

A Contribution to Knowledge of *Gyroporus* (Gyroporaceae, Boletales) in China: Three New Taxa and Amended Descriptions of Two Previous Species

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Abstract

Some species of *Gyroporus* (Gyroporaceae, Boletales) in China are investigated on the basis of morphology and molecular phylogenetic analyses. Six Chinese species are recognized in the present study. Among them, *G. memnonius*, *G. porphyreus* and *G. subglobosus* are new to science; *G. longicystidiatus* and *G. paramjitii* are previously described; and one ambiguous taxon tentatively named *G. cf. castaneus*. A key to known species of *Gyroporus* in China is also provided. A preliminary biogeographical analysis shows that *Gyroporus* in East Asia and Southeast/South Asia are closely related. *Gyroporus longicystidiatus* and *G. paramjitii* are geographically widespread species occurring in East Asia and Southeast/South Asia; *G. cf. castaneus* is a shared species between East Asia and Europe.

Introduction

Gyroporus Quél., originally represented by *G. castaneus* (Bull.) Quél. and *G. cyanescens* (Bull.) Quél. in Europe, is a boletoid genus in Gyroporaceae (Singer) Manfr. Binder & Bresinsky (Boletales) (Quélet 1886; Singer 1986; Binder and Bresinsky 2002). Members of this genus are ectomycorrhizal fungi of many plant families such as Fagaceae, Pinaceae and Myrtaceae (Singer et al. 1983; Agerer 1999; Raidl et al. 2006; Watling 2006, 2008; Wilson et al. 2012). *Gyroporus* is characterized by small to middle-sized basidiomata, whitish, yellowish, yellow-brown to red-brown villous or scaly pileus, white to light yellow, simple pores, a stipe usually concolorous with pileus, stipe chambered or completely hollow, brittle, white context, unchanging or turning blue or purple when injured, short ellipsoid basidiospores, presence of clamp connections (Reijnders 1963; Besl et al. 1973; Gill and Steglich 1987; Agerer 1999; Muñoz 2005; Raidl et al. 2006; Watling 2008; Bessette et al. 2010; Horak 2011; Knudsen and Vesterholt 2012; Wilson et al. 2012; Vizzini et al. 2015; Das et al. 2017; Davoodian et al. 2018; Huang et al. 2021). The genus is distributed in temperate, subtropical and tropical areas of the world (Chiu 1948; Heinemann 1954; Corner 1972; Imazeki et al. 1988; Watling and Li 1999; Bessette et al. 2000; Lannoy and Estadès 2001; Muñoz 2005; Watling and Hills 2005; Zang 2006; Li 2007; Watling 2008; Šutara et al. 2009; Horak 2011; Wilson et al. 2011, 2012; Vizzini et al. 2015; Das et al. 2017; Davoodian et al. 2018; Huang et al. 2021). Most species of this genus are edible (Bessette et al. 2000). Moreover, some interesting secondary metabolites were isolated from the collections identified as *G. castaneus* from China (Wan et al. 1999; Wan 2000). In addition, researchers found that *G. castaneus* has anti-cancer effect, which needed to be further proved (Wu et al. 2013). Besides the edibility and medicinal properties, one species, viz. *G. ammophilus* (M.L. Castro & L. Freire) M.L. Castro & L. Freire has been proved to be toxic, causing severe gastroenteritis when consumed (Castro and Freire 1995).

In China, European *G. castaneus* is also widely reported (Chiu 1948, 1957; Zang 1986; Wu et al. 2013; Tang 2015). Besides this iconic species, *G. atroviolaceus* (Höhn.) E.-J. Gilbert, *G. cyanescens*, *G. longicystidiatus* Nagas. & Hongo, *G. malesicus* Corner and *G. purpurinus* Singer ex Davoodian & Halling were also reported in the country (Zang 1986; Zang et al. 1996; Li and Song 2003; Li 2007). In addition, five new taxa, viz. *G. alpinus* Yan C. Li, C. Huang & Zhu L. Yang, *G. brunneofloccosus* T.H. Li, W.Q. Deng & B. Song, *G. flavocyanescens* Yan C. Li, C. Huang & Zhu L. Yang, *G. pseudomicrosporus* M. Zang and *G. tuberculatosporus* M. Zang were described in China (Zang 1986; Zang et al. 1996; Li et al. 2003; Huang et al. 2021). Recently, abundant collections of *Gyroporus* were made in southwest, southeast, east, south and northeast China, which were carefully examined using morphological and molecular phylogenetic analyses, aiming at discovering more taxa to enrich the diversity of *Gyroporus* in China.

Materials And Methods

Morphological studies

Specimens were collected from temperate, subtropical and tropical regions of China including Jilin, Yunnan, Fujian, Jiangxi, Guangdong and Hainan Provinces. Specimens were described and photographed in the field and deposited in

the Fungal Herbarium of Hainan Medical University (FHMU), Haikou City, Hainan Province of China. Color codes are from Kornerup and Wanscher (1981). Sections of the pileipellis were cut tangentially and halfway between the center and margin of the pileus. Sections of the stipeipellis were taken from the middle part along the longitudinal axis of the stipe. 5% KOH was used as a mounting medium for microscopic studies. All microscopic structures were drawn free hand from rehydrated material. The number of measured basidiospores is given as n/m/p, which indicate that the measurements were made on “n” basidiospores from “m” basidiomata of “p” collections. Dimensions of basidiospores are given as (a)b–c(d), where the range b–c represents a minimum of 90% of the measured values (5th to 95th percentile), and extreme values (a and d), whenever present ($a < 5\text{th percentile}$, $d > 95\text{th percentile}$), are in parentheses. Q refers to the length/width ratio of basidiospores; Qm refers to the average Q of basidiospores \pm sample standard deviation. Box plots for basidiospore size were constructed using statistical software SPSS.

Molecular procedures

Total genomic DNA was obtained with Plant Genomic DNA Kit (TIANGEN Company, China) from materials dried with silica gel according to the manufacturer’s instructions. The primers used for amplifying the nuclear ribosomal large subunit RNA (28S) were LR0R/LR5 (Vilgalys and Hester 1990; James et al. 2006), ITS5/ITS4 (White et al. 1990) for the nuclear rDNA region encompassing the internal transcribed spacers 1 and 2, along with the 5.8S rDNA (ITS), EF1-F/EF1-R (Mikheyev et al. 2006) for the translation elongation factor 1- α gene (*TEF1*), and RPB2-B-F1/RPB2-B-R (Wu et al. 2014) for the RNA polymerase II second largest subunit gene (*RPB2*). PCR reactions were performed with 4 min initial denaturation at 95°C, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at appropriate temperature (50°C for 28S or ITS, 53°C for *TEF1*; 52°C for *RPB2*) for 30 s, extension at 72°C for 120 s and a final extension at 72°C for 7 min. PCR products were checked in 1% (w/v) agarose gels, and positive reactions with a bright single band were purified and directly sequenced using an ABI 3730xl DNA Analyzer (Guangzhou Branch of BGI, China) with the same primers used for PCR amplifications. Forward or reverse sequences were compiled with BioEdit (Hall 1999).

Dataset assembly

Fifty-five sequences (twenty-one of 28S, seventeen of ITS, sixteen of *TEF1*, one of *RPB2*) from seventeen collections were newly generated. Edited sequences were deposited in GenBank; the GenBank accession numbers of 28S, ITS, and *TEF1* are listed in Table 1, and one of *RPB2* from *G. longicystidiatus* Nagas. & Hongo is presented here [N.K. Zeng2974 (FHMU1935): MW354541]. For the combined dataset, the 28S, ITS and *TEF1* sequences were aligned with selected sequences from GenBank and previous studies (Table 1). *Phlebopus marginatus* Watling & N.M. Greg. and *Phlebopus* sp. (REH8795) were chosen as the outgroup inferred from Davoodian et al. (2018). Single-gene phylogenetic trees based on the 28S, ITS, and *TEF1* fragments, respectively, were analyzed to test for phylogenetic conflict. The topologies of the phylogenetic trees based on a single gene were almost identical, indicating that the phylogenetic signals present in the different gene fragments were not in conflict. Then, the sequences of the different genes were aligned using MUSCLE (Edgar 2004), and alignments were purged from unreliably aligned positions and gaps using Gblocks (Castresana 2000). The sequences of the different genes were concatenated using Phyutility v. 2.2 for further analyses (Smith and Dunn 2008).

Table 1
Taxa, vouchers, and GenBank accession numbers of the DNA sequences used in this study

Species	Voucher	Locality	28S	ITS	TEF1	References
<i>Gyroporus</i> aff. <i>austrocastaneus</i>	E4879c	Australasia	FJ710208	—	—	Wilson et al. (2011)
<i>Gyroporus</i> aff. <i>castaneus</i>	E843c	—	EU718170	—	—	Wilson et al. (2011)
<i>Gyroporus</i> aff. <i>castaneus</i>	CM061	Algeria	—	KP826761	—	Unpublished
<i>Gyroporus</i> aff. <i>cyanescens</i>	E486	Australia	EU718173	—	—	Wilson et al. (2011)
<i>Gyroporus</i> aff. <i>cyanescens</i>	REH8819	Western Australia	EU718172	—	—	Wilson et al. (2011)
<i>Gyroporus</i> aff. <i>cyanescens</i>	E5685	Australia	EU718174	—	—	Wilson et al. (2011)
<i>Gyroporus</i> aff. <i>cyanescens</i>	REH8821	Western Australia	EU718139	—	FJ536673	Wilson et al. (2011; 2012)
<i>Gyroporus</i> aff. <i>subalbellus</i>	HONDURAS19-F036a	Honduras	—	MT571529	—	Unpublished
<i>Gyroporus alpinus</i>	LI1478-Strain1	Yunnan, SW China	MW151268	MW149435	—	Huang et al. (2021)
<i>Gyroporus alpinus</i>	LI1478-Strain2	Yunnan, SW China	MW151269	MW149438	—	Huang et al. (2021)
<i>Gyroporus ammophilus</i>	AH:45814	Spain	KX869892	—	—	Crous et al. (2017)
<i>Gyroporus ammophilus</i>	AH:45842	Spain	KX869890	—	—	Crous et al. (2017)
<i>Gyroporus ammophilus</i>	AH:45843	Spain	KX869891	—	—	Crous et al. (2017)
<i>Gyroporus austrobrasiliensis</i>	ICN 184399	Brazil	MF437014	—	—	Magnago et al. (2018)
<i>Gyroporus austrobrasiliensis</i>	ICN 184400	Brazil	MF437015	—	—	Magnago et al. (2018)
<i>Gyroporus austrobrasiliensis</i>	ICN 184402	Brazil	—	MF437001	—	Magnago et al. (2018)
<i>Gyroporus brunneofloccosus</i>	GDGM74638	Guangdong, southern China	MW151266	MW149437	—	Huang et al. (2021)
<i>Gyroporus brunneofloccosus</i>	WU2644	Yunnan, SW China	MW151267	MW149436	—	Huang et al. (2021)
<i>Gyroporus castanaeus</i>	239 - 97	USA	AF336253	—	FJ536670	Binder and Bresinsky (2002); Wilson et al. (2012)

