myanmar	K ₂
	<i>Archaeopelecinus jinzhouensis</i> Shih <i>et al.</i> , 2009	中国 China	J ₂
	<i>Archaeopelecinus tebbi</i> Shih <i>et al.</i> , 2009	中国 China	J ₂
	<i>Azygopelecinus clavatus</i> Feng <i>et al.</i> , 2010	中国 China	K ₁
	<i>Brachypelecinus euthyntus</i> Guo <i>et al.</i> , 2016	缅甸 Myanmar	K ₂
	<i>Cathaypelecinus daohugouensis</i> Shih <i>et al.</i> , 2009	中国 China	J ₂
	<i>Eopelecinus eucallus</i> Zhang, 2005	中国 China	K ₁
	<i>Eopelecinus diminutivum</i> Uchida, 2024	缅甸 Myanmar	K ₂
	<i>Eopelecinus exquisitus</i> Zhang and Rasnitsyn, 2004	俄罗斯 Russia	K ₁
	<i>Eopelecinus fragilis</i> Zhang and Rasnitsyn, 2004	蒙古 Mongolia	K ₁
	<i>Eopelecinus giganteus</i> Zhang, 2005	中国 China	K ₁
	<i>Eopelecinus hodoiporus</i> Zhang, 2005	中国 China	K ₁
	<i>Eopelecinus huangi</i> Liu <i>et al.</i> , 2011	中国 China	K ₁
	<i>Eopelecinus inopinatus</i> Jouault <i>et al.</i> , 2020	缅甸 Myanmar	K ₂
	<i>Eopelecinus laiyangicus</i> Zhang, 2005	中国 China	K ₁
	<i>Eopelecinus leptaleus</i> Zhang, 2005	中国 China	K ₁
	<i>Eopelecinus marechali</i> Jouault, 2021	缅甸 Myanmar	K ₂
	<i>Eopelecinus mecometasomatus</i> Zhang, 2005	中国 China	K ₁
	<i>Eopelecinus mesomicrus</i> Zhang, 2005	中国 China	K ₁
	<i>Eopelecinus minutus</i> Zhang and Rasnitsyn, 2004	蒙古 Mongolia	K ₁
	<i>Eopelecinus pusillus</i> Zhang, 2005	中国 China	K ₁
	<i>Eopelecinus rudis</i> Zhang and Rasnitsyn, 2004	俄罗斯 Russia	K ₁
	<i>Eopelecinus scorpioideus</i> Zhang and Rasnitsyn, 2004	俄罗斯 Russia	K ₁

续表 1 (Table 1 continued)

