TWO NEW CORPROPHILOUS SPECIES OF PSATHYRELLA

ROY WATLING & MARIA JURAND*

ABSTRACT. Two new species, *Psathyrella fimetaria* Watling and *P. coprophila* Watling are described from Scotland. Cultural characteristics are given and their biological significance discussed. A key to the coprophilous species of *Psathyrella* found in the British Isles is given.

INTRODUCTION

With few exceptions, species of *Psathyrella* are generally regarded as difficult to identify because of lack of literature and disagreements as to the interpretation of the often inadequate old descriptions. It was never thought, however, that the coprophilous members of this genus were to be included in this category for they are few in number and fairly well-documented. One of us (R.W.) during a survey of the Isle of Rhum, North Ebudes, found an unknown species of *Psathyrella* growing on pony dung. It was widespread on the island and extremely common in all areas frequented by these animals. Later the same species was found on horse-dung in several localities in the immediate area of the Kindrogan Field Centre, Perthshire.

Since these collections were made it has been found in other localities in Scotland. A collection from Midlothian made by R. F. O. Kemp, which was microscopically similar, was assumed to be referable to the same species. However, cultural characters of the two species were found to be at variance, and a detailed micro-anatomical analysis was made resulting in the finding of several differences between the Midlothian collection, and the Perthshire and Rhum specimens. The Midlothian material has been successfully induced to produce fruit-bodies over several generations. The purpose of this paper is to formally describe the two species as new and discuss various cultural characteristics. It would be safe to say that on classical criteria alone, few would have suspected that two distinct species were involved but now that the differences have been demonstrated there would appear to be little difficulty in separating the two.

TAXONOMY

(R. Watling)

1. Psathyrella fimetaria Watling, **sp. nov.** Fig. 1.

Pileus 5–12 mm, e conico vel conico-convexo conico-expansus vel expansus late umbonatus, castaneus vel badius, sicco pallide-ochraceus vel argillaceo-albidus, ad discum obscuriore coloratus ochraceo-tinctus, jove pluvio striatus, jove sicco leviter ruguloso-atomatus primo, ad partem externam squamulis fibrillosus ad marginem residuis veli fugacibus dispensis. *Lamellae* late adnatae e pallido- vel purpureo-umbrinae, subconfertae ad aciem albidae vel interdum albido-flocculosae. *Stipes* 40–55 × 2–3 mm, aequalis

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vel ad basim leviter interdum flexuosus, albidus vel sursum pallide sordido-brunneolus, ad apicem albo-pruinosus, ad basin albo-vel albido strigulosо-fibrillosus. *Caro* tenuissimo, pilei concolorata, stipites albido. *Sporae* ellipsoideae, poro germinative, 13·5–14·5(–15) × 6·5–7·5(–8) μm. *Basidia* 4-sporigera. *Cystidia* aciei lamellarum praecipue 25–30 × 10·5–15 μm, ad apicem 5·5–7 μm. *Cuticula pilei* cellularis.

Typus: Scotland, Isle of Rhum, *Watling* 7355

Pileus 5–12 mm (up to 14 mm high), conical to convex then expanded, very rich chestnut-brown or bay-brown at first, darker at disc, hardly darkening with age although becoming flushed sepia, striate at margin at first then ½ to ¾ way with age, rapidly drying to become atomate and pale greyish buff to ochraceous; margin with silvery-white veil fibrils. *Stipe* 40–55 × 2–3 mm, equal or slightly swollen at base, whitish throughout only slightly darker towards base at maturity, slightly subtomentose at very base where attached to substrate. *Gills* adnate, sepia-pallid at first, then flushed purplish sepia, soon purple-black, with slightly paler or whitish flocculose margin, slightly mottled as spores mature. *Flesh* white in stipe slightly ochraceous or watery honey in pileus, paler when dry. *Veil* copious at margin of pileus when very young and on stipe, soon becoming lost or adpressed when on stipe.

Spore-mass purple-chestnut. *Basidiospores* ellipsoid in face-view, slightly flattened in side-view, 13·5–14·5(–15) × 6·5–7(–8) μm, thick-walled, dark vinaceous brown with hint of umber in water, unchanged by ammoniacal solutions or Melzer's reagent, although decolorised by concentrated sulphuric acid; apiculus small but distinct, germ-pore obvious c. 1 μm broad, central. *Basidia* 4-spored, 22·5–25 × 11·0–12 μm, clavate, monomorphic, hyaline in water, hardly coloured in KOH or ammoniacal solutions. *Cheilocystidia* numerous, hyaline in water and ammoniacal solutions, elongate lageniform or narrowly lageniform. *Pleurocystidia* present, hyaline, similar to narrowest cheilocystidia, or fusiform, 37–40 × 10·5–11·5 μm (apex—4·5–5 μm), hyaline in ammoniacal solutions. *Pileal surface* composed of broad irregularly rounded, ellipsoid to obovate cells with distinctly brownish coloured walls; *pileocystidia* absent. *Caulocystidia* variable up to 45 μm long × 5·5–10·5 μm, in small clusters, elongate lageniform—subcapitate to clavate, hyaline in water and ammoniacal solutions. *Pileus-trama* of irregularly rounded, ellipsoid to ovate cells, 11·5–18·5 μm broad with strongly coloured walls, flattened and elongate towards the darker base. *Hymenophoral trama* homogeneous with regularly arranged swollen cells, brownish in both water and alkali solutions, dark red-brown in ammoniacal solutions in central zone and immediately beneath pileus-trama. *Clamp-connections* infrequent, only seen in cells of stipe. *Stipe cortex* of elongate cylindric cells, c. 10 μm broad with brownish or dark ochraceous coloured walls. *Veil* very sparse and of elements 3·5–5·5 μm broad.

