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ORIGINAL ARTICLE

Phylogeny and taxonomy of the genus *Anomoloma* (Amylocorticiales, Basidiomycota)

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Abstract *Anomoloma* is a cosmopolitan white rot fungal genus, and it currently contains four species worldwide. In the present study, the species diversity of *Anomoloma* in China is investigated based on morphological characters, and relationships among the species are assessed with phylogenetic analysis based on the internal transcribed spacer (ITS) regions and the large subunit nuclear ribosomal RNA gene (nLSU) sequences. Two new species, *A. luteoalba* and *A. submyceliosum*, are described and illustrated as well as compared with related taxa from other regions of Asia, North America and Europe. Phylogenetic analysis showed that *A. luteoalba* and *A. submyceliosum* are clearly distinct species within *Anomoloma*. A key to all species in this genus is provided.

Keywords Molecular phylogeny · Polypore · Taxonomy · Wood-rotting fungi

Introduction

Anomoloma Niemelä & K.H. Larss. was separated from *Anomoporia* Pouzar by Niemelä et al. (2007) on the basis of decay type and nuclear rDNA sequences data. It is typified by *A. albolutescens* (Romell) Niemelä & K.H. Larss. and currently contains four species: *A. albolutescens*, *A. flavissimum* (Niemelä) Niemelä & K.H. Larss., *A. myceliosum* (Niemelä) Niemelä & K.H. Larss. and *A. rhizosum* Y.C. Dai & Niemelä. The genus is characterized by resupinate, strongly rhizomorphic basidiocarps with white, cream or yellow surfaces; a monomitic hyphal system with clamped generative hyphae; elliptical and slightly thick-walled basidiospores; the species in this genus cause a white rot on woody debris of angiosperm and gymnosperm trees (Niemelä et al. 2007). Recent phylogenetic analysis indicated that *Anomoloma* belongs to the Amylocorticiales (Binder et al. 2010).

During the investigations on the diversity of wood-rotting fungi in subtropical areas of southern China, two new species of *Anomoloma* were identified based on morphological characters and phylogenetic analysis. Illustrated descriptions of the two new species and an identification key to worldwide species of *Anomoloma* and *Anomoporia* are provided.

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Materials and methods

Morphological studies

The examined specimens were deposited in the herbarium of the Institute of Microbiology, Beijing Forestry University (BJFC). Macro-morphological descriptions were based on field notes. Special color terms followed Petersen (1996). Micro-morphological data were obtained from dried specimens, and observed under a light microscope following methods in Li et al. (2014). Sections were studied at a magnification of up to × 1000 using a Nikon E 80i microscope and phase contrast illumination. Drawings were made with the aid of a drawing tube. Microscopic features, measurements and drawings were made from slide preparations stained with cotton blue and Melzer's reagent. Spores were measured from sections cut from the tubes. To represent variation in the size of spores, 5 % of measurements were excluded from each end of the range, and are given in parentheses. The

following abbreviations are used: IKI = Melzer's reagent, IKI– = neither amyloid nor dextrinoid, KOH = 5 % potassium hydroxide, CB = cotton blue, CB– = acyanophilous, L = mean spore length (arithmetic average of all spores), W = mean spore width (arithmetic average of all spores), Q = variation in the L/W ratios between the specimens studied, n (a/b) = number of spores (a) measured from given number (b) of specimens.

Molecular phylogeny

A CTAB (hexadecyltrimethylammonium bromide) rapid plant genome extraction kit (DN14, Aidlab Biotechnologies, Beijing) was used to extract total genomic DNA from dried specimens and to perform the polymerase chain reaction (PCR), according to the manufacturer's instructions with some modifications (Chen et al. 2015). The ITS region was amplified with primer pair ITS5 (GGA AGT AAA AGT CGT AAC AAG G) and ITS4 (TCC TCC GCT TAT TGA TAT GC; White et al. 1990). For the nuclear LSU region, a new primer pair, LR0R-1 (GAC CGT GTA TAA GTT CTC CTG) and LR7-1 (GCT TCT TCA CTG ACC TCC), was designed based on sequences obtained from the National Center for Biotechnology Information (NCBI, GU187559) using Primer-Premier 5 (Premier Biosoft International, Palo Alto, CA, USA). The PCR procedure for ITS was as follows: initial denaturation at 95 °C for 3 min, followed by 35 cycles at 94 °C for 40 s, 54 °C for 45 s and 72 °C for 1 min, and a final extension at 72 °C for 10 min. The PCR procedure for nLSU was as follows: initial denaturation at 94 °C for 1 min, followed by 35 cycles at 94 °C for 30 s, 50 °C for 1 min and 72 °C for 1.5 min, and a final extension at 72 °C for 10 min. The PCR products were purified and sequenced at the Beijing Genomics Institute, China, with the same primers. All newly generated sequences were deposited at GenBank and listed in Table 1.

