INTRODUCTION

In contrast to nuclear DNA, the mitogenome has a maternal mode of inheritance and is usually minimally recombinogenic; it carries genes with comparatively rapid evolutionary rates (Ballard & Whitlock, 2004; Cameron, 2014; Moritz & Brown, 1987; Wolstenholme, 1992). The entire mitogenome is a valuable source of extensive information compared with single genes. Moreover, it exhibits genome-level characteristics, including gene content, base composition, gene organization, and gene secondary structure.
These characteristics have been widely used for species identification as well as phylogenetic, phylogeographic, and genomic evolution studies (Anderson et al., 1981; Chuan et al., 2012; Nelson et al., 2012).

Leafhoppers are the members of a larger group of hemipterans and comprise >22,000 species (Dietrich, 2005). Recently, an increasing number phylogenetic studies have been conducted on leafhoppers using mitogenomic data (Du et al., 2017; Du, Zhang, et al., 2017; Du et al., 2019; Li et al., 2017; Song et al., 2017, 2019; Wang et al., 2020). So far, the data of 143 complete or near-complete mitogenomes of Cicadellidae have been published in the National Center for Biotechnology Information (NCBI) database. Most of these organisms belong to the following subfamilies: Deltocephalinae (58), Cicadellinae (18), and Typhlocybinae (29). However, despite its vast diversity (>1,400 species), knowledge on the mitogenome of Coelidiinae is limited (Li & Fan, 2017; Nielson, 2015; Viraktamath & Meshram, 2019; Wang et al., 2018, 2021; Wang, Fan, et al., 2019; Zhang, 1990). Therefore, sequencing the mitogenomes of Coelidiinae may help enrich population genetics and phylogenetic studies regarding Cicadellidae (Hemiptera).

Most previous studies on Coelidiinae relationships have focused on morphological characteristics. However, the phylogeny of Coelidiinae remains to be explored using mitogenomic data. The lack of mitogenome sequences has limited the expansion of knowledge regarding the molecular evolution and population genetic diversity of this subfamily. Nielson (2015) removed C. biungulata, C. robusta, and five other species from Calodia and created the genus Cladolidia based primarily on the differences in the processes of aedeagus between these groupings. However, the position of the genus Cladolidia within the subfamily is yet to be ascertained (Nielson, 2015).

In the present study, we sequenced two complete mitogenomes of the genus Cladolidia (C. biungulata and C. robusta) using high-throughput sequencing; C. biungulata and C. robusta are the first and second species, respectively, that have been described for this genus. In addition, we described their molecular phylogenetic relationships with 58 leafhopper and 5 treehopper species. Furthermore, this study provides an insight into the identification, phylogeny, conservation genetics, and evolution of Cladolidia and its related species.

2 | MATERIALS AND METHODS

2.1 | Sample collection and DNA extraction

Detailed information on the specimens collected is presented in Table S1. The collected specimens were identified based on their morphological characteristics, as described previously (Li & Fan, 2017; Zhang, 1990). After the species were accurately identified, the specimens were preserved in absolute ethanol and stored at −20°C until genomic DNA extraction. Genomic DNA was extracted from the whole body of adult males after removing the abdomen using DNeasy® Blood & Tissue Kit. In brief, the samples were incubated at 56°C for 6 hr to lyse the cells completely and the total genomic DNA was eluted in 100-μl double-distilled water. The subsequent steps were performed according to the manufacturer’s instructions. After evaluating the extracted genomic DNA quality using 1% agarose gel electrophoresis, it was stored at −20°C until further use. Both the voucher specimens with male genitalia and DNA samples have been deposited at the Institute of Entomology, Guizhou University, Guiyang, China.

