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Research Article

Phylogenetic Systematics of the Species-Groups of *Apanteles* and Related Genera From China Based on Mitogenomes

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The tribe Apantelini *sensu* Mason is the largest tribe within the subfamily Microgastrinae (Hymenoptera: Braconidae). It consists of parasitoids that attack a wide range of families of Lepidoptera and have potential significance for biological control. However, genera (and species-groups) included in this tribe often overlap, and due to the large number of species, they have never been tested extensively at a large scale, such as across the whole mitogenome. This study examined the mitogenomes of 25 species, including 21 newly sequenced species, representing four genera (*Apanteles* Foerster, *Dolichogenidea* Viereck, *Parapanteles* Ashmead, and *Pholetesor* Mason) traditionally regarded as Apantelini in China. Phylogenetic relationships among these species were inferred using MrBayes and IQ-TREE based on four data matrices (PCG123, PCG123 + RNA, PCG12, and AA). The average A + T content of the sequenced mitochondrial genomes was relatively high (86.5%), and gene rearrangements were evident, especially in the *ater* and *taeniaticornis* groups of the genus *Apanteles*. The phylogenetic analysis among these Chinese species revealed key relationships among major species-groups and genera. The genera *Apanteles* and *Dolichogenidea* were clearly separated, but *A. mycetophilus* was identified as a transitional group and very likely represents a different genus. Major species-groups, such as *A. ater* and *D. ultor*, were confirmed to be monophyletic. However, the *A. taeniaticornis* group is no longer supported as a distinct species-group based on the results of the current study, and their members actually belong to the *ater*-group. And we propose a new combination, *Dolichogenidea hyposidrae* comb. nov. (Wilkinson, 1928), based on the molecular data from this study, which cluster the species within the *ultor*-group. Additionally, the relationships between *Dolichogenidea*, *Parapanteles*, and *Pholetesor* are discussed.

Keywords: *Apanteles*; classification; *Dolichogenidea*; gene rearrangements; mitogenomics; *Parapanteles*; *Pholetesor*; phylogeny; species-group

1. Introduction

The subfamily Microgastrinae is important and hyperdiverse, comprising 82 valid genera and more than 3000 described species [1, 2]. Based on ratios of Lepidoptera and Microgastrinae species from several areas, the actual world diversity of Microgastrinae was expected to be between 30,000 and 50,000 species [1]. This high estimate is unsurprising, given their prevalence in most terrestrial habitats and the significant number of undescribed species in major collections.

As parasitoids of almost the entire range of families of Lepidoptera, microgastrine wasps are among the most important potential groups for the biological control of agricultural and forestry lepidopteran pests globally [3].

Two seminal works provided the foundational taxonomic framework for this subfamily. Nixon [4] recognized 20 genera, and reclassified the species within *Apanteles sensu lato* into 44 species-groups to facilitate identification. Mason [5] built upon Nixon's [4, 6] species-groups, recognizing 50 genera and establishing a system that has remained largely stable for the past 40 years. However, not all species within these genera have been adequately addressed, and the system has been challenged by several workers (e.g., [1, 7–12]). Most recently, tribal concepts have either been avoided [13] or deemed inadequate in a recent worldwide checklist [1]. A comprehensive phylogenetic analysis of the subfamily on a worldwide scale is severely needed. While some efforts are progressing, they offer partial resolution of the generic relationships, particularly regarding hyperdiverse genera based on several genes (e.g., [14–16]).

Fernández-Triana et al. [1] separated Microgastrinae into four broadly defined groups, most but not all the tribe Apantelini were included in the *Apanteles* group. The tribe Apantelini *sensu* Mason [5] is the largest in the subfamily Microgastrinae, comprising over 1400 described species worldwide. It is distributed across all geographical regions and accounts for nearly half of the described species in this subfamily [17]. Species within this tribe are characterized by the absence of vein r-m in the fore wing, the propodeum often without a medio-longitudinal carina posteriorly, and the ovipositor sheaths usually longer than half the length of the metatibia and always setose throughout [5]. The concept of Apantelini as defined by Mason [5] is used for convenience, because it is widely recognized that the current tribal and generic classifications of Microgastrinae are imperfect [1, 10]. Ongoing and future phylogenetic studies may challenge and redefine the existing generic concepts [18]. Yu et al. [17] included only the genus *Apanteles* Foerster from China, but their generic concept included *Dolichogenidea*, *Exoryza*, *Iconella*, *Illidops*, and *Pholetesor* as subgenera. Many of these taxa, however, are treated as valid genera by other authors [1, 19–23], despite their morphological similarities. Some generic boundaries remain poorly defined, particularly between *Dolichogenidea* and both *Apanteles* and *Pholetesor* [1, 18].

Apanteles s. str., as defined by Mason [5], included Nixon's [4, 6] *ater*, *caesar*, *crassicornis*, *grandiculus*, *mycetophilus*, *taeniaticornis*, *trifasciatus* species-groups, along with most of the *A. metacarpalis* group. Papp [24–26] later added the *lacteus*- and *laspeyresiella*-groups, which are mainly found in Europe. This genus is the largest mega-genus within Microgastrinae, comprising 681 described species [2], with 137 species in seven species-groups—*ater*, *grandiculus*, *lacteus*, *laspeyresiella*, *metacarpalis*, *mycetophilus*, and *taeniaticornis* have been reported from China [27–30]. The *ater*-group, among them, constitutes 80% of the species in China. *Choeras* is also known from China and has been included in *Apanteles* (e.g., [31]). However, *Choeras* is regarded as one of the most variable genera of Microgastrinae, exhibiting significant morphological and ecological diversity (e.g., [32, 33]). Many Oriental species probably represent lineages distinct from those found in temperate regions, and may warrant placement in different genera [1], as these lineages show unique adaptations and characteristics (Ghafouri Moghaddam, personal observations). Furthermore, the taxonomy of *Choeras* remains unclear due to the high degree of morphological variability, and this genus requires further study to resolve its phylogenetic relationships. Obviously, much more molecular research, particularly using advanced sequencing techniques, is needed to uncover the true phylogenetic secrets of these genera and their species.

Dolichogenidea Viereck is the second-largest genus in Microgastrinae, with 468 species worldwide [34] and 124 from China [20, 21]. Despite the rather subtle morphological differences (as noted by [35]), DNA barcodes typically show that *Dolichogenidea* and *Apanteles* cluster separately [35, 36]. However, *Dolichogenidea* tends to cluster near *Pholetesor*, and both genera appear to be more closely related to each other than to *Apanteles* [1]. *Dolichogenidea* includes two species-groups: the *D. ultor* (76 spp.) and *D. laevigata*-groups (48 spp.) within the Chinese fauna, respectively [20, 21]. And *Exoryza* Mason was recently synonymized under *Dolichogenidea* by Fernandez-Triana et al. [34] with four species from China, making *Exoryza* maybe a third species-group of *Dolichogenidea* in China. The number of species groups for this genus is increasing as more taxa from different regions are examined [23].

The genus *Parapanteles* Ashmead includes 62 described species worldwide, and has recently been recorded from China since Fernández-Triana et al. [1] transferred six Chinese *Dolichogenidea* species: *P. aso* (Nixon), *P. expulsus* (Turner), *P. folia* (Nixon), *P. hemitheae* (Wilkinson), *P. hyposidrae* (Wilkinson), and *P. javensis* (Rohwer) to *Parapanteles* due to their short ovipositor sheaths and inflexible hypopygium. Previously, the genus contained 29 species from Australia, India, and some American countries. However, the boundaries of this genus remain controversial, as it often overlaps with *Dolichogenidea*, *Pholetesor*, and some borderline species of *Apanteles* [1]. The genus was found to be polyphyletic by [37], and its situation remains uncertain until a comprehensive morphological analysis of the boundaries of these genera is completed.

Pholetesor includes 60 described species worldwide [2], with 18 species known from China [19]. The genus was originally based on the *Apanteles circumscriptus* and *A. bucculatricis*-groups of Nixon [4] when it was erected by Mason [5]. Whitfield [38] later revised the Nearctic species of this genus, dividing them into eight species-groups, of which the *P. bedelliae*, *P. ornigis*- and *P. circumscriptus* groups are also reported from China [19].

Apanteles shows overlap with several other genera mentioned above, leading to confusion not only among taxonomists but also for ecologists, biocontrol researchers, and other nontaxonomists worldwide. In China, Liu et al. [19–21, 27–29] have attempted to use the species-group concepts of Nixon [4, 6] and Papp [24–26] to subdivide this mega-genus. However, molecular data, as well as the inclusion of more taxa, are still needed to fully support and validate these results.

Three genes (*COI*, *16S*, and *28S*) were commonly used in early phylogenetic studies of Microgastrinae [14, 39], but these

Table 1: Detailed collection data of the sequenced taxa distributed in China.

Genus	Species-group	Species	Author(s)	Locality	Coordinates
Apanteles	*ater*	sp.	—	Guangdong	114°13′13.47″E, 22°54′26.09″N
Apanteles	*ater*	*altus*	Liu and Chen, 2020	Hunan	110°40′35.61″E, 30°2′59.38″N
Apanteles	*ater*	*dryas*	Nixon, 1965	Hunan	110°54′45.22″E, 30°2′15.96″N
Apanteles	*ater*	*gracilicornis*	Song and Chen, 2004	Hunan	111°31′58.74″E, 28°53′36.17″N
Apanteles	*ater*	*importunus*	Wilkinson, 1928	Hunan	111°42′33.89″E, 29°10′23.00″N
Apanteles	*ater*	*longicoxa*	Liu and Chen, 2020	Hunan	110°54′45.22″E, 30°2′15.96″N
Apanteles	*ater*	*medon*	Nixon, 1965	Hunan	110°54′45.22″E, 30°2′15.96″N
Apanteles	*ater*	*opacus*	(Ashmead, 1905)	Hunan	110°54′45.22″E, 30°2′15.96″N
Apanteles	*ater*	*pachycarinatus*	Song and Chen, 2002	Hunan	110°54′45.22″E, 30°2′15.96″N
Apanteles	*mycetophilus*	*hainanensis*	Liu and Chen, 2015	Hainan	109°30′21.23″E, 19°30′42.34″N
Apanteles	*mycetophilus*	*thoracartus*	Liu and Chen, 2015	Guangdong	112°32′20.70″E, 23°10′3.68″N
Apanteles	*taeniaticornis*	*conon*	Nixon, 1965	Hunan	112°42′55.88″E, 27°16′9.50″N
Dolichogenidea	*laevigata*	*breviventris*	(Ratzeburg, 1848)	Hunan	111°42′33.89″E, 29°10′23.00″N
Dolichogenidea	*laevigata*	*funalicauda*	Liu and Chen, 2018	Hainan	109°49′49.57″E, 18°43′42.58″N
Dolichogenidea	*laevigata*	sp. 1	—	Hunan	112°42′55.88″E, 27°16′9.50″N
Dolichogenidea	*ultor*	*asotae*	(Watanabe, 1932)	Hunan	111°42′33.89″E, 29°10′23.00″N
Dolichogenidea	*ultor*	*caniae*	(Wilkinson, 1928)	Guangdong	113°18′14.19″E, 23°5′41.07″N
Dolichogenidea	*ultor*	*inquisitor*	(Wilkinson, 1928)	Hainan	19°9′31.10″N109°1′48.40″E
Dolichogenidea	*ultor*	*latitergita*	Liu and Chen, 2019	Hunan	112°43′9.15″E, 27°16′2.59″N
Dolichogenidea	*ultor*	*stantoni*	(Ashmead, 1904)	Hunan	110°40′35.61″E, 30°2′59.38″N
Pholetesor	*ornigis*	*salalicus*	Mason, 1959	Hunan	110°54′45.22″E, 30°2′15.96″N

