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Cyptotrama (*Physalacriaceae*, *Agaricales*) from Asia

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ABSTRACT

Cyptotrama was divided into several sections, of which sect. *Xerulina* was often treated as a separate genus by some mycologists. In this study, collections of *Cyptotrama* from East Asia, Southeast Asia, and South Asia were studied. For comparison, materials from North America and New Zealand were analysed. Our multi-gene phylogenetic analyses indicated that *Cyptotrama* is monophyletic and *Xerulina* should be treated as a section within the genus *Cyptotrama*. Different scenarios of morphological character evolution in *Cyptotrama* are discovered. A total of seven species of *Cyptotrama* can be recognized from Asia, three of which, *Cyptotrama angustispora*, *C. glabra*, and *C. shennongjia*, are new to science. Meanwhile, three taxa previously placed in *Xerulina* or *Marasmius* were proved to be members of *Cyptotrama*, and the new combinations, namely *Cyptotrama trogioides*, *C. megaspora*, and *C. myochroa*, are accordingly proposed. A key for the diagnosis of worldwide *Cyptotrama* species is provided.

Introduction

Cyptotrama Singer (1960) is a fungal genus comprising a group of lignicolous, stipitate-pileate, non-radicant, and non-viscid fungi with smooth or floccose pileus, clamped or non-clamped hyphae, and smooth basidiospores. This genus has been placed in *Tricholomataceae* or *Xerulaceae* (Jülich 1981; Singer 1986; Redhead 1987) but later been transferred into *Physalacriaceae* based on molecular evidence (Moncalvo *et al.* 2002; Wilson & Desjardin 2005; Binder *et al.* 2006; Matheny *et al.* 2006), with *Pseudohiatula* Singer as its most closely allied genus (Hao *et al.* 2014; Moreau *et al.* 2015). Four sections (sect. *Cyptotrama*, sect. *Depauperata*, sect. *Xerulina*, and sect. *Aporpotrama*) have been proposed in this genus (Singer 1973, 1986), but the treatment of sect. *Xerulina* has been debated, as some mycologists tended to treat it as a separate genus, viz., *Xerulina* Singer (Singer 1962a; Pegler & Fiard 1983; Pegler & Gardens 1986; Corner 1996; Pegler 1966, 1972, 1977, 1987).

Species of *Cyptotrama* can be found from tropical, subtropical, and temperate regions of different continents (Pegler 1966, 1972, 1977, 1987; Singer 1969, 1973, 1978, 1986, 1989; Pegler & Gardens 1986; Pegler & Fiard 1983; Pegler & Gardens 1986; Moreau *et al.* 2015; Redhead & Ginns 1980). To date, in total 16 species have been described within this genus, most of which were reported from South America (six species) (Singer 1960, 1969, 1973, 1989; Redhead & Ginns 1980), North America (three species) (Singer 1973, 1978; Redhead & Ginns 1980), Central America (Dennis 1970; Pegler & Fiard 1983), and Africa (three species) (Patouillard 1902; Pegler 1966; Singer 1973; Redhead & Ginns 1980; Courtecuisse 1995; De Seynes 1897).

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The only known *Cyptotrama* from Europe, *Cyptotrama fagiphila* Vila *et al*., was described very recently (Moreau *et al*. 2015). Similarly, *Cyptotrama asprata* (Berk.) Redhead & Ginns is the only species documented in Asia (Berkeley 1847; Pegler 1972; Redhead & Ginns 1980; Pegler & Gardens 1986; Yang 1990; Corner 1996; Bi *et al*. 1997; Huang 1998; Wang & Chou 2001; Chou & Chang 2005; Wang & Tong 2011; Wu *et al*. 2011). However, molecular data have shown that *C. asprata* is a species complex represented by at least two species, *C. asprata* and *Cyptotrama chrysopepla* (Berk. & M.A. Curtis) Singer (Moreau *et al*. 2015). Meanwhile, our recent survey of fungal diversity found that abundant *Cyptotrama* with diversified macromorphology can be collected from wide range of Asia. If these collections represent previously recorded *C. asprata* or some hidden new species needs to be further studied.

In this study, multi-gene phylogenetic analyses based on sequences of the internal transcribed spacer region of ribosomal DNA (ITS), the D1–D3 region of the 28s nuc rDNA (28S), and the beta-tubulin gene (*β-tubulin*), together with careful morphological observations, were carried out on our recently collected specimens of Asian *Cyptotrama*. Our goals are: 1) to test if *C.* sect. *Xerulina* should be a section within *Cyptotrama* or a separate genus by using molecular data; 2) to elucidate species diversity of Asian *Cyptotrama* by comparing Asian collections with specimens collected from other parts of the world and with literature records.

Material and methods

Sampling

In total 51 collections of *Cyptotrama* were collected from Laos, Sri Lanka, Canada (Ontario), United States (Massachusetts) and the vast land of China (Table 1). Voucher specimens were deposited in the Herbarium of Cryptogams, Kunming Institute of Botany of the Chinese Academy of Sciences (KUNHKAS). Specimens collected from Indonesia, Malaysia, New Zealand, United States (Michigan) and other parts of China (e.g. Guangdong Prov.) were also included in our study via loan from the Royal Botanic Garden Edinburgh (E), New Zealand Fungal Herbarium Landcare Research (PDD), the Herbarium of the University of Michigan (MICH), the fungal herbarium at the Guangdong Institute of Microbiology (GDGM) and the Herbarium of Mycology of Jilin Agricultural University (HMJAU).

Morphology

Macro-morphological descriptions are based on the field notes and images of basidiomata. Colour codes of the form "10D7" are from Kornerup & Wanscher (1981). Micro-morphological data were obtained from the dried specimens after sectioning and mounting in 5 % KOH solution. In the descriptions of lamellae and basidiospores, the abbreviation [n/m/p] shall mean n basidiospores measured from m basidiomata of p collections; Q is used to mean "length/width ratio" of a spore in side view; and Q_m means average Q of all basidiospores ± sample standard deviation. The descriptive terms of Vellinga & Noordeloos (2001) were followed.

DNA extraction, PCR amplification, and sequencing

Protocols for DNA extraction, PCR, and sequencing followed those in Qin *et al*. (2014) and references therein. Universal primer pairs ITS1/ITS4 (White *et al*. 1990) and LROR/LR5 (Vilgalys & Hester 1990) were used for the amplification of the ITS and the D1–D3 region of the 28S, respectively. For the amplification of the *β-tubulin*, the primer pair TubF/TubR (Qin *et al*. 2014) was employed.

Sequence alignments and phylogenetic analyses

Sequences for each gene marker (Table 1) were carefully checked to exclude possible contamination and were combined with sequences available in GenBank (Supplementary Table 1) to make up three matrices: ITS, 28S, and *β-tubulin*. Each matrix was aligned using Opal 0.3.7 (Wheeler & Kececioglu 2007) separately and manually checked on Bioedit v7.0.9 (Hall 1999) or 4SALE v1.5 (Seibel *et al*. 2006). The aligned sequence lengths of the ITS, 28S, and *β-tubulin* matrices are 953, 874, and 723 bp, respectively.

An incongruence length difference (ILD) test was carried out using Paup 4.0b 10 (Swofford 2002). The test detected no conflicts among ITS, 28S, and *β-tubulin* ($P = 0.11$), suggesting that sequences of these gene makers can be concatenated for phylogenetic analyses. As GenBank holds more sequences of ITS and 28S than that of *β-tubulin*, we firstly constructed a combined ITS-28S dataset to detect the position of *Xerulina* within *Physalacriaceae* (a section of *Cyptotrama* or a separate genus). After this, a combined dataset of ITS, 28S, and *β-tubulin* was used to elucidate the species diversity of Asian species and the relationships among these species. These sequence alignments were deposited at TreeBASE (http://purl.org/phylo/treebase; submission ID17668).

For phylogenetic analyses based on the 28S-ITS and *β-tubulin*-28S-ITS datasets, both Bayesian Inference (BI) and Maximum Likelihood (ML) algorithms were employed. *Armillaria mellea* (Vahl: Fr.) P. Kumm. and *Xerula strigosa* Zhu L. Yang *et al*. were chosen as outgroups, respectively. The substitution model suite for each dataset was chosen using the Akaike Information Criterion (AIC) implemented in MrModeltest v2.3 (Nylander 2004). The HKY + I + G, GTR + I + G, and GTR + I + G models were chosen as the best model for *β-tubulin*, 28S, and ITS respectively for BI analyses. For ML analysis, GTRGAMMAI model was employed. MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003) and RA×ML v7.2.6 (Stamatakis 2006) were used in the ML and BI analyses, respectively. While conducting the analyses, a partitioned mixed model was used by defining *β-tubulin*, 28S, and ITS as independent partitions. All parameters in the ML analysis were kept at their default level, and statistical support was obtained using a rapid nonparametric bootstrapping with 1000 replicates. The BI analysis was performed with running four chains of five million generations and using the stoprul command by setting convergence value as 0.01. Trees were sampled every 100 generations. Subsequently, trees were summarized, and statistic supports were obtained after using the sumt command implemented in MrBayes by discarding the first 25 % generations as burn-ins.

Table 1 – Voucher specimen information and GenBank accession numbers for sequences of Cyptotrama.

