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Coprophilous fungi in New Zealand. I. *Podospora* species with swollen agglutinated perithecial hairs

A. Bell[1]

School of Biological Sciences, Victoria University of Wellington, Wellington, New Zealand

D. P. Mahoney

Department of Biology and Microbiology, California State University, Los Angeles, California 90032

Abstract: New Zealand coprophilous *Podospora* species with swollen agglutinated perithecial hairs include *P. aloides, P. conica, P. curvuloides, P. dakotensis, P. glutinans, P. miniglutinans, P. tetraspora* and *P. vesticola*. Reasons are given for retaining these species in the genus *Podospora* rather than in the genus *Schizothecium*. Species are distinguished by the size and morphology of their ascospores and the number of ascospores per ascus, the agglutinated perithecial hair differences and their *Phialophora* anamorphs, or absence of anamorphs, in agar culture. Descriptions and a key are provided and dung preferences and distributions discussed. *Podospora conica* is proposed as a new combination and *P. curvuloides* is illustrated with transverse striations on its ascospore wall.

Key Words: coprophilous fungi, Lasiosphaeriaceae, New Zealand, *Podospora aloides, P. conica* comb. nov., *P. curvuloides, P. dakotensis, P. glutinans, P. miniglutinans, P. tetraspora, P. vesticola, Schizothecium*, Sordariaceae, taxonomy

INTRODUCTION

Coprophilous fungi have always enjoyed the attention of a relatively large number of mycologists. This may be due in part to the comparative ease with which their preferred substrate can be collected and subsequently interpreted. Being discrete entities, the dung of herbivorous animals can be viewed as tiny self-contained ecosystems that can be studied at leisure in the relative comfort of the laboratory. Among ascomycetous coprophilous fungi, the Sordariaceae, taken in the broad sense (Lundqvist, 1972), and the genus *Podospora* Ces. have received a great deal of attention. Descriptions and keys to species in these taxa have been provided by Cain (1962), Krug and Khan (1989), Malloch and Cain (1971) and Mirza and Cain (1969), by their colleagues and students at the University of Toronto, by Lundqvist (1972) in Sweden and by many others. These, in turn, have attracted other students like ourselves. Species of *Podospora* were known to be well represented in New Zealand (Bell, 1983), yet could benefit from a more detailed treatment.

MATERIALS AND METHODS

The fungi described here were obtained from collections of dung of various herbivorous animals in New Zealand. Each collection, referred to as a sample, was placed in a loosely closed new paper bag and kept air dry at 5 C until it could be incubated in a moist glass container (see Lundqvist, 1972, p. 12; Bell, 1983, p. 14). Attempts were made to sample a wide variety of herbivore dungs throughout the year in as many different ecological districts (McEwen, 1987) as possible. Each dung sample was scrutinized for species of *Podospora* over a period of 12 wk.

We have observed that the dung from domesticated animals that receive regular intestinal drenches to rid them of internal parasites shows a disappointing lack of fungi growing on it. Therefore, we concentrated on collecting dung from wild or grazing animals rather than from those confined to feedlot situations.

These fungi are best observed in their fresh state in water mounts rather than in any other slide mounting medium. Adhesive gelatinous caudae and/or coatings on the ascospores are often destroyed in other mounting media and, even in a water mount, are frequently disrupted through application of a cover slip or upon forcible discharge from the ascus. Semipermanent lactophenol slides, with or without cotton blue, sealed with nail polish or "Glyceel" were prepared for verification purposes. Even here, however, thin-walled structures such as ascospore pedicels, asci and paraphysoid tissue may shrink or disintegrate.

Most observations for illustrations or photography were made from water mounts or from aniline blue lactic acid (0.05 g aniline blue in 100 ml lactic acid) mounts, heated slightly. For clearer views of centrum elements, and a minimum depth of field, best results were achieved by squashing perithecia in water and

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[1] Corresponding author.

transferring the centrum elements to a drop of aniline blue lactic acid. Alternatively, for water mounts, all but the centrum elements were removed. Phase contrast microscopy was essential to the observation and photography of gelatinous structures, e.g., all ascospore caudae in FIGS. 31–42, ascus walls and tips, e.g., FIGS. 19–22, and paraphysoid tissue, FIG. 18.

Attempts were made to culture each species. Perithecia were removed from the dung, cleared of debris either in a drop of sterile distilled water or by pushing through Difco corn meal agar (= CMA) containing 30 μg/ml streptomycin sulfate and 100 units/ml penicillin G and their contents spread on fresh CMA containing the aforementioned antibiotics. After incubation at 22–24 C under continuous fluorescent lighting for 18–36 h, any germinating ascospores were picked off with a sterile needle and transferred to fresh CMA with antibiotics. Since *Podospora* ascospores typically germinated at a very low percentage, we experimented with several techniques to stimulate germination. Techniques we tried included: 1) heat treatment of the ascospores at 55–60 C for 10–20 min (Shear and Dodge, 1927), 2) treatment with 3% hydrogen peroxide for 15–40 min and 3) incorporation of 7 g/L sodium acetate in the CMA medium (Olive and Fantini, 1961). Ultimately, none of these raised the germination percentage. Treatment with 3% hydrogen peroxide for 25 min, however, had the advantage of killing all but the ascospores and thereby negating the need for antibiotics in the CMA.

Cultures were initiated from single germinating ascospores where possible, from germinating ascospore clusters or from the growth of perithecial fragments. Although a variety of agar media were employed, including Difco potato dextrose agar (PDA), Weitzman and Silva-Hutner's agar (WSH) and modified Leonian's agar (Malloch, 1981), the best production of typical teleomorphs and anamorphs was achieved on Difco CMA. If incubating dung samples had been neglected and perithecia had already discharged their ascospores, the situation could be remedied by picking ascospores from the glass lids. If these subsequently grew and sporulated in culture, this was a circuitous way of ascertaining some of the fungi which had been missed.

At least 10 ascospores and usually many more were measured each time a species was observed on dung or in axenic culture, resulting, in most cases, in hundreds of individual measurements for the species overall. The measurement of the ascospores and their number per ascus remain the most reliable characters with which to delineate these *Podospora* species. Other measurements provide only supplementary, corroborative information. Traditionally, taxonomic treatises give measurements for asci and the gelatinous caudae of ascospores together with the measurements of perithecia and other structures. However, not all these measurements are of equal reliability. Asci and caudae are difficult to measure since they are extensible, evanescent and, among these *Podospora* spp., seldom seen in their entirety. Therefore, in the following treatise we deal with ascus and caudal dimensions only in a generalized way.

All references to color of ascospores and mycelia in the following species descriptions were diagnosed according to Rayner (1970). Shapes of perithecia, ascospores and other structures follow those of Snell and Dick (1971).

TAXONOMY

The genus *Podospora* includes those mostly coprophilous pyrenomycetes that are nonstromatic, producing dark pseudoparenchymatous submerged or superficial perithecia. These perithecia may be naked or variously adorned with single, tufted or clustered (= agglutinated) hairs. The most distinctive feature of the genus is the morphology of the ascospores. Each mature ascospore is composed of a dark olivaceous-brown/black ellipsoid cell, attached to which is a smaller, narrowly elongate or papilliform, basal hyaline cell (= pedicel). In addition, various gelatinous appendages (= caudae) are usually present at the apex and base of the spore.

Lundqvist (1972, pp. 52, 69) discusses the position of *Podospora* as a genus in the Lasiosphaeriaceae, segregated from genera such as *Sordaria*, *Gelasinospora* and *Neurospora* which he places in a more restricted Sordariaceae. We accept this placement. A full generic description of *Podospora* can be found in Lundqvist (1972) and Mirza and Cain (1969), although the circumscription of *Podospora* by Lundqvist is narrower than that of Mirza and Cain. For example, Lundqvist has resurrected the generic epithet *Schizothecium* Corda for the species of *Podospora* treated in the present article. Perithecia of these species are adorned with groups of swollen agglutinated hairs, or with prominent protruding peridial cells. In support of this move he emphasized characters which delineate these taxa from the rest of the genus *Podospora*, including the following: 1) ascospores that become transversely septate at a very early stage in their development, 2) pedicels that are plasma-filled and persistent, 3) the lack of interascal filiform paraphyses (pers. comm.), 4) the lack of olivaceous colors in the perithecia (pers. comm.) and 5) peridial cell detail and an anamorph linking them with the genus *Cercophora* Fckl. (pers. comm.).

During our investigations we have paid special attention to these differences. For example, we have found that the ascospores certainly do become septate

at a very early stage in their development, compared with other species of *Podospora* in which immature ascospores remain clavate and single-celled for a longer period of time. But we have not noted the pedicel to be more persistent in this group than in many other species of *Podospora*. In all the species of *Podospora* that we have studied, the pedicel is frequently absent at the time of ascospore germination and plays no part in the germination process. Nor have we found any consistency in the presence or absence of interascal filiform paraphyses among species of *Podospora*. Instead, we find a wide range of interascal tissue and, in some species, an extraascal tissue lining the inner peridium and surrounding the asci. The latter we refer to as "jacket paraphyses" (see FIGS. 6, 9, 17, 18). These are characteristic of, but not exclusive to, the species described here. This jacket and the absence of typical interascal paraphyses do characterize the *Schizothecium* group of *Podospora* species but represent only a variation in centrum structure among *Podospora* species and cannot be a basis for recognizing a separate genus. Studies of centrum development are necessary, and presently lacking, but one such study of *P. tetraspora* and *P. vesticola* currently in progress in our laboratory indicates that interascal tissue is present at least during a portion of perithecial development.

We have not observed any differential colorings or differences in peridial cell detail in the perithecia that may be easily utilized for taxonomic purposes, although differences certainly do exist. Like Lundqvist, Mirza and Cain (1969, p. 2000) use peridial cell detail, "swollen" versus "angular," to differentiate an agglutinated hair group of *Podospora* species, Lundqvist's *Schizothecium* group, from other *Podospora* species. In our opinion, that distinction is too difficult to make to be used in practice.

