A new genus and four new species in the /Psathyrella s.l. clade from China

Tolgor Bau¹, Jun-Qing Yan²

¹ Key Laboratory of Edible Fungal Resources and Utilization (North), Ministry of Agriculture and Rural Affairs, Jilin Agricultural University, Changchun 130118, China ² Jiangxi Key Laboratory for Conservation and Utilization of Fungal Resources, Jiangxi Agricultural University, Nanchang, Jiangxi 330045, China

Corresponding authors: Tolgor Bau (junwusuo@126.com); Jun-Qing Yan (yanjunqing1990@126.com)

Abstract
Based on traditional morphological and phylogenetic analyses (ITS, LSU, tef-1α and β-tub) of psathyrellloid specimens collected from China, four new species are here described: Heteropsathyrella macrocystidia, Psathyrella amygdalinospora, P. piluliformoides, and P. truncatisporoides. H. macrocystidia forms a distinct lineage and groups together with Cystoagaricus, Kauffmania, and Typhrasa in the /Psathyrella s.l. clade, based on the Maximum Likelihood and Bayesian analyses. Thus, the monospecific genus Heteropsathyrella gen. nov. is introduced for the single species. Detailed descriptions, colour photos, and illustrations are presented in this paper.

Keywords
Agaricales, Basidiomycete, four new taxa, Psathyrellaceae, taxonomy

Introduction
Psathyrella (Fr.) Quél. is characterized by usually fragile basidiomata, a hygrophanous pileus, brown to black-brown spore prints, always present cheilocystidia and basidiospores fading to greyish in concentrated sulphuric acid (H₂SO₄) (Kits van Waveren 1985; Örstadius et al. 2015). There are records of more than 1000 names, including synonyms and subspecies, since Fries established the tribe Psathyrella under Agaricus L. (Fries 1838; Smith 1972; Kits van Waveren 1985; Örstadius and Knudsen...
This group has been classified in the Coprinaceae Roze ex Overeem subfamily Psathyrelloideae (Hawksworth et al. 1983; Hawksworth et al. 1995; Kirk et al. 2001) and then incorporated into Psathyrellaceae Vilgalys, Moncalvo & Redhead, based on the study of Redhead et al. (2001). Further studies found that Psathyrella is polyphyletic and Psathyrella s.l. was limited by Örstadius et al. (2015). Psathyrella s.l. consists of five major supported clades: Coprinellus, Cystoagaricus, Kauffmania, Psathyrella s.s., and Typhrasa. Each major clade represents a genus. Hence, Kauffmania Örstadius & E. Larss. and Typhrasa Örstadius & E. Larss. were established, Cystoagaricus Singer emend. Örstadius & E. Larss. was redefined (Örstadius et al. 2015). Most species in Cystoagaricus, Kauffmania, and Typhrasa were incorporated from Psathyrella. Species with cap surface breaking up into dark fibrils or scales were classified into Cystoagaricus. Species having rostrate hymenial cystidia with oily drops were classified into Typhrasa. P. larga (Kauffman) A.H. Sm., which has large basidiomata, scanty veil, and pale spores, was classified into Kauffmania.

As a part of the study of Chinese psathyrellloid species, four new species were discovered, during our investigations in temperate and subtropical regions of China from 2016–2019. Among them was a new species morphologically similar to Psathyrella but phylogenetically distinguished from it, and which formed a separate lineage. We recognize this new taxon as a new genus based on traditional morphological and phylogenetic analyses. In this paper, detailed information on the new taxa is presented.

### Materials and methods

#### Morphological studies

Macroscopic characteristics of fresh specimens were recorded. Colour codes followed Kornerup and Wanscher (1978). Thirty basidiospores, cystidia, and basidia were measured under a microscope in water and 5% aqueous KOH for each specimen. The measurements and Q values are given as (a)b–c(d), in which “a” is the lowest value, “b–c” covers a minimum of 90% of the values and “d” is the highest value. “Q” stands for the ratio of length to width of a spore (Bas 1969; Yu et al. 2020). Photographs of some microscopic characteristics are shown in Suppl. material 1: Figure S1. Specimens were deposited in the Herbarium of Mycology, Jilin Agricultural University (HMJAU).

#### DNA extraction and sequencing

DNA was extracted from dried specimens with the NuClean Plant Genomic DNA kit (CWbio, China). Four regions (ITS, LSU, tef-1a and β-tub) were amplified for the study, which using ITS1/ITS4 (White et al. 1990), LR0R/LR7 (Hopple and Vilgalys 1999), EF983F/EF2218R (Örstadius et al. 2015), and B36f/B12r (Nagy et al. 2011), respectively. PCR was performed using a touchdown program for all regions as follows: 5 min at 95 °C; 1 min at 95 °C; 30 s at 65 °C (add -1 °C per cycle); and 1 min at 72 °C
New genus and new species in /Psathyrella s.l. clade from China

for a cycle of 15 times; 1 min at 95 °C; 30 s at 50 °C; and 1 min at 72 °C for a cycle of 20 times; and 10 min at 72 °C (Yan and Bau 2018b). DNA sequencing was performed by Qing Ke Biotechnology Co., Ltd. (Wuhan City, China), using primers listed above.