科 Family	种 Species	产地 Distribution	年代 Period
Pelecniidae	<i>Eopelecinus strangulatus</i> Wang et al., 2024	缅甸 Myanmar	K ₂
	<i>Eopelecinus shangyuanensis</i> Zhang et al., 2002	中国 China	K ₁
	<i>Eopelecinus similis</i> Zhang et al., 2002	中国 China	K ₁
	<i>Eopelecinus tumidus</i> Liu et al., 2011	中国 China	K ₁
	<i>Eopelecinus vicinus</i> Zhang et al., 2002	中国 China	K ₁
	<i>Eopelecinus yuanjiawaensis</i> Duan and Cheng, 2006	中国 China	K ₁
	<i>Henopelecinus pygmaeus</i> Engel and Grimaldi, 2006	美国 America	K ₂
	<i>Megapelecinus changi</i> Shih et al., 2010	中国 China	K ₁
	<i>Megapelecinus nashi</i> Shih et al., 2010	中国 China	K ₁
	<i>Praescopinus excellens</i> Rasnitsyn, 2008	蒙古 Mongolia	J ₃
	<i>Protopelecinus deformis</i> Zhang and Rasnitsyn, 2004	蒙古 Mongolia	K ₁
	<i>Protopelecinus dubius</i> Zhang and Rasnitsyn, 2004	蒙古 Mongolia	K ₁
	<i>Protopelecinus furtivus</i> Zhang and Rasnitsyn, 2004	俄罗斯 Russia	K ₁
	<i>Protopelecinus regularis</i> Zhang and Rasnitsyn, 2004	俄罗斯 Russia	K ₁
	<i>Sinopelecinus daspletis</i> Zhang and Rasnitsyn, 2006	中国 China	K ₁
	<i>Sinopelecinus delicatus</i> Zhang et al., 2002	中国 China	K ₁
	<i>Sinopelecinus epigaeus</i> Zhang et al., 2002	中国 China	K ₁
	<i>Sinopelecinus hierus</i> Zhang and Rasnitsyn, 2006	中国 China	K ₁
	<i>Sinopelecinus magicus</i> Zhang et al., 2002	中国 China	K ₁
	<i>Sinopelecinus viriosus</i> Zhang et al., 2002	中国 China	K ₁
	<i>Shoushida infera</i> Guo et al., 2016	中国 China	K ₁
	<i>Shoushida regilla</i> Liu et al., 2009	中国 China	K ₁
	<i>Sinopelecinus daspletis</i> Zhang and Rasnitsyn, 2006	中国 China	K ₁
	<i>Sinopelecinus delicatus</i> Zhang et al., 2002	中国 China	K ₁
	<i>Sinopelecinus epigaeus</i> Zhang et al., 2002	中国 China	K ₁
	<i>Sinopelecinus hierus</i> Zhang and Rasnitsyn, 2006	中国 China	K ₁
	<i>Sinopelecinus magicus</i> Zhang et al., 2002	中国 China	K ₁
	<i>Sinopelecinus viriosus</i> Zhang et al., 2002	中国 China	K ₁
	<i>Stelepelecinus longus</i> Guo et al., 2016	中国 China	K ₁
	<i>Stelepelecinus minutus</i> Wang et al., 2024	缅甸 Myanmar	K ₂
	<i>Zoropelecinus periosus</i> Guo et al., 2016	缅甸 Myanmar	K ₂
	<i>Zoropelecinus zigrasi</i> Engel and Grimaldi, 2013	缅甸 Myanmar	K ₂
	<i>Amboserphus beipiaoensis</i> Li et al., 2017	中国 China	K ₁
Mesoserphidae	<i>Amboserphus dimidiatus</i> Li et al., 2016	中国 China	K ₁
	<i>Amboserphus tumidus</i> Li et al., 2016	中国 China	K ₁
	<i>Apiciserphus augustus</i> Li et al., 2016	中国 China	K ₁
	<i>Auliserphus antennatus</i> Rasnitsyn, 1986	哈萨克斯坦 Kazakhstan	J ₃
	<i>Auliserphus brachyurus</i> Rasnitsyn, 1986	哈萨克斯坦 Kazakhstan	J ₃
	<i>Auliserphus caudatus</i> Rasnitsyn, 1986	哈萨克斯坦 Kazakhstan	J ₃
	<i>Auliserphus cretaceus</i> Rasnitsyn, 1990	哈萨克斯坦 Kazakhstan	J ₃
	<i>Auliserphus imperfectus</i> Rasnitsyn, 1986	哈萨克斯坦 Kazakhstan	J ₃
	<i>Auliserphus interstitialis</i> Rasnitsyn, 1986	哈萨克斯坦 Kazakhstan	J ₃
	<i>Auliserphus jurassicus</i> Rasnitsyn, 1986	哈萨克斯坦 Kazakhstan	J ₃
	<i>Auliserphus niger</i> Rasnitsyn, 1986	哈萨克斯坦 Kazakhstan	J ₃

续表 1 (Table 1 continued)