2.2 | Sequence analysis

The two complete mitogenomes of C. biungulata and C. robusta were sequenced by Berry Genomics on the HiSeq 2500 platform (Illumina) with 150-bp paired-end reads. The average insert length was 350 bp, and 6 GB of clean data were obtained. Each mitogenome was assembled using Geneious Prime 2019.2.1 software and based on a mitochondrial reference sequence of Oliidia ritcheriina (MK738125) (Wang, Wang, et al., 2019). The assembled mitochondrial gene sequences were compared with the homologous sequences of O. ritcheriina (MK738125) and Taharana fasciana (KY886913) (Wang et al., 2017; Wang, Wang, et al., 2019), which were retrieved from GenBank and identified via BLAST searches on NCBI to confirm sequence accuracy. We used the MITOS web server and BLAST searches on NCBI (https://blast.ncbi.nlm.nih.gov/Blast.cgi) to annotate the assembled sequences using invertebrate genetic codes (Altschul et al., 1997; Bernt et al., 2013) as well as the search server tRNAscan-SE 1.21 to identify the locations and predict the secondary structure of 22 typical tRNAs (Laslett & Canbäck, 2008; Schattner et al., 2005; Tamura et al., 2013). All rRNA genes were identified based on the locations of adjacent tRNA genes and comparisons with sequences of other leafhopper mitogenomes deposited in NCBI. ORF Finder in Geneious Prime was used to predict 13 protein-coding gene (PCG) locations using invertebrate genetic codes. The mitogenomic map and comparative analysis were performed using CGView comparison tool (Stothard et al., 2017). Furthermore, the relative synonymous codon usage (RSCU) values and codon numbers were calculated using the MEGA version 7.0 program (Sudhir et al., 2016). Finally, chain asymmetry was calculated using the following formulas: AT skew = (A − T)/(A + T) and GC skew = (G − C)/(G + C) (Perna & Kocher, 1995).

2.3 | Phylogenetic analysis

In total, 58 leafhopper and 5 treehopper species were selected to construct the phylogenetic tree after the removal of sequences that were unverified, lacked an accurate scientific name, and were repetitive. Phylogenetic analysis was performed using alignments of the 13 PCGs of leafhopper species with the other complete or near-complete mitogenomes of the treehopper species. The two species of Cosmocosta bipecularis (KP064511) and Tettagades aurapilosa (KM000129) (Yan & Zu, 2019) were used as the outgroup.
These two mitogenomes of Cladolidia contain 10 nucleotides that are dispersed among six intergenic spacers (ranging from 1 to 4 bp), and the longest spacer sequence (4 bp) is located between trnH and nad5, trnA, and trnR. There are a total of 14 overlapping regions (ranging from 1 to 11 bp), and the conserved 11-bp overlapping nucleotide sequence between trnW and tmc is extremely common in Cicadellidae (Du, Zhang, et al., 2017; Du et al., 2019; Wang et al., 2017, 2018, 2020, 2021; Wang, Wang, et al., 2019).

The nucleotide composition of the two Cladolidia species reveals a strong A + T bias in the entire mitogenome, and the A + T contents between C. biungulata and C. robusta are nearly equal (78.2% in C. biungulata and 78.4% in C. robusta). As with other Coelidiinae, the nucleotide composition of the two mitogenomes is clearly biased toward A/T nucleotides, with 13 PCGs, 22 tRNAs, <2 rRNAs, and a control region. This phenomenon to some extent is due to the damage or accumulation of mutations in the mitochondrial DNA (Martin, 1995).

### 3.2 | PCGs and codon usage of Cladolidia mitogenome

A total of 13 PCGs were identified in each of the two Cladolidia mitogenomes. In both mitogenomes, all PCGs use the canonical initiation codon ATN and the canonical stop codon TAA/TAG, except for cox2 and cox3. C. biungulata also harbors nad2, which uses an incomplete stop codon T-. This phenomenon has also been noted in other Coelidiinae insects (Wang et al., 2017; Wang, Wang, et al., 2019). The incomplete stop codons are modified into complete TAA codons via posttranscriptional polyadenylation during mRNA maturation (Perna & Kocher, 1995). Of note, cox1, cox3, and atp6 in each species have the same start and stop codons. The longest PCG is nad5 (1,674 bp), and the shortest is atp8 (150 bp). Only four genes (nad5, nad4, nad4l, and nad1) are present on the N-strand. The other nine genes (cox1, cox2, cox3, atp8, atp6, nad2, nad3, nad6, and cob) are located on the J-strand (Figure 1, Table 1), which is similar to the mitogenome structure of most other Coelidiinae insects (Wang et al., 2017, 2021; Wang, Wang, et al., 2019). The RSCU values and codon number for C. robusta (very similar to C. biungulata) are shown in Figure 2. The most frequently used codon is AUA (Ile, N = 340), followed by AUU (Ile, N = 333), and UUU (Phe, N = 290). However, in previous studies, the most frequently used codon was UUU (Phe) (Wang et al., 2017, 2021; Wang, Wang, et al., 2019). Moreover, the majority of frequently used codons end with A or U (Figure 2). These two factors appear to contribute to the high A + T content of PCGs and the AT bias of the whole mitogenome.

