Whole Genome Sequence of an Edible and Potential Medicinal Fungus, Cordyceps guangdongensis

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ABSTRACT Cordyceps guangdongensis is an edible fungus which was approved as a novel food by the Chinese Ministry of Public Health in 2013. It also has a broad prospect of application in pharmaceutical industries, with many medicinal activities. In this study, the whole genome of C. guangdongensis GD15, a single spore isolate from a wild strain, was sequenced and assembled with Illumina and PacBio sequencing technology. The generated genome is 29.05 Mb in size, comprising nine scaffolds with an average GC content of 57.01%. It is predicted to contain a total of 9150 protein-coding genes. Sequence identification and comparative analysis indicated that the assembled scaffolds contained two complete chromosomes and four single-end chromosomes, showing a high level assembly. Gene annotation revealed a diversity of transposons that could contribute to the genome size and evolution. Besides, approximately 15.57% and 12.01% genes involved in metabolic processes were annotated by KEGG and COG respectively. Genes belonging to CAZymes accounted for 3.15% of the total genes. In addition, 435 transcription factors, involved in various biological processes, were identified. Among the identified transcription factors, the fungal transcription regulatory proteins (18.39%) and fungal-specific transcription factors (19.77%) represented the two largest classes of transcription factors. This genomic resource provided a new insight into better understanding the relevance of phenotypic characters and genetic mechanisms in C. guangdongensis.

KEYWORDS Cordyceps chromosome transporters transcription factors Genome Report

Cordyceps guangdongensis T. H. Li, Q. Y. Lin & B. Song was discovered in Southern China (Lin et al. 2008), and has been successfully cultivated (Lin et al. 2010). Its fruiting body is nontoxic, and was approved as the second novel food of Cordyceps species by the Ministry of Public Health of China in 2013. This fungus is rich in nutrients and bioactive compounds, such as cordycepic acid, adenosine and polysaccharides (Lin et al. 2009; 2010); these contents are similar to those of the traditional Chinese invigorant, Ophiocordyceps sinensis (=Cordyceps sinensis) (Lin et al. 2009). Previous research by the authors’ group indicated that the fruiting bodies of C. guangdongensis possessed various therapeutic properties, including antioxidant activity (Zeng et al. 2009), longevity-increasing activity (Yan et al. 2011), anti-fatigue effect (Yan et al. 2013), curative effect on chronic renal failure (Yan et al. 2012), and anti-inflammatory effect (Yan et al. 2014). These active effects provided great potential for its application in food and medicinal industries. Therefore, it is a matter of cardinal significance to further understand the fruiting body development and metabolic mechanisms of C. guangdongensis, as well as its evolutionary relationship with other related species.

In recent years, whole genome sequencing (WGS) has been widely used to analyze the relevance of phenotypic characters and genetic mechanisms. The rapid development of advanced sequencing techniques and bioinformatic methods makes it more convenient to further explore the mechanisms of fungal development, metabolism, systematic taxonomy, and evolution at the molecular level. To date, numerous genomes of fungi within the order Hypocreales have been published in the Ensembl fungus database (http://fungi.ensembl.org/index.html). Based on the available genome sequences, researchers not only ascertained evolutionary relationship of many fungi (Zheng et al. 2011; Bushley et al. 2013; Xia et al. 2017), but also identified almost 40 medically active product producing gene clusters in different Cordyceps species, such as cyclosporine, oosporein, beauvericin, efrapeptins,
2-pyridone alkaloids, equisetin, emericellamide, tolypin (Zheng et al. 2011; Bushley et al. 2013; Quandt et al. 2015; Kramer and Nodwell 2017; Lu et al. 2017). Meanwhile, various transcription factors (TFs), including bZIP TFs, zinc finger TFs and fungal-specific TFs, were proven to be involved in fruiting body development by transcriptome analysis on the basis of genome sequences (Zheng et al. 2011; Yin et al. 2012; Yang et al. 2016). However, the whole genome sequence for C. guangdongensis is still lacking.