Species	Voucher	Locality	28S	ITS	TEF1	References
<i>Gyroporus castaneus</i>	Gc1	Germany	AF336252	—	FJ536669	Binder and Bresinsky (2002); Wilson et al. (2012)
<i>Gyroporus castanea</i>	G_cast_1-1-2R	USA	—	JX030211	—	Unpublished
<i>Gyroporus castaneus</i>	155–178	Japan	—	AB509594	—	Unpublished
<i>Gyroporus castaneus</i>	3681	USA	—	KM248947	—	Unpublished
<i>Gyroporus castaneus</i>	WA0000071027	Poland	—	MK028888	—	Unpublished
<i>Gyroporus castaneus</i>	156–213	Japan	—	AB509618	—	Unpublished
<i>Gyroporus castaneus</i>	FLAS-F-61844	USA	—	MH212108	—	Unpublished
<i>Gyroporus castaneus</i>	JMP0028	—	—	EU819468	—	Unpublished
<i>Gyroporus castaneus</i>	F:PRL5664	USA	—	GQ166901	—	Unpublished
<i>Gyroporus castaneus</i>	F:PRL5664MAN	USA	—	GQ166887	—	Unpublished
<i>Gyroporus castaneus</i>	FLAS-F-61255	USA	—	MH211836	—	Unpublished
<i>Gyroporus castaneus</i>	F:PRL5948MAN	USA	—	GQ166885	—	Unpublished
<i>Gyroporus castaneus</i>	F:PRL5872MAN	USA	—	GQ166884	—	Unpublished
<i>Gyroporus castaneus</i>	S.D. Russell MycoMap 6269	USA	—	MK532856	—	Unpublished
<i>Gyroporus castaneus</i>	FLAS-F-61497	USA	—	MH211929	—	Unpublished
<i>Gyroporus castaneus</i>	Arora 01 512	—	FJ710209	—	—	Unpublished
<i>Gyroporus castaneus</i>	239 – 97	USA	—	EU718100	—	Wilson et al. (2011)
<i>Gyroporus castaneus</i>	NCJ16	USA	AY612808	—	—	Drehmel et al. (2008)
<i>Gyroporus</i> cf. <i>castaneus</i>	iNaturalist 31940211	USA	—	MN498109	—	Unpublished
<i>Gyroporus</i> cf. <i>castaneus</i>	Y.G. Fan3814 (FHMU3368)	Jilin, NE China	MW352984	MW380861	MW354539	this study

Species	Voucher	Locality	28S	ITS	TEF1	References
<i>Gyroporus cyanescens</i>	FLAS-F-61545	USA	—	MH211963	—	Unpublished
<i>Gyroporus cyanescens</i>	FLAS-F-61205	USA	—	MH211810	—	Unpublished
<i>Gyroporus cyanescens</i>	FLAS-F-61592	USA	—	MH211984	—	Unpublished
<i>Gyroporus cyanescens</i>	FLAS-F-60581	USA	—	MH016792	—	Unpublished
<i>Gyroporus cyanescens</i>	CNV67	—	—	MT345244	—	Unpublished
<i>Gyroporus cyanescens</i>	MCVE:28580	Italy	KT363685	KT363684	—	Vizzini et al. (2015)
<i>Gyroporus cyanescens</i>	17184	Italy	—	JF908785	—	Osmundson et al. (2013)
<i>Gyroporus cyanescens</i>	WA0000071032	Poland	—	MK028893	—	Unpublished
<i>Gyroporus cyanescens</i>	2837	—	—	KM248948	—	Unpublished
<i>Gyroporus cyanescens</i>	MB05-04	—	—	EU718102	—	Unpublished
<i>Gyroporus cyanescens</i>	AH 535	Spain	KX869893	—	—	Crous et al. (2017)
<i>Gyroporus cyanescens</i>	AH 45841	Spain	KX869889	—	—	Crous et al. (2017)
<i>Gyroporus cyanescens</i>	AH 45844	Spain	KX869888	—	—	Crous et al. (2017)
<i>Gyroporus cyanescens</i>	AH:46009	Spain	KY576811	—	—	Unpublished
<i>Gyroporus cyanescens</i>	F1086418	—	EU718167	—	—	Wilson et al. (2011)
<i>Gyroporus cyanescens</i>	Gc2	Germany	EU718168	—	—	Wilson et al. (2011)
<i>Gyroporus cyanescens</i>	Gcy2	Germany	AF336254	—	—	Binder and Bresinsky (2002)
<i>Gyroporus cyanescens</i>	HKAS76672	Heilongjiang, NE China	KF112478	—	KF112311	Wu et al. (2014)
<i>Gyroporus cyanescens</i>	MCVE28580	Italy	KT363685	—	—	Vizzini et al. (2015)
<i>Gyroporus cyanescens</i>	MB 05 - 001	USA	EU718138	—	FJ536672	Wilson et al. (2011, 2012)
<i>Gyroporus cyanescens</i>	REH8758 (E8758c)	Australia	EU718171	—	—	Wilson et al. (2011)

Species	Voucher	Locality	28S	ITS	TEF1	References
<i>Gyroporus cyanescens</i>	REH8804	Thailand	EU718137	—	FJ536671	Wilson et al. (2011; 2012)
<i>Gyroporus cyanescens</i> var. <i>cyanescens</i>	NAMA190	—	—	EU819495	—	Palmer et al. 2008
<i>Gyroporus flavocyanescens</i>	WXL1182	Guizhou, SW China	MW442950	MW440550	—	Huang et al. (2021)
<i>Gyroporus flavocyanescens</i>	WXL1187	Guizhou, SW China	MW442951	MW440551	—	Huang et al. (2021)
<i>Gyroporus lacteus</i>	MCVE 28582	Italy	KT363683	—	—	Vizzini et al. (2015)
<i>Gyroporus longicystidiayus</i>	N.K.Zeng1348 (FHMU900)	Fujian, SE China	MW352975	MW380852	—	this study
<i>Gyroporus longicystidiayus</i>	N.K.Zeng1390 (FHMU937)	Fujian, SE China	MW352972	—	MW354529	this study
<i>Gyroporus longicystidiayus</i>	N.K.Zeng1409 (FHMU954)	Fujian, SE China	MW352980	MW380857	MW354536	this study
<i>Gyroporus longicystidiayus</i>	N.K.Zeng2456 (FHMU1582)	Hainan, southern China	MW352965	MW380845	—	this study
<i>Gyroporus longicystidiayus</i>	N.K.Zeng2974 (FHMU1935)	Hainan, southern China	MW352982	MW380859	MW354537	this study
<i>Gyroporus longicystidiayus</i>	N.K.Zeng3036 (FHMU1997)	Hainan, southern China	MW352983	MW380860	MW354538	this study
<i>Gyroporus longicystidiayus</i>	N.K.Zeng3273 (FHMU2234)	Fujian, SE Chin	MW352966	—	—	this study
<i>Gyroporus longicystidiayus</i>	Y.G. Fan2757 (FHMU3366)	Yunnan, SW China	MW352971	MW380849	MW354528	this study
<i>Gyroporus longicystidiayus</i>	N.K.Zeng4092 (FHMU3367)	Guangdong, southern China	MW352970	—	—	this study
<i>Gyroporus memnonius</i>	N.K.Zeng1378 (FHMU929)	Fujian, SE Chin	MW352979	MW380856	MW354535	this study
<i>Gyroporus memnonius</i>	M.S. Su45 (FHMU3369)	Jangxi, eastern China	MW352981	MW380858	—	this study
<i>Gyroporus paramjitii</i>	KD 162-002	India	MF120285	MF120284	—	Das et al. (2017)
<i>Gyroporus paramjitii</i>	N.K.Zeng3279 (FHMU2240)	Fujian, SE China	MW352967	MW380846	MW354525	this study
<i>Gyroporus paramjitii</i>	N.K.Zeng3282 (FHMU2243)	Fujian, SE China	MW352968	MW380847	MW354526	this study

Species	Voucher	Locality	28S	ITS	TEF1	References
<i>Gyroporus porphyreus</i>	N.K.Zeng1336 (FHMU888)	Fujian, SE China	MW352973	MW380850	MW354530	this study
<i>Gyroporus porphyreus</i>	N.K.Zeng1353 (FHMU905)	Fujian, SE China	MW352976	MW380853	MW354532	this study
<i>Gyroporus porphyreus</i>	N.K.Zeng1366 (FHMU917)	Fujian, SE China	MW352977	MW380854	MW354533	this study
<i>Gyroporus porphyreus</i>	N.K.Zeng1375 (FHMU926)	Fujian, SE China	MW352978	MW380855	MW354534	this study
<i>Gyroporus porphyreus</i>	N.K.Zeng3312 (FHMU2273)	Hainan, southern China	MW352969	MW380848	MW354527	this study
<i>Gyroporus pseudocyanescens</i>	AH:45840	Spain	KY576807	—	—	Unpublished
<i>Gyroporus pseudocyanescens</i>	OKM23719	Western Australia	EU718140	—	—	Wilson et al. (2011)
<i>Gyroporus pseudolacteus</i>	AH 37878	Spain	KX869886	—	—	Crous et al. (2017)
<i>Gyroporus pseudolacteus</i>	AH 39364	Spain	KX869880	—	—	Crous et al. (2017)
<i>Gyroporus pseudolacteus</i>	AH 44522	Spain	KX869887	—	—	Crous et al. (2017)
<i>Gyroporus pseudolacteus</i>	AH 45811	Spain	KX869883	—	—	Crous et al. (2017)
<i>Gyroporus pseudolacteus</i>	AH 45812	Spain	KX869884	—	—	Crous et al. (2017)
<i>Gyroporus pseudolacteus</i>	AH 45848	Spain	KX869881	—	—	Crous et al. (2017)
<i>Gyroporus pseudolacteus</i>	AH 45849	Spain	KX869882	—	—	Crous et al. (2017)
<i>Gyroporus pseudolacteus</i>	AH 45850	Spain	KX869885	—	—	Crous et al. (2017)
<i>Gyroporus pseudolacteus</i>	AH:55729	Spain	KY576806	—	—	Unpublished
<i>Gyroporus purpurinus</i>	PRL3737	USA	EU718141	EU718105	FJ536674	Wilson et al. (2011; 2012)
<i>Gyroporus purpurinuss</i>	Chpn776	USA	—	KX389110	—	Unpublished
<i>Gyroporus</i> sp.	N.K.Zeng1378 (FHMU929)	Fujian, SE Chin	MW352979	MW380856	MW354535	this study
<i>Gyroporus</i> sp.	M.S. Su45 (FHMU3369)	Jangxi, eastern China	MW352981	MW380858	—	this study
<i>Gyroporus</i> sp.	15A_T2_C2	USA	—	KX899069	—	Unpublished

Species	Voucher	Locality	28S	ITS	TEF1	References
<i>Gyroporus</i> sp.	FLAS-F-61541	USA	–	MH211962	–	Unpublished
<i>Gyroporus</i> sp.	FLAS-F-61653	USA	–	MH212028	–	Unpublished
<i>Gyroporus</i> sp.	E8155	Australia	EF561627	–	GU187704	Unpublished; Binder et al. (2010)
<i>Gyroporus</i> sp.	HKAS 52520	Yunnan, SW China	KF112475	–	KF112309	Wu et al. (2014)
<i>Gyroporus</i> sp.	HKAS 63505	Yunnan, SW China	KF112476	–	KF112310	Wu et al. (2014)
<i>Gyroporus</i> sp.	Arora 00-429	Zimbabwe	EU718143	–	FJ536676	Wilson et al. (2011; 2012)
<i>Gyroporus</i> sp.	REH8799	Thailand	EU718142	–	FJ536675	Wilson et al. (2011; 2012)
<i>Gyroporus subalbellus</i>	OKM25477	North America	EU718144	–	FJ536677	Wilson et al. (2011; 2012)
<i>Gyroporus subglobosus</i>	N.K.Zeng1305 (FHMU859)	Fujian, SE China	MW352974	MW380851	MW354531	this study
<i>Gyroporus subglobosus</i>	M. Mu419 (FHMU3364)	Jilin, NE China	MW352985	–	MW354540	this study
<i>Phlebopus marginatus</i>	REH8883	Western Australia	EU718145	–	FJ536678	Wilson et al. (2011; 2012)
<i>Phlebopus portentosus</i>	REH8795	Thailand	FJ153623	–	FJ536680	Wilson et al. (2011; 2012)

Phylogenetic analyses

The combined nuclear dataset (28S + ITS + *TEF1*) was analyzed with Maximum Likelihood (ML) and Bayesian Inference (BI). Maximum likelihood tree generation and bootstrap analyses were performed with the program RAxML 7.2.6 (Stamatakis 2006) running 1000 replicates combined with an ML search. Bayesian analysis with MrBayes 3.1 (Huelsenbeck and Ronquist 2005) implementing the Markov Chain Monte Carlo (MCMC) technique and parameters predetermined with MrModeltest 2.3 (Nylander 2004) was performed. The model of evolution used in the Bayesian analysis was determined with MrModeltest 2.3 (Nylander 2004). For the combined dataset, the best-fit likelihood models of 28S, ITS and *TEF1* were GTR + I + G, HKY + I + G, SYM + I + G, respectively. Bayesian analysis was repeated for five point seven million generations and sampled every 100 generations; trees sampled from the first 25% of the generations were abandoned as burn-in; the average standard deviation of split frequencies was restricted to be below 0.01, and Bayesian Posterior Probabilities (BPP) were then calculated for a majority consensus tree of the retained Bayesian trees.