科 Family	种 Species	产地 Distribution	年代 Period
Mesoserphidae	<i>Auliserphus pallidus</i> Rasnitsyn, 1986	哈萨克斯坦 Kazakhstan	J ₃
	<i>Auliserphus parvulus</i> Rasnitsyn, 1986	哈萨克斯坦 Kazakhstan	J ₃
	<i>Basiserphus loculatus</i> Li et al., 2016	中国 China	K ₁
	<i>Basiserphus longus</i> Li et al., 2016	中国 China	J ₂
	<i>Beipiaoserphus elegans</i> Zhang and Zhang, 2000	中国 China	K ₁
	<i>Beipiaoserphus meridionalis</i> Rasnitsyn, 1994	哈萨克斯坦 Kazakhstan	J ₃
	<i>Campturoserphus gibbus</i> Rasnitsyn, 1986	哈萨克斯坦 Kazakhstan	J ₃
	<i>Campturoserphus obscurus</i> Rasnitsyn, 1986	哈萨克斯坦 Kazakhstan	J ₃
	<i>Campturoserphus pumilus</i> Rasnitsyn, 1986	哈萨克斯坦 Kazakhstan	J ₃
	<i>Choriserphus bellus</i> Li et al., 2016	中国 China	J ₂
	<i>Choriserphus gigantus</i> Li et al., 2016	中国 China	J ₂
	<i>Cretoserphus gomezi</i> Rasnitsyn and Martínez-Delclòs, 2000	西班牙 Spain	K ₁
	<i>Juraserphus modicus</i> Zheng and Chen, 2017	中国 China	J ₂
	<i>Karataoserphus dorsoniger</i> Rasnitsyn, 1994	哈萨克斯坦 Kazakhstan	J ₃
	<i>Lordoserphus cyrturus</i> Rasnitsyn, 1994	哈萨克斯坦 Kazakhstan	J ₃
	<i>Mesoserphus karatavicus</i> Kozlov, 1968	哈萨克斯坦 Kazakhstan	J ₃
	<i>Novserphus ningchengensis</i> Li et al., 2016	中国 China	J ₂
	<i>Otlia ectemnia</i> Zhang, 1992	中国 China	K ₁
	<i>Ozososerphus cuboidus</i> Li et al., 2016	中国 China	J ₂
	<i>Ozososerphus ovatus</i> Li et al., 2016	中国 China	J ₂
	<i>Ozososerphus lepidus</i> Li et al., 2016	中国 China	J ₂
	<i>Scoliuroserphus pallidulus</i> Rasnitsyn, 1986	哈萨克斯坦 Kazakhstan	J ₃
	<i>Scoliuroserphus propodealis</i> Rasnitsyn, 1986	哈萨克斯坦 Kazakhstan	J ₃
	<i>Sinoserphus flexilis</i> Li et al., 2016	中国 China	J ₂
	<i>Sinoserphus grossus</i> Li et al., 2016	中国 China	J ₂
	<i>Sinoserphus lilliana</i> Shih et al., 2011	中国 China	J ₂
	<i>Sinoserphus petilus</i> Li et al., 2016	中国 China	J ₂
	<i>Sinoserphus shihae</i> Shih et al., 2011	中国 China	J ₂
	<i>Sinoserphus wui</i> Shih et al., 2011	中国 China	J ₂
	<i>Turgoserphus sphenogaster</i> Rasnitsyn, 1990	俄罗斯 Russia	J ₁
	<i>Udaserphus transbaicalicus</i> Rasnitsyn, 1983	俄罗斯 Russia	J ₃
	<i>Yanliaoserphus jurassicus</i> Shih et al., 2011	中国 China	J ₂
	<i>Sinchora distorta</i> Kopylov and Zhang, 2015	中国 China	K ₁
	<i>Tanychora liaoningensis</i> Kopylov and Zhang, 2015	中国 China	K ₁
	<i>Tanychora rasnitsyni</i> Kopylov and Zhang, 2015	中国 China	K ₁
	<i>Tanychorella dubia</i> Zhang and Rasnitsyn, 2003	中国 China	K ₁
	<i>Acanthostephanus tenuitubus</i> Ge, Li and Tan, 2025	缅甸 Myanmar	K ₂
Stephanidae	<i>Archaeostephanus corae</i> Engel and Grimaldi, 2004	美国 America	K ₂
	<i>Burmastephanus breviceps</i> Ge and Tan, 2025	缅甸 Myanmar	K ₂
	<i>Kronostephanus zigrasi</i> Engel et al., 2013	缅甸 Myanmar	K ₂
	<i>Lagenostephanus lii</i> Li et al., 2017	缅甸 Myanmar	K ₂
	<i>Tumidistephanus prometheus</i> Ge and Tan, 2023	缅甸 Myanmar	K ₂
	<i>Squamastephanus shihongliangi</i> Ge and Tan, 2025	缅甸 Myanmar	K ₂

