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Fimicolous species of *Coprinopsis* sections *Cinereae, Lanatulae, Radiatae* and *Xenobiae* in Britain, including *Coprinopsis kempii sp. nov*.

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Abstract: The genus *Coprinopsis* as circumscribed by Redhead *et al*. (2001), was divided into 20 sections by Wächter & Melzer (2020) based on an extensive analysis of DNA sequences. As part of a continuing study of sections *Cinereae*, *Lanatulae*, *Picaceae*, *Radiatae* and *Xenobiae* in Britain, the present paper reviews dung inhabiting *Coprinopsis* species in four of these sections (sect. *Picaceae* lacking any dung-inhabiting species). *Coprinopsis villosa* is here reported for the first time in Britain, and the new species *C. kempii*, found on Pony dung at Burnham Beeches, is proposed as well. The species *C. pseudoradiata* has been recorded often from Britain but the relatively few associated fungarium specimens we have been able to examine have failed to match the description or published sequences of that species. Several such collections were of *C. candidolanata*, a species recognised as British in 2013. We have examined the holotype of *C. pseudoradiata* and its ITS sequence matches that of the holotype of *Coprinopsis bicornis*, for which we propose the name *Coprinopsis pseudoradiata* var. *bicornis*.

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INTRODUCTION

Phylogenetic analyses based on sequences of the 28S rDNA region (LSU) by Hopple & Vilgalys (1994, 1999) and Moncalvo *et al*. (2000) demonstrated that *Coprinus* in the broad sense understood until then was not monophyletic. *Coprinus comatus*, the type of the genus, nested in the family *Agaricaceae* along with *C. sterquilinus*, it was separated from the majority of species previously included in the genus *Coprinus*. These species formed a large clade, intermixed with many *Psathyrella* and some other species. Redhead *et al*. (2001) reviewed the accumulating DNA phylogenetic evidence, the past application of names and earlier Coprinoid studies. They delineated three genera within a new family, *Psathyrellaceae*, namely: *Coprinellus*, *Coprinopsis* and *Parasola*.

Schafer (2010a) transferred nine subsections of *Coprinus* sensu Uljé (2005), as sections of *Parasola* (sect. *Glabri* and *Auricomi*), *Coprinellus* (sect. *Setulosi*, *Micacei* and *Domestici*) and *Coprinopsis* (sect. *Atramentarii*, *Alachuani*, *Narcotici* and *Nivei*); the remainder comprising species in *Coprinus* s. str. Unfortunately, three of the sections (*Coprinellus* sect. *Setulosi*, *Coprinopsis* sect. *Alachuani* and *Parasola* sect. *glabri*) were incorrectly named. The genus name should have been applied to each section as autonym since the section included the genus type. In any case, the morphology-based classifications were shown to require revision on the basis of molecular studies of the *Psathyrellaceae*, particularly Nagy *et al*. (2012, 2013a, b), Örstadius *et al*. (2015), and Szarkándi *et al*. (2017). More recently, in a major revision supported by extensive analysis of the molecular phylogeny, Wächter & Melzer (2020) proposed an arrangement that added two new Coprinoid genera: *Narcissea* and *Tulosesus*. A much larger number of more narrowly defined sections was proposed, including 20 sections of *Coprinopsis*. However, the generic name *Tulosesus* is illegitimate since it includes a species that is the accepted lectotype of an earlier legitimate genus, *Agaricus ephemerus* Bull. (1789), the genus being *Ephemerocybe* Fayod (1889), discussed by Donk (1962) and Redhead *et al*. (2001). Species in *Tulosesus* have therefore been transferred to *Ephemerocybe* by Yang *et al*. (2025).

The present study provides a review of British fimicolous species in sections *Lanatulae*, *Cinereae* and *Radiatae*. These sections comprise species with veil in chains of filamentous cells, often narrowing obtusely at the septa, like chains of sausages, and often forming pointed tufts on the cap (Uljé & Noordeloos 1999, Schafer 2010a). *Coprinopsis* section *Lanatulae* originally included common and much collected or studied species like *C. lagopus* and *C. cinerea*. However, a proportion of species in sect. *Lanatulae* were moved by Wächter & Melzer (2020) to the new sections *Radiatae* and *Cinereae*, with several distributed in other sections.

Other species in *Coprinopsis* section *Xenobiae* and section *Picaceae* are treated in the present work as well. These sections

include somewhat similar species having thin walled, filamentous veil that is branched and/or diverticulate but lacks the Lanatulae-type veil. The phylogenetic analysis aims to clarify the checklist of British species comparing published sequences and newly found British collections. The paper provides a key and detailed morphological descriptions of British fimicolous species in these sections.

After *C. candidolanata* was recorded (from north-east Yorkshire) in 2013 and added to the Checklist of British and Irish Basidiomycetes (CBIB) in Update 7 (Ainsworth & Henrici 2016), the following fimicolous species were on the British list, grouped in the sections proposed by Wächter & Melzer (2020):

a) Sect. *Cinereae*: *C. cinerea*.
b) Sect. *Radiatae*: *C. radiata*, *C. candidolanata*.
c) Sect. *Xenobiae*: *C. luteocephala* and *C. xenobia*.
d) Indetermined section: *C. bicornis* and *C. pseudoradiata*.

The species *C. macrocephala*, reported on dung or other substrates, has been distinguished from *C. radiata* on the basis of fruitbody size and spore size (Orton & Watling 1979, Uljé 2005) but sequences of specimens with such characteristics have consistently matched *C. radiata* in phylogenetic studies and any distinction from that species is unclear (Nagy *et al*. 2013, Wächter & Melzer 2020).

New collections identified as these species or close to these species were examined morphologically and by molecular phylogeny in the present work. One collection from the City of London Corporation's Burnham Beeches nature reserve, sporulating on Exmoor Pony dung in 2017 and subsequent years, had been recognised as morphologically distinct from other species and was included in the present study.

MATERIALS AND METHODS

Morphological studies

Newly collected specimens were photographed in situ, taking notes of the macroscopic characters, habitat and associations, or when sporulating later in lab. Collections were examined fresh, when possible, or dried soon after collection. Dried material was examined after soaking in either 10 % aqueous ammonia or in Congo Red solution followed by washing off with aqueous ammonia. A Leica MZ APO dissecting microscope at magnifications from ×8 to ×80 was used to examine the fruitbody for the presence of cystidia, veil and other critical features. Slides were examined at up to ×1000 in oil in a Leica DMLS trinocular microscope. Microscopic structures were photographed through the eyepiece or with an attached camera or from a screen with an attached video camera. Spores and other features were measured from the photographs.

Collections are either deposited at the Royal Botanic Gardens at Kew (referred to by the designation K(M) or K-, followed by the accession number), or are deposited in the Keiths Wood Research Fungarium managed by Derek Schafer.

DNA extraction, amplification and sequencing

Total DNA was extracted from dry specimens employing a modified protocol based on Murray & Thompson (1980). PCR reactions (Mullis & Faloona 1987) included 35 cycles with an annealing temperature of 54 ºC. The primers ITS1F, ITS1, ITS4 and NLB4 (White et al. 1990, Gardes & Bruns 1993, Martin & Rygiewicz 2005) were employed to amplify the ITS rDNA region, and in some cases, LR0R and LR5 (Vilgalys & Hester 1990, Cubeta et al. 1991) were used for the 28S rDNA region, and EF1-983F, EF1-1567R and EF1- 2218R (Rehner & Buckley 2005) for the translation elongation factor 1a (tef1) gene. PCR products were checked in 1 % agarose gels, and amplicons were sequenced with one or both PCR primers. Sequences were corrected to remove reading errors in chromatograms.

One of the samples (the holotype of *C. pseudoradiata* at Geneva, Kuhner 19440417) was extracted with a special protocol using a prior treatment with PTB coupled with Promega EZNA Forensic DNA extraction kit (Stielow *et al.* 2012, modified from Erickson *et al.* 2005). The resulting DNA was sent for PCR amplification of ITS1 region (primers ITS1F + ITS2) and NGS sequencing to StabVida (Caparica, Portugal).

Alignments and phylogenetic analyses

BLASTn (Altschul *et al.* 1990) was used to select the most closely related ITS rDNA sequences from the International Nucleotide Sequence Database Collaboration public database (INSDC, Arita *et al*. 2021). The sequences retrieved were mainly from studies conducted by Wächter & Melzer (2020). All sequences (Supplementary Table 1) were first aligned in MEGA v. 5.0 (Tamura *et al.* 2011) with its Clustal W application and then realigned manually as needed to establish positional homology. Aligned sequences were loaded in MrBayes v. 3.2.6 (Ronquist *et al.* 2012), where a Bayesian analysis was performed (single partition, GTR+G+I model, two simultaneous runs, four chains, temperature set to 0.2, sampling every 100th generation) until the average split frequencies between the simultaneous runs fell below 0.01 after 2.09 M generations. Finally, a full search for the best-scoring maximum likelihood tree was performed in RAxML v. 8.2.12 (Stamatakis 2014) using the standard search algorithm (single partition, GTRGAMMAI model, 2000 bootstrap replications). The significance threshold was set above 0.95 for posterior probability (PP) and 70 % bootstrap proportions (BP).

RESULTS

The ITS rDNA sequences obtained from the fimicolous collections studied in the present work nest in five major clades of genus *Coprinopsis* (Fig 1), corresponding to the sections *Cinereae*, *Lanatulae*, *Radiatae* and *Xenobiae* delineated in Wächter & Melzer (2020) except that the *C. pseudoradiata/ C. bicornis/ C. scobicola* clade in our phylogram occupies an intermediate position between the core of this section and the sister clade, sect. *Radiatae*. We feel this is best accommodated by including this group of species in sect. *Radiatae*, but results do not support this taxonomic decision, probably because of the insufficient information provided by ITS rDNA alone. Based on these results and morphological observations, the following British species are here identified:

1) *Coprinopsis kempii*. In sect. *Radiatae*, four collections of a *Coprinopsis* on pony dung from Burnham Beeches nest

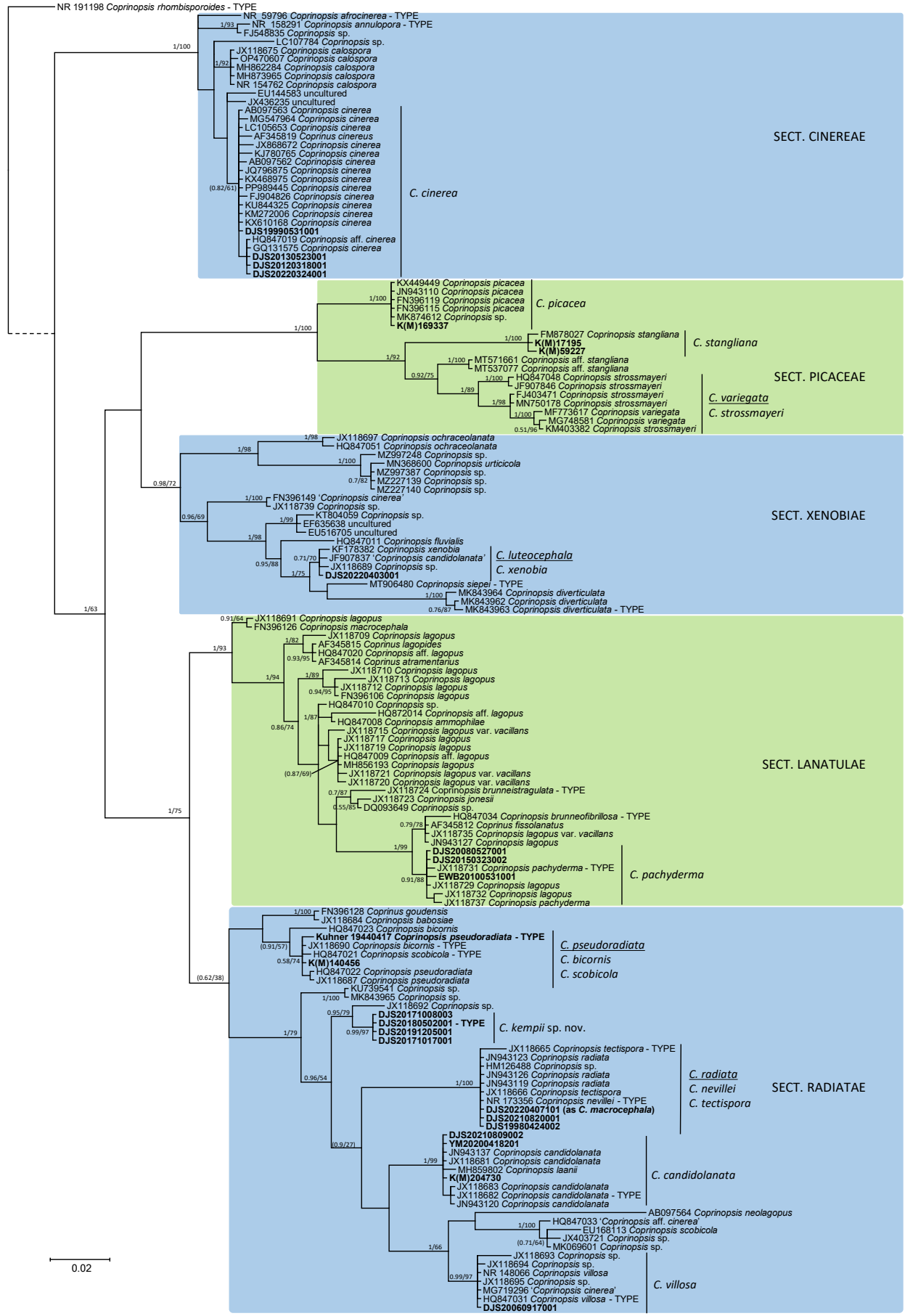


Fig. 1. A 50 % majority rule ITS rDNA consensus phylogram of selected sequences of *Coprinopsis* sects. *Cinereae*, *Lanatulae*, *Picaceae*, *Radiatae* and *Xenobiae* (with *C. rhombisporoides* Voto & Deschuyteneer from sect. *Coprinopsis* as outgroup) obtained using MrBayes from 2925 sampled trees. Nodes were annotated if they were supported by ≥ 0.95 Bayesian posterior probability (left) or ≥ 70 % maximum likelihood bootstrap proportions (right). Nonsignificant support values are exceptionally represented inside parentheses. Sequences newly generated in this study are in bold.

in a clade distinct from sequences of other species and we propose here that they comprise a new species, *Coprinopsis kempii*, which is formally introduced below. This species has veil with strings of generally unbranched thin-walled cells mixed with branched, diverticulate (but not coralloid) filamentous cells. Clamp connections are present in both forms of veil cell. Sequence JX118692, a collection from Sweden (SZMC-NL-3193), reported as *Coprinopsis* sp. 2 in Nagy *et al*. (2013), may also belong here.

2) *Coprinopsis radiata*. Two *C. radiata* collections from Burnham Beeches: DJS20210820001, a collection from August 2021 on Pony dung and DJS20220407101, collected in April 2022 on deer (probably Muntjak) dung; and one, DJS19980424002 on a cow dung/straw heap in Whitchurch in April 1998, all in Buckinghamshire, nest with sequences of other collections of this species from around the world. *Coprinopsis tectispora*, a lignicolous species with a dissociating dark perispore described by Van de Bogart (1979) from Washington State (USA) was reported from Britain by Schafer (2010b). This collection, from Oxfordshire, Schafer 20090720001 was sequenced in Nagy *et al*. (2013), and its ITS rDNA (Genbank JX118666) matches the sequences of the Burnham Beeches and Whitchurch *C. radiata* collections in our phylogram. One of those collections, DJS20220407101, on deer dung, was tentatively identified as *C. macrocephala* (following Uljé 2005), with large, broad spores. However, it also nests in the clade with *C. radiata* and *C. tectispora*. The holotype of *C. nevillei* (Garcia & Vellinga 2010; LIP GG08090401; GenBank ITS: NR 173356) also belongs in this clade, despite its growing on a stem of *Polygonatum* and not on dung, as noted by Wächter & Melzer (2020; on page 1253); the species epithet is misspelled.

3) *Coprinopsis candidolanata*. Also in sect. *Radiatae*, three collections of *C. candidolanata*: K(M)204730 from north-east Yorkshire in 2013; YM20200418201 from east Norfolk in 2020; and DJS20210809002, from Burnham Beeches, Buckinghamshire in 2021 nest in a monophyletic clade along with six published sequences of that species. Of these, JX118682, appears to be the holotype from Italy (Uljé *et al.* 2000), but no herbarium code is indicated. The species is characterised by veil comprising strings of unbranched, sausage-shaped filamentous cells mixed with branched and highly diverticulate/coralloid cells, a lack of clamp connections, spores ellipsoid to ovoid, occasionally more or less cylindrical in face view, ellipsoid, sometimes slightly flattened on one side in side view; around 8–10 × 5–7 µm. An ITS sequence (MH859802) of a culture sample identified with the earlier name *C. laanii* Kits van Wav. (CBS 476.70, United Kingdom, 10 Sep. 1969, *R.F.O. Kemp*) nests in this clade too, but this conflicts with another ITS sequence of the same culture (GQ249276) that was included in Wächter & Melzer (2020), nesting in sect. *Narcoticae*. *Coprinopsis laanii* is a very distinctive species with spores that have a strongly developed, erratic and undulating perispore and typical sect. *Narcoticae* ornamented globose veil, so the MH859802 identification must be incorrect, possibly because of some failure of procedure or contamination.

