Morphology and molecular study of three new Cordycipitoid fungi and its related species collected from Jilin Province, northeast China

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Abstract
Cordyceps species are notable medicinal fungi in China, which are pathogenic on insects and exhibit high biodiversity in tropical and subtropical regions. Recently, three new Cordyceps species, Cordyceps changchunensis and Cordyceps jingyuetanensis growing on pupae of Lepidoptera and Cordyceps changbaiensis growing on larvae of Lepidoptera, were found in Jilin Province, China and are described, based on morphological and ecological characteristics. These three new species are similar to the Cordyceps militaris group, but are distinctly distinguishable from the known species. Cordyceps changchunensis, characterised by its small and light yellow to orange stromata which is occasionally forked, covered with white mycelium at the base of stipe, globose to ovoid perithecia, is macroscopically similar to Cordyceps militaris. Cordyceps changbaiensis is clearly discriminated from other Cordyceps species by its white to orange and branched stromata, clavate to cylindrical fertile apical portion, immersed and globose to ovoid perithecia. Moreover, unbranched, clavate and orange to light red stromata, almond-shaped to ovoid and immersed perithecia separate Cordyceps jingyuetanensis from other Cordyceps species. nrITS, nrLSU and EF-1α sequences were undertaken and phylogenetic trees, based on Maximum Likelihood and Bayesian Inference analysis showed that the three new species clustered with Cordyceps militaris, but formed individual clades, as well as confirmed the results of our morphological study.

Keywords
Cordyceps, host, new species, phylogenetic study, relationship
Introduction

The family Cordycipitaceae belongs to Hypocreales with plant-, animal- and fungus-based nutrition modes (Sung et al. 2007; Vega et al. 2009). The species of Cordycipitaceae are a wide variety which infect invertebrates and, in the tropics and subtropics, are known to have the highest species diversity (Kobayasi 1941, 1982). According to current data, over 900 species of Cordycipitoid fungi are reported worldwide (Yan and Bau 2015; Zha et al. 2018). In China, more than 146 species are recorded (Yan and Bau 2015).

Cordycipitoid fungi were first described in 1753 as *Clavaria militaris* L., later being recognised as *Cordyceps militaris* (L.) Fr. The genus *Cordyceps* Fr. was established by Fries in 1818, encompassing over 450 species (Kobayasi 1982; Luangsa-ard et al. 2007). Compared with a large number of species, subdivisions into infrageneric groups, for example, subgenera and sections, have been proposed in the *Cordyceps* classification, traditionally based on morphological and ecological characters (Stensrud et al. 2005). The classification of *Cordyceps*, based on the studies of Kobayasi (1941, 1983), three subgenera, *C. subg. Cordyceps*, *C. subg. Ophiocordyceps* and *C. subg. Neocordyceps* were recognised. Subg. *Cordyceps* was characterised by the production of either immersed or superficial perithecia, which are approximately at right angles to the surface of stroma and ascospores break into part-spores at maturity. Mains proposed a different viewpoint, two subgenera, *C. subg. Cryptocordyceps* and *C. subg. Racemella*, were added (Mains 1958). Based on nrITS, nrSSU, nrLSU, EF-1α, RPB1, RPB2, TUB and ATP6 sequences, the phylogenetic study implied that the Cordycipitoid fungi belong to six genera (*Cordyceps* Fr., *Metacordyceps* G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *Tyrannicordyceps* Kepler & Spatafora, *Elaphocordyceps* G.H. Sung & Spatafora, *Ophiocordyceps* Petch and *Polycephalomyces* Kobayasi) across three families, Cordycipitaceae, Clavicipitaceae and Ophiocordycipitaceae (Sung et al. 2007; Yan and Bau 2015).

The host of Cordycipitoid fungi is varied and the fungi are always parasitic on larvae of swifts, pupae of Lepidoptera, spiders etc. Cordycipitoid fungi have a strong relationship with the environment and its host (Zha et al. 2019).

In this study, three new species of *Cordyceps* are reported, based on morphology and molecular studies. Furthermore, the relationship between the host and *Cordyceps* species is analysed.

Material and methods

Sampling and morphological studies

The specimens were photographed in situ. The size of the stromata was measured when fresh. After examination and description of the fresh macroscopic characters, the specimens were dried in an electric drier at 40–45 °C.
Descriptions of macroscopic characters were based on field notes and photographs. The colours correspond to the “Flora of British fungi: colour identification chart” (Royal Botanic Garden 1969). The dried specimens were rehydrated in 94% ethanol for microscopic examination and then mounted in 3% potassium hydroxide (KOH), 1% Congo Red, Cotton Blue and Melzer’s Reagent (Torres et al. 2005), along with a Zeiss Axio Lab. A1 microscope for observation. For each species, a minimum of 40 part-spores was measured from two different ascocarps, part-spores are given as length × width (l × w). The specimens examined are deposited in the Herbarium of Mycology of Jilin Agricultural University (HMJAU).