Besides the sequences generated from this study, other reference taxa for our phylogenetic analysis were selected from GenBank, and the original publications of the phylogenetic analyses contributing the sequences were referenced in Table 1. Sequences were aligned in MAFFT 6 (Katoh and Toh 2008; http://mafft.cbrc.jp/alignment/server/) using the "G-INS-I" strategy and manually adjusted in BioEdit (Hall 1999). Sequence alignments were deposited at TreeBase (submission ID 18429; www.treebase.org). Sequences of *Jaapia argillacea* Bres. and *J. ochroleuca* (Bres.) Nannf. & J. Erikss. obtained from GenBank were used as outgroups to root trees following Binder et al. (2010).

Maximum parsimony (MP) analysis was applied to the combined dataset of ITS and nLSU sequences. Tree construction was performed in PAUP* version 4.0b10 (Swofford 2002). All characters were equally weighted and gaps were treated as missing data. Trees were inferred using the heuristic search option with tree bisection and reconnection (TBR) branch swapping and 1000 random sequence additions. Max-trees were set to 5000, branches of zero length were collapsed and all parsimonious trees were saved. Clade robustness was assessed using a bootstrap (BT) analysis with 1000 replicates (Felsenstein 1985). Descriptive tree statistics tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index (HI) were calculated for each maximum parsimonious tree (MPT) generated. DNA sequence data was also analyzed using maximum likelihood (ML) analysis; ML analysis was conducted with RAxML-HPC2 on Abe through the Cipres Science Gateway (www.phylo.org) involving 1000 replicates under the GTRGAMMA model, with all model parameters estimated by the program. In addition, 1000 rapid bootstrap replicates were run with the GTRCAT model. Phylogenetic trees were visualized using Treeview (Page 1996).

Bayesian inference (BI) was also applied to the combined dataset. Substitution models suitable for each partition in the dataset were determined using Akaike information criterion (AIC) implemented in MrModeltest2.3 (Posada and Crandall 1998; Nylander 2004). The general time reversible (GTR) model was estimated as the best-fit evolution model for all partitions in the combined dataset. BI was calculated with MrBayes3.1.2 (Ronquist and Huelsenbeck 2003) with a GTR model of DNA substitution and an invgamma distribution rate variation across sites. Four Markov chains were run for two runs from random starting trees for 2 million generations of the combined ITS and nLSU dataset and sampled every 100 generations. The burn-in was set to discard the first 25 % of the trees. A majority rule consensus tree of all remaining trees was calculated. Branches that received bootstrap support for maximum parsimony (MP), maximum likelihood (BS) and Bayesian posterior probabilities (BPP) greater than or equal to 75 % (MP/BS) and 0.95 (BPP) were considered as significantly supported, respectively.

Results

The combined ITS and nLSU dataset included sequences from 53 fungal samples representing 29 taxa. The dataset had an aligned length of 1587 characters, including gaps, of which 954 characters are constant, 127 are variable and parsimony-uninformative, and 506 are parsimony-informative. MP analysis yielded 40 equally parsimonious trees (length = 1860, CI = 0.537, RI = 0.762, RC = 0.409, HI = 0.463), and a strict consensus tree of these trees is shown in Fig. 1. The best model for the combined ITS and nLSU partition was a GTR + I + G model. BI analysis resulted in a similar topology.