Note: All taxa examined in the current study from China were based on female specimens.

markers provided low bootstrap support for many branches and failed to adequately resolve generic relationships except for some terminal nodes [13]. The addition of four nuclear markers in subsequent studies offered slight improvement, but still conflicts between the morphological and molecular data remained [40]. To achieve better phylogenetic resolution for this group, more genes and larger datasets are required [13, 40]. A recent phylogenomic study on Braconidae (Jasso-Martinez et al. [41]) made significant progress by using a genomic-scale dataset based on ultra-conserved elements (UCEs) with comprehensive taxon sampling. Their analysis of 43 genera of Microgastrinae revealed that the New Zealand genus *Kiwigaster* was sister to the remaining Microgastrinae taxa. and the monophyly of *Microplitis* group *sensu* Fernandes-Triana et al. [1] (with representatives of *Alloplitis* + *Philoplitis* + *Snellenius* + *Jenopappius* + *Microplitis*) was well supported. However, the relationships among other mega-genera remain largely unresolved due to insufficient taxon sampling (most of the genera were represented by a single individual). Nevertheless, clearer patterns have emerged for some groups (e.g., *Pholetesor* + *Shireplitis*; *Glyptapanteles* + *Lathrapanteles* + *Sathon*; *Exoryza* + *Parapanteles*). Future studies, incorporating broader sampling, will likely build upon these findings.

To date, only a limited number of complete or near-complete mitochondrial genomes of Microgastrinae wasps have been available in GenBank/NCBI (https://www.ncbi.nlm.nih.gov/). Moreover, no research has yet been published utilizing mitochondrial genomes to analyze the phylogenetic relationships across genera or species-groups of Microgastrinae. In this work, as an initial study, we provide new insights into this group, shedding light on its phylogenomic relationships and contributing to a deeper understanding of its evolutionary dynamics.

2. Materials and Methods

Specimens were collected using hand netting and Malaise traps (MTs) in Guangdong, Hainan, and Hunan provinces (Table 1). The collected specimens were stored in 100% ethanol and kept at −80°C prior to DNA extraction. Genomic DNA was extracted, quantified, sequenced, assembled, and annotated following the protocol described by Liu et al. [42]. Voucher specimens are deposited in the Laboratory of Hunan University of Arts and Science, Changde, China. All mitochondrial genomes have been submitted to GenBank under the accession numbers PV802262−PV802281 and MZ958824.

The base compositions and codon usages (RSCU) in each sequence were calculated following the methods described by Yuan et al. [43]. Two sequences of *Dolichogenidea* from NCBI, one of *Parapanteles* and one of *Pholetesor*, in addition to the 21 mitochondrial genomes we sequenced, were downloaded from NCBI for comparison and analysis of this group (Table 2). *Choeras* Mason is not included here since, as presently understood, it is clearly a polyphyletic assemblage of species, some of which may eventually be placed in different genera [1]. Gene arrangements of mitochondrial genomes across these genera were compared using 25 representative mitochondrial genomes, covering four genera traditionally or morphologically recognized as Chinese Apantelini. These sequences, along with three outgroup sequences representing two subfamilies of Braconidae (Cardiochilinae and Miracinae), and one distinct lineage of Microplitini from the subfamily Microgastrinae,

Table 2: Details on the 28 mitochondrial genomes of the microgastroid complex along with three outgroups used in this study.

Genus	Species-group	Species	Author(s)	Accession no.
Outgroups				
Cardiochiles	—	*fuscipennis*	Szépligeti, 1900	KF385870
Mirax	—	sp.	—	KJ412471
Microplitis	—	*manilae*	Ashmead, 1904	OP651893
Ingroups				
Apanteles	*ater*	sp.	—	PV802275
Apanteles	*ater*	*altus*	Liu and Chen, 2020	MZ958824
Apanteles	*ater*	*dryas*	Nixon, 1965	PV802270
Apanteles	*ater*	*gracilicornis*	Song and Chen, 2004	PV802268
Apanteles	*ater*	*importunus*	Wilkinson, 1928	PV802276
Apanteles	*ater*	*longicoxa*	Liu and Chen, 2020	PV802264
Apanteles	*ater*	*medon*	Nixon, 1965	PV802269
Apanteles	*ater*	*opacus*	(Ashmead, 1905)	PV802266
Apanteles	*ater*	*pachycarinatus*	Song and Chen, 2002	PV802278
Apanteles	*mycetophilus*	*hainanensis*	Liu and Chen, 2015	PV802272
Apanteles	*mycetophilus*	*thoracartus*	Liu and Chen, 2015	PV802271
Apanteles	*taeniaticornis*	*conon*	Nixon, 1965	PV802267
Dolichogenidea	*laevigata*	*breviventris*	(Ratzeburg, 1848)	PV802262
Dolichogenidea	*laevigata*	*funalicauda*	Liu and Chen, 2018	PV802273
Dolichogenidea	*laevigata*	sp. 1	—	PV802277
Dolichogenidea	*ultor*	*gelechiidivoris*	Marsh, 1975	OR099831
Dolichogenidea	*ultor*	sp. 2	—	KT215851
Dolichogenidea	*ultor*	*asotae*	(Watanabe, 1932)	PV802281
Dolichogenidea	*ultor*	*caniae*	(Wilkinson, 1928)	PV802274
Dolichogenidea	*ultor*	*inquisitor*	(Wilkinson, 1928)	PV802265
Dolichogenidea	*ultor*	*latitergita*	Liu and Chen, 2019	PV802279
Dolichogenidea	*ultor*	*stantoni*	(Ashmead, 1904)	PV802280
Dolichogenidea	*ultor*	*hyposidrae*	Wilkinson, 1928	OP741149
Pholetesor	*ornigis*	*salalicus*	Mason, 1959	PV802263
Pholetesor	*ultor*	sp.	—	KT215846

which are phylogenomically closest to Apantelini species, were included in the phylogenetic analyses (Table 2).

Four data matrices were chosen for phylogenetic inferences, that is DNA sequences of all 1st, 2nd and 3rd codon positions of protein-coding genes (PCGs) (PCG123), DNA sequences of all 1st and 2nd codon positions of PCGs (PCG12), DNA sequences of all protein-coding and RNA genes (PCG + RNA), and amino acid sequences of all PCGs (AA). The methods for Bayesian inference (BI) analyses and maximum likelihood (ML) analyses followed Liu et al. [42].

ML and BI analyses were performed using IQ-TREE v2.2.2.7 [44] and MrBayes v3.2.6 [45], respectively. For Bayesian analyses, chains were sampled every 1000 generations over a total of 50 million generations, and effective sample size (ESS) values were assessed using Tracer v1.7 [46]. A burn-in of 25% was applied, and the remaining trees were used to generate a majority-rule consensus tree with posterior probabilities (PPs) of clades. Optimal partitioning strategy and models were selected using PartitionFinder v2.1.12. All trees were visualized using FigTree v1.4.4 [47] and subsequently refined with Adobe Illustrator and Adobe Photoshop.

3. Results

3.1. General Features of the Mitochondrial Genomes. We sequenced the mitochondrial genomes of 21 species from six species-groups belonging to the genera *Apanteles*, *Dolichogenidea*, and *Pholetesor*, covering the main groups of the traditional tribe Apantelini in China. Mitochondrial genomes were reported for the first time from China for the genus *Apanteles s. str*., with 13 sequences: nine species from the *ater*-group: *A.* sp., *A. altus* Liu and Chen, *A. dryas* Nixon, *A. gracilicornis* Song and Chen, *A. importunus* Wilkinson, *A. longicoxa* Liu and Chen, *A. medon* Nixon, *A. opacus* (Ashmead), and *A. pachycarinatus* Song and Chen; two species from the *mycetophilus*-group: *A. hainanensis* Liu and Chen and *A. thoracartus* Liu and Chen; and one species from the *taeniaticornis*-group: *A. conon* Nixon.

For the genus *Dolichogenidea*, we sequenced eight species from two species-groups, *viz*., three species from the *laevigata*-group: *D. breviventris* (Ratzeburg), *D. funalicauda* Liu and Chen, and *D.* sp. 1; five species from the *ultor*-group: *D. asotae* (Watanabe), *D. caniae* (Wilkinson), *D. inquisitor* (Wilkinson),

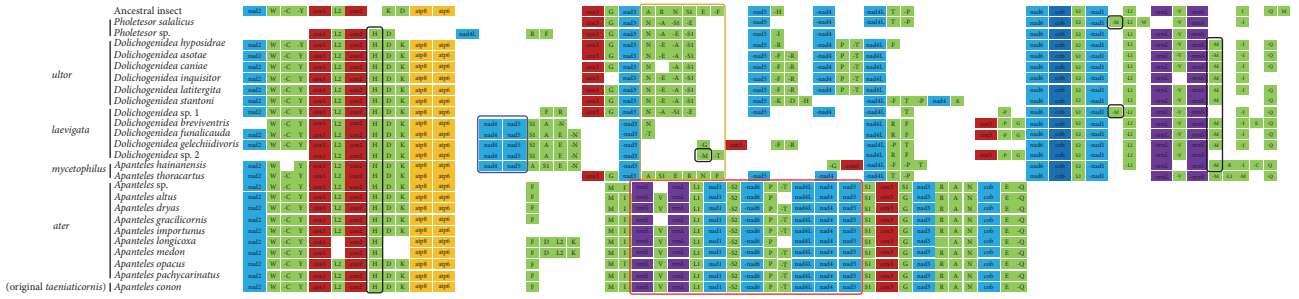

FIGURE 1: Gene rearrangement in 25 mitochondrial genomes.