Data analyses

ITS1+5.8S+ITS2 sequences of four new species were tested with BLAST in GenBank, species sharing over 95% similarity are selected. Based on the BLAST results, morphological similarities and then compared to the research of Örstadius et al. (2015) and Yan and Bau (2018a). Totally, 176 sequences of 46 taxa, including 4 regions (ITS, LSU, tef-1α, and β-tub) which divided into 7 partitions (ITS, LSU, Tef 1st, Tef 2nd, Tef 3rd, Tub 1st, and Tub 2nd) were downloaded for phylogenetic analyses. The details are presented in Table 1. Sequences were aligned by the online version of the multiple sequence alignment program MAFFT v7 (Katoh and Standley 2013) and were manually adjusted in BIOEDIT v7.1.3.0 (Hall 1999). Phylogenetic analyses were conducted using Bayesian inference (BI) in MRBAYES v3.2.6 (Ronquist and Huelsenbeck 2003) and maximum likelihood (ML) in IQTREE v1.5.6 (Nguyen et al. 2014). For BI analyses, the best model was selected by AIC in MRMODELTEST 2.3, and gaps were treated as missing data (Nylander 2004; Örstadius et al. 2015). Four Markov chains (MCMCs) were run for two million generations, with sampling every 100th generation. The first 25% of trees were discarded (Ronquist and Huelsenbeck 2003). ML analyses were executed by applying the ultrafast bootstrap approximation with 1000 replicates. The sequence alignment was deposited in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S27605?x-access-code=ad75ae6bd4198ca6d44a895863bc1b&format=html).

Results

Phylogenetic results

The aligned complete dataset consisted of 54 taxa and 2606 characters (ITS 711 bp, LSU 829 bp, Tef 1st 69 bp, Tef 2nd 136 bp, Tef 3rd 497 bp, Tub 1st 125 bp, and Tub 2nd 239 bp). Due to the different number of models supported by Mrbayes and IQtree, the best models are calculated separately, and the results are as follows: the best models for Bayesian analysis were GTR+I+G for the ITS, LSU, Tef 3rd, and Tub 2nd, HKY+I for Tef 1st, SYM+G for Tef 2nd, and SYM+I+G for Tub 1st; the best models for ML analysis were TIM2+F+I+G4 for the ITS and LSU, TNe+FQ+I for Tef 1st and Tef 2nd, TIM2+F+G4 for Tef 3rd, TIMe+FQ+G4 for Tub 1st, and HKY+F+G4 for Tub 2nd.

For Bayes analysis, the average standard deviation of split frequencies less than 0.01 after 610 thousand generations. The Bayesian inference (BI) and ML bootstrap proportions are shown in the Bayesian tree (Fig. 1). In addition, the ML tree is shown in Suppl. material 2: Figure S2. The phylogenetic tree analyses recovered 8 major supported clades
Table 1. Sequences used in this study. Newly generated sequences are in bold.