Table 1 Species, specimens, and GenBank accession number of sequences used in this study

Species	Specimen no.	GenBank no.	
		ITS	nLSU
Amyloathelia crassiuscula	GB/K169-796	DQ144610	DQ144610
Amylocorticium cebennense	HHB-2808	GU187505	GU187561
A. cebennense	JS24813	AY463376	AY586627
A. subincarnatum	AS_95	AY463377	AY586628
A. subsulphureum	GB/M Ryberg	DQ144611	DQ144611
A. subsulphureum	HHB-13817	GU187506	GU187562
Amyloxenasma allantosporum	4527	GU187498	GU187666
Anomoloma albolutescens	CFMR:L-6088	GU187507	GU187563
A. albolutescens	H/RP 3549	DQ144612	DQ144612
A. albolutescens	Wei 2772	KT954951[a]	–
A. flavissimum	H/TN 6397	DQ144613	DQ144613
A. flavissimum	Dai 2968a	KT954952[a]	KT954966[a]
A. flavissimum	Cui 9699	KT954954[a]	KT954968[a]
A. flavissimum	Cui 12303	KT954955[a]	KT954969[a]
A. flavissimum	Cui 12188	KT954956[a]	KT954970[a]
A. flavissimum	Cui 10058	KT954953[a]	KT954967[a]
A. flavissimum	Cui 12108	KT954957[a]	KT954971[a]
A. luteoalba	Cui 2687	KT954961[a]	KT954975[a]
A. luteoalba	Cui 8686	KT954962[a]	KT954976[a]
A. myceliosum	CFMR:MJL-4413	GU187500	GU187559
A. rhizosum	H/YD 4031	DQ144616	DQ144616
A. rhizosum	Cui 9717	KT954958[a]	KT954972[a]
A. rhizosum	Cui 10589	KT954959[a]	KT954973[a]
A. rhizosum	Cui 10618	KT954960[a]	KT954974[a]
A. submyceliosum	Dai 7402	KT954963[a]	KT954977[a]
A. submyceliosum	Cui 2942	KT954965[a]	–
A. submyceliosum	Dai 7402-2	KT954964[a]	KT954978[a]
Anomoporia bombycina	CFMR:L-6240	GU187508	GU187564
A. bombycina	GGu612	AY463378	AY586629
A. kamtschatica	GB/M Edman K426	–	DQ144615
A. kamtschatica	KHL11072	AY463379	AY586630
A. vesiculosa	O/M Nunez 934	DQ144617	DQ144617
A. vesiculosa	Dai 5657	KT954949[a]	–
A. vesiculosa	Cui 9523	KT954950[a]	–
Athelopsis lacerata	KHL s.n.	–	GU187669
Athelia rolfsii	AFTOL-664	DQ484061	AY635773
Ceraceomyces americanus	FP-102188	KP135409	KP135277
C. serpens	HHB-15692-Sp	KP135031	KP135200
C. tessulatus	KHL 8474	AY463391	AY586642
C. sublaevis	FP-101245-Sp	KP135029	GU187607
Hypochniciellum subillaqueatum	KHL 8493	AY463431	AY586679
Irpicodon pendulus	GB/B.Norden	DQ144619	DQ144619
Jaapia argillacea	CBS252.74	GU187524	GU187581
J. argillacea	KHL 11734	EU118636	EU118636
J. ochroleuca	KHL 8433	EU118637	EU118637
Leptosporomyces septentrionalis	JS16122	GU187497	GU187664
Pilcaturopsis crispa	AFTOL-1924	DQ494686	DQ470820
P. crispa	FP-101310-SP	DQ534576	AY293203

Table 1 (continued)

Species	Specimen no.	GenBank no.	
		ITS	nLSU
Podoserpula pusio	RH9929	KP191968	KP191769
P. pusio	AFTOL-1522	DQ494688	DQ470821
P. pusio	H. Lepp 329	GU187555	EF535271
Serpulomyces borealis	L-8014	GU187512	GU187570
S. borealis	KHL 8432	EU118610	EU118610

[a] Newly generated sequences for this study

The phylogenetic tree (Fig. 1) inferred from the combined ITS and nLSU sequences demonstrates two new lineages; collections from subtropical areas in southern China on angiosperm wood formed one lineage (MP = 100 %, BS = 100 %, BPP = 1.00), while collections from subtropical areas in southern China on gymnosperm wood formed another lineage (MP = 99 %, BS = 99 %, BPP = 0.99). They are considered as distinct phylogenetic species.