Scientific name	Herbarium no.	Collection no.	GenBank accession nos.			Locality
			ITS	28S	β-tubulin	
Cyptotrama angustispora	HKAS 78639 (type)	Zhu L. Yang5681	**KR607194**	**KR607154**	–	Attapeu, Laos
C. asprata	HKAS 60303	Z.-W. Ge2627	KJ024098	KJ024103	**KR607101**	Limushan, Qiongzhong County, Hainan, China
C. asprata	HKAS 76282	S. Karunarathna38	KJ024099	KJ024104	–	Sinharaja, Sri Lanka
C. asprata	HKAS 78634	Zhu L. Yang5676	**KR607193**	**KR607153**	**KR607114**	Attapeu, Laos
C. asprata	TENN59472	–	–	HM005084	–	Hawaii, United States
C. asprata	RV98/78	–	–	AF261353	–	–
C. asprata	CL/Mart03.156 (LIP)	–	KM588682	–	–	Martinique, France
C. asprata	DED6391	–	DQ097355	–	–	United States
C. asprata	–	–	AB509791	–	–	Yakushima, Japan
C. asprata	–	–	AB509972	–	–	Yakushima, Japan
C. asprata	ASIS21363	–	KF668296	–	–	Korea?
C. asprata	ASIS22554	–	KF668317	–	–	Korea?
C. asprata	GDGM 25312	T.-H. Li, *et al.*	**KR607186**	**KR607145**	–	Shakou, Shimentai, Yingde County, Guangdong, China
C. asprata	GDGM 25421	T.-H. Li, *et al.*	**KR607187**	**KR607146**	–	Yinghong, Shimentai, Yingde, Guangdong, China
C. asprata	GDGM 27630	Y.-J. Li, *et al.*	**KR607185**	**KR607144**	–	Chebaling, Shixing County, Guangdong, China
C. asprata	HMJAU 24814	T. Bau	**KR607191**	**KR607151**	**KR607121**	Guishan, Shiling County, Yunnan, China
C. asprata	HKAS 76285	B. Feng1244	**KR607180**	**KR607139**	**KR607119**	Mingchi Forest Amusement Park, Yilan County, Taiwan, China
C. asprata	HKAS 49302	Z.-W. Ge807	**KR607192**	**KR607152**	**KR607122**	Wengda, Seda County, Sichuan, China
C. asprata	HKAS 70373	Z.-W. Ge2868	**KR607178**	**KR607137**	**KR607118**	Daweishan, Pingbian County, Yunnan, China
C. asprata	HKAS 70545	Z.-W. Ge3041	**KR607179**	**KR607138**	**KR607125**	Zixishan Forest Park, Chuxiong, Yunnan, China
C. asprata	HKAS 76286	Y.-J. Hao781	**KR607190**	**KR607150**	**KR607120**	Jiuxiang, Yiliang County, Yunnan, China
C. asprata	HKAS 83076	Y.-J. Hao1285	**KR607176**	**KR607135**	**KR607130**	Wuliangshan, Nanjian County, Yunnan, China
C. asprata	HKAS 84622	L.-H. Han326	**KR607189**	**KR607149**	**KR607127**	Gaoligongshan, Longyang District, Yunnan, China
C. asprata	HKAS 53393	Y.-C. Li1048	**KR607174**	**KR607133**	**KR607116**	Mangshan, Yizhang County, Hunan, China
C. asprata	HKAS 76284	J. Qin647	**KR607182**	**KR607141**	**KR607132**	Kunming Botanic Garden, Kunming, Yunnan, China
C. asprata	HKAS 83324	J. Qin907	–	**KR607147**	**KR607128**	Gaoligongshan, Longyang District, Yunnan, China
C. asprata	HKAS 83342	J. Qin925	**KR607188**	**KR607148**	**KR607129**	Gaoligongshan, Longyang District, Yunnan, China
C. asprata	PDD 78164	P. Catcheside	**KR607177**	**KR607136**	–	Katikati, Odey Road, Puketoki Track, Bay of Plenty, New Zealand
C. asprata	HKAS 75447	X.-H. Wang3137	**KR607181**	**KR607140**	–	Longdoushe Forest Farm, shixing county, Guangdong, China
C. asprata	HKAS 76287	N.-K. Zeng302	**KR607184**	**KR607143**	**KR607124**	National Forest Park of Limushan, Qiongzhong County, Hainan, China
C. asprata	HKAS 76289	N.-K. Zeng410	**KR607183**	**KR607142**	**KR607126**	Wuzhishan, Wuzhishan City, Hainan, China
C. asprata	HKAS 73936	X.-T. Zhu541	**KR607175**	**KR607134**	**KR607117**	Tanhe, Cheng County, Gansu, China
C. chrysopepla	HKAS 59934	Z.-W. Ge2258	**KR607197**	**KR607156**	**KR607113**	Mount Monadnock, New Hampshire, Massachusetts, United States
C. chrysopepla	TENN59440	–	–	HM005083	–	North Carolina, United States
C. chrysopepla	TENN60561	–	–	HM005081	–	Tennessee, United States
C. chrysopepla	DAOM157066	–	–	AF042642	–	Gatineau County, Quebec, Canada
C. fagiphila	BRNM 751955 (Holotype)	–	KM588683	KM588686	–	Spain
C. fagiphila	SEST09081503	–	KM588684	KM588687	–	Spain
C. glabra	HKAS 50484 (type)	Zhu L. Yang4687	**KR607207**	**KR607168**	–	Ailaoshan, Jingdong County, Yunnan, China
C. glabra	HKAS 78616	Zhu L. Yang5658	**KR607205**	**KR607166**	**KR607102**	Attapeu, Laos
C. glabra	HKAS 78629	Zhu L. Yang5671	**KR607206**	**KR607167**	**KR607103**	Attapeu, Laos

(*continued on next page*)

Table 1 – (continued)

Scientific name	Herbarium no.	Collection no.	GenBank accession nos.			Locality
			ITS	28S	β-tubulin	
C. glabra	HKAS 70344	Z.-W. Ge2839	**KR607210**	**KR607171**	**KR607108**	Daweishan, Heping, Pingbian County, Yunnan, China
C. glabra	HKAS 71568	Y.-J. Hao459	**KR607209**	**KR607170**	**KR607111**	Houqiao, Tengchong county, Yunnan, China
C. glabra	HKAS 83102	Y.-J. Hao1312	**KR607204**	**KR607165**	**KR607107**	Wuliangshan, Nanjian County, Yunnan, China
C. glabra	HKAS 84629	L.-H. Han333	**KR607199**	**KR607160**	–	Gaoligongshan, Longyang District, Yunnan, China
C. glabra	HKAS 52507	Y.-C. Li820	**KR607208**	**KR607169**	**KR607110**	Ecology station of Ailaoshan, Jingdong County, Yunnan, China
C. glabra	HKAS 86991	X.-B. Liu339	**KR607203**	**KR607164**	**KR607105**	Gaoligongshan, Longyang District, Yunnan, China
C. glabra	HKAS 73271	J. Qin285	**KR607212**	**KR607173**	–	Mangbang, Tengchong County, Yunnan, China
C. glabra	HKAS 83298	J. Qin881	**KR607201**	**KR607162**	**KR607104**	Luoboyakou, Zhen'an, Longlin County, Yunnan, China
C. glabra	HKAS 83313	J. Qin896	**KR607200**	**KR607161**	**KR607106**	Gaoligongshan, Longyang District, Yunnan, China
C. glabra	HKAS 83322	J. Qin905	**KR607202**	**KR607163**	–	Gaoligongshan, Longyang District, Yunnan, China
C. glabra	HKAS 56938	L.-P. Tang981	**KR607211**	**KR607172**	**KR607109**	Wuliangshan, Nanjian County, Yunnan, China
C. glabra	HKAS 87681	K. Zhao440	**KR607198**	**KR607159**	–	Dadugang, Jinghong, Yunnan, China
C. shennongjia	HKAS 75559 (type)	Q. Cai805	**KR607195**	**KR607155**	–	Muyu, Shennongjia, Hubei, China
C. shennongjia	HKAS 77959	J. Qin558	**KR607196**	**KR607156**	–	Muyu, Shennongjia, Hubei, China

Boldface: sequences generated in this study.

Results

Molecular phylogeny

The phylogenetic trees inferred from the ITS-28S and ITS-28S-*β-tubulin* matrices show similar topologies (as Figs 1 and 2). All species of *Cyptotrama* clustered together as a monophyly in *Physalacriaceae* with *Pseudohiatula* as its sister group. Within *Cyptotrama*, six phylogenetic species were recognized, which morphologically represent three sections (sect. *Aporpotrama*, sect. *Cyptotrama*, and sect. *Xerulina*). A new species collected from Asia, *Cyptotrama glabra* Zhu L. Yang & J. Qin, formed the basal group of *Cyptotrama*.

Taxonomy

Cyptotrama Singer
Lilloa 30: 375, 1960.
Xerulina Singer, Sydowia 15: 59, 1962 ("1961").

Basidiomata small to medium, collybioid to marasmioid, fleshy to papery.

Pileus plano-convex to hemispherical, glabrous, rugose, and striate, or covered with verrucous or granular squamules; pileipellis dry. Lamellae adnexed to adnate, white, cream to yellow, usually distant. Stipe subcylindrical, glabrous or floccose; basal slightly enlarged, non-radicate. Annulus absent. Context white, unchanged when bruised, spore print usually white to cream.

Hymenophoral trama bilateral to regular. Basidiospores ovoid, ellipsoid, cylindrical, amygdaliform to limoniform, inamyloid, thin-walled, smooth, colourless and hyaline. Basidia clavate, 4-spored; basidioles fusiform, with acute apex; clamps present or absent. Cheilocystidia and pleurocystidia present in most species.

When pileus glabrous, pileipellis epithelium to hymeniderm, composed of clavate, broad clavate, globose to sphaero-pedunculate cells, sometimes intermixed with pileocystidia; when pileus covered by squamules, squamules composed of inflated chained thick-walled cells; pileocystidia absent; pileipellis under squamules usually an epithelium or hymeniderm, composed of clavate, broad clavate cells. When stipe glabrous, caulocystidia are usually present; when stipe with squamules composed of hyphae with differentiated terminal cells. Clamp connections present or absent.

Type: *Cyptotrama macrobasidia* Singer.

Habitat: on rotten wood in forests. Saprotrophic.

Distribution: Pantropic to sub-cosmopolitan.

Cyptotrama angustispora Zhu L. Yang & J. Qin, **sp. nov.** Figs 3A and 4

MycoBank: MB 811964.

Etymology: referring to the narrow basidiospores.

Type: **Laos:** *Attapeu*: Medicinal Biodiversity Preserve, alt. 540 m, on rotten wood of broadleaf trees, 28 Apr. 2013, *Zhu L. Yang*5681 (HKAS 78639).

Pileus 1.5–5 cm in diam, dry, convex to applanate, surface finely radially rugose, centre often slightly depressed; surface

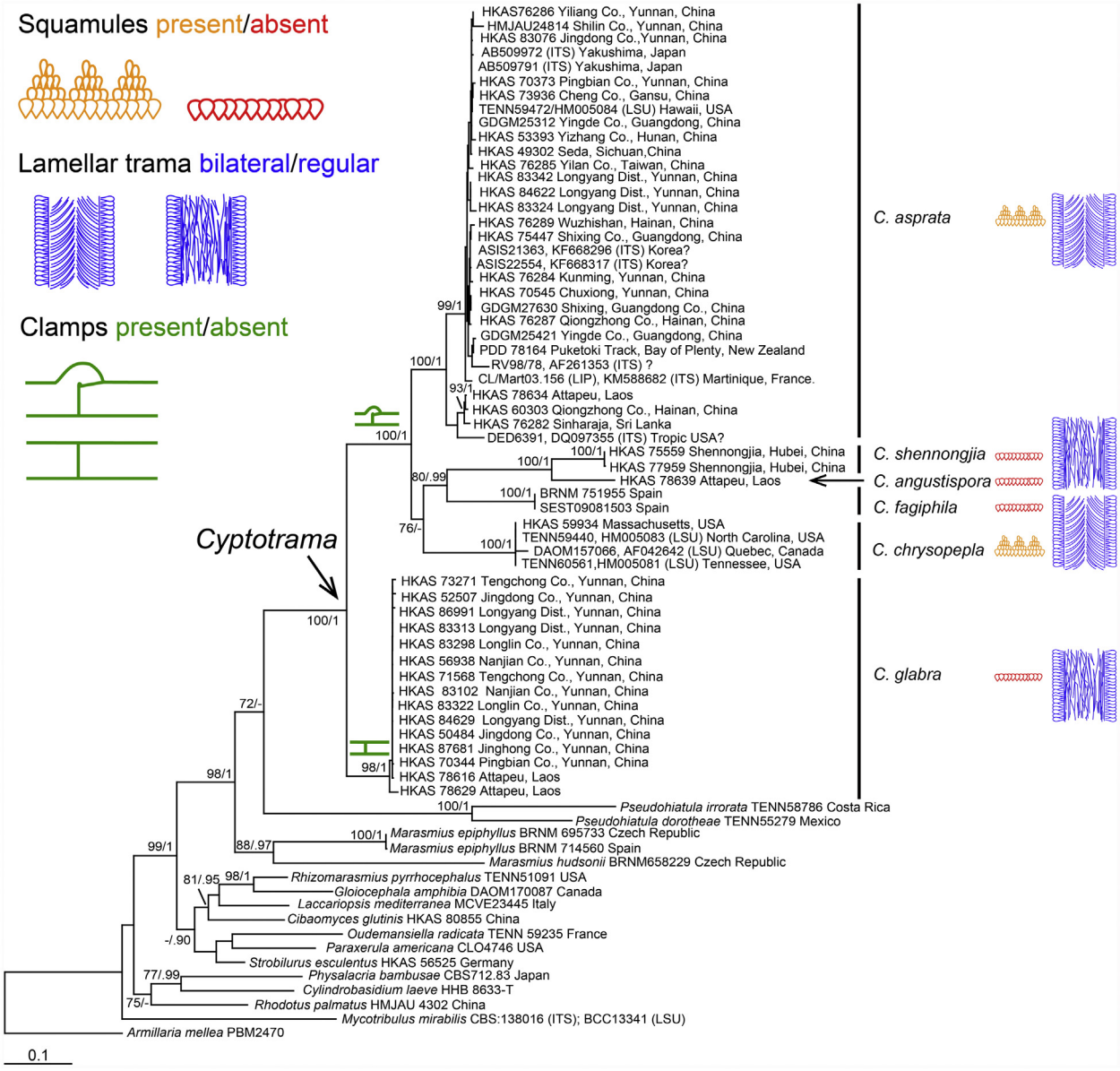

Fig 1 – ML tree of 16 generic clades within *Physalacriaceae* inferred from the concatenated 28S-ITS sequences. Bootstrap values (>50 %), together with Bayesian Posterior Probabilities (>0.90) are indicated along nodes.