| Taxon | Voucher | Locality | ITS | LSU | tef-1x | β-Tub |
|-------|---------|----------|-----|-----|--------|--------|
| Coprinellus christianopolitanus | LO141-08 type | Sweden | KC992944 | KC992944 | KJ732823 | – |
| C. disseminatus | SZMC-NL-2337 | Sweden | FM878017 | FM876274 | – | FN396282 |
| C. silvicola | LO172-08 | Sweden | KC992943 | KC992943 | KJ732822 | KJ649911 |
| C. truncorum | SZMC-NL-1101 | Sweden | FM878006 | FM876262 | FM897225 | FN396328 |
| Cyanogaeacorus | Ramsholm800927 | Finland | KC992945 | KC992945 | – | – |
| Hypholoma maraquamunus | – | Sweden | – | – | – | – |
| C. olivaceogriseus | WK 8/15/63-5 (MICH) Type | USA | KC992948 | KC992948 | – | – |
| C. syrphoides | LÖ191-92 | Sweden | KC992949 | KC992949 | – | – |
| C. squamosiceps | Laeso448035 | Ecuador | KC992950 | – | – | – |
| C. strigilosporus | E. Nagase 97/40 | – | – | – | – | – |
| Heterophairella | HMJAU37802 Type | China:Jilin | MW405102 | MW413559 | MW411004 | MW410997 |
| – macrocytoida | – | – | – | – | – | – |
| H. macrocytoida | HMJAU37803 | China:Jilin | MW405101 | MW413538 | MW411003 | – |
| H. macrocytoida | HMJAU37912 | China:Jilin | MW405103 | MW413560 | MW411005 | – |
| Kauflania larga | LAS97-054 | Sweden | DQ389695 | DQ389695 | – | – |
| K. larga | LÖ223-90 | Sweden | DQ389694 | DQ389694 | KJ732824 | KJ649912 |
| Pastbyrella abieticola | Sminh8673 (MICH) Type | USA | KC992891 | KC992891 | – | – |
| P. amylodinonpora | HMJAU37952 Type | China:Sichuan | MW405104 | MW413536 | MW410999 | MW410991 |
| P. amylodinonpora | HMJAU37504 | China:Sichuan | MW405105 | – | – | – |
| P. cowenii | GE02.007 (PC) Type | France | KC992890 | KC992890 | – | – |
| P. estivana | ZT12073 | NewZealand | KC992925 | KC992925 | – | KJ649900 |
| P. fagenophila | LÖ210-85 (M) Type | Sweden | KC992902 | KC992902 | – | KJ649979 |
| P. fennocanadica | HMJAU37918 | China:Heilongjiang | MG374723 | MW413365 | MW411000 | MW410993 |
| P. fennocanadica | LO84-05 Type | Sweden | KC992905 | KC992905 | KJ732790 | KJ648881 |
| P. fennocanadica | LO99-96 | Sweden | KC992904 | KC992904 | KJ732791 | KJ648882 |
| P. fusca | LO87-04 | Sweden | KC992892 | KC992892 | KJ732779 | – |
| P. macrocytis | LO103-98 | Sweden | DQ389700 | – | KJ732810 | KJ649901 |
| P. noli-tangere | LO83-03 Neotype | Sweden | DQ389713 | DQ389713 | – | KJ649901 |
| P. oboensis | HMJAU37936 | China:Yunnan | MT429164 | MW413566 | – | MW410996 |
| P. oboensis | DED 8234 Type | SaoTomé | NR148107 | – | – | – |
| P. olivipila | LÖ93-02 | Sweden | DQ389722 | DQ389722 | KJ732817 | KJ649906 |
| P. panaeoloides | LO4-03 | Sweden | DQ389719 | DQ389719 | KJ732782 | KJ648873 |
| P. panaeoloides | HMJAU36936 | China:Jilin | MG374733 | MH155958 | – | MH161165 |
| P. pertinax | HMJAU6830 | China:Jilin | MG374735 | – | – | MW410995 |
| P. pertinax | LO259-91 Neotype | Sweden | DQ389701 | DQ389701 | KJ732809 | – |
| P. piliformis | HMJAU37922 | China:Heilongjiang | MG374716 | MW413364 | MW411001 | MW410994 |
| P. piliformis | LO162-02 | Germany | DQ389699 | DQ389699 | KJ732808 | KJ648899 |
| P. piliformisides | HMJAU37923 Type | China:Yunnan | MW405106 | MW413362 | MW411002 | – |
| P. pygmaea | LO97-04 | Sweden | DQ389718 | DQ389718 | KJ732811 | KJ649902 |
| P. pygmaea | HMJAU37850 | China:Jilin | MG374744 | MH155959 | MH161170 | MH161166 |
| P. rybergii | LÖ37-06 Type | Sweden | KC992893 | KC992893 | KJ732781 | KJ648872 |
| P. saponacea | HMJUA 37935 | China:Shanxi | MH155965 | MH155960 | – | MH161167 |
| P. saponacea | LO204-96 | Sweden | DQ389717 | – | KJ732780 | KJ648871 |
| P. seminuda | Smith34901 (MICH) Type | USA | KC992907 | KC992907 | – | – |
| P. senex | HMJAU4450 | China:InnerMongolia | MG374732 | – | – | MW410992 |
| P. senex | LO115-02 | Germany | DQ389712 | DQ389712 | KJ648880 | – |
| P. truncatiporoides | HMJAU37947 Type | China:Zhejiang | MW405107 | MW413363 | MW410998 | MW410990 |
| P. truncatiporoides | HMJAU57045 | China:Zhejiang | MW405108 | – | – | – |
| Phellodermia | Smith70162 (MICH) Type | USA | KC992906 | KC992906 | – | – |
| Typhrasa gossypina | Schumacher024 | Germany | KC992946 | KC992946 | KJ732825 | – |
| T. nanispora | Bart090706 Type | Austria | KC992947 | KC992947 | – | – |
| Outgroup | – | – | – | – | – | – |
| Coprinopsis cineraria | CBM-FB-24142 Type | Japan | KC992962 | – | – | – |
| C. maeae | JV06-179 Type | Denmark | KC992965 | KC992965 | – | KJ649202 |
| C. submicronpora | AH27055 Type | Spain | KC992959 | KC992959 | – | KJ649918 |
| C. udicola | AM1240 Type | Germany | KC992967 | KC992967 | KJ732831 | KJ649222 |
| C. udincola | Smith34903 (MICH) Type | USA | KC992960 | KC992960 | – | – |
New genus and new species in /Psathyrella s.l. clade from China

(6 genera), with a high statistical support value (BPP ≥ 0.95, bootstrap ≥ 75). They are *Psathyrella* (including 3 clades), *Coprinellus*, *Kauffmania*, *Cystoagaricus*, *Typhrasa*, and the new genus – *Heteropsathyrella*. *P. amygdalinospora*, *P. piluliformoides*, *P. truncatisporoides* were separated into individual lineages and are independent from the close taxa in *Psathyrella*. *P. amygdalinospora* forms a distinct lineage in the /pygmaea clade, *P. piluliformoides* belongs to /piluliformis and groups together with *P. oboensis* Desjardin & B.A. Perry, and *P. truncatisporoides* belongs to /noli-tangere and groups together with