Comparative analysis revealed that the mitogenome of Coelidiinae is a conservative poly-T (with 28–31 bp) structure (Figure 3). Such a large poly-T structure is not found in the mitogenomes of other leafhoppers; hence, we hypothesized that this particular structure serves as a DNA barcode for the subfamily.
All 22 tRNAs of C. biungulata and C. robusta mitogenomes were identified; they ranged from 57 to 68 bp in length. Among the tRNA genes, 14 are located on the J-strand and 8 on the N-strand, which is the coding pattern observed in almost all Cicadellidae mitogenomes (Du, Zhang, et al., 2017; Du et al., 2019; Wang et al., 2017, 2018, 2020, 2021; Wang, Wang, et al., 2019). The 22 tRNA genes in the two Cladolidia species were identified, and their secondary structures are shown in Figure 4. All these gene products are folded into the typical cloverleaf secondary structure, except trnS1, which lacks the dihydrouridine (DHU) arm; the loss of the DHU arm in trnS1 is

### TABLE 1 Organization of the Cladolidia robusta/C. biungulata mitogenome

| Gene     | Direction | Length (bp) | Start | Stop | Anticodon | Intergenic nucleotides | AT content (%) |
|----------|-----------|-------------|-------|------|-----------|------------------------|----------------|
| trnI     | J         | 62          | –     | –    | GAT       |                        | 77.4           |
| trnQ     | N         | 67          | –     | –    | TTG       | –                      | 79.1/77.6      |
| trnM     | J         | 68/66       | –     | –    | CAT       | –1/0                   | 75/74.2        |
| nad2     | J         | 955/957     | ATT   | T/TA | –         | 0                      | 82.1/82.7      |
| tmW      | J         | 62          | –     | –    | TCA       | 0/-2                   | 80.680.6       |
| tmC      | N         | 57/65       | –     | –    | GCA       | -8/-11                 | 84.2/84.6      |
| tmY      | N         | 63/62       | –     | –    | GTA       | 0/-5                   | 79.4/79        |
| cox1     | J         | 1,536       | ATG   | TAA  | –         | 2                      | 71.5/72.5      |
| trnL1(UUR)| J       | 67/68       | –     | –    | TAA       | 0                      | 82.1/82.4      |
| cox2     | J         | 676         | ATT   | T    | –         | 0                      | 76.5/79.5      |
| tmK      | J         | 71          | –     | –    | CTT       | 0                      | 76.1/77.5      |
| tmD      | J         | 64          | –     | –    | GTC       | -1/0                   | 85.9/84.4      |
| atp8     | J         | 150         | ATA   | TAA  | –         | 1/0                    | 82/82.7        |
| atp6     | J         | 636         | ATA   | TAA  | –         | -1                     | 76.3/77.7      |
| cox3     | J         | 778         | ATG   | T    | –         | 0                      | 73.5/73.8      |
| tmG      | J         | 61/63       | –     | –    | TCC       | 0/-2                   | 75.4/79.4      |
| nad3     | J         | 354         | ATA   | TAG  | –         | 0                      | 79.1/80.4      |
| trnA     | J         | 61          | –     | –    | TGC       | -2                     | 80.3           |
| tmR      | J         | 59/63       | –     | –    | TCG       | 4/1                    | 74.6           |
| tmN      | J         | 64          | –     | –    | GTT       | -1/-2                  | 78.1/76.6      |
| trnS1    | J         | 62          | –     | –    | GCT       | -1                     | 7.169.4        |
| tmE      | J         | 63          | –     | –    | TTC       | -1                     | 87.3/87.3      |
| tmF      | J         | 67          | –     | –    | GAA       | -1                     | 82.1/83.6      |
| nad5     | N         | 1,674       | ATT   | TAA  | –         | -1                     | 77.4/77.9      |
| trnH     | N         | 60          | –     | –    | GTG       | 0                      | 75/78.3        |
| nad4     | N         | 1,308       | ATT/  | TAG  | TAA       | -1                     | 77.8/78        |
| nad4l    | N         | 276         | ATG   | TAA/TAG| –         | 2                      | 83.7/84.4      |
| tmT      | J         | 65          | –     | –    | TGT       | 2                      | 87.7           |
| tmP      | N         | 62          | –     | –    | TGG       | 0                      | 74.2/75.8      |
| nad6     | J         | 474         | ATT   | TAA  | –         | 4/2                    | 82.3/80.8      |
| cob      | J         | 1,122/1,126 | ATA/ATC| TAA | –         | 0                      | 73.5/74.1      |
| tmS2(UCN)| J       | 61/64       | –     | –    | TGA       | 1/-1                   | 82/79.7        |
| nad1     | N         | 939         | ATT   | TAA  | –         | -4/-7                  | 77.2/78.4      |
| trnL2(CUN)| N      | 68          | –     | –    | TAG       | 0                      | 75/79.4        |
| rrnL     | N         | 1,186/1,182 | –     | –    | –         | 0                      | 82.82.2        |
| tmV      | N         | 60          | –     | –    | TAC       | 0                      | 73.3/75        |
| rrnS     | N         | 779/730     | –     | –    | –         | 0                      | 81.6/81.5      |
| CR       |           | 1,016/1,199 | –     | –    | –         | 0                      | 84/82.5        |
a typical feature in Cicadellidae mitogenomes (Wang et al., 2017, 2018; Wang, Wang, et al., 2019). The combined length of tRNA genes of \( C. \) biungulata and \( C. \) robusta is 1,411 bp and 1,394 bp, with A + T contents of 79.4% and 78.9%, respectively. \( \text{rrnS} \) is located between \( \text{trnL2} \) (CUN) and \( \text{trnV} \), whereas \( \text{rrnL} \) is flanked by \( \text{trnV} \) and the control region (Figure 1, Table 2). Two rRNA genes, \( \text{rrnS} \) and \( \text{rrnL} \), in \( C. \) biungulata and \( C. \) robusta have the same total length (2,222 bp).

