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Amylosporus succulentus sp. nov. (Russulales, Basidiomycota) evidenced by morphological characters and phylogenetic analysis

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Abstract – Three polypore specimens were collected from Hainan, southern China. They are described and illustrated here as a new species, *Amylosporus succulentus*, based on a combination of morphological characters and phylogenetic (ITS and nLSU sequences) data. It is characterized by poroid basidiocarps, both simple septate and clamped generative hyphae, hymenial hyphae without clamp connections, and finely asperulate and amyloid basidiospores. These characters are typical for *Amylosporus*. In the phylogenetic perspective, *A. succulentus* is closely related to *A. campbellii*, the generic type, and nested within the Wrightoporiaceae clade. A key to accepted species of *Amylosporus* worldwide is provided.

Molecular phylogeny / Polypore / Taxonomy / Wood-inhabiting fungi / Wrightoporiaceae

INTRODUCTION

Amylosporus Ryvarden (1973), typified by *A. campbellii* (Berk.) Ryvarden, was introduced for an annual growth habit, poroid basidiocarps, both simple septate and clamped generative hyphae, hymenial hyphae without clamp connections, and finely asperulate and amyloid basidiospores (David & Rajchenberg, 1985, 1987; Hattori, 2008). Four species were recorded worldwide in *Amylosporus*, namely *A. bracei* (Murrill) A. David & Rajchenb., *A. campbellii*, *A. iobapha* (Pat.) A. David & Rajchenb., and *A. ryvardenii* Stalpers.

During studies on the polypores from southern China, three specimens previously identified as *A. campbellii* were re-studied, and they respresent in fact an undescribed species based on morphological characters and phylogenetic analysis of ITS and nLSU sequences. Its illustrated description is provided along with an identification key to the five accepted species of *Amylosporus.*

MATERIAL AND METHODS

Morphological studies

The studied specimens are deposited at the herbaria of the Institute of Microbiology, Beijing Forestry University (BJFC) and the Institute of Applied

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Ecology, Chinese Academy of Sciences (IFP). The microscopic routines followed Li *et al.* (2014). Sections were studied at magnification up to × 1000 using a Nikon E80i microscope and phase contrast illumination. Drawings were made with the aid of a drawing tube. Microscopic features, measurements and drawings were made from slide preparations stained with Cotton Blue and Melzer's reagent. Spores were measured from sections cut from the tubes. Presenting the variation in the size of the spores, 5% of measurements were excluded from each end of the range, and were given in parentheses. Basidiospore spine lengths were not included in the measurements. In the text the following abbreviations were used: IKI = Melzer's reagent, IKI+ = amyloid, IKI– = non-dextrinoid and non-amyloid, KOH = 5% potassium hydroxide, CB = Cotton Blue, CB+ = cyanophilous, CB– = acyanophilous, L = mean spore length (arithmetic average of all spores), W = mean spore width (arithmetic average of all spores), Q = variation in the L/W ratios between the specimens studied, n = number of spores measured from given number of specimens. Special color terms followed Petersen (1996).

Molecular procedures and phylogenetic analysis

A CTAB rapid plant genome extraction kit (China) was used to obtain PCR products from dried specimens, according to the manufacturer's instructions with some modifications (Chen & Cui, 2014). The DNA was amplified with the primers: ITS4 and ITS5 or ITS1 for ITS (White *et al.*, 1990), and LR0R and LR7 or LR5 for nLSU (http://www.biology.duke.edu/fungi/mycolab/primers.htm). The PCR procedure for ITS was as follows: initial denaturation at 95°C for 3 min, followed by 35 cycles at 94°C for 40 s, 54°C for 45 s and 72°C for 1 min, and a final extension of 72°C for 10 min. The PCR procedure for nLSU was as follows: initial denaturation at 94°C for 1 min, followed by 35 cycles at 94°C for 30 s, 50°C for 1 min and 72°C for 1.5 min, and a final extension of 72°C for 10 min. The PCR products were purified and sequenced in Beijing Genomics Institute, China, with the same primers.

The dataset in our phylogenetic analysis was extended from the previous studies on Russulales (mainly from Larsson & Larsson, 2003, Miller *et al.*, 2006, Larsson, 2007). Sequences generated for this study were aligned with additional sequences downloaded from GenBank (Table 1) using BioEdit (Hall, 1999) and ClustalX (Thompson *et al.*, 1997). Prior to phylogenetic analysis, ambiguous sequences at the start and the end were deleted and gaps were manually adjusted to optimize the alignment. Sequence alignment was deposited at TreeBase (http://purl.org/phylo/treebase; submission ID 16140).