![Phylogram generated by Bayesian inference (BI) analysis based on sequences of a concatenated data set from four nuclear genes (ITS, LSU, tef-1α and β-tub), rooted with *Coprinopsis* spp. Bayesian inference (BI-PP) ≥ 0.95 and ML bootstrap proportions (ML-BP) ≥ 75 are shown as BI-PP/ML-BP. ● indicates newly described taxa.](image-url)
P. rybergii Örstedius & E. Larss. H. macrocystidia forms a distinct lineage and groups together with the lineage consisting of Cystoagaricus, Kauffmania, and Typhrasa.

**Taxonomy**

*Heteropsathyrella* T. Bau & J.Q. Yan, gen. nov.
MycoBank No: 838372

**Remarks.** Pileus hygrophanous, tawny to brown, non-deliquescent. Veil present. Lamellae adnexed. Stipe central, hollow. Basidiospores ellipsoid to subellipsoid, smooth, brown in 5% KOH, pale mouse grey in H₂SO₄. Hymenium hyaline. Basidia monomorphic. Pseudoparaphyses abundant and regularly distributed. Pleurocystidia and cheilocystidia present. Pileipellis composed of saccate to subglobose cells covered by a 1 cell deep layer of periclinal hyphae which are covered by scattered and irregular deposits dissolving in 5% KOH.

**Etymology.** *Heteropsathyrella*, referring to its morphological similarity to *Psathyrella*.

**Type species.** *Heteropsathyrella macrocystidia* T. Bau & J.Q. Yan, sp. nov.

*Heteropsathyrella macrocystidia* T. Bau & J.Q. Yan, sp. nov.
MycoBank No: 838373
Figs 2a–c, 3

**Etymology.** *macrocystidia*, referring to its large pleurocystidia, which are up to 83 μm long.

**Type.** CHINA. Changbai Mountain, Antu County, Yanbian Korean Autonomous Prefecture, Jun-Qing Yan, Herbarium of Mycology, Jilin Agricultural University (HM-JAU37802).

**Diagnosis.** Differs from *Psathyrella epimyces* by saprophytic and abundant pseudoparaphyses.

Pileus 35–70 mm broad, obtusely conic when young, expanding to plane, with a small obtuse umbo, hygrophanous, tawny to brown (7C6–7D7), darker at center (7E7), striate up to 2/3 from margin, becoming dirty white as pileus dries (7A1–7B2). Veil scattered, small, white (7A1), fibrillose, evanescent. Context hygrophanous, thin and fragile, approximately 1.0–1.5 mm at the centre. Lamellae 3.0–6.0 mm broad, crowded, adnexed, dirty white (7A1–7B2), becoming pale brown to brown (7E7–7F7) as spores mature, edge white (7A1) and even. Stipe 35–100 mm long, 5.0–15 mm thick, white (7A1), cylindrical, gradually thickening towards base, fragile, hollow, but context thick, surface uneven, with small grainy bulb, covered with small, white, evanescent fibrils. Odour and taste indistinctive. Spore print grey brown (7E3–7E4).

Spores 7.8–9.2 × 4.9–5.4 μm, Q = 1.6–1.8, elongated-ellipsoid in face view, in profile flattened on one side, pale brown in water, darker brown in 5% KOH, smooth, with or without 1–2 guttules, germ pore indistinct, approximately 1.0 μm in diam. Basidia 26–34 × 7.3–9.8 μm, clavate, hyaline, 4- or 2-spored. Pseudoparaphyses abundant and regular distribution. Pleurocystidia 59–83 × 12–20 μm, abundant, utriform
New genus and new species in /Psathyrella s.l. clade from China

with broadly obtuse apex, slightly thick-walled, glabrous or covered by irregular deposits, base tapering to a long stipe. Cheilocystidia 37–56 × 9.8–17 μm, utriform to fusoid with obtuse apex, base tapering to a short stipe. Caulocystidia 29–61 × 12–22 μm, caespitose, various, utriform, fusoid or utriform with abrupt narrow neck terminating in a capitellum, base tapering to a long or short stipe. Trama of gills irregular. Pileipellis a 1–2-cell-deep layer of vesiculose cells, up to 61 μm long, covered by a 1-cell-deep layer of periclinal hyphae which are approximately 3.6 μm in diam and covered by scattered and irregular deposition dissolving in 5% KOH. Clamps present.

Habit and habitat. Scattered on mossy rotten wood in mixed forests of larch and birch.

Other specimens examined. China. Changbai Mountain, Antu County, Yanbian Korean Autonomous Prefecture, Jun-Qing Yan, 16 July 2016, HMJAU37803; 28 July 2017, HMJAU37912.