K₁: 早白垩世; K₂: 晚白垩世; J₁: 早侏罗世; J₂: 中侏罗世; J₃: 晚侏罗世。K₁: Early Cretaceous; K₂: Late Cretaceous; J₁: Early Jurassic; J₂: Middle Jurassic; J₃: Late Jurassic.

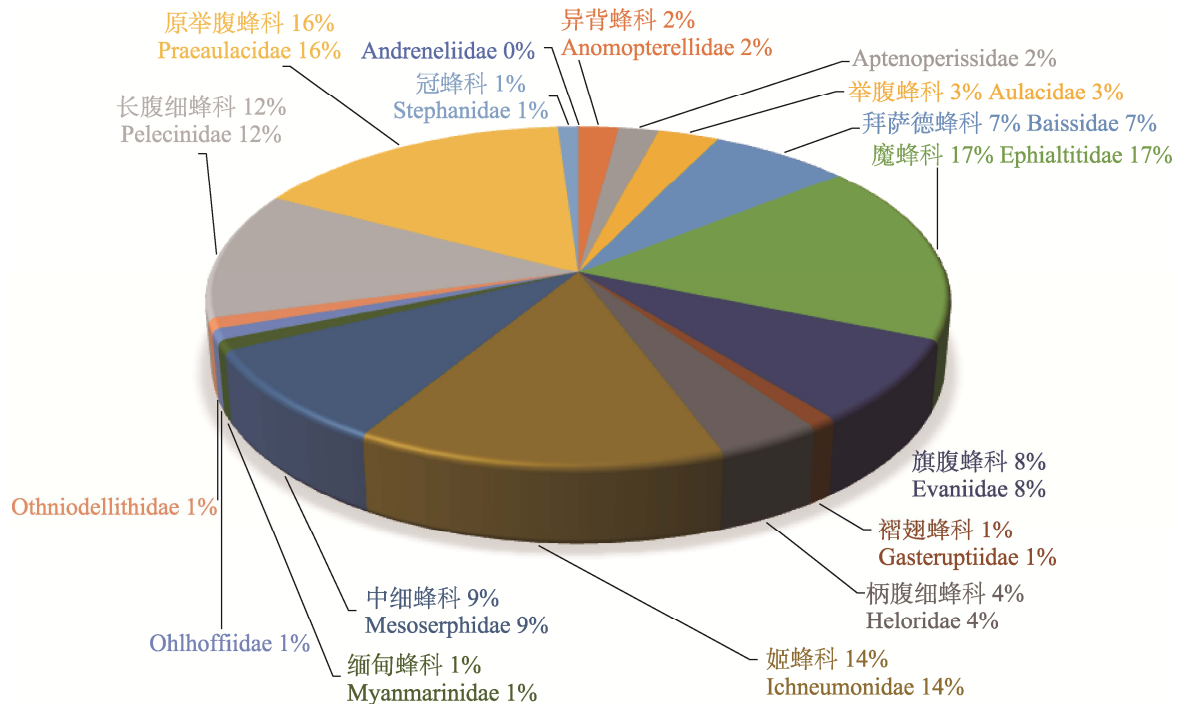


图 2 中生代寄生蜂化石主要类群

Fig. 2 Families of parasitic wasps in Mesozoic

1.3 寄生蜂化石时代特征

从中生代不同地质时期物种分布来看, 侏罗纪和白垩纪各个阶段都有寄生蜂化石发现(图 3), 其中侏罗世 164 种, 包括早侏罗世 7 种, 中侏罗世 80 种, 晚侏罗世 77 种; 白垩纪 329 种, 包括早白垩世 152 种, 晚白垩世 177 种。Whitfield 曾推测旗腹蜂总科在侏罗纪和白垩纪物种的分布格局可能与其内部各科寄生习性的差异及寄主的多样性有关(Whitfield, 1998)。而白垩纪早期植物化石的发现不断为被子植物的起源提供新见解, 认为许多植物的辐射伴随被子植物出现并促使被子植物迅速崛起, 占据陆地和许多水生生态系统(Shi *et al.*, 2021)。寄生蜂白垩纪物种量相较侏罗纪成倍增加, 这可能与白垩纪被子植物的兴起密切相关。

2 2000 年来我国寄生蜂化石系统发育研究概况

2000 年后, 在个别类群中, 如长腹细蜂科中, 基于 16 个属的 22 个形态特征进行支序系统学分