Phylogenetic analysis was done as in Li & Cui (2013). Maximum parsimony (MP) analysis was applied to the combined ITS and nLSU dataset. The sequences of *Sistotrema brinkmannii* (Bres.) J. Erikss., *S. coronilla* (Höhn.) Donk ex D.P. Rogers, *S. muscicola* (Pers.) S. Lundell and *S. sernanderi* (Litsch.) Donk were used as outgroups following Larsson & Larsson (2003). The tree construction procedure was performed in PAUP* version 4.0b10 (Swofford, 2002). All characters were equally weighted and gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1000 random sequence additions. Max-trees were set to 5000, branches of zero length were collapsed and all parsimonious trees were saved. Clade robustness was assessed using a bootstrap (BT) analysis with 1000 replicates (Felsenstein, 1985). Descriptive tree statistics tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and homoplasy index

Table 1. A list of species, specimens and GenBank accession number of sequences used in this study. New sequences are shown in bold

Species	*Sample no.*	*Locality*	*GenBank accessions*	
			ITS	*nLSU*
Albatrellus ovinus (Schaeff.) Kotl. & Pouzar	PV 22-89	–	AF506396	AF506396
Albatrellus subrubescens (Murrill) Pouzar	PV 154-95	–	AF506395	AF506395
Aleurocystidiellum disciforme (DC.) Boidin *et al.*	NH 13003	Russia	AF506402	AF506402
Aleurocystidiellum subcruentatum (Berk. & M.A. Curtis) P.A. Lemke	NH 12874	Germany	AF506403	AF506403
Aleurodiscus amorphus (Pers.) J. Schröt.	KHL 4240	Sweden	AF506397	AF506397
Amylosporus bracei (Murrill) A. David & Rajchenb.	1008/77	USA	**KM267724**	KJ807076
Amylosporus campbellii (Berk.) Ryvarden	0806/20a	Jamaica	JF692200	KJ807077
A. succulentus Jia J. Chen & L.L. Shen	Dai 7802	China	**KM213669**	**KM213671**
A. succulentus	Dai 7803	China	**KM213668**	**KM213670**
Amylostereum areolatum (Chaillet ex Fr.) Boidin	NH 8041	Romania	AF506405	AF506405
Amylostereum laevigatum (Fr.) Boidin	NH 2863	Sweden	AF506407	AF506407
Auriscalpium vulgare Gray	EL 33-95	Sweden	AF506375	AF506375
Boidinia aculeata (Sheng H. Wu) E. Larss. & K.H. Larss.	Wu 890714-52	China	AF506433	AF506433
Boidinia granulata Sheng H. Wu	Wu 9209-34	China	AY048880	AY048880
Boidinia propinqua (H.S. Jacks. & Dearden) Hjortstam & Ryvarden	KHL 10931	Jamaica	AF506379	AF506379
Bondarzewia montana (Quél.) Singer	–	Canada	DQ200923	DQ234539
Bondarzewia podocarpi Y.C. Dai	Dai 9261	China	KJ583207	KJ583221
Byssoporia terrestris (DC.) M.J. Larsen & Zak	Hjm 18172	Sweden	DQ389664	DQ389664
Dentipellicula taiwaniana (Sheng H. Wu) Y.C. Dai & L.W. Zhou	Dai 10867	China	JQ349115	JQ349101
Dentipellis fragilis (Pers.) Donk	Dai 12550	China	JQ349110	JQ349096
Dentipellis parmastoi (Nikol.) Stalpers	Cui 8513	China	JQ349113	JQ349099
Dentipellopsis dacrydicola Y.C. Dai & L.W. Zhou	Dai 12004	China	JQ349104	JQ349089
Dentipratulum bialoviesense Doma_ski	GG 1645	France	AF506389	AF506389
Echinodontium tinctorium (Ellis & Everh.) Ellis & Everh	NH 6695	Canada	AF506430	AF506430
Gloeocystidiellum bisporum Boidin et al.	KHL 11135	Norway	AY048877	AY048877
Gloeocystidiellum clavuligerum (Höhn. & Litsch.) Nakasone	NH 11185	Spain	AF310088	AF310088
Gloeocystidiellum compactum Sheng H. Wu	Wu 880615-21	China	AF506434	AF506434
Gloeocystidiellum formosanum Sheng H. Wu	Wu 9404-16	China	AF506439	AF506439
Gloeocystidiellum porosum (Berk. & M.A. Curtis) Donk	NH 10434	Denmark	AF310094	AF310094
Gloeocystidiopsis cryptacanthus (Pat.) E. Larss. & K.H. Larss.	KHL 10334	Puerto Rico	AF506442	AF506442
Gloeodontia discolor (Berk. & M.A. Curtis) Boidin	KHL 10099	Puerto Rico	AF506445	AF506445
Gloeodontia pyramidata (Berk. & M.A. Curtis) Hjortstam	Ryvarden 15502	Colombia	AF506446	AF506446