Psathyrella amygdalinospora T. Bau & J.Q. Yan, sp. nov.
MycoBank No: 838374
Figs 2d–f, 4

Etymology. Referring to the spore shape.
Type. **China.** Scenic Spot of Kangding Love Song (Mugecuo), Kangding City, Tibetan Autonomous Prefecture of Garzê, Sichuan Province, 30°08′49.19″N, 101°51′39.18″E, 3790 m, 21 August 2017, Jun-Qing Yan, Herbarium of Mycology, Jilin Agricultural University (HMJAU 37952).

**Diagnosis.** Differs from *P. obtusata* by its spores, ovoid in front view, amygdali-form in profile and dark brown and gradually becoming black-brown in 5% KOH.

Pileus 15–25 mm broad, paraboloid, hygrophanous, chestnut (8F6–8F7), becoming dirty white (8A1–8B1) as pileus dries. Veil not observed. Context approximately 2.0 mm at the centre, fragile, concolorous with pileus. Lamellae 4.0 mm, light brown (8D3–8D5), edges white (8A1), even. Stipes 45–60 mm long, 2.5–3.0 mm thick, fragile, hollow, cylindrical, equal or slightly expanded at base, dirty white (8A1–8B1). Odour and taste indistinctive.

---

**Figure 3.** *Heteropsathyrella macrocystidia* (HMJAU37802) **a** basidiomata **b** basidiospores **c** basidia **d** pileipellis **e** pleurocystidia **f** cheilocystidia **g** caulocystidia. Scale bars: = 10 mm (**a**); 10 μm (**b–g**).
Spores 8.8–9.7 × 4.9–5.8 μm, Q = 1.5–1.9, ovoid in front view, amygdaliform in profile, reddish brown in water, dark brown and gradually becoming black-brown in 5% KOH, inamyloid, smooth, germ pore absent. Basidia 17–20 × 7.3–9.8 μm, clavate, hyaline, 4-spored. Pleurocystidia abundant, 44–68 × 9.8–13 μm, fusiform to narrowly utriform, thin-walled, apex obtuse to subacute, rarely subcapitate. Pleurocystidioid cheilocystidia abundant, 22–32 × 7.3–12 μm, fusiform to utriform, short mucronate or obtuse at apex, rarely mixed with pyriform cells. Trama of gills irregular. Pileipellis consisting of a 1–2-cell-deep layer of subglobose cells that were 30–40 μm broad. Clamps present.

Figure 4. *Psathyrella amygdalinospora* (HMJAU37952) a basidiomata b basidiospores c basidia d pileipellis e pleurocystidia f cheilocystidia. Scale bars: 10 mm (a); 10 μm (b–f).
Habit and habitat. Scattered on mosses in mixed forests of Cunninghamia spp., Pinus spp. and Quercus semecarpifolia.

Other specimens examined. CHINA. Scenic Spot of Kangding Love Song (Mugecuo), Kangding City, Tibetan Autonomous Prefecture of Garzê, Sichuan Province, 22 August 2017, Jun-Qing Yan, HMJAU57044.

Psathyrella piluliformoides T. Bau & J.Q. Yan, sp. nov.
MycoBank No: 838375
Figs 2g, h, 5

Etymology. Reference to its characteristics similar to Psathyrella piluliformis.

Type. CHINA. Kunming Institute of Botany, Kunming City, Yunnan Province, 9 September 2017, Herbarium of Mycology, Jilin Agricultural University (HMJAU37923).

Diagnosis. Differs from Psathyrella piluliformis by having ring and yellow amorphous incrustation at the apex of pleurocystidia.

Pileus 50–60 mm broad, plane, hygrophanous, brown (7C7–7D7) at centre, pale (6B6–6B7) at margin, smooth, striations indistinct at margin. Context thin and fragile, approximately 2.0 mm at the centre, same colour as pileus. Lamellae approximately 4.0 mm, very closed, pale coffee (6C5–6D5), edges paler and even (6B4). Stipe 5.5 mm long, 5.0 mm thick, fragile, cylindrical, hollow, slightly thickened towards base, white (6A1) at apex, base slightly brown, with white evanescent squama. Ring present at 1/3 from stipe apex.

Spores 5.6–6.3 × 3.1–4.4 μm, Q = 1.3–1.9, ellipsoid to oblong-ellipsoid, in profile flattened on one side, pale brown in water, dirty brown in 5% KOH, inamyloid, smooth, germ pore distinct, truncate, 1.1–1.9 μm broad. Basidia 15–18 × 4.9–6.1 μm, clavate, hyaline, 4- or 2-spored. Pleurocystidia 39–54 × 11–15 μm, abundant, utriform to narrowly utriform, or lageniform, rarely fusiform, thick-walled or thin-walled, apex obtuse or broadly obtuse, covered by yellow amorphous incrustation, dissolving in 5% KOH. Cheilocystidia scattered, 24–37 × 9.8–15 μm, utriform, thick-walled or thin-walled, apex obtuse or broadly obtuse, mixed with subglobose to spheropドルDU cells, cells 11–16 × 9.8–14 μm, slightly thick-walled or not. Trama of gills irregular. Pileipellis consisting of a 2–3-cell-deep layer of subglobose cells 34–40 μm broad. Clamps present.