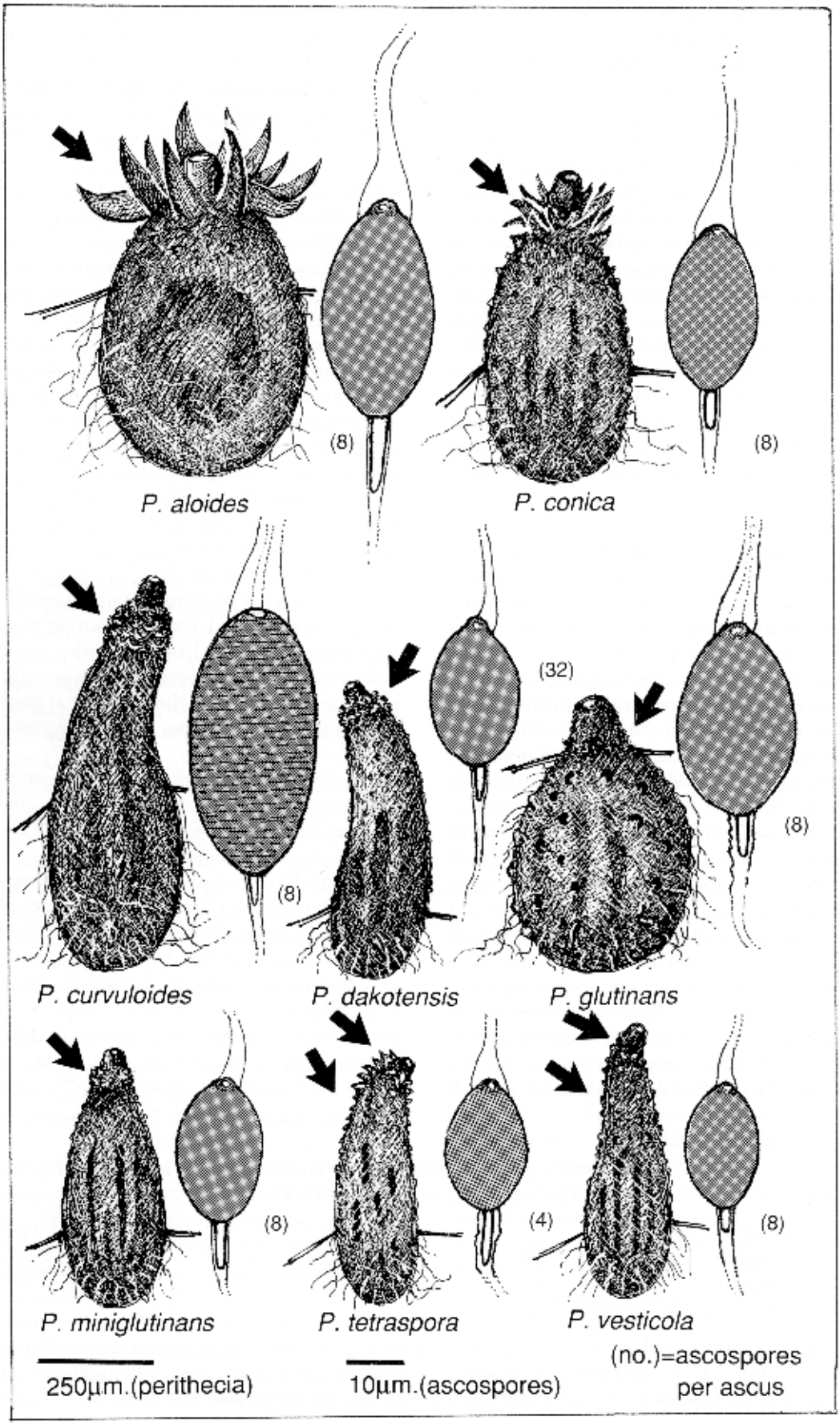
This leaves the question of the anamorph and its use as a taxonomic criterion for separating species from *Podospora*. This paper shows that some taxa transferred by Lundqvist to *Schizothecium* do produce an anamorph belonging to the form genus *Phialophora* Medlar as does *Cercophora mirabilis* Fckl. However, these are not the only species of *Podospora* or the only genera of Ascomycetes that have a *Phialophora* anamorph. We have found that *Podospora communis* (Speg.) Niessl and an undescribed *Podospora* on which we are working, both species without agglutinated hairs, produce a *Phialophora* anamorph in CMA culture. Also many other described *Podospora* species are still undescribed in agar culture and may have *Phialophora* anamorphs. As noted by Domsch et al. (1980, p. 620), "*Phialophora* is a rather heterogenous assemblage of anamorphs of unrelated Ascomycetes." Although in time different sections of the genus *Phialophora*, or its generic segregates, may be found associated with particular ascomycete genera, more information must be forthcoming before this is possible. At present we do not know whether the *Phialophora* anamorphs of *Podospora* species described here are unique to this group of species or not. Within the group they are certainly similar to each other; in fact six of the species, *Podospora aloides*, *P. comica*, *P. curvuloides*, *P. glutinans*, *P. tetraspora* and *P. vesticola*, exhibit virtually indistinguishable anamorphs. Only *P. dakotensis* and *P. miniglutinans* lack an anamorph.

While we recognize that the species of *Podospora* described herein do have certain morphological characteristics that bind them, including a sum total of characters ably noted by Lundqvist, we do not consider these sufficient to warrant the generic distinction of *Schizothecium*. Given the evidence at hand, we prefer to continue treating these fungi as species of the genus *Podospora*.

Lundqvist (1972) states that there are some 31 named species within his *Schizothecium* group, some of which are possibly synonyms, and Mirza and Cain (1969) detail 17 named species. To date we have found eight species in New Zealand which are distinguished from each other in the following key. As viewed intermingled on the dung, perithecia of these species are often difficult to distinguish, due to their variability, yet we can distinguish "typical" perithecia of each species. Illustrations of these perithecia together with details of ascospore morphology appear in FIG. 1. Photographs of perithecia and ascospores are presented in FIGS. 2–15 and FIGS. 16 and 19–43, respectively.

KEY TO NEW ZEALAND SPECIES OF *PODOSPORA* WITH SWOLLEN AGGLUTINATED PERITHECIAL HAIRS

1. Asci each containing four ascospores ..... (7) *P. tetraspora*
1. Asci each containing >four ascospores 2
2. Asci each containing 32 ascospores ..... (4) *P. dakotensis*
2. Asci each containing eight ascospores 3
3. Perithecia adorned with triangular groups of agglutinated hairs approx. 230 μm long, ascospores 31–37 × 16–20 μm ..... (1) *P. aloides*
3. Perithecia adorned with agglutinated hairs that are shorter, or the ascospores smaller, or both 4


(8)
P. aloides
(8)
P. conica
(8)
P. curvuloides
(32)
P. dakotensis
(8)
P. glutinans
(8)
P. miniglutinans
(4)
(8)
P. tetraspora
P. vesticola
250µm.(perithecia)
10µm.(ascospores)
(no.)=ascospores per ascus

4. Ascospores with dark cell (38–)40–55(–58) × (17–)20–25(–29) μm usually finely transversely striated, pedicel 4–6(–7) × 2 μm ..... (3) *P. curvuloides*
4. Ascospores with dark cell dimensions smaller, without transverse striations 5
5. Ascospore dark cell 31–37 × 21–27 μm, pedicel 8–15 × 2–3 μm ..... (5) *P. glutinans*
5. Ascospore dark cell dimensions smaller 6
6. Perithecia adorned with triangular groups of agglutinated hairs which are each 30–110 μm long, dark cell of ascospore 22–29(–31) × 13–18 μm, pedicel (5–)7–12(–16) × 2–2.5 μm ..... (2) *P. conica*
6. Perithecia adorned with a collar of much smaller agglutinated hairs or with agglutinated hairs scattered and consisting mostly of one to few inflated cells, ascospores smaller 7
7. Perithecia adorned with a short collar of agglutinated hairs each <30 μm long, ascospore dark cell (19–)21–24(–25) × 13–15(–16) μm, pedicel 7–8 × 2 μm ..... (6) *P. miniglutinans*
7. Perithecia adorned with scattered agglutinated hairs consisting mostly of one to few inflated cells, ascospore dark cell 17–20(–22) × 10–12 μm, pedicel 5–7(–8) × 2 μm ..... (8) *P. vesticola*

1. *Podospora aloides* (Fckl.) Mirza & Cain, Canad. J. Bot. 47: 2004. 1969. FIGS. 1, 48

= *Sordaria curvula* de Bary var. *aloides* (Fckl.) Wint., Bot. Zeitung 31: 485. 1873.
= *Schizothecium aloides* (Fckl.) Lundq., Symb. Bot. Upsal. 20(1): 253. 1972.

Characteristics on dung. Perithecia maturing within the first 2 wk of dung incubation, scattered, sparse, mostly submerged in the loose straw-like surface of the substrate, broadly pyriform to ovoid, ca 1.5 × 1 mm; venter subglobose, semitransparent, with pseudoparenchymatous peridium consisting of swollen angular cells and bearing scattered inflated cells and long flexuous hyphae; neck dark, velvety in appearance, covered with anticlinally arranged, blunt, dark-tipped cells. Triangular groups of agglutinated hairs radiating from the base of the neck and frequently curved upward obscuring the neck and ostiole; each grouping ca 230 × 70 μm, acuminate from the merging of adjacent individual hairs; the latter moderately attenuated, each consisting of a row of elongated, slightly swollen, thick-walled, brownish cells. *Interascal tissue* and *jacket paraphyses* as in *P. conica*. *Asci* cylindrically clavate, long-stalked, with simple apices; containing eight irregularly biseriate ascospores. *Ascospores* with dark cell ellipsoid 31–37 × 16–20 μm, olivaceous black, bearing an apical germ pore; pedicel hyaline, straight or slightly curved, covered with a thin gelatinous sheath, 12–14 × 2 μm. Caudae at the spore extremities, long, single, whip-like; one at the tip of the pedicel and the other over the germ pore, the latter broader and sometimes with a central light region appearing to extend upward from the germ pore.

Herbarium specimens examined. NEW ZEALAND. N. ISLAND: Waikawa Beach, on cow dung, 11 Jul. 1992, *A. Bell* (WELTU[2] 597). SWITZERLAND. Lucienstieg near Ragaz, on cow dung, as *Sordaria aloides* Fckl., date unknown, *Barbey-Boissier 678* (LECTOTYPE, G).

Comments. Podospora aloides is apparently rare in New Zealand. It has been found on only three dung samples, including one from a previous study (Bell, 1983). All of our New Zealand records and most of those elsewhere have been from cattle dung. Some of the countries or regions where *P. aloides* has been reported include Canada, Europe, Kenya, and the United States (Krug and Khan, 1989; Lundqvist, 1972; Mirza and Cain, 1969).

This species is very similar to *P. conica*, but larger in all respects. To date we have been unsuccessful in culturing it and are, therefore, unable to verify the *Phialophora*-like anamorph illustrated by Mirza and Cain (1969, p. 2005). Their illustration and description resemble ours for the *Phialophora* state of *P. conica* (FIGS. 43–45, 49). They also report a small, but distinct, apical ring at the ascus tip which we have not seen, although such a structure is sometimes visible in asci of our *P. conica* and *P. tetraspora*.