Results

The combined *Gyroporus* dataset (28S + ITS + *TEF1*) consisted of 107 taxa and 2566 nucleotide sites, and the alignment was deposited in TreeBASE (S27451). The phylogram with branch lengths generated from BI, including the support values is shown in Fig. 1. The topologies of the phylogenetic trees based on the combined dataset generated from ML and BI analyses were almost identical, but statistical support showed slight differences.

The present molecular data indicate that the Chinese collections of *Gyroporus* were grouped into ten independent lineages (1, 2, 3, 4, 5, 6, 7, 8, 9, and 10) (Fig. 1). Lineage 1, with strong statistical support (BS = 100%, PP = 1.0), included two collections (WXL1187 and WXL1182) of *G. flavocyanescens*, both from southwestern China; in lineage 2, two specimens of *G. alpinus* (LI1478-Strain1 and LI1478-Strain2) both from southwestern China grouped together with high statistical supported (BS = 99, PP = 1); lineage 3, with strong statistical support (BS = 100, PP = 1), included two collections of *G. brunneofloccosus* (GDGM74638 and WU2644) from southern China and southwestern China, respectively; in lineage 4, one collection numbered FHMU929 from southeastern China, and another one numbered FHMU3369 from eastern China grouped together with strong statistical support (BS = 100, PP = 1); in lineage 5, one collection numbered FHMU3368 and one material labeled as *G. castaneus*, both from northeastern China, and one collection also labeled as *G. castaneus* from Germany grouped together with 59% bootstrap support; in lineage 6, one specimen numbered FHMU3366 from southwestern China and four collections numbered FHMU900, FHMU937, FHMU954, FHMU2234, respectively, all from southeastern China, four entries numbered FHMU1582, FHMU1935, FHMU1997, FHMU3367, respectively, all from southern China, and one collection labeled *Gyroporus* sp. (REH8799) from Thailand grouped together with high statistical support (BS = 100, PP = 1); lineage 7, one specimen labeled *Gyroporus* sp. (HKAS52520) from southwestern China; in lineage 8, one collection numbered FHMU3364 from northeastern China, and another one numbered FHMU859 from southeastern China grouped together with strong statistical support (BS = 100, PP = 1); lineage 9 including four collections numbered FHMU888, FHMU905, FHMU917, FHMU926, respectively, from southeastern China, one accession numbered FHMU2273 from southern China, and one specimen identified as *G. castaneus* from Japan was strongly supported (BS = 100, PP = 1); in lineage 10, two samples numbered FHMU2240 and FHMU2243, respectively, from southeastern China, one collection labeled *Gyroporus* sp. (HKAS63505) from southwestern China, one specimen named *G. castaneus* from Thailand and the holotype of *G. paramjitii* K. Das, D. Chakraborty & Vizzini (2017: 671) grouped together with strong statistical supported (BS = 100, PP = 1) (Fig. 1).

Taxonomy

Gyroporus **cf.** *castaneus* (Bull. : Fr.) Quél., Enchir. Fung.: 161, 1886

Figure 2a–c and Fig. 4

Basidiomata medium-sized. **Pileus** 7.9–10 cm diam., convex when young, then applanate; margin uplifted when old; surface dry, subtomentose, yellow (5A5) to yellow-brown (5B6); context 0.9–1.1 cm in thickness in the center of the pileus, white, unchanging in color when injured. **Hymenophore** poroid, depressed around apex of stipe; pores subrounded to angular, 0.3–0.5 mm diam, white (1A1) when young, then brown-yellow (5A6), unchanging in color when bruised; tubes 0.6–0.8 cm in length, white (1A1) to light yellow (1A2), unchanging in color when injured. **Stipe** 11–14 × 2.7–3.4 cm, central, subcylindric, brittle, hollow; surface dry, subtomentose, yellow-brown (4B5) to orange-brown (5B5); context white (1A1), brown (5B6) in age, unchanging in color when injured; annulus absent; basal mycelium white (1A1). **Odor** indistinct.

Basidia 20–30 × 9–14 μm, clavate, thin-walled, 4-spored, colorless in KOH; sterigmata 2–6 μm long. **Basidiospores** [40/2/1] 8–10(–11) × (4–)4.5–6(–7) μm, Q = (1.5–)1.6–2.1(–2.2), Qm = 1.81 ± 0.16, oval to ellipsoid, slightly thick-walled (up to 0.5 μm), yellow-brown in KOH, smooth. **Hymenophoral trama** composed of thin- to slightly thick-walled (up to 0.5 μm) hyphae, 4–16 μm wide, colorless in KOH. **Cheilocystidia** 17–26 × 6–12 μm, subfusiform or fusiform, thin-walled, colorless in KOH, no encrustations. **Pleurocystidia** 15–32 × 7–13 μm, subfusiform or fusiform, thin-walled, colorless in KOH, no encrustations. **Pileipellis** a trichoderm 80–120 μm in thickness, composed of thin- to slightly thick-

walled (up to 1 μm), light yellow in KOH hyphae 5–15 μm in width; terminal cells 30–80 \times 10–13 μm , clavate or subcylindrical, with obtuse apex. **Pileal trama** made up of hyphae 5–17 μm in diam., slightly thick-walled (up to 1 μm), light yellow in KOH. **Stipitipellis** a trichoderm-like structure 60–90 μm in thickness, composed of thin- to slightly thick-walled (up to 1 μm), 5–12 μm wide, light yellow in KOH, emergent hyphae with clavate terminal cells (31–66 \times 6–11 μm). **Stipe trama** composed of cylindrical, light yellow in KOH, slightly thick-walled (0.8–1 μm), interwoven hyphae 4–17 μm diam. **Clamp connections** present in all tissues.

Habitat

Scattered on the ground in forests dominated by fagaceous trees.

Known distribution

Northeastern, southeastern and eastern China.

Specimens examined: CHINA. Jilin Province: Yongan City, Changbaishan National Nature Reserve, elev. 1300 m, 10 August 2019, Y.G. Fan3814 (FHMU3368). Fujian Province: Zhangping City, Xinqiao Town, Chengkou Village, elev. 350 m, 4 August 2013, N.K. Zeng1378 (FHMU929). Jiangxi Province: Nanchang City, Campus of Jiangxi University of Traditional Chinese Medicine, elev. 75 m, 4 June 2014, M.S. Su45 (FHMU3369).

Notes

Two Chinese collections both from northeastern China phylogenetically clustered with one specimen identified as *G. castaneus* from Germany with low statistical support (Fig. 1); however, morphological features of our specimen match with the descriptions of *G. castaneus* (Heinemann and Rammeloo 1979; Moser 1983; Castro and Freire 1995). It is well known that *G. castaneus* was originally described from Europe (Quélet 1886), however, the collections named "*G. castaneus*" from Europe were resolved in more than one lineage of the tree (Fig. 1), the true *G. castaneus* should be redefined in the future. For the time being, the specimens from northeastern China (Fig. 1) are tentatively named *G. cf. castaneus*.

Gyroporus longicystidiatus Nagasawa & Hongo, Rep. Tottori Mycological Inst. 39: 18, 2001

Figure 2d–i and Fig. 5

Basidiomata small to medium-sized. **Pileus** 2.7–9 cm diam., hemispheric, convex when young, then applanate; margin decurved when young, sometimes recurved when old; surface dry, subtomentose, drab, yellow-brown (4B5) to dark yellow-brown (4B8); context 0.3–1.1 cm in thickness in the center of the pileus, white (1A1), unchanging in color when injured. **Hymenophore** poroid, depressed around apex of stipe; pores subrounded to angular, 0.1–1 mm diam, white (1A1) when young, then light yellow (1A4), unchanging in color when bruised; tubes 0.2–0.7 cm in length, white (1A1) to light yellow (1A6), unchanging in color when injured. **Stipe** 3–7 \times 0.6–2 cm, central, subcylindric, base slightly enlarged (2–2.5 cm), brittle, hollow; surface dry, subtomentose, light yellowish brown (5B5), light brown (5C5), brown (5D6); context white (1A1), unchanging in color when injured; annulus absent; basal mycelium grayish white (1B1) to white (1A1). **Odor** indistinct.

Basidia 20–33 \times 10–14 μm , clavate, thin-walled, 4-spored, colorless in KOH; sterigmata 2–6 μm long. **Basidiospores** [220/11/7] (6–)7–9 (–11) \times (3–)3.5–6 (–6.5) μm , $Q = (1.2\text{--})1.3\text{--}2(-2.7)$, $Q_m = 1.56 \pm 0.24$, oval to ellipsoid, slightly thick-walled (up to 0.5 μm), yellowish brown in KOH, smooth. **Hymenophoral trama** composed of thin- to slightly thick-walled (up to 0.5 μm) hyphae, 4–15 μm wide, colorless in KOH. **Cheilocystidia** 23–98 \times 9–21 μm , subfusiform or fusiform, thin-walled, colorless in KOH, no encrustations. **Pleurocystidia** 38–140 \times 12–21 μm , subfusiform or fusiform,

thin-walled, colorless in KOH, no encrustations. **Pileipellis** a trichoderm 70–100 µm in thickness, consisting of thin- to slightly thick-walled (up to 1 µm), light yellow in KOH, hyphae, 6–13 µm in width; terminal cells 41–69 × 9–11 µm, subfusiform, narrowly clavate or subcylindrical, with obtuse apex. **Pileal trama** made up of hyphae 4–18 µm in diameter, slightly thick-walled (0.8–1 µm), light yellow in KOH. **Stipitipellis** a trichoderm-like structure 60–100 µm in thickness, composed of thin- to slightly thick-walled (up to 1 µm), 5–11 µm wide, light yellow in KOH, emergent hyphae with subfusiform, fusiform or clavate terminal cells (25–40 × 7–14 µm). **Stipe trama** composed of cylindrical, light yellow in KOH, slightly thick-walled (0.8–1 µm), interwoven hyphae 3–15 µm wide. **Clamp connections** present in all tissues.

Habitat

Solitary, scattered or gregarious on the ground in forests dominated by fagaceous trees.

Known distribution

Eastern (Chang et al. 2001; Chou et al. 2005), southwestern (Li 2007), southeastern and southern China; Japan (Nagasawa 2001); Thailand (Davoodian et al. 2018).

Specimens examined: CHINA. Hainan Province: Qiongzong County, Yinggeling National Nature Reserve, elev. 650 m, 1 August 2015, N.K. Zeng2456 (FHMU1582); same location, 26 May 2017, N.K. Zeng2974 (FHMU1935). Fujian Province: Zhangping City, Xinqiao Town, Chengkou Village, elev. 350 m, 1 August 2013, N.K. Zeng1348 (FHMU900); same location, 7 August 2013, N.K. Zeng1390 (FHMU937); same location, 13 August 2013, N.K. Zeng1409 (FHMU954); Yongan City, Tianbaoyan National Nature Reserve, elev. 380 m, 17 August 2017, N.K. Zeng3273 (FHMU2234); Yunnan Province: Baoshan City, Baihualing, elev. 1000 m, 8 July 2018, Y.G. Fan2757 (FHMU3366).