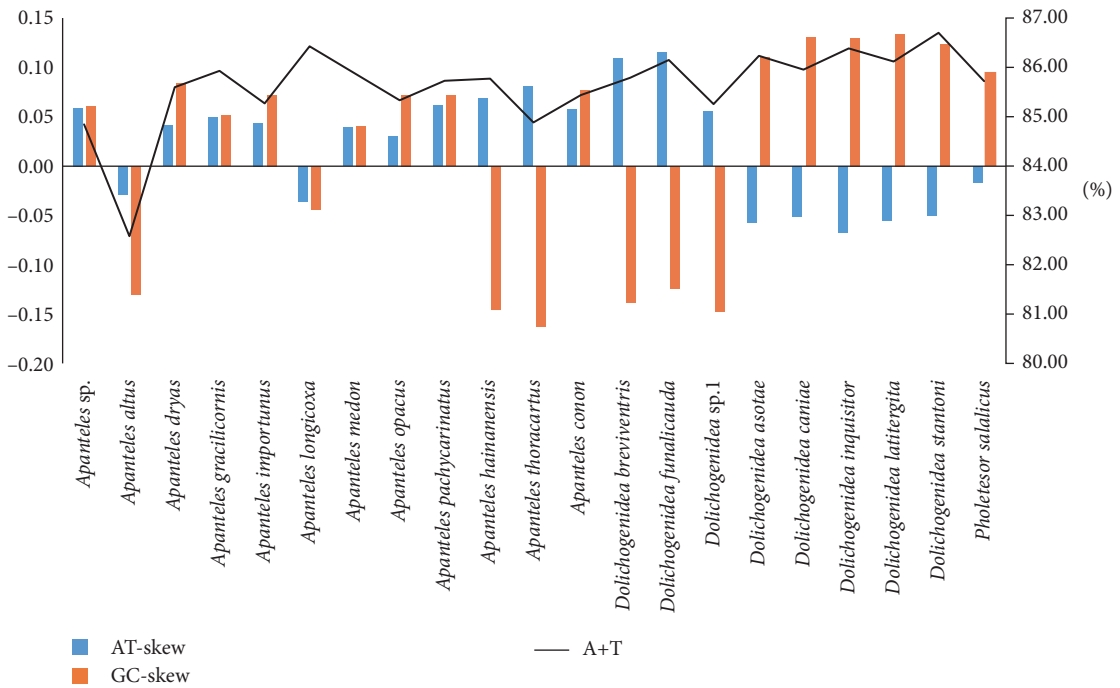

FIGURE 2: Base composition and protein-coding genes (PCGs).

D. latitergita Liu and Chen, and *D. stantoni* (Ashmead). Additionally, for the genus *Pholetesor*, we sequenced *P. salalicus* Mason from the *ornigis*-group (Table 1).

The 21 mitogenomes ranged in size from 15,231 bp in *Apanteles conon* Nixon, to 17,908 bp in *Dolichogenidea stantoni* (Ashmead), with the exception of the poorly sequenced *P. salalicus* Mason, which had a length of 10,841 bp. All protein-coding and rRNA genes were successfully obtained, except for *cox1*, *cox2*, *nad2*, *atp6*, *atp8*, and *rrnL* in *P. salalicus* (Figure 1).

The average A + T content for the sequenced regions of the mitochondrial genomes of three genera was relatively high (86.5%), ranging from 83.4% in *Apanteles altus* to 87.4% in *P. salalicus*, with no significant differences observed between different genera or species-groups. When compared to other available mitochondrial genomes from NCBI within this group and other orders, this A + T content is not exceptional [48, 49]. These results were consistent with those for the 13 PCGs (Figure 2). In these genera, the AT-skew was positive in 13 out of 21 species, while the GC-skew was negative in 7 out of 21 species (Figure 2). Comparatively, a positive AT-skew and a negative GC-skew are common in most insect species [50]. The highest and lowest AT-skew values were observed in *Apanteles thoracartus* (0.080) and *Dolichogenidea inquisitor* (−0.068), respectively. For GC-skew, the highest and lowest values were found in *Apanteles dryas* (0.084) and *A. thoracartus* (−0.164), respectively.

The relative synonymous codon usages (RSCUs) in all the sequenced mitochondrial genomes are shown in Figures 3 and 4. UAA (with an average RSCU of 4.11) was consistently the most frequent codon, except in *Dolichogenidea caniae*, where AGG (2.74) was the most common. These results indicated a strong preference for A and T, particularly at the third codon position, which is consistent with findings in other hymenopteran studies [43, 48, 51].

The PCGs, excluding stop codons, contain between 3361 codons in *P. salalicus* to 5241 codons in *Dolichogenidea stantoni*. Seven AT-rich codons—AAA (Lys), AAU (Asn), AUU (Ile), UUA (Leu), AUA (Met), UUU (Phe), and UAU (Tyr)—were the most frequently used codons across all sequences,

Figure 3: Relative synonymous codon usage (RSCU) of protein-coding genes (PCGs) in new sequenced mitochondrial genomes, part I (*Apanteles*).

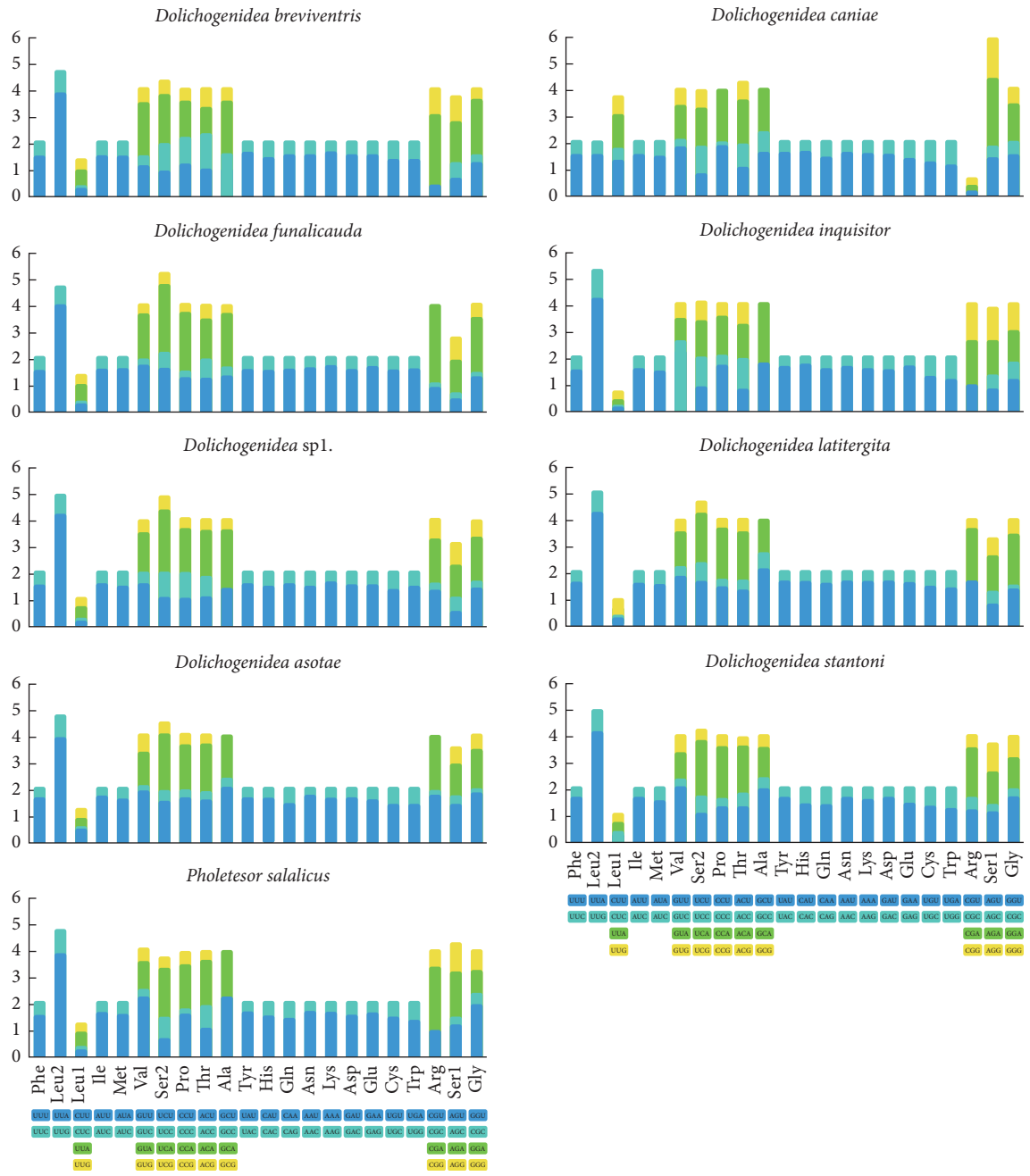

FIGURE 4: Relative synonymous codon usage (RSCU) of protein-coding genes (PCGs), part II (*Dolihogenidea* and *Pholetesor*).

which corresponds to the high A + T content observed in these mitogenomes.

3.2. Gene Rearrangement. Generally, gene rearrangements were evident in these genera when compared with the ancestral type of *Drosophila melanogaster* Meigen (Figure 1), especially for the *ater*- and *taeniaticornis*-groups of the genus *Apanteles*. *Parapanteles*, *Pholetesor*, the entire *ultor* species-group, one species from the *laevigata*-group (*D.* sp. 1) in *Dolichogenidea*, and one *mycetophilus* species (*A. thoracartus*) from *Apanteles* showed the same or nearly the same conserved gene arrangements of PCGs and rRNA genes as in the ancestral type. However, other species from the *laevigata*-group of *Dolichogenidea* and a species of the *mycetophilus*-group in *Apanteles* (*A. hainanensis*) exhibited inverse transpositions of the genes *nad4* and *nad5* (blue box in Figure 1), indicating that these groups might have undergone more complex rearrangements compared to others.