In order to acquire abundant molecular information to effectively explore the genetic characteristics of C. guangdongensis, the whole genome of C. guangdongensis was sequenced for the first time in this study. At the assembly level, the types of transposable elements and transcriptional factors (TFs) were further analyzed. This genomic resource provides a new insight to better understand the relevance of phenotypic characters and genetic mechanisms in C. guangdongensis.

MATERIAL AND METHODS

Fungal strains and DNA extraction

The sample used for the whole genome sequencing and assembly was isolated from the strain GDGM30035 (wild fruiting bodies of C. guangdongensis). The strain was cultured on PDA medium at 23 ± 1°C for four weeks. Aqueous suspensions of fungal spores were prepared by pouring sterile distilled water onto the sporulated cultures and gently scrubbing the agar surface. The sporule suspension was collected by passing the aqueous fungal suspensions through four layers of sterile cheesecloth to remove mycelial fragments. The sporule suspension was diluted to 1×10^7 conidia ml^-1 using a hemocytometer, and was coated on the PDA medium covered with cellophane. A single colony (C. guangdongensis GD15) was transferred onto a new PDA medium and was cultured three times. For DNA isolation, the strain was cultured on a PDA medium, which was covered with cellophane in advance. Genomic DNA from a 7-day-old fungal colony was extracted using CTAB-based extraction buffer (Watanabe et al. 2010). The DNA concentration was determined using UV-Vis spectrophotometer (BioSpec-nano). The integrity of the DNA was detected using 0.8% agarose gel, and the purity of the DNA was analyzed with PCR using 16S rRNA primers.

Genome sequencing and assembly

The genome of C. guangdongensis GD15 was sequenced at the Beijing Genomics Institute at Shenzhen with the hybrid of Illumina HiSeq2000 and the PacBio sequencing platform. The PacBio sequencing approach could provide previously unprecedented sequencing read lengths (>2kb), and get better sequencing depth. The next generation sequencing approach has also been widely used in various species. It has been proven to be involved in fruiting body development by transcriptome analysis on the basis of genome sequences (Zheng et al. 2011; Yin et al. 2012; Yang et al. 2016). However, the whole genome sequence for C. guangdongensis is still lacking.

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Functional annotation

Structural and functional annotations of genes were performed according to various databases of ARDB (Antibiotic Resistance Genes Database) (Liu and Pop 2009), CAZymes (Carbohydrate-Active enZymes Database) (Cantarel et al. 2009), COG (Cluster of Orthologous Groups) (Tatusov et al. 2003), GO (Gene Ontology) (Ashburner et al. 2000), IPR (InterPro Protein Families Database) (Kanehisa et al. 2006), NR (Non-Redundant Protein Database) (Yuan and Zhang 2013), P450 (Magrane et al. 2011), PHI (Pathogen Host Interactions) (Torto-Alalibo et al. 2009), SwissProt (Magrane et al. 2011), T3SS (Type III Secretion System Effector protein) (Vargas et al. 2012), TrEMBL (O’Donovan et al. 2002), VFDB (Virulence Factors of Pathogenic Bacteria) (Chen et al. 2016), IPR (InterPro Protein Families Database) (Mitchell et al. 2015), KOG (Eukaryotic Orthologous Groups) (Tatusov et al. 2003), and NOG (Non-supervised Orthologous Groups) (Huerta-Ceps et al. 2016). Transcription factors were annotated according to their InterPro IDs in the Fungal Transcription Factor Database (Wilson et al. 2008).

Data availability

The genome sequencing project has been deposited at GenBank under the accession number NRQP00000000. The BioProject designation for this project is PRNA399600. Figure S1 shows the length and quality distributions of PacBio reads. Figure S2 shows the BUSCO analysis of the completeness of the assembly results. Figure S3 shows the distribution of gene length predicted in the C. guangdongensis genome. Table S1 shows the genome sequences used to analyze the chromosome. Table S2 shows the genome annotation of proteins in C. guangdongensis genome. Table S3 shows the transposable element classification in C. guangdongensis. Supplemental material available at Figshare: https://figshare.com/s/6ad2d1f775328ca704c4a.