Table 1. A list of species, specimens and GenBank accession number of sequences used in this study. New sequences are shown in bold *(continued)*

Species	*Sample no.*	*Locality*	*GenBank accessions*	
			ITS	*nLSU*
Gloeopeniophorella convolvens (P. Karst.) Boidin *et al.*	KHL 10103	Puerto Rico	AF506435	AF506435
Gloiodon nigrescens (Petch) Maas Geest.	Desjardin 7287	Bali	AF506450	AF506450
Gloiodon strigosus (Sw.) P. Karst.	JS 26147	Norway	AF506449	AF506449
Gloiothele lactescens (Berk.) Hjortstam	EL 8-98	Sweden	AF506453	AF506453
Hericium alpestre Pers.	NH 13240	Russia	AF506457	AF506457
Hericium americanum Ginns	DAOM F-21467	Canada	AF506458	AF506458
Hericium erinaceus (Bull.) Pers.	NH 12163	Russia	AF506460	AF506460
Heterobasidion annosum (Fr.) Bref.	06129/6	Russia	KJ583211	KJ583225
Heterobasidion parviporum Niemelä & Korhonen	04121/3	Finland	KJ583212	KJ583226
Lactarius leonis Kytöv.	SJ 91016	Sweden	AF506411	AF506411
Laxitextum bicolor (Pers.) Lentz	NH 5166	Sweden	AF310102	AF310102
Lentinellus omphalodes (Fr.) P. Karst.	JJ 2077	Sweden	AF506418	AF506418
Lentinellus ursinus (Fr.) Kühner	EL 73-97	USA	AF506419	AF506419
Megalocystidium luridum (Bres.) Jülich	KHL 8635	Norway	AF506422	AF506422
Peniophora pini (Schleich.) Boidin	Hjm 18143	Sweden	EU118651	EU118651
Polyporoletus sublividus Snell	JA 030918	–	DQ389663	DQ389663
Pseudoxenasma verrucisporum K.H. Larss. & Hjortstam	EL 34-95	Sweden	AF506426	AF506426
Russula violacea Quél.	SJ 93009	Sweden	AF506465	AF506465
Scytinostroma ochroleucum (Bres. & Torrend) Donk	TAA 159869	Australia	AF506468	AF506468
Scytinostroma odoratum (Fr.) Donk	KHL 8546	Sweden	AF506469	AF506469
Sistotrema brinkmannii (Bres.) J. Erikss.	NH 11412	Turkey	AF506473	AF506473
Sistotrema coronilla (Höhn. & Litsch.) Donk ex D.P. Rogers	NH 7598	Canada	AF506475	AF506475
Sistotrema muscicola (Pers.) S. Lundell	KHL 8791	Sweden	AF506474	AF506474
Sistotrema sernanderi (Litsch.) Donk	KHL 8576	Sweden	AF506476	AF506476
Stereum hirsutum (Willd.) Pers.	NH 7960	Romania	AF506479	AF506479
Vararia ochroleuca (Bourdot & Galzin) Donk	JS 24400	Norway	AF506485	AF506485
Wrightoporia austrosinensis Y.C. Dai	Dai 11579	China	KJ807065	KJ807073
Wrightoporia avellanea (Bres.) Pouzar	E 7088	–	AJ537507	AJ537507
W. avellanea	Ryvarden 41710	Jamaica	AF506488	AF506488
Wrightoporia casuarinicola Y.C. Dai & B.K. Cui	Dai 6914	China	KJ807068	–
Wrightoporia lenta (Overh. & J. Lowe) Pouzar	Cui 7804	China	KJ513292	KJ807081
W. lenta	Dai 10462	China	KJ513291	KJ807082
Wrightoporia rubella Y.C. Dai	Dai 9233	China	KJ807071	KJ807084
W. subavellanea Jia J. Chen & B.K. Cui	Dai 11484	China	KJ513295	KJ807085
W. subavellanea	Dai 11488	China	KJ513296	KJ807086
W. subavellanea	Dai 11492	China	KJ513297	KJ807087
Wrightoporia tropicalis (Cooke) Ryvarden	TFM F-16446	Japan	KJ807072	KJ807088
W. tropicalis	Ryvarden 45363	Belize	KJ513294	KJ807089