On horse and pony dung, solitary or in small groups, sometimes attached in twos and threes at base, Isle of Rhum, 25 viii 1964, *Watling* 7355 (Type) & *Watling* 7356; Kilmory, Isle of Rhum, 26 viii 1964, *Watling* 7357; 17 viii 1967 & 3 ix 1968, Kindrogan, Perthshire, *Watling* 7440; 22 viii 1970, Straloch, Perthshire, *Watling* 7441 & 7470.

Recognised by lack of pink-edged gills, presence of pleurocystidia, a copious veil when very young and size and shape of basidiospores.

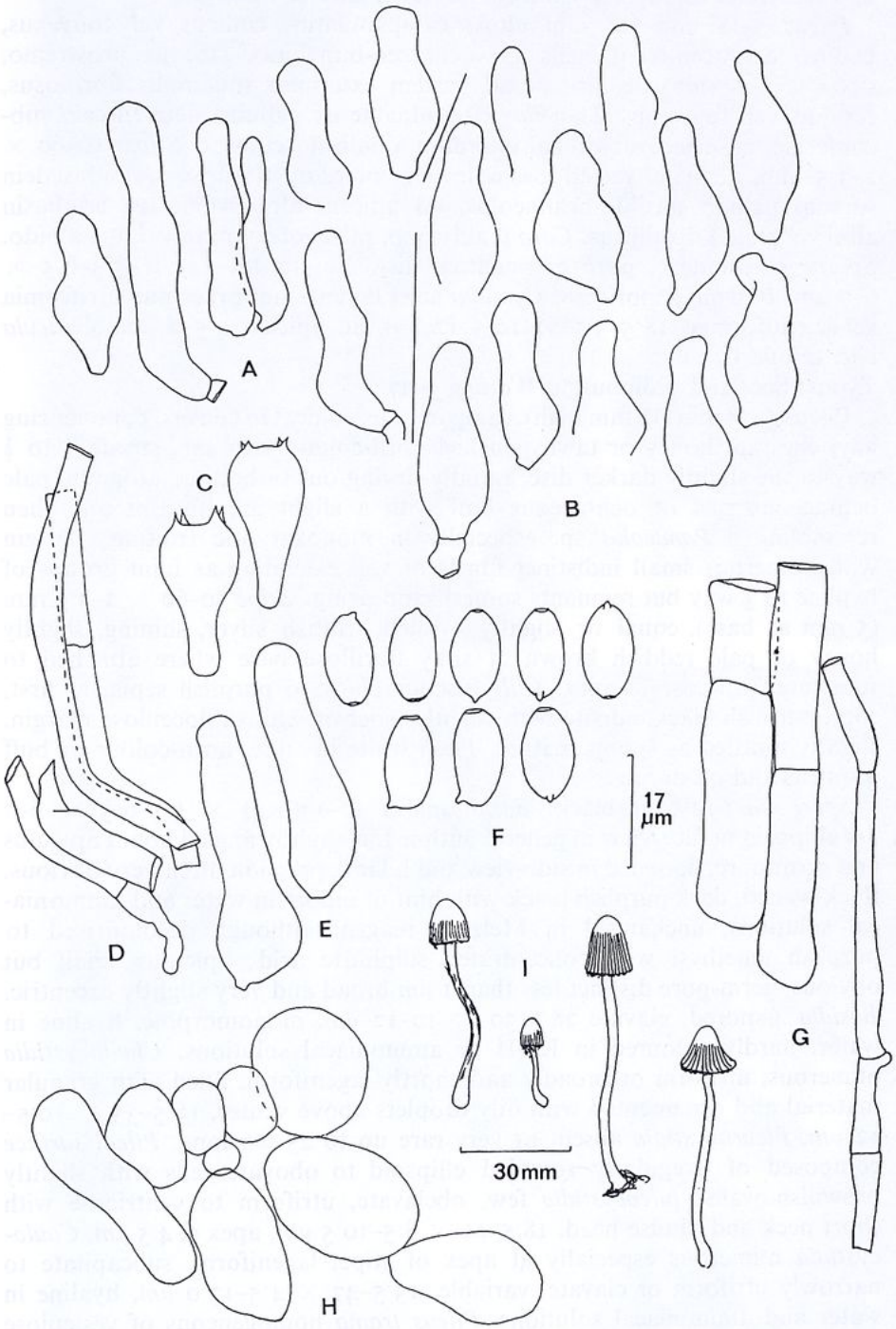

FIG. 1. *Psathyrella fimetaria*: A, caulocystidia; B, cheilocystidia; C, basidia; D, veil-elements; E, pleurocystidia; F, basidiospores; G, cortical cells of stipe; H, pileal surface; I, habit-sketch. Magnification of all microscope structures as indicated.