析, 阐明在 1.65 亿年间长腹细蜂翅脉特征的演化(Shih *et al.*, 2010), 如 Rs_1 在原始类群中直且伸达前翅前缘, 接近翅端部(图 4: A-C), 进化类群和现生类群到达翅边缘(图 4: G, H), 而 *Shoushida regilla*(图 4: E)则代表了一种过渡形态; Rs_2 在原始类群中缺失或极短, 在进化类群则发育良好, 并与 Rs 、 $2r-rs$ 及 Rs_1 共同构成“X”型翅脉结构, (图 4: E-H), 过渡类型 *Brachypelecinus euthyntus*(图 4: D)则具有发育不完全的 Rs_2 , 未延伸至翅端。长腹细蜂的翅脉演化从原始的直脉结构逐步过渡到复杂的“X”型分叉, 反映出其在飞行能力、体型演变以及寄生策略适应方面的系统发育趋势。琥珀化石的发现极大丰富了翅脉演化阶段的证据, 为理解中生代昆虫的辐射适应提供了关键线索。除翅脉演化, 雄性长腹细蜂的腹部各节也具有明显的演化路线(Guo *et al.*, 2016), 第一条演化路径从腹部非常宽阔逐渐变化形成腹部宽度明显变窄(图 5: A-C), 进一步演化至腹部各节愈加修长且柄后腹第一节形状更加规则, 似矩形, 末端逐渐加宽(图 5: D-G), 最终形成特化形态(图 5: H, I); 第二条演化路径从腹部非常宽阔变化形成柄后腹

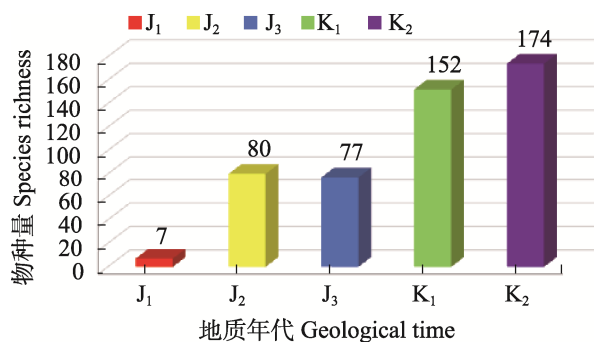


图3 中生代寄生蜂化石时代分布

Fig. 3 Distribution of parasitic wasps in Mesozoic

J₁: 早侏罗世; J₂: 中侏罗世; J₃: 晚侏罗世;K₁: 早白垩世; K₂: 晚白垩世。J₁: Early Jurassic; J₂: Middle Jurassic; J₃: Late Jurassic;K₁: Early Cretaceous; K₂: Late Cretaceous.