pale grey, brownish, cement-coloured (4C2, 4C3), but centre darker (grey to dark grey, 4D3, 4E4); margin finely striate, barely with yellowish tinge. Lamellae sinuate, distant, with lamellulae; cream to yellowish (2A2–2A5, 2B5–2B6), up to 6 mm wide; edge yellowish, yellow to sulphur-yellow, with greenish tinge. Stipe 3–5 cm in length, 2–5 mm in diam, subcylindrical, fistulose, basal part slightly enlarged; surface whitish to cream, with fine whitish squamules. Context of pileus and stipe thin, whitish to cream.

Basidiospores (Fig 4A) [90/4/1] (6) 6.5–9 × (2.3) 2.5–3.5 μm, [Q = (2) 2.17–3.2 (3.4), Q_m = 2.64 ± 0.31], cylindrical, thin-walled, smooth, colourless and hyaline, non-amyloid, non-dextrinoid. Basidia (Fig 4B) 23–28 × 4.5–6.5 μm, clavate, 4-spored, sometimes colourless and hyaline, usually with yellowish brown intracellular pigment; sterigmata 4–5 μm long. Basidioles (Fig 4B) abundant, 19–27 × 5–8 μm, fusiform with subacute apices, thin-walled, colourless and hyaline. Cheilocystidia and pleurocystidia absent. Lamellae edge (Fig 4C) composed of crowdedly arranged fusiform basidioles with subacute apices, 23–32 × 3–6 μm, thin walled (≤1.5 μm thick), colourless and hyaline, occasionally pyriform to nearly sphaero-pedunculate, 23–33 × 7–10 μm. Subhymenium ca. 15 μm thick, composed of branching hyphal segments, 3–4 (5) μm in diam; clamps abundant. Lamellar trama ca. 200–500 μm in width, composed of irregularly arranged to interwoven (not bilateral) filamentous hyphae (4–16 μm wide) becoming broader and gelatinized towards the median, slender and not gelatinous towards the subhymenium.

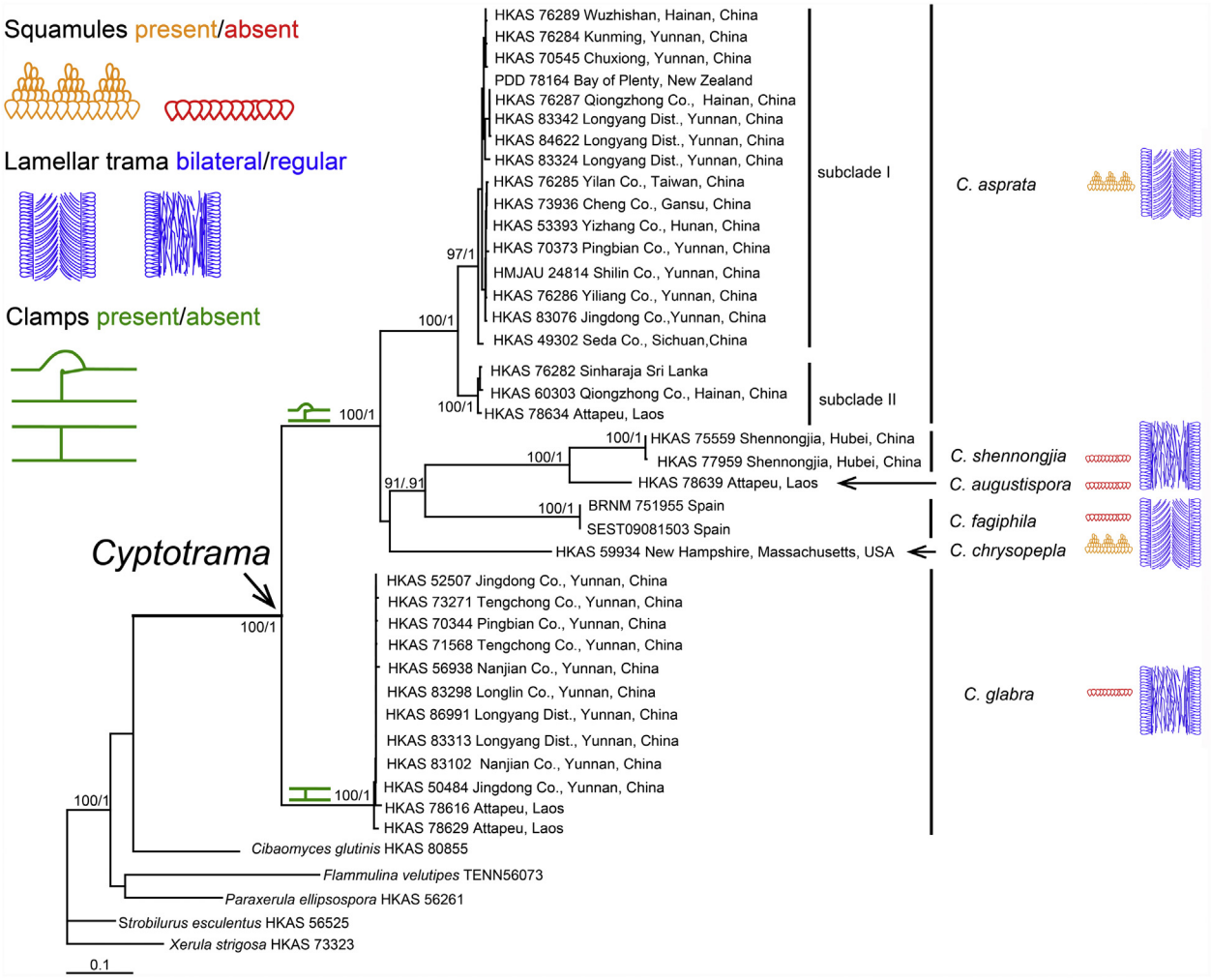

Fig 2 – ML tree of *Cyptotrama* inferred from the Matrix of the concatenated 28S, ITS and *β-tubulin* sequences. Bootstrap values (>50 %), together with Bayesian Posterior Probabilities (>0.90) are indicated along nodes.

Pileocystidia (Fig 4E) scattered, 55–70 × 8–12 μm, sinuate, clavate, but lower part inflated, with mastoid apices and slender clavate peduncules. Pileipellis (Fig 4F) an epithelium to epithelioid hymeniderm, ca. 30–50 μm thick, composed of 1–2 layers of sub-globose, sphaero-pedunculate to pyriform inflated cells, 20–33 × 10–25 μm. Caulocystidia (Fig 4D) scattered to closely arranged as a trichoderm-like structure, perpendicular to stipe, 70–160 × 5–8 μm, mostly cylindrical, flexuose to narrowly clavate, colourless and hyaline, thin walled (≤0.5 μm). Stipitipellis composed of vertically arranged, sometimes branching hyphae 2–8 μm wide. Trama of stipe composed of vertically arranged filamentous to slightly inflated hyphae 2–12 μm in diam. Clamp connections common in all parts of basidiomata.

Habitat and known distribution: on rotten wood of broadleaf trees in a tropical forest at alt. 540 m; in early summer, in Laos.

Comments: *Cyptotrama shennongjia* looks like *C. angustispora* but differs from the latter by broader basidiospores (see below). *Cyptotrama fagiphila* resembles *C. angustispora* by the greyish pileus and the presence of clamp connections. However, *C. fagiphila* can be distinguished from the latter by its bilateral lamellar trama, broader basidiospores (8–11 × 5–6.5 μm) and the absence of pileocystidia (Moreau *et al.* 2015). *Marasmius batistae* Singer, originally described from Brazil, resembles *C. angustispora* by the combination of a grey glabrous pileus, a hymeniform pileipellis with pileocystidia, the irregular lamellar trama, the absence of pleurocystidia and cheilocystidia, the cylindrical caulocystidia, the nearly identical inamyloid basidiospores (5.5–8.8 × 2.5–3.8 μm) and the presence of clamp connections. However, it differs from the latter by its whitish lamellae and capitate pileocystidia (Singer 1965, 1976).

Cyptotrama glabra Zhu L. Yang & J. Qin, **sp. nov.** Figs 3B, C and 5

MycoBank: MB 811965.

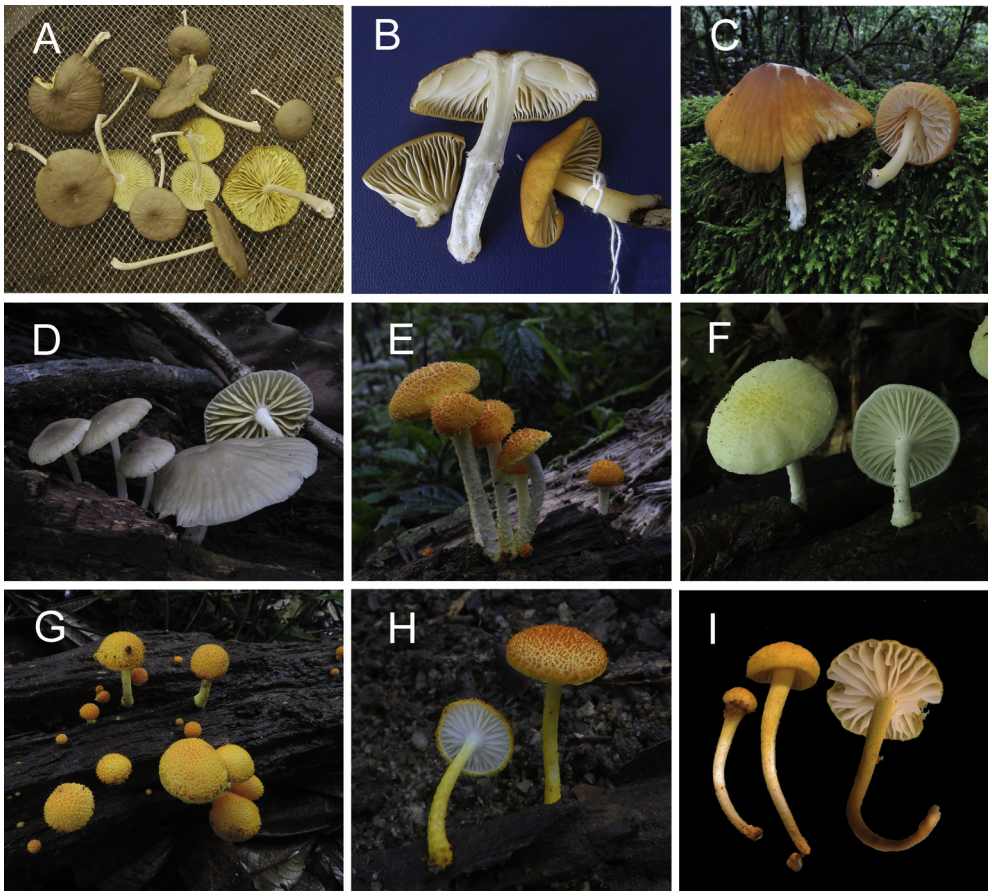

Fig 3 – Basidiomata of *Cyptotrama*. (A). *C. angustispora* (HKAS 78639, Type). (B, C). *C. glabra* (HKAS 50484, Type). (D). *C. shennongjia* (HKAS 75559, Type). (E–H). *C. asprata* (HKAS 70373, HKAS 75447, HKAS 83324, and HKAS 60303). (I). *C. chrysopepla* (HKAS 59934).