**DNA extraction, PCR amplification and sequencing**

Total DNA was extracted from dried specimens using the NuClean Plant Genomic DNA Kit (Kangwei Century Biotechnology Company Limited, Beijing, China). Sequences of the internal transcribed spacer region (ITS), nuclear large ribosomal subunits (LSU) and translation elongation factor 1-alpha (EF-1α) were used for phylogenetic analysis. The ITS sequence was amplified using the primer pair ITS4 and ITS5 (White et al. 1990), LSU sequence was amplified using the primer pair LROR and LR7 (Stensrud et al. 2005) and EF-1α sequence was amplified using the primer pair 983F and 2218R (Castlebury et al. 2004).

Reaction programmes followed Yan and Bau (2015), Castillo et al. (2018) and Ban et al. (2015), respectively. PCR products were visualised via UV light after electrophoresis on 1% agarose gels stained with ethidium bromide and purified using Genview High-Efficiency Agarose Gels DNA Purification Kit (Gen-View Scientific Inc., Galveston, TX, USA). The purified PCR products were sent to Sangon Biotech Limited Company (Shanghai, China) for sequencing using the Sanger method. The new sequences were deposited in GenBank.

**Data analysis**

Based on the results of BLAST and morphological similarities, the sequences obtained and related to these samples are listed in Table 1. A dataset comprising of sequences from this study, 31 representative sequences showing the highest similarity to *Cordyceps* spp. and the outgroup *Metacordyceps taii* (Z.Q. Liang & A.Y. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *Metarhizium yongmunense* (G.H. Sung, J.M. Sung & Spatafora) Kepler, S.A. Rehner & Humber, *Nigelia martiale* (Speg.) Luangsa-ard & Thanakitp., *Ophiocordyceps* spp. and *Tolypocladium ophioglossoides* (J.F. Gmel.) C.A. Quandt, Kepler & Spatafora, retrieved from GenBank, were aligned with using ClustalX (Thompson et al. 1997), MACSE V2.03 (Ranwez et al. 2018) and MAFFT (Katoh and Standley 2013), then manually adjusted in BioEdit (Hall 1999). The datasets were aligned first and then, nrITS, nrLSU and EF-1α sequences were combined with Mesquite. The tree construction procedure was performed in PAUP* ver-
Table 1. Voucher information and GenBank accession numbers of ITS, LSU and EF-1α DNA sequences of *Cordyceps changchunensis*, *Cordyceps changbaiensis*, *Cordyceps jingyuetanensis* and related species used in this study.

