Hygrophorus annulatus, a new edible member of H. olivaceoalbus-complex from southwestern China

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ABSTRACT

Members of Hygrophorus olivaceoalbus-complex or olive waxcaps have both ecological and economic significance. European and North American species diversity of this fungal group has been presented in recent molecular phylogenetic studies, but no Chinese materials were included. In this study, a phylogenetic overview of the H. olivaceoalbus-complex based on internal transcribed spacer (ITS) sequences was made, and a local popular edible species from southwestern China was described as a new species H. annulatus. This new species is characterized by grayish brown, olive brown to dark brown pileus disc, inflexed to deflexed pileus margin, obvious and dark brown annulus, basidiospores measuring (8.0–)8.5–11.0(–12.0) × 5.0–7.5(–8.0) μm, and the distribution in subalpine forests dominated by Abies and/or Picea in southwestern China.

Keywords: Basidiomycota, Hygrophoraceae, olive waxcaps, phylogeny, taxonomy

Article history: Received 30 July 2020, Revised 13 January 2021, Accepted 14 January 2021, Available online 20 March 2021.
and dried in a Dörrex dehydrator (Stockli, Switzerland) or other electric driers at 50 °C overnight. Macro-morphological characters were noted from the specimen records and photographs. Color names and codes were given according to Kornerup and Wanscher (1978). Micro-morphological characters of the dry specimens were observed and measured using AX10 light microscopy and ZEN 2 lite software (Carl Zeiss Inc., Oberkochen, Germany). Dry tissues were rehydrated in water to observe colors and gelatinous zones of pileipellis, and in 5% KOH then mounted with 1% Congo red to measure basidiospores, basidia, pileipellis, stiptippellis, and hymenophoral trama. For each individual, 20 basidiospores and 10 basidia were randomly selected and measured. Q value refers to the length/width ratio of basidiospores and basidia. Size and Q value dimensions of basidiospores and basidia are described with the notation (a–)b–c(–d): the range ‘b–c’ represents 90% of the measured values, and ‘a’ and ‘d’ represent extreme values. Q_m/L_m/W_m refers to the average of Q values/length/width ± standard deviation. Specimens are deposited in the Fungarium of Guangdong Institute of Microbiology (GDGM), the Herbarium of Mycology, Academia Sinica (HMAS), the Herbarium of Cryptogams at the Kunming Institute of Botany, Chinese Academy of Sciences (KUNHKS), and the Mycological Herbarium of Soil and Fertilizer Institute, Sichuan Academy of Agricultural Sciences (SAAS).

Genomic DNA was extracted from the dry specimens using the HiPure Fungus DNA Mini Kit (Magen Biotech Co., Ltd., Guangzhou, China) according to the manufacturer’s instructions. Sequences of nuclear ribosomal ITS region were amplified by Polymerase Chain Reaction (PCR), using primers ITS1F and ITS4 (White et al., 1990; Gardes & Bruns, 1993). The PCR procedure for ITS was as follows: initial denaturation at 94 °C for 5 min, followed by 35 cycles at 94 °C for 40 s, 52 °C for 40 s and 72 °C for 1 min, and a final extension of 72 °C for 8 min. Amplified PCR products were cleaned and sequenced by Beijing Luhe Co., Limited (Guangzhou, China) on an ABI 3730 DNA sequencer analyzer (Applied Biosystems, Foster City, CA, USA) with the same primers. Raw ab initio sequences of both directions were assembled and unrecognized starting and ending base pairs were trimmed using SeqMan software version 7.1.0 (DNASTAR, Inc.). The consensus sequences have been deposited in GenBank (accession nos. MT758317–MT758341).

Phylogenetic analyses were conducted to elucidate the phylogenetic position of the Chinese specimens and to examine the relationships among the members of the H. olivaceoalbus-complex. Fifty-eight downloaded and 25 newly generated ITS sequences of the H. olivaceoalbus-complex were included as the ingroup, H. bakerensis A.H. Sm. & Hesler and H. tennesseensis A.H. Sm. & Hesler were selected as the outgroup following the results of Moreau et al. (2018). Sequences were aligned with MAFFT (Multiple Alignment using Fast Fourier Transform) online service version 7 using auto strategy (Katoh & Standley, 2013). The alignment dataset was deposited in TreeBASE (submission ID: 27067). Best-fit models for IQ-TREE and MrBayes were selected according to BIC criterion using ModelFinder (Kalyaanamoorthy et al., 2017) in PhyloSuite (Zhang et al., 2020). Maximum Likelihood (ML) analyses were performed on IQ-TREE under the TPM2u+G+F model for 5000 ultrafast bootstraps (BS) (Minh et al., 2013; Nguyen et al., 2015). Bayesian analyses were implemented using MrBayes (Ronquist et al., 2012) on the CIPRES Science Gateway (www.phylome.org) under the HKY+G+F model, in which the initial 25% of sampled data were discarded as burn-in. The trees were viewed and edited in ITOL (Interactive Tree of Life) web server (Letunic & Bork, 2016).