4) *Coprinopsis villosa*. Another clade in sect. *Radiatae* includes the holotype of *C. villosa*, SZMC-NL-1758 (Nagy *et al.* 2013, GenBank ITS: HQ847031). A 2006 collection on horse dung from Whippendell Woods in Hertfordshire, DJS20060917001, has cap veil with strings of generally unbranched thin-walled cells, brownish coloured at the apex, mixed with branched but very narrow and not diverticulate filamentous cells. It was recorded when collected as *C. pseudoradiata* but, in the present study, was found to nest in the *C. villosa* clade. This is reported here as the first collection of *C. villosa* from Britain. It has slightly smaller spores than described by Nagy *et al.* (2013) for the holotype, but the average spore size matches that of the earlier Hawaii collection (Keirle *et al.* 2004).

5) *Coprinopsis pseudoradiata*. The ITS rDNA-based phylogram (Fig. 1) does not confirm a direct relationship between *C. pseudoradiata* and sect. *Lanatulae* s. str., but an apparent (not significant) relation with sect. *Radiatae*. The holotype of *C. pseudoradiata*, Kühner 19440417, originally deposited at Lyon herbarium (LY, Kühner & Josserand 1944, Watling 1976), now at Geneva herbarium (G), was examined in this study. The species has veil in strings of unbranched filamentous cells, narrowing obtusely towards the septa, interspersed with some narrower, cylindrical cells. The broader cells vary distinctly in length and breadth, including some very broad, occasionally even spherical terminal cells and some sequences of very short cells within the strings. This somewhat irregular structure is similar to the veil of *C. bicornis*. Clamp connections are present; spores are slightly narrower than those of *C. candidolanata* but otherwise of similar size to that species. We provide here a description of the species based on our recent study of the holotype and its published studies, Kühner & Josserand (1944) and Watling (1976).

There are more than 80 records of *C. pseudoradiata* from Britain (Richardson 2015; FRDBI). However, most are without fungarium collections. A 1998 collection from the New Forest in the herbarium of the Royal Botanic Gardens at Kew, identified when collected as *C. pseudoradiata*, was sequenced in the present study and nested in the *C. candidolanata* clade. A 1999 collection from Lodore Wood in Cumberland, also determined when collected as *C. pseudoradiata*, was here re-determined morphologically as *C. candidolanata*, but failed to provide a DNA sequence. Indeed, with one remaining collection, deposited at Kew as *C. pseudoradiata*, failing to provide a sequence and no collections from Britain being found at RBG Edinburgh, we have no sequence as yet of a four-spored British collection of *C. pseudoradiata*.

Our phylogram seems to agree with the results of Nagy *et al*. (2013), which showed that sequences of the two-spored *C. bicornis* type, collections of *C. pseudoradiata* from Norway and the British type of *C. scobicola* clustered closely in their phylogenetic tree, despite the morphological differences. However, the present analysis obtained only a partially significant support for this clade (PP 0.58, ML 74), so its status needs to be confirmed with additional information from protein-coding genes. In any case, our study of the *C. pseudoradiata* holotype suggests it could be closely related with the *C. bicornis* and *C. scobicola* types phylogenetically. Morphologically, the veil characteristics are similar, but spores in *C. bicornis* are somewhat larger. On this basis, we feel that the combination *C. pseudoradiata* var. *bicornis* would be more appropriate for this taxon. The morphological and substrate differences with *C. scobicola* are greater. Further study of additional collections and genes may support it as a close sister species. The issue of two-spored versus four-spored taxa is discussed further below.

6) *Coprinopsis pachyderma*. The remaining (non-fimicolous) sequences in sect. *Lanatulae* analysed in the present work mainly consist of the *C. lagopus* complex. This non-fimicolous species complex was considered in Nagy *et al.* (2013) to be largely unresolved, identifying six phylogenetic species (PS1 to PS6) among other unresolved clades. Wächter & Melzer (2020) identified seven unresolved clades labelled as /lagopus A to /lagopus G but attached the names *C. brunneofibrillosa* and *C. pachyderma* to clades that, together, correspond to the Nagy *et al.* (2013) PS6. We have included three British collections of *C. pachyderma* in our phylogram. DJS20080527001 (E6) is a collection among wood chip in Buckinghamshire in 2008 and DJS20150323002 (F6) is a collection growing in mulch inside the Palm House at Kew in 2015; both were identified as *C. pachyderma*. The third collection, EWB20100531001, was tentatively identified as *C. cinerea* in 2010 but its sequence matched *C. pachyderma* as well. Its morphology and habitat also matched *C. pachyderma* when re-examined. These three sequences nest in a clade with other collections of *C. pachyderma*, including the holotype FVDB 3237 (GenBank ITS: JX118731). It should be noted that sequence JX118737 (Uljé1273) in that clade is a Derek Reid collection from England, Chichester, discussed in Uljé & Noordeloos (1999) and not from the Netherlands as listed in Nagy *et al.* (2013).

7) *Coprinopsis stangliana*. In sect. *Picaceae*, K(M)17195 is the 1991 collection of *C. stangliana* from Box Hill, Surrey described in Henrici & Læssøe (1993); K(M)59227 is a 1998 Derek Schafer collection of that species from Wytham Woods, Oxford.

8) *Coprinopsis picacea*. K(M)169337 is a 2010 Andy Overall collection from Hampstead Heath.

9) *Coprinopsis variegata/strossmayeri*. Sequence MN750178 (Douglas *et al*. 2020) is the first British record in this complex.

10) *Coprinopsis luteocephala*. In sect. *Xenobiae*, DJS20220403001 is a 2022 Derek Schafer collection identified as *C. luteocephala* on cow dung from Burnham Beeches. We regard *C. luteocephala* as probably synonymous with *C. xenobia* but perhaps in need of further study including type sequencing if possible, *C. luteocephala* appearing to have the earlier date (Watling 1972). In the clade, sequence JF907837 (*C. candidolanata*) was reviewed in Wächter & Melzer (2020) and considered to be a misidentification.

11) *Coprinopsis cinerea*. In sect. *Cinereae*. The description is based on four collections: DJS19990531001 is a collection from Whitchurch, Buckinghamshire growing on a cow dung-straw heap in May 1999; DJS20130523001 is a collection from near Clough Wood in Derbyshire in May 2013 on a similar substrate; DJS20120318001 was collected in March 2012 from Whitchurch on a cow/horse dung heap and DJS20220324001 was collected on a horse dung/straw heap in Knebworth, Hertfordshire in March 2022.

Key to fimicolous species of the studied *Coprinopsis* sections in Britain

The following key is provided to distinguish the different fimicolus species studied in the present work. When substrate association is less clear, a broader range of taxa needs to be considered and keys to a larger range of possible species have to be considered.

All species are deliquescent as they develop and drop spores; all, except *C. luteocephala, C. siepei* and some collections of *C. villosa*, have veil initially of white silvery threads, s.m. made of strings of thin-walled sausage-shaped or rounded cells ("*Lanatuli*-type veil"), and grow on either pure dung or dung mixed with vegetation (especially on dung/straw heaps). The veil components may also include a variety of other cell types and may colour the veil initially or as the basidiocarp matures.

1. Cap veil with *Lanatulae*-type veil either entirely or mixed with diverticulate veil.....2

1. Cap veil entirely of branched, diverticulate, mainly thin-walled cells, turning yellow in maturing fruitbodies, or entirely of narrow cylindrical hyphae, 6–14 µm wide.....9

2. Average spore length in mature fruitbodies >12 µm; cap veil substantially all of *Lanatuli* type.....3

2. Average spore length in mature fruitbodies <12 µm; cap veil may include substantial proportion of diverticulate or other cell types.....4

3. Spores with germ pore raised, detaching in KOH, robust fleshy species with stipe up to 150 × 15 mm, cap yellowish with greyish veil, spores 11–14.5 × 7.5–8.5 µm, on herbivorous dung or vegetable waste..... ***C. annulopora*** (not British)

3. Spores with germ pore not raised and not detaching in KOH.....***C. radiata***

4. Basidia 2-spored.....***C. pseudoradiata* var. *bicornis***

4. Basidia 4-spored.....5

5. Cap veil includes diverticulate cells (Figs 2, 8, 19).....6

5. Cap veil does not include significant amounts of diverticulate cells; additional narrower filamentous, branched or unbranched veil may or may not be present (Figs 5–6, 11, 12, 17)..... 7

6. Diverticulate veil cells with coralloid excrescences, clamp connections absent.....***C. candidolanata***

6. Diverticulate veil cells with narrower, less rounded excrescences, clamp connections present.....***C. kempii***

7. Average breadth of spores >5.75 µm; veil substantially of regular *Lanatuli* type cells or chestnut brown in part and with very narrow additional components.....8

7. Average breadth of spores <5.75 µm; veil varied and irregular with large rounded cells varying in length along the strings, mixed with strings of cylindrical cells 3 to 14 µm wide .....***C. pseudoradiata* var. *pseudoradiata***

8. Spores on average 9–11 × 6–7 µm., some having a protruding germ pore with a detachable cap; veil generally of *Lanatuli* type, varying from wide cells at the base to narrow at the tip; a robust species, often in small bunches, stipe firm at the base; common e.g. on dung-straw heaps but not generally on pure dung.....***C. cinerea***

8. Spores on average 8.5–12 × 6–7.5 µm, ellipsoid to ovoid in frontal view, ellipsoid to subamygdaloid or sometimes slightly phaseoliform in lateral view; immature spores have an epispore layer initially in longitudinal ridges, giving them a cog-wheel shape in end view and some spores may present with fragments of perispore (Fig. 17); veil chestnut brown or at least brownish towards the top of the cap; mixed, with strings of sausage-shaped cells and narrow smooth filamentous hyphae, mostly < 4 µm wide; less robust species found so far only on horse dung.....***C. villosa***

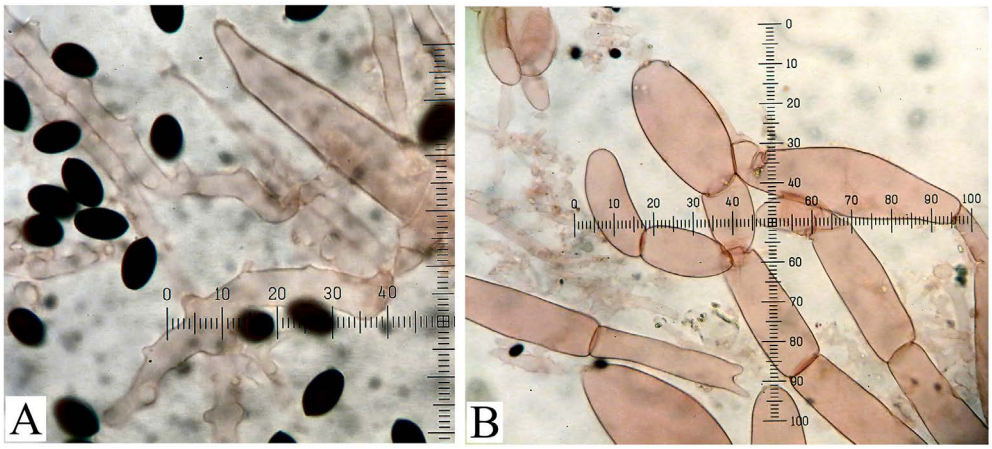


Fig. 2. *Coprinopsis candidolanata* cap veil. **A.** x1000, scale division = 1 µm. **B.** x400, scale division = 2.5 µm.

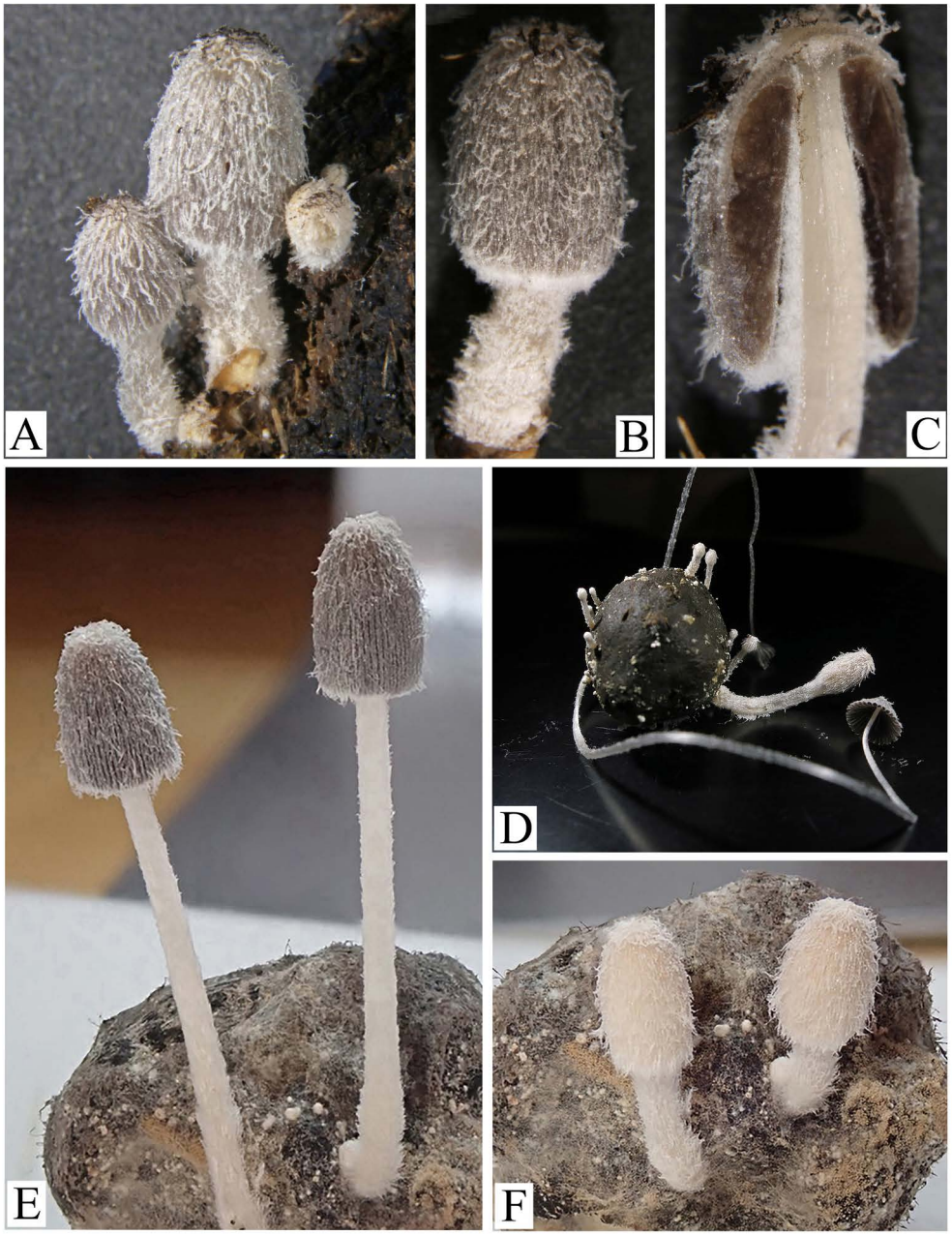


Fig. 3. *Coprinopsis candidolanata* fruitbodies. **A, B, C.** DJS20210809002, on cow dung, Burnham Beeches. **D.** DJS20230923101, on sheep dung, Strensall Common. **E, F.** YM20200418201, on deer dung, Martham Broad, photo Yvonne Mynett.