Moreover, for the *ater*- and *taeniaticornis*-groups of *Apanteles*, a large inverse transpositions cluster, including *nad5* to

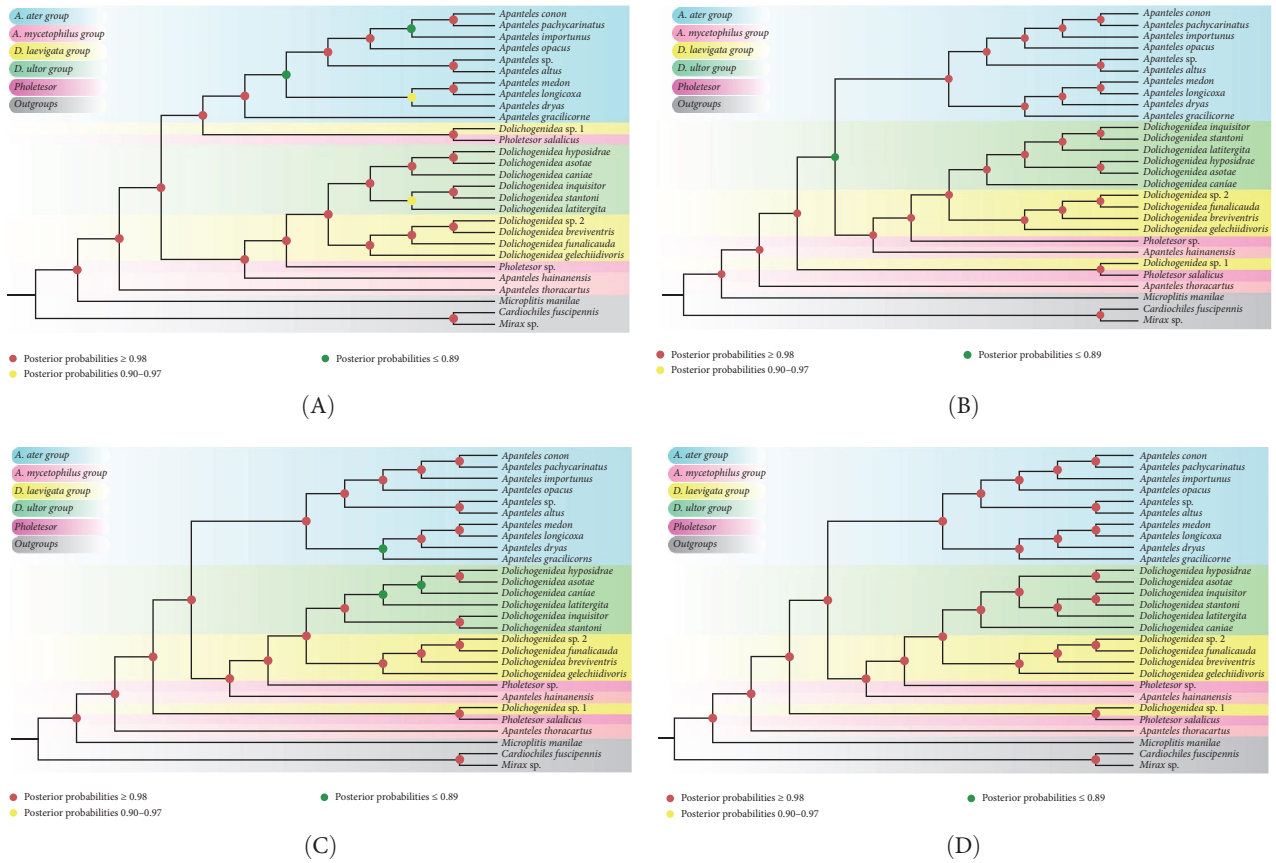

FIGURE 5: Phylogenetic bayesian trees of 25 species using different matrices: (A) the matrices of AA; (B) the matrices of PCG12; (C) the matrices of PCG123; (D) the matrices of rRNA. Nodes with posterior probabilities values: ≥ 0.98 (red dots), 0.90–0.97 (yellow dots), ≤ 0.89 (green dots).

rrnS (red box in Figure 1), was observed. This cluster might represent a specific evolutionary event that distinguishes these groups from others, possibly linked to adaptive, biological, or ecological factors. Not surprisingly, tRNA genes had the highest frequency of rearrangement, followed by PCGs and rRNA genes in this study. We speculate that the higher frequency of rearrangements in tRNA genes could suggest a more flexible mitochondrial genome structure in these species, potentially linked to the unique metabolic or physiological demands of these groups.

The tRNA genes located in the tRNA clusters had a relatively higher frequency of rearrangement, such as the cluster between *nad3* and *nad5* (orange box in Figure 1). This could imply that the clustering of certain tRNA genes might play a role in regulating mitochondrial gene expression and that variations in the clustering patterns might reflect specific evolutionary adaptations. Besides, *trnH* and *trnM* (black box in Figure 1) showed inverse transpositions in all sequences compared to the ancestral type, which may indicate a common evolutionary trend across Microgastrinae that further supports the role of gene rearrangements in shaping their mitochondrial genome evolution.

3.3. Phylogenetic Analyses of Some Species-Groups. Phylogenetic relationships were inferred using MrBayes and IQ-TREE based on four data matrices (AA, PCG12, PCG123, rRNA), resulting in eight tree topologies (Figures 5 and 6). Generally, the support values of the corresponding nodes in the BI phylogenetic tree were relatively higher than those in the ML trees for each data matrix in this study. This supports the finding that MrBayes performs more reliably than ML methods in the mitochondrial phylogenomic analysis of this group, consistent with other studies in the order Hymenoptera [42, 51–53]. The higher support in BI trees suggests that the Bayesian method may better handle the complexities of mitochondrial genome evolution in Microgastrinae, potentially due to its ability to model evolutionary processes more flexibly.

The topologies inferred using BI analyses from all data matrices almost always displayed the highest support values at every node (Figure 5A–D). Additionally, the obtained topologies from ML analyses showed the highest support values at most nodes; however, some nodes had moderate or weak support values (Figure 6A–D). In these phylogenetic trees, most species-groups of the genera *Apanteles* and *Dolichogenidea* clustered together in both BI and ML analyses with strong support values, except for two *mycetophilus* species in the genus *Apanteles*, which were placed in relatively remote branches, suggesting distinct evolutionary trajectories. Although the topology from the data matrix of AA in both BI and ML analyses showed that two species of the *mycetophilus*-group

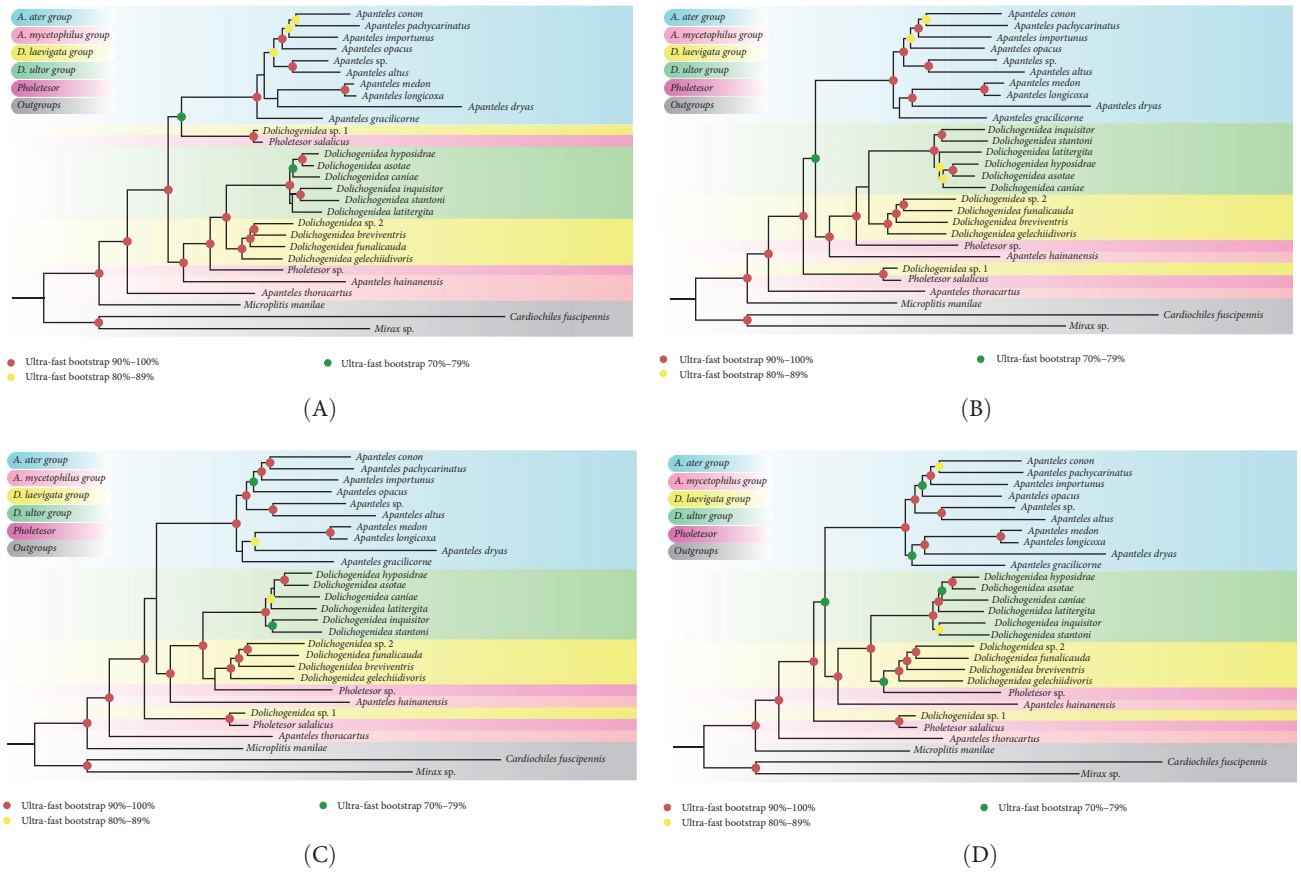

FIGURE 6: Phylogenetic maximum likelihood trees of 25 species using different matrices: (A) the matrices of AA; (B) the matrices of PCG12; (C) the matrices of PCG123; (D) the matrices of rRNA. Nodes with ultra-fast bootstrap support values: 90%–100% (red dots), 80%–89% (yellow dots), 70%–79% (green dots).

are close to each other, they are not clustered together (Figures 5A and 7A). Within *Apanteles*, the *taeniaticornis*-group clustered with the *ater*-group as sister to *A. pachycarinatus*, indicating a closer relationship between these groups (Figures 5A–D and 6A–D). This clustering of the *taeniaticornis*-group with the *ater*-group was supported by strong values in BI analyses across all data matrices (Figure 5A–D), as well as in the data matrix of PCG123 in ML analysis (Figure 6C). Other topologies obtained from the data matrices of AA, PCG12, and rRNA showed moderate support values but still clustered together, forming a sister group (Figure 6A,B,D). This finding challenges some previous taxonomic classifications and may suggest more complicated evolutionary patterns within the genus.