Etymology: referring to the glabrous pileus.

Type: **China**: *Yunnan*: Ailaoshan, Jingdong County, alt. 2500 m, on rotten wood of broadleaf trees, 20 Jul. 2006, *Zhu L. Yang*4687 (HKAS 50484).

Pileus 3–7 cm in diam, dry, convex to applanate, centre often slightly depressed; centre cinnamon (5D5–5D8), but other parts of pileus ochraceous yellow (4A8, 4B8, 4C8), becoming paler when mature; margin incurved, orange-yellow (4A6–4A8, 5B7–5B8) with long, faintly translucent striations; colour of pileus becoming pinkish (13A3, 13A4) then olivaceous grey to brown (29C2–29C3, 5E5) when dryed. Lamellae adnexed to nearly free, distant with a few lamellulae, cream, yellowish to whitish orange, up to 12 mm in height, 1 mm in thickness. Stipe 3–5 cm in length, 3–8 mm in diam, subcylindrical, hollow, not inflated; surface cream to white, glabrous, sometimes with orange yellow tinge. Context of pileus and stipe white.

Basidiospores (Fig 5A) [150/7/6] (9) 9.5–11 (12.5) × (4) 4.5–6 (7) μm, [Q = (1.42) 1.75–2.22 (2.62), Q_m = 1.99 ± 0.19], oblong to cylindrical, thin-walled, smooth, colourless and hyaline, non-amyloid, non-dextrinoid. Basidia (Fig 5B) 35–40 × 7–8.5 μm, clavate to narrowly clavate, 4-spored; sterigmata 4–5 μm long. Basidioles (Fig 5B) very abundant, 28–38 × 4–6 μm, fusiform with subacute apices, thin-walled, colourless. Cheilocystidia (Fig 5E) forming a sterile band along the lamellae edge, crowded, clavate to broadly clavate, slightly thick-walled (≤1.5 μm thick), colourless and hyaline, 20–40 × 9–25 μm, sometimes pyriform to sphaero-pedunculate, 40–60 × 20–35 μm. Pleurocystidia (Fig 5D) present, but scattered (70–120 × 12–25 μm), subfusiform, slightly thick-walled (≤1.5 μm thick), colourless and hyaline, with narrow to acute apex. Subhymenium ca. 20 μm in thickness, composed of branching hyphal segments, 3–4 (5) μm in diam, septa without clamps. Lamellar trama (Fig 5B) ca. 250–400 μm in width, composed of mostly irregularly arranged to interwoven (not bilateral) filamentous hyphae (3–15 μm wide) becoming broader and somewhat gelatinized towards the median, becoming slender and somewhat regularly towards the subhymenium and not gelatinous. Pileocystidia absent. Pileipellis (Fig 5F) an epithelium of 30–50 μm thick, composed of 1–3 layers of subglobose, broadly clavate, ovoid to obovoid cells (10–40 × 8–35 μm). Caulocystidia (Fig 5C) scattered to gregarious, mostly broadly clavate to sphaero-pedunculate, 20–50 × 10–20 μm, sometimes lageniform to subfusiform, 35–70 × 10–17 μm, colourless and hyaline, thin walled (≤0.5 μm). Stipitipellis (Fig 5C) composed of vertically

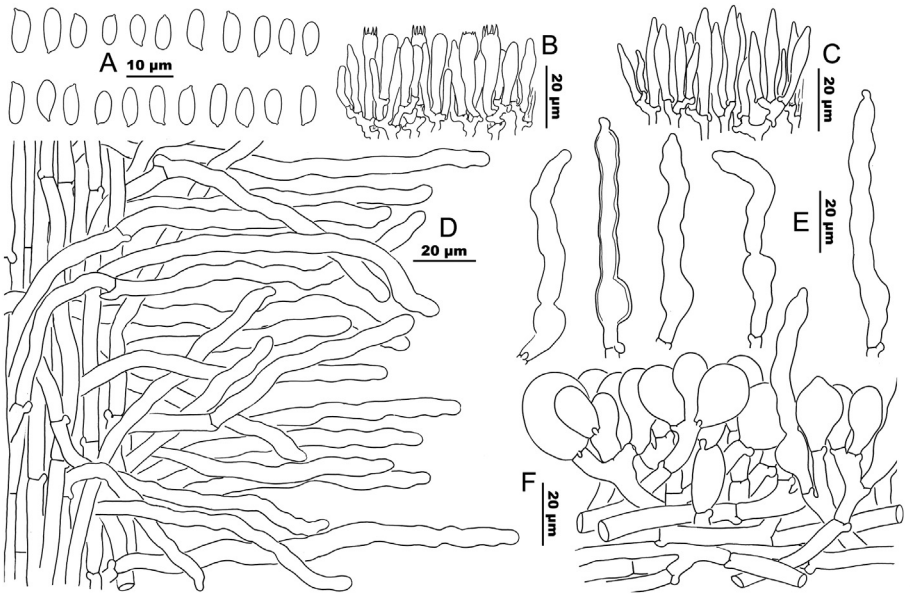

Fig 4 – Microscopic features of *Cyptotrama angustispora* (HKAS 78639, Type). (A). Basidiospores; (B). Basidia; (C). Lamellae edge; (D). Stipitipellis, and caulocystidia; (E). Pileocystidia; (F). Pileipellis.

arranged, branching and sometimes anastomosing hyphae 2–10 μm wide. Trama of stipe composed of vertically arranged filamentous to inflated hyphae 2–25 μm in diam.

Habitat and known distribution: on rotten wood of broad-leaf trees in tropical and subtropical forests; in summer at alt. 300–2600 m in Southwestern China and Laos.

Other specimens examined: **China**: *Guangdong*: Heishiding, Fengkai County, alt. 650 m, 27 Mar. 2012, *F. Li* 97 (HKAS 88116); same location, 24 Apr. 2012, *F. Li* 138 (HKAS 88115); same location, 29 Mar. 2013, *F. Li* 1200 (HKAS 78549). *Yunnan*: Ailaoshan, Jingdong County, 14 Jul. 2007, *Y.-C. Li*820 (HKAS 52507); Baihualing, Longyang District, 25 Jul. 2003, *Zhu L. Yang*3868 (HKAS 42875); Bawan Town, Longyang District, 17 Sept. 2002, *H.-C. Wang*70 (HKAS 41651); same location, 19 Sept. 2002, *H.-*

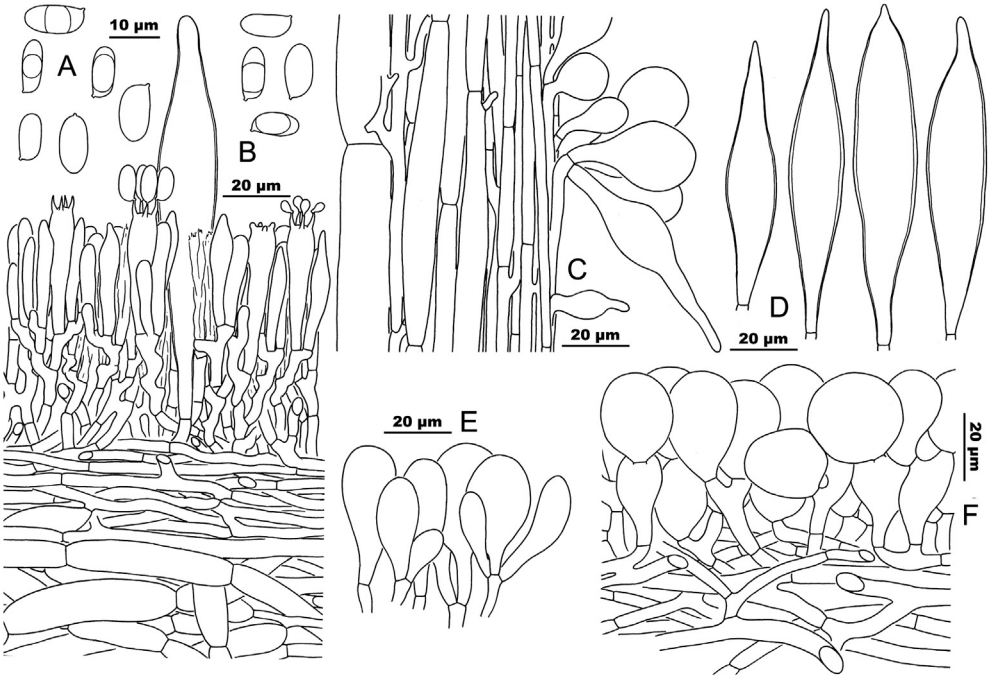

Fig 5 – Microscopic features of *Cyptotrama glabra* (HKAS 50484, Type). (A). Basidiospores; (B). Hymenium; (C). Stipitipellis, and caulocystidia; (D). Pleurocystidia; (E). Cheilocystidia; (F). Pileipellis.