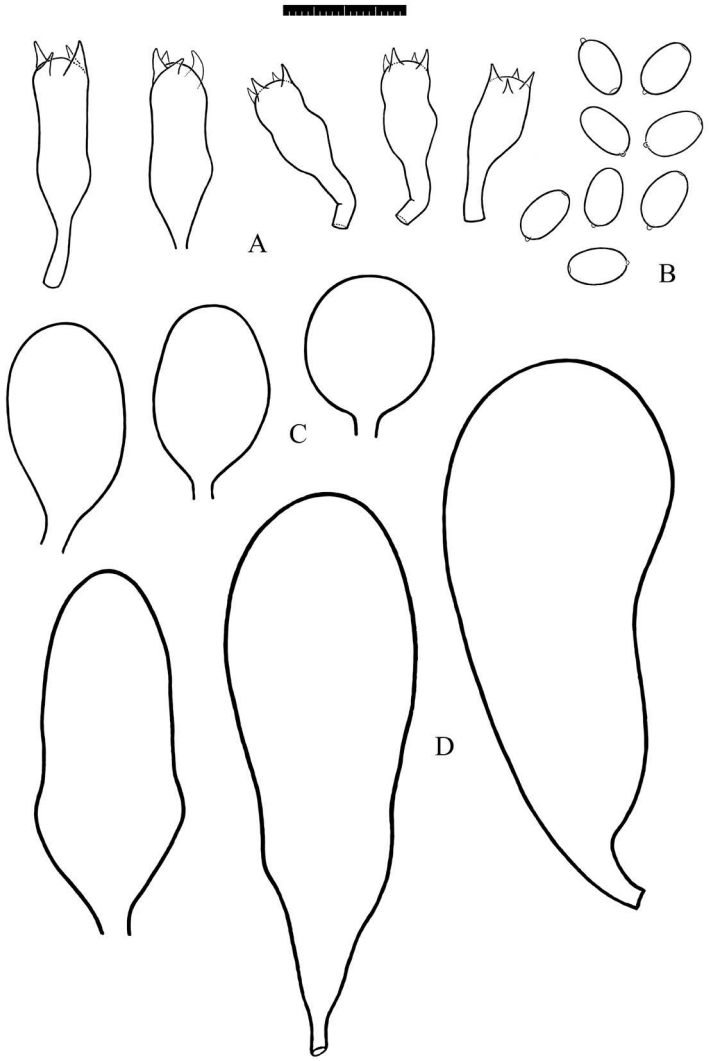


Fig. 4. *Coprinopsis candidolanata.* **A.** Basidia. **B.** Spores. **C.** Cheilocystidia. **D.** Pleurocystidia. Scale bar = 20 µm.

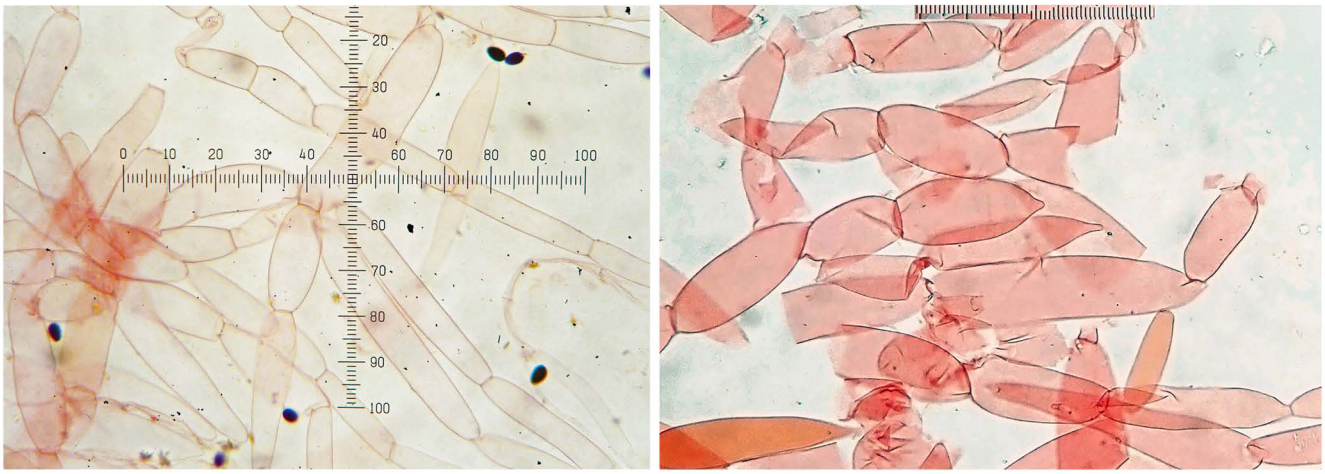


Fig. 5. *Coprinopsis cinerea* DJS20120318001, on cow/horse dung-straw heap, Cap veil x400. Scale division 2.5 µm.

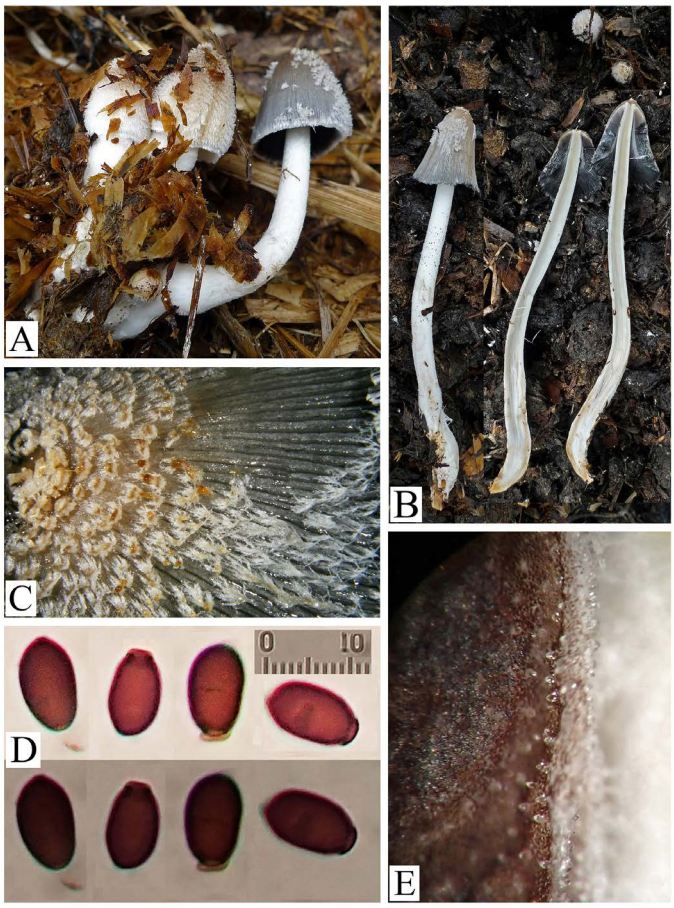


Fig. 6. *Coprinopsis cinerea.* **A, B.** Basidiocarps, DJS20120318001 on cow/horse dung-straw heap**.** C. Cap veil, DJS20120318001 on cow/horse dung-straw heap. **D.** DJS20130523001, Spores x1000, upper four lightened to show germ pore, scale division 1 µm. **E.** DJS20220324001, gill.

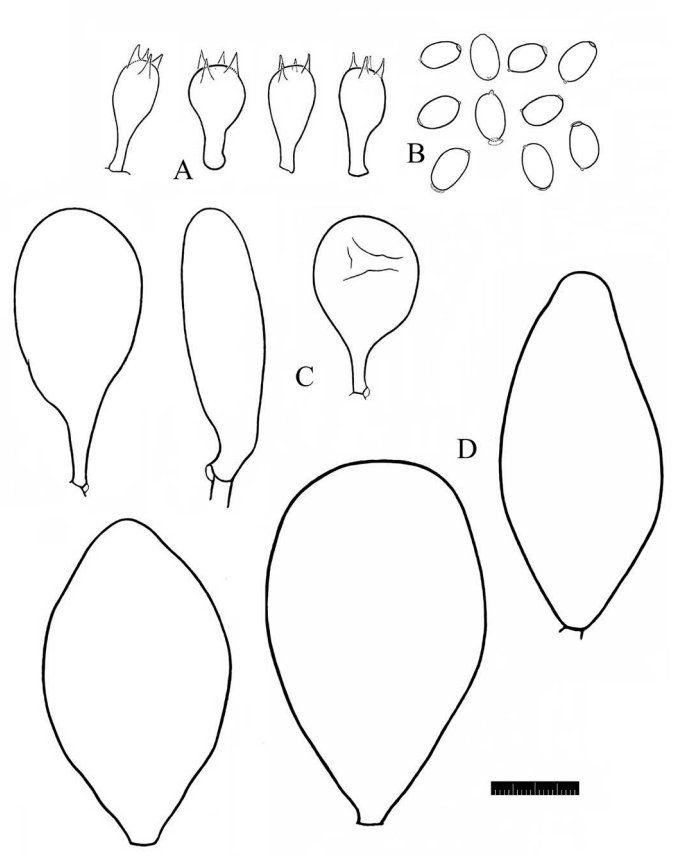


Fig. 7. *Coprinopsis cinerea* basidia. **A.** Spores. **B.** Cheilocystidia. **C.** Pleurocystidia. **D.** Scale bar = 20 µm.

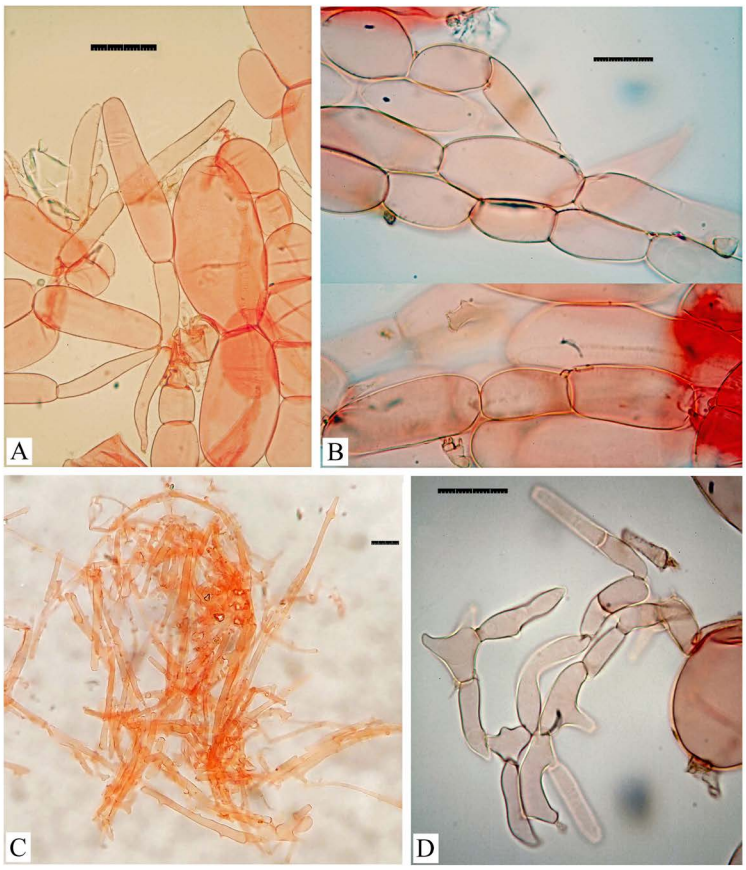


Fig. 8. *Coprinopsis kempii*. **A.** DJS20171008003, cap veil x400. **B.** DJS20171017001, cap veil x1000. **C.** DJS20191117001, cap veil x1000. **D.** DJS20171017001, cap veil x1000. Scale bar = 20 µm.

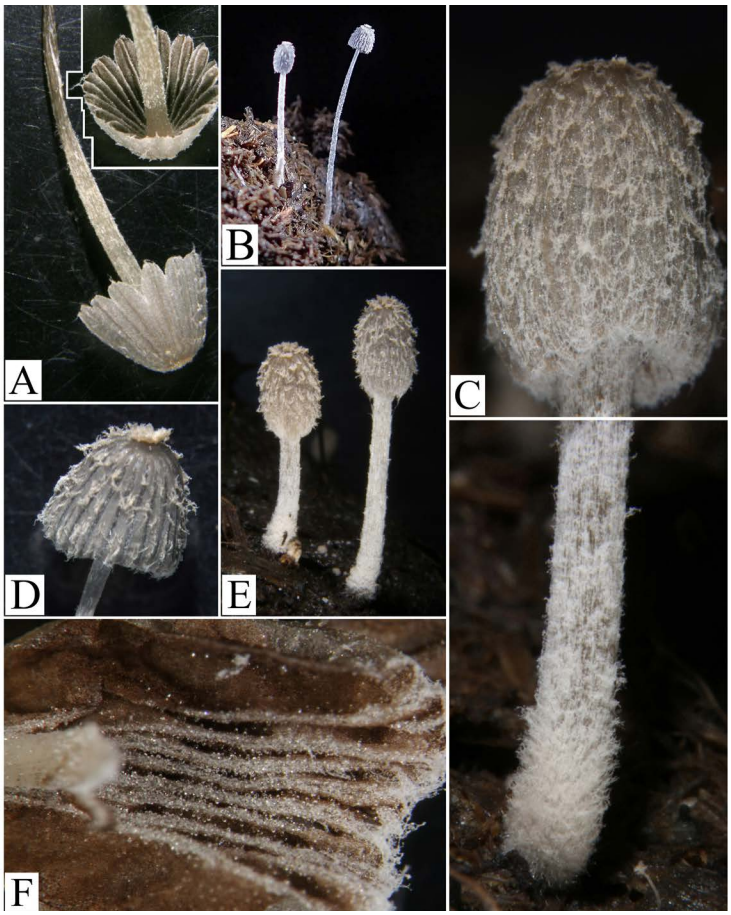


Fig. 9. *Coprinopsis kempii* on Pony dung, from Burnham Beeches. **A.** DJS20191117001, basidiocarps. **B, D.** DJS20180502001, K-M1447368, basidiocarps. **C, E.** DJS20191205001, basidiocarps. **F.** DJS20191205001, gills.

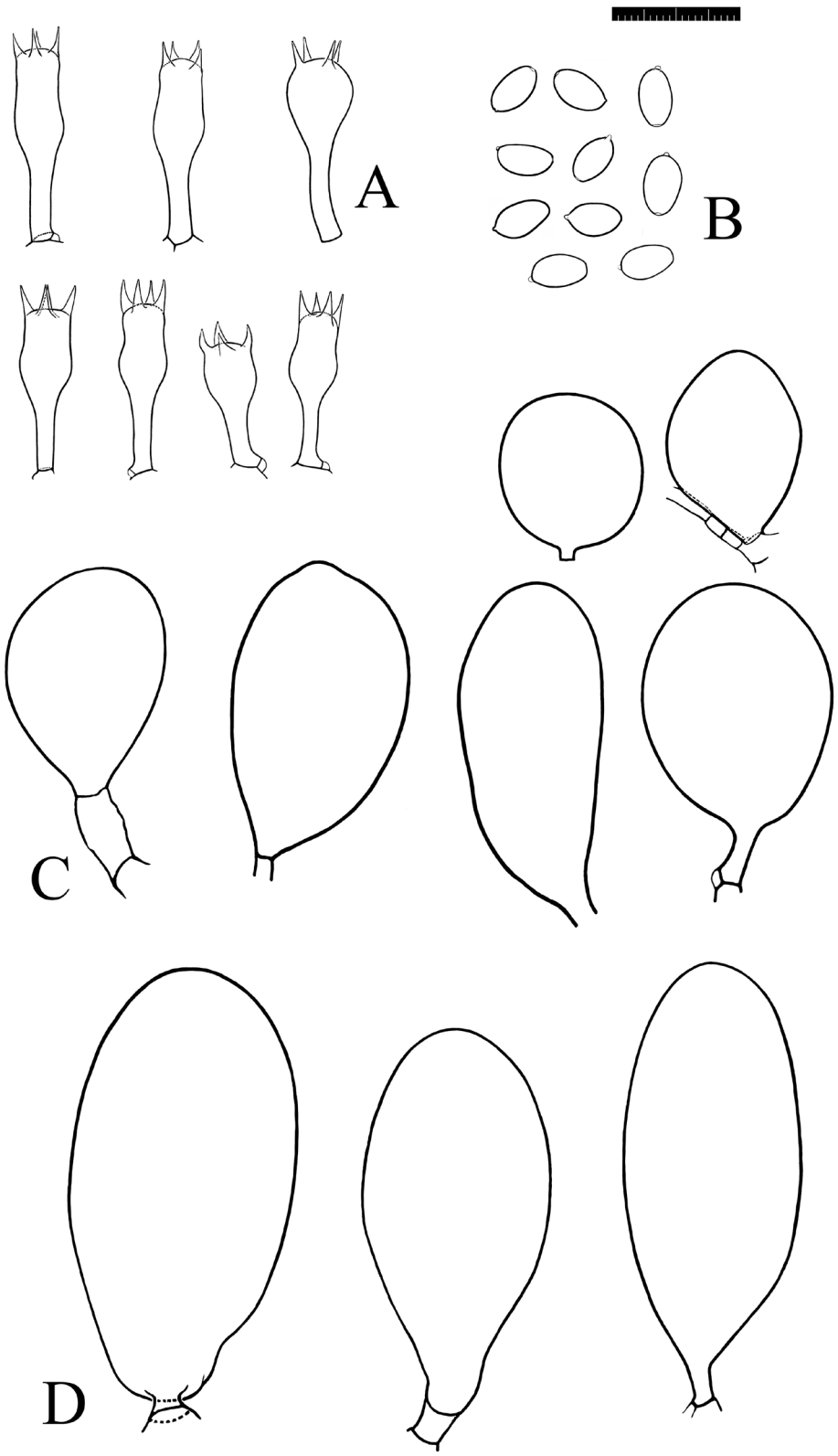


Fig. 10. *Coprinopsis kempii.* **A.** Basidia. **B.** Spores. **C.** Cheilocystidia. **D.** Pleurocystidia. Scale bar = 20 µm.