In contrast, within *Dolichogenidea*, the major groups *ultor* and *laevigata* often remained well-separated as sister groups in both BI and ML analyses, supporting the traditional distinction between these two groups (Figures 5A–D and 6A–D). The two clades of the *ultor*- and *laevigata*-groups were supported by strong values in BI analyses across all data matrices (Figures 5A–D), as well as in all data matrices in ML analyses (Figure 6A,C,D), except for the PCG12 matrix, which showed weak support (Figure 6B). However, *Dolichogenidea* sp. 1 was sister to the representative of *Pholetesor* with strong support values in both BI and ML analyses (Figures 5A–D and 6A–D). The genus *Parapanteles* had the species *P. hyposidrae* grouped within the *ultor*-group of *Dolichogenidea* with strong support values in both BI and ML analyses; consequently, we transferred the species to the *ultor*-group (Figures 5A–D and 6A–D). These observations demonstrated the complex intergeneric relationships within Microgastrinae.

Two of the obtained trees from the AA data matrix in both BI and ML analyses presented the same topology for all taxa, differing only in support values (Figures 5A and 6A). The *ater*-group was completely identical and consistently placed in the same position across all obtained trees from both BI and ML analyses (Figures 5A–D and 6A–D). Other obtained trees from the remaining data matrices (PCG12, PCG123, rRNA) in both BI and ML analyses displayed the same topologies, with only small changes in the internal branches of *Dolichogenidea* and *Apanteles* (Figures 5B–D and 6B–D). For example, in the *ultor*-group, *D. latitergita* formed a sister group with *D. caniae* and *D. asotae* in the PCG123 matrix under BI analysis, whereas in the rRNA matrix under BI analysis, *D. latitergita* formed a sister group with *D. stantoni* and *D. inquisitor*. Similarly, species of the *mycetophilus*-group clustered with the *Dolichogenidea* clade in both BI and ML analyses, particularly in the PCG12, PCG123, and rRNA data matrices. This suggests a

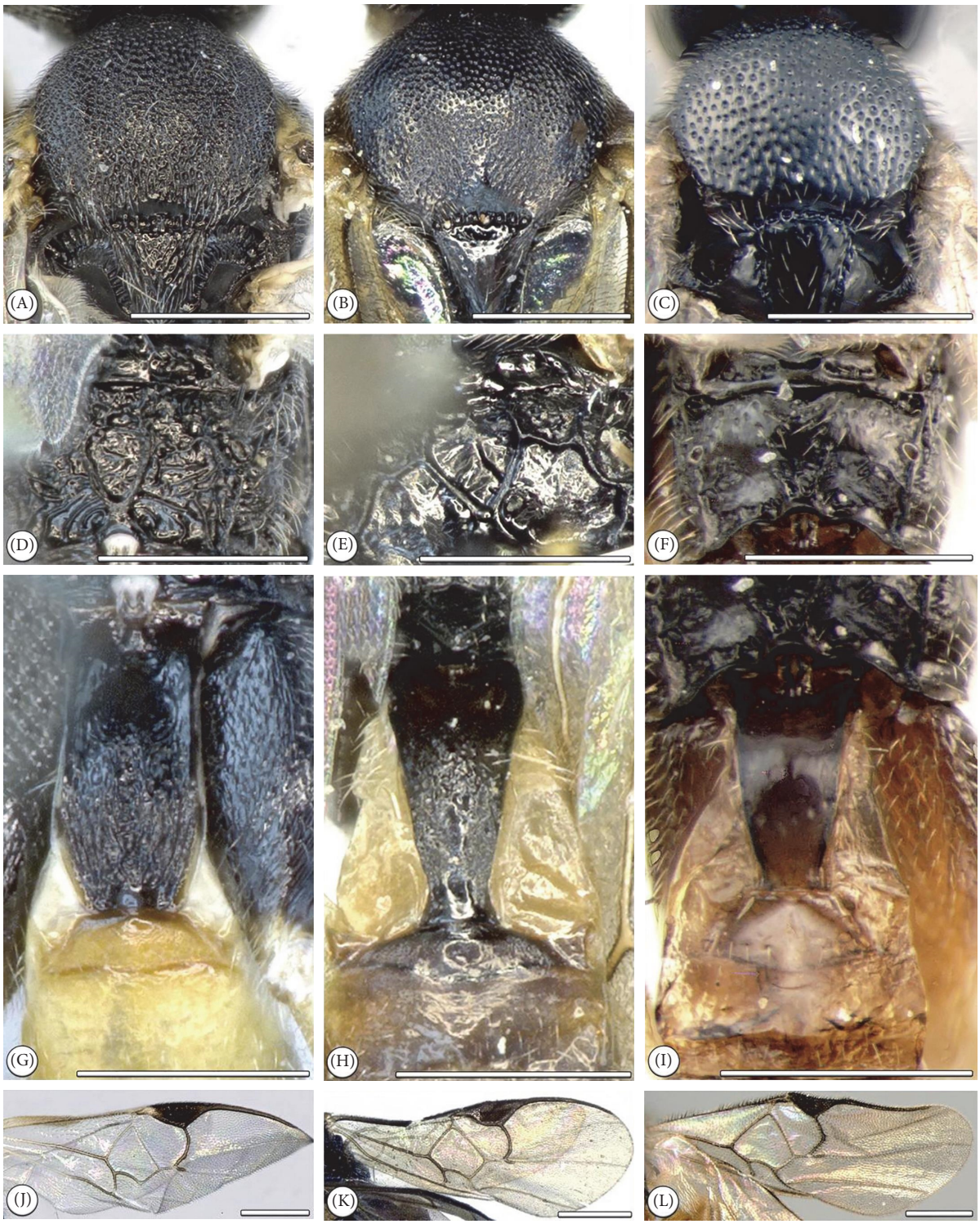

FIGURE 7: Distinct features of *Apanteles* species-groups distributed in China: (A, D, G, J) *Apanteles longicoxa* Liu and Chen, 2020; (B, E, H, K) *Apanteles conon* Nixon, 1965; (C, F, I, K) *Apanteles thoracartus* Liu and Chen, 2015; (A–C) mesoscutum, dorsal view; (D–F) propodeum, dorsal view; (G–I) T1–T3, dorsal view; (J–L) fore wing. Scale bars: 0.5 mm.

relatively stable relationship between these genera across different tree constructions. Additionally, *P. salalicus* and *Dolichogenidea* sp. 1 were unexpectedly grouped with the *ater*-group of *Apanteles* in BI and ML analyses using the AA data matrix (Figures 5A and 6A). However, in other data matrices from both BI and ML analyses, these species (*P. salalicus* and *Dolichogenidea* sp. 1) were placed as sister to the two major clades of *Apanteles* and *Dolichogenidea*, without considering *A. thoracartus* (Figures 5B–D and 6C–D). These two species most likely belong to the same genus, which shows the problem in

the morphological circumscription of both genera. However, this unexpected grouping was strongly supported in BI analysis, while it received weak support in ML analysis, indicating that these relationships are uncertain and not strongly corroborated by the data. The observed uncertainties and inconsistencies across trees highlight the complexity of resolving phylogenetic relationships within this group and emphasizes the need for more detailed and comprehensive analyses in future studies.

4. Discussion

4.1. Informative Mitochondrial Sequences and Phylogenetic Results. Comparative analysis of the four Chinese genera from China provides valuable insights into the phylogenetic relationships within microgastrine wasps. Similar to other members of Hymenoptera, these taxa showed high A + T content, frequent gene rearrangement, and a strong base composition bias, consistent with findings from previous studies [43, 48, 53, 54].

Gene rearrangements are usually confined to specific lineages and can be useful for phylogenetic reconstruction at lower taxonomic levels [55]. Insights from studies on Aculeata provide valuable information for resolving phylogenetic relationships within this group [42, 56]. In our study, species from the genus *Apanteles*, particularly those in the *ater*- and *taeniaticornis*-groups, exhibited more frequent gene rearrangements compared to other related genera from China. These two species-groups showed identical patterns of rearrangement in rRNA genes, PCGs, and even the sequenced tRNA genes, aligning with all the phylogenetic results in this study. Morphologically, the *taeniaticornis*-group (characterized by strongly wedged-shaped tergite 1, distinctly concave hind wing beyond its widest part, and strong rugosities on the apical part of the mesoscutum) represents an extremity within the *ater*-group (Figure 7; Table 3; [4, 30]). *Apanteles taeniaticornis* group is not clearly distinct from the *A. ater* group *sensu lato* [4]. Instead, it gradually transitions into the *ater*-group through certain intermediate species, such as *A. cestius* [4]. Thus, Nixon [4] reinforced the idea that the boundaries between these groups are not sharply defined, implying a continuum of characteristics rather than distinct, isolated groups. Our molecular analyses support Nixon's hypothesis, confirming that the *taeniaticornis*-group is not an isolated group and that its members actually belong to the *ater*-group. Hence, the genomic data support the inclusion of the *taeniaticornis*-group within the *ater*-group.

The *mycetophilus*-group of *Apanteles* is probably paraphyletic, for the two species do not cluster together across all topologies, reflecting its complexity. This is further corroborated by shared gene rearrangements, such as the *nad4* and *nad5* transpositions, where *A. hainanensis* aligns with the *laevigata*-group and also with the whole *Dolichogenidea* clade (Figures 5A and 6A), and *A. thoracartus* aligns with the whole clade (of *Apanteles*, *Dolichogenidea*, *Parapanteles* and *Pholetesor*) except outgroups (Figures 5B–D and 6B–D). This may also be an indication that at least some of the characters used to define *Apanteles* are plesiomorphic, especially the ones to define the *mycetophilus*-group.