In \( \text{Cladolidia} \), the A + T (81.8%) contents are the same and AT skews can be either positive or negative. The 22 tRNA and 2 rRNA genes are highly conserved, particularly \( \text{trnI} \), \( \text{trnA} \), \( \text{trnR} \), and \( \text{trnE} \), and the secondary structures are exactly the same between \( C. \) biungulata and \( C. \) robusta.

3.4 | Control region of \( \text{Cladolidia} \) mitogenome

The control regions are located between \( \text{rrnS} \) and \( \text{trnI} \), with lengths of 1,016 (\( C. \) biungulata) and 1,199 bp (\( C. \) robusta), respectively. The control region has the highest A + T content (83% and 82.5%) among the two complete \( C. \) biungulata and \( C. \) robusta mitogenomes (Table 2). Comparative analysis of the base composition of every component of the Coelidiinae mitogenomes indicated that the control regions have the highest A + T content, ranging from 82.5% (\( C. \) robusta) to 85.9% (\( O. \) obliqua). In the control region, both AT and GC skew are negative, indicating that T and C are more abundant than A and G. The GC content was the most significant factor in determining the
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3.5 | Phylogenetic relationship

By detecting the base heterogeneity of mitogenome datasets used for constructing a phylogenetic tree, we can determine whether the base heterogeneity of each dataset will cause a major error in the tree construction process (Li et al., 2015; Liu et al., 2018; Morgan et al., 2013; Sheffield et al., 2009; Song et al., 2016; Timmermans et al., 2015). On the basis of the calculation results obtained from the AliGROOVE (Kück et al., 2014) software, the heterogeneity of PCG12 and AA datasets in the mitogenomic data of Cicadellidae is weak (Figure 5). Hence, the two datasets could be used to construct a phylogenetic tree.