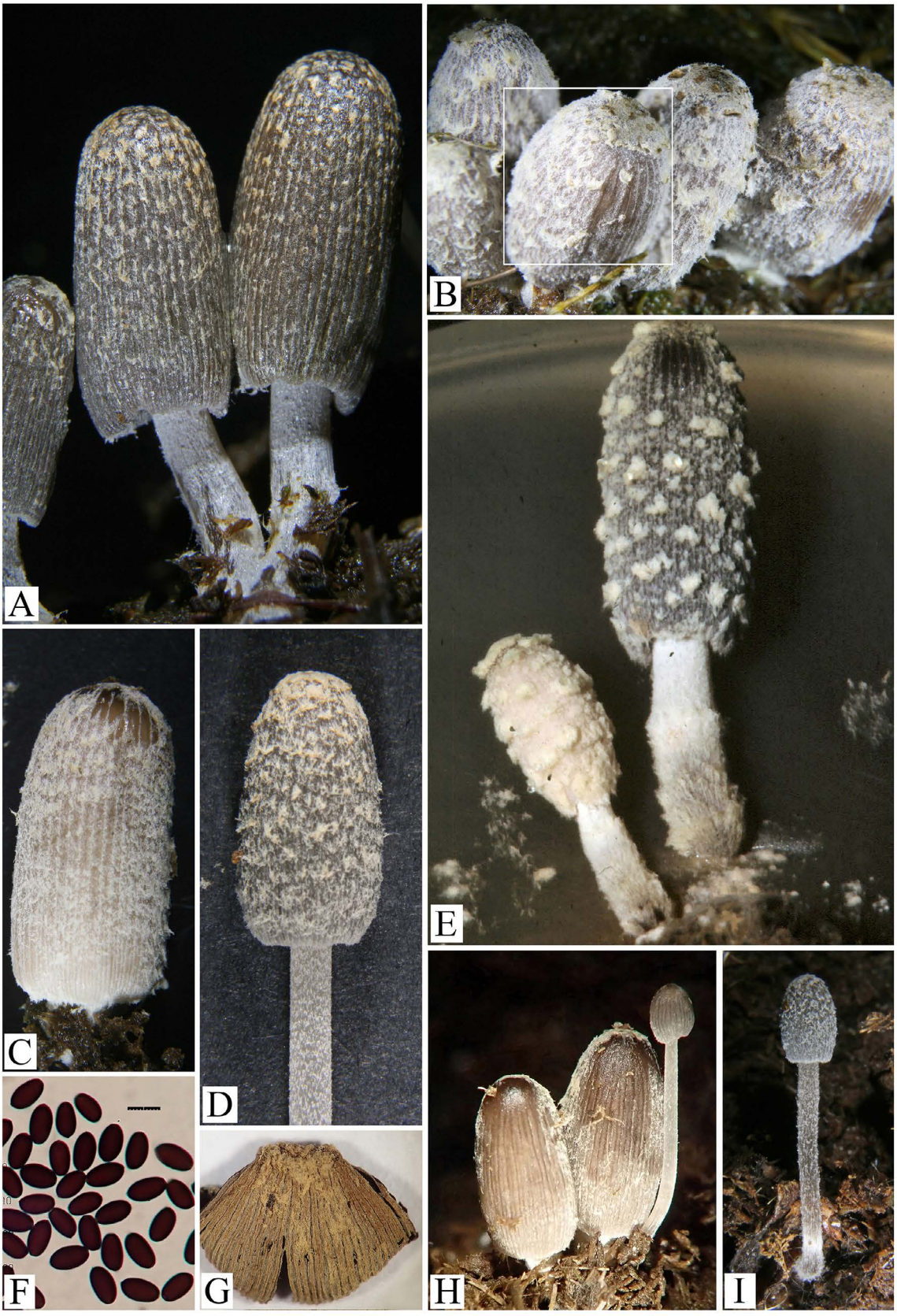


Fig. 11 *Coprinopsis luteocephala.* **A, B, C.** DJS20100810001, basidiocarps. **D.** DJS20220403001 **E.** Fruitbodies growing from culture, photo R F O Kemp, January 1973. **F.** DJS20100810001, spores; x1000, scale bar = 10 µm. **G.** DJS20171102003, fungarium specimen. **H.** DJS20250403001, basidiocarps. **I.** DJS20220401002, basidiocarp.

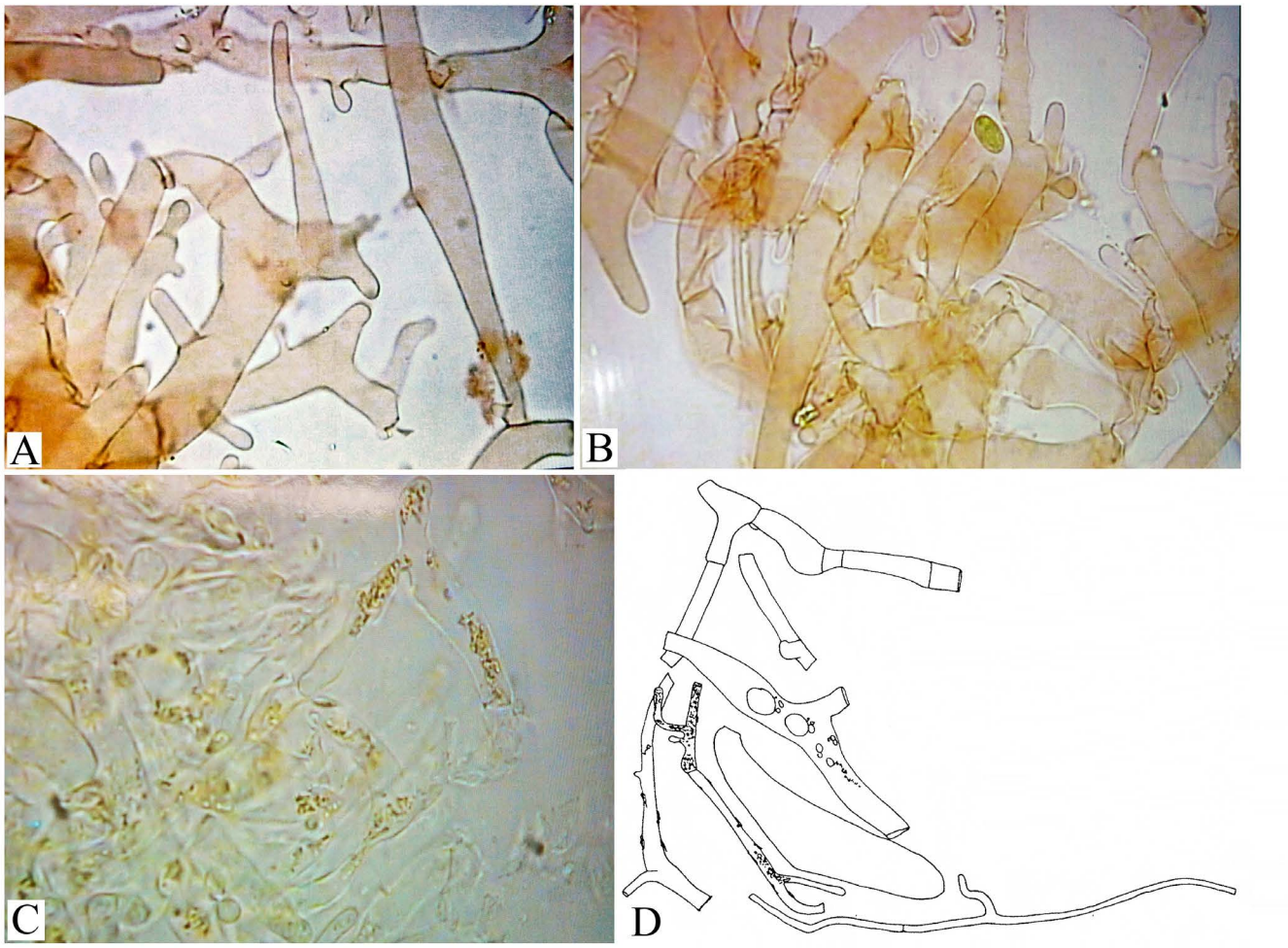


Fig. 12. *Coprinopsis luteocephala*, DJS20100810001. **A, B.** Veil stained in congo red. **C.** Veil in aqueous ammonia showing yellow inclusions. **D.** Veil illustration from Orton & Watling (1997) showing yellow contents and encrustation.

9. Cap veil entirely of branched, diverticulate, mainly thin-walled cells, turning yellow in maturing basidiocarps; spores ellipsoid or cylindrical, average length 9.5–11.5 µm, average breadth 5–6.5 µm; small species, unopened cap up to 18 mm.....***C. luteocephala***

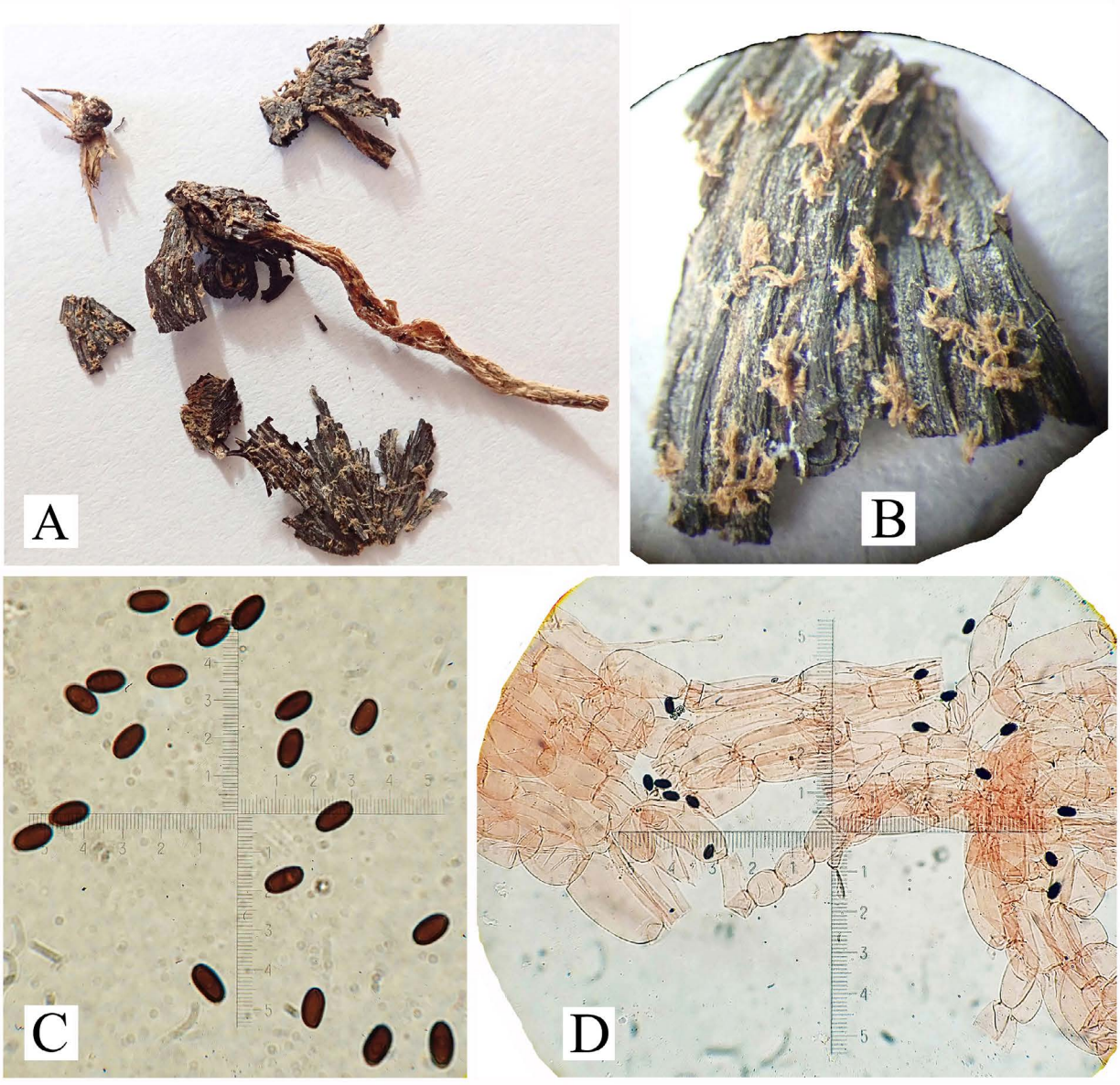
9. Cap veil entirely of narrow cylindrical hyphae, 6–14 µm wide; spores 13-15 (16) × 8–9 µm; larger species, unopened cap 37 mm.....***C. siepei*** (not British)

Taxonomy

Coprinopsis candidolanata (Doveri & Uljé) Keirle *et al.*, Figs 2–4.

Cap: unopened, 3–6 × 2–4 mm, ovoid to ellipsoid, expanding conical/campanulate then finally applanate to upturned/concave, up to 12 mm diam., white to pale grey tinged ochre at the centre beneath the veil; becoming grooved as it expands; veil densely covering the cap in elongate but irregular, fibrous-woolly white fibrils running down from the apex towards the rim. *Stipe*: up to 60 × 0.6–1.2 mm, cylindrical, becoming curled and narrower as it expands, initially densely covered with veil, becoming smooth as it extends. *Gills*: moderately crowded, L = 15 to 30, l = 0–3, narrow, white becoming dark, with a white edge and glistening dots (pleurocystidia) on the gill face visible as the spores mature. *Spores*: 7.6–11.5 × 4.6–6.6 µm, Q = 1.45–2.08; average L = 9.4 (9.0–10.0), average B = 5.7 (5.5–5.9), average Q = 1.67 (1.63–1.71), ellipsoid to ovoid in face view, often somewhat flattened on one side in side view, rarely cylindrical; with a central germ pore ±1.5 µm wide. *Basidia*: 19–33 × 8–10 µm, four–spored without a clamp at the base; polymorphic, the longer basidia with a median constriction. *Cheilocystidia*: densely covering the gill edge, 26–54 × 19–28 µm, globose, ovoid, ellipsoid or broadly utriform. *Pleurocystidia*: 40–90 × 18–30 µm, ellipsoid, ovoid, utriform or cylindrical, sometimes with a median restriction; with a generally short basal stem occasionally tapering narrowly towards it. *Veil*: a mixture of: (a) almost entirely unbranched chains of elongate cells, narrowing at the septa and varying from broadly ellipsoid or sub-globose to cylindrical or fusiform, 23–80 × 10–45 µm, the chains mostly terminating in narrow cylindrical hyphae, 7–15 µm wide; with (b) branched, diverticulate to coralloid filamentous hyphae. *Clamp connections* absent; occasionally, what appear to be pseudo-clamps are found on the wider veil but clamps are absent from narrower hyphae and from the base of basidia.

Habitat: Found on sheep, deer and cow dung in the UK.



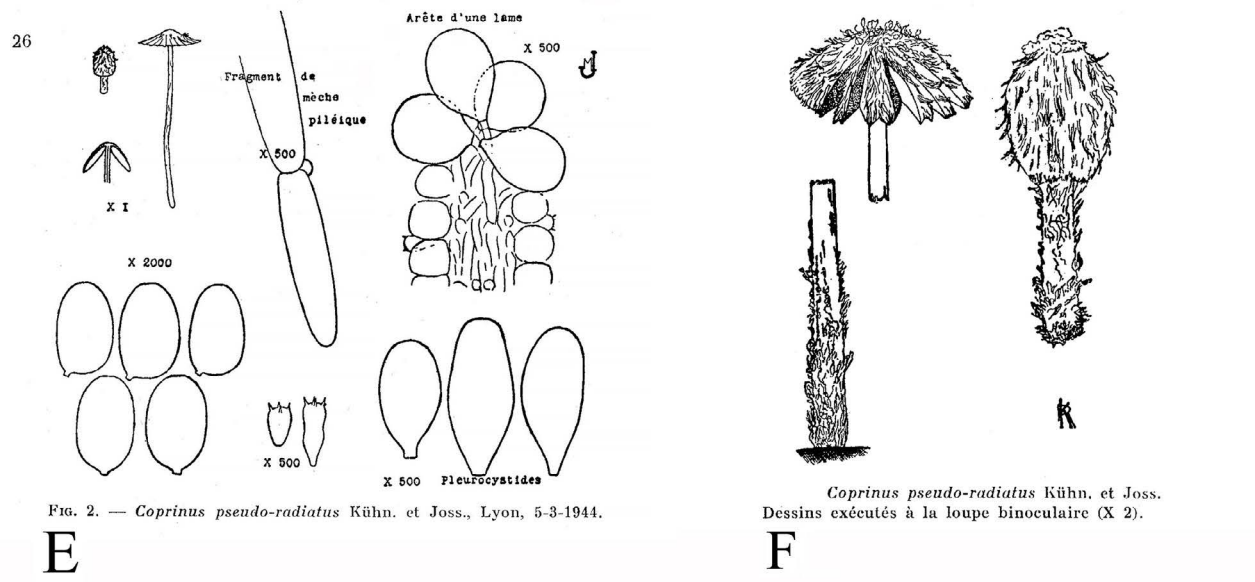


Fig. 2. — *Coprinus pseudo-radiatus* Kühn. et Joss., Lyon, 5-3-1944.