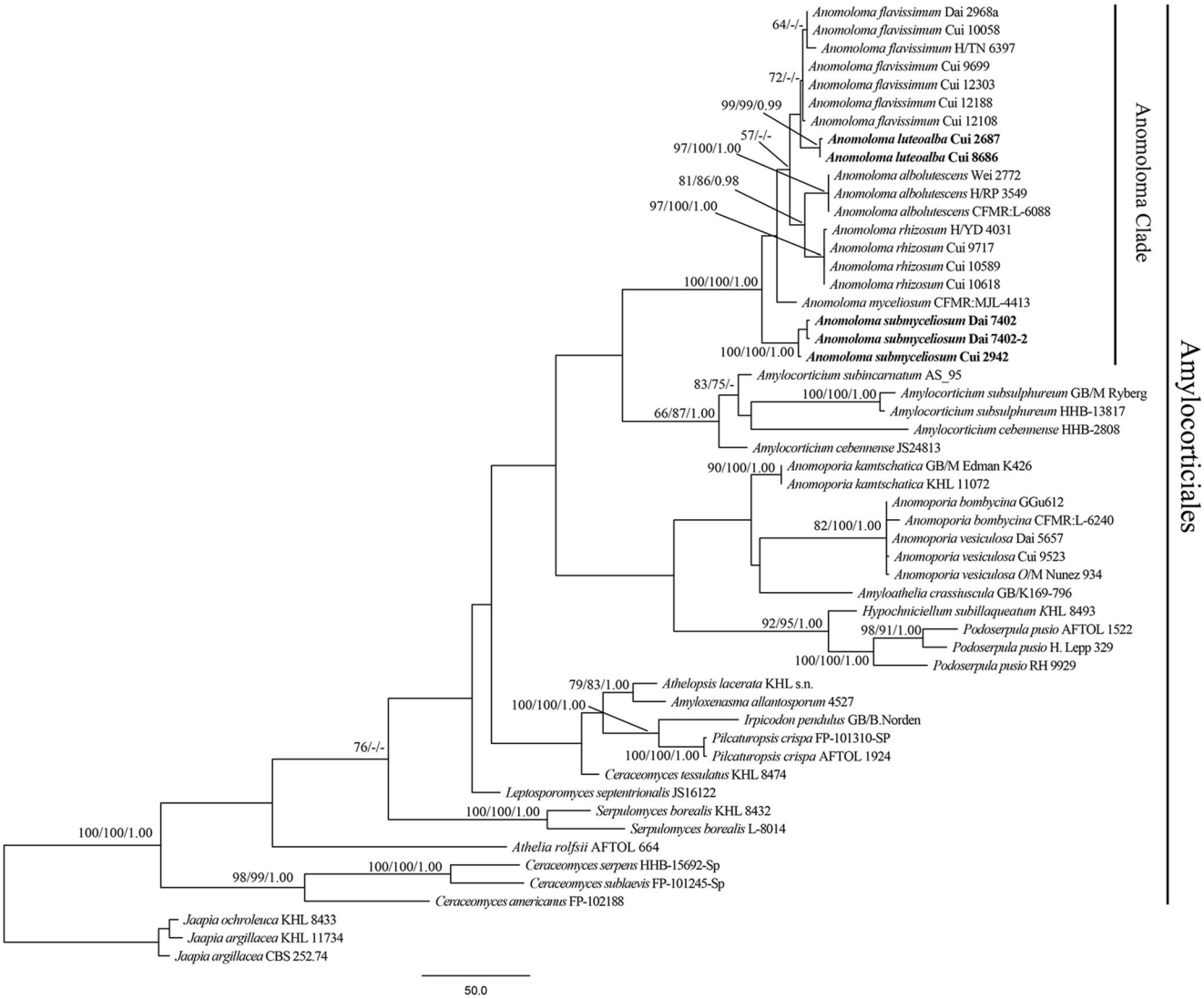

Fig. 1 Maximum parsimony strict consensus tree illustrating the phylogeny of *Anomoloma* and related species, based on combined ITS and nLSU sequences. Branches are labeled with parsimony bootstrap proportions higher than 50 % and Bayesian posterior probabilities more than 0.95, respectively

Taxonomy

Anomoloma luteoalba J. Song & B.K. Cui, sp. nov. (Figs. 2a and 3)

MycoBank no.: MB 815368

Anomoloma luteoalba is characterized by the following combined characters: cream to yellowish pore surface, 5–6 angular pores per mm, yellow rhizomorphs, ellipsoid basidiospores of 3–3.5 × 2–2.5 μm, and absence of cystidia.