2. Psathyrella coprophila Watling, **sp. nov.** Fig. 2 & Plate 3.

Pileus 5–18 mm (18 mm altus) campanulatus, conicus vel convexus, badius, ochraceo-ferrugineus vel ochraceo-bubalinus, striatus prostremo, sicco leviter atomatus primo, ad partem externum squamulis fibrillosus, residuis veli fugacibus. *Lamellae* late adnatae ex pallidae dein fuscae, subconfertae, ad aciem albido vel interdum albido-flocculosae. *Stipes* 50–60 × 2–3·5 mm, aequalis vel ad basin leviter interdum flexuosus, albidus dein sursum pallide sordido-brunneolus, ad apicem albo-pruinosus, ad basin albo vel albido fibrillosus. *Caro* tenuissimo, pilei concolorata, stipitis albido. *Sporae* ellipsoideae, poro germinativo distincte, 12–13(–14) × 5·5–6·5 × 6–7 μm. *Basidia* 4-sporigera, *Cystidia* aciei lamellarum praecipue utriformia vel lageniformia, 18·5–3·5 × 10·5–12 μm, ad apicem 4·5–6 μm. *Cuticula pilei* cellularis.

Typus: Scotland, Edinburgh, *Watling* 3947.

Pileus 5–18 mm (18 mm high), campanulate, conical to convex, commencing bay, chestnut honey or tawny flushed horn-colour with age, striate ¼ to ½ way to the slightly darker disc, rapidly drying out to become atomate, pale ochraceous rust or ochraceous buff with a slight greyish tint and then resembling a *Panaeolus* sp. especially in monokaryotic fruiting; margin with numerous small indistinct fibrils of veil extending as faint groups of hyphae to ½ way but remnants soon disappearing. *Stipe* 50–60 × 2–3·5 mm (5 mm at base), equal or slightly swollen, whitish silver, shining, slightly honey or pale reddish brown at silky fibrillose base where attached to substrate, pruinose at apex. *Gills* fuscous black to purplish sepia, at first, soon purplish black, adnate with slightly paler or whitish flocculose margin, slightly mottled as spores mature. *Flesh* white in stipe, horn-colour or buff in pileus and on drying.

Spore-mass fuscous black. *Basidiospores* 12–13(–14) × 5·5–6·5 × 6–7 μm ellipsoid in face-view in general outline but slightly angled about apiculus and germ-pore, flattened in side-view and hilar depression often very obvious, thick-walled, dark purplish black with hint of umber in water and ammoniacal solutions, unchanged in Melzer's reagent although decolourised to purplish amethyst with concentrated sulphuric acid; apiculus small but obvious, germ-pore distinct less than 1 μm broad and very slightly excentric. *Basidia* 4-spored, clavate 28·5–30 × 10–12 μm, monomorphic, hyaline in water, hardly coloured in KOH or ammoniacal solutions. *Cheilocystidia* numerous, utriform or broadly and shortly lageniform, filled with granular material and ornamented with oily droplets above venter, 16·5–35 × 10·5–12 μm. *Pleurocystidia* absent or very rare up to 25 μm long. *Pileal surface* composed of irregularly rounded ellipsoid to obovate cells with slightly brownish walls; *pileocystidia* few, obclavate, utriform to ventricose with short neck and obtuse head, 18·5–21 × 8·5–10·5 μm, apex c. 4·5 μm. *Caulocystidia* numerous especially at apex of stipe, lageniform, subcapitate to narrowly utriform or clavate, variable, 13·5–47 × 4·5–13·0 μm, hyaline in water and ammoniacal solutions. *Pileus trama* homogeneous of vesiculose cells up to 20 μm broad with or without slightly brownish walls in water and alkali. *Hymenophoral trama* homogeneous, composed of regularly arranged swollen cells, hyaline in water or slightly brownish in ammoniacal solutions. *Clamp-connections* present, numerous on cortical cells of stipe. *Veil* remnants on pileus of hyaline, filamentous cells, 3·5–8 μm broad with