Coprinus pseudo-radiatus Kühn. et Joss.
Dessins exécutés à la loupe binoculaire (X 2).

Fig. 13. *Coprinopsis pseudoradiata* var. *pseudoradiata.* **A, B.** Holotype at Geneva. **C.** Spores from holotype x1000, scale division = 0.8 µm. **D.** Veil from holotype x400, scale division = 2 µm. **E, F.** drawings from Kühner & Josserand (1944).

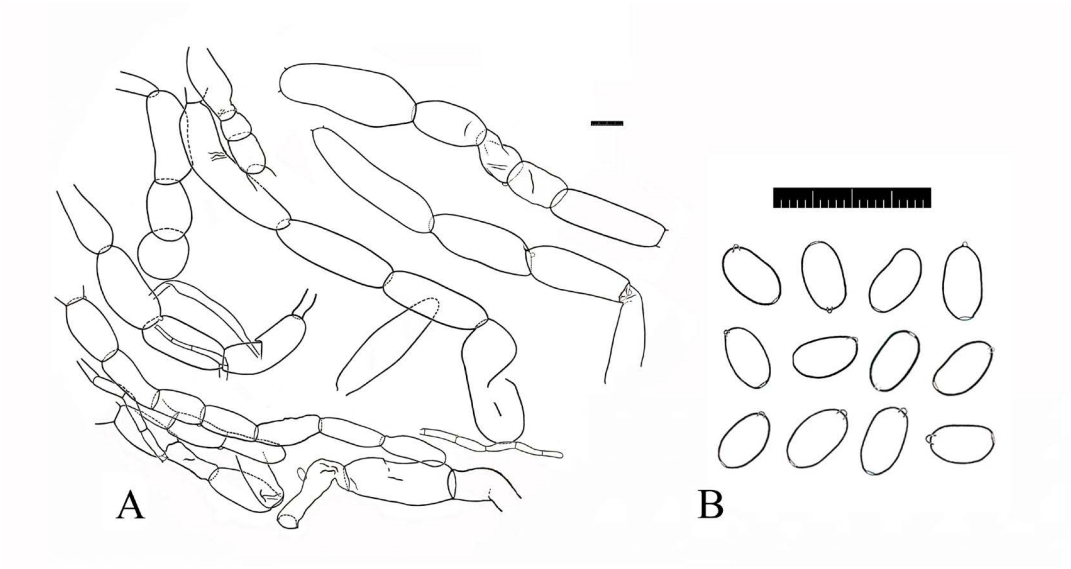


Fig. 14. *Coprinopsis pseudoradiata* var. *pseudoradiata*, holotype at Geneva. **A.** Veil. **B.** Spores. Scale bar = 20 µm.

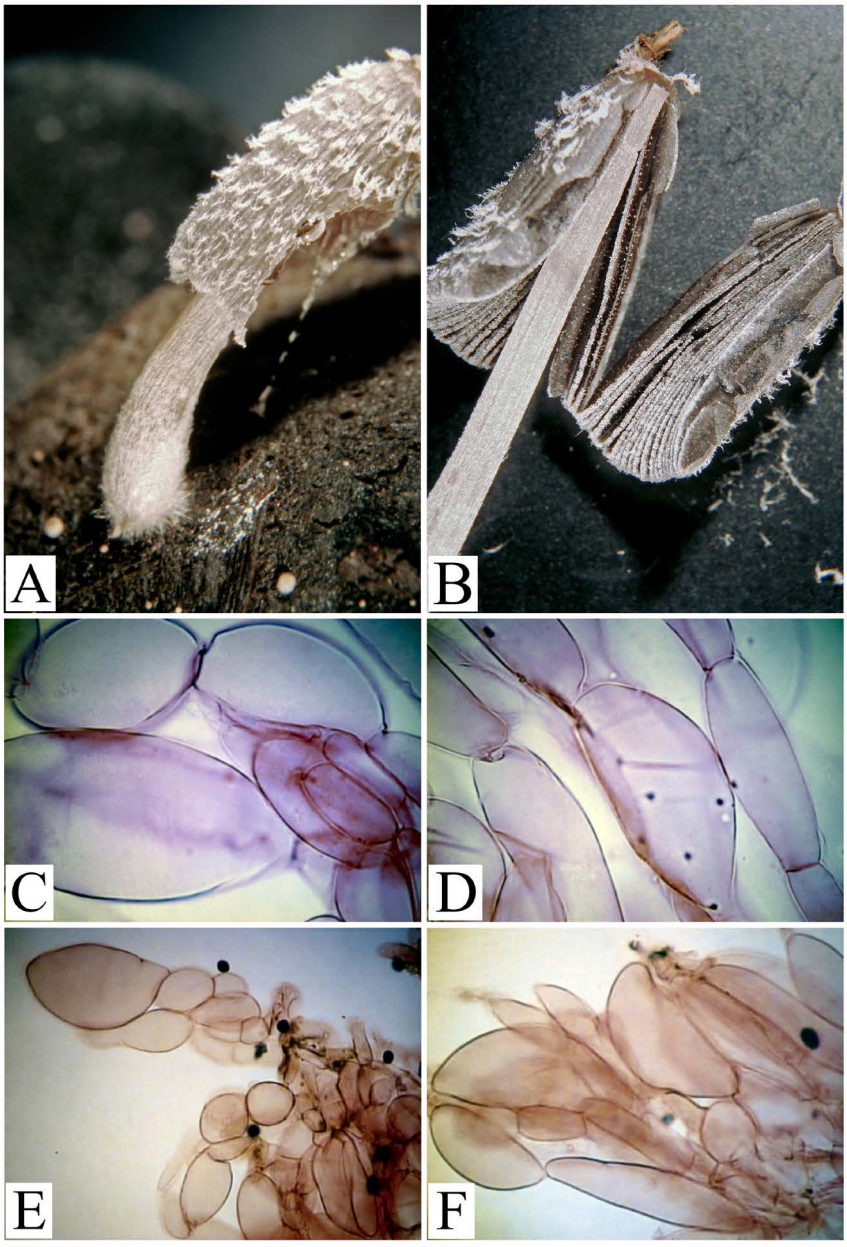


Fig. 15. *Coprinopsis pseudoradiata* var. *bicornis.* **A, B.** DJS20051007001, K(M)140456, basidiocarp. **C, D.** DJS20051007001, K(M)140456, veil. **E, F.** DJS20051017001, veil.

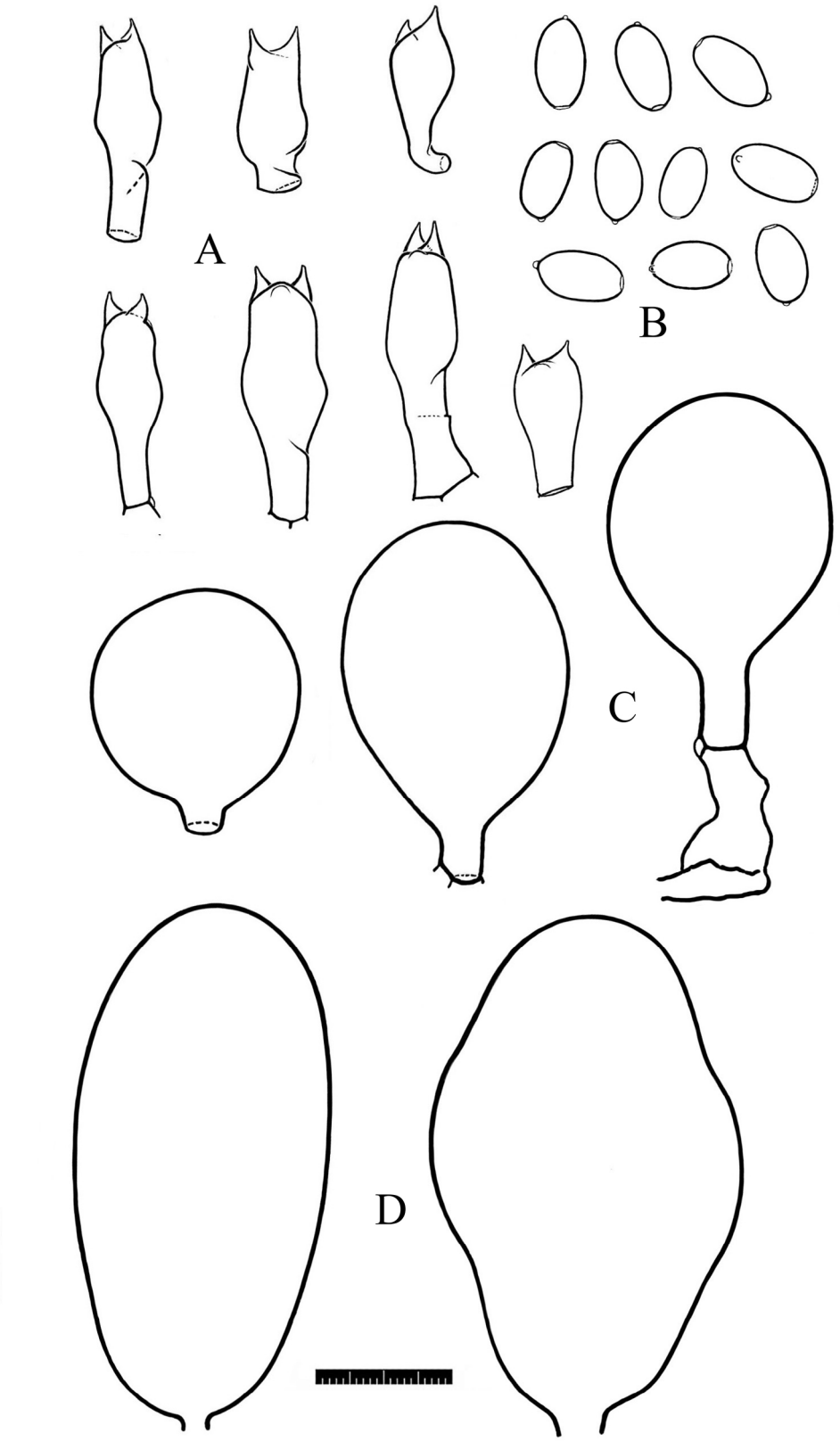


Fig. 16. *Coprinopsis pseudoradiata* var. *bicornis.* **A.** Basidia. **B.** Spores. **C.** Cheilocystidia. **D.** Pleurocystidia. Scale bar = 20 µm.

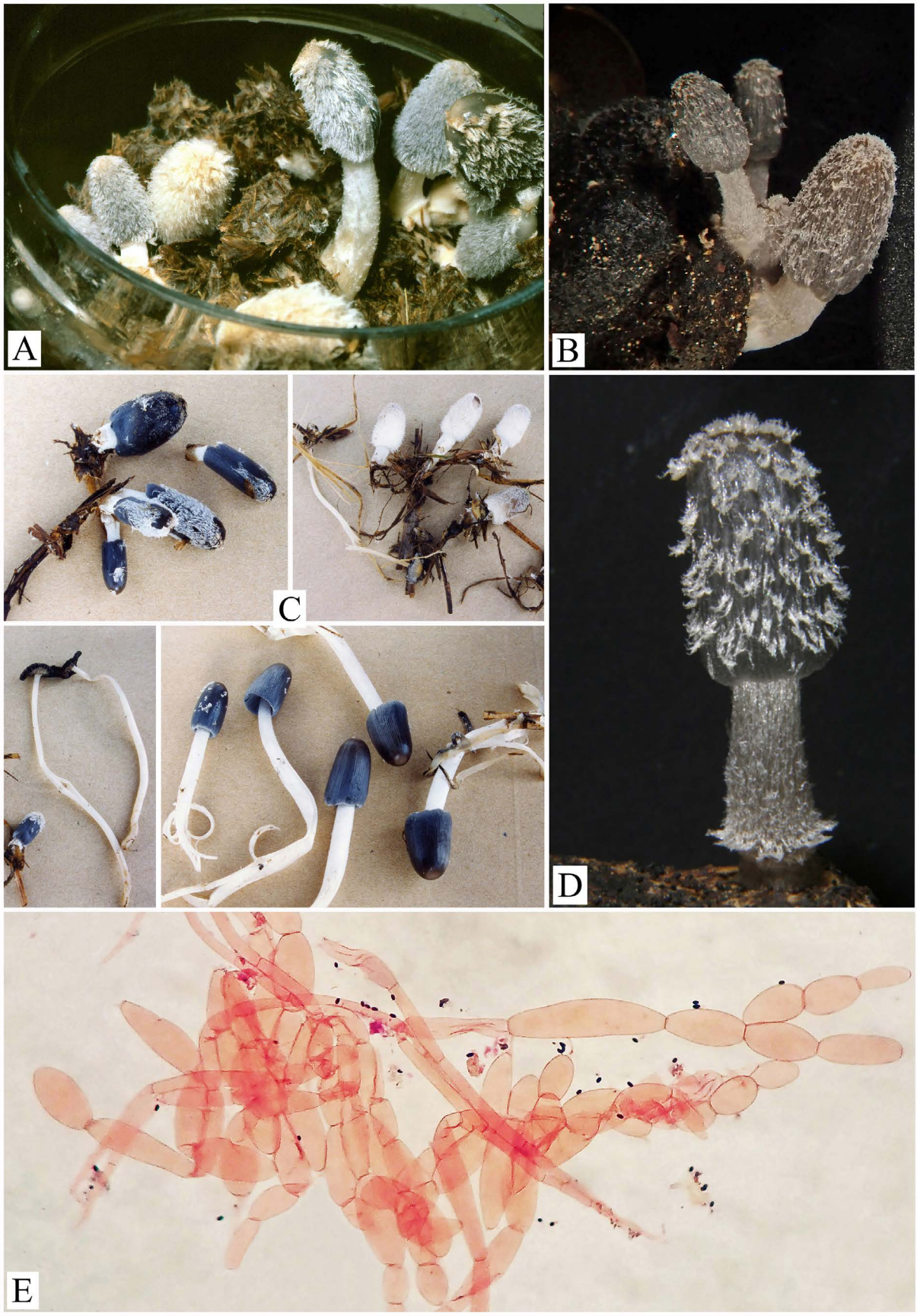


Fig. 17. *Coprinopsis radiata.* **A** Basidiocarps growing in horse dung culture, photo RFO Kemp, 1970. **B.** DJS20220407101, on deer dung. **C.** DJS19980424002 from horse dung/straw heap. **D.** DJS20210820001, on pony dung. **E.** DJS20200610001, cap veil x100 stained in congo red.

Specimens examined: **England**, Cumberland, Lodore Wood, on sheep dung, 1 Sep. 1999, *D.J. Schafer*, DJS19990901101; Yorkshire, Strensall Common, on incubated sheep dung, 22 to 23 Sep. 2013, *M. Greaves*, K(M)204730, DJS20130923101; Norfolk, Martham Broad, on deer dung, 18 Apr. 2020, *Y. Mynett*, YM20200418201; Buckinghamshire, Burnham Beeches, on cow dung, 9 Aug. 2021, *D.J. Schafer*, DJS20210809002.

Notes: This is a widespread species in Britain and some earlier records of *Coprinopsis pseudoradiata* have been of *C. candidolanata*. It can be distinguished from that species by the presence of diverticulate/coralloid veil on the cap, along with the *Lanatuli* type veil and from *C. kempii* by the coralloid veil and lack of clamp connections.

Coprinopsis cinerea (Schaeff.) Redhead *et al.*, Figs 5–7.