(HI) were calculated for each maximum parsimonious tree (MPT) generated. Phylogenetic trees were visualized using Treeview (Page, 1996).

MrModeltest2.3 (Nylander, 2004) was used to determine the best-fit evolution model for the combined dataset for bayesian inference (BI). BI was calculated with MrBayes3.1.2 (Ronquist & Huelsenbeck, 2003) with a general time reversible (GTR) model of DNA substitution and an invgamma distribution rate variation across sites. Four Markov chains were run for 2 runs from random starting trees for 5 million generations of the combined ITS and nLSU dataset, and sampled every 100 generations. The burn-in was set to discard the first 25% of the trees. A majority rule consensus tree of all remaining trees was calculated. Branches that received bootstrap support for MP and bayesian posterior probabilities (BPP) greater than or equal to 75% (MP) and 0.95 (BPP) respectively were considered as significantly supported.

RESULTS

The ITS+nLSU dataset included sequences from 70 fungal specimens representing 64 taxa. The dataset had an aligned length of 2098 characters in the dataset, of which 1010 characters are constant, 173 are variable and parsimony-uninformative, and 915 are parsimony-informative. Maximum parsimony analysis yielded one equally parsimonious tree (TL = 6291, CI = 0.349, RI = 0.586, RC = 0.205, HI = 0.651), and the maximum parsimonious tree was shown in Fig. 1. Best model estimated and applied in the BI was "GTR+I+G" with equal frequency of nucleotides. Both MP and BI trees resulted in similar topologies. Only the MP tree was provided. Both bootstrap values (≥ 50%) and BPPs (≥ 0.95) were showed at the nodes (Fig. 1).

The newly sequenced specimens from southern China were embedded in the Wrightoporiaceae calde as a distinct lineage, and had a close relationship with *Amylosporus campbellii* (80% MP and 1.00 BPPs). In addition, *A. bracei*, *A. campbellii*, *A. succulentus*, *Wrightoporia casuarinicola* Y.C. Dai & B.K. Cui, and *W. rubella* Y.C. Dai formed a distinct and well supported clade (80% MP and 1.00 BPPs) that appears weakly related to *W. lenta* (Overh. & J. Lowe) Pouzar, the type species of *Wrightoporia.*

TAXONOMY

Amylosporus succulentus Jia J. Chen & L.L. Shen, **sp. nov.** **Figs 2-3**

MycoBank: MB 809943

Original diagnosis: Differs from other *Amylospus* species by juicy fruiting body when fresh, pileate basidiocarps with a cream to pinkish violet pore surface, dextrinoid and hyaline skeletal hyphae, distinctly inflated contextual skeletal hyphae in KOH, presence of gloeoplerous hyphae and cystidioles, and ellipsoid, slightly thick-walled, and cyanophilous basidiospores measuring 4.2-5.2 × 3-3.8 µm.

HOLOTYPUS: **CHINA,** Hainan Province, Haikou, Jinniuling Park, on lawn, 1 Sep 2006, Y.C Dai, Dai 7802 (BJFC; IFP).