2. **Podospora conica** (Fckl.) Bell & Mahoney, comb. nov.

FIGS. 1, 2–4, 7, 17, 19, 20, 31, 32, 43–45, 49

≡ *Cercophora conica* Fckl., Jahrb. Nass. Ver. Naturk. 23–24: 245. 1870.
= *Podospora curvula* (de Bary ex Winter) Niessl, Hedwigia 22: 156. 1883.
≡ *Schizothecium conicum* (Fckl.) Lundq., Symb. Bot. Upsal. 20(1): 253. 1972.

[2] The fungal portion of this herbarium is separately housed and separately numbered.

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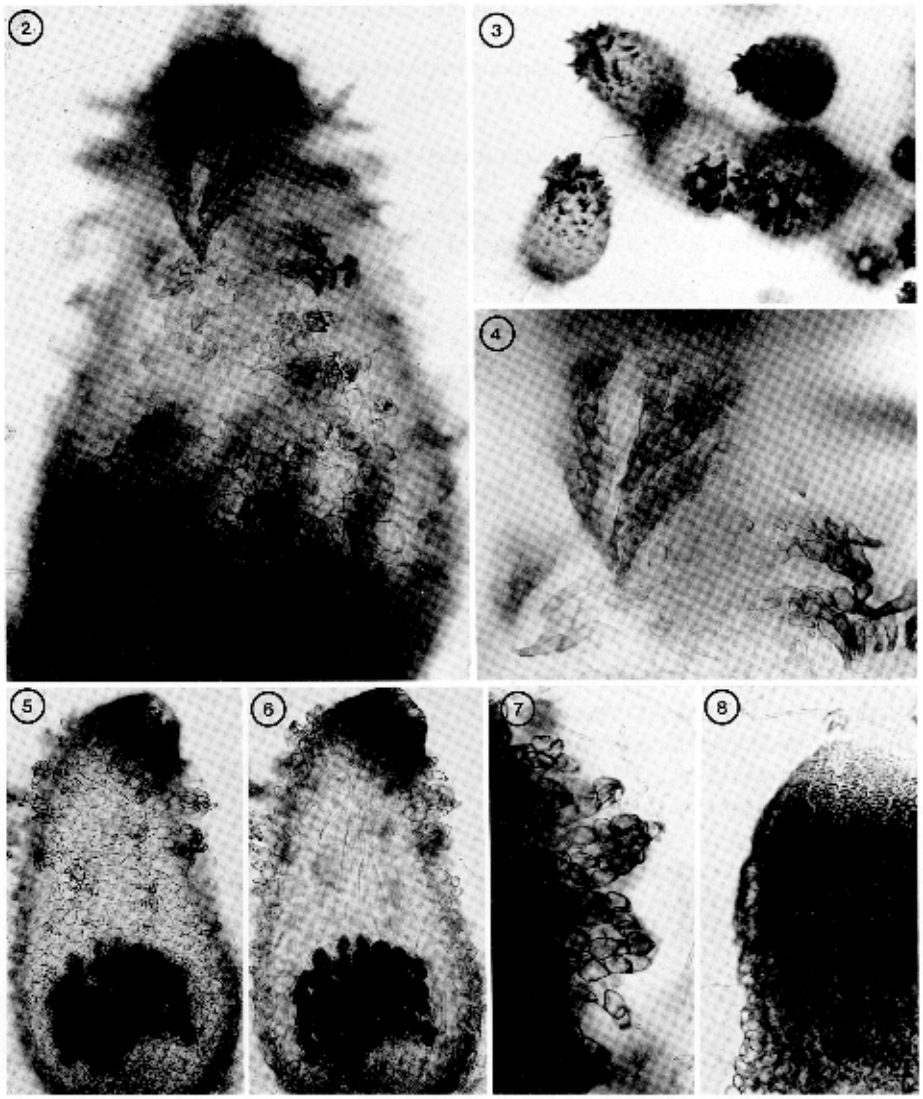
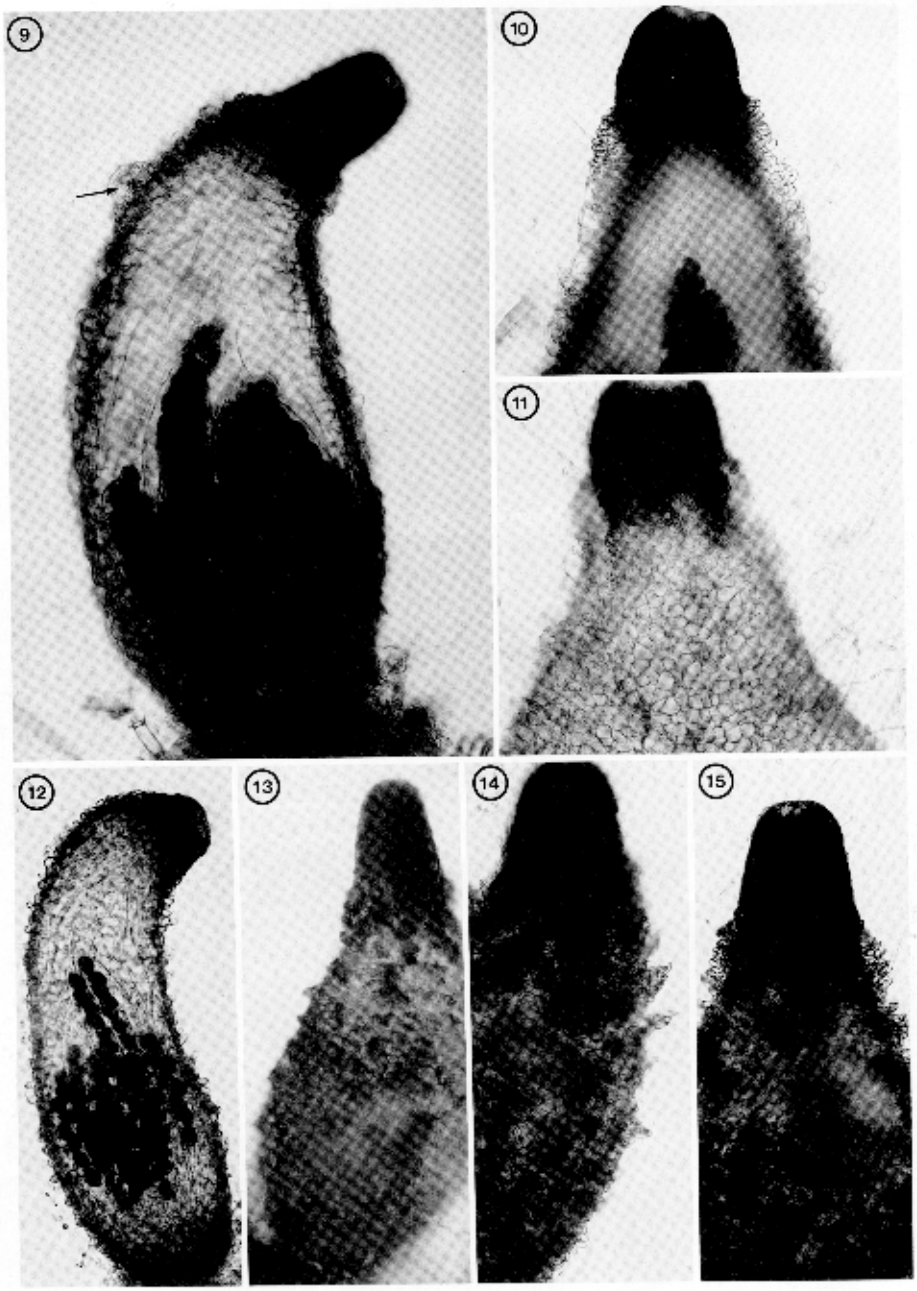
FIG. 1. Diagram illustrating the morphology of typical perithecia, agglutinated hairs (arrowed) and mature ascospores of eight species of *Podospora*. Numbers in brackets refer to the number of ascospores per ascus.