| Species name                  | Specimen/Strain number | Host/Substratum                  | GenBank accession numbers | References                                                                 |
|-------------------------------|------------------------|----------------------------------|---------------------------|-----------------------------------------------------------------------------|
|                               |                        |                                  |                           |                                                                             |
| *Akanthomyces lecanii*        | CBS101247              | Homopteran                       | JN649836                  | (Kepler et al. 2012)                                                        |
| *A. tuberculatus*             | NBRC106949             | Lepidoptera                      | JN943318                  | (Kepler et al. 2017; Schoch et al. 2012)                                    |
| *Blackwellomyces cardinalis*  | CBS113414              | Lepidoptera                      | MH862930                  | (Sung et al. 2007; Yu et al. 2019)                                          |
| *B. pseudomilitaris*          | NBRC101411             | Lepidoptera                      | JN943308                  | (Mongkolsamrit et al. 2020; Schoch et al. 2012)                              |
| *Cordyceps bassiana*          | IFO4848                | Lepidoptera                      | AB027382                  | (Kepler et al. 2012; Schoch et al. 2012)                                    |
| *C. bifusispora*              | ARS5690/EFCC8260       | Lepidoptera                      | AY245627                  | (Kuo et al. 2005; Sung et al. 2007)                                         |
| *C. brongniartii*             | NBRC101395             | Lepidoptera pupae                | JN943298                  | (Kepler et al. 2012; Schoch et al. 2012)                                    |
| *C. cateniobliqua*            | CBS153.83              | Lepidoptera                      | MH861560                  | (Vu et al. 2019)                                                            |
| *C. changbaiensis*            | HMJAU48255             | Lepidoptera                      | MW893252                  | This study                                                                  |
| *C. changbaiensis*            | HMJAU48260             | Lepidoptera                      | MW893270                  | This study                                                                  |
| *C. changchunensis*           | HMJAU48251             | Lepidoptera                      | MW893249                  | This study                                                                  |
| *C. changchunensis*           | HMJAU48252             | Lepidoptera                      | MW893250                  | This study                                                                  |
| *C. changchunensis*           | HMJAU48259             | Lepidoptera                      | MW893251                  | This study                                                                  |
| *C. changchunensis*           | BCC75734/TBRC7274      | Coleopteran larvae               | KT261594                  | (Mongkolsamrit et al. 2018; Tasanathai et al. 2016)                          |
| *C. coleopterorum*            | CBS110.73              | Coleoptera                       | AY624177                  | (Kepler et al. 2012; Luangsa-Ard et al. 2005)                                |
| *C. exasperata*               | MCA2155                | Lepidoptera                      | MF416542                  | (Kepler et al. 2017)                                                        |
| *C. farinosa*                 | CBS111113              | Lepidoptera                      | MF416554                  | (Kepler et al. 2017; Luangsa-Ard et al. 2005)                                |
| *C. fumosorosea*              | CBS244.31              | Coleoptera                       | AY624182                  | (Kepler et al. 2017; Luangsa-Ard et al. 2005)                                |
| *C. hepialidicola*            |                       | Lepidoptera                      | AF315649                  | Unpublished                                                                 |
| *C. jingyuetanensis*          | HMJAU48253             | Lepidoptera                      | MW893253                  | This study                                                                  |
| *C. jingyuetanensis*          | HMJAU48261             | Lepidoptera                      | MW893271                  | This study                                                                  |
| *C. kyushuensis*              | HMAS78115              | Lepidoptera                      | EF368021                  | (Sung et al. 2007; Wang et al. 2008)                                         |
| *C. militaris*                | OSC3623                | Lepidoptera pupae                | JN049825                  | (Sung et al. 2007)                                                          |
| *C. militaris*                | HMJAU48256             | Lepidoptera pupae                | MW888227                  | This study                                                                  |
| *C. moravotii*                | BCC55820/TBRC7276      | Hymenoptera                      | KT261589                  | (Mongkolsamrit et al. 2018; Tasanathai et al. 2016)                          |
| *C. ninchukispora*            | BCC30937               | Lepidoptera                      | FJ765274                  | (Kepler et al. 2017)                                                        |
| *C. ningxiaensis*             | HMJAU25074             | Diptera                          | MF309668                  | (Yan and Bau 2015)                                                          |
| *C. polyarthra*               | 6578                   | Lepidoptera                      | AJ536548                  | Unpublished                                                                 |
| *C. pruinosa*                 | ARSEF5413              | Lepidoptera                      | JN049826                  | (Kepler et al. 2012; Zha et al. 2019)                                        |
| *C. qingchengensis*           | MFLU17-1022            | Lepidoptera                      | KY423506                  | (Zha et al. 2019)                                                           |
| *C. rosea*                    | Spt09-053              | Lepidoptera                      | MF416536                  | (Kepler et al. 2017)                                                        |
| *C. roseostromata*            | ARSEF4870              | Larva, not specified             | AY245637                  | (Kuo et al. 2005; Sung et al. 2001)                                          |
| *C. scarabaeicola*            | ARSEF5689              | Coleoptera                       | JN049827                  | (Kepler et al. 2012; Sung et al. 2007)                                       |
| *C. scarabaeicola*            | Arsef5689              | Coleoptera                       | JN049827                  | (Kepler et al. 2012; Sung et al. 2001)                                       |
| *Cordyceps* sp.              | HMJAU48254             | Lepidoptera                      | MW888228                  | This study                                                                  |
|                               |                        |                                  | MW893280                  |                                                                             |
|                               |                        |                                  | MZ616771                  |                                                                             |
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| Species name                        | Specimen/Strain number | Host/Substratum | GenBank accession numbers | References                                |
|------------------------------------|------------------------|-----------------|---------------------------|-------------------------------------------|
| C. spegazzinii                     | ARSEF7850              | Diptera         | DQ196435 DQ196435 GU734752 | (Torres et al. 2005)                      |
| C. taishanensis                    | A-1                    | Lepidoptera     | FJ008927                  | Unpublished                               |
| C. tenuipes                        | TBRC7266               | Lepidoptera     | MF140742 MF140828         | (Mongkolsamrit et al. 2018; Vu et al. 2019) |
| Isaria cicadae                     | GACP07071701           | Hemiptera       | KX017277 KM761212 MT268245 | (Zhi et al. 2021)                          |
| L. japonica                        | BCC2808                | Lepidoptera     | AY624199                  | (Luangsa-Ard et al. 2005)                 |
| Metarhizium yong-munense           | EFCC2131               | Lepidoptera     | JN040856 EF468833 EF468770 | (Kepler et al. 2012; Sung et al. 2007)    |
| Metacordyceps taii                 | ARSEF5714              | Lepidoptera     | JN040829 AF543787 AF543775 | (Sung et al. 2007)                        |
| Nigelia maritae                    | HMAS197472(S)          | Coleoptera      | JN040881 JF415975 JF416016 | (Kepler et al. 2012)                      |
| Ophiocordyceps acicularis          | OSC12858/OSC110987     | Coleoptera      | JN040820 DQ518757 DQ522326 | (Kepler et al. 2012)                      |
| O. clavata                         | NBRC106961             | Coleoptera      | JN943327 JN941414 MH879672 | (Schoch et al. 2012)                      |
| O. guacilis                        | EFCC8572               | Lepidoptera     | HM142942 EF468811 EF468751 | (Sung et al. 2007; Zhong et al. 2010)     |
| O. rubiginosoperi-thecata           | NBRC106966             | Coleoptera      | JN943344 JN941437         | (Schoch et al. 2012)                      |
| O. sinensis                        | ARSEF6282              | Lepidopteran pupae | HM595981 HM595885 EF468767 | (Chan et al. 2011; Sung et al. 2007)      |
| Tolyphocladium ophioglossoides      | NBRC106331             | Elaphomyces sp. | JN943320 JN941408         | (Schoch et al. 2012)                      |

sion 4.0b10 (Swofford 2002) as described by Jiang et al. (Jiang et al. 2011). All characters were equally weighted and gaps were treated as missing data.