Notes: *Gyroporus longicystidiatus*, a species originally described from Japan (Nagasawa 2001) and later reported in China (Chang et al. 2001; Chou et al. 2005; Li 2007; Davoodian et al. 2018), is well characterized by a drab pileus, long and wide cystidia, and elliptical basidiospores with $Q_m = 1.56 \pm 0.24$. Our new collections match well with the protologue of *G. longicystidiatus*, except that the pleurocystidia were described as “absent” by Nagasawa (2001) whereas they are present in our specimens. Moreover, one new collection (FHMU1935) and true *G. longicystidiatus* defined by Davoodian et al. (2018) grouped together with strong statistical support based on *RPB2* sequences (data not shown), which further proved that our specimens are conspecific. Besides Chinese collections, a single accession labeled *Gyroporus sp.* (REH8799) from Thailand should also be identified as *G. longicystidiatus* as inferred from our phylogenetic tree (Fig. 1).

Gyroporus memnonius N.K. Zeng, H.J. Xie & M.S. Su, sp. nov.

Figure 3l–m and Fig. 6

MycoBank: MB838353

Diagnosis

Characterized by a small to medium-sized basidioma, a dark brown pileus, a yellowish brown stipe, elliptical basidiospores with $Q_m = 2.07 \pm 0.23$, and a distribution in subtropical area of Asia.

Etymology

Latin “*memonius*” refers to the new species has a pileus colored with dark brown.

Holotype: CHINA. Fujian Province: Zhangping City, Xinqiao Town, Chengkou Village, elev. 350 m, 4 August 2013, N.K. Zeng1378 (FHMU929).

Basidiomata small to medium-sized. **Pileus** 4.8–6 cm diam., convex when young, then applanate; margin decurved; surface dry, subtomentose, dark brown (5D7); context about 0.8 cm in thickness in the center of the pileus, white (1A1), unchanging in color when injured. **Hymenophore poroid**, depressed around apex of stipe; pores subrounded to angular, about 0.5 mm diam., white (1A1), then yellow (1A4), unchanging in color when bruised; tubes about 0.6 cm in length, white (1A1), unchanging in color when injured. **Stipe** 4–6 × 1–2 cm, central, subcylindric, base slightly enlarged, brittle, hollow; surface dry, subtomentose, brown-yellow (3A6) to yellow-brown (4B6); context white (1A1), unchanging in color when injured; annulus absent; basal mycelium white (1A1). **Odor** indistinct.

Basidia 19–25 × 6 µm, clavate, thin-walled, 4-spored, colorless in KOH; sterigmata 2–5 µm long. **Basidiospores** [40/2/2] 8–10 × 4–5 µm, $Q = (1.78-)1.8-2.5$, $Q_m = 2.07 \pm 0.23$, subfusiform to ellipsoid, slightly thick-walled (up to 0.5 µm), yellowish brown in KOH, smooth. **Hymenophoral trama** composed of thin- to slightly thick-walled (up to 0.5 µm) hyphae, 3–10 µm wide, colorless in KOH. **Cheilocystidia** 15–32 × 4–9 µm, subfusiform or fusiform, thin-walled, colorless in KOH, no encrustations. **Pleurocystidia** 17–40 × 4–10 µm, subfusiform or fusiform, thin-walled, colorless in KOH, no encrustation. **Pileipellis** a trichoderm 60–100 µm in thickness, composed of thin- to slightly thick-walled (up to 1 µm), light yellow in KOH, hyphae 5–13 µm in width; terminal cell 38–105 × 9–15 µm, clavate or subcylindrical, with obtuse apex. **Pileal trama** made up of hyphae 4–15 µm in diameter, slightly thick-walled (1 µm), light yellow in KOH. **Stipitipellis** a trichoderm-like structure 40–85 µm in thickness, composed of thin- to slightly thick-walled (up to 1 µm), 4–12 µm wide, light yellow in KOH, emergent hyphae with subfusiform, fusiform or clavate terminal cells (25–53 × 6–14 µm). **Stipe trama** composed of cylindrical, light yellow in KOH, slightly thick-walled (up to 1 µm), interwoven hyphae 4–15 µm wide. **Clamp connections** present in all tissues.

Habitat

Solitary on the ground in forests dominated by fagaceous trees.

Known distribution

Southeastern China.

Additional specimen examined: CHINA. Jiangxi Province: Nanchang City, Campus of Jiangxi University of Traditional Chinese Medicine, elev. 75 m, M.S. Su45 (FHMU3369).

Notes: *Gyroporus memnonius* looks like *G. ammophilus*, *G. castaneus*, *G. paramjitii* K. Das, D. Chakraborty & Vizzini, *G. punctatus* Lj.N. Vassiljeva and *G. tuberculatosporus*. However, *G. ammophilus* has a large basidioma [pileus up to 15 (–20) cm], surfaces of the pileus and the stipe colored with salmon to brown, tubes and pores salmon to straw-color, becoming brown when young, a context salmon-color to pinkish cream, finally bluish, larger basidiospores measuring 8.5–12 × 4–5.5 (–6.5) µm, and a distribution in coniferous forests of Europe (Castro and Freire 1995); *G. castaneus* has a larger basidioma (up to 10 cm), larger basidiospores measuring 8–12 (–14) × 4.5–6 (–7) µm, and a distribution in Europe (Heinemann and Rammeloo 1979; Moser 1983; Castro and Freire 1995); *G. paramjitii*, a species originally described from India, has a dark brown stipe, and larger basidiospores measuring (7.5–) 8–11.6 (–13) × (4.8–) 5–6.6 (–7) µm (Das et al. 2017); *G. punctatus*, a species originally described from former Soviet Union, has a smaller basidioma, a rugulose-reticulate pileus, a rugulose stipe, and wider basidiospores measuring (7.2–) 7.8–10.4 (–12) × 4.8–6 µm (Vassiljeva 1950; Nagasawa 2001); Chinese *G. tuberculatosporus* has a larger basidioma (pileus up to 10 cm), surfaces of the pileus and the stipe colored with yellowish brown, and larger basidiospores measuring 9–11.3 × 5–8.7 µm (Zang et al. 2006).

Phylogenetically, *G. memnonius* is genetically distant from *G. ammophilus* and *G. paramjitii*; it is closely related to collections named *G. castaneus* from northeastern China, Europe, USA, respectively (Fig. 1). Phylogenetic relationships of *G. memnonius* to *G. punctatus* and *G. tuberculatosporus* are unknown due to a lack of DNA sequences from the latter two.

Gyroporus paramjitii K. Das, D. Chakraborty & Vizzini, *Nordic J. Bot.* 35(6): 671, 2017

Figure 3a–b and Fig. 7

Basidiomata small-sized. **Pileus** 2.5–5 cm diam., convex when young, then applanate; margin decurved; surface dry, densely covered with red-brown (6C7), orange-brown (5B8) to dark red-brown (6C8) squamules; context 0.7–1 cm in thickness in the center of the pileus, white (1A1), unchanging in color when injured. **Hymenophore** poroid, depressed around apex of stipe; pores subrounded to angular, about 0.5 mm diam, white (1A1), then yellow (1A4), unchanging in color when bruised; tubes 0.6–0.8 cm in length, white (1A1), then yellowish (2A6), unchanging in color when injured. **Stipe** 3–4 × 0.4–1 cm, central, subcylindric, base slightly enlarged, brittle, hollow; surface dry, tomentose, red-brown (5B8) to dark red-brown (6D8); context white (1A1), unchanging in color when injured; annulus absent; basal mycelium white (1A1). **Odor** indistinct.

Basidia 11–16 × 6 μm, clavate, thin-walled, 4-spored, colorless in KOH; sterigmata 2–6 μm long. **Basidiospores** [140/7/2] 7–9 × (4–)5–6 μm, Q = (1.2–)1.4–1.8(–2), Qm = 1.59 ± 0.13, oval to ellipsoid, slightly thick-walled (up to 0.5 μm), yellowish brown in KOH, smooth. **Hymenophoral trama** composed of thin- to slightly thick-walled (up to 0.8 μm) hyphae, 4–16 μm wide, colorless in KOH. **Cheilocystidia** 20–41 × 5–15 μm, subfusiform or fusiform, thin-walled, colorless in KOH, no encrustations. **Pleurocystidia** 20–43 × 7–15 μm, subfusiform or fusiform, thin-walled, colorless in KOH, no encrustations. **Pileipellis** a trichoderm 80–120 μm in thickness, composed of thin- to slightly thick-walled (up to 1 μm), colorless in KOH, hyphae 4–16(–20) μm in width; terminal cells 20–65 × 11–20 μm, subfusiform, clavate or subcylindrical, with obtuse apex. **Pileal trama** made up of hyphae 4–18 μm in diameter, slightly thick-walled (0.8–1 μm), colorless in KOH. **Stipitipellis** a trichoderm-like structure 60–90 μm in thickness, composed of thin- to slightly thick-walled (up to 1 μm), 5–13(–18) μm wide, light yellow in KOH, emergent hyphae with subfusiform, fusiform or clavate terminal cells (35–65 × 7–22 μm). **Stipe trama** composed of cylindrical, light yellow in KOH, thin- to slightly thick-walled (up to 1 μm), interwoven hyphae, 5–19 μm wide. **Clamp connections** present in all tissues.

Habitat

Gregarious on the ground in forests dominated by fagaceous trees.

Known distribution

Southeastern and southwestern China (Yang et al. 2021); India (Das et al. 2017).

Specimens examined: CHINA. Fujian Province: Yongan City, Tianbaoyan National Nature Reserve, elev. 380 m, 17 August 2017, N.K. Zeng3279, 3282 (FHMU2240, 2243).

Notes: Our molecular phylogenetic analyses indicate that Chinese collections and the holotype of *G. paramjitii*, a species originally described from India (Das et al. 2017), grouped together with strong statistical support (Fig. 1), which indicates that our new specimens should be recognized as *G. paramjitii*. Morphologically, our new collections match well with the protologue of *G. paramjitii* (Das et al. 2017), except that the size of cheilocystidia is slightly different, those from Indian collections being 27–45 × 5–7 μm (Das et al. 2017), whereas cheilocystidia from Chinese specimens are 20–35 × 7–13 μm. The diagnostic morphological features of *G. paramjitii* are summarized as follows: a small basidioma, a pileus covered with red-brown to dark red-brown squamules, oval to ellipsoid basidiospores with Qm = 1.59 ± 0.13, relatively

short hymenial cystidia, and the hyphae in the pileipellis usually with cystidioid terminal cells. Besides the aforementioned collections, two vouchers labeled *G. castanaeus* (RWH8804) from Thailand and *G. sp.* (HKAS63505) from southwestern China, respectively, should also be identified as *G. paramjitii* as inferred from our phylogenetic tree (Fig. 1).

Gyroporus porphyreus N.K. Zeng, H.J. Xie & Zhi Q. Liang, sp. nov.

Figure 3c–h and Fig. 8

MycoBank: MB838354

Diagnosis

Characterized by a small to medium-sized basidioma, a pileus colored with yellow-brown, brown to red-brown when young, then purple, a brown, pale red-brown to red-brown stipe, oval to ellipsoid basidiospores with $Q_m = 1.67 \pm 0.34$, relatively short hymenial cystidia, and a distribution in subtropical region of China.

Etymology

Latin “*porphyreus*” refers to the pileus of the new species colored with purple when old.

Holotype: CHINA. Fujian Province: Zhangping City, Xinqiao Town, Chengkou Village, elev. 350 m, 3 August 2013, N.K. Zeng1366 (FHMU917).

Basidiomata small to medium-sized. **Pileus** 3–7 cm diam., convex when young, then applanate; margin recurved; surface dry, tomentose, yellow-brown (4A5), brown (5A6-5B8) to red-brown (7C4) when young, then purple (7C4); context 0.5–0.7 cm in thickness in the center of the pileus, white (1A1), unchanging in color when injured. **Hymenophore** poroid, nearly adnate to slightly depressed around apex of stipe; pores subrounded to angular, 0.3–0.5 mm diam, white when young, then yellow to yellow-brown (1A1-5A6), unchanging in color when bruised; tubes 0.3–0.5 cm in length, yellowish (2A5), unchanging in color when injured. **Stipe** 3–5.5 × 0.7–1.8 cm, central, subcylindric, base slightly enlarged, brittle, hollow; surface dry, tomentose, brown (6D6), pale red-brown (7C5) to red-brown (8E6); context white (1A1), unchanging in color when injured; annulus absent; basal mycelium white (1A1). **Odor** indistinct.