Cap: unopened, 15–40 × 12–30 mm, ovoid, ellipsoid or cylindrical-ellipsoid, expanding conical/campanulate then finally applanate to concave with upturned margin, up to 55 mm diam.; initially white below the veil, tinged ochre at the centre, becoming darker and grooved as it expands; densely covered in white threads of veil forming pointed upturned tufts as the cap expands, colouring ochre/brown towards the centre when mature. *Stipe*: 40–120 × 3–8 mm, white, covered with fine fibrillose veil, cylindrical or narrowing upwards from the swollen base, which is often tinged pale buff; the base may taper to a long root and is firm and solid, often growing in fasciculate groups on rich substrates. *Gills*: crowded, L = 40 to 60, white becoming dark, with a white edge, which liquefies rapidly as the spores mature from the cap rim towards the stipe; glistening dots (pleurocystidia) visible on the gill face as the spores mature. *Spores*: 9.1–13.0 × 5.6–7.5 µm, Q = 1.46–1.84; average L = 10.8 (10.5–11.0) µm, average B = 6.6 (6.4–7.1) µm, average Q = 1.64 (1.53–1.70); ellipsoid to ovoid, occasionally cylindrical or with a straight edge on one side, with a central germ pore 1.3 to 2 µm wide, often presenting with a protruding truncate annuliform bulge, comprising a cap that covers the germ pore and loosens and detaches in aqueous ammonia or KOH. *Basidia*: 17–29 × 9–12.5 µm. four-spored with clamps at the base, polymorphic, the longer basidia with a median constriction. *Cheilocystidia*: 31–74 × 15–38 µm; densely covering the gill edge; predominantly globose, subglobose to broadly ellipsoid, varying towards ovoid, broadly utriform or oblong, rarely broadly conical. *Pleurocystidia*: 64–122 × 30–47 µm; obovoid, broadly utriform, elongate-ovoid; generally, with a short, truncate pedicel and often with remains of tissue from an opposing gill attached at the apex. *Veil*: predominantly composed of strings of thin-walled sausage shaped cells, varying in breadth along the string, the broader cells narrowing towards a broad septum; some narrow, branched and diverticulate veil may also be present.

Habitat: Very common on large dung-straw heaps in Britain, particularly at the stage when heated by microbial activity; generally, on rotting vegetation or mixed dung and vegetation, rather than on pure dung.

Specimens examined: **England**, Buckinghamshire, Whitchurch, on cow/horse dung/straw heap, 31 May 1999, *D.J. Schafer*, DJS19990531001; Buckinghamshire, Whitchurch, on cow/horse dung-straw heap, 18 Mar. 2012, *D.J. Schafer*, DJS20120318001; Derbyshire, Clough Wood, on cow dung-straw heap, 23 May 2013, *D.J. Schafer*, DJS20130523001; Hertfordshire, New Wood, Knebworth, on horse/dung straw heap, 24 Mar. 2022, *D.J. Schafer*, DJS20220324001.

Notes: On rich substrates, this is easily recognised by its robust fruitbodies, often more or less fasciculate, rooting with a firm slightly buff-coloured base to the stipe and spores around 10.5–11 × 6.5–7 µm, some usually with a raised germ pore. The germ pore cap can be found more easily in dried mature specimens and has only been reported in sect. *Cinereae*.

Coprinopsis kempii D.J. Schaf., ***sp. nov.*** MB 862709. Figs 8–10.

Etymology: Named after the mycologist Dr. Roger Kemp, who studied the breeding behaviour of these species extensively at the University of Edinburgh and recognised the existence of undescribed "*Lanatuli*" species with diverticulate veil.

Diagnosis: Small deliquescing agaric with white tufted to tangled filamentous veil; the veil comprising elongate or rounded cells in strings mixed with narrower branched and diverticulate filamentous cells, both with clamp connections; more or less ellipsoid spores, dark brown to blackish, around 8.5–9 × 5 µm with a central germ pore; on Exmoor Pony dung.

Typus: **England**, Buckinghamshire, Burnham Beeches, on Exmoor Pony dung, *D.J. Schafer*, 2 May 2018, DJS20180502001 (**holotype** K-M1447368).

Other specimens examined: **England**, Buckinghamshire, Burnham Beeches, on Exmoor Pony dung, 8 Oct. 2017, *D.J. Schafer*, DJS20171008003; Ibid. 17 Oct. 2017, *D.J. Schafer*, DJS20171017001; Ibid. 17 Nov. 2019, *D.J. Schafer*, DJS20191117001; Ibid. 5 Dec. 2019, DJS20191205001.

Description: *Cap:* unopened, 2.5–5.5 × 1.5–3 mm, ovoid to ellipsoid, expanding conical/campanulate, becoming grooved as it expands and sometimes splitting along alternate gills, then finally applanate to upturned/concave, up to 9 mm diam.; white to pale grey tinged ochre at the centre beneath the veil; veil covering the cap in tangled, fibrous-woolly white fibrils forming downward pointing irregular tufts and often a patch or cap at the apex. *Stipe:* 4.5–30 × 0.7–1.1 mm, cylindrical, hollow, narrowing upwards as it expands; initially covered with veil, becoming more or less smooth as it extends but with a dense band of upwardly pointing veil at the base. *Gills*: not crowded, L = 12 to 24, l = 0–2, narrow, white becoming dark, with a white edge and glistening dots (pleurocystidia) on the gill face visible as the spores mature. *Spores:* 7.6–10.0 × 4.5–6.0 µm, Q = 1.54–1.90; average L = 8.7 (8.3–8.9), average B = 5.1 (5.0–5.2), average Q = 1.71 (1.66–1.75); ellipsoid to ovoid in face view, often slightly less curved on one side in side view but not significantly lentiform (flattened), rarely cylindrical; with a central germ pore ±1.6 µm wide. *Basidia:* 19–26 ×

7–8 µm, four-spored with clamps at the base, polymorphic, the longer basidia with a median constriction; surrounded by 4–6 pseudoparaphyses. *Cheilocystidia*: densely covering the gill edge, 22–40 × 17.5–32 µm, globose, subglobose or broadly ellipsoid. *Pleurocystidia*: 53–68 × 22–29 µm, ellipsoid, broadly ellipsoid or oblong**.** *Veil*: a mixture of: (a) chains of generally unbranched thin-walled cells of widely varying breadth and length; some sausage-shaped, some as short as they are broad, narrowing at the septa; some chains tapering along their length; some changing abruptly to narrower cylindrical strings of cells not always narrowing at the septa; and (b) frequently branched diverticulate but not coralloid cylindrical cells, breadth 2.5–8 µm. *Clamp connections* present in both types of veil.

Habitat: So far only found on Exmoor Pony dung at the type location.

Notes: Distinguished from the macroscopically similar *C. pseudoradiata* by the presence of diverticulate veil and from *C. candidolanata* by the less coralloid diverticulate veil with clamp connections. Many species in *Coprinopsis* section *Coprinopsis* also have diverticulate veil but lack *Lanatuli* type veil.

Coprinopsis luteocephala (Watling) Redhead *et al.*, Figs 11, 12.

Cap: made of primordia densely covered in felty white veil; unopened cap up to 18 mm high, 8 to 22 mm broad, cylindrical to acorn shaped with domed or more conical top; veil breaking up into felty-fibrillose patches at the centre and fibrillose strands and tufts towards the rim as the cap expands, taking on a varying amount of yellow colour with some veil patches brownish ochre at the centre. The cap below the veil initially light greyish, brown in the centre, translucently striate then grooved, becoming dark brown then grey black before opening conical, convex, flat and finally upturned at the rim. *Gills*: crowded, greyish becoming violaceous black as the spores mature, gill edge silvery white, gill face dotted with scattered silvery white dots (pleurocystidia), edge becoming wet and black as the gills open and deliquesce. *Stipe*: expanding up to 60 mm long, 1.5–2.5 at the base, tapering to 0.5–1.5 mm towards the cap, initially covered in white to yellow veil. *Spores*: dark brown, purplish date; ellipsoid or cylindrical, rounded at the apiculus end, slightly conical towards the germ pore; in side view the edge nearest the apiculus is less rounded than the other side. Spore length 9.0–12.3 µm (average 10.1 to 11.2 µm, overall 10.8 µm), breadth 5.0–6.9 µm (average 5.5–6.2 µm, overall 5.8 µm); germ pore 1.5–2 µm. wide. *Basidia*: four spored, 17–27 × 7–10 µm, four-spored with clamps at the base, polymorphic, the longer basidia with a median constriction. *Cheilocystidia*: 20–65 × 15–55 µm, globose, broadly oblong or ellipsoid, ovoid or obovoid, densely packed along the gill edge. *Pleurocystidia*: 60–105 × 30–45 µm, ellipsoid, ovoid or utriform, scattered but easily seen with a hand lens against the background of dark spores. *Cap surface*: a cutis but of short, broad elements. *Veil*: made of filamentous cells, breadth varying between 2 and 12 µm, irregularly branched and diverticulate with excrescences generally cylindrical with rounded ends; thin walled with some slight thickening of the narrower hyphae; many veil cells with yellow intracellular material and extracellular encrustation (Fig. 12).

Habitat: On cow and horse dung, one collection possibly on wild boar dung; widespread in Britain but rarely recorded.

Specimens examined: **Scotland**, East Perthshire, Dalreoch, on the remains of a cow dung heap, 10 Aug. 2010, *D.J. Schafer*, DJS20100810001. **England**, West Gloucestershire, Forest of Dean, Woorgreens Lake, on old (probably wild boar) dung in lakeside woodland, 2 Nov. 2017, *D.J. Schafer*, DJS20171102003; Buckinghamshire, Burnham Beeches on cow dung in mire, 1 & 3 Apr. 2022, *D.J. Schafer*, DJS20220401002, DJS20220403001; Norfolk, Sweet Briar Marshes, on cow dung, 3 Apr. 2025, *D.J. Schafer*, DJS20250403001.

Notes The yellow and diverticulate veil, spore size and shape, and fimicolous substrate characterise *C. luteocephala*. The yellow colour, however, develops during the growth of the fruitbody and young, fruitbodies can appear completely white, some trace of yellow colour usually visible on close examination with a hand lens. Under moist conditions, the veil may collapse to a thin layer in patches that darken at the centre to a brownish ochre colour. The status of the closely related *C. xenobia* is discussed below.

Coprinopsis pseudoradiata (Kühner & Joss. ex Watling) Redhead *et al.* **var. *pseudoradiata***, Figs 13, 14.

Description based on Kühner & Josserand (1944), Watling (1976), and Uljé & Noordeloos (1999) or our examination of the type where indicated. *Cap:* unopened 3–6 × 2–4 µm, ellipsoid, acorn-shaped to ovoid, opening campanulate then convex/flattened 6–15 (–23) mm; covered initially in pale whitish, silvery grey or grey-brown easily detached pointed tufts of radial fibrils, dividing as the cap expands, striate except at the grey-brown centre, eventually splitting and deliquescing. *Gills*: moderately crowded, thin, narrow, white, becoming black as the spores mature. *Stipe*: 15–55 × 0.5–2.3 mm; equal or tapering towards the apex; often swollen at the base, hollow covered in fluffy veil, particularly towards the base, becoming glabrous. *Spores*: (from holotype) ellipsoid, slightly flattened on one side, cylindrical with rounded or obtusely conical ends, some slightly phaseoliform or obtuse at the germ-pore end; 7.6–10.0 × 4.4–5.6 µm, average length 8.7 µm, average breadth 5.0 µm, Q 1.52–2.07, average Q 1.75; *Basidia*: 15–30 × 6–8 µm, 4-spored, polymorphic, some clavate-obconical, measuring e.g. 15 × 8 µm, the other constricted cylindric, reported to measure 26 × 8 µm (Kühner & Josserand 1944) or 18–32 × 8–10 µm surrounded by 3–6 pseudoparaphyses (Uljé & Noordeloos 1999). *Cheilocystidia*: overabundant, very shortly elliptical or sub-globose, reported to measure 30–40 × 22–28 µm (Kühner & Josserand 1944) and 25–60 × 15–28 µm (Uljé & Noordeloos 1999), with a (sub)globose or ellipsoid to oblong or (sub) utrifom shape. *Pleurocystidia*: not very numerous, more frequent near the ridge, most often elliptical-ovoid, rarely a little contracted below the apex, reported to measure 25–60 × 16–26 µm (Kühner & Josserand, 1944) (sometimes 76–107 × 28–32 µm, never

seeming to be attached at both ends, but presenting a free end that is always very broadly rounded-obtuse) or 30–80 × 20–30 µm (Uljé & Noordeloos 1999, ellipsoid to oblong, utriform or subcylindric). *Veil*: (from holotype) substantially comprising strings of thin-walled sausage-shaped cells, generally inflated and obtusely constricted at the septum; breadth varying along the length of the strings and between different strings, the broader cells usually more constricted at the septum; varying further in that some strings have cells with length similar to their breadth; some strings terminated with broad rounded or broadly fusiform cells at one end, some abruptly changing to narrower cylindrical cells; the narrower cells essentially unbranched and not diverticulate but occasional branching to narrow hyphae occurs on cells of various breadths; many strings of narrower cylindrical cells diam. 3–14 µm wide, some with external encrustation also frequent (Figs 11, 12).

Habitat: On horse dung (Kühner & Josserand, 1944); two collections from Norway have been sequenced (Nagy *et al*. 2013) but their substrate is not described; Uljé & Noordeloos (1999) describe it as "Growing solitary in small groups or fasciculate on pure dung or mixed dung, rarely (seemingly) on soil. Rather rare but widespread in Europe".

Specimens examined: **France**, Lyon, on horse dung, 17 Apr. 1944, *R. Kühner* (holotype, at Geneva Herbarium); Ibid. 18 Apr. 1944, *R. Kühner* (at Geneva Herbarium).

Notes: Recognised by its small, narrow spores and the lack of branched/diverticulate veil cells. DNA confirmed collections from Britain are still not available, only one record of the var. bicornis in 2005 has been found and sequenced.

Coprinopsis pseudoradiata* var. *bicornis (Uljé & Horvers) Redhead *et al.*, Figs 15, 16.

Cap: unopened, 18 × 8 mm, cylindric-ellipsoid, pale grey, covered in white fibrillose veil; veil breaking up into tangled but pointed and upturned flocks, slightly greyish and remaining as an unbroken patch at the top of the cap. *Gills*: initially crowded, L 25 or more, narrow, white, becoming grey and then black as the spores mature; gill edge white, densely covered in tightly packed, rounded cystidia; gill face dotted with hyaline dots, comprising pleurocystidia. *Stipe*: hairy flocculose, 34 mm long, tapering from 2 mm wide at the apex to 4 mm at the somewhat swollen base, which is densely covered in veil. *Spores*: ellipsoid, ovoid, sometimes somewhat flattened on one side, cylindrical with rounded or rounded-conical ends or slightly phaseoliform, broader/offset at one end; 10.5–13.5 × 6.5–8.0 µm, average length 12.0 µm, average breadth 7.1 µm; Q 1.50 to 1.95, average Q 1.69; germ pore ± 2 µm. *Basidia*: 19–35 × 8.0–12.0 µm, average length 25 µm, average breadth 9.7 µm, two-spored, surrounded by 3-5 pseudoparaphyses; polymorphic, the longer basidia with a median constriction. *Cheilocystidia*: densely covering the gill edge, 37–64 × 24–41 µm, globose, subglobose or broadly ellipsoid/ovoid, occasionally oblong. *Pleurocystidia*: 65–85 × 37–47 µm, broadly ellipsoid, ovoid or subutriform. *Veil*: strings of thin-walled sausage-shaped cells, generally inflated and obtusely constricted at the septum; breadth varying along the length of the strings and between different strings, the broader cells usually more constricted at the septum; some very broad cells present and some strings have cells with length similar to their breadth; strings often terminated with broad rounded or broadly fusiform cells at one end, other strings with narrower cylindrical cells terminating a string of broader cells; no diverticulate cells observed.

Habitat: found only once in Britain on horse dung in October 2005. Uljé & Horvers (1999) reported finding it only twice in the Netherlands on horse and cow dung respectively.

Specimens examined: England, Buckinghamshire, Hampden Common, on horse dung, 7 Oct. 2005, *D.J. Schafer*, DJS20051007001, K(M)140456; Ibid. 17 Oct. 2005, *D.J. Schafer*, DJS20051017001.

Notes: The basidia often have slight swellings at the apex between the sterigma, looking like incipient sterigma. These are not collapsed sterigma and the basidia are consistently two-spored.

Coprinopsis radiata (Bolton) Redhead *et al.*, Figs 17, 18.