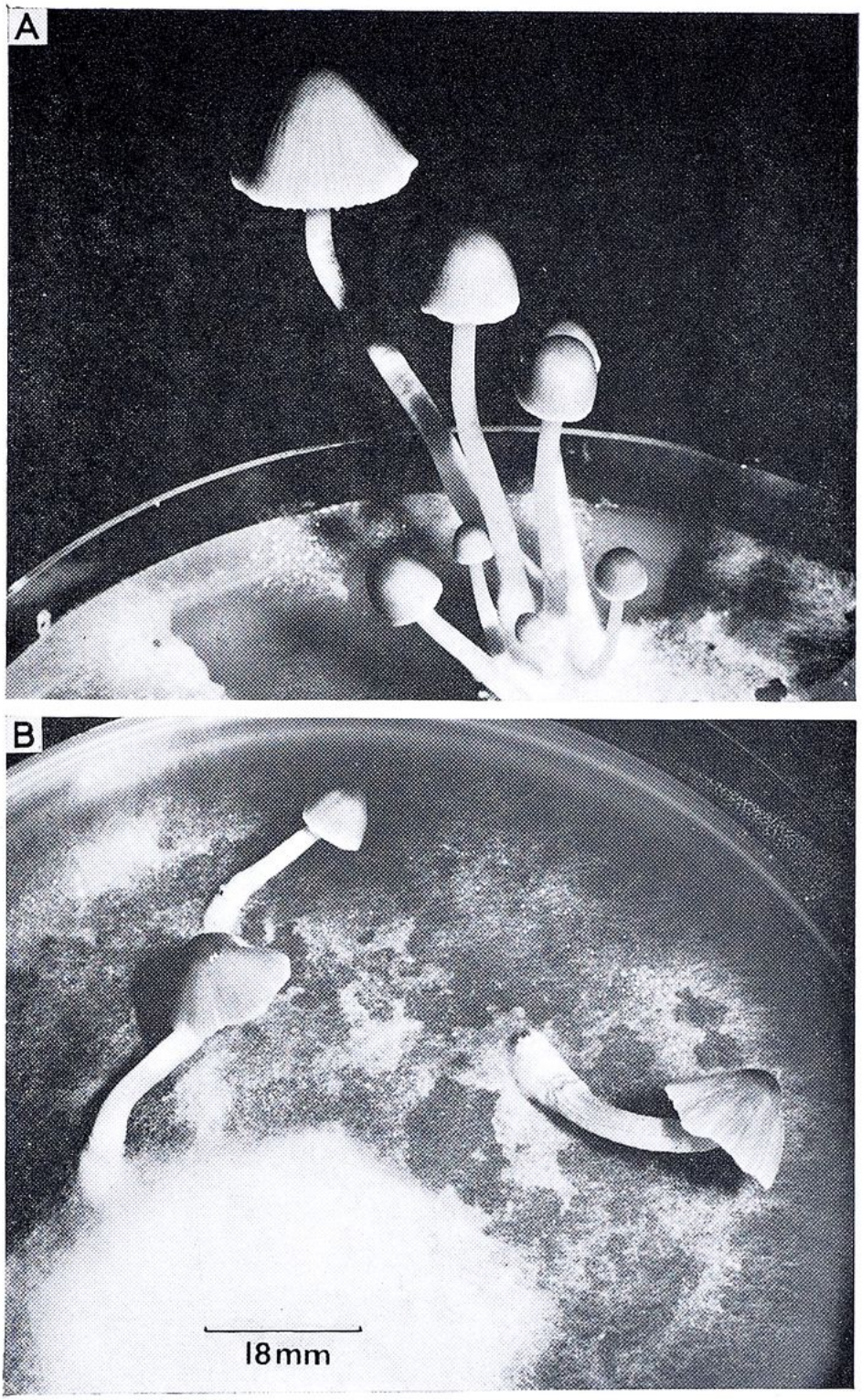

PLATE 3. Fruit-bodies of *Psathyrella coprophila* grown in culture: A, dikaryotic fruit-bodies; B, monokaryotic fruit-bodies. Size as indicated.