Habit and habitat. Solitary on moss.

Psathyrella truncatisporoides T. Bau & J.Q. Yan, sp. nov.
MycoBank No: 838378
Figs 2i, 6

Etymology. Referring to the truncate spore.
New genus and new species in *Psathyrella s.l.* clade from China

**Type.** China. Wulingken, Baishanzhu, Qingyuan County, Lishui City, Zhejiang Province, Tolgor Bau, Jun-Qing Yan, 16 August 2015, Herbarium of Mycology, Jilin Agricultural University (HMJAU37947).

**Diagnosis.** Differs from *P. rybergii* by its shorter spores (6.8–7.8 μm).

Pileus 8.0–13 mm broad, spreading broadly conical to plane, hygrophanous, pale brown (7C6–7D7), white (7A1–7B1) at margin, striate up to 2/3 from margin. Veil of a thin coating of white to dirty white (7A1–7B1) fibrils, evanescent. Context thin and very fragile, same colour as pileus, approximately 1.0 mm at centre. Lamellae approximately

---

**Figure 5.** *Psathyrella piluliformoides* (HMJAU37923) a basidiomata b basidiospores c basidia d pileipellis e pleurocystidia f cheilocystidia. Scale bars: 10 mm (a); 10 μm (b–f).
1.5 mm broad, pale brown (7B4–7C4), close, adnate, margin even. Stipes 10–25 mm long, approximately 1.5 mm thick, white (7A1), fragile, hollow, smooth but irregularly lumpy, with the base slightly expanding or not. Odour and taste indistinctive.

Spores (5.8)6.8–7.8(8.3) × 4.4–4.9 μm, Q=1.2–1.8, broadly ellipsoid to ellipsoid, in profile flattened on one side, inamyloid, smooth, apex obviously truncate, germ pore distinct, 1.5–2.4 μm broad. Basidia 13–17 × 6.1–7.3 μm, clavate, 4-spored. Pleurocystidia 37–49 × 12–16 μm, utriform to broadly utriform, with obtuse to broad apex, base tapering to a long or short stipe, thin-walled. Cheilocystidia 19–31 × 7.3–12 μm, abundant, similar to pleurocystidia, rarely spheropedunculate, rarely with crystals. Trama of gills irregular. Pileipellis a hymeniderm with 29–39 μm broad cells. Clamps present.

Figure 6. *Psathyrella truncatisporoides* (HMJAU37947) a basidiomata b basidiospores c basidia d pileipellis e pleurocystidia f cheilocystidia. Scale bars: 10 mm (a); 10 μm (b–f).
Habit and habitat. Scattered, terrestrial, in bamboo forest.

Other specimens examined. China. Wulingken, Baishanzhu, Qingyuan County, Lishui City, Zhejiang Province, Tolgor Bau, Jun-Qing Yan, 18 August 2015, HM-JAU57045.

Discussion

The species in the family Psathyrellaceae can be roughly divided into two types by macromorphology: psathyrelloid and coprinoid. *Heteropsathyrella* is macromorphologically similar to *Psathyrella* s.s. but phylogenetically and micromorphologically distinguished from it, differing in the special pileipellis which composed of utriform to subglobose cells covered by a 1 cell deep layer of periclinal hyphae and abundant pseudoparaphyses. There are no other genera in this family, like *Heteropsathyrella*, that match the characteristics of psathyrelloid basidiomata, lamellae adnexed, basidia monomorphic, pseudoparaphyses abundant and pileipellis composed of a cellular subpellis below a hyphal suprapellis covered by scattered and irregular deposits, which dissolve in 5% KOH. Based on the study of this family (Smith 1972; Kits van Waveren 1985; Nagy et al. 2013; Örstadius et al. 2015), a detailed feature comparison between *Heteropsathyrella* and related genera are shown in Table 2. The type species, *H. macrocystidia*, is characterized by stout basidiomata, large pleurocystidia up to 80 μm long, and the generic characters above cited. Thus, this taxon is obviously unique and distinguished from all known species. In the case of not comparing the pileipellis and pseudoparaphyses, few species have the aspect of *H. macrocystidia*: *P. epimyces* (Peck) A.H. Sm. has stout basidiomata, and large pleurocystidia up to 70 μm long, but parasitic on *Coprinus*- or *Coprinopsis*- species (Smith 1972); *P. parvifibrillosa* A.H. Sm. and *P. lauricola* A.H. Sm. & Hesler has large pleurocystidia up to 70 μm long, but basidiomata small, and the shape of pleurocystidia are fusoid and utriform without long stipe at the base, respectively (Smith 1972).