第一节显著加长且腹节 6 节, 其余各节逐渐变小 (图 5: J), 目前长腹细蜂子遗类群属于后者 (图 5: K), 这表明了第二条演化路径可能代表长腹细蜂自早白垩世相对原始腹部形态向现生形态演化的主流趋势。

此外, 在中细蜂科中, 基于 20 个属的 22 个特征开展支序系统学研究, 发现其前翅 1M 脉、1cu-a 脉、2m-cu 脉和 2cu-a 脉的 7 种不同组合类型 pa、pp、aa、ip、pi、ia 和 ii (Li *et al.*, 2016);

又如冠蜂科中, 选用 19 个类群的 34 个形态特征基于形态矩阵进行支序系统学分析, 发现早在晚白垩世早期 (100 Ma), 冠蜂科内部就出现了亚科的分化。Schlettereriinae 亚科作为一单系的支持特征是后足基节背侧具有齿状结构。Stephanidae 的第一腹节背板和腹板融合可能是一个逆转现象 (Li *et al.*, 2017b)。后续的研究对于冠蜂科内部物种做了重新厘定, 将 *Tichostephanus* 转移至褶翅蜂科 (Jouault *et al.*, 2020; Ge *et al.*, 2023; Wang *et al.*, 2024a; Ge *et al.*, 2025)。近年来, 现生膜翅目系统学研究不断取得重要成果, Peters 等 (2017) 选取了膜翅目 173 个物种的 3 256 个蛋白质编码基因开展系统发育研究, 研究结果推测现存膜翅目类群大约在 2.81 亿年前开始多元化, 寄生蜂独立为一个单系群, 而原始寄生蜂很可能是距今 2.47 亿年前单一寄主的寄生蜂后代 (Peters *et al.*, 2017)。但当考虑化石类群后, 各类群的关系变得混乱。所以目前尚没有完全基于化石形态特征或大比例加入化石形态特征的寄生蜂支序系统学研究, 仅在个别类群做了初步尝试。如旗腹蜂总科中, 选取旗腹蜂总科 63 个物种的 81 个形态特征, 结合现生 12 个物种的基因序列 (COI、16S

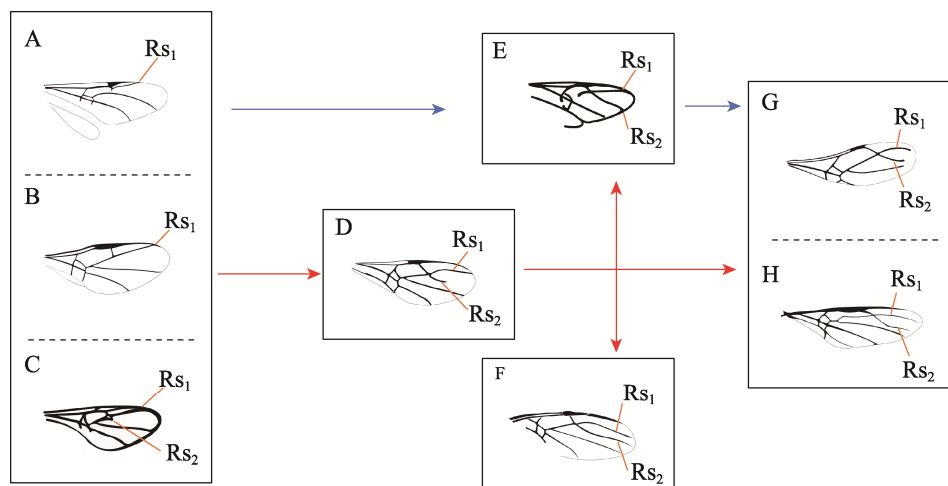


图4 长腹细蜂翅脉演化示意图

Fig. 4 The evolution pathway of wing venation in Peleciniidae

A. *Megapelecinus Changi*; B. *Cathaypelecinus daohugouensis*; C. *Archaeopelecinus tebbi*; D. *Brachypelecinus euthyntus*;E. *Shoushida regilla*; F. *Zoropelecinus zigrasi*; G. *Pelecinopteron tubniforme*; H. *Pelecinus Polyturator*.蓝色箭头和红色箭头分别为 Rs₁ 和 Rs₂ 的演化历程。Blue arrow and red arrow represent the evolutionary history of Rs₁ and Rs₂, respectively.