MrModeltest 2.3 was used to determine the best fitting substitution model for each dataset for Bayesian Inference, which was calculated with MrBayes 3.2.6 with a general time-reversible DNA substitution model and a gamma distribution rate variation across sites (Ronquist and Huelsenbeck 2003). Four Markov chains were run for two runs from random starting trees for four million generations until the split deviation frequency value was < 0.01 and trees were sampled every 100 generations. raxmlGUI 2.0 (Edler et al. 2020) was used for Maximum Likelihood (ML) analysis with 1,000 bootstrap replicates using the GTRGAMMA algorithm to perform a tree inference and search for optimal topology (Vizzini et al. 2015).

Results

Phylogenetic analysis

The phylogenetic tree, based on ITS from Bayesian analysis, included sequences from 46 fungal samples representing 43 taxa and the results are shown in Fig. 1. According to the phylogenetic tree, the three new species gather into one branch with C. militaris, C. roseostromata Kobayasi & Shimizu, C. taishanensis B. Liu, P.G. Yuan & J.Z. Cao, C. kyushuensis A. Kawam. and C. hepialidicola Kobayasi & Shimizu, but the species C. jingyuetanensis does not gather into one branch by itself. Meanwhile, the genus Cordyceps was divided into three independent clades. Furthermore, Cordyceps and Akanthomyces Lebert are a sister clade to Blackwellomyces Spatafora & Luangsara-ard.
Figure 1. Phylogenetic tree of Cordycepitiod fungi, based on ITS from Bayesian analysis; self-examined sequences are shown in bold.

For these reasons, the combined ITS, LSU and EF-1α dataset including 121 fungal samples representing 48 taxa was used for analysis and the results are shown in Fig. 2. In these data, the three new species are in three independent clades included in the *C. militaris* complex, *C. jingyuetanensis* was close to *C. hepialidicola* Kobayasi & Shimizu and is different from Fig. 1. From the phylogenetic tree (Fig. 2), the species of *Cordyceps* are mainly divided into three independent clades. Moreover, the family Cordycipitaceae clustered into three clades and the genus *Akanthomyces* formed a sister clade to the genus *Cordyceps*.

**Taxonomy**

*Cordyceps changchunensis* J.J. Hu, Bo Zhang & Y. Li, sp. nov.

MycoBank No: 839249

Figs 3, 4

**Holotype.** China. Jilin Province: Changchun City, Jingyuetan National Forest Park, 43.77°N, 125.47°E, 27 August 2018, Jia-Jun Hu, Bo Zhang & Gui-Ping Zhao (HMJAU 48251, holotype, GenBank Acc. nos.: ITS = MW893249, LSU = MW893274, EF-1α = MZ616769).
**Etymology.** *changchunensis*: referring to Changchun, the location of the holotype.

**Diagnosis.** *Cordyceps changchunensis* can be easily differentiated from closely-related species *C. militaris* by its unique host, smaller stromata, immersed perithecia and larger part-spores (2.6–6 × 1.0–1.4 μm).

**Description.** Sexual Morph. Stromata 2.4–4.5 cm long, single or multiple, solitary to gregarious, arising from pupa; branched, sometimes single at base, then branched into two forks. Fertile apical portion, orange, clavate to globose, sometimes irregular, 2.0–3.5 cm long and 0.4–0.6 cm wide, distinctly distinguishable from the stipe. Sterile stipe fleshy, light yellow to orange, cylindrical, 1.3–3.3 cm long and ca. 0.4 cm wide, usually with white mycelium at the base. Perithecia immersed at right angles to the surface of the fruiting body, globose to ovoid, 180–600 × 180–520 μm, with a thick wall about 10–15 μm. **Asci** cylindrical, 80–300 × 2.5–5 μm, 8–spored, apex of ascus hemispherical, 3.0–4.0 × 2.0–3.0 μm.
Part-spores oblong, 2.6–6 × 1.0–1.4 μm, smooth, hyaline in 3% KOH, thin-walled, inamyloid.

Asexual Morph. Unknown.

Host. Growing on pupae of Lepidoptera.

Other specimens examined. China. Jilin Province: Changchun City, Jingyuetan National Forest Park, 20 August 2015, Bo Zhang (HMJAU 48259, GenBank Acc. nos.: ITS = MW893251, LSU = MW893276, EF-1α = MZ616773); Changchun City, Jingyuetan National Forest Park, 18 August 2018, Bo Zhang (HMJAU 48252, isotype, GenBank Acc. nos.: ITS = MW893250, LSU = MW893275, EF-1α = MZ616775).

Distribution. China (Jilin Province).

Note. C. changchunensis is easily confused with C. militaris due to highly similar morphology and sharing the same habitat. Morphologically, the stromata of C. militaris are larger than C. changchunensis, single or gregarious, larger perithecia.