Holotype. **CHINA**. Zhejiang Prov., Lin'an, Tianmushan Nature Reserve, on fallen trunk of *Pinus*, 11 Ocotober 2005, *Cui 2687* (BJFC 000044).

Etymology. luteoalba (Lat.): referring to the cream to yellowish pore surface.

Fruitbody. Basidiomata annual, resupinate, felty or softly corky, without odor or taste when fresh, corky upon drying, up to 20 cm long, 5 cm wide, and 1 mm thick at centre. Sterile margin irregular, up to 1 cm wide, thinning out, cinnamon buff when dry; yellow rhizomorphs arising from margin and penetrating into decayed wood. Pore surface cream to yellowish when dry; pores angular, 5–6 per mm; dissepiments thin, entire. Subiculum cream to pale buff when dry, felty, up to 0.7 mm thick. Tubes concolorous with pore surface, softly corky, up to 0.3 mm long.

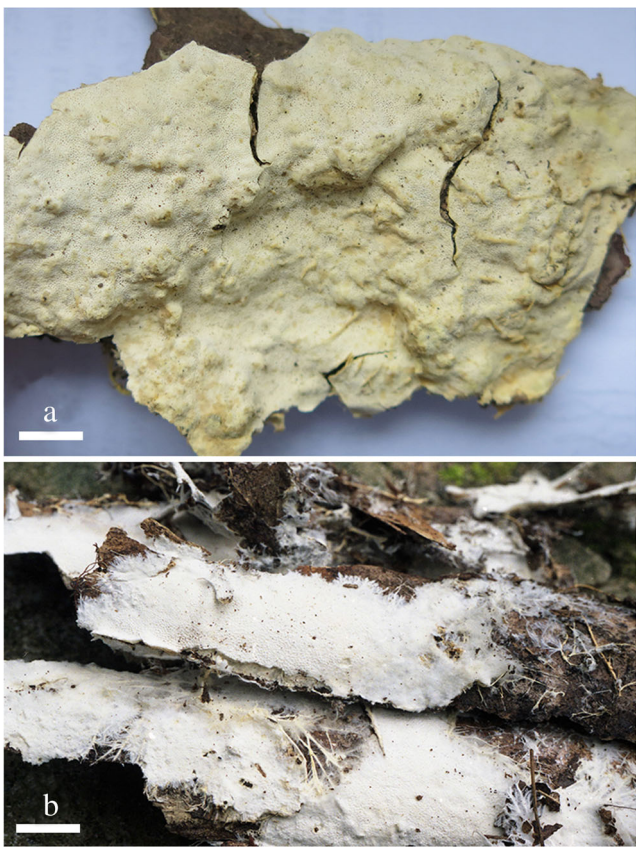

Fig. 2 Basidiomata of *Anomoloma* species. **a.** *A. luteoalba*; **b.** *A. submyceliosum*. *Bars*: **a** = 1.5 cm, **b** = 2 cm

Hyphal structure. Hyphal system monomitic; generative hyphae with clamp connections, CB–, IKI–; tissues unchanged in KOH.

Subiculum. Generative hyphae hyaline, thin- to slightly thick-walled with a wide lumen, frequently branched, interwoven, 2–5 μm in diam. Hyphae close to the substrate often covered with minute hyaline crystals.

Tubes. Generative hyphae hyaline, thin-walled, frequently branched, interwoven, 2–3 μm in diam. Cystidia and cystidioles absent. Basidia clavate, bearing four sterigmata and a basal clamp connection, 20–25 × 4–5 μm; basidioles in shape similar to basidia, but smaller.

Spores. Basidiospores ellipsoid, hyaline, slightly thick-walled, smooth, amyloid, CB–, 3–3.5 × 2–2.5 μm, L = 3.2 μm, W = 2.18 μm, Q = 1.41–1.49 (n = 40/2).

Type of rot. A white rot.

Additional specimen (paratype) examined: **CHINA**. Anhui Prov., She County, Qingliangfeng Nature Reserve, on fallen trunk of *Pinus*, 14 December 2009, *Cui 8686* (BJFC 007175).