Basidia 21–30 × 11–13.5 μm, clavate, thin-walled, 4-spored, colorless in KOH; sterigmata 2–8 μm long. **Basidiospores** [240/12/5] (6.5–)7–10.5(–11) × (3.5–)4–5.5 (–6) μm, $Q = (1.27–)1.4–2.56(–2.67)$, $Q_m = 1.67 \pm 0.34$, oval to ellipsoid, slightly thick-walled (up to 0.5 μm), yellowish brown in KOH, smooth. **Hymenophoral trama** composed of thin- to slightly thick-walled (up to 0.5 μm) hyphae, 4–10 μm wide, colorless in KOH. **Cheilocystidia** 19–22 × 7–11 μm, subfusiform or fusiform, thin-walled, colorless in KOH, no encrustations. **Pleurocystidia** 21–42 × 9–14.5 μm, subfusiform or fusiform, thin-walled, colorless in KOH, no encrustations. **Pileipellis** a trichoderm about 130 μm in thickness, composed of thin- to slightly thick-walled (up to 1 μm), light yellow in KOH, hyphae 6–12 μm in width; terminal cells (31–)60–95 × 7–13 μm, subfusiform or subcylindrical, with obtuse apex. **Pileal trama** made up of hyphae 4–18 μm in diameter, slightly thick-walled (up to 1 μm), light yellow in KOH. **Stipitipellis** a trichoderm-like structure about 100 μm in thickness, composed of thin- to slightly thick-walled (up to 1 μm), 5–12 μm wide, light yellow in KOH, emergent hyphae with subfusiform, fusiform or clavate terminal cells (26–100 × 9–11 μm). **Stipe trama** composed of cylindrical, light yellow in KOH, slightly thick-walled (0.8–1 μm), interwoven hyphae, 5–17 μm wide. **Clamp connections** present in all tissues.

Habitat

Solitary or scattered on the ground in forests dominated by fagaceous trees.

Known distribution

Southeastern China.

Additional specimens examined: CHINA. Fujian Province: Zhangping City, Xinqiao Town, Chengkou Village, elev. 350 m, 30 July 2013, N.K. Zeng1336 (FHMU888); same location, 1 August 2013, N.K. Zeng1353 (FHMU905); same location, 3 August 2013, N.K. Zeng1375 (FHMU926); same location, 22 August 2017, N.K. Zeng3312 (FHMU3131).

Notes

The pileus of *G. atroviolaceus* and *G. purpurinus* is also tinged with purple, however, *G. atroviolaceus*, a species firstly described from Indonesia, has a pileus colored with black besides purple, wider basidiospores measuring $8.5\text{--}10 \times 6\text{--}6.5 \mu\text{m}$, and longer cystidia (Corner 1972; Horak 2011); *G. purpurinus* has larger basidiospores measuring $8\text{--}11\text{--}(12) \times (4\text{--})4.8\text{--}7 \mu\text{m}$, narrower cystidia measuring $23\text{--}50 \times 3.3\text{--}8 \mu\text{m}$, and a distribution in the eastern United States and adjacent Mexico and Canada (Davoodian and Halling 2013). Besides, *G. porphyreus* also resembles *G. borealis* Davoodian, O. Asher, Sturgeon, Ammirati & Delaney and *G. smithii* Davoodian. Nevertheless, *G. borealis* has slightly longer basidiospores measuring $(8.0\text{--})8.8\text{--}11\text{--}(12) \times 4.8\text{--}5.6\text{--}(6.4) \mu\text{m}$, narrower cheilocystidia measuring $31.2\text{--}36.8 \times 6.4\text{--}8 \mu\text{m}$ without observing pleurocystidia and was recorded under planted landscape trees in Washington, USA; *G. smithii* has narrower cystidia measuring $24\text{--}36 \times 4\text{--}8 \mu\text{m}$, thicker pileipellis hyphae $6\text{--}20 \mu\text{m}$ broad and distributing in USA (Davoodian et al. 2020). Phylogenetically, *G. porphyreus* is distant from *G. purpurinus*. Phylogenetic relationships of *G. porphyreus* with *G. atroviolaceus* is unknown due to a lack of DNA sequences from the latter. Moreover, we also noted that *G. porphyreus* is phylogenetically related to the European *G. ammophilus* (Fig. 1). However, *G. ammophilus* has a large basidioma [up to $15\text{--}(20)$ cm], surfaces of the pileus and the stipe colored with salmon to brown, tubes and pores salmon to straw-color, becoming brown with age, a context salmon-color to pinkish cream and finally bluish, longer basidiospores measuring $8.5\text{--}12 \times 4\text{--}5.5\text{--}(6.5) \mu\text{m}$, and a distribution in coniferous forests (Castro and Freire 1995). In addition, our molecular data also indicate that one collection labeled *G. castaneus* from Japan and specimens of *G. porphyreus* grouped together with strong statistical support (Fig. 1), indicating that the Japanese material should be identified as *G. porphyreus*.

Gyroporus subglobosus N.K. Zeng, H.J. Xie, L.P. Tang & M. Mu sp. nov.

Figure 3i–j and Fig. 9

MycoBank: MB838355

Diagnosis

Characterized by a small basidioma with a yellowish brown, red-brown to dark brown pileus, a brown to red-brown stipe, subglobose to ellipsoid basidiospores with $Q_m = 1.38 \pm 0.17$, and relatively short hymenial cystidia.

Etymology

Latin “*subglobosus*” refers to the subglobose basidiospores of the new species.

Holotype: CHINA. Jilin Province: Tonghua City, Yuhuangshan Park, elev. 400 m, 26 August 2019, M. Mu419 (FHMU3364).

Basidiomata small-sized. **Pileus** 2.5–3 cm diam., convex when young, then applanate; margin uplifted when old; surface dry, subtomentose, sometimes slightly rimose in age, yellow-brown (4B7), red-brown (7D6) to dark brown (5C7); context about 0.2 cm in thickness in the center of the pileus, white (1A1), unchanging in color when injured. **Hymenophore** poroid, depressed around apex of stipe; pores subrounded to angular, 0.5–1 mm diam, white when young, then yellow

(1A2), unchanging in color when bruised; tubes 0.5–0.8 cm in length, yellowish (1A4), unchanging in color when injured. **Stipe** 5–8 × 0.8–1 cm, central, subcylindrical, base slightly enlarged, brittle, hollow; surface dry, subtomentose, brown (6C6) to red-brown (7C6); context white (1A1), unchanging in color when injured; annulus absent; basal mycelium white (1A1). **Odor** indistinct.

Basidia 20–29 × 11–15 µm, clavate, thin-walled, 4-spored, colorless in KOH; sterigmata 2–6 µm long. **Basidiospores** [40/2/2] 6.5–9.5(–10) × 5–7 µm, Q = 1.1–1.5(–1.9), Qm = 1.38 ± 0.17, subglobose to ellipsoid, slightly thick-walled (up to 0.5 µm), light yellow in KOH, smooth. **Hymenophoral trama** composed of thin- to slightly thick-walled (up to 0.5 µm) hyphae, 4–15 µm wide, colorless in KOH. **Cheilocystidia** 18–21 × 5–7.5 µm, subfusiform or fusiform, thin-walled, colorless in KOH, no encrustations. **Pleurocystidia** 17–35 × 7.5–10 µm, clavate, subfusiform to fusiform, thin-walled, colorless in KOH, no encrustations. **Pileipellis** a trichoderm 90–160 µm in thickness, composed of thin- to slightly thick-walled (up to 1 µm), light yellow in KOH, hyphae 4–14 µm in width; terminal cells 29–72 × 6–11.5 µm, clavate, subfusiform or fusiform, with obtuse apex. **Pileal trama** made up of hyphae 4–15 µm in diameter, thin- to slightly thick-walled (up to 1 µm), light yellow in KOH. **Stipitipellis** a trichoderm-like structure 50–100 µm in thickness, composed of thin- to slightly thick-walled (up to 1 µm), 5–10 µm wide, light yellow in KOH, emergent hyphae with clavate, broadly clavate or subfusiform terminal cells (20–55 × 7–12 µm). **Stipe trama** composed of cylindrical, light yellow in KOH, thin- to slightly thick-walled (up to 1 µm), interwoven hyphae, 5–18 µm wide. **Clamp connections** present in all tissues.

Habitat

Scattered on the ground in forests dominated by *Pinus koraiensis* Siebold et Zuccarini, *Quercus mongolica* Fischer ex Ledebour, or *Castanopsis kawakamii* Hayata.

Known distribution

Northeastern and southeastern China.

Additional specimen examined: CHINA. Fujian Province: Zhangping City, Xinqiao Town, Chengkou Village, elev. 350 m, 28 July 2013, N.K. Zeng1305 (FHMU859)

Notes

Morphologically, *G. subglobosus* looks like *G. austrobrasiliensis* A.C. Magnago & R.M. Silveira, *G. castanaeus*, *G. malesicus*, *G. mcnabbii* Davoodian, Bougher & Halling, *G. paramjitii* and *G. madagascariensis* Buyck, O. Asher & Davoodian. However, *G. austrobrasiliensis* has surfaces of pileus and stipe tinged with orange, smaller basidiospores measuring (6–) 7–8 × 5–6 µm, pileipellis hyphae usually with subclavate terminal cells, and a distribution in Brazil (Magnago et al. 2018); *G. castanaeus* has a larger basidioma (more than 10 cm), longer basidiospores measuring 8–12 (–14) × 4.5–6 (–7) µm, and a distribution in Europe (Heinemann and Rammeloo 1979; Moser 1983; Castro and Freire 1995); Malaysian *G. malesicus* has a very small basidioma, narrower basidiospores measuring 9–10 × 5–5.5 µm, and absence of clamp connections (Corner 1972; Horak 2011); *G. mcnabbii* has a larger basidioma (pileus up to 9 cm), longer basidiospores measuring (7.6–)8.4–10.7(–11.9) × (4.9–)5.5–6.7(–7) µm, and a distribution in Australia (Davoodian et al. 2018); *G. paramjitii* has a dark brown stipe, longer basidiospores measuring (7.5–) 8–11.6 (–13) × (4.8–) 5–6.6 (–7) µm, and longer cheilocystidia (Das et al. 2017); *G. madagascariensis* has shorter and narrower basidiospores measuring 6.7–8.4(–9.1) × 4.1–5.2 µm, tubes that some areas discoloring to orange but lacking for cheilocystidia and pleurocystidia (Davoodian et al. 2020). Phylogenetically, *G. subglobosus* is distant from *G. austrobrasiliensis*, *G. castanaeus* and *G. paramjitii*. Phylogenetic relationships of *G. subglobosus* to *G. malesicus* and *G. mcnabbii* are unknown due to a lack of DNA sequences from the latter two.