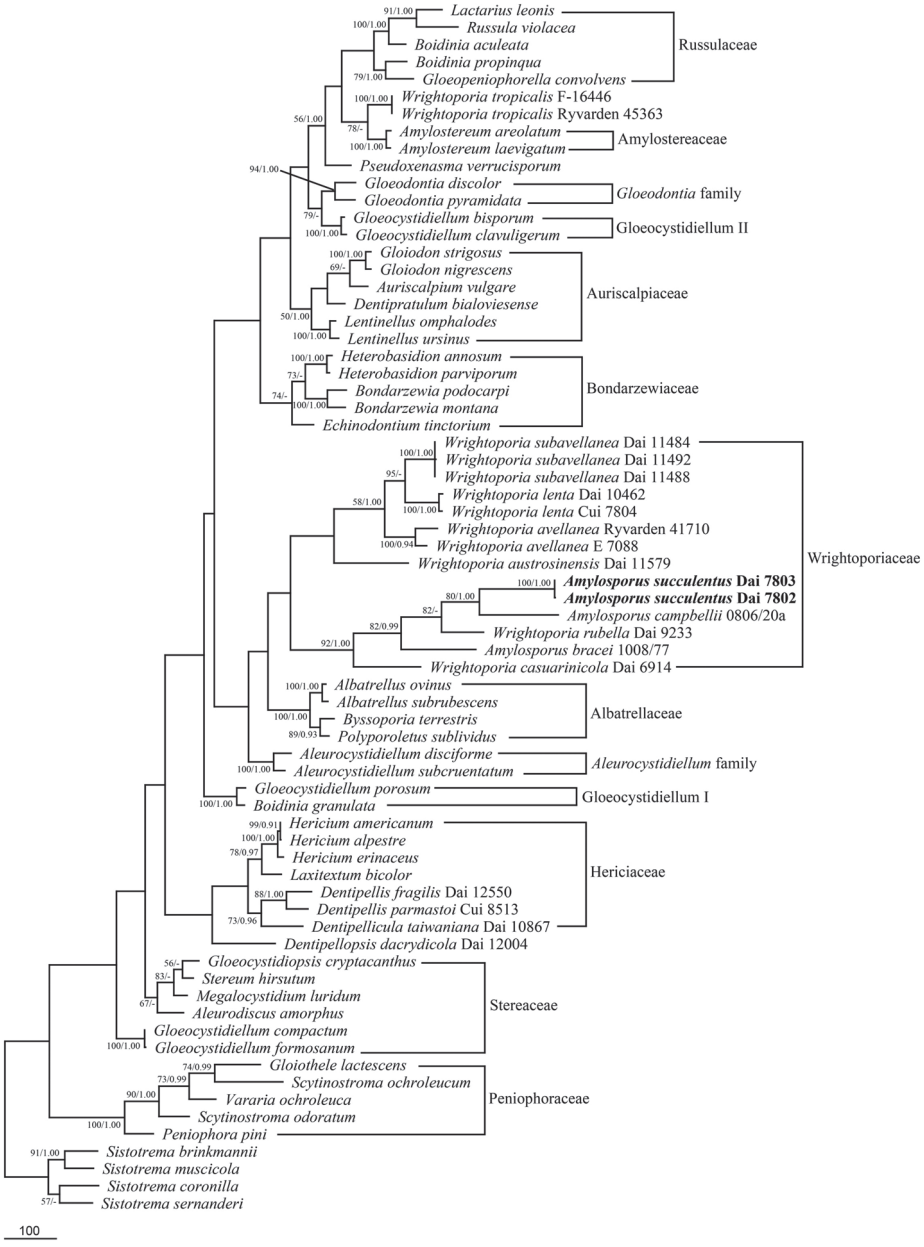


Fig. 1. Strict consensus tree illustrating the phylogeny of the new species and related species generated by Maximum parsimony based on ITS + nLSU sequences. Parsimony bootstrap proportions (before the slash markers) higher than 50% and Bayesian posterior probabilities (after the slash markers) more than 0.95 are indicated along branches.