Figure 3. Morphological characters of Cordyceps changchunensis (HMJAU 48251, holotype) a, b, e stromata and host of Cordyceps changchunensis c surface of fertile apex of ascostroma d host of Cordyceps changchunensis f–h apex of ascus i–k ascus l–n part-spores. Scale bars: 1 cm (a, b); 2 mm (c, e); 1 mm (d); 10 μm (f–h); 50 μm (i–k); 5 μm (l–n).
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(500–1089 × 132–264 μm) and smaller part-spores (2–4 × 1 μm) (Li et al. 2015). In the phylogenetic analysis, the three specimens of *C. changchunensis* were placed in separate monophyletic lineages (BPP = 0.91, MLBS = 78%).

*Cordyceps changbaiensis* J.J. Hu, Bo Zhang & Y. Li, sp. nov.

MycoBank No: 839250

Figs 5, 6

**Holotype.** CHINA. Jilin Province, Yanbian Korean Autonomous Prefecture, Antu County, Changbai Mountain, 42.19°N, 128.18°E, 4 September 2019, Jia-Jun Hu & Bo Zhang (HMJAU 48255, holotype, GenBank Acc. nos.: ITS = MW893252, LSU = MW893277, EF-1α = MZ616772).

**Etymology.** *changbaiensis*: referring to Mt. Changbai, the location of the holotype.

**Diagnosis.** The species is characterised by orange to white and branched stromata, globose to ovoid perithecia and larger part-spores (3.0–7.0 × 1.0–1.4 μm).

**Description.** **Sexual Morph.** **Stromata** 2.4–5.2 cm long, single or multiple, solitary, arising from the head of the host insect covered with white mycelia. **Fertile apical portion**, orange to clavate to cylindrical, 0.6–1.5 cm long and 0.2–0.6 cm wide, obviously distinguishable from the stipe. **Sterile stipe** fleshy, white to light yellow, cylindrical, 1.8–3.7 cm long and 0.2–0.5 cm wide. **Perithecia** immersed to the surface of the fruiting body, globose to ovoid, 120–230 × 90–170 μm, with a thick wall about 15 μm. **Asci** cylindrical, 225–625 × 4–5 μm, 8-spored, apex of ascus hemispherical, 3.0–4.0 × 2.2–3.2 μm. **Part-spores** oblong, 3.0–7.0 × 1.0–1.4 μm, smooth, hyaline in 3% KOH, thin-walled, inamyloid.

**Asexual Morph.** Unknown.

**Host.** Growing on larvae of Lepidoptera.

**Distribution.** China (Jilin Province).

**Other specimens examined.** CHINA. Jilin Province: Baishan City, Fusong County, Quanyang Town, 42.30°N, 127.29°E, 22 August 2021, Jia-Jun Hu, Bo Zhang & Gui-
Ping Zhao (HMJAU 482260, isotype, GenBank Acc. nos.: ITS = MW893270, LSU = MW893272, EF-1α = MZ616774)

**Note.** *C. changbaiensis* has orange to white and branched stromata. Morphologically, *C. roseostromata* Kobayasi & Shimizu is similar to *C. changbaiensis* due to the single or branched stromata. *C. kyushuensis* A. Kawam. is also close to *C. changbaiensis* because of the host and the stromata being similar in colour. However, both *C. roseostromata* and *C. kyushuensis* have a larger perithecia and smaller part-spores. Furthermore, the stromata of *C. kyushuensis* is gregarious or fascicled and grows from the head or abdomen of the host (Li et al. 2015); *C. roseostromata* has pyriform perithecia and host on larva of Coleoptera (Kobayasi 1983). In the phylogenetic analysis, *C. changbaiensis* was placed in separate monophyletic lineages (BPP = 0.95, MLBS = 97%) and formed a sister relationship with *C. rosea*.
**Cordyceps jinyuetanensis** J.J. Hu, Bo Zhang & Y. Li, sp. nov.

MycoBank No: 839251

Figs 7, 8

**Holotype.** CHINA. Jilin Province: Changchun City, Jingyuetan National Forest Park, 43.80°N, 125.50°E, 27 August 2018, Jia-Jun Hu, Bo Zhang & Gui-Ping Zhao (HMJAU 48253, holotype, GenBank Acc. nos.: ITS = MW893253, LSU = MW893278, EF-1α = MZ616770).

**Etymology.** jinyuetanensis: referring to Jingyuetan National Forest Park, the location of the holotype.

**Diagnosis.** *C. jinyuetanensis* is different from other species by growing on pupae, orange to light red stromata, immersed and almond-shaped to ovoid perithecia.