Key to Gyroporus species known from China

1. Context changing blue when injured.....2
1. Context unchanging in color when injured.....5
2. Pileus dark brown, brown to light red-brown, without any yellow or orange tinge.....*G. brunneofloccosus*
2. Pileus ivory yellow, greyish-yellow or flavous, grey-yellow, yellowish-brown, grey-orange to brownish-yellow.....3
3. Basidioma distributed in alpine mixed forests dominated by *Abies* sp., *Picea* sp. and *Quercus semicarpifolia*; pileus small to medium-sized 3–6 cm wide.....*G. alpinus*
3. Basidioma distributed in tropical forests dominated by *Lithocarpus* spp., *Castanea* spp. and *Quercus* spp.; pileus large 6–10 cm wide.....4
4. Pileus initially flavous to dull yellow or grey-yellow and then grey-orange to greyish-orange.....*G. flavocyanescens*
4. Pileus yellowish brown.....*G. tuberculatosporus*
5. Cystidia long (up to 100 µm).....*G. longicystidiatus*
5. Cystidia relatively short (up to 45 µm).....6
6. Basidiospores subglobose to ellipsoid ($Q_m < 1.5$).....*G. subglobosus*
6. Basidiospores oval to ellipsoid ($Q_m > 1.5$)7
7. Pileus colored yellow-brown, brown to red-brown when young, then purple.....*G. porphyreus*
7. Pileus colored with yellow, yellow-brown, orange-brown, red-brown, dark brown to dark red-brown, without purple tinge.....8
8. Pileus densely covered with red-brown, orange-brown to dark red-brown squamules, and hyphae in the pileipellis usually with cystidioid terminal cells.....*G. paramjitii*

8. Pileus tomentose to subtomentose, yellow, yellow-brown to dark brown, and hyphae in the pileipellis usually without cystidioid terminal cells.....9

9. Pileus smaller (up to 6 cm), basidiospores narrower measuring 4–5 μm , and a distribution in subtropical area.....*G. memnonius*

9. Pileus larger (up to 10 cm), basidiospores wider measuring (4–)4.5–6(–7) μm , and a distribution in a temperate area.....*G. cf. castaneus*

Discussion

Gyroporus castaneus complex

Species of *Gyroporus* are easily recognized at genus level. However, taxa of the genus are difficult to distinguish due to the shortage of molecular phylogenetic studies and apparent morphological convergence in previous studies (Corner 1972; Singer et al. 1983; Castro and Freire 1995; Bougher and Syme 1998). With the rapid development of molecular phylogenetic analyses, many previously described taxa have been re-evaluated, providing a better understanding of the diversity of *Gyroporus* worldwide (Vizzini et al. 2015; Das et al. 2017; Davoodian et al. 2018; Magnago et al. 2018; Huang et al. 2021). For example, *G. castaneus*, originally described from Europe, was believed to be a widely distributed species in the world. Conversely, recent studies indicated that *G. castaneus* represents a species complex rather than a single widespread species. Our molecular data also show that collections named *G. castaneus* resolved in several different parts of the tree (Fig. 1). Interestingly, specimens of *G. castaneus* from Europe resolved in more than one part of the tree (Fig. 1). The true *G. castaneus* may just be restricted to a wide area comprising Europe, temperate and subtropical regions of Asia (Fig. 2), a hypothesis that should be confirmed with more collections and DNA sequences from the holotype locality of the species. In China, *G. castaneus* s. l. likely occurs in temperate and subtropical regions of China, collections identified as *G. castaneus* from tropical areas of the country are certainly to be referred to other species (Davoodian and Halling 2013). As for *G. cyanescens*, it also resolved in several different parts of the tree (Fig. 1), which indicated *G. cyanescens* also represents a species complex rather than a single widespread species.

Species diversity of *Gyroporus* from China

In the present study, unexpected abundant species diversity was revealed in China, and ten lineages of *Gyroporus* were uncovered (Fig. 1). Three (lineages 4, 8 and 9) are described as new: *Gyroporus memnonius*, *G. subglobosus* and *G. porphyreus*; five (lineages 1, 2, 3, 6 and 10) are previously described taxa: *Gyroporus flavocyanescens*, *Gyroporus alpinus*, *Gyroporus brunneofloccosus*, *G. longicystidiatus* and *G. paramjitii*; one (lineage 5) is tentatively named *G. cf. castaneus*; and one (lineage 7) is not described due to the paucity of material. Besides the aforementioned species, there are two additional taxa described from China, viz. *G. pseudomicrosporus* and *G. tuberculatosporus*. It is worth noting that *G. pseudomicrosporus* is not a true *Gyroporus* (Dr. N. Davoodian, private communications). At the same time, we also noted that basidiospores of *G. tuberculatosporus* were described as “tuberculatae” (Zang et al. 1996), but they are smooth according to our re-examinations of the holotype, moreover, the species is a member of *G. cyanescens* complex (Dr. N. Davoodian, private communications). In the future, more collections from a wide area (including the type locality), and more DNA sequences are expected for elucidating their true taxonomic relationships to other *Gyroporus* species. In previous studies, *G. atroviolaceus*, *G. cyanescens*, *G. malesicus* and *G. purpurinus* were also reported in China (Zang 1986; Zang et al. 1996; Li and Song 2003), yet their occurrence in the country remains to be confirmed.

Phylogenetic relationships and geographic divergence of *Gyroporus*

Recent phylogenetic studies have uncovered useful information concerning

the phylogeny and geography of *Gyroporus* (Davoodian et al. 2018). Our molecular data based on three-locus DNA sequences with a number of additional collections

from East Asia provide new insights. It is evident there are common or allied species shared between East Asia and Europe/North America as inferred from our data set (Fig. 1). For example, collections tentatively named *G. cf. castaneus* as occurring in temperate areas of East Asia and Europe was uncovered. Similar scenarios have been documented for many other fungi (Tang et al. 2013; Cui et al. 2016; Huang et al. 2020). The affinities of *Gyroporus* species between East Asia and Southeast/South Asia are evident (Fig. 1), both regions share two common taxa, i.e., *G. longicystidiatus* (East Asia-Southeast Asia) and *G. paramjitii* (East Asia-South Asia). In addition, *G. longicystidiatus* and *G. porphyreus* both occur in China and Japan.

Declarations

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Authors' contributions Conceptualization: Zhi-Qun Liang and Nian-Kai Zeng; Methodology: Hui-Jing Xie; Performing the experiment: Hui-Jing Xie; Formal analysis: Hui-Jing Xie and Zhi-Qun Liang; Resources: Nian-Kai Zeng, Li-Ping Tang, Man Mu, Yu-Guang Fan and Shuai Jiang; Writing—original draft preparation: Hui-Jing Xie; Writing—review and editing: Zhi-Qun Liang and Nian-Kai Zeng; Supervision: Nian-Kai Zeng; Project administration: Nian-Kai Zeng; Funding acquisition: Nian-Kai Zeng and Hui-Jing Xie. All authors have read and agreed to the published version of the manuscript.

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Data availability The sequence data generated in this study are deposited in NCBI GenBank.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Figures

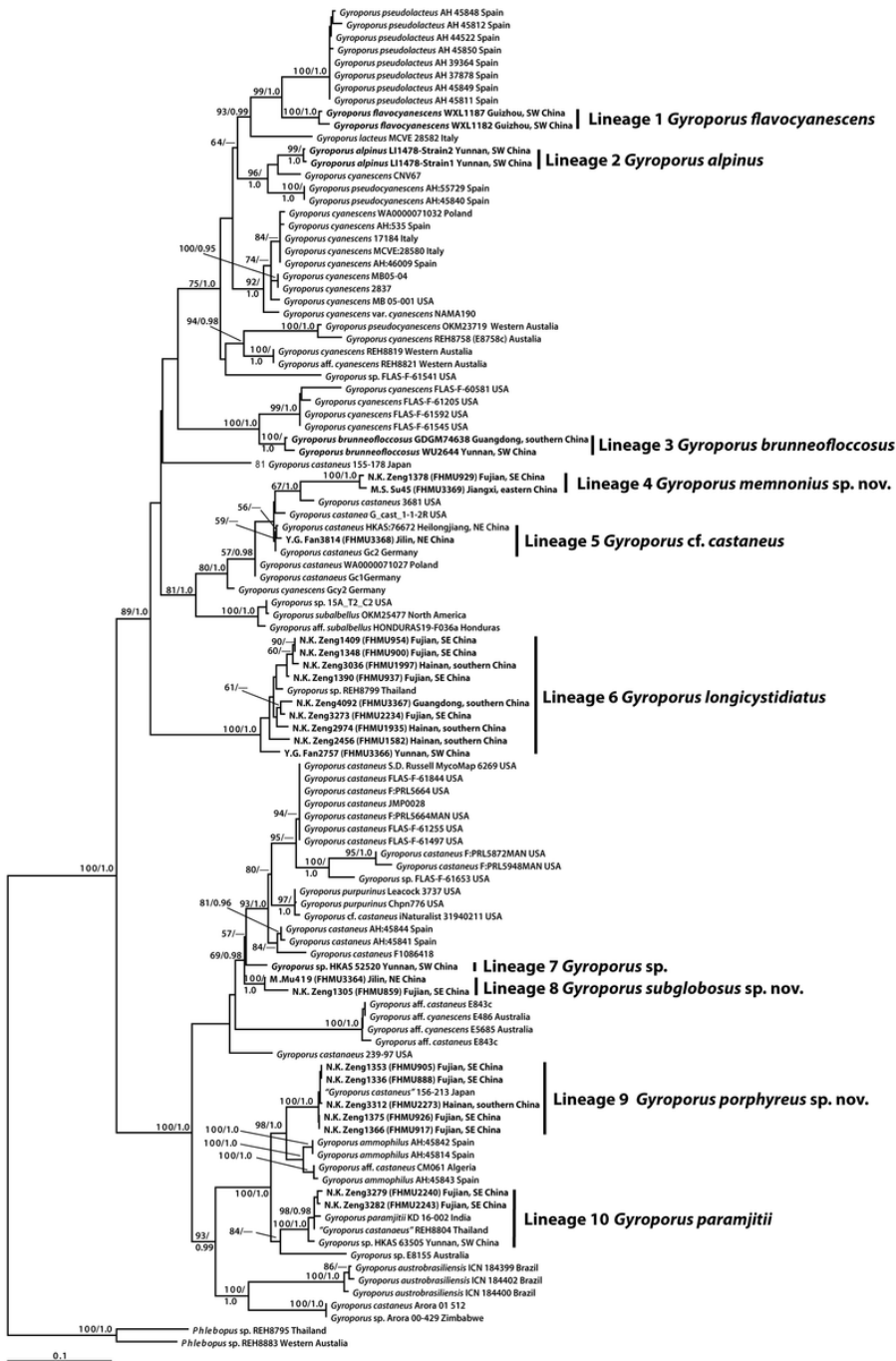


Figure 1

Phylogram inferred from a combined (rDNA 28S, ITS and TEF1) dataset using BS/PP. BS $\geq 70\%$ and PP ≥ 0.95 are indicated above or below the branches as RAxML BS/PP. SE = southeast; SW = southwest; NE = northeast.



Figure 2

Basidiomata of *Gyroporus* species. a–c *G. cf. castaneus* (a–c from FHMU3368). d–i *G. longicystidiatus* (d from FHMU900; e from FHMU954; f from FHMU1997; g from FHMU937; h, i from FHMU1935); *G. memnonius* (FHMU929, holotype). Photos: a–c, Y.G. Fan; d–m, N.K. Zeng.



Figure 3

Basidiomata of *Gyroporus* species. a–b *G. paramjitii* (a from FHMU2240; b from FHMU2243). c–h *G. porphyreus* (c from FHMU1336; d from FHMU905; e from FHMU2273; f–h from FHMU917, holotype). i–j *G. subglobosus* (FHMU3364, holotype). Photos: a–h, N.K. Zeng; i–j, M. Mu.