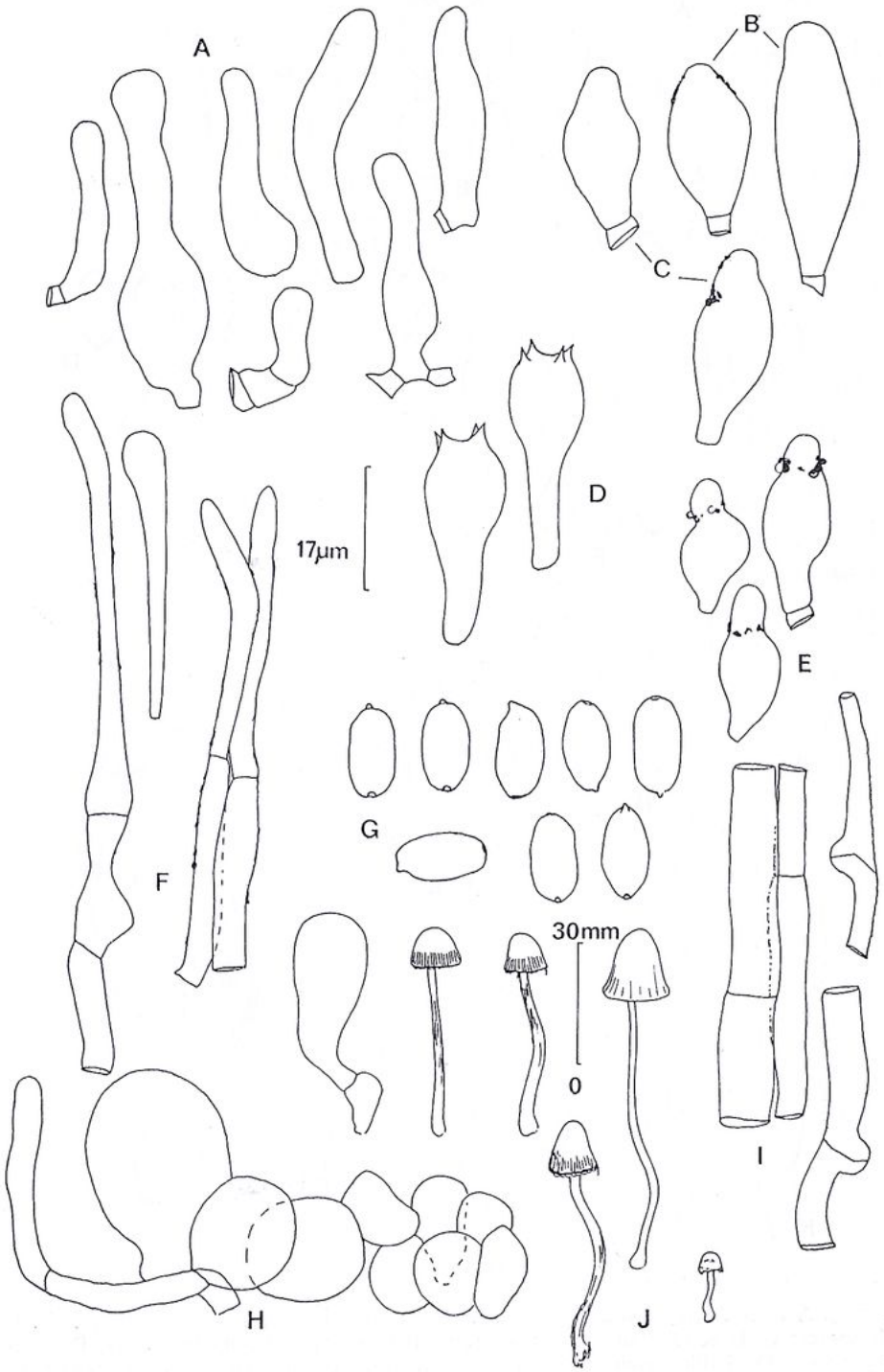

FIG. 2. *Psathyrella coprophila*: A, caulocystidia; B, cheilocystidia; (from culture) C, cheilocystidia (from original collection); D, basidia; E, pleurocystidia; F, veil-elements; G, basidiospores; H, pileal surface; I, cortical cells of stipe; J, habit-sketch. Magnification of all microscope structures as indicated.