BI and ML analyses using 13PCGs12 and the AA datasets generated phylogenetic trees with two topologies (Figures 6, 7, S8, and S9). The monophyly of each subfamily was generally well supported in the family Cicadellidae, which is consistent with the findings of some previous molecular phylogenetic studies (Du, Zhang, et al., 2017; Du et al., 2019; Wang et al., 2017, 2018, 2020, 2021; Wang, Wang, et al., 2019). However, this finding is different from that of the studies by (Xue et al., 2020) and (Dietrich et al., 2017). They supported the inclusion of Macropsini and Idiocerini as the tribes of Eurymelinae. The phylogenetic relationships determined in our study do not support this inclusion, possibly owing to the use of molecular data different from those of previous studies and the limited mitogenomic data evaluation in our study; therefore, multiple gene types and more taxa should be sampled in the future to resolve this issue. Our analyses confirm that lassinae is a sister group of codon bias among organisms, which is consistent with the general tendency of the complete mitogenome.

FIGURE 2 Relative synonymous codon usage (RSCU) and codon number of Cladolidia robusta

FIGURE 3 Poly-T structure of ND5 in the subfamily Coelidiinae
FIGURE 4  Predicted secondary structures of the 22 tRNAs of Cladolidia biungulata mitogenome. "*" indicates the sites without a codon in Cladolidia robusta
| Region            | Length | AT content% | AT skew | GC skew |
|-------------------|--------|-------------|---------|---------|
| **Cladolidia biungulata** |        |             |         |         |
| Whole             | 15,376 | 78.2        | 0.16    | -0.24   |
| 13 PCGs           | 1,411  | 79.4        | 0.18    | -0.26   |
| 22 tRNAs          | 1,394  | 78.9        | 0.12    | -0.14   |
| 2 rRNAs           | 1,972  | 81.8        | 0.18    | -0.27   |
| Control region    | 1,199  | 83          | -0.02   | -0.01   |
| **Cladolidia robusta** |        |             |         |         |
| Whole             | 15,247 | 78.4        | 0.16    | -0.24   |
| 13 PCGs           | 1,394  | 78.9        | 0.18    | -0.25   |
| 22 tRNAs          | 1,402  | 79.5        | 0.11    | -0.10   |
| 2 rRNAs           | 1,956  | 81.8        | 0.17    | -0.27   |
| Control region    | 1,016  | 82.5        | 0.01    | -0.09   |

Abbreviation: PCG, protein-coding gene.
**Figure 5** Heterogeneity of amino acids (left) and PCG12 (right) in the mitogenome of Cicadellidae. Differences in heterogeneity between sequences are represented by color, with dark red (−1) to dark blue (+1) representing differences from heavy to light. PCG, protein-coding gene.

**Figure 6** Phylogenetic tree of Cicadellidae species inferred via Bayesian analyses of the amino acid datasets.
FIGURE 7  Phylogenetic tree Cicadellidae species inferred via maximum likelihood analyses of the amino acid datasets
Coelidiinae. Nine species of Coelidiinae are clustered together, and all phylogenetic relationships demonstrated a high nodal support in both ML (bootstrap support [BS] > 90) and BI (posterior probabilities [PP] = 1.00) analyses. These results provide substantial support for these two species (C. biungulata and C. robusta) being the members of the Coelidiinae subfamily and Cicadellidae family.