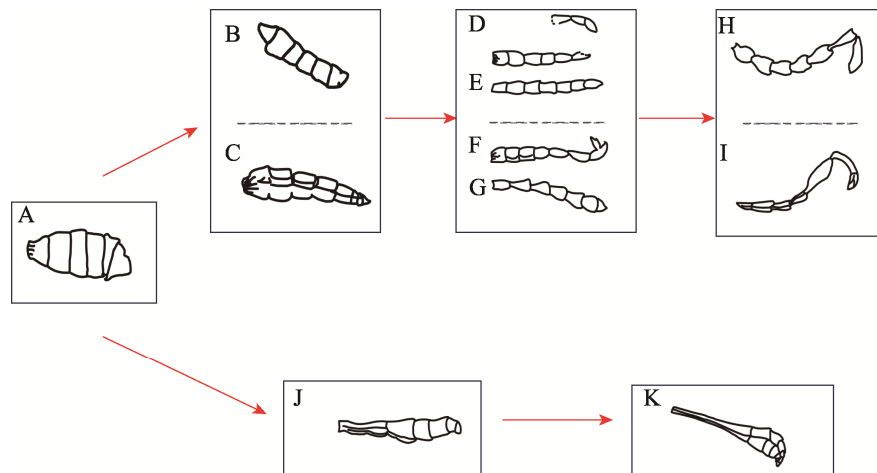


图5 长腹细蜂科雄性柄后腹从祖征形态到衍征形态演化路线示意图

Fig. 5 The evolution pathway of male metasoma in Peleciniidae

A. *Iscopinus simplex* Zhang and Rasnitsyn, 2004; B. *Iscopinus baissicus* Kozlov, 1974; C. *Praescopinus excellens* Rasnitsyn, 2008; D. *Protopelecinus regularis* Zhang and Rasnitsyn, 2004; E. *Sinopelecinus viriosus* Zhang, Rasnitsyn and Zhang, 2002; F. *Abropelecinus annulatus* Feng, Shih, Ren and Liu, 2010; G. *Azygopelecinus clavatus* Feng, Shih, Ren and Liu, 2010; H. *Henopelecinus pygmaeus* Engel and Grimaldi, 2006; I. *Pelecinopterion tubuliforme* Brues, 1933; J. *Stelepelecinus longus* Guo, Shih and Ren, 2016; K. *Pelecinus thoracicus* Klug, 1841.

和 28S) 进行全证据支序系统学分析, 为了使结果更接近自然谱系, 建议现生类群和化石类群所占比例应该相当 (Li *et al.*, 2018a)。Jouault 等 (2022) 利用 Bayesian 法和化石的出生-死亡模型对旗腹蜂总科做了新的系统发育研究, 并对各科的分化时间进行估计和验证。综上, 寄生蜂化石系统发育的研究仍有较大拓展空间。

3 2000 年来我国寄生蜂化石寄生行为研究案例

由于受到化石标本保存情况的限制, 昆虫化石研究中对于行为生态方面的研究相对困难。2016 年, 根据新发现的魔蜂科标本 (图 6: A), 研究人员提出蜂腰演化的三条路线, 即从魔蜂科非常宽阔的蜂腰结合结构向侏罗纪的绝灭科夸父科、现生冠蜂科以及典型的旗腹蜂式蜂腰结合方式转变 (Li *et al.*, 2016)。然而, 关于寄生习性的化石证据长期缺乏, 近年来随着缅甸琥珀三维标本的补充, 我国学者在寄生蜂化石寄生行为研究方面取得了重要进展。