RESULTS AND DISCUSSION

Whole-genome assembly

A total of 3,926,378,523 reads representing a cumulative size of 3.926 Gb were generated, including 13,392,532 and 3,912,985,991 reads...
from Illumina and PacBio sequencing platforms, respectively. The PacBio sequencing results showed high quality polymerase reads and subreads (Figure S1). After filtering out the low quality reads, a total of 3,484,503,143 reads were assembled into nine scaffolds with N50 of 7.88 Mb from ~183 average coverage. In addition, a total length of 29.05 Mb with a 57.01% GC content was obtained (Figure 1A). Based on the Illumina sequencing data, the predicted genome size by K-mer analysis was 31.58Mb; the total size of the combined assembly closely matched this estimated size (91.98%). Compared to the previously reported draft genomes listed in Table 1. The completeness of the assembly results was evaluated by comparing with the BUSCO set of 1315 fungal orthologs. According to the results, a total of 1295 set appeared complete in the C. guangdongensis gene sets; this indicated an estimated completeness of 98.5%, with only 0.99% missing (Figure S2). These results indicated that our assembly is relatively contiguous.

**Chromosome analysis**

Sequence analysis of telomeric repeats was used to estimate the number of chromosomes in the C. guangdongensis genome according to the method described by Zheng et al. (2011). The characteristic telomeric repeats (TTAGGG/CCCTAA)n were found at either 5ʹ or 3ʹ terminal of six scaffolds, of which the telomeric repeats were found at both ends of scaffolds one and three, suggesting that the two scaffolds are complete chromosomes. The lengths of the two complete chromosomes were about 8.81 Mba and 5.00 Mba, respectively. Single-ended telomeric repeats were found at four scaffolds, including the start of scaffolds four and six, the ends of scaffolds two and five, suggesting that these four scaffolds extended to the telomeres. The lengths of the four candidate scaffolds were about 7.88, 4.50, 2.05, and 0.61 Mba, respectively. The remaining three scaffolds contained no telomeric repeats, possibly due to incompleteness of the scaffold sequence data (Table 2, Table S1). Furthermore, on scaffold seven, 14 genes were identified which belonged to the core genes of mitochondrial genome, indicating that this scaffold represents mitochondrial genome sequence. Previous researches showed that the haploid genome of C. militaris contains seven chromosomes (Kramer and Nodwell 2017), and Cordyceps subsessilis (=Tolypocladium inflatum) also contains seven chromosomes (Stimberg et al. 1992). Taking into consideration the chromosome number of these related species and the present telomeric repeats analysis, it was inferred that C. guangdongensis may also possibly contain seven chromosomes. This hypothesis should be further proved with karyotype analysis.

**Genome features and annotation**

As shown in Table 3, a total of 9150 protein-coding genes were predicted in the genome, including 31 rRNA, 111 tRNA, 121 sRNA, 25 snRNA and 26 miRNA. The cumulative length of the total number of genes accounted for 56.35% of the whole genome sequence length, and the lengths of most genes were in the range of 200-5000bp (Figure S3). There was a large proportion of exons (48.29%), with a maximum number of 29,548, and the number of introns was 20,398, with a total length of 2.34 Mba (8.06%). The total number of ncRNA was 314, representing 0.4% of the genome assembly; this suggested that ncRNA formed only a small proportion of the overall genome size (Figure 1B).

Of the 9150 identified genes, 8486 genes (92.74%) were annotated using the databases described in the methods section (Table S2). This present paper mainly focused on the genes involved in metabolic processes. Among all the genes predicted, approximately 48.90% (4475) were annotated by KEGG pathway, and in these genes, 15.57% (1425) of the total predicted genes were involved in metabolism accounted for the major proportion. Genes classified into functional categories based on the COG analysis accounted for 24.43% (2236), and in these genes, 12.01% (1099) of the total predicted genes were involved in metabolic processes, and approximately 2.01% (184) of the total predicted genes were related to the biosynthesis, transportation, and catabolism of secondary metabolites (Figure 2). The percentage of genes encoding CAZymes was 3.15% (289); these genes were contributed to substrate degradation processes in nutrition for fungal development and reproduction. Among the genes related to CAZymes, 103 genes encoding glycoside hydrolases (GHs) accounted for the largest proportion (1.12%) of the total predicted genes, followed by 78 genes encoding carbohydrate-binding modules (CBMs) (0.85%),