Anomoloma submyceliosum J. Song & B.K. Cui, sp. nov. (Figs. 2b and 4)

MycoBank no.: MB 815369

Anomoloma submyceliosum is characterized by the following combined characters: white pore surface and rhizomorphs, 2–3 angular pores per mm, ellipsoid basidiospores of 3–4.2 × 2–2.7 μm, and growth on angiosperm wood in subtropical areas.

Holotype. **CHINA**. Fujian Prov., Wuyishan, Longfeng Valley, on angiosperm stump, 17 October 2005, *Cui 2942* (holotype, BJFC 000070).

Etymology. submyceliosum (Lat.): referring to the morphological similarity to *Anomoloma myceliosum*.

Fruitbody. Basidiomata annual, resupinate, felty or softly corky, without odor or taste when fresh, up to 15 cm long, 4–8 cm wide, and 1.2 mm thick at centre. Sterile margin irregular, white, thinning out, up to 1.5 cm wide; radiciform and thread-like, white rhizomorphs arising from margin and penetrating into decayed wood. Pore surface white when fresh, becoming cream to cream buff when dry; pores angular, 2–3 per mm; dissepiments thin, entire. Subiculum white when fresh, becoming cream to buff when dry, felty, up to 0.8 mm thick. Tubes concolorous with pore surface, softly corky, up to 0.4 mm long.

Hyphal structure. Hyphal system monomitic; generative hyphae with clamp connections, IKI–, CB–; tissues unchanged in KOH.

Subiculum. Generative hyphae hyaline, slightly thick-walled with a wide lumen, frequently branched, interwoven, 2.2–4.5 μm in diam. Hyphae close to the substrate often covered with minute hyaline crystals.

Tubes. Generative hyphae hyaline, thin- to slightly thick-walled, frequently branched, interwoven, 2–3 μm in diam. Cystidia and cystidioles absent. Basidia clavate, bearing four sterigmata and a basal clamp connection, 23–30 × 5–6 μm; basidioles in shape similar to basidia, but smaller.