2024 年, 首都师范大学任东教授研究团队发现了一类非常有趣的寄生蜂——墙冠褶翅蜂

Tichostephanus longus (图 6: B), 隶属于旗腹蜂总科现生褶翅蜂科。墙冠褶翅蜂保存了非常重要的几个特征, (1) 头部具有一排明显的“齿状”突起结构, 该结构普遍存在于木质寄生性昆虫中, 在成虫从寄主体内咬出通道时支撑头部; (2) 产卵器鞘存在横纹, 这种结构在寄生蜂产卵初期能够协助支撑、固定产卵器, 随着钻孔的进行, 产卵器鞘逐渐弯曲, 为进一步穿刺提供支撑; (3) 产卵器鞘顶端具有特化的“瓶刷”状感受器, 由许多规则排列的板状刚毛组成, 每根成片状的刚毛都非常薄, 具有平行的纵向脊延伸到边缘, 且刚毛基部都具有明显的毛点窝。这种异常扩大的板状刚毛在现生的寄生蜂中都没有观察到。考虑到感受器的着生位置, 这种独特的感受器可能在宿主定位中发挥作用, 很可能接收机械刺激或者化学刺激, 以探测来自寄主的振动或捕获空气中的化学分子。特征与功能的统一性暗示这一白垩纪寄生蜂很可能具备一种独特的寄主定位方式 (Wang *et al.*, 2024a)。

2025 年, 任东教授团队又描述了一类已经灭绝的寄生蜂——海妖肿腿蜂 *Sirenobethylus charybdis* (图 6: C), 隶属于青蜂总科灭绝海妖肿腿蜂科, 揭示了 1 亿年前白垩纪一类腹部末

端特化的寄生蜂控制宿主的寄生机制。海妖肿腿蜂的腹部末端格外膨大, 特化为一个类似“捕蝇器”的结构。CT 扫描显示, 第 6 节腹板向后延伸, 加宽加厚, 背面布满了“板状”硬刚毛; 第 7 腹板同样向后延长加宽, 呈近乎透明的柔韧的一片, “盖”在第 6 腹板的硬刚毛之上; 第 6 腹板向下弯曲与第 7 腹板之间形成一个可以张合的“捕捉”装置。第 6 节腹板后缘伸出了一排长长的、柔软的“触感”刚毛, 作用可能是“感知”宿主的精确位置。一旦宿主靠近, 第 6 节腹板张合, 就可以“抓住”宿主。而第 7 腹板后缘中间凹槽类似通道, 为短而尖的产卵器刺蜇寄主进行产卵提供便利 (Wu *et al.*, 2025)。

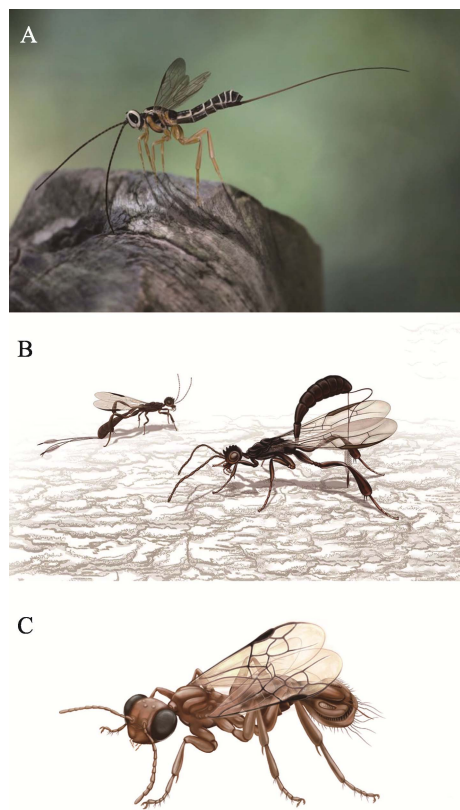


图 6 寄生行为研究代表化石复原图
Fig. 6 The 3D reconstruction images of parastitoid wasp

A. 魔蜂科; B. 褶翅蜂科; C. 海妖肿腿蜂科。
A. Ephialtitidae; B. Gasteruptionidae; C. Sirenobethylidae.

4 总结与展望

综上, 2000 年后我国寄生蜂化石研究在分类

学, 系统学和特征与功能演化方面都取得了一定的研究成果, 在寄生蜂演化历史及其与生态系统互动的多维度方面研究尚有诸多上升空间。未来的研究可进一步整合化石与现生类群的多源数据 (如形态学、分子生物学和古生态学), 应用显微 CT、三维重建及同步辐射成像等技术, 构建全证据系统发育框架, 以解析关键特征的演化轨迹及其适应性意义。

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