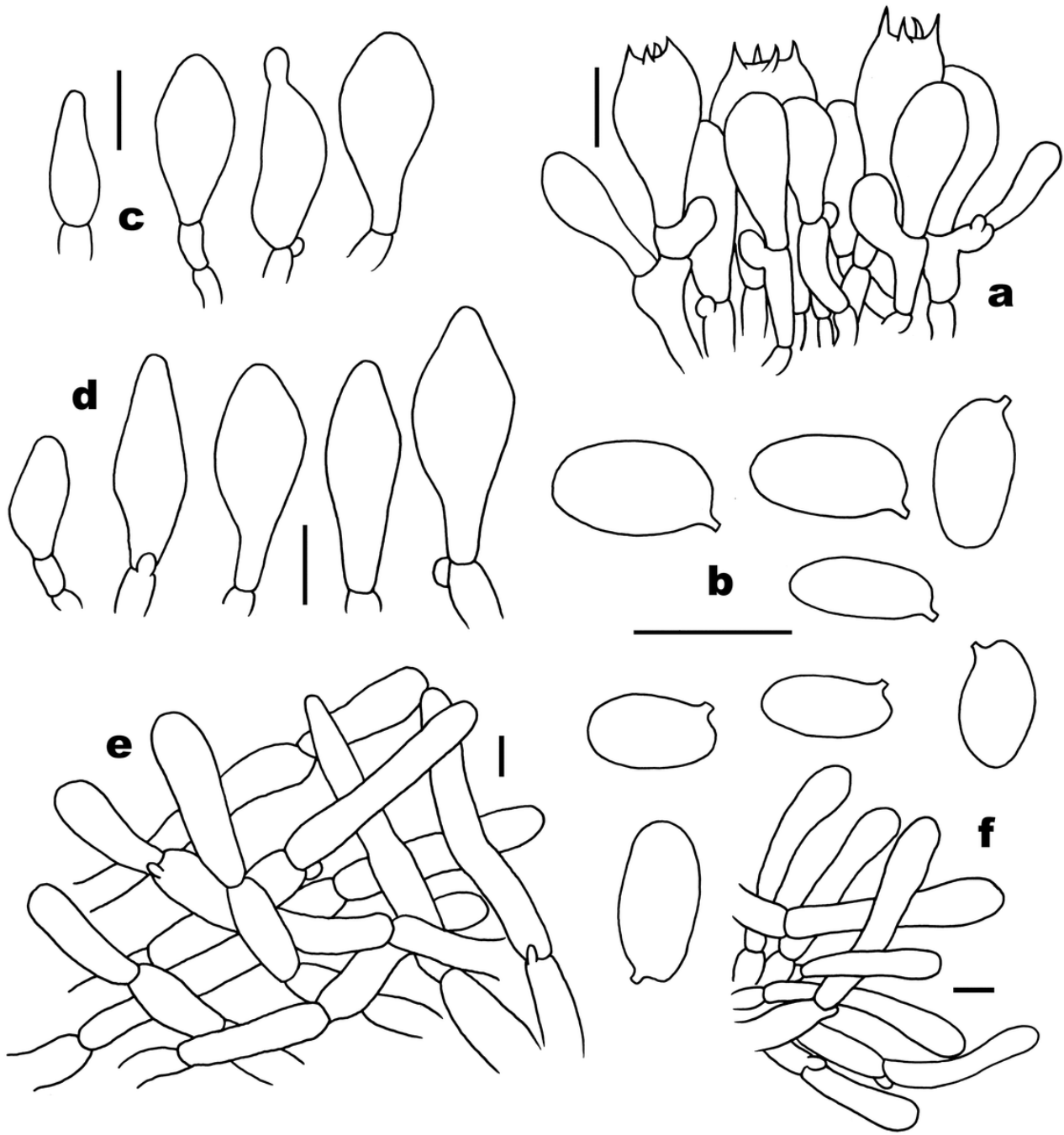


Figure 4

Microscopic features of *Gyroporus* cf. *castaneus* (FHMU3368). a Basidia. b Basidiospores. c Cheilocystidia. d Pleurocystidia. e Pileipellis. f Stipitipellis. Bars = 10 μ m. Drawings by H.J. Xie.

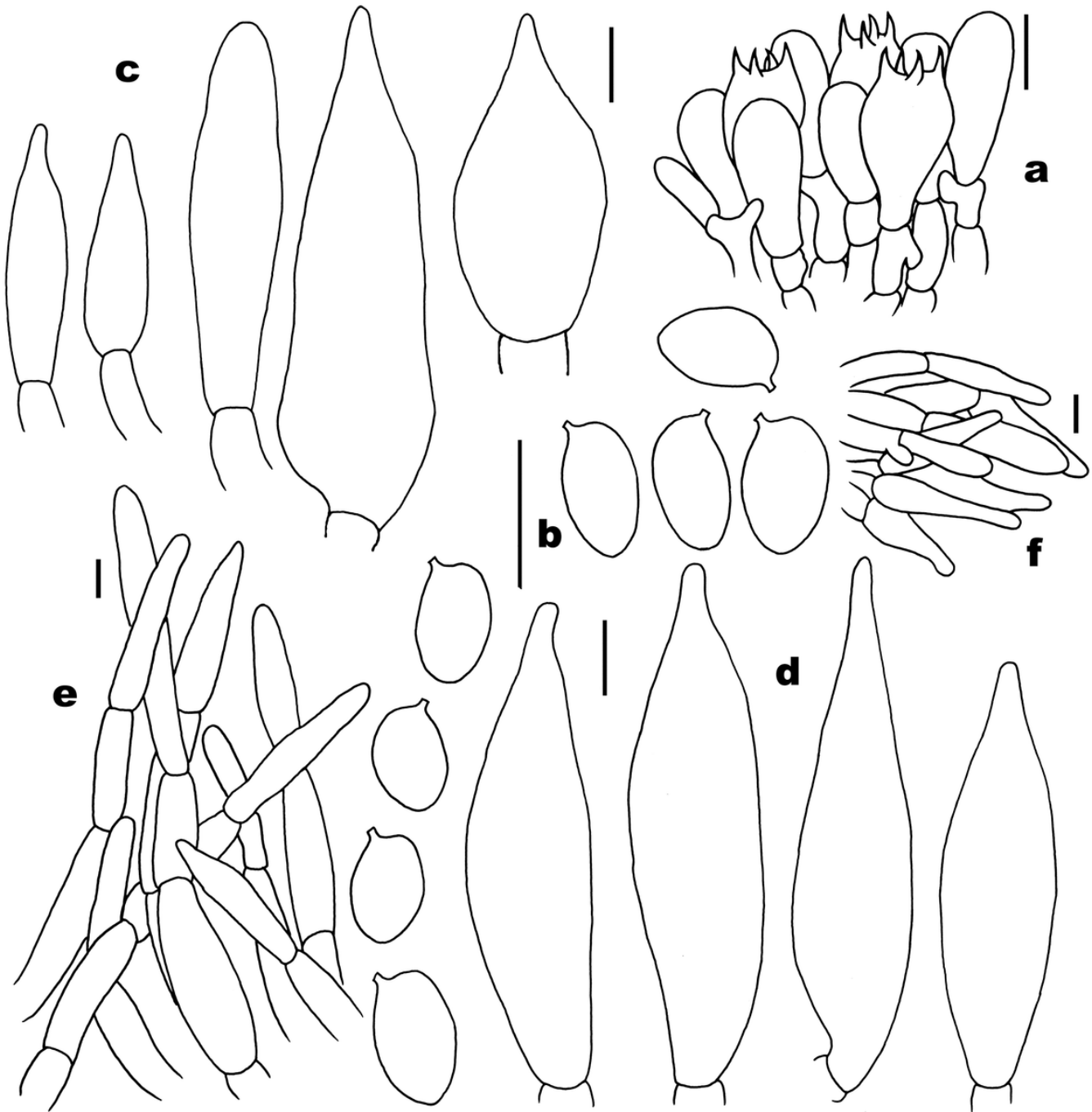


Figure 5

Microscopic features of *Gyroporus longicystidiatus* (FHMU1935). a Basidia. b Basidiospores. c Cheilocystidia. d Pleurocystidia. e Pileipellis. f Stipitipellis. Bars = 10 μ m. Drawings by H.J. Xie.

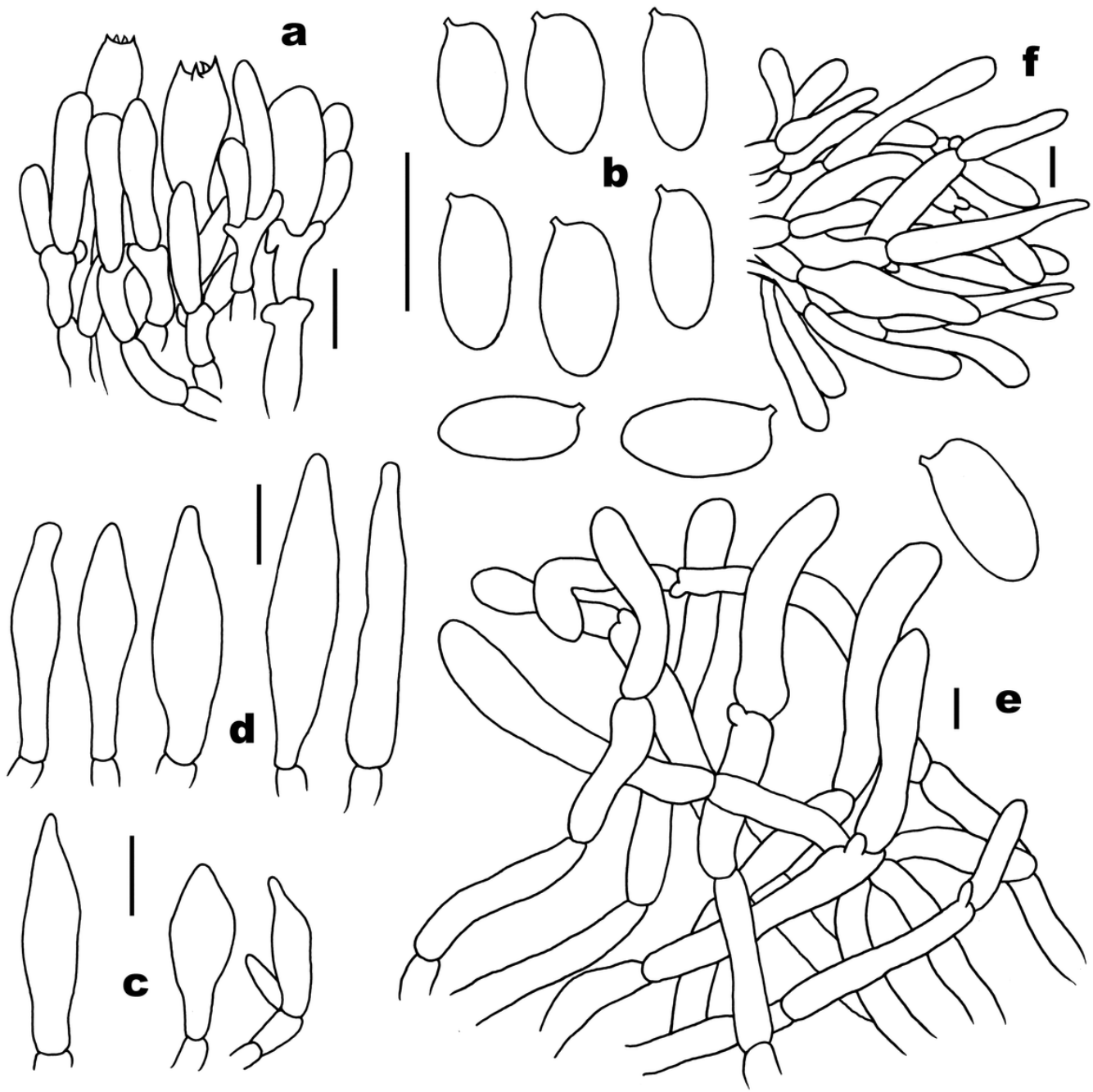


Figure 6

Microscopic features of *Gyroporus memnonius* (FHMU929, holotype). a Basidia. b Basidiospores. c Cheilocystidia. d Pleurocystidia. e Pileipellis. f Stipitipellis. Bars = 10 μm . Drawings by H.J. Xie.