4 | DISCUSSION

The results of all analyses performed in the present study clearly support the 12 included cicadellidae subfamilies being monophyletic groups. The BI tree showed the following relationship within Membracoidea: (Deltoccephalinae + (Treehoppers + ((Megophthalminae + (Macropsinae + (Hylicinae + (Coelidiinae + fassinae))) + (Idiocerinae + (Cicadellinae + (Typhlocybinae + (Mileewinae + (Evacanthinae + Ledrinae)))))))) (Figure 6, S8, and S9). However, the ML tree showed the following phylogenetic relationships: (Ledrinae + (Evacanthinae + (Mileewinae + (Typhlocybinae + (Cicadellinae + (Idiocerinae + (Macropsinae + (Megophthalminae + Hylicinae)+ (Deltoccephalinae + (Treehoppers + (Coelidiinae + fassinae) +)))))))) (Figure 7). In all BI analyses with higher approval ratings than ML analyses, this phenomenon is commonly noted in the analyses performed in previous studies; other recent analyses of relationships among some leafhopper subfamilies have yielded trees with low support for many deep internal branches (Wang et al., 2018, 2020). These two relationships of BI analyses and ML analyses differ primarily in the positions of Deltoccephalinae and Ledrinae. In ML-AA analysis, Ledrinae occupied the basal branch of leafhopper species in all phylogenetic analyses. This further confirms that the subfamily Ledrinae is an ancient group of leafhoppers, which is consistent with the findings of previous molecular phylogenetic studies (Du, Zhang et al., 2017; Du et al., 2019; Wang et al., 2017, 2018, 2020, 2021; Wang, Wang et al., 2019). However, Deltoccephalinae, rather than Ledrinae, occupied the basal branch of leafhopper species in other (BI-AA, BI/ML-PCG12) phylogenetic analyses. Our analyses confirm that fassinae and Coelidiinae are assigned to the sister groups of treehoppers, Macropsinae, and Megophthalminae with high approval ratings (ML, BS = 100; BI, PP = 1.00); this result is different from that observed in previous studies (Du et al., 2019; Wang et al., 2017, 2018, 2020, 2021; Wang, Wang et al., 2019). In the present study, phylogenetic relationships showed that the subfamily Megophthalminae is a sister group of Macropsinae instead of treehoppers.

In all analyses, the two species of the genus Cladolidia also clustered closely with the genus Taharana; the results showed that the genus Cladolidia is a monophyly group. However, the genus Olidiana was not classified as monophyletic and can be divided into three branches. The three species O. Ritcheriina, Olidiana sp., and O. Ritcheri also clustered closely to the genus Taharana. The remaining species were split into two clades: one included O. Longistika, O. Obligua, and O. Alata and the other included only one species (O. Tongmaiensis). This conclusion was further confirmed based on significant differences in their morphological characteristics, which were characterized by body color, shape, and the position of the processes on the aedeagus shaft. Therefore, on the basis of the complete mitogenome phylogenetic analysis and the comparison of morphological characteristics, we propose that Olidiana is not monophyletic; hence, this genus may need taxonomic revisions. Future studies on both the morphological and molecular characteristics of additional species are warranted to reveal phylogenetic relationships within Coelidiinae.

ACKNOWLEDGMENTS

This research was supported by the National Natural Science Foundation of China (No. 31672342); the Program of Excellent Innovation Talents, Guizhou Province, China [Grant number 20206003]; and the Guizhou Province Graduate Research Fund YJSCXJH[2020]073. We also wish to thank Dr. Hongpin Zhang and Yalin Yao (Institute of Entomology, Guizhou University, Guiyang, China) for providing specimens in this study and two anonymous reviewers for reading the manuscript and making a lot of very valuable suggestion.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

Xianyi Wang: Formal analysis (equal); Investigation (lead); Methodology (lead); Writing—original draft (equal); Writing—review & editing (equal). Jiajia Wang: Conceptualization (equal); Investigation (equal); Methodology (equal); Writing—review & editing (equal). Renhui Dai: Conceptualization (equal); Formal analysis (equal); Writing—original draft (equal); Writing—review & editing (equal).

DATA AVAILABILITY STATEMENT

GenBank accession numbers: Cladolidia biungulata (MW406474) and Cladolidia robusta (MW406475). These two datasets 13PCG12 dataset (first and second codons of 13 PCGs, 6,676 bp); AA dataset, the amino acid sequences of 13 PCGs, 3,338 bp were deposited in Dryad: https://doi.org/10.5061/dryad.zkh1893b3).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Wang, X., Wang, J., & Dai, R. (2021). Structural features of the mitogenome of the leafhopper genus Cladoldia (Hemiptera: Cicadellidae: Coelidiinae) and phylogenetic implications in Cicadellidae. Ecology and Evolution, 11, 12554-12566. https://doi.org/10.1002/ece3.8001