Parapanteles hyposidrae was grouped with the *ultor*-group of Chinese *Dolichogenidea* in Liu et al. [21] but was later transferred to the genus *Parapanteles* by Fernández-Triana et al. [1]. In our study, this species showed the same gene arrangement as members of the *ultor*-group and consistently grouped within this group across all topologies. This highlights the problematic separation of *Parapanteles* and *Dolichogenidea*, as shown in Jasso-Martinez et al. [41]'s phylogeny where *Parapanteles* grouped together with *Exoryza* (the latter was transferred to *Dolichogenidea* by Fernández-Triana et al. [34]) when no other *Dolichogenidea* representatives available. We refrain from making definitive taxonomic decisions at this stage for these two genera until further studies focusing on host associations and identifying the best characters to define the boundaries of these genera are conducted and more *Parapanteles* representatives are available. But, at least, we can propose here a new combination for *hyposidrae***comb. nov.** as *Dolichogenidea*, acknowledging *D. hyposidrae* is morphologically distinct (inflexible hypopygium and very short ovipositor sheaths) from other *Dolichogenidea*. It perfectly proved the speculation of Fernández-Triana et al. [1] that some species of *Parapanteles* with available DNA barcodes cluster within *Dolichogenidea* could just be considered as species within that genus, with short ovipositor sheaths and an inflexible hypopygium.

In our study, *Pholetesor* is always polyphyletic: one is sister to one *laevigata*-group of *Dolichogenidea* (*D.* sp. 1), and the other is sister to the rest of *Dolichogenidea* in all BI analyses, showing its close relationship with *Dolichogenidea*. And the close relationship between *P. salicatus* and *D.* sp. 1 is well supported in all analyses, which coincidentally agrees with the similar appearance of the propodeum in both taxa (cf. D and F in Figure 8). However, minor gene rearrangement changes, such as those in *nad4L*, were observed when compared to *Dolichogenidea*. Jasso-Martínez et al. [41] recovered *Pholetesor* as closely related to *Shireplitis* Fernandez-Triana and Ward, 2013 and distant from the other related genera discussed in this study, but it worth to note that *Dolichogenidea* was not included in that study except *Exoryza*. Despite this, the relationships among these taxa suggest clear evolutionary connections that warrant further investigation.

Dolichogenidea, including two species-groups, *laevigata* and *ultor*, shows a distinct gene rearrangements pattern for all species compared to *Apanteles*, and the two species groups separated well across all analyses with only one exception of *D.* sp. 1, showing *laevigata*-group may not monophyletic. *Dolichogenidea* sp. 2, which lacks further morphological information in NCBI, is inferred to belong to the *laevigata*-group based on its gene rearrangement pattern of *nad4* and *nad5* and its position in the phylogenetic topologies. However, until more study is done, we tentatively retain it within the *laevigata*-group.

These findings suggest a potential association between gene arrangement and sequence evolution, consistent with observations in other studies [42, 56, 57].

4.2. Implications for Classification of Species-Groups. This study represents the first comprehensive effort to use mitochondrial genomes for comparing and reconstructing relationships among some important species-groups and genera of

Table 3: The differences among the species-groups of three genera (Hymenoptera, Braconidae, Microgatrinae) distributed in China (Figures 7 and 8; for more details, see [19–21, 28–30].

Genus	***Apanteles***			***Dolichogenidea***		***Pholetesor***
Character/ group	***ater***	***mycetophilus***	***taeniaticornis*** [a]	***laevigata***	***ultor***	***ornigis***
Mesoscutum	Always with a trace of striations or punctate with striations at posterior end of the imaginary course of the notauli	Strongly shining, with very small, mostly well-separated punctures, punctuation tends to fade out on the posterior half	Densely, coarsely rugose-punctate to reticulate-punctate, interspaces of punctures on mesoscutum obviously bigger than their diameter, largely polished at middle and posterior parts	Punctate, variable in density and size, punctuation rarely confluent giving an impression of rugose surface	More or less finely punctate, without a trace of longitudinal striation at the posterior end of the imaginary course of the notauli	Shallowly punctate anteriorly to virtually impunctate posteriorly
Propodeum	Rugose, with a median U-shaped areola, posterolateral areas, if it is delimited at all, as long as or slightly higher than wide	Without trace of a median carina or areolation, On the whole smooth and shining, except for traces of punctation across the dorsal surface and some short rugae radiating from the nucha	With complete, sharply defined areolation, setoseless	Without areola or longitudinal carina, though often with an areola like U-shaped impression, boarded with short pait of carinae or rugae below, rugose to polished all over	With a well-marked areola usually pentagonal, posterolateral areas always distinctly wider that high	Without areola and transverse carinae, with two series of ridges diverging obliquely from nucha
T1	Usually parallel- or subparallel-sided and narrowing at its posterior third, its posterior horizontal surface with a longitudinal trough	Usually markedly narrowed towards apex, long, more or less wedge-shaped, punctate and with faint rugosity on each side at apex, more coarsely sculptured against the polished tip	Narrowly wedge-shaped, not strongly constricted apically, its horizontal surface at least twice as long as wide across the hump, obscure with obsolescent punctures laterally, longitudinal channel obvious with transversal carinae inside, apical tubercle highly polished and smooth	Usually parallel- or subparallel-sided, rarely a little narrowed or widened behind or with arched sides, usually rugulose-subrugulose, or smooth to polished, rarely strongly rugose, with more or less punctuation	Usually parallel-sided, sometimes slightly widened or indistinctly constricted apically but never wedge-shaped	Subparallel-sided to posteriorly narrowing, usually much longer than broad, coarsely sculptured; rarely broadening weakly posteriorly and not much longer than broad
T2	Usually distinctly shorter than T3	Transverse, trapezoidal and smooth and polished	Shiny and polished, transverse, slightly curved apically.	Transverse, distinctly shorter than T3, usually rugulose-subrugulose, or smooth to polished, rarely strongly rugose, with more or less punctuation	Shorter than T3	Broadly trapezoidal to subtriangular, coarsely sculptured, slightly to much shorter than III down midline
Vannal lobe	Usually concave or at most straight, beyond its widest part and often without setae	Beyond its widest part, more or less straight and virtually without projecting setae	More or less concave, beyond its widest part of hind wing	Beyond its widest part evenly convex and always with distinct setae fringe throughout	Margin of the vannal lobe more or less convex and evenly thickly setose	Weakly flattened subapically, evenly fringed with short setae
R1 (Metacarp)	Usually longer than pterostigma	Usually longer than pterostigma	Mostly longer than pterostigma	Usually longer than pterostigma	Distinctly longer than pterostigma	Longer than pterostigma

[a]The status of this species group was revised in the current study, and its species were moved to the *A. ater* group. However, we have included their previously used differential characters for quick morphological comparison.

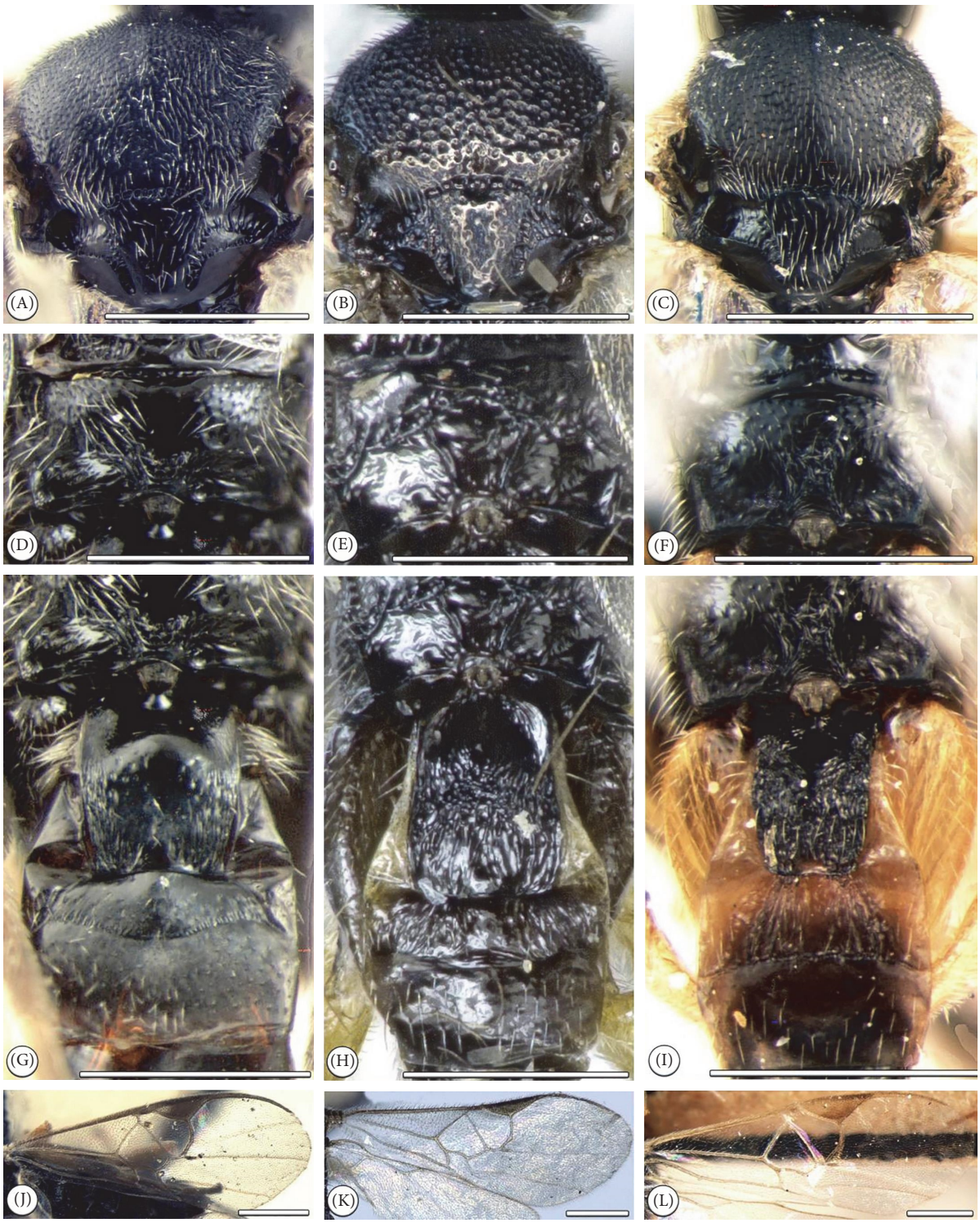

FIGURE 8: Distinct features of *Dolichogenidea* and *Pholetesor* species-groups distributed in China. (A, D, G, J) *Dolichogenidea breviventris* (Ratzeburg, 1848); (B, E, H, K) *Dolichogenidea caniae* (Wilkinson, 1928); (C, F, I, K) *Pholetesor salalicus* Mason, 1959; (A–C) mesoscutum, dorsal view; (D–F) propodeum, dorsal view; (G–I) T1–T3, dorsal view; (J–L) fore wing. Scale bars: 0.5 mm.