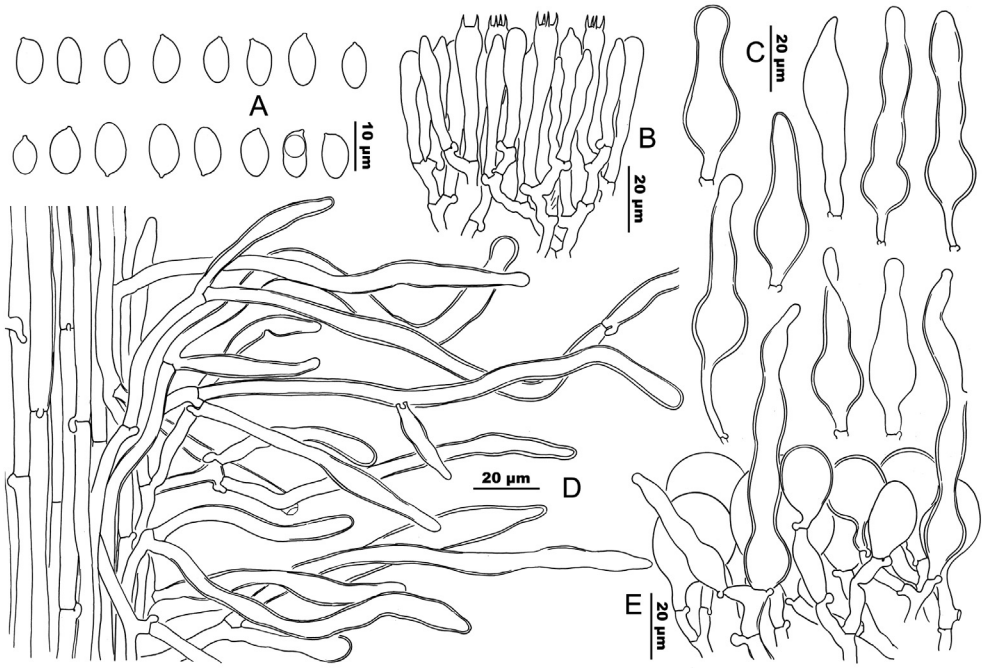

Fig 6 – Microscopic features of *Cyptotrama shennongjia* (HKAS 75559, Type). (A). Basidiospores; (B). Hymenium; (C). Pileocystidia; (D). Stipitipellis, and caulocystidia; (E). Pileipellis.

*C. Wang*90 (HKAS 41663); National Nature Reserve of Gaoligongshan, Longyang District, alt. 2230 m, 17 Jun. 2014, *J. Qin*896 (HKAS 83313); same location, alt. 2230 m, 18 Jun. 2014, *J. Qin*905 (HKAS 83322); same location, 19 Jun. 2014, *L.-H. Han*333 (HKAS 84629); same location, alt. 2207 m, 30 Jun. 2014, *X.-B. Liu*339 (HKAS 86991); Wuliangshan, Nanjian County, 28 Jul. 2009, *L.-P. Tang*981 (HKAS 56938); same location, 4 Aug. 2014, *Y.-J. Hao*1312 (HKAS 83102); Mangbang town, Tengchong County, 9 Aug. 2011, *J. Qin*285 (HKAS 73271); Wuhe Town, Tengchong County, 11 Aug. 2011, *J. Qin*313 (HKAS 73299); Houqiao Town, Tengchong County, 10 Aug. 2011, *Y.-J. Hao*459 (HKAS 71568); Daweishan, Pingbian County, 7 May 2011, *Z.-W. Ge*2839 (HKAS 70344); Luoboyakou, Zhen'an Town, Longling County, alt. 2560 m, 16 Jun. 2014, *J. Qin*881 (HKAS 83298); Dadugang, Jinhong, *K. Zhao*440 (HKAS 87681). **Laos:** Attepeu, alt. 300 m, 26 Apr. 2013, *Zhu L. Yang*5658 (HKAS 78616); same location, 27 Apr. 2013, *Zhu L. Yang*5671 (HKAS 78629).

Comments: *Cyptotrama hygrocyboides* Singer and *C. pauper* Singer resemble this species by the glabrous pileus, and the absence of clamp connections, but they both are reported to be red or rose-coloured, with pileocystidia and a bilateral lamellar trama (Singer 1969, 1989). The absence of pleurocystidia also makes *C. pauper* different from the other two species. In tropic Asia, *Marasmius trogioides* Corner (≡ *C. trogioides*, see below), and *M. trogioides* var. *megaspora* Corner (≡ *C. megaspora*, see below) may be closely related to this species (Corner 1996). The colour of *M. trogioides* is cinnamon fawn, fulvous ochraceous, to fuscous brown. *Marasmius trogioides* var. *megaspora* has larger basidiospores (10.5–13.5 × 6–7 μm). Both taxa have thin-walled cheilocystidia, while those of *C. glabra* are slightly thick-walled.

Cyptotrama shennongjia Zhu L. Yang & J. Qin, **sp. nov.** Figs 3D and 6

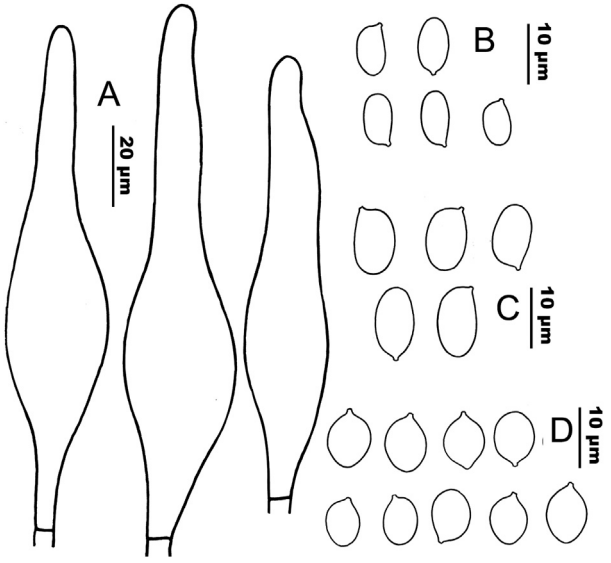

Fig 7 – Microscopic features of *Cyptotrama trogioides* (E00192255), *C. megaspora* (E00192181, Type) and *C. macrobasidia* (MICH10533, Isotype). (A). Pleurocystidia of *C. trogioides*; (B). Basidiospores of *C. trogioides*; (C). Basidiospores of *C. megaspora*; (D). Basidiospores of *C. macrobasidia*.

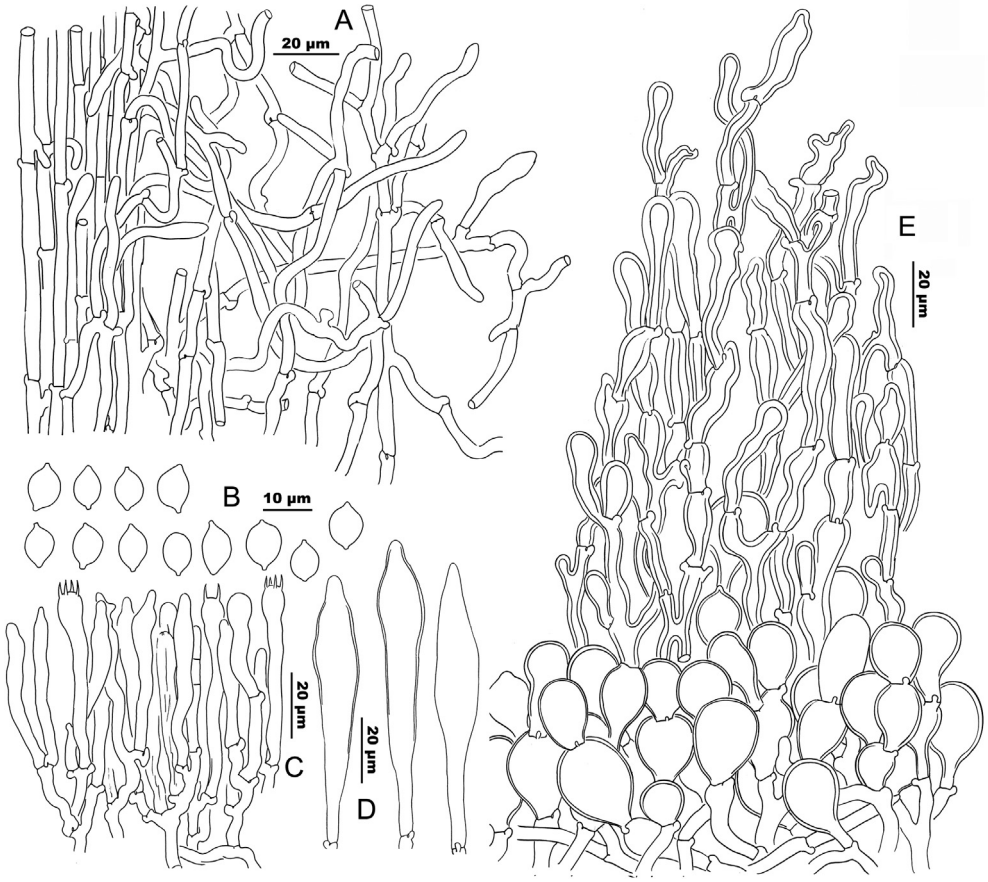

Fig 8 – Microscopic features of *Cyptotrama asprata* (HKAS 83324). (A). Structure of squamules on stipe and stipitipellis; (B). Basidiospores; (C). Basidia; (D). Hymenophoral cystidia (cheilocystidia and pleurocystidia); (E). Structure of squamules on pileus and pileipellis.

MycoBank: MB 811963.

Etymology: referring to the locality of the type.

Type: **China:** *Hubei*: Muyu Town, Shennongjia, 31°29′23″N, 110°21′33″E, alt. 1800 m, on rotten wood of *Quercus* trees, 16 Jul. 2012, *Q. Cai*805 (HKAS 75559).

Pileus 2–3.5 cm in diam, applanate, greyish, grey to yellowish grey (4B1, 4C1), striate. Lamellae yellowish to yellow (2A2–2A5), adnate to adnexed, thin and distant, up to 8 mm in height, with lamellulae, intervenose. Stipe 2–3 cm in length, 2–4.5 mm in diam, subcylindrical, hollow; surface dirty white to cream, with fine whitish squamules. Context of pileus and stipe thin, whitish to cream, colour unchanging when cut.

Basidiospores (Fig 6A) [65/2/2] (7) 7.5–9.5 (10.5) × 4–6 μm, [Q = (1.4) 1.5–2.12 (2.25), Q_m = 1.79 ± 0.2], oblong, thin-walled, smooth, colourless and hyaline, non-amyloid, non-dextrinoid. Basidia (Fig 6B) 28–50 × (5) 6–7 (8) μm, 4-spored, clavate; sterigmata up to 4.5–5 μm in length. Basidioles (Fig 6B) 25–33 × 5–7 μm, fusoid, with subacute apex. Cheilocystidia and pleurocystidia absent. Lamellae edge fertile. Lamellar trama 100–250 μm wide, irregular to interwoven, not bilateral; hyphae 4–18 μm wide, thin to slightly thick walled (ca. 1 μm). Pileocystidia (Fig 6C) abundant, 53–100 × 14–17 μm, lageniform, ventricose, broadly fusiform, thin-walled, colourless. Pileipellis (Fig 6E) an epithelioid hymeniderm composed of subglobose, globose, sphaeropedunculate to obovoid cells, 24–50 × 15–30 μm. Caulocystidia (Fig 6D) scattered to gregarious, subcylindrical, subfusiform to narrowly clavate, 3–11 μm in diam, slightly thick-walled (ca. 1 μm), colourless, branching, clamped. Stipitipellis composed of vertically arranged, branching and sometimes anastomosing hyphae 2–10 μm wide. Trama of stipe composed of vertically arranged 3–11 μm wide, thin-to slightly thick-walled hyphae.

Habitat and known distribution: on rotten wood of broadleaf trees in subtropical forests; in summer at alt. 1800 m in central China.

Other specimen examined: **China:** *Hubei*: Muyu Town, Shennongjia, alt. 1800 m, 16 Jul. 2012, *J. Qin*558 (HKAS 77959).