For several of the already formally described and circumscribed clades within *Psathyrella*, phylogenetic analyses suggest that they include a morphologically heterogeneous assemblage of species, and morphological characterization is difficult (Örstadius et al. 2015). The boundaries between species in the *noli-tangere* clade are difficult to characterize; these taxa share the characteristics of spores less than 10 μm long, and utriform, fusiform, lageniform or transition-type pleurocystidia present at the same time. The new species *P. amygdalinospora* forms an independent lineage and differs from the others in spores being ovoid in front view, amygdaliform in profile, and germ pore being absent. Macromorphologically, this species is similar to *P. obtusata* (Pers.) A.H. Sm. and *P. fulvescens* (Romagn.) M.M. Moser ex A.H. Sm, but the spores of *P. obtusata* are ellipsoid to oblong-ellipsoid and pale yellow in 5% KOH (Örstadius and Knudsen 2012), while *P. fulvescens* has an obvious germ pore (Smith 1972).

*P. amygdalinospora* can be classified into section *Pennatae* in Kits van Waveren’s classification system (Kits van Waveren 1985) and in subsection *Limicolae* in Smith’s
Table 2. A summary of morphological characteristics used to discriminate the ten genera.

|                  | Coprinellus | Coprinopsis | Cystoagaricus | Heterophaebryla | Homophron | Kauffmania | Lacrymaria | Pansola | Psathyrella | Typhrasa |
|------------------|-------------|-------------|---------------|-----------------|-----------|------------|------------|---------|-------------|---------|
| **Veil**         | subglobose cdls, hyphae, or absent | hyphae | hyphae | absent | hyphae | hyphae | absent | hyphae, rarely subglobose cells | hyphae |
| **Cap or lamellae** | fully, partilly, or non-deliquescent | deliquescent, rarely non-deliquescent | non-deliquescent | non-deliquescent | non-deliquescent | non-deliquescent | non-deliquescent | non-deliquescent | non-deliquescent | non-deliquescent |
| **Spore surface** | smooth, rarely warty | smooth, rarely warty or with myxosporium | smooth | smooth | smooth | often warty | smooth | smooth, rarely granulose or with myxosporium | smooth |
| **Basidia**      | mono-, di-, tri-, or tetramorphic | Dimorphic | monomorphic | monomorphic | monomorphic | monomorphic | mono- to dimorphic | monomorphic | monomorphic | monomorphic |
| **Pseudoparaphyses** | present | present, rarely absent | absent | present | absent | absent | absent | present | rarely present | absent |
| **Pileipellis**  | hymeniderm to paraderm | Cutis | paraderm | hymeniderm to paraderm | hymeniderm to paraderm | hymeniderm | hymeniderm | hymeniderm, paraderm, rarely cutis | hymeniderm to paraderm |
| **Pileocystidia** | often present | Absent | absent | abundant and regular distribution | simple hairs sometimes present | absent | absent | very rarely present | absent |
| **Sclerocystidia** | sometimes present | Absent | absent | absent | absent | absent | absent | absent | absent | absent |
classification system (Smith 1972). The closest related species can be separated as follows: the pleurocystidia of *P. pennata* (Fr.) A. Pearson & Dennis are fusoid-ventricose with an acute apex and thickened wall (Kits van Waveren 1985); the spores of *P. borealis* A.H. Sm. are ellipsoid and have an obvious germ pore (Smith 1972).

The species in the /pygmaea clade share abundant cheilocystidia and utriform pleurocystidia. The new species *P. truncatisporoides* forms a distinct lineage and groups together with *P. rybergii* Örstedius & E. Larss. in this clade. The closely related *P. rybergii* differs in having spore lengths of 8.5–9.5 μm. Macromorphologically, there are hardly any other species that match the characteristics of *P. truncatisporoides* and they can be separated as follows: *P. rubiginosa* A. H. Sm. has subdistant lamellae and a very inconspicuous germ pores (Smith 1972); the pleurocystidia of *P. noli-tangere* (Fr.) A. Pearson & Dennis are narrowly utriform to lageniform and rarely forked (Kits van Waveren 1985); the spores of *P. elliptispora* A.H. Sm. are 8.0–11.0 μm long (Smith 1972).

The morphological boundary of the /piluliformis clade is basically the same as that of section *Hydrophilae* delineated by Kits van Waveren (1985). The new species *P. piluliformoides* forms a distinct lineage in this clade and can be separated by having an obvious ring. The closely related *P. oboensis* also exhibits very closed lamellae but differs in absence of a ring and clavate-mucronate pleurocystidia. Few species have been described resembling *P. piluliformoides* and they can be separated as follows: *P. piluliformis* (Bull.) P.D. Orton has no ring and without yellow amorphous incrustation at the apex of pleurocystidia (Örstedius and Knudsen 2012); *P. laevissima* (Romagn.) Singer has mucronate pleurocystidia (Kits van Waveren 1985).

**Acknowledgements**

This work was supported by the National Natural Science Foundation of China (32070010 and 31960008) and Jiangxi Provincial Natural Science Foundation (20202BABL213041). Sincere thanks to the anonymous reviewers of this manuscript.

**References**

Bas C (1969) Morphology and subdivision of *Amanita* and a monograph of its section *Lepidella*. Persoonia 5: 96–97.