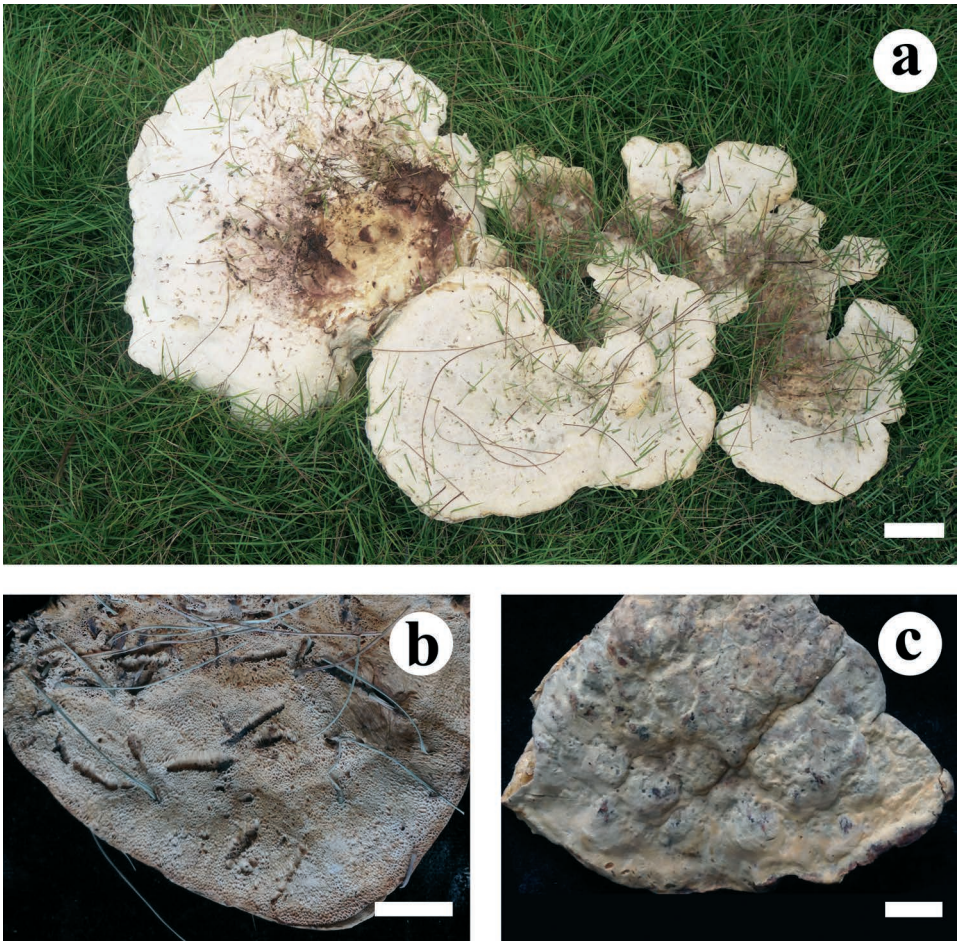
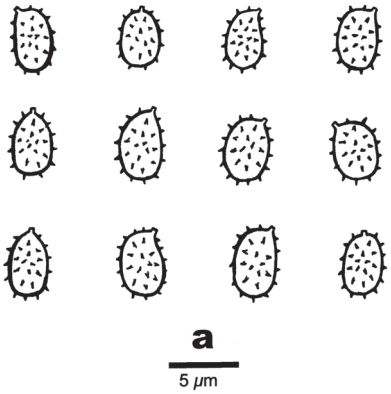
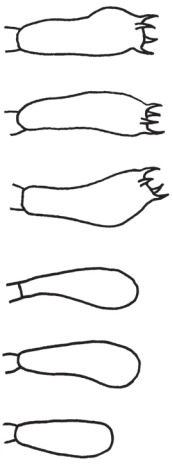


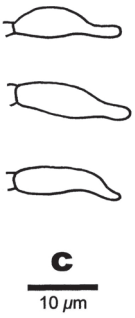
Fig. 2. Basidiocarp of *Amylosoporus succulentus* from the holotype. **a.** Fresh basidiocarp in the wild. **b-c.** Dried basidiocarp. Bars a, b, c = 1 cm.

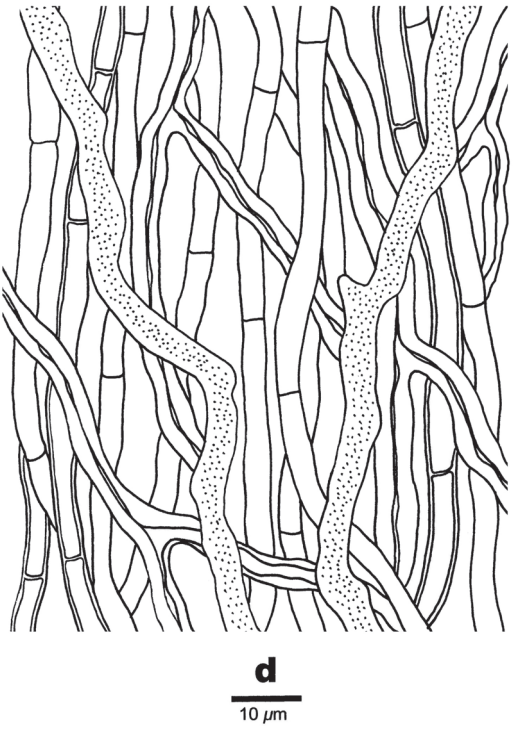
Etymology. succulentus (Lat.): referring to watery and juice fruiting body of the species when fresh.