Cap: unopened, up to 2.4 × 1.2–1.9 mm, or much smaller, depending on the substrate; cylindric-ellipsoid to ellipsoid, initially densely covered in white veil, the surface beneath revealed as the cap grows before expanding, initially white at the rim, light brown then brown towards the top, becoming rapidly darker, grey and then black, striate, expanding conical, campanulate then flattened with upturned rim; veil white to pale silvery grey, densely hairy covering the cap, then breaking up into pointed upturned tufts, browning at the tips as it matures. *Stipe*: up to 80 × 7 mm or much narrower, white, fragile, hollow, tapering towards the apex; often with a root into the substrate. *Gills*: narrow, tightly packed together and initially joined at the gill edge by cystidia; separating as the cap expands, the edge remaining white, the face becoming rapidly grey, then black as the spores mature, covered in glistening hyaline dots (pleurocystidia) visible against the dark background. *Spores*: 11.2–17.4 × 6.2–10.0 µm, Q = 1.53–2.18; average L = 14.4 (13.4–15.6), average B = 8.0 (7.1–8.8), average Q = 1.81 (1.72–1.89); ellipsoid, ellipsoid with one straight side or cylindrical with obtusely conical or rounded ends; with a central germ pore ± 1.8 µm wide. *Basidia*: 16–38 × 8–13 µm, 4-spored with clamps at the base, polymorphic, the longer basidia with a median constriction; surrounded by 3–5 pseudoparaphyses. *Cheilocystidia*: densely covering the gill edge, 30–77 × 20–42 µm, globose, subglobose, ovoid, obovoid or utriform. *Pleurocystidia*: 60–151 × 24–68 µm, ellipsoid, broadly utriform to cylindric ovoid. *Veil*: strings of sausage-shaped cells, up to 80 µm wide at the base, tapering to less than 10 µm at the tip. *Clamp connections* present.

Habitat: On dung from a variety of herbivore species. Also found on rotting wood or vegetation.

Specimens examined: **England**, Buckinghamshire, Whitchurch, on horse/cow dung-straw heap, 24 Apr. 1998, *D.J. Schafer*, DJS19980424002; Buckinghamshire, Burnham Beeches, on pony dung, 20 Aug. 2021, *D.J. Schafer*,

DJS20210820001; Buckinghamshire, Burnham Beeches, on deer dung, 7 Apr. 2022, *D.J. Schafer*, DJS20220407101.

Notes: Common in Britain on dung of cow, deer, horse, rabbit and sheep; also on dung-straw heaps. Forming small fruitbodies on smaller dung pellets but also larger fruitbodies on more extensive substrate such as dung-straw heaps. Also found on non-dung substrates, where the presence of some cylindrical spores (with rounded ends) distinguish it from *C. lagopus* agg. Described earlier as a small species, Kemp (1975, 1985) showed that small specimens of *C. radiata* re-grown on sterile media could produce much larger basidiocarps (see Fig. 17, A). Specimens identified as *C. macrocephala*, distinguished by larger basidiocarps and spore size, were shown by Kemp (1985), with the exception of two specimens collected by P.D. Orton, to be interfertile with *C. radiata* in laboratory studies. Nagy *et al*. (2013) observed a high morphological plasticity in spore shape and basidiome size in *C. radiata* coupled with negligible genetic divergence, species identified as *C. macrocephala* and *C. tectispora* nesting in the *C. radiata* clade. The former has to be regarded for the moment as a dubious species but a search for further material matching the description of Orton & Watling (1979), with coarse veil and broad spores, might provide collections that are distinct phylogenetically. *Coprinopsis tectispora*, distinguished by large dark spores with a detachable perispore (Van de Bogart 1979, Schafer 2010b) and a soil or wood chip substrate, matches *C. radiata* phylogenetically despite its morphological differences. So, unless further collections or sequences of further loci prove otherwise, it appears also to be *C. radiata*.

Coprinopsis villosa L. Nagy *et al.*, Figs 19, 20.

Cap: unopened up to 25 mm high × 10 mm wide (British collection 8 mm × 3.5 mm unopened when collected), ellipsoid to cylindrical with conical apex, covered with finely fibrillose to hairy veil; becoming applanate and deliquescing,

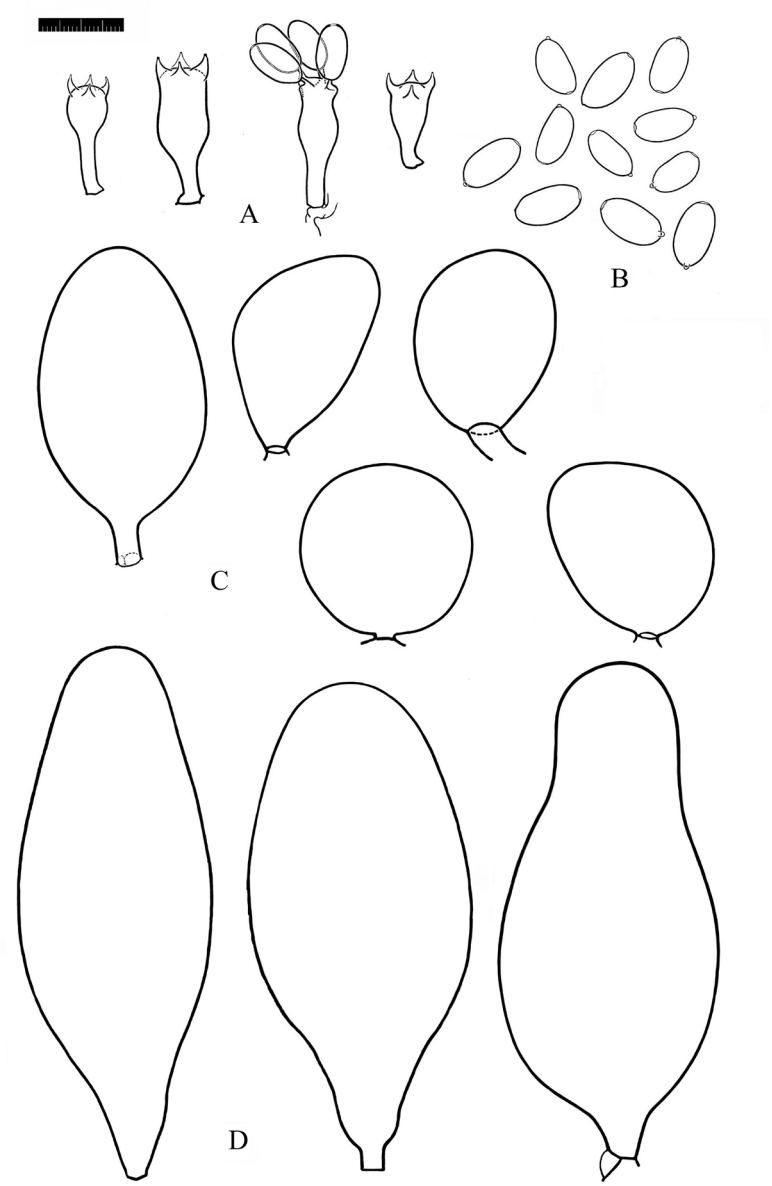


Fig. 18. *Coprinopsis radiata.* **A.** Basidia. **B.** Spores. **C.** Cheilocystidia. **D.** Pleurocystidia. Scale bar = 20 µm.

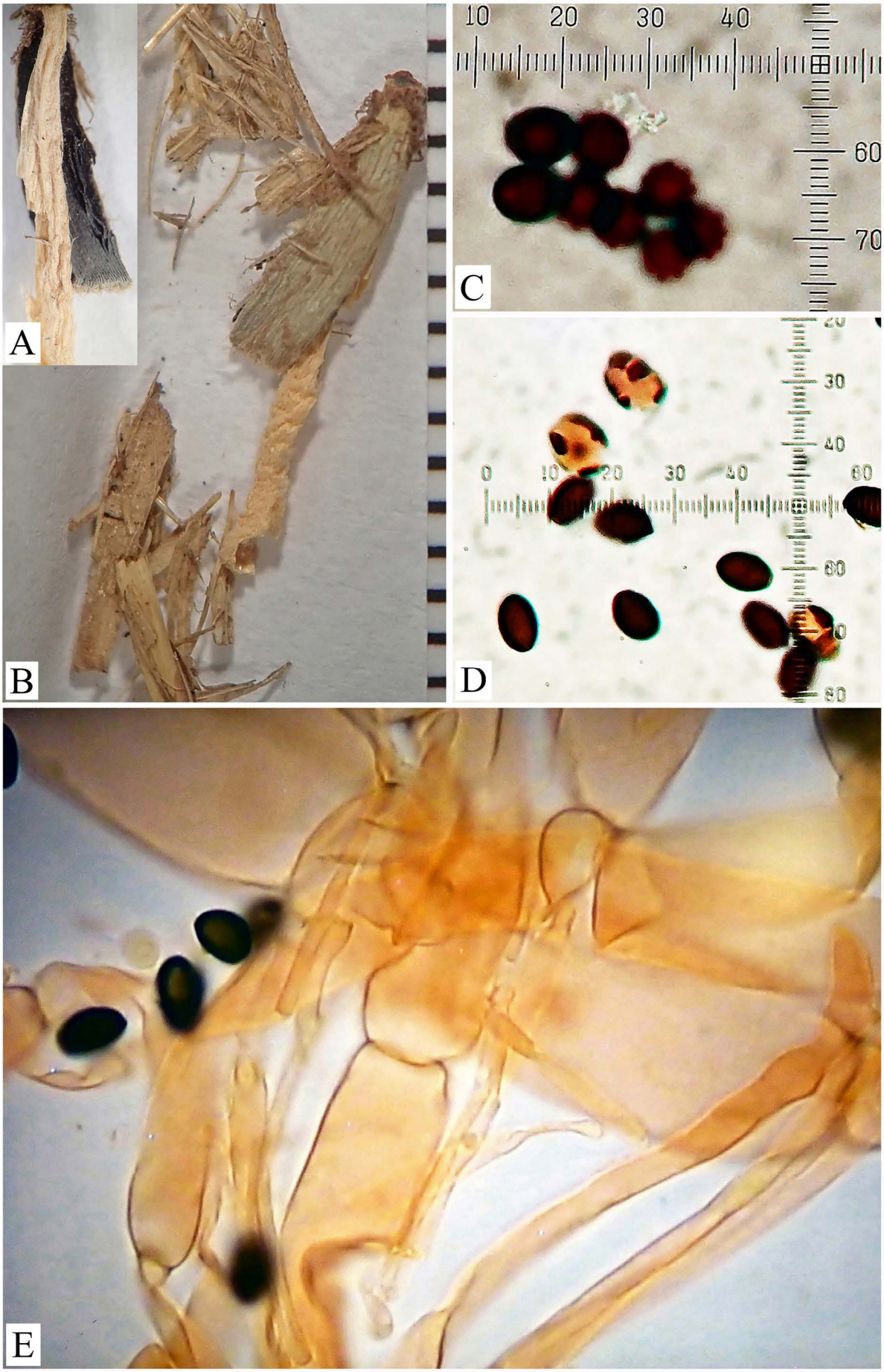


Fig. 19. *Coprinopsis villosa* DJS20060917001 (K-M1447369). **A, B.** Fungarium specimen. **C**. Young spores in quadrats from dried specimen with cog-wheel profile. **D.** Spores with dark exospore breaking into patches (scale divisions C & D = 1 µm.). **E.** Veil stained with congo red × 1000.

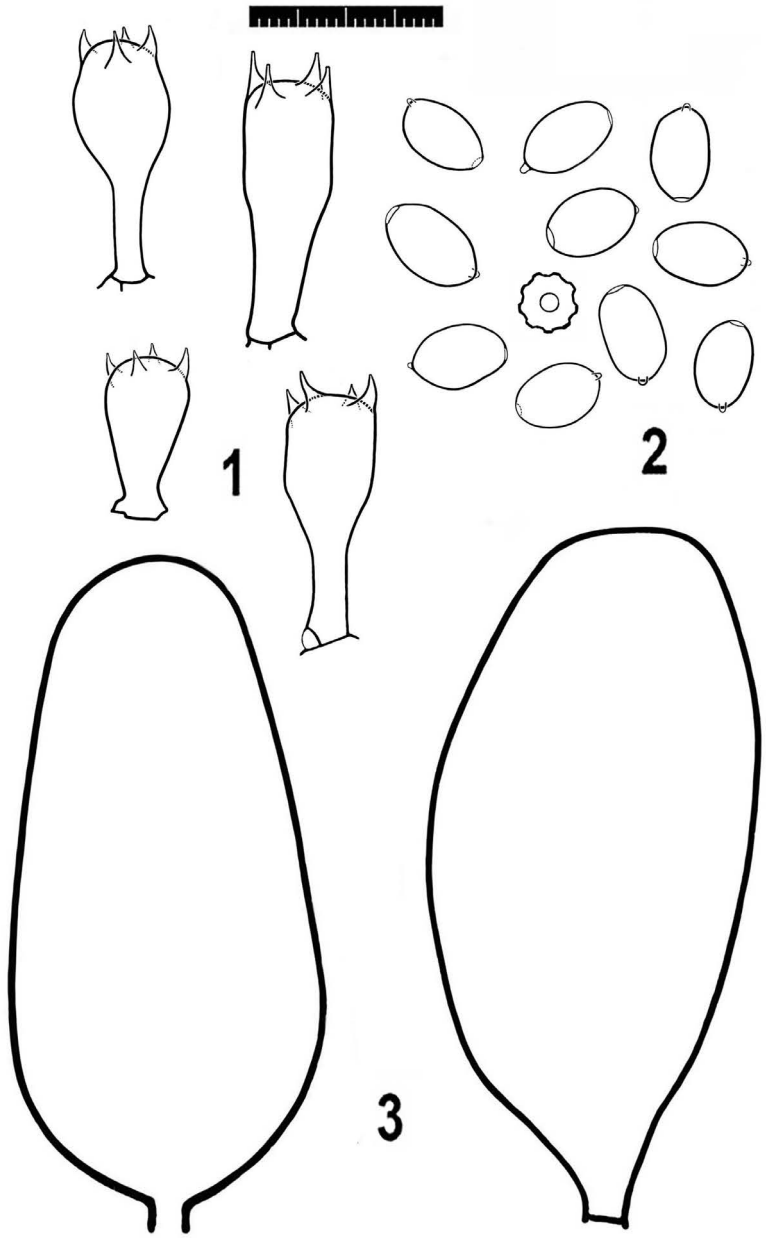


Fig. 20. *Coprinopsis villosa*. **A.** Basidia. **B.** Spores. **C.** Pleurocystidia. Scale bar = 20 µm.

up to 35 mm diam; veil: white, reddish-brown towards the apex, or completely chestnut brown. *Stipe*: up to 90 mm × 5 mm, white with white floccose, finely fibrillose veil (British collection 15 mm × 3.5 mm. *Gills*: crowded, free. *Spores*: ellipsoid to ovoid in frontal view, ellipsoid to subamygdaloid or sometimes slightly phaseoliform in lateral view, regular, not lentiform in polar view; reported to measure a) 9.8–12 × 6.0–7.8 µm on average 11.1 × 7.1 µm, Q reported to be 1.47–1.64, Qav = 1.57 (Nagy *et al*. 2013) b) 7.6–14.4 × 4.8–9.2 µm, on average 10.2 ± 1.5 × 6.0 ± 0.9 µm, Q = 1.5–1.9, Qav = 1.7 (Keirle *et al*. 2004); c) 8.5–11.0 × 5.0–6.8 µm, on average 9.6 × 6.1 µm, Q = 1.31–1.78, Qav = 1.58 (British collection); dark brown with thick wall; immature spores in polar view often presenting a cog-wheel profile and some spores with irregular patches of perispore. *Basidia*: 17–35 × 7–12 µm, on average 25 × 9 µm; 4-spored with clamps at the base, polymorphic, the longer basidia with a median constriction; surrounded by 4–6 pseudoparaphyses. *Cheilocystidia*: 10–21 µm diam., globose, subglobose, a few utriform (British collection globose, 13 × 14 µm). *Pleurocystidia*: 42–70 × 26–30 µm, ellipsoid or utriform, (British collection 70 × 32 & 72 x 33 µm). *Veil*: a mixture of (a) strings of thin-walled sausage shaped cells, varying in breadth along the string but tapering towards the tip, the broader cells narrowing towards a broad septum and (b) long, narrow hyphae, branched but not diverticulate, tapering from 5 µm to (the predominant elements) 2 µm wide.

Habitat: so far always on horse dung.
Specimen examined: **England**, Hertfordshire, Whippendell

Wood, on horse dung, 17 Sep. 2006, *D.J. Schafer*, DJS20060917001, K-M1447369.

Notes: The species is distinguished by its spore shape and size, broader than *C. pseudoradiata*, lacking the raised germ pore with detachable cap of *C. cinerea*, and by its veil of two types, including very narrow smooth hyphae, branched but not diverticulate and brown coloured, at least towards the centre of the cap. In addition, the cog-wheel shape of some young spores is very distinctive when present.