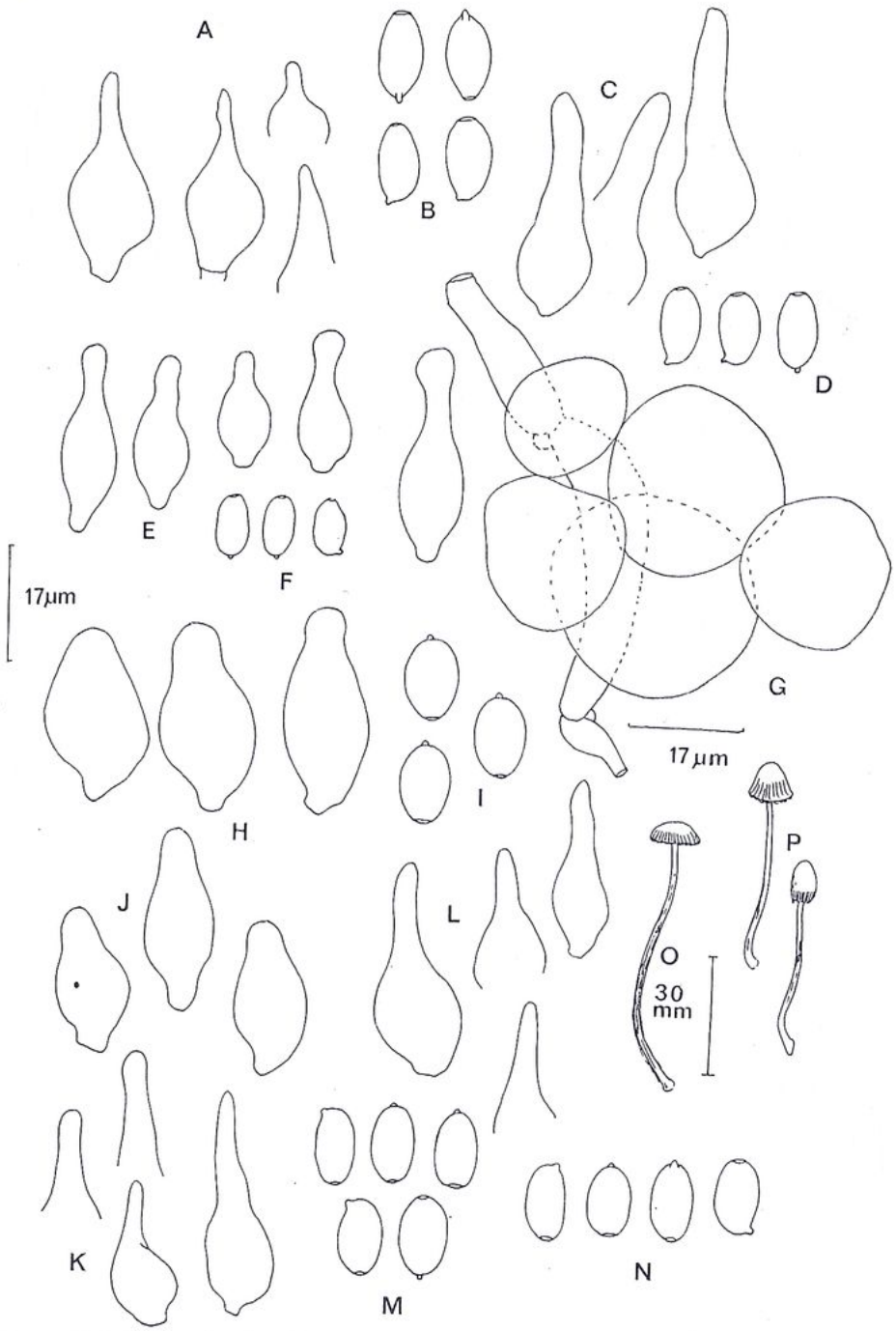

FIG. 3. A & B, *Psathyrella* aff. *stercoraria*: *Orton* 2193 in E; A, cheilocystidia; B, basidiospores; C, D & O, *Psathyrella stercoraria*, *Watling* 7359; C, cheilocystidia; D, basidiospores; O, habit-sketch; E–G, *Psathyrella sphaerocystis*: (type—*Orton* 2193); E, cheilocystidia; F, basidiospores; G, veil-constituents; H–J & P, *Psathyrella* aff. *coprophila*, *Watling* 5069; H, cheilocystidia; I, basidiospores; J, pleurocystidia; P, habit-sketch; K–N, *Psathyrella coprobia*; K, cheilocystidia & N, basidiospores (from *Watling* 7358 Scotland); L, cheilocystidia & M, basidiospores (from *Watling* 3514, Idaho U.S.A.). Magnification as indicated.

slightly irregular wall ornamentation. *Stipe cortex* of elongate, cylindric cells 4–8 μm broad.

On horse dung, solitary or in small groups, Blackford Glen, Edinburgh, 1 xi 1966, *Watling* 3947, legit *R. F. O. Kemp* (subsequently in culture, *Watling* 5063, 5064 and 6020).

P. coprophila freely produces fruit-bodies in Petri-dishes on agar-surfaces but these are more variable than those found in nature. The largest sized fruit-bodies resemble the size of *P. fimetaria* collected on Rhum. *P. fimetaria* is normally more of a robust species.

P. coprophila can be distinguished by the white margin to the gills, thin, fugacious white veil which is very easily lost on handling or at maturity, size of basidiospores and honey to tawny pileus-colour. It is separable morphologically from *P. fimetaria* in size, basidiospore-shape and sparsity of pleurocystidia.

Discussion

The spore-size and the dark colour of the spore-print place both these species in *Psathyrella* subgenus *Psathyrella*. Both these newly proposed species lack the pink-edged gills typical of *P. stercoraria* Kühn. & Joss. Both species differ from *P. coprobia* by the lack of the copious, white flocculose veil and paler pileus-colour, although they would appear to be fairly closely related. The Rhum collections were at first referred to Smith's interpretation of *Psathyrella coprobia* (J. Lange) A. H. Smith as outlined in the notes accompanying the '*New Check list of British Agarics and Boleti*' (Dennis et al., 1960). However, referring to Smith's original description and his personal notes, the emphasis placed on basidiospore-size by the British authors would appear too great. One of us (R.W.) has collected typical *P. coprobia* in the western United States in the presence of A. H. Smith, and the European (Fig. 3 K & L) and American (Fig. 3 M & N) concepts agree.*

Searching the literature has failed to find a name for either of our fungi. The recently described *P. sphaerocystis* P. D. Orton (Fig. 3 E–G) differs markedly in the presence of a mealy-granular veil. *P. stercoraria* (Fig. 3 C, D & O), which has been seen recently in Scotland, is also unrelated in the characters of the cheilocystidia, although it is similar in the size of the basidiospores and the fugacious veil remnants; it is a very small fungus. The presence or absence of a pink-edged gill is a difficult character to determine and almost impossible in dried material. However, fruit-bodies at all stages of development have been available for both *P. fimetaria* and *P. coprophila* and no evidence of a red-line at the gill-edge, at any stage during the life-history, has been found.