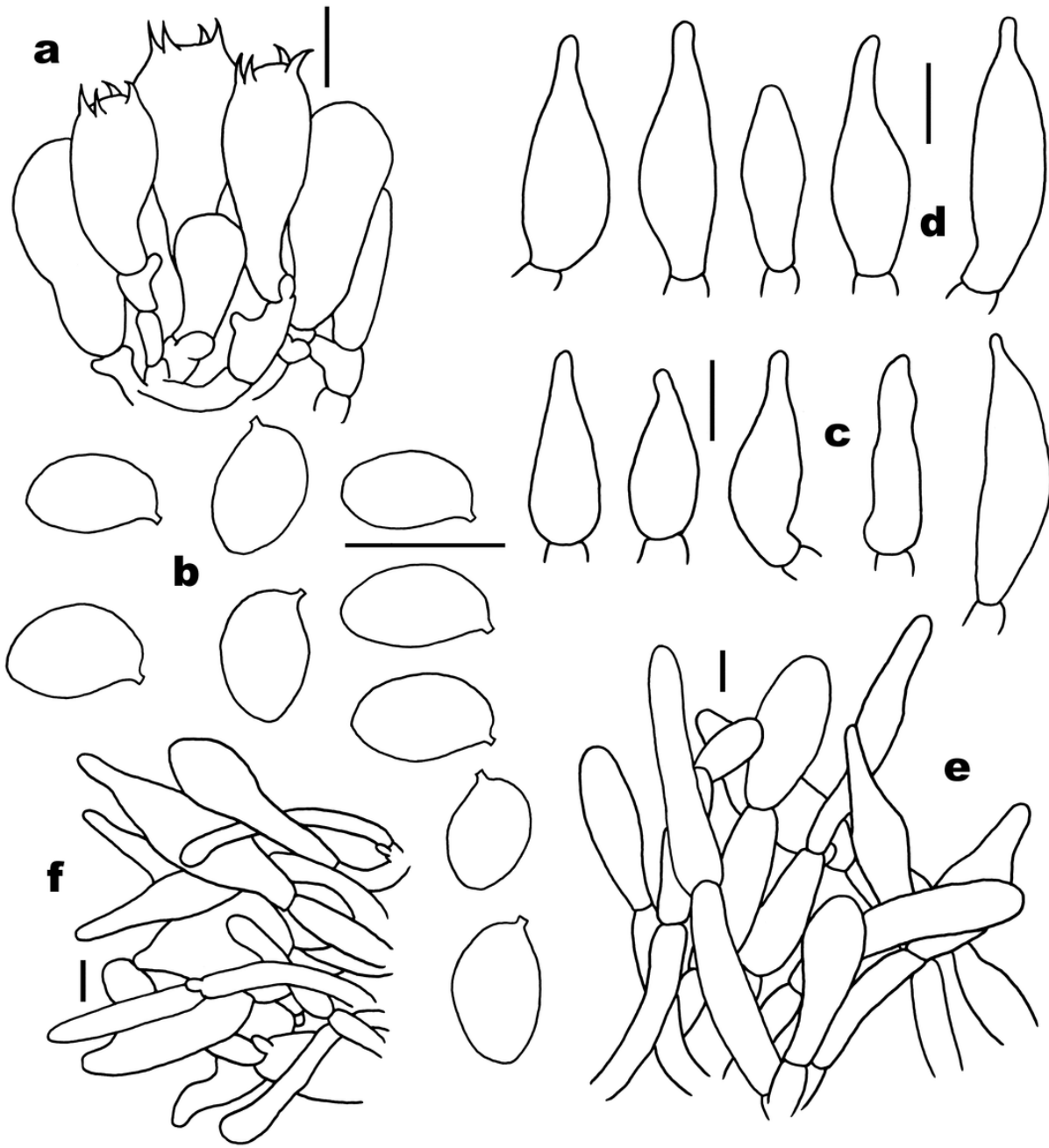


Figure 7

Microscopic features of *Gyroporus paramjitii* (FHMU2240). a Basidia. b Basidiospores. c Cheilocystidia. d Pleurocystidia. e Pileipellis. f Stipitipellis. Bars = 10 μ m. Drawings by H.J. Xie.

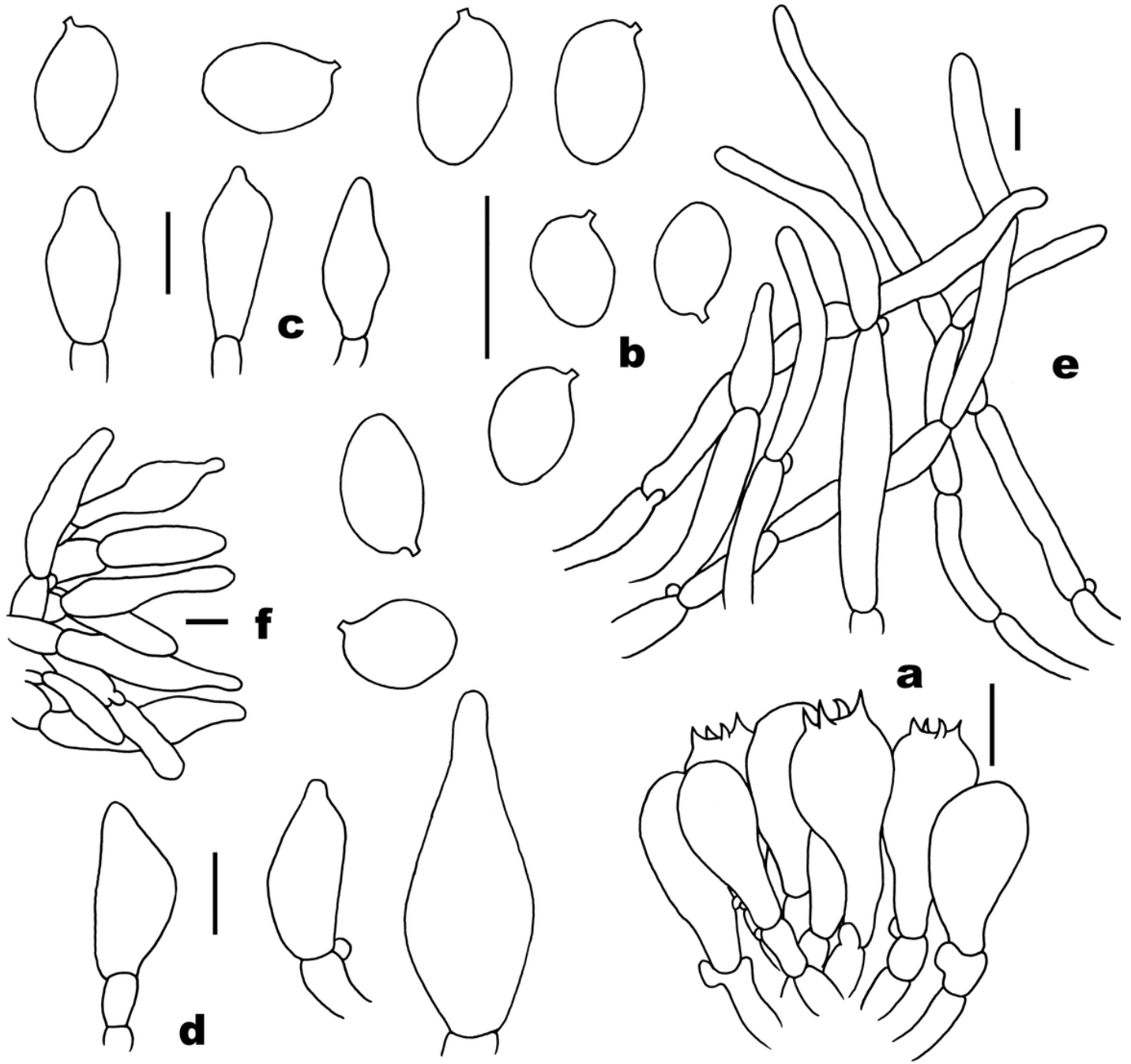


Figure 8

Microscopic features of *Gyroporus porphyreus* (FHMU917, holotype). a Basidia. b Basidiospores. c Cheilocystidia. d Pleurocystidia. e Pileipellis. f Stipitipellis. Bars = 10 μ m. Drawings by H.J. Xie.

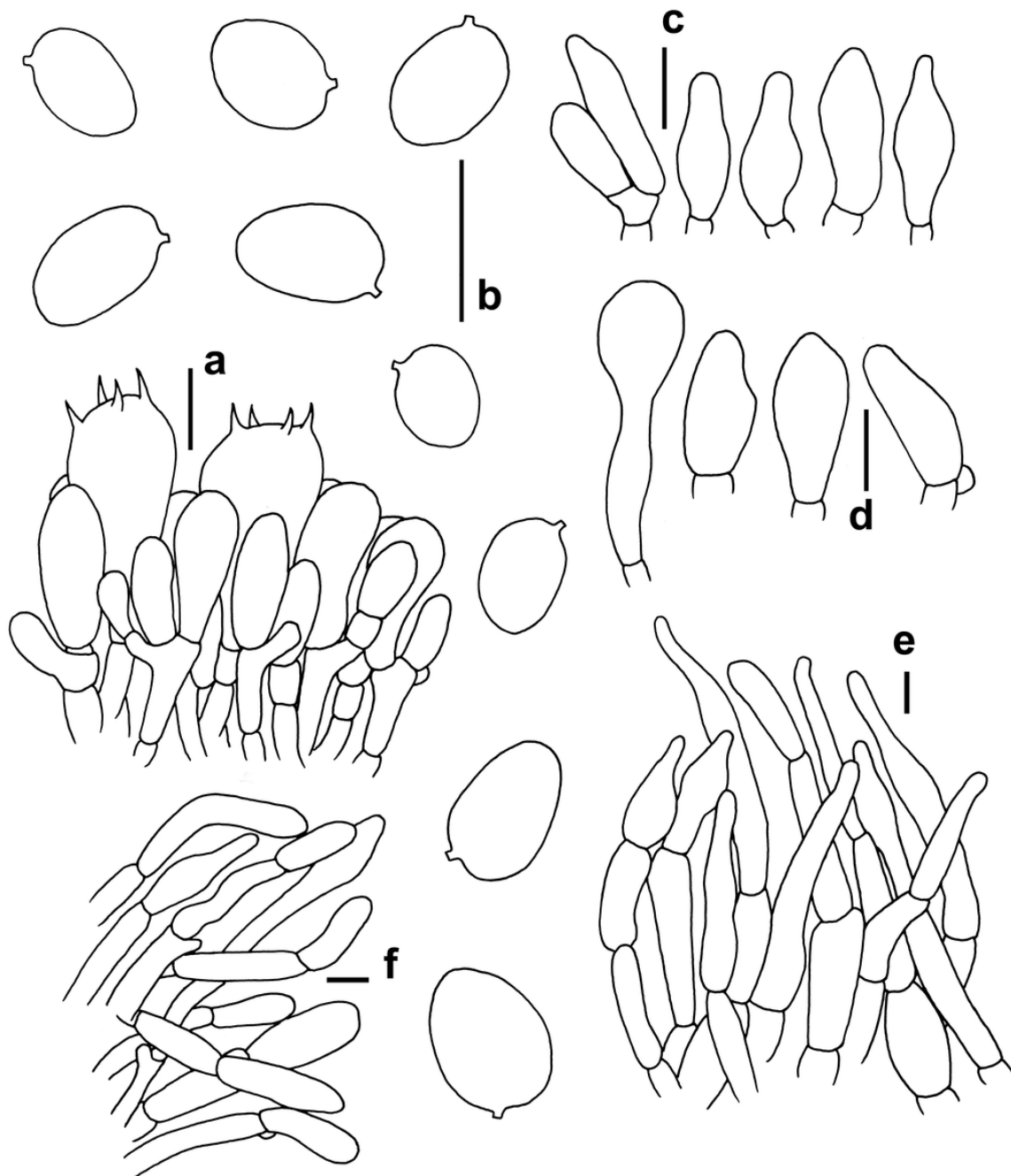


Figure 9

Microscopic features of *Gyroporus subglobosus* (FHMU3364, holotype). a Basidia. b Basidiospores. c Cheilocystidia. d Pleurocystidia. e Pileipellis. f Stipitipellis. Bars = 10 μ m. Drawings by H.J. Xie.