Basidiocarps annual, pileate, centrally to laterally stipitate, solitary or a few confluent, watery and juice when fresh, without odour or taste, becoming corky and light in weight upon drying. Pileus more or less circular, projecting up to 7 cm long, 15 cm wide, 4 cm thick at the base, sometimes lobed, becoming thinner towards margins; margins undulating, obtuse to acute. Pileal surface cream to greyish violet when fresh, becoming pinkish buff to clay-buff when dry, azonate. Pore surface cream to pinkish violet when fresh, buff upon drying; pores angular, 2-4 per mm; dissepiments thin, lacerate. Context cream and watery when fresh, pinkish buff and corky when dry, up to 3 cm thick. Tubes buff and brittle when dry, up to 1cm long. Stipe short and thick, buff and corky when dry, up to 1 cm long. **Type of rot.** White rot.









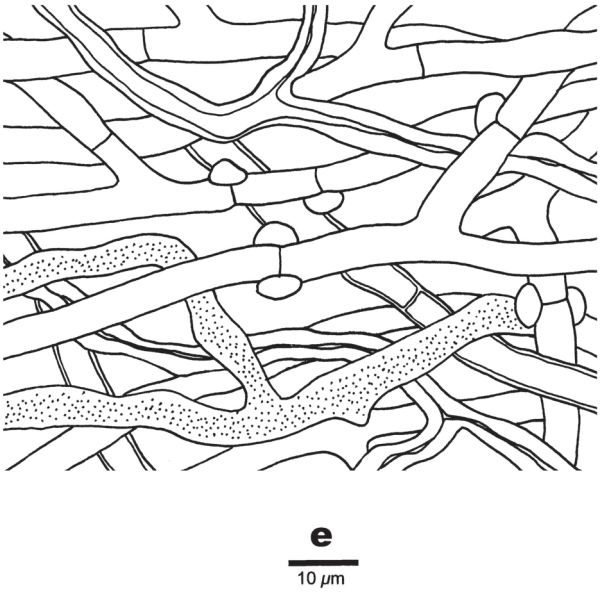


Fig. 3. Microscopic structures of *Amylosporus succulentus* (drawn from the holotype). **a.** Basidiospores. **b.** Basidia and basidioles. **c.** Cystidioles. **d.** Hyphae from trama. **e.** Hyphae from subiculum. *Bars*: a. 5 μm; b-e. 10 μm.

Hyphal system dimitic; tramal generative hyphae with simple septa only, contextual generative hyphae with both simple septa and double or multiple clamp connections; skeletal hyphae dextrinoid, CB+; contextual skeletal hyphae distinctly inflated in KOH, up to 20 µm in diam. **Context** Generative hyphae domidant, hyaline, thin- to slightly thick-walled, frequently branched, 4-10 µm in diam; skeletal hyphae frequent, thick-walled with a narrow to wide lumen, freuqently branched, flexuous, loosely interwoven, 3-8 µm in diam; gloeoplerous hyphae occasionally present, thin-walled with granular to oily contents appearing refractive in phase contrast illumination, up to 12 µm in diam. **Tubes** Generative hyphae common to dominant, hyaline, thin- to slightly thick-walled, rarely branched, subparallel along the tubes, 3-6 µm in diam; skeletal hyphae common, thick-walled with a narrow to wide lumen, freuqently branched, flexuous, loosely interwoven, 3-8 µm in diam; gloeoplerous hyphae frequently present, thin-walled with granular to oily contents appearing refractive in phase contrast illumination, up to 9 µm in diam. Cystidia absent, but cystidioles present, thin-walled, fusoid, tapering, 13-18 × 3-4 µm; basidia clavate, with four sterigmata and a basal simple septum, 15-20 × 5-8 µm; basidioles in shape similar to basidia, but slightly smaller. **Basidiospores** ellipsoid, hyaline, slightly thick-walled, finely asperulate, IKI+, CB+, (4.0-)4.2-5.2(-5.4) × (2.8-)3-3.8(-4) µm, L = 4.73 µm, W = 3.14 µm, Q = 1.46-1.52 (n = 60/2).

Additional specimens examined: *Amylosporus succulentus* — **CHINA**, Hainan Province, Haikou, Jinniuling Park, on lawn, 1 Sep 2006, Y.C Dai, Dai 7803 (BJFC; IFP) & 7808 (IFP).