Key to the British species of Coprophilous Psathyrella

1 Veil composed of globose, ellipsoid or vesiculose cells; basidiospores 8–9 × 4·5–5·5μm . *P. sphaerocystis* P. D. Orton, 1964

\+ Veil when present composed of filamentous cells; basidiospores over 9 μm long 2

* *Watling* 3514, Hughes Fork, Upper Priest River, Idaho, U.S.A. (E).

2 Basidiospores over 6 μm wide (13–16 × 7–8 μm); pileus ochraceous brown soon becoming alutaceous or ochraceous cream, or ivory; gills brownish . *P. albidula* (Romagn.) Moser, 1955

\+ Basidiospores rarely wider than 6 μm, or if up to 6·5 μm then 13 μm or less in length 3

3 Pileus convex to semiglobate, red-brown and entirely covered in white, floccose veil remnants; basidiospores 10–12 × 5·5–6 μm . . . *P. coprobia* (J. Lange) A. H. Smith, 1941

\+ Pileus campanulate, smooth but for occasional remnants of veil when young 4

4 Gill-margin coloured reddish; pileus small up to 8 mm broad *P. stercoraria* Kühn. & Joss.,* 1957

\+ Gill-margin not red, white or only slightly paler than gill-face . 5

5 Basidiospores 10·5–11·5 × 8–8·5 μm *P.* aff. *coprophila* Watling (Fig. 3 H–J)

\+ Basidiospores 12 μm or over in length, less than 8 μm in breadth 6

6 Pleurocystidia present; basidiospores 12–13(–14) × 5·5–6·5 × 6–7 μm . . . . . *P. coprophila* Watling

\+ Pleurocystidia scarce; basidiospores 13·5–14·5(–15) × 6·5–7·5 (–8) μm . . . . . *P. fimetaria* Watling

Culture studies

(M. K. Jurand)

In both *P. coprophila* and *P. fimetaria* all mycelia were grown from the spores of one fruit-body only. The fruit-body of *P. coprophila* was the type specimen from Midlothian and the fruit-body of *P. fimetaria* was collected in Perthshire (*Watling* 7470).

All descriptions and experimental studies were made on mycelia grown on agar plates at 20°C on horse dung extract medium (Lange 1952).

1. P. coprophila Watling

Macroscopic characters. Monocaryotic mycelial colony growing to 37–46 mm diameter in 7 days, mainly submerged, almost transparent, later producing varying amounts of aerial growth, then appearing sparsely woolly, often patchy; aerial hyphae frequently with glistening droplets. Margin of colony regular.

Dikaryotic mycelial colony growing to 60–65 mm diameter in 7 days, with strong radial growth lines; aerial hyphae less frequent than in monokaryons. Margin of colony regular.

Microscopic characters. Basidiospores germinating within 24 hours to form an irregularly branched colony.

Monokaryotic mycelium with no clamp-connections; hyphal diameter at first branch 2·9–3·7 μm. Angle of side branches 45°–65°. Oidia cylindrical 3·0–4·5 × 1·2 μm, borne on aerial hyphae in wet heads, which later coalesce to form droplets.

* A collection made by Orton related to this species is illustrated in Fig. 3 A & B (Surlingham, Norfolk, 27 vii 1960, *Orton* 2193). This collection, however, differs in size of fruit-body and several anatomical details.

Dikaryotic mycelium with clamp-connections at most septa; hyphal diameter at clamp-connections 3·7–5·0 μm. Angle of side branches 25°–45°. Dikaryotic hyphae only rarely producing monokaryotic side branches which bear oidial heads.

Fruiting in culture. Dikaryons form primordia after about 14 days of incubation in the light and mature fruit-bodies after about 20 days. (Plate 3A).

Some monokaryotic strains form monokaryotic fruit bodies after three to four weeks of incubation in the light (Plate 3B).

A comparison of dikaryotic and monokaryotic fruit bodies in *P. coprophila* is summarised below.

	Dikaryotic	*Monokaryotic*
Colour of cap	snuff-brown	fulvous
Size of cap	5–15 mm	5–10 mm
Length of stipe	20–50 mm	10–35 mm
Posture of stipe	erect	almost prostrate
Colour of gill	cigar brown	fawn
Colour of gill edge	cigar brown	fawn
Spore density	abundant	few
Colour of spore print	fuscous black	—
Spore size	12·5–14·0 × 6·5 μm	12·5–14·0 × 6·5 μm
Spore no. per basidium	4	4
Pleurocystidia	absent or infrequent	abundant
Cheilocystidia	present	present

Most of the differences shown above are the direct effect of differences in spore-density. The main diagnostic character of a monokaryotic fruit-body is the absence or low density of spore-print. The only difference which is independent of spore density is stipe posture. The stipes of dikaryotic fruit-bodies are firm and erect while those of monokaryotic fruit-bodies lack directed growth. This is thought to be due to a difference in their response to gravity.