**Description.** **Sexual Morph.** **Stromata** 4–4.5 cm long, multiple, solitary, arising from pupae of Lepidoptera. **Fertile apical** portion, orange to light red, clavate, 0.8–1.3 cm long and 0.1–0.2 cm wide, obviously distinguishable from the stipe. **Sterile stipe** fleshy, light yellow to orange, cylindrical, 2.7–3.7 cm long and 0.1–0.2 cm wide, usually with white mycelium at the base. **Perithecia** immersed to the surface of the fruiting body, almond-shaped to ovoid, 220–340 × 110–220 μm, with a thick wall about 15–20 μm. **Asci** cylindrical, 225–475 × 3–5 μm, 8-spored, apex of ascus hemispherical to irregular, 3.0–4.0 × 1.4–2.8 μm. **Part-spores** oblong, 2.8–5.0 × 1.0–1.4 μm, smooth, hyaline in 3% KOH, thin-walled, inamyloid.

**Asexual Morph.** Unknown.

**Host.** Growing on pupae of Lepidoptera.

**Distribution.** China (Jilin Province).

**Other specimen examined.** CHINA. Jilin Province: Baishan City, Fusong County, Quanyang Town, 42.30°N, 127.29°E, 22 August 2021, Jia-Jun Hu, Bo Zhang & Gui-Ping Zhao (HMJAU 482261, isotype, GenBank Acc. nos.: ITS = MW893271, LSU = MW893273)

**Note.** A review of literature revealed that there are about 20 species of Cordycepioid fungi growing on pupae, like the unusual medicinal fungi *O. sinensis* (Berk.)
Figure 7. Morphological characters of *Cordyceps jingyuetanensis* (HMJAU 48253, holotype) a stromata and host of *Cordyceps jingyuetanensis* b host of *Cordyceps jingyuetanensis* c, d surface of fertile apex of ascostroma e, f part-spores g–k ascus l–o apex of ascus. Scale bars: 1 cm (a); 2 mm (b, c); 500 μm (d); 5 μm (e, f); 20 μm (g–k); 10 μm (l–o).

G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *C. militaris, I. cicadae* Miq. and also like the two new species, *C. ningxiaensis* T. Bau & J.Q. Yan and *C. qingchengensis* L.S. Zha & T.C. Wen, reported from China in 2015 and 2019. Nevertheless, *C. jingyuetanensis* is different from these Cordycipitiod species; *C. ningxiaensis* grows
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I. *cicadaceae* grows on the pupae of Hemiptera and the stromata of *C. qingchengensis* are yellow, single or branched on the top. *C. hepialidicola* Kobayasi & Shimizu from Japan is similar to *C. jingyuetanensis* in its phylogenetic relationship, but there are distinct morphological differences. Morphologically, the stromata of *C. hepialidicola* are multiple, branched on the top sometimes, grow from the head of larva of Hepialida or Lepidoptera, have larger perithecia (300–350 × 500 μm) and smaller part-spores (3–4 × 1 μm) (Kobayasi 1983). In the phylogenetic analysis, *C. changbaiensis* was placed in separate monophyletic lineages (BPP = 0.92, MLBS = 79%).

**Cordyceps militaris** (L.) Fr., *Observ. mycol.* (Havniæa) 2: 317 (cancellans) (1818)

Fig. 9

**Specimens examined.** China. Yunnan Province: Qujin City, Huize County, 26.24°N, 103.25°E, 30 July 2019, Jia-Jun Hu, Bo Zhang & Di-Zhe Guo (HMJAU 48256, GenBank Acc. nos.: ITS = MW888227, LSU = MW893279); Jilin Province: Changchun City, Jingyuetan National Forest Park, 43.80°N, 125.50°E, 25 August 2018, Jia-Jun Hu & Yong-Lan Tuo (HMJAU 48257); Changchun City, Jingyuetan National Forest Park, 43.80°N, 125.50°E, 25 August 2018, Jia-Jun Hu, Bo Zhang & Gui-Ping Zhao (HMJAU 48258); Tonghua City, Ji’an County, Wunvfeng National Forest Park, 41.28°N, 126.14°E, 25 August 2019, Yong-Lan Tuo (HMJAU 48262); Heilongjiang Province: Daxing’an Mountains, Shuanghe National Reserve, 52.44°N, 125.40°E, 23 June 2019, Di-Zhe Guo (HMJAU 48263).