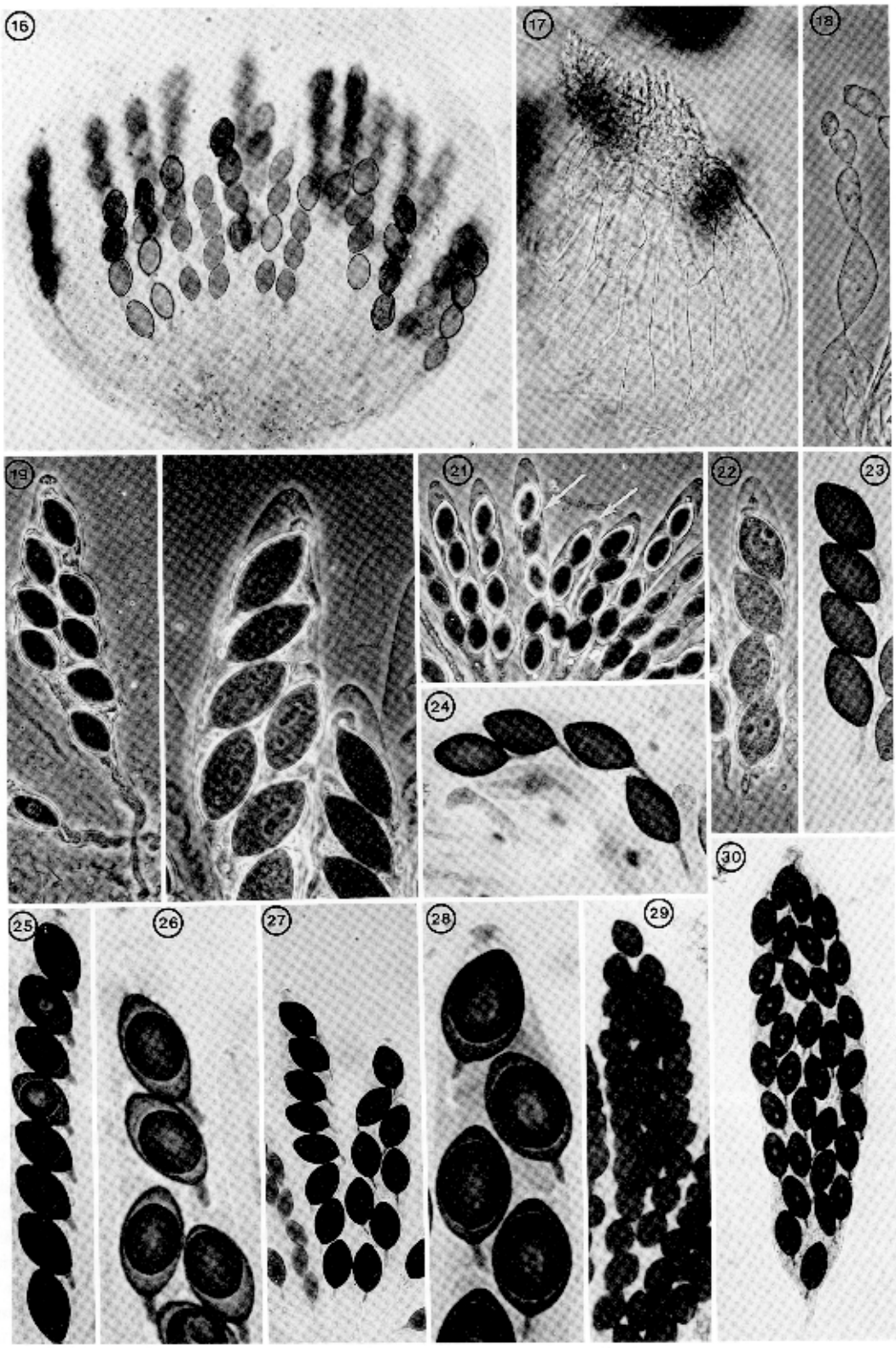


FIGS. 2–8. Perithecia. 2–4. *Podospora conica*, WELTU 593. 2, 4. Same perithecium showing triangular groups of agglutinated hairs typical of the species; × 170 and × 340. 3. Perithecia from the same culture as those figured in FIGS. 2 and 4, further emphasizing the position of larger triangular groups near the base of the neck and smaller triangular groups over the venter; × 40. 5, 6. *P. tetraspora*, WELTU 609. Same perithecium: FIG. 5 focused on the pseudoparenchymatous outer peridium and agglutinated hairs; in FIG. 6 focused on the ascospores and the vertically elongated hyaline jacket paraphyses that surround the asci; × 170. 7. *P. conica*, WELTU 592, showing one type of agglutinated hair variation among strains of this species. Here individual hairs of each triangular grouping adhere less tightly and are more swollen and less attenuated, particularly the apical cells. Compare with the agglutinated hair groupings in FIG. 4; × 340. 8. *P. dakotensis*, WELTU 596, showing the outer peridial layer of the perithecial neck. This consists of vertical rows of small, crowded, anticlinally elongated cells with blunt, darkly pigmented, thickened outer walls. The long axis of these cells is partially visible along the left margin of the neck; × 340. FIGS. 2–8. All perithecia are from CMA axenic cultures. Perithecia were photographed in water slide mounts except in FIG. 3 where they appear in situ on the colony surface.

Characteristics on dung. Perithecia usually maturing within the first 3 wk of dung incubation, mostly gregarious, semi-immersed to superficial, pyriform, 430–950 × 230–650 μm; neck dark, ca 100 μm high, appearing velvety with its outer peridium of short, even-sized, anticlinally arranged, blunt, dark-tipped cells; triangular groups of prominent agglutinated hairs arising at the base of the neck, variable in size, 30–110 μm long; each triangular group hyaline to pale brown and composed of ca three to five short hairs joined laterally; each hair of three to four slightly to moderately swollen, elongate cells with the terminal cell pointed and usually with a thicker, darker, distal cell wall; smaller triangular groups forming a graded



FIGS. 9–15. Perithecia. 9–11. *Podospora dakotensis*. 9. WELTU 595. Perithecium in median optical section, showing internal asci, ascospores, vertically elongated hyaline jacket paraphyses and a low collar of short agglutinated hairs at the base of the black neck. Material at the arrow is debris from the dung. 10, 11. WELTU 596. Same perithecium, unsquashed and squashed, respectively. 10. Median focus, showing a more prominent perithecial collar than was seen in the strain in FIG. 9. 11. Focus on the pseudoparenchymatous outer peridial layer. 12–15. *P. vesticola*. 12. WELTU 612. Perithecium with 1- to 2-celled hairs scattered over the venter. Hair agglutinations are not obvious. 13–15. WELTU 611. A strain of this species with obvious agglutinated hairs. 13, 14. Showing small triangular groups of agglutinated hairs scattered over the venter (seen best along the left perithecial margin in FIG. 13 and the right margin in FIG. 14). 15. A less typical perithecium, but from the same colony that produced the perithecia in FIGS. 13 and 14, showing short agglutinated hairs forming a low collar at the base of the neck. FIGS. 9–12 and 14, 15, × 170; FIG. 13, × 110. FIGS. 9–15. All perithecia are from CMA axenic cultures except those in FIGS. 9 and 12 which were mounted directly from the dung. Perithecia were photographed in water slide mounts except in FIG. 13 where the perithecium appears in situ on the colony surface.



FIGS. 16–30. Centrum elements. 16. *Podospora tetraspora*, WELTU 608. Entire centrum; × 340. 17. *P. conica*, WELTU 592. Centrum, showing only the vertically elongate, hyaline jacket paraphyses; × 340. 18. *P. vesticola*, WELTU 489. Single jacket paraphysis, believed to develop with age from hyaline centrum elements like those illustrated in FIG. 17; × 340. 19–30. Asci with ascospores. 19, 20. *P. conica*, WELTU 593. Mature and slightly immature ascospores, respectively, showing basal pedicels and apical caudae on the spores and a plug of material at the ascus tip. A rarely seen apical ring is represented by

series over the venter with single inflated cells on the lower venter. Venter peridium pseudoparenchymatous, thin, membranaceous, semitransparent, consisting of light brown, angular to swollen-angular cells. *Interascal tissue* absent among mature asci. *Jacket paraphyses*, located at the centrum periphery (see TAXONOMY section), composed of simple chains of hyaline, thin-walled, inflated cells that decrease in size distally to their free ends above the mature asci. *Asci* cylindrically clavate, long-stalked, ca 200 × 30 μm, containing eight irregularly biseriate ascospores; apices simple with a cytoplasmic plug, infrequently with a small apical ring. *Ascospores* consisting of an ellipsoid olivaceous-black cell 22–29(–31) × 13–18 μm, bearing an apical germ pore and a basal hyaline pedicel (5–) 7–12(–16) × 2–2.5 μm; the upper end of the dark cell frequently darker and slightly lemoniform or umbonate in the region of the germ pore. Upper and lower caudae single, hyaline, long and whip-like; the upper cauda broader and situated over the germ pore, or appearing slightly eccentric to it, the lower one at the apex of the pedicel and continuous with a thin gelatinous sheath over the pedicel.

Characteristics in culture. Colonies center-inoculated onto CMA in 9-cm plastic petri dishes, spreading slowly, 35–45 mm in diam in 2 wk under continuous fluorescent light at 22–24 C, producing an appressed grey-olivaceous mycelium. *Perithecia* concentrated in the colony center; morphological features as given above. *Anamorph* a *Phialophora*, produced in abundance in all axenic cultures examined from 10 different dung samples. *Phialides* borne singly and sessile from separate, or fascicled, surface substrate or low aerial hyphae; frequently arranged side by side, opposite each other or in irregular whorls along the hyphae; hyaline, smooth, variously shaped but usually pyriform with a flared apical collarette, mostly 6–10(–16) × 3–5 μm. *Phialoconidia* hyaline, smooth, broadly obovoid with a truncate base, mostly 3 × 2 μm; usually collecting in a glioid mass at the phialide apex, or occasionally forming a short chain. *Aleuriospores* sparse, solitary, sessile on substrate hyphae or terminal on short branches, smooth, hyaline, moderately thin-walled, globose to obovoid, slightly larger than the phialoconidia to ca 4 μm long.

Ascospore germination is characterized by the formation of a globose vesicle, 10–13 μm in diam, which forms over the germ pore and from which one to several hyphae emerge. In cultures of WELTU 592, these young hyphae immediately produce phialides (FIG. 43), a feature not observed at this early stage among other strains of *P. conica* or among other species in this study.

Herbarium specimens examined. GERMANY. Locality unknown, on cow dung (?), as *Cercophora conica* Fckl., herb. Barbey-Boissier s. n. (TYPE, G), this collection also has *Cercophora mirabilis* Fckl. on it, and Fuckel (1870) writes that these two fungi occurred together; Waldwiesen bei Eberbach, on cow dung, as *Sordaria curvula* de Bary var. *coronata* Wint., date unknown, herb. Barbey-Boissier 679 (G); Oestrich, on cow dung, as *Sordaria curvula* de Bary, date unknown, herb. Barbey-Boissier 680 (G), this is the LECTOTYPE of *Cercophora conica* Fckl. NEW ZEALAND. N. ISLAND: Waikawa Beach, sand dune vegetation, on rabbit dung, 11 Aug. 1992, *A. Bell* (WELTU 603); Wainuiomata, along Wainuiomata River, on red deer dung, 16 Feb. 1988, *F. Kell* (WELTU 592); E. of Wellington, Rimutaka Forest Park, Orongorongo Valley, on cow dung, 16 May 1972, *B. Bell* (WELTU 124). S. ISLAND: Along Buller River near Owens Pub, on cow dung, 7 May 1990, *A. Bell and D. Mahoney* (WELTU 593).

Cultures deposited. Living CMA cultures from WELTU 592 have been deposited as IMI 361008, ATCC 90643 and CBS 128.94.