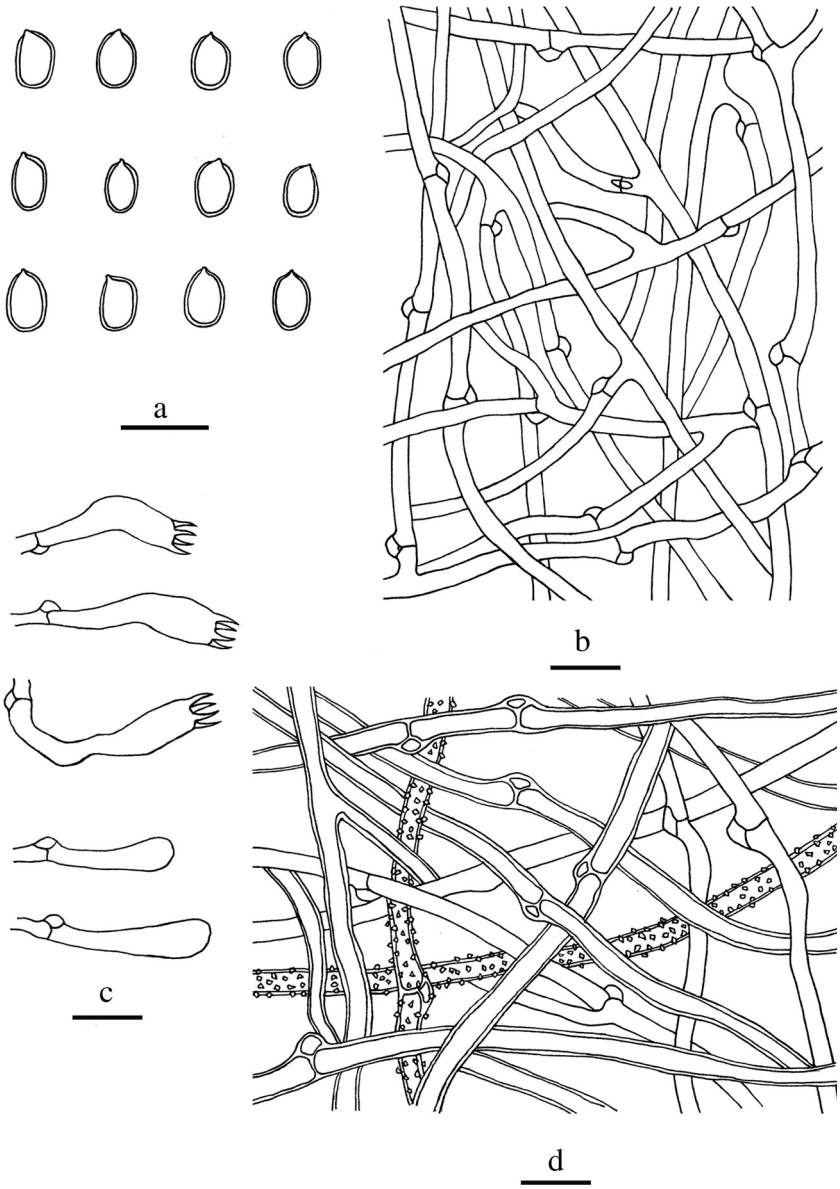

Fig. 3 Microscopic structures of *Anomoloma luteoalba* (drawn from the holotype). **a**. Basidiospores; **b**. Basidia and basidioles; **c**. Hyphae from trama; **d**. Hyphae from Subiculum. *Bars*: **a** = 5 μm; **b–d** = 10 μm

Spores. Basidiospores ellipsoid, hyaline, slightly thick-walled, smooth, amyloid, CB–, 3–4.2(−4.5) × 2–2.7 μm, L = 3.74 μm, W = 2.32 μm, Q = 1.54–1.69 (*n* = 60/2).

Type of rot. A white rot.

Additional specimens (paratypes) examined: **CHINA**. Fujian Prov., Wuyishan, Wuyishan Nature Reserve, Taoyuanyu, on rotten angiosperm wood, 22 Ocotober 2005, *Dai 7402* (BJFC 000067), *Dai 7402–2* (BJFC 000071).

Discussion

Previously, species of *Anomoloma* were treated in *Anomoporia* (Niemelä 1994). The two genera were separated by phylogenetic analysis based on rDNA sequences data (Niemelä et al. 2007). In the present study, phylogenetic analyses of *Anomoloma* using ITS and nLSU sequences reflect the overall structure of the Amylocorticiales as defined by Binder et al. (2010). The phylogeny shows that *Anomoloma* forms a monophyletic clade and is clearly separated from *Anomoporia*; the species with a yellowish pore surface gather together and form a weakly supported group; two new species in China were identified and strongly supported (Fig. 1).

Anomoloma flavissimum clusters together with *A. luteoalba* phylogenetically (Fig. 1), and it is similar to *A. luteoalba* by its yellow rhizomorphs and by growing on gymnosperm wood; however, *A. flavissimum* differs from *A. luteoalba* in producing a bright chrome or sulphur yellow pore surface, vesicular cystidia, slightly larger pores (4–5 per mm) and basidiospores (3–4 × 2–3 μm, Núñez and Ryvarden 2001). *Anomoloma rhizosum* also resembles *A. luteoalba* by its yellowish buff, pinkish buff or buff yellow pore surface and