2. P. fimetaria Watling

Macroscopic characters. Monokaryotic mycelial colony growing to 16–25 mm diameter in 7 days, mainly submerged almost transparent; aerial hyphae few. Margin of colony regular.

Dikaryotic mycelial colony growing to 35–38 mm diameter in 7 days. Growth mainly submerged at first, then woolly aerial hyphae produced abundantly in patches. Margin of colony regular.

Microscopic characters. Basidiospores germinating to produce at first a long unbranched hypha, later a sparsely branched colony.

Monokaryotic mycelium with no clamp-connections, hyphal diameter at first branch 3·3–4·2 μm. Side branches fewer than in *P. coprophila*, set at an angle of 50°–70°. Oidia cylindrical, borne on submerged hyphae; aerial droplets of coalesced oidial heads formed less frequently than in *P. coprophila.*

Dikaryotic mycelium with clamp-connections at most septa; hyphal diameter at clamp-connections (2·9)–3·3–4·2 μm. Angle of side branches 50°–70°.

Fruiting in culture. No mature fruit bodies were obtained, but primordia occasionally formed in cultures contaminated with bacteria.

EXPERIMENTAL STUDIES

Breeding Systems. Both *P. coprophila* and *P. fimetaria* are heterothallic and have mating alleles at a single locus (bipolar). *P. coprophila* was shown to be a bipolar species by Kemp (personal communication) by crossing strains grown from several basidiospore tetrads. The spores of each tetrad were isolated with a micromanipulator. The breeding system of *P. fimetaria* was shown to be bipolar by using monokaryotic mycelia grown from basidiospores obtained from a spore-print. Ten monokaryotic mycelia were cross-mated in all combinations.

Nuclear Migration. In many Basidiomycetes a monokaryotic mycelium can be rapidly dikaryotised by the migration of nuclei into it from a dikaryotic inoculum. Dikaryotisation also occurs when two compatible monokaryons come into contact.

An experiment was designed to test whether migration of nuclei from a dikaryon into a monokaryon occurs in *P. coprophila* and *P. fimetaria.* In each species six different monokaryons, each replicated twice, were used with the same dikaryon. The monokaryotic colonies were allowed to grow till the plates were almost covered with mycelium. The original inoculum was then removed and replaced by a dikaryotic inoculum of the same species. To test the rate of nuclear migration, plugs 5 mm apart were taken every 24 hours, and were examined later for the presence of clamp-connections. In this way the distance travelled by the dikaryotizing nuclei was estimated.

It was found that the nuclei of *P. coprophila* migrated, on average, the radial distance of 47 mm in 7 days, a rate approximately 1·5 times as great as the growth rate of the dikaryon. The nuclei of *P. fimetaria* did not migrate at all even by the fifth day of sampling.

If these results are indicative of what happens in other populations of both species in nature then their implications may be considerable. In natural populations of *P. coprophila* nuclear migration might allow an established monokaryon to be dikaryotized by a secondarily established mycelium of the same species, thus giving rise to a mycelium mosaic. In natural populations of *P. fimetaria* the mycelia probably remain more individually distinct. This difference in migration potential may have played a part in the evolution of the two species.

Intersterility between the species. The intersterility of *P. coprophila* and *P. fimetaria* was tested by mycelial mating and oidial homing.

a) *Mycelial mating.* Four monokaryons, two of each mating type, of each species were crossed in all combinations. No dikaryons were formed.

This indicates that representative populations of two species are intersterile when allowed to meet in the artificial environment of the agar plate. In nature this genetical isolation would have permitted morphological divergence of the two taxa.

b) *Oidial homing.* Oidial homing, first observed by Kemp (1970) is a reaction between hyphae and oidia of the same species. When oidia are smeared on the edge of a monokaryotic colony the hyphal tips grow towards the oidia and later fuse with them. The directed growth of the hyphal tips

towards the oidia can be clearly seen under the low power of the microscope and the whole test can take less than one hour.

An experiment was designed to test the hyphal homing in both species using strains of different mating types. The results showed that reciprocal tests between the species never gave any reaction but that within both *P. coprophila* and *P. fimetaria*, monokaryotic hyphae fuse with the oidia of their own species regardless of mating type. Dikaryotic hyphae can also home, but the reaction is less distinct than that of a monokaryon.

The results of the homing experiment agree with those of the mycelial mating experiment. Both suggest that *P. coprophila* and *P. fimetaria* are reproductively isolated.

Conclusion

The results show that experimental studies can be of use to the fungal taxonomist, both as a source of characters and as a means of confirming the validity of taxa. In this case the type of breeding system and the presence of nuclear migration may be used as taxonomic characters along with morphological ones. The mycelial mating and homing experiments have been used to test the biological status of the two taxa. Their unambiguous results independently confirmed the conclusions reached by morphological considerations.

Acknowledgments

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