DISCUSSION

Section *Lanatulae*

In the present work, the holotype of *C. pseudoradiata* at Geneva, dated 17 April 1944, was sequenced with some difficulty using next generation sequencing and produced an ITS sequence that most closely matched *C. bicornis* and was close to sequences of *C. pseudoradiata* collected from Norway, published in Nagy *et al*. (2013). Our study of the holotype has also confirmed the similarity to *C. bicornis* in veil structure and the distinction from other species, including *C. kempii*. On the basis of the similar ITS sequences and the shared morphological traits, there is clearly a case for reducing the status of *C. bicornis* to a synonym of the earlier *C. pseudoradiata*. Nagy *et al*. (2013) refrained from making that change, but the genetic data obtained in the present work from the holotype of *C. pseudoradiata* and the observations on the veil structure of both species allow more reliable conclusions to be drawn. The difference in spore size (*C. bicornis* having larger spores) as well as the two-spored basidia, are nevertheless remarkable features that need to be taken into account, so we feel that the transfer of *C. bicornis* to an infraspecific rank is better than a plain synonymy with *C. pseudoradiata*. The nomenclatural code proposes two main infraspecific ranks (variety and form), but it does not define them accurately, so their usage is not formally regulated. While each term seems to have a different original meaning (and could therefore be used in different cases), there is no scientific consensus about it. Since the code states that variety is hierarchically superior, its usage would avoid unnecessary taxonomic complications, and is therefore chosen here to accommodate these specimens, as *C. pseudoradiata* var. *bicornis*. In some cases, species with nearly-identical ITS sequences show significant differences in other genes, so sequencing additional markers (*TEF1, RPB2*) from *C. bicornis* and *C. pseudoradiata* could still support a partial or a recent complete reproductive isolation (speciation). However, we think this would be rare, as ITS sequences would be very similar to each other, or present a few apomorphic mutations, instead of the observed scattered variability. The analysis of additional samples and genes will surely clarify this issue, but in case that 'cryptic' species are found inside this clade, the taxonomic status of other synonyms in *Coprinopsis* should be investigated as well (i.e. *C. radiata*, *C. nevillei* and *C. tectispora*; *C. variegata* and *C. strossmayeri*). The position of *C. scobicola*, which also nests in the same clade in our phylogram, as well as in those of Nagy *et al*. (2013) and Wächter & Melzer (2020), is not so clear. Differences in spore shape and size and in substrate preference suggest that, although it may deserve to be accommodated in another infraspecific rank, further collections and sequencing are necessary to confirm this. Further study may provide correlation of these traits and clearer nomenclatural assignments but, alternatively, may reflect a less settled pattern of speciation in closely related two- and four-spored species, as discussed below.

The phylogenetic analysis in the present work also suggests that the clade including *C. pseudoradiata* and *C. pseudoradiata* var. *bicornis* is maybe related to sect. *Radiatae*. On the basis of these results, sect. *Lanatulae* does not have any fimicolous species, providing an ecological distinction from sect. *Radiatae*, although this needs to be studied further before making that assertion. Additional information should be analysed to draw more reliable conclusions, as other scenarios are possible too: e.g. an independent origin.

The remaining species in sect. *Lanatulae* particularly include the *Coprinopsis lagopus* species complex, which represents approximately 20 % of *Coprinopsis* records in Britain. Further study of collections morphologically and by sequencing is continuing in an effort to clarify the species that are present. *Coprinopsis pachyderma* provides an example of what is possible. Collections of this species, including the type, were included, along with others identified as *C. lagopus* in phylogenetic species PS6 of Nagy *et al.* (2013). The subsequent study of Wächter & Melzer (2020) divided this clade into two, attaching the names of the known species, *C. pachyderma* and *C. brunneofibrillosa* one to each clade. The ITS sequences of two collections in the present work, DJS20080527001 and DJS20150323002, which were identified before sequencing as C. pachyderma, nest in that clade.

Also in sect. *Lanatulae*, the two sequences FN396128 and JX118684 are of *C. babosiae*, a species found on rotting wood and bark in forests in Hungary, possibly associated with *Populus alba*, and described in Nagy *et al*. (2013). The sequence FN396128 was reported initially as *C. goudensis* but was presumably a misidentification, since it was subsequently included in the formal description of *C. babosiae*. This species has not been reported from Britain.

Section *Radiatae*

Coprinopsis candidolanata appears to be quite common in Britain and has previously been mistaken for *C. pseudoradiata*, although it is not clear how many of the previous records of that species have been misidentified and further collections in this group of species will be very helpful in clarifying the position.

The morphological differences supporting *C. kempii* as a new species, particularly the veil structure with diverticulate veil elements and clamp connections, are supported by the phylogenetic analysis, which places the species in a distinct clade in section *Radiatae*. Morphological characters separate it from *C. candidolanata* and *C. villosa* in that section and from *C. pseudoradiat*a in section *Lanatulae*, species with somewhat similar spores.

Coprinopsis villosa was provisionally described from Hawaii, USA, (Keirle *et al*. 2004) and formally proposed in Nagy *et al*. (2013) with additional material from Germany,

Hungary and Sweden. The British collection, DJS20060917001 from Whippendell Wood in Hertfordshire was made in 2006 and misidentified as *C. pseudoradiata* but re-examined as part of the present study. Its sequence and characters matched those of *C. villosa* and the collection is reported here as the first British collection of this species. The species is distinguished by its spore shape and size, broader than *C. pseudoradiata*, lacking the raised germ pore with detachable cap of *C. cinerea*, and by its veil of two types, including very narrow smooth hyphae, branched but not diverticulate. The veil is described as chestnut brown in Nagy *et al*. (2013) but as white, often with brownish or reddish tones near the disc, in Keirle *et al*. (2004). The British collection has veil matching the Hawaiian description and also spore size closer to that material. There is also a remarkable feature of the spores described in the Hawaiian collection. Less mature specimens were reported as having wall pigment developing in longitudinal ridges, presenting a cog-wheel appearance in end view. This was observed in the British collection and was also accompanied by some spores having the complete dark exospore breaking up into patches (Fig. 19).

Coprinopsis radiata is common and widespread in Britain on a variety of dung substrates, often mixed with vegetation such as straw. The species *C. macrocephala*, basionym Agaricus macrocephalus Berk., was described as a fimicolous species by Berkeley (1836) and, as *Coprinus macrocephalus*, by Berkeley (1860). In other respects, the original description could match various fimicolous *Coprinopsis* species. It was distinguished from *C. radiata* by Orton & Watling (1979) mainly on the basis of fruitbody size and breadth of spores but Kemp (1975, 1985) showed that small specimens of *C. radiata* re-grown on sterile media could produce much larger basidiomata (see Fig. 17A). Specimens identified as *C. macrocephala*, distinguished by larger fruitbodies and spore size, were shown by Kemp (1985), with the exception of two specimens collected by P.D. Orton, to be interfertile with *C. radiata* in laboratory studies. Nagy *et al*. (2013) observed a high morphological plasticity in spore shape and basidiome size in *C. radiata* coupled with negligible genetic divergence, species identified as *C. macrocephala* and *C. tectispora* nesting in the *C. radiata* clade. Coprinopsis macrocephala has to be regarded for the moment as a dubious species but a search for further material matching the description of *C. macrocephala* by Orton & Watling (1979), with coarse veil and broad spores, might provide collections that are distinct phylogenetically. Coprinopsis tectispora, distinguished by large dark spores with a detachable perispore (Van de Bogart 1979, Schafer 2010b) and a soil or wood chip substrate, matches *C. radiata* phylogenetically despite its morphological differences. So, unless further collections or sequences of further loci prove otherwise, it appears also to be *C. radiata*.

The type of *C. nevillei* also nests in this clade and, as noted in Wächter & Melzer (2020) this appears to be another synonym, despite it being found growing on a plant stem.

Section *Cinereae*

In this section, only one species, *C. cinerea*, has been reported from Britain so far. This is a very common and widespread species, also much studied as a model species in fungal biology and one of the earliest species to have a complete genome of one of its strains sequenced (Stajich *et al*. 2010). Four UK collections were sequenced in the present study. The two species, *C. radiata* and *C. cinerea* occur commonly on dung/straw heaps in Britain, the latter often associated with a stage in the life of the dung heap when microbial action makes it hot. Both can have a rooting base to the stipe but *C. radiata* has a fragile, hollow stipe; *C. cinerea* is generally larger and has a firmer stipe, still hollow but often with a rather firm, solid base and root. *C. cinerea* has another distinguishing feature relating to the germ pore that, surprisingly, seems to have been noted only recently. The germ pore has been known to be sometimes raised with the appearance of a collar but Gierczyk *et al*. (2014), see also Mešić *et al*. (2018), point out that this is caused by a detachable translucent cap (like a contact lens, Figs 6–7). This seems to be more readily seen in mature spores, especially in aqueous KOH and when dried fungarium collections are examined. *Coprinopsis cinerea* is well separated in our phylogram, as in those of Nagy *et al*. (2013) and Wächter & Melzer (2020), from other species with similar veil.

Two other species with a detaching cover to the germ pore are in this section: *C. annulopora* and *C. afrocinerea*. The former is fimicolous, growing on herbivorous dung, a robust fleshy species with large spores (11–14.5 × 7.5–8.5 µm). The latter grows on sandy/gravel soil or rotten wood and has smaller spores. Neither has yet been recorded from Britain.

Also in sect. *Cinereae* is the remarkable *C. calospora*, found only once in Europe, in the Netherlands (Uljé & Bas 1993) growing indoors on a *Yucca* plant and recognised by its spores covered with large rounded nodules. It has been reported recently growing on a rotting wood building plank in the Dominican Republic (Voto & Angelini 2025) and there is a sequence reported from USA (GenBank OP470607).

Section *Xenobiae*

This section includes two fimicolous species described from Britain: *C. luteocephala* (Watling 1972) and *C. xenobia* (Orton 1976), both from Scotland. Uljé & Noordeloos (1997) distinguished these two species on the basis of veil colour and spore size but referred to Italian collections where the spore size matched *C. luteocephala* but colour was lacking, concluding that one variable taxon was probably involved. Ruiz *et al.* (2013) described collections of *C. xenobia* from Spain and reviewed the relationship with *C. luteocephala*, including phylogeny, concluding that, although more exhaustive molecular studies with more genes and collections were needed, the synonymy hypothesis was the most plausible. We studied four British collections: from Scotland in 2010, from the Forest of Dean in 2017, from Buckinghamshire in 2022 and from Norfolk in 2025. The 2010 collection was particularly useful, providing primordia and more developed stages of sporulating from one site over several days. The primordia are covered in white veil, which develops yellow colouration as the fruitbody matures, the colour intensity varying depending on the conditions. Using a hand lens, the presence of yellow tones can often be seen in collections that initially appear colourless. The yellow colour is associated with intracellular vacuolar material in the veil

cells, as described for the holotype in Watling (1972) and the photograph by R.K.O. Kemp (Fig. 11E) shows fruitbodies arising from a culture, probably of the holotype. We consider the two species to be synonymous. *C. luteocephala* has the earlier date and we are applying this name to all four collections. Clearly, however, it would be valuable to sequence the holotypes of each to confirm this assessment.

No other fimicolous species in sect. *Xenobiae* are known from Britain but the recently described *C. siepei*, described from Germany (Bender & Melzer, 2021) grows on horse straw manure and should be looked for in Britain. It has veil entirely of narrow cylindrical hyphae, 6–14 µm wide and large spores 13–15(–16) × 8–9 µm.

Section *Picaceae*

Two British species, *C. picacea* and *C. stangliana*, and one species complex, *C. strossmayeri/variegata* belong in this section, which does not include any fimicolous species. All have large basidiocarps with patches of felty veil on the cap.

Coprinopsis picacea is a common find in British woodland, especially among leaf litter in *Fagus* woodland. It is easily recognised with white patches of veil contrasting with the dark underlying cap; a skatole-based unpleasant odour and large spores are also distinctive. The sequence of one British collection, K(M)169337 collected by Andy Overall from Hampstead Heath in 2010 is included in the phylogram.

A first British collection from Rugby of the *C. strossmayeri/variegata* complex was reported in Douglas *et al.* (2020), comparing its ITS sequence with sequences from various parts of the world, and is included in our phylogram. A deeper study needs to be undertaken to define species boundaries and establish names for what may be as many as eight different species. The oldest name derives from *Coprinus variegatus* Peck (1873) but the potential synonymy has been generally ignored, with American records using *Coprinopsis variegata* and European *C. strossmayeri*, which derives from *Coprinus strossmayeri* Schulzer (1879).

Two collections of *C. stangliana* from Britain are included in the phylogram. K(M)17195 is the 1991 collection of *C. stangliana* from Box Hill, Surrey described in Henrici & Læssøe (1993) as a species of unimproved grassland on calcareous soil. At the time, surprise was expressed that such a distinctive species in such a location had not been found before in Britain, although two earlier collections from that site, in 1977 and 1987 were identified and reported in that paper. Subsequently, a 1948 record from that site by Dr. R.W.G. Dennis was added to the database, presumably from an herbarium specimen. The 1993 report was followed by a number of records from other parts of Britain, including one, K(M)59227, from Wytham woods in Oxfordshire, which we have sequenced and included in the phylogram. The woodland locality was surprising, albeit in a grassy clearing in the wood. Very few British records have been added in recent years and *C. stangliana* appears to be genuinely rare in Britain.

Two sequences, MT571666 and MT537077, labelled *C.* aff. *stangliana*, form a distinct clade in our phylogram. Presumably, these are collections reported in Bougher (2006) from Western Australia as *C. stangliana*, but differences were noted from European collections and a molecular phylogenetic study promised. They appear to represent a new species. Clearly, it would be valuable to sequence the holotype of *C. stangliana*, a 1986 collection from Germany, deposited at M herbarium.

Sect. *Lanatulae* includes numerous clades with some collections identified as *C. lagopus* in each clade, a fact already reported by Nagy *et al.* (2013) and Wächter & Melzer (2020), and observed in the present analyses too. More collections belonging to these clades need to be sequenced to ascertain which of them are actually present in Britain and find distinctive characteristics allowing them to be assigned to known or new species corresponding to these clades.

Two-spored versus four-spored taxa in the coprinoid *Psathyrellaceae*

In many genera, different collections of species may be found with varying proportions of two- and four-spored basidia in their fruitbodies, the character often being regarded as a variable phenotypic feature unrelated to reproductive isolation, justifying distinction only as a form or, occasionally, variety, depending on the different concepts of these ranks. In the coprinoid *Psathyrellaceae*, in contrast, taxa are generally exclusively four-spored or have basidia with fewer sterigmata but not four. The distinction between four-spored and other otherwise similar taxa is also reflected in extensive laboratory mating studies (Lange 1952, Kemp 1970, 1975). Kemp (1975) reported that two-spored taxa were never found to be interfertile with four-spored taxa in his studies and described a form of speciation as a process in which incompatibility occurred at the hyphal level, morphological and other changes taking place later as a consequence. This and similar considerations were reflected in the four-spored versus two (or three)-spored character being regarded as justifying distinction at the species level along with other morphological features in the coprinoid genera.

However, phylogenetic studies, for example Nagy *et al*. (2013), Wächter & Melzer (2020), Schafer *et al*. (2022) have identified pairs of 2-spored and 4-spored taxa that are not separated in typical phylograms and often have essentially identical ITS sequences. In our present study, as reported in Nagy *et al*. (2013), *C. bicornis* nests alongside the 4-spored *C. pseudoradiata* in an unresolved clade that includes another morphologically distinct but phylogenetically close two-spored species, *C. scobicola.* In Schafer *et al*. (2022), *Parasola cuniculorum* is shown to be phylogenetically distinct from the 4-spored *P. misera* but to have a 4-spored form (found in Cyprus and recently in our present study at Burnham Beeches in Britain) that is not distinct from 2-spored *P. cuniculorum* in our phylograms. A 2-spored taxon, *Ephemerocybe callina* var. *miionis*, phylogenetically not distinct from *E. callina* var. *callina*, was also reported from Cyprus in that study. In Wächter & Melzer (2020), the 4-spored *E. fuscocystidiata* is distinguished from, but close to the 2-spored *E. amphithalla* and *Coprinopsis rugosobispora* is distinguished (but subject to the need for further investigations) from the four spored *C. phlyctidospora* and collection "Schafer 601", also a 2-spored taxon, is included in the *C. phlyctidospora* clade.

We do not have the resources or expertise to explore this issue further, but several scenarios are possible. A very recent speciation (a complete genetic-driven reproductive

isolation) could have not had time to fix any distinctive mutation in the phylogenetic markers studied in this work. Also, reproductive isolation could be just partial (with occasional interbreeding events), leading to no visible diagnostic mutations fixed yet. These phenomena could be the cause of the unresolved phylogeny in the clade that includes *Coprinopsis pseudoradiata*, *C. pseudoradiata* var. *bicornis* and *C. scobicola* and, from the point of view of field mycology, we think it remains important to distinguish, record and keep collections of such taxa as a basis for analysing processes of speciation in the future. Additional information to solve this issue could be obtained from mating studies, protein-coding genes and genomic studies.

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Conflict of interest: The authors declare that there is no conflict of interest.

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Supplementary Material: http://fuse-journal.org/

Supplementary Table 1. Species studied, and associated data.