Comments. This common coprophile has generally been referred to as *Podospora curvula* de Bary, based

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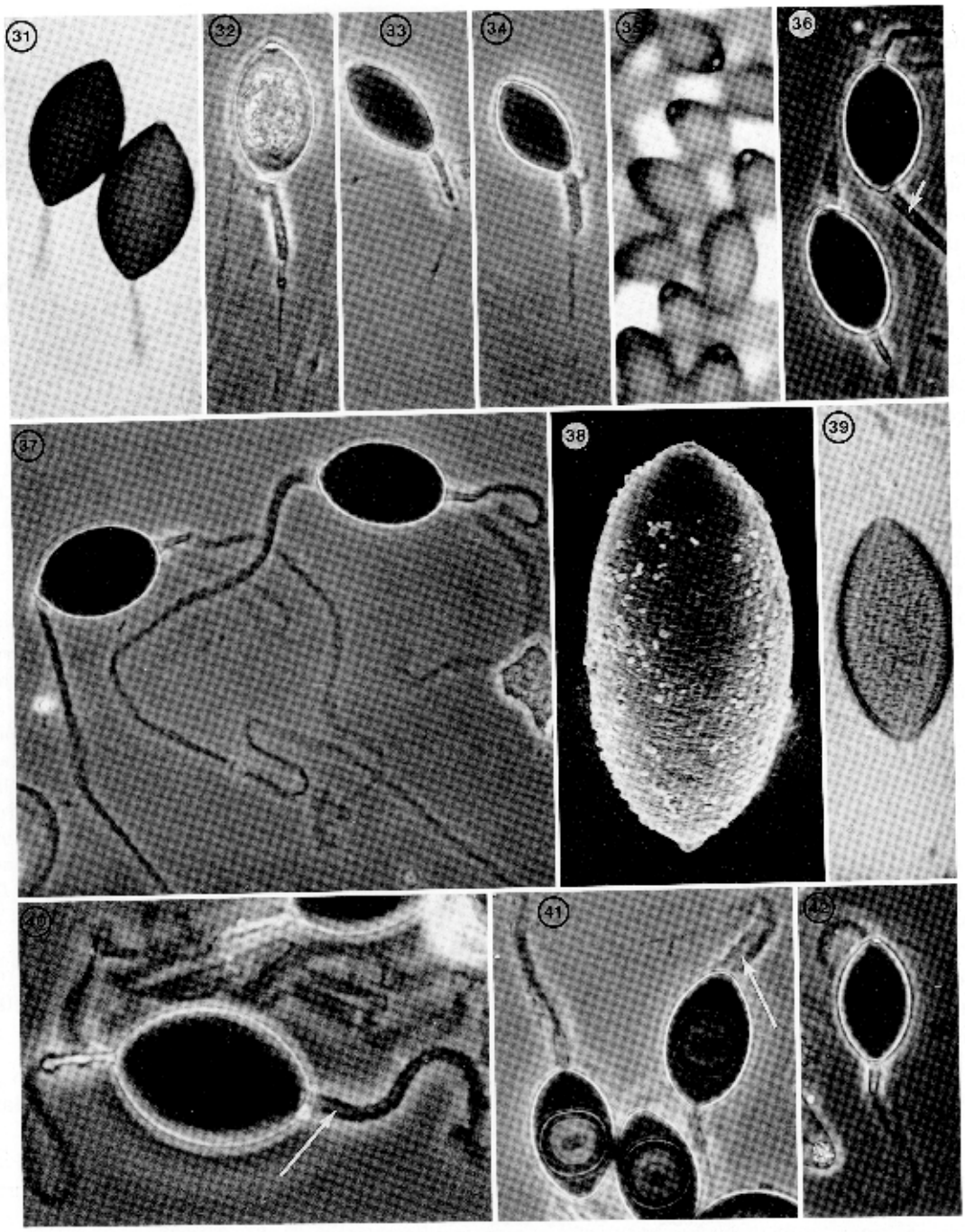
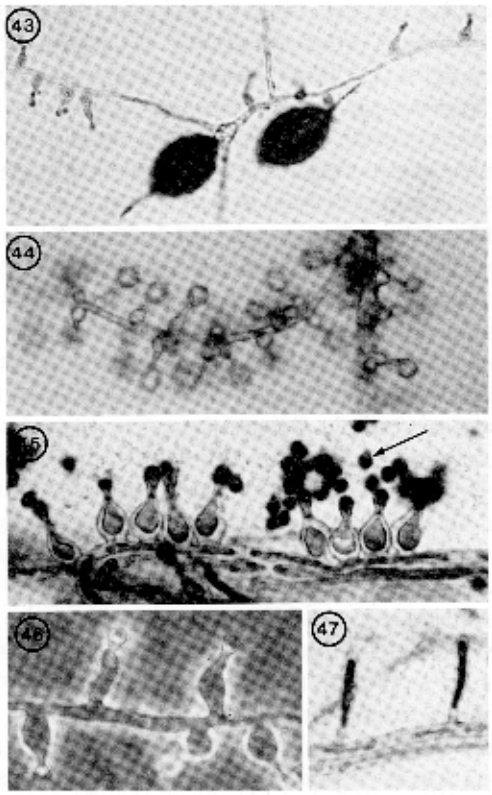
two light refractive dots in the ascus tip of FIG. 19; × 340 and × 560, respectively. 21–24. *P. tetraspora* showing mature (FIGS. 21, 23, 24) and immature (FIG. 22) ascospores with basal pedicels, faint apical and basal caudae (best seen in FIGS. 22 and 23), apical germ pores (FIGS. 23, 24) and plugs at the ascus tips (FIGS. 21, 22 and faintly in 23). Arrows in FIG. 21 indicate the occasional five- and three-spored asci. 21. WELTU 610; × 340. 22–24. WELTU 609; × 560. 25, 26. *P. vesticola*, WELTU 611, showing a plug in the ascus tips and ascospores with de Bary bubbles and basal pedicels. 25. The more typical uniseriate arrangement of ascospores; × 560. 26. Biseriate ascospore arrangement. The uppermost ascospore exhibits an apical cauda that extends above the germ pore; × 840. 27, 28. *P. miniglutinans*, WELTU 605, showing plugs at the ascus tips, ascospores with de Bary bubbles and basal caudae extending downward from the pedicels. 27. Asci with uniseriate, and more typical biseriate, ascospore arrangements; × 340. 28. Demonstrates that the gelatinous basal cauda is continuous with a thin gelatinous sheath that covers the pedicel; × 840. 29, 30. *P. dakotensis*, WELTU 594 and 600, respectively; × 340. Thirty two-spored asci in two views: "natural" and flattened, respectively. 30. Showing ascospore pedicels, de Bary bubbles and a weakly staining plug at the ascus tip. FIGS. 16–30. All photos were prepared from species grown in CMA axenic culture except FIG. 29 which was mounted directly from the dung. Aniline blue lactic acid slide mounts were used except for FIGS. 17, 18 and 29 which were water mounts.



FIGS. 31–42. Ascospores. 31, 32. *Podospora conica,* WELTU 592. 31. Dark cells and pedicels only. 32. Freshly discharged ascospore on the petri dish lid, showing a stretched basal cauda, a faint apical cauda and caudae of other ascospores in the background. 33–35. *P. tetraspora,* WELTU 609. 33, 34. Ascospores on the petri dish lid as in FIG. 32. 34. Showing an infrequently seen extra gelatinous cauda near the base of the pedicel. 35. Demonstrating more concentrated pigmentation of the dark cell in the area surrounding the germ pore. 36, 37. *P. dakotensis,* WELTU 596. 36. Arrow indicating a light central area in the apical cauda. 37. "Complete" caudae on two ascospores. 38, 39. *P. curvuloides.* 38. Scanning electron micrograph (SEM) of fresh ascospores from CMA cultures of WELTU 599, showing low transverse ridges on the spore wall; × 1460. 39. The low transverse ridges appear as fine striations. From R. F. Cain's original slide (TYPE, TRTC 35466). 40. *P. glutinans,* WELTU 602. 41. *P. miniglutinans,* WELTU 606, with de Bary bubbles. 40, 41. Arrows indicating a light central area in the apical cauda. 42. *P. vesticola,* WELTU 489. FIGS. 31–42. All figures, except the SEM, × 840. Ascospores were photographed in water except those in FIGS. 31, 35 and 41 (aniline blue lactic acid mounts), in FIG. 38 (the SEM) and in FIG. 39 (mounting medium unknown). The source of most ascospores was axenic CMA-cultured perithecia, although those of FIGS. 36, 39, 40 and 42 were from dung perithecia.



FIGS. 43–47. *Phialophora* anamorphs of *Podospora* species and hyphal branches in *P. miniglutinans*. 43–45. *P. conica*. 43. WELTU 592. Freshly discharged ascospores photographed on the petri dish lid. Left-hand spore has germinated and phialides and conidia are visible along the germ hyphae; × 450. 44, 45. WELTU 603. 44. Low aerial hyphae bearing numerous phialides, each with a ball of conidia at its apex. Photographed in situ on the colony surface; × 450. 45. Phialides with flared collarettes and conidia. Arrow indicates a conidium with a truncate base; × 1120. 46. *P. curvuloides*, WELTU 598. Phialides with flared collarettes; × 1120. 47. *P. miniglutinans*, WELTU 607, showing two right-angle, hyphal side branches; × 1120. FIGS. 43–47. Photographed from CMA axenic cultures. FIGS. 43, 45, 47. Mounted in cotton blue lactophenol. FIG. 46. Mounted in water.

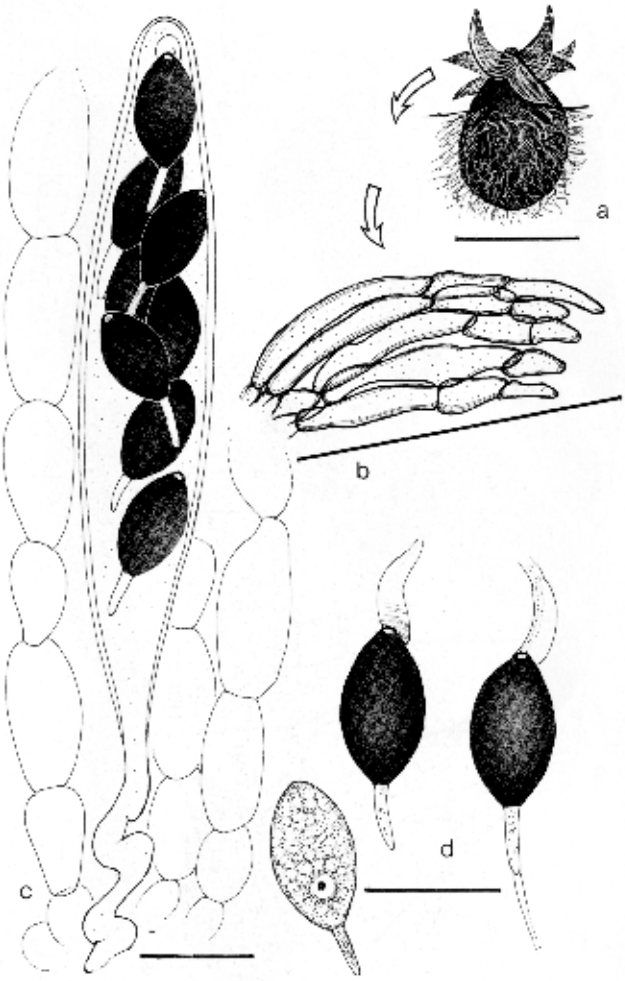


FIG. 48. *Podospora aloides*. a. Habit sketch of perithecium. b. Agglutinated hairs of the perithecium (arrows). c. Ascus, mature ascospores and jacket paraphyses. d. Two mature ascospores and an immature unpigmented ascospore showing a nucleus. Scale = 1 mm for (a), 200 μm for (b), 35 μm for (c), 30 μm for (d).

upon *Sordaria curvula* de Bary (1866). As noted by Lundqvist (1972), this is an invalid name because it is not based upon a published description or diagnosis. Krug and Khan (1989) favor the specific epithet *fimicola*, based upon *Schizothecium fimicolum* of Corda (1838). However, since there is no type of Corda's species and since his "diagnosis is incomplete in that it lacks spore measurements" (Krug and Khan, 1989, p. 1178), we consider that the next earliest legitimate name should be based upon Fuckel's *Cercophora conica* (1870), for which there is herbarium material and an adequate description. The nomenclature of *P. conica* is discussed further by Lundqvist (1972) and Krug and Khan (1989).