![Image](image_url)

**Figure 1** General genomic features of Cordyceps guangdongensis. A, I, scaffolds, the different colors represented different scaffolds; II, gene density, represented as the number of genes per 100 kb, increased in color intensity from light blue, to dark blue, dark, dark red, and light red. The density of non-coding RNA increased in color intensity from dark blue, to light blue, white, light, red, and dark red; III, percentage of coverage of repetitive sequences, increased in color intensity from light green, to dark green, dark, dark red, and light red; IV, GC content estimated by the percentage of G + C in 100 kb. B, Genomic element density including genic and nongenic features of the overall genome assembly length including 40.5% non-annotated sequences.
and then 66 genes encoding glycosyl transferases (GTs) (0.72%). Genes acted as auxiliary activities (AAs) accounted for 0.32%. In addition, genes belonging to the carbohydrate esterases (CEs) and polysaccharide lyases (PLs) had much lower percentages of about 0.13% and 0.01% of the total predicted genes, respectively. Since the genes relevant to CAZymes in *Pleurotus eryngii* were not only involved in decomposition of organic materials, but also primordium differentiation and fruiting body development (Xie et al. 2018), the CAZymes genes identified in *C. guangdongensis* could likely be also involved in primordium differentiation and fruiting body development. These results are beneficial and provide the basis to further study the genetic and molecular mechanisms underlying fruiting body development.

**Repetitive elements**

The cumulative sequences of repetitive elements identified in *C. guangdongensis* genome occupied 2.77% of the assembly sequences. The tandem repeats represented 1.42% of the genome assembly, with a total length of 412,989 bp; and the TEs represented 1.35% of the genome assembly with a total length of 393,608 bp. The total number of TE families analyzed with RepeatMasker in the genome assembly was 1534, of which 1527 (99.5%) belonged to the known TEs, including 1033 retrotransposons (Class I) and 494 DNA transposons (Class II); the remaining TEs could not be classified at the time of this study (Table 4 and Table S3).

Class I retrotransposons can be mainly divided into three groups of TEs, including LINE, LTR, and SINE; each group contains several subgroups. Retrotransposons, particularly L1, Copia, DIRS, ERV1, Gypsy, Pao, Alu, etc., are the easiest to be annotated; they are also the most abundant transposons in fungi (Suarez et al. 2018). Class II DNA transposons contain a lot of known groups and some unclassified members. Among the transposons, hAT, MULE, PIF-Harb and Tc1-Mariner were reported to be extraordinarily abundant in fungi, whereas transposons CMC and piggyBac have limited taxonomic distribution and seem to exist in only a few fungal taxa (Muszewska et al. 2017). Other transposons, including P, Sola, Dada, Ginger, Zisupton, and Merlin, had been identified only in a handful of species (Kojima and Jurka 2013; Iyer et al. 2014; Majerek et al. 2014).

Previous studies indicated that TEs contributed to genome size expansion and evolution (Cordaux and Batzer 2009; Sun et al. 2012) and played crucial roles in a wide range of biological events, including organism development (Kano et al. 2009; Garcia-Perez et al. 2016), regulation (Elbarbary et al. 2016) and differentiation (Morales-Hernández et al. 2016). In addition, they sometimes act as novel promoters to activate the transcription process (Faulkner et al. 2009; Mita and Boeke 2016). Therefore, the abundance in *C. guangdongensis* would be more significant in this regard; they should be noted and further studied for their application in fungal taxonomy and regulatory roles in fruiting body development.