### Taxonomy

**Hygrophorus annulatus** C.Q. Wang & T.H. Li, sp. nov.

MycoBank no.: MB 836177.

**Diagnosis:** *Hygrophorus annulatus* differs from the other species of *H. olivaceoalbus*-complex by the DNA sequences, obvious and dark brown annulus, shorter basidiospores measuring (8.0–)8.5–11.0(–12.0) × 5.0–7.5(–8.0) μm, and the distribution in subalpine forests dominated by *Abies forrestii* Coltn.-Rog., *A. georgei* Orr, *Picea asperata* Mast., *P. likiangensis* (Franch.) Pritz. in southwestern China.

Type: CHINA. Sichuan Province, Garze Tibetan Autononomous Prefecture, Kangding City, Mugecuo, on the ground of a forest dominated by *Picea asperata*, 30°11′N, 101°54′E, elev. ca 3400 m, 4 Aug 2015, M. Zhang (GDDM45124, holotype).

Gene sequence ex-holotype: MT758324 (ITS).

**Etymology:** annulatus means annulate, referring to the well-developed ring on the stipe.

Pileus (20–)40–70(–100) mm, hemispherical to convex when young, becoming subumbonate, plano-convex or aplonate when mature, greyish brown (6E3–4), olive brown (4F3–7) to dark brown (6F3–7) at disc, lighter towards the margin, light brown (6D4), brownish gray (6G2) to gray (6B1, 6C1) from outer zone of disc to pileus margin, sticky when wet; margin involute at the beginning and then inflexed to deflexed, entire to irregularly fissured, even to wavy. Context up to 12 mm thick, white, soft. Lamellae narrowly adnate with a decurrent tooth or subdecurrent, up to 5 mm broad, subdistant, white, sometimes with pinkish tint, waxy, with 1–3 lamellulae of different lengths between two complete lamellae; edge even, concolorous. Stipe 60–150 × 5–20 mm, central, subcylindrical, nearly equal to slightly tapering upwards, solid, with a brownish annulus or partial veil at upper part of stipe, white above the annulus, covered with greyish to dark brown (6F4–7) fibers below, which usually form several vague to rather clear annular stripes or bands, usually with white mycelium at base. Annulus superior, at an area of about 1 cm below the stipe apex when mature, as one or two layers of fibrous veil, connecting pileus margin and stipe when young, leaving a strong dark brown (concolorous with pileus disc) annulus and usually a weaker (concolorous to the pileus margin) ring on the stipe when mature, fibrous. Odor and taste mild. Edible.

Basidiospores (8.0–)8.5–11.0(–12.0) × 5.0–7.5(–8.0) μm, *L_m* = 10.0 ± 0.9, *W_m* = 6.3 ± 0.8, *Q* = (1.33–)1.36–1.82(–1.83), *Q_m* = 1.60 ± 0.12, ellipsoid to elongate, thin-walled, hyaline in KOH. Basidia (37.0–)41.0–65.0(–71.0) × (7.5–)8.0–11.0(12.5) μm, *L_m* = 51.8 ± 9.2, *W_m* = 10 ± 1.2, *Q* = 4.2–6.8, *Q_m* = 5.26 ± 0.82, clavate, 4-spored, thin-walled; sterigmata 4.5–8.5 μm long. Subhymenium ramose, composed of hyphae 3–13 mm wide. Hymenophoral trama divergent, consisting of parallel with slightly interwoven septate hyphae; hyphae 30–85 × 4–12 μm, thin-walled, hyaline. Pileipellis an ixocutis to ixotrichoderm, 80–380 μm thick, covering with a gelatinous zone measuring 80–340 μm thick; hyphal elements 3–5 μm wide, thin-walled; stiptippellis an ixocutis; hyphae 3–5 μm wide, thin-walled, with brown intracellular pigment. Clamp-connections present in all tissues.

Habitat and known distribution: solitary to scattered on the ground in subalpine coniferous forests or coniferous and broad-leaved mixed forests, under various spruces and/or firs, particularly *A. forrestii*, *A. georgei*, *P. asperata*, *P. likiangensis*. So far only known from Sichuan, Tibet, and Yunnan in southwestern China, mostly found at elevations between 3000 m and 4300 m.