Comments: The grey pileus, yellow lamellae and the pileocystidia of *Cyptotrama shennongjia* recall those of *C. angustispora*. However, *C. shennongjia* differs from *C. angustispora* by the broader basidiospores. The basidiospores of *C. shennongjia* resemble those of *C. fagiphila*, but the latter species has bilateral lamellar trama and possesses no pileocystidia (Moreau *et al.* 2015).

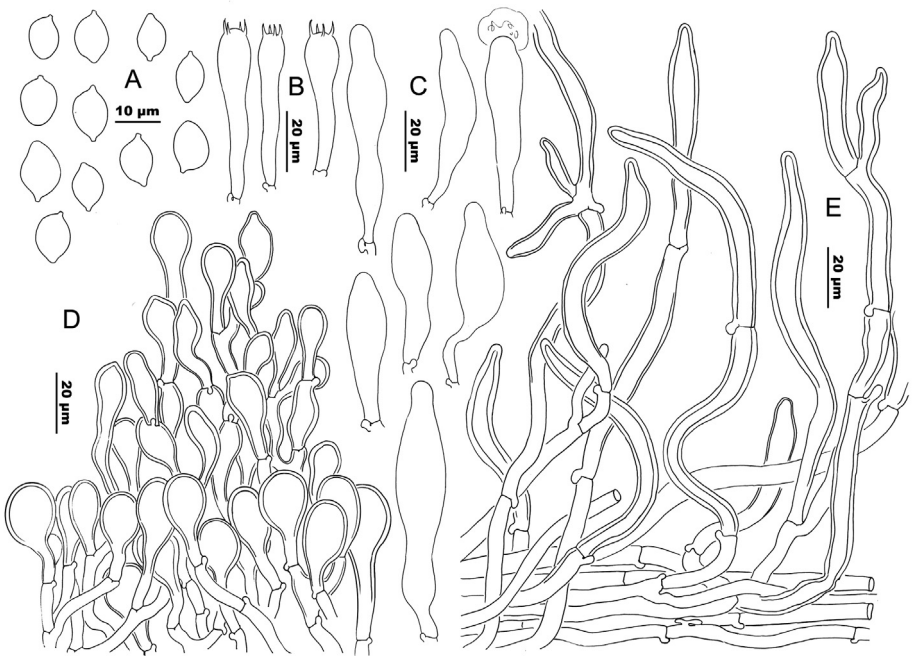

Fig 9 – Microscopic features of *Cyptotrama chrysopepla*. (A). Basidiospores (MICH139013 and HKAS 59934); (B). Basidia (HKAS 59934); (C). Hymenophoral cystidia (cheilocystidia and pleurocystidia, MICH139013 and HKAS 59934); (D). Structure of squamules on pileus and pileipellis (HKAS 59934) (E). Structure of squamules on stipe and stipitipellis (MICH139013).

Cyptotrama trogioides (Corner) Zhu L. Yang & J. Qin, **comb. nov.** Fig 7A, B

MycoBank: MB 811975.

Basionym: *Marasmius trogioides* Corner, Nova Hedwigia, Beih. 111: 105 (1996)

Pileus 3–9 cm in diam, convex then applanate with depressed centre, smooth or irregularly rugose, glabrous, dry, pruinate, bright cinnamon fawn to fulvous ochraceous, fuscous brown over the centre; margin incurved at first, exceeding the gills, sub-striate. Lamellae adnexed to free, thick, waxy, sub-distant, not intervenose, white to cream. Stipe 3–6 cm in length, 3–8 mm in diam, 5–9 mm at the abrupt and slightly dilated base waxy cartilaginous, hollow, or with fibrillose pith, finely pruinose, shining white. Context of pileus and stipe white, colour unchanging when cut.

Basidiospores (Fig 7B) [60/3/3] 7–10 (10.5) × 4–5 (5.5) μm, [Q = (1.5) 1.55–2.22 (2.33), Q_m = 1.94 ± 0.21], oblong, thin-walled, smooth, colourless and hyaline, non-amyloid, non-dextrinoid. Basidia 33–42 × 6–8 μm, 4-spored, clavate; sterigmata ca. 4 μm long. Lamellar edge sterile. Cheilocystidia 25–80 × 8–20 μm, clavate, thin to slightly thick walled. Pleurocystidia (Fig 7A) 50–120 × 15–25 μm, fusiform, clavate to subcylindrical, thin walled (≤0.5 μm), with attenuate apex, rarely acute. Pileocystidia absent. Pileipellis an epithelioid hymeniderm composed of broad clavate to obpyriform cells, 28–70 × 15–35 μm, thin walled. Caulocystidia cluster to scattered, mostly broadly clavate, 25–50 × 10–20 μm, colourless and hyaline, thin walled. Stipitipellis composed of vertically arranged, branching and sometimes anastomosing hyphae 2–8 μm wide. Trama of stipe composed of vertically arranged filamentous to inflated hyphae 3–20 μm in diam.

Type locality: Indonesia.

Habitat and known distribution: on rotten wood in tropical forests; only known from Indonesia.

Specimens examined: **Indonesia:** *Borneo*: Kinabalu, alt. 1600 m, 8 Feb. 1964, *E.J.H. Corner RSNB* 5277 (Record No. 206852, E00192255); Pinosula Plateau, Kinabalu, alt. 1600 m, 17 Mar. 1964, *E.J.H. Corner RSNB* 5824 (Record No. 206858, E00192194); Mesilau, Kinabalu, alt. 1600 m, 8 Apr. 1964, *E.J.H. Corner RSNB* 8155A (Record No. 206853, E00192254, Type!)

Comments: *Cyptotrama glabra* looks like *C. trogioides* but differs from the latter by the orange colour of pileus. Furthermore, the pleurocystidia of *C. trogioides* were found to be thin-walled, with an attenuate apex, whereas these of *C. glabra* are thick-walled with acute apex.

Cyptotrama megaspora (Corner) Zhu L. Yang & J. Qin, **comb. nov., state. nov.** Fig 7C

MycoBank: MB 811976.

Basionym: *Marasmius trogioides* var. *megaspora* Corner, Nova Hedwigia, Beih. 111: 105 (1996)

Pileus 2–5.5 cm in diam, orange fawn to orange ochraceous, centre subfuscous when young, finely scurfy pruinose. Lamellae paler concolourous with the pileus, whitish to the edge. Stipe 2–4 cm in length, ca. 3.5 mm in diam, base enlarged (6–9 mm), pale yellowish white.

Basidiospores (Fig 7C) [20/1/1] (9) 10–12.5 × (5) 6–7 μm, [Q = (1.5) 1.66–1.92, Q_m = 1.75 ± 0.1], oblong, colourless.

Basidia 40–50 × 7.5–9 μm, 4-spored, clavate; sterigmata 4–5.5 μm. Cheilocystidia 25–70 × 11–24 μm, clavate, thin to slightly thick walled. Pleurocystidia 50–130 × 11–23 μm, fusiform, clavate to subcylindrical, thin walled (≤0.5 μm), with attenuate apex. Pileocystidia absent. Pileipellis an epithelioid hymeniderm composed of broad clavate cells. Caulocystidia cluster to scattered, mostly broadly clavate, 25–60 × 7–15 μm, colourless and hyaline, thin walled. Stipitipellis composed of vertically arranged, branching and sometimes anastomosing hyphae. Trama of stipe composed of vertically arranged filamentous to inflated hyphae 7–25 μm in diam.

Habitat and known distribution: on rotten wood in a tropical forest; only known from Malaysia.

Type locality: Malaya (Malaysia).

Specimens examined: **Malaysia**: Cameron highland, Pahang, alt. 1800 m, 3 Oct. 1966, *E.J.H. Corner s. n.* (Record no. 206863, E00192181, Type!)

Comments: This species resembles *Cyptotrama glabra* by having an orange ochraceous pileus. However, *C. glabra* can be distinguished by its thick-walled (≤1.5 μm) pleurocystidia and smaller basidiospores. The spore sizes of *C. glabra* are 9.5–11 (12.5) × (4) 4.5–6 (7) μm, while those of *C. megaspora* measured by Corner were 10.5–13.5 × 6–7 μm (Corner 1996).

Cyptotrama myochroa (Sacc.) Zhu L. Yang & J. Qin, **comb. nov.**

MycoBank: MB 811977.

Basionym: *Clitocybe myochroa* Sacc., 1887. Syll. fung. (Abellini) 5: 193.
Xerulina myochroa (Sacc.) Pegler, 1986. Kew Bull., Addit. Ser. 12: 208.

Type Study: Pegler. 1986. Kew Bull., Addit. Ser. 12: 208.

Type locality: Central Province, Sir Lanka.

Habitat and known distribution: on dead sticks; only known from Sri Lanka.

Comments: *Cyptotrama myochroa* is characterized by the greyish brown pileus covered by darker brown squamules, white adnate lamellae, elongated amygdaliform to cylindrical fusoid basidiospores (11–14 × 4–5 μm) and the absence of lamellar cystidia (Pegler & Gardens 1986). *Cyptotrama deseynesiana* (Pegler) Redhead & Ginns, originally described from Africa, resembles *C. myochroa* in the brown squamules on the pileus, the presence of clamp connections, but differs from the latter by the presence of cheilocystidia and much smaller basidiospores (De Seynes 1897; Pegler 1966; Redhead & Ginns 1980). *Cyptotrama lachnocephala* Singer, originally described from Africa, differs from *C. myochroa* by the ochraceous pileus, the presence of pleurocystidia and shorter limoniform to ellipsoid basidiospores (Patouillard 1902; Pegler 1966; Singer 1973). *Cyptotrama granulosa* (Romell) Redhead & Ginns, originally described from Juan Fernandeza Island of South Pacific Ocean, differs from *C. myochroa* by the presence of cheilocystidia and distinctly smaller ellipsoid to ovoid basidiospores 6.3–8 × 3.5 μm (Romell 1926; Redhead & Ginns 1980).

Cyptotrama asprata (Berk.) Redhead & Ginns Figs 3E–H and 8

Pileus 1–3 (5) cm, convex, hemispherical to applanate, whitish, cream to yellow, densely covered by orange, golden yellow to lemon-coloured (3A4–3A8, 4A4–4A8, 5A8) squamules, becoming whitish yellow when mature; usually not striate. Lamellae adnate to slightly decurrent, up to 5 mm in height, not intervenose, not forked, distant, white to cream, with lamellulae. Stipe 1.5–6 cm in length, 0.2–0.5 cm in diam, cylindrical or enlarged at base, fistulose, concoluorous with pileus, floccose. Context thin, white. Odour indistinct.