Although frequently observed on incubating dung, this species has proven unrewarding in axenic culture. Few of its ascospores germinate by methods attempted to date (see MATERIALS AND METHODS) so most of our 10 cultures originated from the growth of perithecial fragments or from germination within an ascospore cluster. Perithecia, usually present on the original CMA petri dishes, frequently decline in numbers or disappear altogether with subsequent subculturing. Only two cultures were originally isolated from single germinating ascospores and both failed to produce perithecia. Heterothallism is a possibility although further work is necessary. Presently the WELTU 592 culture, isolated from growth of an ascospore cluster, is being investigated in this regard. It is our only strain of *P. conica* with a high percentage of as-

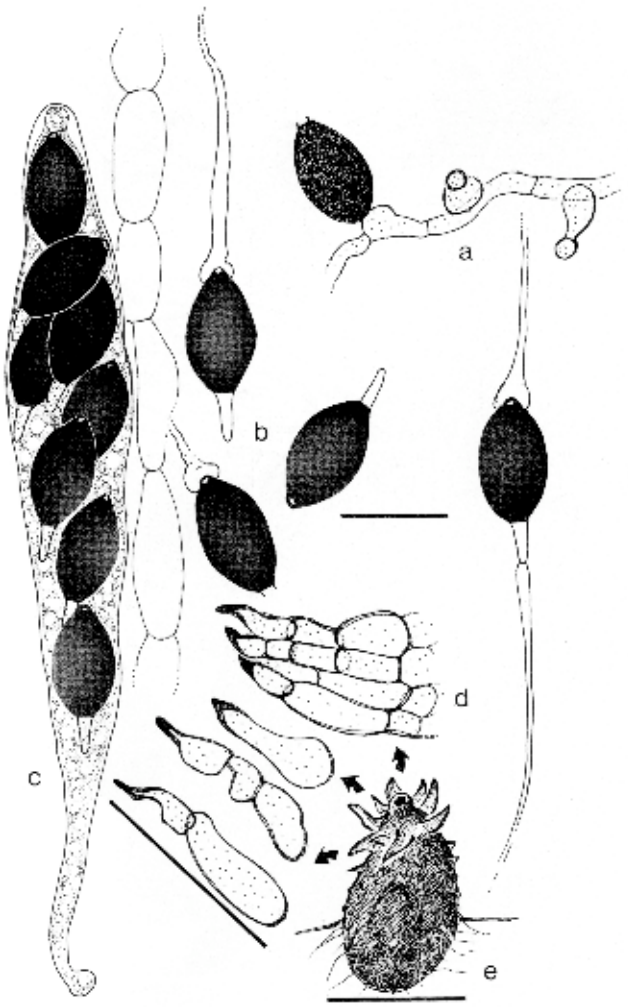


FIG. 49. *Podospora conica*. a. Germinating ascospore showing production of anamorph on the germination hypha. b. Mature ascospores. c. Ascus and jacket paraphysis. d. Agglutinated hairs of the perithecium (arrows). e. Habit sketch of perithecium. Scale = 25 μm for (a), (b) and (c), 50 μm for (d), 0.5 mm for (e).

cospore germination (untreated, fresh ascospores) and sustained perithecial production.

Podospora conica is the most frequently observed species of *Podospora* in New Zealand, in this study occurring on 40 samples of dung from cattle (6), deer (2), goat (3), horse (5), opossum (3), rabbit (13), sheep (6) and sheep/goat? (2). In previous investigations (Bell, 1983), it was also recorded on dung of birds and wallabies. A wide range of dung collection sites is represented ranging from the "close to subtropical" far north (McEwen, 1987, sheet 1, p. 4) to the southeastern and western coasts of the South Island. Numerous reports also indicate its broad distribution on herbivore dung in temperate areas worldwide, a selection including Algeria, Argentina, Canada, Chile, Germany, Japan, Kenya (elev. 9000 ft.; Krug and Khan, 1989), Spain, Sweden, Tanzania, United Kingdom, United States and Uruguay (Barrasa and Solans, 1989; Furuya and Udagawa, 1972; Garcia-Zorrón, 1973, 1975; Krug and Khan, 1989; Lundqvist, 1972; Mirza and Cain, 1969).

With the above-mentioned diversity of dung observations (teleomorph only) and with records from 10 cultured isolates (teleomorph and anamorph), we had the opportunity to examine strain variability within this species. Aside from the expected strains with ascospores, perithecia and agglutinated hairs in the lower or upper portions of their size range for the species, we noted other variations. Most strains had triangular groups of agglutinated hairs that were composed of closely adhering hairs with only slightly swollen elongate cells (FIGS. 1, 2–4, 49), but other, less common, strains had triangular groupings with more loosely adhering hairs whose cells were less elongate and more swollen (FIG. 7). Among the asci, most strains exhibited no specialization of the ascus tip, although rarely certain strains produced some asci with a small apical ring (FIG. 19). Only *P. tetraspora*, of the species treated here, had a similar ring which was also rarely seen. Mirza and Cain (1969) report a small apical ring as a regular feature in asci of both species. Among the many ascospores examined, however, we did not see the small, fugaceous gelatinous cauda at the base of the ascospore pedicel, which these authors also noted. Such a cauda was rarely seen in the closely related *P. tetraspora* (FIG. 34), but is not included in Mirza and Cain's description of that species (1969).

Apart from size differences, certain agglutinated hair differences, differences in ascospore number per ascus and the presence or absence of an anamorph, all eight species treated here share many morphological similarities with *P. conica*, notably the descriptions of their perithecial neck and venter peridia, jacket paraphyses, ascospore dark cells and pedicels (except *P. curvuloides*), gelatinous caudae, the thin gelatinous covering on their pedicels and their globose germination vesicles. Because of these similarities and because *P. conica* is so well represented in New Zealand, we will use it as a focus of comparison and abbreviate the treatment of other species where they duplicate or strongly overlap with it.

3. *Podospora curvuloides* Cain, Canad. J. Bot. 40: 453. 1962. FIGS. 1, 38, 39, 46, 50

Characteristics on dung. *Perithecia* maturing after 1–2 months of dung incubation, sparse to moderately abundant, gregarious, submerged in the dung with the upper half of the venter or only the neck protruding, often in a reclining or semireclining position, pyriform, 750–1000 × 400–500 μm; neck dark and vel-

vety, ca 125 μm long; venter semitransparent; neck and venter peridia as described for *P. conica*; agglutinated hairs short, inconspicuous, usually forming a poorly developed mound-like collar at the base of the neck with small scattered, bluntly conical groupings over the upper venter; individual hairs of the collar and scattered groupings often indistinct, consisting of one to few, hyaline to light brownish, thin-walled inflated cells with the terminal cell more elongate and narrowing apically to a bluntly rounded, slightly thickened, darker end wall; numerous long brown flexuous hyphae covering the lower venter. *Interascal tissue* and *jacket paraphyses* as in *P. conica*. *Asci* cylindrically clavate, containing eight ascospores initially arranged irregularly uniseriately, often biseriate with age or in slide mounts; apex simple with a cytoplasmic plug. *Ascospores* consisting of a large olivaceous-black ellipsoid cell whose entire surface is delicately, but distinctly, ornamented with numerous transverse striations formed by low ridges of the cell wall, (38–)40–55(–58) × (17–)20–25(–29) μm and a small, smooth, basal, hyaline pedicel 4–6(–7) × 2 μm; germ pore small, located at the slightly umbonate, darker apex of the large cell; caudae single, long and whip-like, one at the end of the pedicel and continuous with a thin gelatinous sheath over the pedicel, the other much broader, arising around the germ pore and containing a conspicuous central light region that appears to extend upward from the pore.

Characteristics in culture. Colonies on CMA inoculated and incubated as described for *P. conica*; spreading slowly, approximately 35 mm in diam in 3 wk; mycelial growth grey olivaceous, mostly submerged with low grey aerial hyphae in central regions. *Perithecia* maturing in 5–7 wk, sparse to moderately abundant in central regions, immersed to semi-immersed in the agar; morphological features as described on dung. *Anamorph* a *Phialophora* produced in abundance in all axenic cultures prepared from four different dung samples. *Phialides* numerous, borne singly and sessile along separate, or fascicled, surface substrate or low aerial hyphae; hyaline, smooth, variously shaped but usually symmetrically to asymmetrically pyriform with a flared apical collarette, mostly 7–12 × 3–4 μm. *Phialoconidia* hyaline, smooth, broadly obovoid with a truncate base, 2–3 × 2–2.5 μm; collecting in a glioid mass at the phialide apex, or occasionally forming a short chain.

Ascospore germination as described for *P. conica*; germination percentage low.