Micrograstrinae within China. As the largest genus in Microgastrinae, *Apanteles* has often overlapped with other closely related genera. However, the relationships among these genera and their species-groups have never been discussed using mitogenomes data before. Our findings demonstrate that *Dolichogenidea* is clearly distinct from *Apanteles*, supported not only by gene arrangement patterns but also by phylogenetic analyses, consistent with the DNA barcoding result reported by Smith et al. [36]. Key species-groups such as *ater*, *ultor*, and *laevigata* were testified to be noticeably different in gene

arrangement and phylogenetic position, confirming the validity of these groups as distinct systematic units for future studies. Our findings are consistent with the study conducted by Aman-Zuki et al. [58], whose phylogenetic analyses showed that each species group, including *ater* and *ultor*, was monophyletic. Conversely, some species-groups within *Apanteles* remain problematic. The *mycetophilus*-group appears paraphyletic in our analyses, which is different from Aman-Zuki et al. [58]. The discrepancy may stem from the limitations of their study, which included only a few genetic markers and a restricted number of taxa. Such constraints can lead to incomplete phylogenetic resolution, potentially overlooking cryptic diversity or misrepresenting evolutionary relationships. In contrast, our approach, which utilizes a more comprehensive mitochondrial dataset, provides a more robust perspective on the phylogenetic placement of the *mycetophilus*-group within the broader context of Microgastrinae. However, both studies found that species classified in this group are recovered outside the *Apanteles* clade, indicating that species within this clade very likely represent a different genus (or genera). The *taeniaticornis*-group, which clusters within the *ater*-group and shares identical gene arrangement, is proposed to no longer be considered as a separate species-group. These findings provide valuable insights for refining the taxonomic and systematic frameworks of *Apanteles* and Microgastrinae as a whole.

Additionally, *Parapanteles* may be a synonym of *Dolichogenidea* (possibly at best considered a subgenus). Jasso-Martínez et al. [41], using UCE data, revealed that *Parapanteles* is closely related to *Exoryza* and distant from *Apanteles* and *Pholetesor*. However, *Exoryza* was recently transferred to *Dolichogenidea* by Fernández-Triana et al. [34], strengthening our forementioned synonym finding.

Finally, while *Pholetesor* appears less closely related to *Apanteles*, *Exoryza* (*Dolichogenidea*), and *Parapanteles* as suggested by Jasso-Martínez et al. [41], our study indicates some degree of similarity between *Pholetesor* and the *laevigata*-group of *Dolichogenidea*. This underscores the complex phylogenetic relationships among these genera, highlighting the need for further studies incorporating diverse molecular data, expanded taxon sampling, and comprehensive morphological analyses to fully resolve these issues.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Disclosure

All authors have read and agreed to the published version of the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

Conceptualization, methodology, validation, formal analysis, investigation, data curation: Zhen Liu, Geng Lu, and Shi-qi Chen. Writing – original draft preparation: Zhen Liu. Writing – review and editing: Zhen Liu, Cornelis van Achterberg, Mostafa Ghafouri Moghaddam, Buntika A. Butcher, Xue-Xin Chen, and Andrew Polaszek.

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References

[1] J. Fernández-Triana, M. R. Shaw, C. Boudreault, M. Beaudin, and G. R. Broad, "Annotated and Illustrated World Checklist of Microgastrinae Parasitoid Wasps (Hymenoptera, Braconidae)," *ZooKeys* 920 (2020): 1–1089.

[2] M. Ghafouri Moghaddam, J. L. Fernandez-Triana, and D. Ward, "Microgastrinae Wasps of the World," 2025, http://microgastrinae.myspecies.info/ [Accessed on January 17, 2025].

[3] J. B. Whitfield, "Subfamily Microgastrinae. Manual of the New World Genera of the Family Braconidae (Hymenoptera)," *International Society of Hymenopterists. Special Publication* 1 (1997): 333–364.

[4] G. E. J. Nixon, "A Reclassification of the Tribe Microgasterini (Hymenoptera: Braconidae)," *Bulletin of the British Museum (Natural History). Entomology. Supplement* 2 (1965): 1–284.

[5] W. R. M. Mason, "The Polyphyletic Nature of, *Apanteles*, Foerster (Hymenoptera: Braconidae): A Phylogeny and Reclassification of Microgastrinae," *Memoirs of the Entomological Society of Canada* 113, no. S115 (1981): 1–147.

[6] G. E. J. Nixon, "A Revision of the North-Western European Species of the *vitripennis*, *pallipes*, *octonarius*, *triangulator*, *fraternus*, *formosus*, *parasitellae*, *metacarpalis* and *circumscriptus* -Groups of *Apanteles* Förster (Hymenoptera, Braconidae)," *Bulletin of Entomological Research* 63, no. 2 (1973): 169–230.

[7] A. D. Austin, "Revision of the Enigmatic Australasian Genus, *Miropotes*, Nixon (Hymenoptera: Braconidae: Microgastrinae), With Comments on the Phylogenetic Importance of the Female Ovipositor System," *Systematic Entomology* 15, no. 1 (1990): 43–68.

[8] A. D. Austin and P. C. Dangerfield, "Synopsis of Australasian Microgastrinae (Hymenoptera: Braconidae), With a Key to Genera and Description of New Taxa," *Invertebrate Taxonomy* 6, no. 1 (1992): 1–76.

[9] J. B. Whitfield, "Annotated Checklist of the Microgastrinae of North America North of Mexico (Hymenoptera: Braconidae)," *Journal of the Kansas Entomological Society* 68, no. 3 (1995): 245–262.

[10] C. van Achterberg, "Western Palaearctic Genera of the Subfamily Microgastrinae: A Reappraisal of the Generic and Tribal Division (Hymenoptera: Braconidae)," in *Parasitic Wasps: Evolution, Systematics, Biodiversity and Biological Control. Agroinform, Budapest*, ed. G. Melika and G. Thuróczy, (2003): 19–35.

[11] J. Fernández-Triana, "Eight New Species and an Annotated Checklist of Microgastrinae (Hymenoptera: Braconidae) From Canada and Alaska," *ZooKeys* 63 (2010): 1–53.

[12] A. K. Walker, I. J. Kitching, and A. D. Austin, "A Reassessment of the Phylogenetic Relationships Within the Microgastrinae (Hymenoptera: Braconidae)," *Cladistics* 6, no. 3 (1990): 291–306.

[13] J. B. Whitfield, A. D. Austin, and J. L. Fernandez-Triana, "Systematics, Biology, and Evolution of Microgastrine Parasitoid Wasps," *Annual Review of Entomology* 63, no. 1 (2018): 389–406.

[14] J. B. Whitfield, P. Mardulyn, A. D. Austin, and M. Dowton, "Phylogenetic Relationships Among Microgastrine Braconid Wasp Genera Based on Data From the 16S, COI and 28S Genes and Morphology," *Systematic Entomology* 27, no. 3 (2002): 337–359.

[15] N. Murphy, J. C. Banks, J. B. Whitfield, and A. D. Austin, "Phylogeny of the Parasitic Microgastroid Subfamilies (Hymenoptera: Braconidae) Based on Sequence Data From Seven Genes, With an Improved Time Estimate of the Origin of the Lineage," *Molecular Phylogenetics and Evolution* 47, no. 1 (2008): 378–395.

[16] P. Abdoli, A. A. Talebi, N. G. Kavallieratos, R. Khosravi, and F. Bidari, "Contribution to the Phylogeny of Microgastrinae (Hymenoptera: Braconidae) Based on Mitochondrial COI and Nuclear 28S rDNA Genes, With Comments on the Identity of *Pholetesor circumscriptus* (Nees, 1834)," *Journal of Insect Biodiversity and Systematics* 10, no. 4 (2024): 965–981.

[17] D. S. Yu, C. van Achterberg, and K. Horstmann, "World Ichneumonoidea 2015. Taxonomy, Biology, Morphology and Distribution," (Nepean, Ottawa, Canada.[database on flash-drive], Nepean, Ottawa, Canada.).

[18] M. R. Shaw, A. Höcherl, and J. Fernández-Triana, "An Illustrated Key to European Genera of Microgastrinae Parasitoid Wasps (Hymenoptera, Braconidae) With a Recent Historical and Biological Perspective and a Guide to Available Species-Level Identification Resources," *ZooKeys* 1212 (2024): 285–316.

[19] Z. Liu, J. H. He, and X. X. Chen, "The Genus, *Pholetesor*, Mason, 1981 (Hymenoptera, Braconidae, Microgastrinae) From China, With Descriptions of Eleven New Species," *Zootaxa* 4150, no. 4 (2016): 351–387.

[20] Z. Liu, J. H. He, and Chen, "The *laevigata*-Group of the Genus, *Dolichogenidea*, Mason, 1981 From China, With Descriptions of 26 New Species," *Zootaxa* 4436, no. 1 (2018): 1–74.

[21] Z. Liu, J. H. He, X. X. Chen, A. Gupta, and M. G. Moghaddam, "The *ultor*-Group of the Genus, *Dolichogenidea*, Viereck (Hymenoptera, Braconidae, Microgastrinae) From China With the Descriptions of Thirty-Nine New Species," *Zootaxa* 4710, no. 1 (2019): 1–134.

[22] E. P. Fagan-Jeffries, S. J. Cooper, and A. D. Austin, "Three New Species of, *Dolichogenidea*, Viereck (Hymenoptera, Braconidae, Microgastrinae) From Australia With Exceptionally Long Ovipositors," *Journal of Hymenoptera Research* 64 (2018): 177–190.

[23] J. Fernández-Triana, C. Boudreault, T. Dapkey, M. A. Smith, W. Hallwachs, and D. Janzen, "A Revision of *Dolichogenidea* (Hymenoptera, Braconidae, Microgastrinae) With the Second Mediotergite Broadly Rectangular From Area de Conservación Guanacaste, Costa Rica," *ZooKeys* 835 (2019): 87–123.