Fries E (1838) Epicrisis Systematis Mycologici. seu synopsis Hymenomycetum. Uppsala, Sweden.

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic acids symposium series 41: 95–98. https://doi.org/10.1021/bk-1999-0734.ch008

Hawksworth DL, Kirk PM, Sutton BC, Pegler DN (1995) Ainsworth & Bisby’s Dictionary of the Fungi (8th edn.) The Cambridge University Press, UK.

Hawksworth DL, Sutton BC, Ainsworth GC (1983) Ainsworth and Bisby's Dictionary of the Fungi (7th edn.). Commonwealth mycological institute, Surrey.
Hopple JJ, Vilgalys R (1999) Phylogenetic relationships in the mushroom genus *Coprinus* and dark-spored allies based on sequence data from the nuclear gene coding for the large ribosomal subunit RNA: divergent domains, outgroups, and monophyly. Molecular Phylogenetics & Evolution 13(1): 1–19. https://doi.org/10.1006/mpev.1999.0634

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology & Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/mst010

Kirk PM, Cannon PF, David J, Stalpers JA (2001) Ainsworth and Bisby’s dictionary of the fungi (9th edn.). CABI publishing.

Kits van Waveren E (1985) The Dutch. French and British species of *Psathyrella*. Persoonia 2: 1–284.

Körnerup A, Wanscher JHK (1978) The methuen handbook of colour 3rd edn. Eyre Methuen Ltd. Reprint., London.

Nagy LG, Vágvolgyi C, Papp T (2013) Morphological characterization of clades of the Psathyrellaceae (Agaricales) inferred from a multigene phylogeny. Mycological Progress 12: 505–517. https://doi.org/10.1007/s11557-012-0857-3

Nagy LG, Walther G, Házi J, Vágvolgyi C, Papp T (2011) Understanding the Evolutionary Processes of Fungal Fruiting Bodies: Correlated Evolution and Divergence Times in the Psathyrellaceae. Systematic Biology 60: 303–317. https://doi.org/10.1093/sysbio/syr005

Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ (2014) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular biology and evolution 32: 268–274. https://doi.org/10.1037/molbev/msu300

Nylander J (2004) MrModeltest 2.3. Computer program and documentation distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala.

Örstadius L, Knudsen H (2012) *Psathyrella* (Fr.) Quél. In: Knudsen H, Vesterholt J (Eds) Funga Nordica Agaricoid, boletoid, cyphelloid and gasteroid genera. Nordsvamp, Copenhagen, 586–623.

Örstadius L, Ryberg M, Larsson E (2015) Molecular phylogenetics and taxonomy in Psathyrellaceae (Agaricales) with focus on psathyrellloid species: introduction of three new genera and 18 new species. Mycological Progress 14: 1–42. https://doi.org/10.1007/s11557-015-1047-x

Redhead SA, Vilgalys R, Moncalvo JM, Johnson J, Hopple JS (2001) *Coprinus* Pers. and the disposition of *Coprinus* species sensu lato. Taxon 50(1): 203–241. https://doi.org/10.2307/1224525

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Smith AH (1972) The North American species of *Psathyrella*. The New York Botanical Garden 24: 1–633.

White TJ, Bruns TD, Lee SB, Taylor JW, Innis MA, Gelfand DH, Sninsky JJ (1990) Amplification and direct sequencing of Fungal Ribosomal RNA Genes for phylogenetics. Academic Press, San Diego, 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Yan JQ, Bau T (2018a) The Northeast Chinese species of *Psathyrella* (Agaricales, Psathyrellaceae). MycoKeys 33: 85–102. https://doi.org/10.3897/mycokeys.33.24704
Supplementary material 1

Figure S1. Photographs under the microscope
Authors: Tolgor Bau, Jun-Qing Yan
Data type: images
Explanation note: *Heteropsathyrella macrocystidia*: a. Basidiospores, Basidia, Pseudo-paraphyses, and Pleurocystidia; b. Marginal cell; c. Pileipellis; *Psathyrella amygdalinospora*: d. Basidiospores; e. Pleurocystidia; f. Marginal cell; *P. piluliformoides*: g. Basidiospores; h1. Apex of pleurocystidia covered by yellow amorphous incrustation in water; h2. Pleurocystidia; i. Marginal cell; *P. truncatisporoides*: j. Basidiospores; k. Pleurocystidia; l. Marginal cell. Observed under 5% aqueous KOH. Congo Red was used as a stain when necessary. Scale bars: 10 μm.
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/mycokeys.80.65123.suppl1

Supplementary material 2

Figure S2. Phylogram generated by maximum likelihood (ML) analysis
Authors: Tolgor Bau, Jun-Qing Yan
Data type: phylogenetic
Explanation note: Phylogram generated by maximum likelihood (ML) analysis based on sequences of a concatenated data set from four nuclear genes (ITS, LSU, Tef-1α and β-tub) rooted with *Coprinopsis* spp. ML bootstrap proportion (ML-BP) > 75% is shown ● indicates newly described species.
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/mycokeys.80.65123.suppl2