**Note.** *C. militaris* is a widely distributed species and also a well-known medicinal fungus in China. At this time, we collected samples from many different places. The morphological evidence shows no apparent differences between each other. However, the habitat is markedly different.
| Species                      | Host                          | Stromata                                                                 | Fertile part                                      | Perithecia                                                                 | Asci                                                                 | Ascospores                        | Reference                      |
|-----------------------------|-------------------------------|-------------------------------------------------------------------------|--------------------------------------------------|---------------------------------------------------------------------------|----------------------------------------------------------------------|-----------------------------------|---------------------------------|
| *Beauveria bassiana*        | Larvae of Lepidoptera        | Single or several, unbranched, slender and cylindrical, brownish-yellow to yellowish | 18.7–33.3 × 2.8–8.0 mm                          | Elliptical, 610–720 × 230–320 μm, immersed to surface                   | Cylindrical, 230–590 × 3.5–4.0 μm with asci cap 3.6–4.0 μm in diameter | Filamentous, 300–570 × 1.0 μm, not broken into part-spores | (Li et al. 2001)                |
| *Blackwellomyces pseudomilitaris* | Larvae of Lepidoptera        | Single or cluster, simple or branched, cylindrical, white to white-orange | 15–30 × 0.9–3 mm                                 | Elongate-ellipsoid or elongate-ovoid, 290–570 × 120–245 μm, superficial | Filiform, 290–410 × 5–6 μm                                          | Filiform, 280–390 × 1.0 μm, not broken into part-spores | (Hywel-Jones 1994)              |
| *Cordyceps bicuspidata*     | Larvae of Lepidoptera        | Simple, cylindrical, clavate, whitish                                   | 6 × 1.3 mm                                      | Pyriform, with protruding apices, yellowish, 500 × 150–170 μm, immersed | Cylindrical, 200–220 × 5–4.5 μm                                          | Bifusiform, 145–220 μm in length, central part filiform about 0.4 μm wide, terminal parts narrowly fusiform, about 30 × 1.6 μm and 3 septate | (Eriksson 1982)                 |
| *C. hyshuensis*             | Larvae of Lepidoptera        | Cluster, cylindrical, Light yellow to orange red                        | 20–30 × 5–8 mm                                  | Elliptical, 300–500 × 200–300 μm, half-buried                          | Cylindrical, 3–4.5 μm wide                                         | Short cylindrical, part-spores 5–7 × 0.7–1 μm                           | (Guo and Li 2000; Li et al. 2015) |
| *C. militaris*              | Lepidopteran pupae            | Single or several, clavate, orange                                      | 10–20 × 2.5–3.5 mm                              | Conical, half-buried                                                     | Clavate, 300–400 × 4–5 μm                                         | Filiform, part spores 2–3 × 1 μm                                  | (Li et al. 2015)                |
| *C. ningxiaensis*           | Fly pupae (Diptera)           | One to two in a group, clavate, orange                                  | 1.2–1.5 × 1.2–2.8 mm                            | Ellipsoid to ovoid, 288–400 × 103–240 μm, with a wall about 10 μm thick, loosely embedded at right angles to the surface | Cylindrical, 168–205 × (3.7–4.1–5.5) μm, with oblate spheroid or hemispherical refractive cap 3.4–3.8 × 2.9–3.4 μm at apex | Filiform, irregularly multisepitate, part-spores 3.6–7.8 × 1.0–1.4 μm | (Yan and Bau 2015)              |
| *C. polyarthra*             | Larvae of Lepidoptera        | Cespitose, narrowly clavate, light yellow to reddish-brown              | 2–8 × 1.3–3 mm                                  | Ovoid, 250–450 × 125–250 μm, brown, with a definite wall 25 μm thick, embedded at right angles to the surface | Cylindrical, 150–260 × 3–4 μm, with a 1.5–2 μm thick cap             | Filiform, part-spores 4–6 × 0.75–1 μm                                 | (Mains 1958)                   |
| *C. pruinosa*               | Larvae of Lepidoptera        | Solitary or several, clavate, orange to red                             | 2–8 × 1–3 mm                                    | Ovoid to fusiform, 360–400 × 130–200 μm, crowded, red, ordinal in orientation, immersed | Cylindrical, 100–200 × 2.5–4 μm                                      | Filiform, part-spores 4–6 × 1 μm                                     | (Li et al. 2015)                |
| *C. qingchengensis*         | Lepidopteran pupae            | Branched, yellow                                                        | 7–9 × 2.0–2.5 mm                                 | Ovoid but apex sharply pointed, 335–490 × 145–240 μm, partially immersed at right angle to the surface | Cylindrical, 180–200 × 2.4–4.0 μm wide, caps hemispherical, 1.8–2.2 × 2.5–3.2 μm | Filiform, 180–220 × 0.45–0.65 μm, not at all bifusiform and not broken into part-spores | (Zha et al. 2019)              |
| *C. rhinostromata*          | Larva, not specified          | Single or branched                                                       | 1.2–5 × 1.5–2.2 mm                               | Pyriform, 280–300 × 140–160 μm, Superficial                            | 3–3.5 × 2.5–3 μm                                                   | 4–5 × 1 μm                                      | (Kobayasi 1983)                |
| *C. changhunensis*          | Lepidopteran pupae            | Single or multiple, clavate, orange                                     | 2.0–3.5 × 0.4–0.6 mm                            | Globose to ovoid, 180–600 × 180–520 μm, with a thick wall about 10–15 μm, partially immersed at right angles to the surface | Cylindrical, 80–300 × 2.5–5 μm, caps hemispheric, 3.0–4.0 × 2.0–3.0 μm at apex | Oblong, 2.6–6 × 1.0–1.4 μm                                     | This study                     |
| *C. changbaiensis*          | Larvae of Lepidoptera        | Single or multiple, clavate, white to orange                           | 0.6–1.5 × 0.2–0.6 mm                             | Globose to ovoid, 120–230 × 90–170 μm, with a thick wall about 15 μm, immersed to surface | Cylindrical, 225–265 × 4–5 μm, caps hemispherical, 3.0–4.0 × 2.2–3.2 μm at apex | Oblong, 3.0–7.0 × 1.0–1.4 μm                                     | This study                     |
| *C. jingyuetanensis*        | Lepidopteran pupae            | Single or multiple, clavate, orange to light red                       | 0.8–1.3 × 0.1–0.2 mm                             | Almond-shaped to ovoid, 220–340 × 110–220 μm, with a thick wall about 15–20 μm, immersed to surface | Cylindrical, 225–475 × 3–5 μm, caps hemispherical to irregular, 3.0–4.0 × 1.4–2.8 μm at apex | Oblong, 2.8–5.0 × 1.0–1.4 μm                                     | This study                     |
Figure 9. Macrocharacter of *Cordyceps militaris* a–e stromata and host of *Cordyceps militaris* (a collected from Daxing’an Mountains, Heilongjiang Province b collected from Ji’an County, Tonghua City, Jilin Province c, e collected from Changchun City, Jilin Province d collected from Qujin City, Huize County, Yunnan Province). Scale bars: 1 cm (a–e).