Basidiospores (Fig 8B) [156/7/6] 7–10 (11) × 4.5–7.5 (8.5) μm, [Q = (1) 1.17–1.67 (1.9), $Q_m = 1.41 \pm 0.16$], ellipsoid-limoniform to broadly ellipsoid, thin-walled, smooth, colourless and hyaline, non-amyloid, non-dextrinoid. Basidia (Fig 8C) 4-spored, 28 (40)–60 × 6–8 μm, clavate, colourless and hyaline; sterigmata 5–6 μm long. Basidioles (Fig 8C) abundant, 39–58 × 4–7.5 μm, fusiform with subacute apices, thin-walled, colourless. Cheilocystidia (Fig 8D) and pleurocystidia both present and similar in size and form, scattered, 50–90 × 9–16 μm, fusiform with acute to subacute apices, thin-to slightly thick-walled (≤1 μm thick), colourless and hyaline. Subhymenium ca. 25–35 μm in thickness, composed of branching hyphal segments, 3–4 (5) μm in diam, clamps abundant. Lamellar trama ca. 400–1200 μm in width, bilateral to weakly bilateral, composed of thin-walled filamentous hyphae (2–16 μm wide), becoming broader and gelatinized towards the median. Pileocystidia absent. Squamules (Fig 8E) on pileus composed of inflated chained, narrowly clavate, cylindrical to fusiform cells, 15–70 × 4–15 μm, thick-walled (1–4 μm), golden yellow to brownish yellow. Pileipellis (Fig 8E) under squamules an epithelium, composed of 1–3 layers, broad ellipsoid, subglobose, obovoid to sphaeropedunculate cells, 25–39 × 13–27 μm, thin to slightly thick walled (≤1 μm), nearly colourless. Squamules on stipe (Fig 8A) composed of interwoven, sometimes anastomosing filamentous to narrowly cylindrical hyphae 3–5 μm wide, thin walled (<1 μm), colourless to yellowish, hyaline, mixed with few terminal cells, 25–38 × 5–10 μm, slightly thick-walled (ca. 1 μm). Stipitipellis composed of vertically arranged, colourless to yellowish filamentous hyphae, 3–9 μm in diam. Trama of stipe composed of vertically arranged, nearly colourless hyphae, 3–15 μm in diam. Clamp connections abundant.

Type locality: Central Province, Sir Lanka.

Habitat and known distribution: on rotten wood; widely distributed in tropical, subtropical or even temperate regions of many parts of the world.

Specimens examined: **China:** *Gansu*: Tanhe Town, Cheng County, 22 Aug. 2011, *X.-T. Zhu*541 (HKAS 73936). *Guangdong*: Shakou Town, Yingde County, 23 Apr. 2008, *T.-H. Li et al.* (GDGM 25312); Yinghong Town, Yingde County, 25 Apr. 2008, *T.-H. Li et al.* (GDGM 25421); Chebaling, Shixing County, 29 Sept. 2010, *Y.-J. Li et al.* (GDGM 27630); Longdoushe Forest Farm, Shixing county, 14 Sept. 2011, *X.-H. Wang*3137 (HKAS 75447). *Hainan*: Limushan, Qiongzhong County, alt. 890 m, 5 Aug. 2010, *Z.-W. Ge*2627 (HKAS 60303); same location, 3 Jun. 2009, *N.-K. Zeng*235 (HKAS 76288); same location, 22 Jul. 2009, *N.-K. Zeng*302 (HKAS 76287); Wuzhishan, alt. 861 m, 2 Aug. 2009, *N.-K. Zeng*410 (HKAS 76289). *Hubei*: Muyu Town, Shennongjia, 15 Jul. 2012, *J. Qin*531 (HKAS 76283). *Hunan*: Mangshan, Yizhang County, *Y.-C. Li*1048 (HKAS 53393). *Yunnan*: Kunming Botanic Garden, Kunming, 10 Oct. 2012, *J. Qin*647 (HKAS

76284); Qiongzhusi, Kunming, 28 Jul. 2013, *G. Wu*1152 (HKAS80526); Jiuxiang, Yiliang County, 22 Sept. 2012, *Y.-J. Hao*781 (HKAS 76286); Guishan, Shilin County, 28 Jul. 2011, *T. Bau* (HMJAU 24814); Daweishan, Pingbian County, 8 May 2011, *Z.-W. Ge*2868 (HKAS 70373); Zixishan, Chuxiong, 11 Sept. 2011, *Z.-W. Ge*3041 (HKAS 70545); Dadugang, Jinghong, 30 Jun. 2014, *Z.-W. Ge*3534 (HKAS 84372); Xishuangbanna Tropical Botanic Garden, Menglun Town, Jinghong, 28 Nov. 2014, *G. Wu*1352 (HKAS 88114); Wuliangshan, Nanjian County, *Y.-J. Hao*1285 (HKAS 83076); National Nature Reserve of Gaoligongshan, Longling County, alt. 2200 m, 19 Jun. 2014, *L.-H. Han*326 (HKAS 84622); same location, alt. 2050 m, 18 Jun. 2014, *J. Qin*907 (HKAS 83324); same location, alt. 2200 m, 19 Jun. 2014, *J. Qin*925 (HKAS 83342); The Lijiang Alpine Botanic Garden, Yulong County, 24 Jul. 2008, *L.-P. Tang*478 (HKAS 54709). *Sichuan*: Wenda Town, Seda County, 7 Aug. 2005, *Z.-W. Ge*807 (HKAS 49302). *Taiwan*: Mingchi Forest Amusement Park, Yilan County, 13 Sept. 2012, *B. Feng*1244 (HKAS 76285). **Laos:** Attapeu, alt. 530 m, 28 Apr. 2013, *Zhu L. Yang*5676 (HKAS 78634). **New Zealand:** Odey Road, Puketoki Track, Bay of Plenty, 6 May 2003, *P. Catcheside* (PDD 78164). **Sir Lanka**: Sinharja, 28 Aug. 2011, *S. Karunarathna*38 (HKAS 76282).

Comments: *Cyptotrama asprata* was originally described from Sri Lanka. It's commonly known as the golden-scruffy *Collybia* and widespread in South and Southeast Asia (Sri Lanka, and Laos), East Asia (China, Japan, Korea), New Zealand, Hawaii, and Central America (Martinique, France) (Berkeley 1847; Redhead & Ginns 1980; Yang 1990; Moreau *et al.* 2015; Figs 1 and 2; Supplementary Fig 1). *Cyptotrama chrysopepla*, originally described from Cuba (Berkeley & Curtis 1868) and then found in North America, resembles *C. asprata* in its' gold yellow and scruffy appearance, but differs by the smaller squamules, the hymeniderm pileipellis, thick walled elements in squamules of stipe, the non-acute subcapitate pleurocystidia and larger basidiospores [8.5–12 (13) × (6) 6.5–8.5 (10) μm] (Fig 9; see below).

Cyptotrama chrysopepla (Berk. & M.A. Curtis) Singer Figs 3I and 9

Pileus 1–3 cm, convex, hemispherical to applanate, orange, golden yellow, lemon-coloured (3A5–3A8, 4A5–4A8), densely covered with fine squamules, dry, striate. Lamellae adnexed to slightly decurrent, white to cream, pale orange when dried, 2–3 mm in height, moderately distant, sometimes intervenose, occasionally forked, with lamellulae. Stipe 1.5–4 cm in length, 2–4 mm in diam, cylindrical or tapering downwards, concolourous with pileus, with fine squamules. Context thin, white.

Basidiospores (Fig 9A) [124/5/5] 8.5–12 (13) × (6) 6.5–8.5 (10) μm, [Q = (1.14) 1.22–1.57 (1.66), Q_m = 1.37 ± 0.11], ellipsoid-limoniform, thin-walled, smooth, colourless and hyaline, non-amyloid, non-dextrinoid. Basidia (Fig 9B) 45–57 × 8–11 μm. Pleurocystidia (Fig 9C) abundant, 50–96 × 11–18 μm, fusiform, narrowly utriform, subcapitate, thin-to slightly thick-walled (≤1 μm), encrusted. Cheilocystidia (Fig 9C) similar to pleurocystidia, 50–65 × 8–10 μm, thin-to slightly thick-walled (≤1 μm), encrusted. Lamellar trama sub-bilateral, 200–1300 μm wide; hyphae 3–8 (12) μm wide. Pileocystidia absent. Squamules (Fig 9D) on pileus composed of inflated chained clavate, subfusiform to subcylindrical cells, 25–39 × 13–27 μm, thick-walled (1.5–3.5 μm), golden yellow to brownish yellow. Pileipellis (Fig 9D) under squamules a hymeniderm, composed of clavate, broad clavate, 12–35 (40) × 10–15 (20) μm, thick walled (1–1.5 μm), yellowish to brownish yellow. Squamules (Fig 9E) on stipe nearly a trichodermial structure composed of cylindrical, narrowly clavate, subfusiform to flexuose hyphae 4–12 (16) μm wide, thick-walled (≤2.5 μm), colourless and hyaline. Trama of stipe composed of vertically arranged thin-to slightly thick-walled (0.5–1 μm) filamentous hyphae 3–8 (13) μm wide. Clamp connections common in all parts of basidiomata.

Type Locality: Cuba.

Habitat and known distribution: on rotten wood; known from Canada, United States and Cuba (Berkeley & Curtis 1868; Dennis 1970; Moreau *et al.* 2015).

Specimens examined: **Canada**: Deer Run, Dundas Valley, Hamilton, Ontario, alt. 200 m, B. Feng 2003 (HKAS 91482). **United States**: *Massachusetts*: Mount Monadnock, Hampshire, *Z.-W. Ge*2258 (HKAS 59934). *Michigan*: Pigeon lake Field Station, Bayfield, Wisconsin, 6 Jul. 1971, *S.J. Mazzer* 6458 (MICH139010); Waterloo State Recreation Area, Washtenaw County, 26 Jun. 1981, *A.H. Smith* 91328 (MICH139011); Rifle River Area, Ogemaw County, 15 Jul. 1975, *A.H. Smith* 85562 (MICH139013); Silver river, Dynamite Hill road, Baraga County, 9 Aug. 1969, *J.F. Ammirati* 3576 (MICH139012).

Comments: *Cyptotrama chrysopepla* used to be treated as a synonym of *C. asprata* (Aberdeen 1962; Redhead & Ginns 1980; Pegler & Fiard 1983; Pegler & Gardens 1986; Pegler 1987; Corner 1996). In our analysis, close phylogenetic relationship between *C. chrysopepla* and *C. asprata* was not supported. The latter differs from *C. chrysopepla* by its epithelium pileipellis, thin walled elements of squamules on stipe and attenuate to cylindrical hymenophoral cystidia (Fig 8).

Key to species of *Cyptotrama*

A key for 21 species of *Cyptotrama* is provided based on morphological characters and geographic distributions (Romell 1926; Pegler 1966; Redhead & Ginns 1980; Pegler & Gardens 1986; Singer 1953, 1964, 1969, 1973, 1978, 1986, 1989; Corner 1996; Moreau *et al.* 2015). Because an ITS sequence generated from the holotype of *Cyptotrama songolarum* Courtec. shares 100 % identity with a sequence accessible in GenBank identified as *Termitomyces eurhizus* (Berk.) R. Heim (Moreau *et al.* 2015), *C. songolarum* is excluded from the key below.