Herbarium specimens examined. AUSTRALIA. NEW SOUTH WALES: 18 km NW of Adaminaby, on rabbit dung (?), as *Schizothecium curvuloides* (Cain) Lundq., 5 Apr. 1981, *Tibell 12094-k* (UPS). TASMANIA: 10 km ESE of Huonville, on hare dung (*Lepus europeus*), as *Schizothecium rimosum* Lundq., 8 Mar. 1980, *Tibell 11285-q* (UPS); Mt. Field Natl. Park, 0.5 km SE of Lake Dobson, 42°41'S, 146°36'E, alt. ca 1000 m, on wombat droppings (*Vombatus ursinus*), as *Schizothecium rimosum* Lundq., 6 Mar. 1981, *Tibell 11194-f* (UPS); same locality, W. shore of Lake Dobson, alt. 1040 m, on wombat droppings, as *Schizothecium* n. sp. Lundq., 5 Mar. 1981, *Tibell 11045-d* (UPS, WELTU 560). BRAZIL. RIO GRANDE DO SUL: São Leopoldo, on cow dung, as *Podospora curvuloides* Cain, 11 Mar. 1936 (date collected by Alfons Theobald), 25 Feb. 1938 (date dung incubated) (TYPE, TRTC 35446). KENYA. Mt. Kenya, Timau Track, elev. 11 000 ft., 0°0'S, 37°19'E, on cow dung, as *Podospora curvuloides* Cain, 14 Jul. 1966, *Cain, Griffin and Krug 66.641q* (TRTC); Mt. Londiani Forest, on cow dung, as *Schizothecium curvuloides* (Cain) Lundq., 20

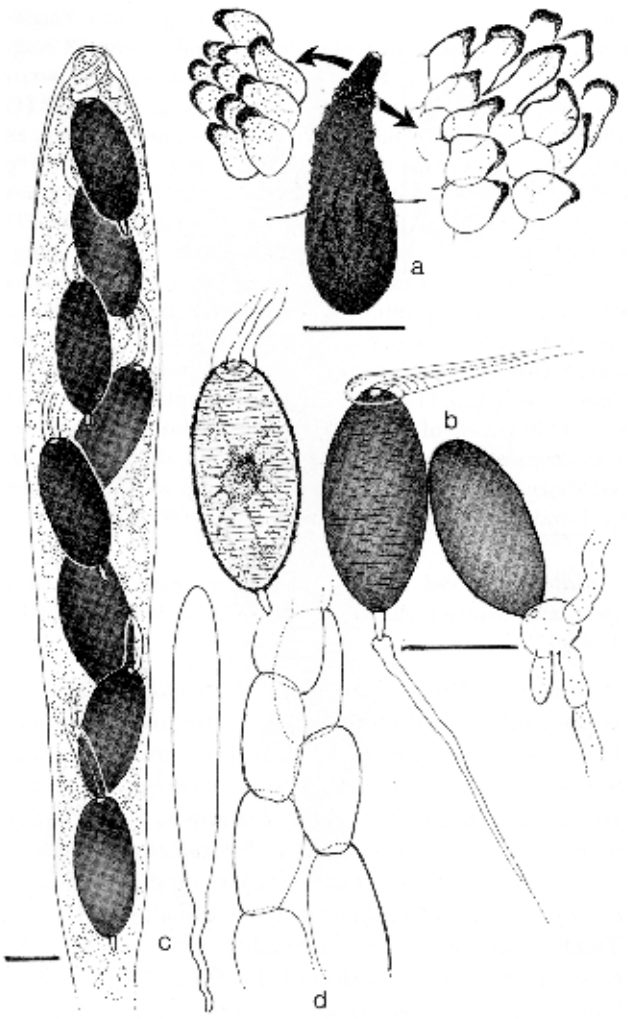


FIG. 50. *Podospora curvuloides*. a. Habit sketch of perithecium showing details of neck cells and agglutinated hairs (arrows). b. Three ascospores, left ascospore showing nucleus and ascospore wall in optical section, middle ascospore showing surface striations, pedicel and caudae, right ascospore with germination vesicle and germ hyphae. c. Asci. d. Jacket paraphyses. Scale = 0.5 mm for (a), 25 μm for (b), 15 μm for (c) and (d).

Jan. 1970, *Lundq. 6514-e* (UPS). MEXICO. JALISCO: Zapotlanejo, on cow dung, as *Podospora curvuloides* Cain, 18 Aug. 1960 (TRTC 36769). PUEBLA: N. of Tehuacan, on burro dung, as *Podospora curvuloides* Cain, 13 Aug. 1961 (TRTC 40888). OAXACA: 32 miles NW of Oaxaca, on cow dung, as *Podospora curvuloides* Cain, 19 Aug. 1961, *Cain C1959q* (TRTC). NEW ZEALAND. N. ISLAND: N. of Houhora, on horse dung, 6 Feb. 1991, *A. Bell and D. Mahoney* (WELTU 598); E. Wairarapa near Riversdale Beach, on goat dung, 14 Aug. 1991, *K. Cloud* (WELTU 599). S. ISLAND: Banks Peninsula, on sheep dung, as *Schizothecium* n. sp. Lundq., 1 Jan. 1981, *Tibell s. n.* (UPS, WELTU 568); Banks Peninsula, on sheep dung, as *Schizothecium rimosum* Lundq., 1 Jan. 1981, *Tibell s. n.* (WELTU 386); Banks Peninsula, Mt. Herbert Forest, 8 km S. of Diamond Harbour, on cow dung, as *Schizothecium rimosum* Lundq., *Tibell 9406-h*, slide only (UPS); NE shore of Lake Lyndon, on cow dung, as *Schizothecium* sp. Lundq., 25 Sept. 1980, *Tibell 8989-d* (WELTU 359).

Cultures deposited. Living CMA cultures from WELTU 599 have been deposited as IMI 361009, ATCC 90644 and CBS 129.94.

Comments. During this study *P. curvuloides* was encountered on six dung samples, horse (5) and goat (1), from collection sites located on both the North and South Islands. Previously it was observed on South Island cattle dung (Bell, 1983). Lundqvist has recorded it, as *Schizothecium rimosum* and *Schizothecium* spp. (see Herbarium specimens examined), from sheep and cow dung on the South Island in collections made by Leif Tibell. Our own results probably underestimate the frequency and distribution of this fungus in New Zealand, since we have looked at less horse and cattle dung than dung from other herbivores. If present on a dung sample, however, it is unlikely to be overlooked even though the perithecia are mostly submerged, because it appears later in the incubation period when there is little else to distract the observer. Other countries where this species has been found include Australia, Brazil, Kenya, Mexico and Peru (Cain, 1962; Krug and Khan, 1989; Lundqvist, pers. comm.; Mirza and Cain, 1969).

Podospora curvuloides is the only species of *Podospora* with an ornamented surface on its ascospores (FIGS. 1, 38, 39, 50). Its delicate transverse striations are reported here for the first time although they are present on the ascospores of the type specimen (FIG. 39) and on those from nearly all of the collections we have examined. We could not find them on the Tibell 12094-k collection from Australia. They are most easily seen on slightly immature, less pigmented ascospores where they appear as finger print-like ridges. The dark pigment of mature ascospores makes it difficult to see them under normal light microscopy. The New Zealand collections of *P. curvuloides* have ascospores with larger dark cells than are cited by Mirza and Cain (1969), 31–41 × 17–20 μm versus mostly 40–55 × 20–25 μm. Their dimensions for the pedicel, 4–5 × 1.5–2 μm, are similar to our own. It was this larger size of the dark cell and its striated surface that led us to examine collections from other countries. We have now observed a variety of collections and find that there is a variation in ascospore size between these collections and our own. Apart from this larger size, however, the ascospores are alike in all other respects, including the fine striations present on the dark cell. In our opinion all are representative of the same species. Ascospore measurements for various herbarium collections are given below:

Collection details	Ascospore dark cell	Pedicel
P. curvuloides Tibell 12094-k (UPS): Australia	35–39 × 20–23 μm	6 × 2 μm
P. curvuloides TRTC 35446 (TYPE): Brazil	36–41 × 23–27 μm	5 × 2 μm
P. curvuloides Cain et al. 66.641q (TRTC): Kenya	31–38 × 17–23 μm	6 × 2 μm
P. curvuloides Lundq. 6514-e (UPS): Kenya	35–42 × 19–21 μm	
P. curvuloides TRTC 36769: Mexico	34–36 × 19–23 μm	
P. curvuloides TRTC 40888: Mexico	35–42 × 19–28 μm	5 × 2 μm
P. curvuloides Cain C1959g (TRTC): Mexico	30–36 × 17–20 μm	
P. curvuloides Tibell 11194-f (UPS): Tasmania	40–44 × 18–24 μm	5 × 2 μm
P. curvuloides Tibell 11285-q (UPS): Tasmania	40–46 × 21–23 μm	

Our axenic cultures of *P. curvuloides* no longer produce perithecia upon transfer to fresh media. In fact, most of the cultures yielded relatively few perithecia during their initial growth on CMA. All produced and continue to produce an abundant *Phialophora* anamorph. Attempts to stimulate perithecia on cultures of WELTU 599 through the use of PDA, modified Leonian's and WSH agars have yielded only a few fertile perithecia after 6 wk of incubation on WSH only. The homothallic or heterothallic nature of the species remains in doubt, although the few single as-

cospore initiated cultures have failed to produce perithecia.

Certain perithecial features of *P. curvuloides* resemble those of *P. glutinans*. Both share similar agglutinated hairs, numerous long brown flexuous hyphae and perithecia largely immersed in the substrate. Differences in perithecial shape and ascospore characters, however, easily distinguish the two.

4. *Podospora dakotensis* (Griff.) Mirza & Cain, Canad. J. Bot. 47: 2016. 1969.

FIGS. 1, 8–11, 29, 30, 36, 37, 51

= *Pleurage dakotensis* Griff., Mem. Torrey Bot. Club 11: 87. 1901.

≡ *Schizothecium dakotensis* (Griff.) Lundq., Symb. Bot. Upsal. 20(1): 254. 1972.

Characteristics on dung. Mature *perithecia* first observed after 2–10 wk of dung incubation, gregarious to scattered, mostly superficial, narrowly pyriform, 400–850 × 200–375 μm; venter semitransparent with a pseudoparenchymatous peridium of globose to subglobose or swollen angular cells; neck dark, smooth, with peridium as described for *P. conica*; a distinct mound-like collar of short agglutinated hairs at the base of the neck, individual hairs of this collar often indistinct and consisting of one to several, hyaline to light brownish, thin-walled swollen cells, the terminal cell of each hair more elongate, narrowing apically, with a bluntly rounded, slightly thickened, darkened outer wall; smaller, less conspicuous, mounds of swollen cells scattered over the venter. *Interascal tissue* and *jacket paraphyses* as in *P. conica*. *Asci* clavate, containing 32 irregularly multiseriate ascospores; stipe short, abruptly narrowing beneath the spore-bearing region; apex simple with a cytoplasmic plug. *Ascospores* consisting of an ellipsoid dark cell (19–)21–25 × (11–)12–15(–16) μm and a hyaline, narrowly cylindrical, basal pedicel 5–7(–8) × 1.5–2 μm; germ pore at the faintly umbonate, darker apex of the dark cell; caudae single, long and whip-like, one arising at the tip of the pedicel and continuous with a thin gelatinous covering over the pedicel, the other broader and arising over the germ pore, or eccentric to it, with a faint central light region appearing to extend upward from the pore.

Characteristics in culture. Colonies on CMA inoculated and incubated as described for *P. conica*; spreading slowly, ca 30–35 mm in diam in 3 wk; mycelial growth grey olivaceous and mostly submerged. *Perithecia* maturing in approximately 3 wk, superficial to semi-immersed in the agar surface, numerous, evenly scattered or in central regions; morphological features as described on dung. *Anamorph* none.