Key to reported species in this study

1. Stromata arise from pupae ................................................................. 2
   – Stromata arise from larvae................................................. *Cordyceps changbaiensis*
2. Stromata branched into two forks sometimes..... *Cordyceps changchunensis*
   – Stromata not branched ................................................................. 3
3. Part-spores over 3 μm .............................................. *Cordyceps jingyuetanensis*
   – Part-spores less than 3 μm................................................... *Cordyceps militaris*

Discussion

In this study, three new species, collected from northeast China in the *Cordyceps militaris* group, are described. In previous work, about 38 species were recognised as
belonging to the *C. militaris* group (Yan and Bau 2015). ML and BI analysis recognised four well-supported clades, one is Cordycipitaceae, the others are Clavicipitaceae and Ophiocordycipitaceae (Fig. 2). Moreover, the Cordycipitaceae branch is mainly divided into three clades, the *Akanthomyces* clade near the *Cordyceps* clade, implies a closer biological relationship.

The previous studies have revealed that the genus *Cordyceps* was not monophyletic (Artjariyasripong et al. 2001), the species of *Isaria* was nested within *Cordyceps* (Kepler et al. 2017) and our phylogenetic analysis also shows a similar result. *Cordyceps* clade consisted of three major subclades designated as clade 1, clade 2 and clade 3 (Fig. 2). Nearly all the subclades in *Cordyceps* clade were strongly supported.

Clade 1, including nine *Cordyceps* spp. and two *Isaria* spp. *I. cicadae*, based on Chinese sequences, gathers into one branch with *Cordyceps* species. What is known as *I. cicadae* in China, named on a Brazilian specimen, is of confused classification status, due to the teleomorph having remained undiscovered. In China, *C. cicadae* Massae has been regarded as a teleomorph of *I. cicadae* as well as a teleomorph of *O. sobolifera* (Hill ex Watson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora and referred to as *C. sobolifera* (Hill ex Watson) Berk. & Broome. Until recently, the teleomorph was discovered in Mt. Jinggang, Jiangxi Province, China and both teleomorph and anamorph existed on some specimens, with the morphology of the anamorph consistent with those, "*I. cicadae*", harvested throughout southern China, significantly different from the type specimen of *I. cicadae*. For this reason, it was published as a new species named *C. chanhua* Z.Z. Li, F.G. Luan, Hywel-Jones, C.R. Li & S.L. Zhang (Zhi et al. 2021). Furthermore, *I. japonica* Yasuda reported from Japan, exhibits exceptionally high affinity with the genus *Cordyceps*. The teleomorph, however, still remains a mystery and a more intensive study is needed. Clade 2 consists of *C. scarabaecola* Kobayasi, *C. bassiana* Z.Z. Li, C.R. Li, B. Huang & M.Z. Fan and *C. brongniartii* Shimazu. Yellow stromata seem to be a synapomorphic character of clade 2. Clade 3 included 15 *Cordyceps* spp. However, clade 3 did not form a monophyletic group. *C. ninchukispora* (C.H. Su & H.H. Wang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *C. chiangdaoensis* Tasan., Thanakitp., Khons. & Luangsa-ard, *C. pruinosa* Petch and *C. morakotii* Thanakitp., Thanakitp. & Luangsa-ard gather into one branch. *Cordyceps* spp. of clade 3A all arise from pupae. Clade 3B includes 11 *Cordyceps* spp., seven known *Cordyceps* spp., one unidentified *Cordyceps* sp. and our three new species. Being visually similar to *Cordyceps militaris* seems to be a synapomorphic character of clade 3B.

About 60% of *Cordyceps* sensu lato species are recorded on two insect orders—Coleoptera and Lepidoptera (Shrestha et al. 2016). Host preferences have been variously implemented in taxonomic work, so this is also in *Cordyceps*. Host associations, when superimposed on phylogeny, suggested that some groups of taxa have conserved the endoparasite-host interactions to some extent; however, several host shifts have occurred during the evolution of *Cordyceps* (Stensrud et al. 2005). In *Cordyceps* species, hosts were considered as having low significance as a phylogenetic character, but are the most crucial feature in morphological aspects (Torres et al. 2005).
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