1. Pileus floccose (covered with squamules) 2
Pileus glabrous to subglabrous 10

2(1) Lamellae distant; clamp connections present..... 3
Lamellae closed; clamp connections absent..... **depauperata** Singer (1978)

3(2) Pileus golden yellow to orange 4
Pileus ochraceous, brown, or olive-umber to glaucous..... 6

4(3) Basidiospores usually limoniform or citriform; cheilocystidia similar to pleurocystidia; pleurocystidia scattered; lamellar trama bilateral..... 5

Basidiospores not limoniform or citriform; cheilocystidia vesiculose; pleurocystidia rare or absent; lamellar trama regular ..... **verruculosa** Singer (1964)

5(4) Hymenophoral cystidia subacute; pileipellis an epithelium; elements of squamules on stipe thin walled; widespread in subtropical (or even temperate) and tropical areas **asprata**
Hymenophoral cystidia attenuate cylindrical; pileipellis a hymeniderm; elements of squamules on stipe thick walled; only known from North America to Central America ..... **chrysopepla**

6(3) Basidiospores 11–14 × 4–5 μm; hymenophoral cystidia absent. Sri Lanka ..... **myochroa**
Basidiospores shorter; hymenophoral cystidia present or absent. Africa, South America or South Oceania 7

7(6) Pileus olive-umber to glaucous; basidiospores 9–12 × 6–7.5 μm ..... **costesii** (Speg.) Singer (1973)
Pileus never with olivaceous tinge; basidiospores shorter, less than 9 μm long 8

8(7) Basidiospores 4.5–6.4 μm wide (Patouillard, 1902); cheilocystidia absent; pleurocystidia present ..... **lachnocephala**
Basidiospores narrower, to 3.5 μm wide; cheilocystidia present; pleurocystidia absent 9

9(8) Basidiospores 3.5–5.8 × 2–3.2 μm; cheilocystidia narrowly lageniform, only known from Africa ..... **deseynesiana**
Basidiospores 6.3–8 × 3.5 μm, cheilocystidia clavate to cylindrical, reported from South Oceania (Juan Fernández Islands) ..... **granulosa**

10(1) Clamp connections present 11
Clamp connections absent 17

11(10) Pileus 15–60 mm, grey to greyish; basidiospores ellipsoid, oblong to narrowly ellipsoid; lamellae white, cream to yellow; lamellar trama bilateral or not. Eurasia 12
Pileus 5–25 mm, ochraceous, dark orange, dark brown or white; basidiospores globose to subglobose; lamellae white; lamellar trama bilateral to sub-bilateral. South America 14

12(11) Lamellae white to cream yellow; pileocystidia absent; lamellar trama bilateral. Europe (Spain) ..... **fagiphila**
Lamellae yellow; pileocystidia present; lamellar trama not bilateral. Asia 13

13(12) Basidiospores narrower, 6.5–9 × 2.5–3.5 μm. Laos ..... **angustispora**
Basidiospores broader, 7.5–9.5 × 4–6 μm. Central China ..... **shennongjia**

14(11) Pileus dark brown or white; basidiospores longer (over 10 μm long), ellipsoid to oblong 15
Pileus ochraceous to dark orange; basidiospores shorter (up to 9 μm), broad ellipsoid to subglobose 16

15(14) Pileus ca. 19–25 mm, black brown to dark brown. Mexico ..... **dennisii** Singer (1973)
Pileus ca. 5 mm, snow white. Brazil ..... **nivea**

16(14) Pileus ca. 20 mm, ochraceous with a slight flesh tinge; basidiospores 8.2–9 × (6) 7–7.5 μm; cheilocystidia undifferentiated; pleurocystidia 65–70 × 9.5–13 μm, ventricose-subampullaceous, with subcapitate to moderately narrowed apices, thin walled. Bolivia ..... **macrobasidia**
Pileus ca. 5–9 mm, dark orange, cinnamomeous when dried; basidiospores 6.5–7 × 5–6.5 μm; cystidia dimorphic: both thin-walled and thick-walled cystidia present. Argentina ..... **platensis** Singer (1969)

17(10) Pileus red to rose. South America 18
Pileus orange to yellowish brown. Asia 19

18(17) Lamellae cream-coloured; cheilocystidia similar to pleurocystidia, 62–176 × 10–24 μm, thick walled (0.8–1 μm). Chile ..... **hygrocyboides**
Lamellae white; cheilocystidia inconspicuous (17–26 × 4.5–8.5 μm); pleurocystidia absent. Brazil ..... **pauper**

19(17) Pileus cinnamon fawn, fulvous ochraceous, fuscous brown; lamellae cream to white. Indonesia ..... **trogioides**
Pileus orange to dark orange; lamellae pale orange 20

20(19) Basidiospores 10.5–13.5 × 6–7 μm; pleurocystidia thin-walled. Malaysia ..... **megaspora**
Basidiospores 9.5–11 × 4.5–6 μm; pleurocystidia thick-walled. China and Laos ..... **glabra**

Discussion

In the genus *Cyptotrama*, four sections, namely sect. *Cyptotrama*, sect. *Depauperata*, sect. *Xerulina* and sect. *Aporpotrama*, were proposed by Singer (1973, 1986). Although Singer (1986) stated that "*Xerulina* is too closely related to *Cyptotrama* to be kept in a different genus", some mycologists preferred to treat *Xerulina* as a separate genus (Pegler 1966, 1972, 1977, 1987; Pegler & Gardens 1986; Corner 1996). In our molecular phylogenetic analyses, two species of *Xerulina*, *Xerulina chrysopepla* (≡ *Cyptotrama chrysopepla*, the generic type of *Xerulina*) and *Xerulina asprata* (≡ *Cyptotrama asprata*) were included. It was found that they formed a well-supported clade with *Cyptotrama shennongjia*, *C. angustispora*, and *C. fagiphila*, which can be morphologically placed in sect. *Cyptotrama*. Thus, it is reasonable to follow Singer (1973, 1986) to treat *Xerulina* as a section of *Cyptotrama*, even though the molecular data of the type species of *Cyptotrama* (*Cyptotrama macrobasidia* Singer) is currently not available. The isotype material of *C. macrobasidia* (Singer B577, MICH10533, Fig 7D) is not available to us for molecular study, due to its scarceness.

The bilateral (divergent) lamellar trama has been used as one of the key diagnostic characters to distinguish *Cyptotrama* from its allied genera (Singer 1960, Pegler & Gardens 1986; Singer 1986), despite the fact that *Cyptotrama verruculosa* (Singer) Singer, *C. deseynesiana* and *C. lachnocephala* have regular lamellar trama (Singer 1964; Pegler 1966). In this study, we found that the lamellar trama of *C. angustispora*, *C. glabra*, and *C. shennongjia* is slightly bilateral, irregular to regular, depending on the stages of development. In our opinion, the bilateral lamellar trama, which can be also observed in species of several genera of *Physalacriaceae*, namely *Pseudohiatula* (Singer 1962b, 1964, 1982; Dennis 1968), *Flammulina* (Singer 1964; Redhead *et al.* 2000), *Armillaria* (Motta & Korhonen 1986; Berube & Dessureault 1988) and *Xerula* (Petersen & Baroni

2007), can't be used as a reliable character to separate *Cyptotrama* from its allied genera in the family.

In the infrageneric system of *Cyptotrama* proposed by Singer (Singer 1986), the erection of four sections was mainly based on the combination of two features: the floccose/glabrous pileus and the presence/absence of clamp connections. Our phylogenetic analyses on six species of this genus found that the species with floccose pileus (*C. asprata* and *C. chrysopepla*) didn't cluster together (Figs 1 and 2), indicating that the squamules on the pileus would have originated at least twice in *Cyptotrama*. In contrast, all species with clamp connections formed a well-supported clade, and so did the one without clamp connections. This would indicate that the presence of clamp connections could be an important character for the infrageneric treatment. However, its validity still needs to be checked by adding more species in the phylogenetic studies. Besides, the structure of stipe surface (with squamules or caulocystidia) showed obvious discrepancies among species of *Cyptotrama*, and could be effectively employed for species delimitation of *Cyptotrama*, yet has been ignored or undervalued in the earlier studies.

Prior to this study, Asian *Cyptotrama* species has been poorly addressed, with only a single species, *C. asprata*, reported from the vast region. Our morphological and molecular studies uncovered three new species. Meanwhile, we found that three taxa, which were previously placed in *Marasmius* and *Xerulina*, namely *Marasmius trogioides*, *M. trogioides var. megaspora*, and *Xerulina myochroa*, should be transferred to *Cyptotrama*. Our study thus increased the species of Asian *Cyptotrama* from one to seven, which has exceeded the number of species in South America. In the heterogeneous *Marasmius* Fr. (*Marasmiaceae*), many taxa were found to be members of *Physalacriaceae* (Petersen 2000; Ronikier & Ronikier 2011; Hao *et al.* 2014; Jenkinson *et al.* 2014; Moreau *et al.* 2015). *Marasmius batistae* Singer (Singer 1965, 1976) might also be a *Cyptotrama*, given its similarity with *C. angustispora*.

Our study also provided some new insights into the distribution pattern of *Cyptotrama*. Within the six *Cyptotrama* species supported by molecular data (Figs 1 and 2), most of them were found to be endemic or restricted to certain regions. However, the wide disjunctive distribution of *C. asprata* is really striking and might be a result of long-distance dispersal because genetic divergences among samples from different geographical locations are often subtle (Figs 1 and 2, Supplementary Fig 1). In previous morphological studies, *C. asprata* was supposed to be a widespread species in North America, South America, South Africa, Asia, Australia, and Oceania (Berkeley 1847; Redhead & Ginns 1980; Wood 1983; Pegler & Gardens 1986; Yang 1990; Corner 1996; Hemmes & Desjardin 2002; Hosoya *et al.* 2006), and, thus, *C. chrysopepla*, a species originally described from North America, was consequently treated as a synonym of *C. asprata* (Aberdeen 1962; Pegler 1972, 1977, 1987; Redhead & Ginns 1980; Wood 1983; Pegler & Gardens 1986; Hemmes & Desjardin 2002). Moreau *et al.* (2015) found that *C. asprata* and *C. chrysopepla* are different species, then designated the North American samples as *C. chrysopepla* and labelled collections from East-Asia and Central America as *C. asprata* s. str. Our phylogenetic analyses based on extensive sampling (Figs 1 and 2; Supplementary Fig 1) confirmed that *C. asprata* s. str. can be also found from North America (DED6391) and expanded its distribution to New Zealand and different areas of Asia (Laos and several provinces in China). *Cyptotrama chrysopepla* can be distinguished from *C. asprata* by the pileipellis (Figs 8E and 9D), the pleurocystidia (Figs 8D and 9C) and the elements of squamules on stipe (Figs 8A and 9E).

It is worth noting that *C. asprata* can be divided into two subclades in our molecular analyses. The subclade I was formed by three tropical Asian specimens (HKAS 78634, Laos; HKAS 60303, Hainan, China; HKAS 76282, Sri Lanka) and one North American collection (DED6391), while the subclade II comprised of samples collected from subtropical (or even temperate) and tropical areas. Our morphological study found that three specimens within subclade I (DED6391 not observed) have relatively narrower basidiospores and shorter basidia than those of subclade II. The basidiospores and basidia size of subclade I measured are [70/3/3] (6.5) 7–9 (9.5) × (4) 4.5–6 (7) μm, [Q = 1.16–1.77 (1.9), Q_m = 1.47 ± 0.16] and 28–40 × 6–8 μm. For specimens of subclade II, the size of basidiospores are [86/4/3] (7.5) 8–10 (11) × (5) 5.5–8 (8.5) μm, [Q = (1) 1.13–1.67 (1.8), Q_m = 1.37 ± 0.15], while the size of basidia are (35) 48–60 × 6–8 μm. Given the fact that the observed difference between these two subclades are subtle and that the distribution of the two subclades are partially sympatric (for example, Hainan Province of China), we tend to treat them as a single species.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.funbio.2016.01.009.

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