[24] J. Papp, "A Survey of the European Species of, the *lacteus*-, *longipalpis*-, *ultor*-, *butalidis*- and *vipio*-Group," in *Annales Historico-Naturales Musei Nationalis Hungarici*, 73, (1981): 263–291.

[25] J. Papp, "A Survey of the European Species of, the *laspeyresiella*-, *merula*-, *falcatus*- and *validus*-Group," in *Annales Historico-Naturales Musei Nationalis Hungarici*, 74, (1982): 255–267.

[26] J. Papp, "A Survey of the European Species of the *carbonarius*-, *circumscriptus*-, *fraternus*-, *pallipes*- *parasitellae*-, *vitripennis*-, *liparidis*-, *octonarius*- *and thompsoni*-group," in *Annales Historico-Naturales Musei Nationalis Hungarici*, 75, (1983): 247–283.

[27] Z. Liu, J. H. He, and X. X. Chen, "The *grandiculus*- and *metacarpalis*-Group of the Genus, *Apanteles*, Foerster, 1862 (Hymenoptera, Braconidae, Microgastrinae) From China, With Descriptions of Eight New Species," *Zootaxa* 3765, no. 5 (2014): 435–457.

[28] Z. Liu, J. H. He, and X. X. Chen, "The *lacteus*-, *laspeyresiella*- and *mycetophilus*-Groups of, *Apanteles*, Foerster, 1862 (Hymenoptera, Braconidae, Microgastrinae) in China, With Descriptions of Eight New Species," *Zootaxa* 3949, no. 3 (2015): 370–392.

[29] Z. Liu, J. H. He, X. X. Chen, and G. Ankita, "The *ater*-Group of the Genus, *Apanteles*, Foerster (Hymenoptera, Braconidae, Microgastrinae) From China With the Descriptions of Forty-Eight New Species," *Zootaxa* 4807, no. 1 (2020): 001–205.

[30] Z. Liu and X.-X. Chen, "The *taeniaticornis*-Group of Genus, *Apanteles*, Foerster (Hymenoptera, Braconidae, Microgastrinae) From China With One New Species," *Journal of Hymenoptera Research* 96 (2023): 21–31.

[31] S. N. Song, J. H. He, and X. X. Chen, "The Subgenus, *Choeras*, Mason, 1981 of Genus, *Apanteles*, Foerster, 1862 (Hymenoptera, Braconidae, Microgastrinae) From China, With Descriptions of Eighteen New Species," *Zootaxa* 3754, no. 5 (2014): 501–554.

[32] M. Ghafouri Moghaddam, E. Rakhshani, C. Van Achterberg, and A. A. Mokhtari, "Study of the Iranian Species of, *Choeras*, Mason (Hymenoptera: Braconidae: Microgastrinae), With the Description of a New Species," *Zootaxa* 4446, no. 4 (2018): 455–476.

[33] M. Ghafouri Moghaddam, D. C. Arias-Penna, and M. Heidari Latibari, "Notes on the Genus, *Choeras*, Mason, 1981 (Hymenoptera: Ichneumonoidea, Braconidae, Microgastrinae) From Iran," *Tijdschrift Voor Entomologie* 165, no. 1–3 (2022): 37–48.

[34] J. L. Fernandez-Triana, C. Boudreault, J. B. Whitfield, et al., "A Revision of the Parasitoid Wasp Genus, *Dolichogenidea*, Viereck (Hymenoptera, Braconidae) in the Neotropical Region, With the Description of 102 New Species," *ZooKeys* 1237 (2025): 1–250.

[35] J. Fernández-Triana, J. B. Whitfield, J. J. Rodriguez, et al., "Review of *Apanteles Sensu Stricto* (Hymenoptera, Braconidae, Microgastrinae) From Area De Conservación Guanacaste, Northwestern Costa Rica, With Keys to All Described Species From Mesoamerica," *ZooKeys* 383 (2014): 1–565.

[36] M. A. Smith, J. L. Fernández-Triana, E. Eveleigh, et al., "DNA Barcoding and the Taxonomy of Microgastrinae Wasps (Hymenoptera, Braconidae): Impacts After 8 Years and Nearly 20 000 Sequences," *Molecular Ecology Resources* 13, no. 2 (2013): 168–176.

[37] K. S. Parks, D. H. Janzen, W. Hallwachs, et al., "A Five-Gene Molecular Phylogeny Reveals, *Parapanteles*, Ashmead (Hymenoptera: Braconidae) to be Polyphyletic as Currently Composed," *Molecular Phylogenetics and Evolution* 150 (2020): 106859.

[38] J. B. Whitfield, "Revision of the Nearctic Species of the Genus, *Pholetesor*, Mason (Hymenoptera: Braconidae)," *Zootaxa* 1144, no. 1 (2006): 3–94.

[39] P. Mardulyn and J. B. Whitfield, "Phylogenetic Signal in the COI, 16S, and 28S Genes for Inferring Relationships Among Genera of Microgastrinae (Hymenoptera; Braconidae): Evidence of a High Diversification Rate in This Group of Parasitoids," *Molecular Phylogenetics and Evolution* 12, no. 3 (1999): 282–294.

[40] J. C. Banks and J. B. Whitfield, "Dissecting the Ancient Rapid Radiation of Microgastrine Wasp Genera Using Additional Nuclear Genes," *Molecular Phylogenetics and Evolution* 41, no. 3 (2006): 690–703.

[41] J. M. Jasso-Martínez, B. F. Santos, A. Zaldívar-Riverón, et al., "Phylogenomics of Braconid Wasps (Hymenoptera, Braconidae) Sheds Light on Classification and the Evolution of Parasitoid Life-History Traits," *Molecular Phylogenetics and Evolution* 173 (2022): 107452.

[42] Z. Liu, C. Van Achterberg, and H. Chen, "Mitochondrial Phylogenomics of Scoliidae From China, With Evidence to Challenge the Former Placement of the Colpa Group," *Insects* 15, no. 10 (2024): 758.

[43] R. Z. Yuan, J. J. Zhou, X. H. Shu, X. Q. Ye, P. Tang, and X.-X. Chen, "The Mitochondrial Genome of *Chelonus formosanus* (Hymenoptera: Braconidae) With Novel Gene Orders and Phylogenetic Implications," *Archives of Insect Biochemistry and Physiology* 111, no. 1 (2022): e21870.

[44] B. Q. Minh, H. A. Schmidt, O. Chernomor, et al., "IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era," *Molecular Biology and Evolution* 37, no. 5 (2020): 1530–1534.

[45] F. Ronquist, M. Teslenko, P. van Der Mark, et al., "MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space," *Systematic Biology* 61, no. 3 (2012): 539–542.

[46] A. Rambaut, A. J. Drummond, D. Xie, G. Baele, and M. A. Suchard, "Posterior Summarisation in Bayesian Phylogenetics Using tracer 1.7," *Systematic Biology* 67, no. 5 (2018): 901–904.

[47] A. Rambaut, "FigTree, v.1.4.4. Computer Program Distributed by the Author," 2018, [Accessed 01 October 2023], http://tree.bio.ed.ac.uk/software/figtree/.

[48] D. D. Xiao, Z. Q. Wang, J. C. Zhu, X. G. Zhou, P. Tang, and X.-X. Chen, "The Mitochondrial Genomes of Two Parasitoid Wasps *Protapanteles immunis* and *Parapanteles hyposidrae* (Hymenoptera: Braconidae) With Phylogenetic Implications and Novel Gene Rearrangements," *Genes* 14, no. 1 (2023): 230.

[49] D. Oliveira, R. Raychoudhury, D. V. Lavrov, and J. H. Werren, "Rapidly Evolving Mitochondrial Genome and Directional Selection in Mitochondrial Genes in the Parasitic Wasp *Nasonia* (Hymenoptera: Pteromalidae)," *Molecular Biology and Evolution* 25, no. 10 (2008): 2167–2180.

[50] M. T. P. Gilbert, S. J. Wei, M. Shi, et al., "New Views on Strand Asymmetry in Insect Mitochondrial Genomes," *PLoS ONE* 5, no. 9 (2010): e12708.

[51] L.-S. Huang, Z. Liu, H.-Y. Chen, and X.-X. Chen, "Two Mitochondrial Genomes of Genus, *Megacampsomeris*, Betrem, 1928 (Hymenoptera: Scoliidae) With Their Phylogenetic Implications," *Journal of Asia-Pacific Entomology* 26, no. 2 (2023): 102067.

[52] M. Dowton, S. L. Cameron, A. D. Austin, and M. F. Whiting, "Phylogenetic Approaches for the Analysis of Mitochondrial Genome Sequence Data in the Hymenoptera—A Lineage With Both Rapidly and Slowly Evolving Mitochondrial Genomes," *Molecular Phylogenetics and Evolution* 52, no. 2 (2009): 512–519.

[53] S.-J. Wei, Q. Li, K. van Achterberg, and X.-X. Chen, "Two Mitochondrial Genomes From the Families Bethylidae and Mutillidae: Independent Rearrangement of Proteincoding Genes and Higher-Level Phylogeny of the Hymenoptera," *Molecular Phylogenetics and Evolution* 77 (2014): 1–10.

[54] M. Dowton and A. D. Austin, "Evidence for AT-Transversion Bias in Wasp (Hymenoptera: Symphyta) Mitochondrial Genes and its Implications for the Origin of Parasitism," *Journal of Molecular Evolution* 44, no. 4 (1997): 398–405.

[55] P. Tang, J. C. Zhu, B. Y. Zheng, et al., "Mitochondrial phylogenomics of the Hymenoptera," *Molecular Phylogenetics and Evolution* 131 (2018): 8–18.

[56] R. Shao, M. Dowton, A. Murrell, and S. C. Barker, "Rates of Gene Rearrangement and Nucleotide Substitution are Correlated in the Mitochondrial Genomes of Insects," *Molecular Biology and Evolution* 20, no. 10 (2003): 1612–1619.

[57] X.-Y. Zheng, L.-J. Cao, P.-Y. Chen, et al., "Comparative Mitogenomics and Phylogenetics of the Stinging Wasps (Hymenoptera: Aculeata)," *Molecular Phylogenetics and Evolution* 159 (2021): 107–119.

[58] A. Aman-Zuki, M. A. Mohammed, B. M. Zain, and S. Yaakop, "Phylogenetic Relationships of Five Oriental Apanteles Species-Groups (Hymenoptera: Braconidae: Microgastrinae) by Concatenating Four Molecular Markers," *Journal of Asia-Pacific Entomology* 22, no. 1 (2019): 341–352.