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doi: 10.47371/mycosci.2021.01.001

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Fig. 1. Phylogenetic relationship among the members of *Hygrophorus olivaceoalbus*-complex generated from ITS dataset using maximum likelihood analysis. For downloaded sequences, species names, GenBank/UNITE numbers, and origins are consecutively listed; for newly generated sequences, species names, voucher numbers, GenBank numbers, and origins are consecutively listed. The sequence generated from basidioma (●), root tip (▲), or soil (●) is marked. Host trees are added at the end with brackets if known. The tree scale means the number of substitutions per site. The IQ-TREE bootstrap support values (BS ≥ 50%) and Bayesian posterior probabilities (PP ≥ 0.5) are indicated by the numbers around the branches (BS/PP).
Additional specimens examined: CHINA. Sichuan Province: Daocheng County, Sangdui Town, on the ground of a forest dominated by *Picea*, 29°11′9.87″N, 100°5′31.99″E, elev. 4089 m, 19 Aug 2019, X.H. Wang 6210 (KUN-HKAS 107620); Jiuzhaigou County, Jiuzhaigou, 11 Sep 2012, X.L. He (SAAS 407); Li County, Miyaluo Town, near Dalangba village, 31°43′23.41″N, 102°44′40.91″E, elev. 3054 m, 24 Aug 2019, X.H. Wang 6454 (KUN-HKAS 107623); Kangding City, Xinduqiao Town, road from Xinduqiao to Gaoersi (old 318 national highway), on the ground of a forest dominated by *Picea*, 30°03′52.51″N, 101°24′45.87″E, elev. 3903 m, 21 Aug 2019,
X.H. Wang 6338 (KUN-HKAS 107621); Luding County, Yajiangeng Mt., on the ground of a spruce forest, 29°55′03.30″N, 101°59′18.43″E, 27 Aug 2019, X.H. Wang 6570 (KUN-HKAS 107624); Yajiang County, on the ground of a forest dominated by Abies and Quercus, 30°05′36″N, 101°29′53″E, elevated 3.702 m, 19 Aug 2016, Z.X. Wu, L.H. Sun & T.Z. Wei (HMAS 280974); Yajiang County, Jianziwanshan, on the ground of a forest dominated by Picea, 30°07′11.13″N, 100°42′35.34″E, elevated 4.259 m, 20 Aug 2019, X.H. Wang 6263 (KUN-HKAS 107622). Tibet Autonomous Region: Bomi County, Zhulonggou, on the ground of a mixed forest with Picea and Rhododendron, 29°49′16″N, 95°45′22″E, elevated 2.894 m, 19 Sep 2016, Z.P. Song (GDGM 47445); Nyingchi City, Lalung Town, 29°45′55″N, 94°44′2″E, elevated 3.361 m, 19 Sep 2016, Z.P. Song (GDGM 47447); Nyingchi City, 18 Sep 2016, Z.P. Song (GDGM 47200). Yunnan Province: Ninglang Yi Autonomous County, Miaomianzhang, on the ground of a forest with Picea, Pinus and Quercus sect. Heterobalanus, 27°33′24.31″N, 100°40′08.01″E, elevated 3.282 m, 24 Sep 2019, X.H. Wang 7084 (KUN-HKAS 107625); Shangri-la County, 28°00′25.36″N, 99°42′35.06″E, elevated 3.529 m, 16 Aug 2019, X.H. Wang 6078 (KUN-HKAS 107619).

In the phylogenetic analysis, the ingroup sequences were grouped into six lineages (groups Ia, Ib, II, III, IV, and V; Fig. 1) defined in this study. Group I, supported with 100% BS/1 PP, comprised two clades (group Ia and group Ib). Clade Ia (74% BS) was composed of 33 isolates of basidiomata, soils and plant root tips from Europe (Estonia, Finland, France, Germany, Italy, Latvia, Norway, Slovakia, and Sweden) and one from Canada. Clade Ib (81% BS/0.88 PP) was formed by 13 isolates from Europe (Estonia, Finland, and Sweden). Group II, supported with 94% BS, contained 25 samples from Sichuan, Tibet, and Yunnan, all in southwestern China. Group III, supported with 90% BS/1 PP, comprised four samples from Canada and one sample from France. Group IV was a well-supported (95% BS/1 PP) lineage consisting of two samples from Sweden. Group V was a moderately supported (73% BS/0.69 PP) lineage that included two samples from Canada and a sample from America. Hygrophorus bakersensis and H. tennessensis formed an outgroup clade sibling to the ingroup with BS 100%/1 PP.