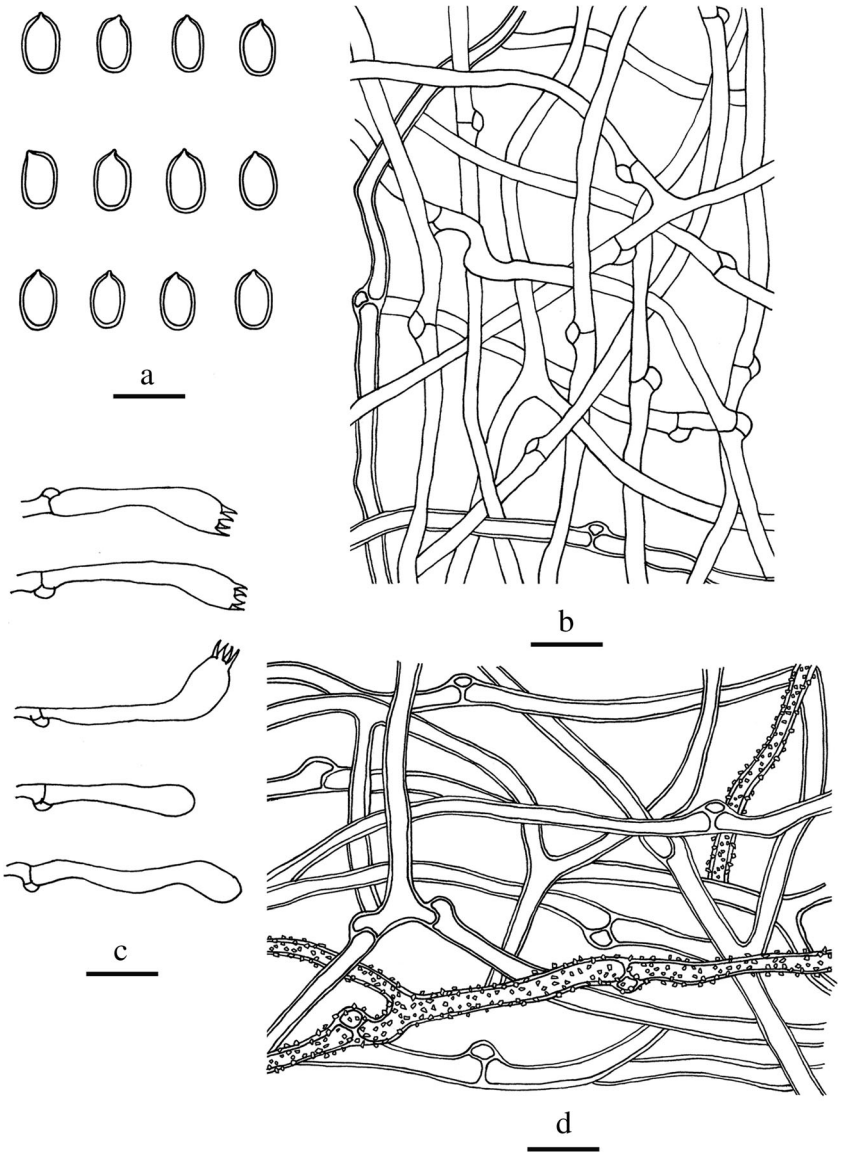

Fig. 4 Microscopic structures of *Anomoloma submyceliosum* (drawn from the holotype). **a**. Basidiospores; **b**. Basidia and basidioles; **c**. Hyphae from trama; **d**. Hyphae from Subiculum. *Bars*: **a** = 5 μm; **b–d** = 10 μm

yellow rhizomorphs; however, *A. rhizosum* differs from *A. luteoalba* by producing larger pores (4–5 per mm) and basidiospores (4.1–5.3 × 3–4 μm), and thin- to thick-walled generative hyphae in the subiculum (Niemelä et al. 2007). *Anomoloma myceliosum* may be confused with *A. submyceliosum* by its white pore surface and rhizomorphs; nevertheless, *A. myceliosum* is distinguished from *A. submyceliosum* by its larger basidiospores (3.5–4.5 × 2.5–3 μm), growing on gymnosperm wood and circumboreal temperate distribution (Núñez and Ryvarden 2001).

Key to accepted species of *Anomoloma* and *Anomoporia* worldwide

1 Basidiospores usually > 5 μm in length 2

1* Basidiospores usually < 5 μm in length 3

2 Basidiocarps salmon pink, vesicular cells present in the context *Anomoporia versiculosa*

2* Basidiocarps violet-brown or lavender, vesicular cells absent in the context *Anomoporia bombycina*

3 Rhizomorphs present 4

3* Rhizomorphs absent *Anomoporia kamtschatica*

4 Pore surface and rhizomorphs white 5

4* Pore surface and rhizomorphs cream buff to yellow 6

5 Basidiospores 3–4.2 × 2–2.7 μm; mainly growing on angiosperm wood *Anomoloma submyceliosum*

5* Basidiospores 3.5–4.5 × 2.5–3 μm; mainly growing on gymnosperm wood *Anomoloma myceliosum*

6 Pores < 4 per mm *Anomoloma albolutescens*

6* Pores > 4 per mm 7

7 Basidiospores usually > 4 μm in length *Anomoloma rhizosum*

7* Basidiospores usually < 4 μm in length 8

8 Pore surface bright chrome or sulphur yellow; vesicular cystidia present *Anomoloma flavissimum*

8* Pore surface cream to yellowish; vesicular cystidia absent *Anomoloma luteoalba*

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