DISCUSSION

Morphologically, *Amylosporus succulentus* is characterized by an annual growth habit, watery and juicy fruiting body when fresh, pileate basidiocarps with a cream to pinkish violet pore surface, both simple septate and clamped generative hyphae, hymenial hyphae without clamp connections, dextrinoid and hyaline skeletal hyphae, distinctly inflated contextual skeletal hyphae in KOH, presence of gloeoplerous hyphae and cystidioles, and ellipsoid, slightly thick-walled, finely asperulate, amyloid and cyanophilous basidiospores which are 4.2-5.2 × 3-3.8 µm. Phylogenetically, two samples of *A. succulentus* formed a distinct lineage with strong supports (100% MP, 1.00 BPPs) and are distant from other taxa in the genus or other genera. *Amylosporus succulentus* was embedded in the lineage of the Wrightoporiaceae and clustered with *A. campbellii*. Both morphology and rDNA sequence data confirmed that the two samples represent a new species in *Amylosporus*.

Amylosporus succulentus is closely related to *A. campbellii* according to our rDNA phylogeny (Fig. 1). Morphologically, *A. succulentus* may be confused with *A. campbellii*, as they produce pileate basidiocarps, similar sized pores (2-4 per mm in *A. campbellii*), and presence of gloeoplerous hyphae. However, *A. campbellii* can be readily distinguished from *A. succulentus* by its non-dextrinoid and pale golden yellow skeletal hyphae.

Previously, *Amylosporus campbellii* was reported in China (Dai, 2007, 2012), but the identifications were based only on morphological characters. According to the combination of morphological features and rDNA sequences

data, the Chinese samples turned out to be different from *A. campbellii* originally described from India, and they are described here as a new species, *A. succulentus*. It should be noted that previously many Chinese polypores were named after already described species on the basis of morphology only, and in fact many of them were later proven to be undescribed species using molecular studies, such as species in *Albatrellus, Hymenochaete, Heterobasidion*, *Perenniporia*, *Phellinidium*, *Phylloporia*, *Polyporus* etc. (Cui *et al*., 2008; He & Dai, 2012; Zhou & Dai, 2012; Cui & Dai, 2013; Zhao & Cui, 2013; Zhao *et al.*, 2013; Chen *et al.*, 2014; Dai *et al*., 2014; Zhou *et al.*, 2014).

Amylosporus succulentus may be confused with *A. bracei* in producing a pinkish violet pore surface and dextrinoid skeletal hyphae. However, *A. bracei* differs from *A. succulentus* in its resupinate to effused-reflexed basidiocarps with rhizomorphs, smaller pores (5-7 per mm), absence of gloeoplerous hyphae, and smaller basidiospores (3-3.5 × 2.5 μm, Ryvarden, 2000). Moreover, the two species are different in the ITS and nLSU rDNA-based phylogenetic analysis (Fig. 1).

Amylosporus is a white-rot fungal genus belonging to the Russulales. The previous studies on *Amylosporus* were mainly based on morphological characters (Ryvarden, 1977; David & Rajchenberg, 1985; Stalpers, 1996). Recently, Chen & Cui (2014) proved that *Amylosporus* was a polyphyletic genus and closely related with *Wrightoporia casuarinicola* and *W. rubella*. However, relationships among species of *Amylosporus* appear ambiguous (Fig. 1). Species of *Amylosporus* were embedded in the Wrightoporiaceae clade. Nevertheless, species of *Wrightoporia* with simple septate generative hyphae clustered with species of *Amylosporus*, then formed a different group (92% MP and 1.00 BPPs) that appears distant from the type species, *W. lenta.* Species in this clade are characterized by hymenial hyphae without clamp connections, differing from other species of *Wrightoporia*. A further study on subdivision and phylogeny of all the species of *Wrightoporia* s.l. and *Amylosporus* is badly needed by wider taxa sampling and more conserved gene markers.

KEY TO ACCEPTED SPECIES OF *AMYLOSPORUS* WORLDWIDE

1. Basidiocarps pileate 2
1. Basidiocarps resupinate to effused-reflexed 3

2. Skeletal hyphae dextrinoid . . . . . *A. succulentus*
2. Skeletal hyphae non-dextrinoid . . . . . *A. campbellii*

3. Tramal generative hyphae > 3 μm in diam 4
3. Tramal generative hyphae < 3 μm in diam. . . . . *A. iobapha*

4. Basidiospores > 4 μm long. . . . . *A. ryvardenii*
4. Basidiospores < 4 μm long. . . . . *A. bracei*

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