**Table 2 Chromosome analysis of Cordyceps guangdongensis GD15 genomic sequence**

| Scaffold | Size (bp) | Start Telomere | End Telomere | Judge | chromosome |
|----------|-----------|----------------|--------------|--------|------------|
| Scaffold1 | 8,817,043 | CCCTAA         | TTAGGG       | double-end | Complete chromosome |
| Scaffold2 | 7,881,840 | No             | TTAGGG       | single-ended | Chromosome fragment |
| Scaffold3 | 5,000,199 | CCCTAA         | TTAGGG       | double-end | Complete chromosome |
| Scaffold4 | 4,508,454 | CCCTAA         | No           | single-ended | Chromosome fragment |
| Scaffold5 | 2,058,248 | No             | TTAGGG       | single-ended | Chromosome fragment |
| Scaffold6 | 614,660  | CCCTAA         | No           | No       | Mitochondrial genome |
| Scaffold7 | 75,887   | No             | No           | No       | Fragment |
| Scaffold8 | 68,140   | No             | No           | No       | Fragment |
| Scaffold9 | 31,250   | No             | No           | No       | Fragment |
Zn₂Cys₆-type TFs, GATA-type TFs, bZIP TFs, and CHCC-type TFs, were differentially expressed during fruiting body developmental stages (Zheng et al. 2011). Hence, this information could help explore the regulatory mechanisms of TFs in fruiting body development in *C. guangdongensis*.

**Conclusion**

High quality genome sequencing of *C. guangdongensis* was presented in this study. Two complete chromosomes and four single-end chromosomes were assembled through genome sequence analysis. In the genomic sequences, diverse transposable elements were identified,

**Figure 2** COG functional classification of proteins in the *Cordyceps guangdongensis* genome.
which may contribute to genome size and evolution. Moreover, transcription factors in the genome of *C. guangdongensis* were identified and classified; these transcription factors may facilitate further studies of fruiting body development. And above all, knowledge about the genome sequence of *C. guangdongensis* will reveal more detailed molecular information and facilitate further studies of fruiting body development and identification of secondary metabolites in *C. guangdongensis*.

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![Figure 3](image-url)

**Figure 3** Transcription factors analysis in the *Cordyceps guangdongensis* genome.

### Table 4 Transposable element repeat class analysis in *Cordyceps guangdongensis*

| Repeat element family | Number of unique elements in family | cumulative length (bp) | % of genome assembly |
|-----------------------|-------------------------------------|------------------------|----------------------|
| Class I - Retrotransposons |                                      |                        |                      |
| LINE                  | 343                                 | 57,004                 | 0.19618              |
| L1                    | 14                                  | 660                    |                      |
| others                | 329                                 | 56,344                 |                      |
| LTR                   | 661                                 | 259,862                | 0.89435              |
| Copia                 | 269                                 | 174,266                |                      |
| DIRS                  | 4                                   | 324                    |                      |
| ERV1                  | 17                                  | 1,170                  |                      |
| Gypsy                 | 314                                 | 79,093                 |                      |
| Pao                   | 17                                  | 1,741                  |                      |
| others                | 40                                  | 3,268                  |                      |
| SINE                  | 15                                  | 1,304                  | 0.00448              |
| Alu                   | 1                                   | 51                     |                      |
| Others                | 14                                  | 1,253                  |                      |
| others                | 14                                  | 1,154                  | 0.00397              |
| Class II - DNA Transposons |                                    |                        |                      |
| CMC-EnSpm             | 44                                  | 3,001                  |                      |
| Dada                  | 8                                   | 485                    |                      |
| Ginger                | 2                                   | 141                    |                      |
| hAT                   | 4                                   | 440                    |                      |
| Merlin                | 3                                   | 108                    |                      |
| MULE-MuDR             | 29                                  | 4,628                  |                      |
| P                     | 2                                   | 134                    |                      |
| PIF-Harbinger         | 11                                  | 729                    |                      |
| PiggyBac              | 63                                  | 19,337                 |                      |
| Sola                  | 29                                  | 1,840                  |                      |
| TcMar-Tc1             | 14                                  | 3,780                  |                      |
| Zisuption             | 1                                   | 88                     |                      |
| others                | 284                                 | 39,028                 |                      |
| Unclassified          | 7                                   | 545                    | 0.00187              |
| Total                 | 1,534                               | 393,608                | 1.35466              |
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