Phylogenetically, the Asian and North American populations of the H. olivaceoalbus-complex are distinct from those known species. With regards to the number of sequences within the H. olivaceoalbus-complex, 50 European and 8 American ITS sequences were available in public databases; no Asian sequence was available in these public databases. In this study, 25 sequences from China were added. Sequences from soils and plant roots provide more samples for the phylogenetic analysis. With regards to the sequence origins within the H. olivaceoalbus-complex, the number of sequences from basidiomata, soils and plant root tips are 47, 32, and 4, respectively; within the H. olivaceoalbus clade, the numbers were 14, 30, and 4, respectively.

ITS sequences seem to be useful for specific delimitation of H. olivaceoalbus-complex, and this is in agreement with results presented in Moreau et al. (2018), the genus Hygrophorus and other groups within the genus (Endo et al., 2018; Naseer et al., 2019; Larsson & Bendiksen, 2020; Wang & Li, 2020; Wang et al., 2020). The supported five species level clades within the H. olivaceoalbus-complex have been recognized in the ML tree based on the phylogenetic analysis of the ITS dataset (Fig. 1).

Morphologically, the Chinese samples have the following distinctive features: a grayish brown, olive brown to dark brown pileus disc, strong dark brown annulus, and basidiospores measuring (8.0–)8.5–11.0(–12.0) × 5.0–7.5(–8.0) μm. The samples should be treated as a new species belonging to the H. olivaceoalbus-complex. This new species is similar to H. fuscoalbus, H. korhonenii and H. olivaceoalbus. However, H. fuscoalbus differs in the robust basidiomata, concolorous pileus, almost white annulus or rings, and lighter stipe color (Candusso, 1997; https://www.gbif.org/occurrence/1099011067). Hygrophorus korhonenii differs in the more prominent pileus umbo, longer basidiospores (10.0–14.0 μm), and always associated with P. abies in Fennoscandia (Harmaja, 1985; Læssøe & Petersen, 2019). Hygrophorus olivaceoalbus differs in its lighter annulus or rings, slightly more distant lamellae, and bigger basidiospores [12–14(–15) × 6.5–7.5(–8.2) μm in Candusso (1997), 10–16 × 7–8.5 μm in Læssøe and Petersen (2019)]. To some extent, the new species is similar to H. persoonii Arnolds, which was originally described from Belgium. However, H. persoonii is different from H. annulatus for having a much thicker gelatinous zone on the pileus, a white and floccose stipe apex, and a mycorrhizal association with Quercus (Candusso, 1997; Campo, 2015; Læssøe & Petersen, 2019).

In this study, 25 specimens from 12 localities of H. annulatus were obtained. The wide sampling allows us to evaluate the intra-specific morphological variation and determine the reliable features for species identification. In mature basidiomata, the pileus diameters and the lamellar widths are stable among different individuals. The colors of pileus discs and rings are more stable than the colors of the other parts of pileus and stipe. In addition, the position of annulus is relatively constant, usually located at about 1 cm away from the stipe apex, irrespective of the stipe length.

Ecologically, all examined samples of H. annulatus were collected in coniferous forests or forests with coniferous trees, mostly in P. asperata or P. likiangensis dominated forests and rarely in A. forestii or A. georgei dominated forests. Hygrophorus annulatus seems to have lower host specificity than H. olivaceoalbus, which is so far only known from P. abies dominated forests. More investigations are needed to further understand the ecological preferences of H. annulatus and its related taxa.

Acknowledgments

The authors sincerely thank the editors and anonymous reviewers for their efforts and contributions towards this manuscript. Sincere acknowledgements are expressed to Z.P. Song, Z.X. Wu and L.H. Sun for collecting the voucher specimens; to Y.J. Yao and L. Yang for the loan of sequences from HMAS; to J.Y. Xu, Z.Q. Zhang, W. Zhang and B. Cao for providing plant information. This study is supported by the National Natural Science Foundation of China (Nos. 31800013, 31700021, 31770041, 31270072), the Biodiversity Survey and Assessment Project of the Ministry of Ecology and Environment, China (No. 2019JI2096001006), the Science and Technology Planning Project of Guangdong Province, China (Nos. 2019121202005, 2018B030324001), the GDAS’ Project of Science and Technology Development (Nos. 2020GDASYL-20200104013, 2017GDASCX-0102), the Special Funds for the Young Scholars of Taxonomy of the Chinese Academy of Sciences (ZSBR-001), and the Public Health Service Project of the National Administration of Traditional Chinese Medicine (No. 201407002-6).

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