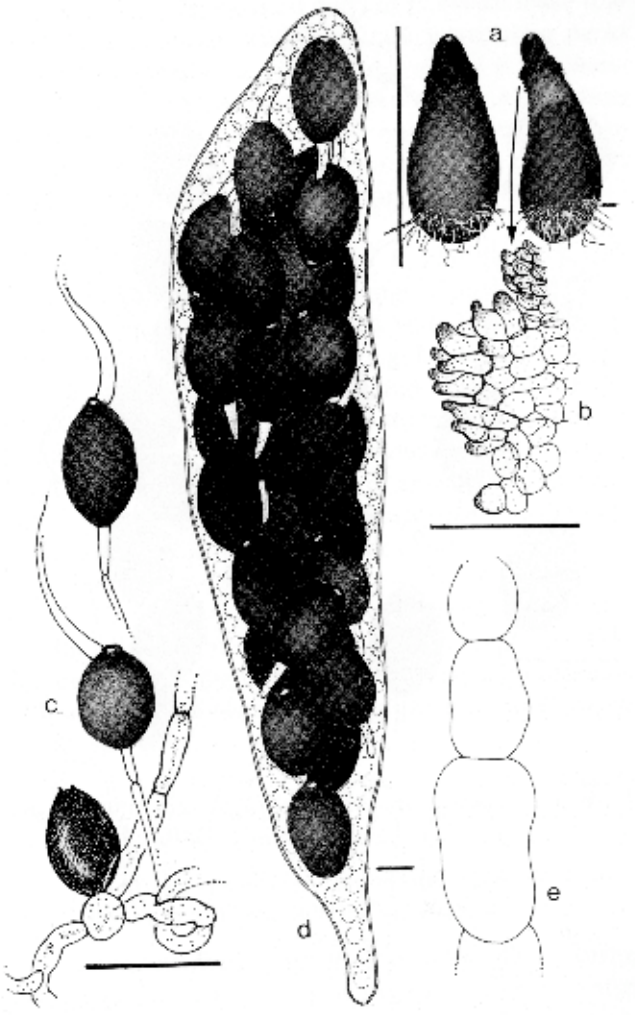


FIG. 51. *Podospora dakotensis*. a. Habit sketches of two perithecia. b. Collar of agglutinated hairs (arrow). c. Two mature ascospores together with a germinating ascospore. d. Mature ascus. e. Jacket paraphysis. Scale = 0.5 mm for (a), 25 μm for (b) and (c), 10 μm for (d) and (e).

Homothallic. Colonies inoculated with single germinating ascospores yielding fertile perithecia. Ascospore germination as described for *P. conica*; germination percentage low.

Herbarium specimens examined. NEW ZEALAND. N. ISLAND: Cape Reinga, on cow dung, 7 Feb. 1991, *A. Bell and D. Mahoney* (WELTU 600); Kawhia, near Te Kauri Lodge, on sheep/goat (?) dung, 20 May 1988, *A. Bell, K. Churchill and D. Mahoney* (WELTU 596); Matauri Bay, on sheep dung, 7 Feb. 1991, *A. Bell and D. Mahoney* (WELTU 613); Tararua Mts., Penn Creek track, on opossum dung, 4 Sep. 1987, *A. Bell and D. Mahoney* (WELTU 595); Waikawa Beach, sand dune vegetation, on rabbit dung, 26 Feb. 1992, *D. Mahoney and H. Keena* (WELTU 594). USA. NEW JERSEY: Fort Lee, on rabbit dung, as *Pleurage dakotensis* Griff. (represented by one slide only), Jan. 1900, s. n., proposed LECTOTYPE

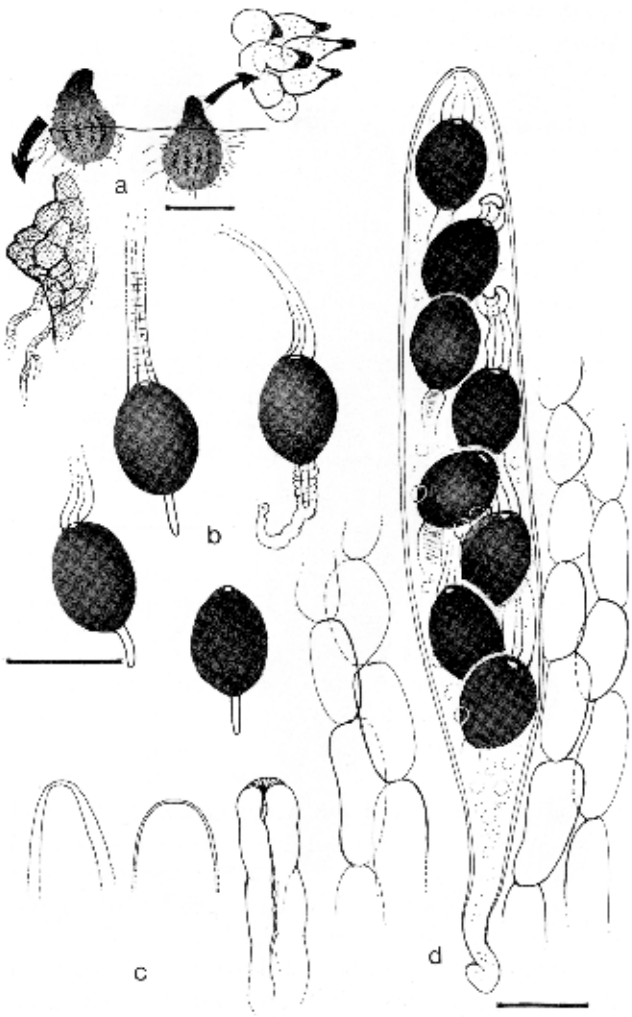


FIG. 52. *Podospora glutinans*. a. Habit sketches of two perithecia with details of neck cells and agglutinated hairs (arrows). b. Mature ascospores. c. Ascus tips; right-hand ascus has discharged its contents. d. Mature ascus and jacket paraphyses. Scale = 0.5 mm for (a), 35 μm for (b), (c) and (d).

(NY). Original TYPE collected at Brookings, S. Dakota, Nov. 1899, is missing.

Cultures deposited. Living CMA cultures from WELTU 613 have been deposited as IMI 361010, ATCC 90645 and CBS 130.94.

Comments. We have encountered this species on seventeen samples of dung including rabbit (5), cattle (2), sheep (2), sheep/goat? (1), goat (1), opossum (1) and horse (5). Eleven different ecological districts (McEwen, 1987) are represented, ranging from the far north of the North Island to the west coast of the South Island. Although common in New Zealand, *P. dakotensis* may be underestimated because it frequently grows accompanied on the dung by other species such as *P. conica*, *P. tetraspora* and *P. miniglutinans*, and is easily overlooked. Its distinctive perithecial collar is not evident beneath a dissecting microscope so slide mounts are essential to verify its presence. This factor may, in part, also account for the wide variation recorded for the times of appearance of mature perithecia (2–10 wk). Elsewhere *P. dakotensis* has been reported from Canada, Japan, Mexico, Spain and the United States (Furuya and Udagawa, 1972; Lundqvist, 1972; Mirza and Cain, 1969).

Our six axenic cultures of *P. dakotensis*, representing six different dung samples, all produce numerous perithecia on CMA and continue to do so after several transfers to fresh media. Corn meal agar cultures of *P. tetraspora* and *P. miniglutinans* also share this feature. The latter species is the only other species in this study that, like *P. dakotensis*, lacks a *Phialophora* anamorph. Perhaps not unrelated to this fact are the similarities shared by their perithecia. Perithecia of both have the same distinctive collar of agglutinated hairs. Perithecia of *P. curvuloides* and *P. glutinans* also have collars but these are inconspicuous and often poorly developed.

5. *Podospora glutinans* (Cain) Cain, Canad. J. Bot. 40: 460. 1962. FIGS. 1, 40, 52

= *Schizothecium glutinans* (Cain) Lundq., Symb. Bot. Upsal. 20(1): 254. 1972.
= *Sordaria glutinans* Cain, Univ. Toronto Stud., Biol. Ser. 38: 40. 1937.

Characteristics on dung. Mature *perithecia* first observed after 2–8 wk of dung incubation, sparse, usually submerged in the dung with only the neck protruding, broadly pyriform, 700–900 × 440–500 μm; venter subglobose to broadly ovoid, semitransparent; neck dark, ca 150 μm long; venter and neck peridia as in *P. conica*; agglutinated hairs inconspicuous, poorly developed, usually less than 20 μm long, consisting of groups of swollen, pale brown, thin-walled cells arranged in low triangular mounds two to three cells high, scattered more or less evenly over the upper ⅔'s of the venter and often forming a poorly defined collar at the base of the neck; long brown flexuous hyphae common over the lower venter. *Interascal tissue* and *jacket paraphyses* as in *P. conica*. *Asci* broadly cylindrical, containing eight obliquely uniseriate, occasionally biseriate, ascospores; apices simple. *Ascospores* consisting of a broadly ellipsoid, olivaceous-black cell 31–37 × 21–27 μm with a small germ pore at the slightly darker, faintly umbonate apex and a hyaline, straight or slightly curved, basal pedicel 8–15 × 2–3 μm; caudae single, long and whip-like, one at the apex of the pedicel and continuous with a thin gelatinous sheath over the pedicel, the other somewhat broader and situated over

the germ pore with a central light region often appearing to extend upward from the pore.

Characteristics in culture. Colonies from WELTU 601 center-inoculated onto CMA, incubation conditions as for *P. conica*; gradually spreading, ca 8 cm in diam in 3 wk, olivaceous grey, appressed, with mycelial growth mostly submerged in the medium. *Perithecia* observed only once during the third month of growth on a medium consisting of four steam-sterilized rabbit pellets over which CMA had been poured, and then only in localized areas contaminated with a species of *Cladosporium*; fertile, completely submerged in the agar, or with portions of the neck protruding; morphological features as described from dung. *Anamorph* a *Phialophora*, absent or sparsely produced in initial cultures, more abundant after subsequent transfers to fresh media (but still requiring observation techniques described under the Comments for *P. tetraspora*) and best seen in CMA cultures augmented with steam-sterilized rabbit pellets or gamma-ray-sterilized opossum dung. *Phialides* solitary, scattered, borne sessile on surface substrate hyphae, hyaline, smooth, varying in shape from long, narrow and hypha-like to slightly swollen in middle or basal regions to pyriform like those of *P. conica*, always with a flared apical collarette; 10–22 × 2–5 μm. *Phialoconidia* hyaline, smooth, with a single, large, centric to eccentric blue-staining guttule (in cotton blue lactophenol), subglobose to broadly obovoid with a truncate base, 2–3 × 2–2.5 μm, gathering in a glioid mass at the phialide apex, or occasionally forming a short chain.

Ascospore germination, as described for *P. conica*.

Herbarium specimens examined. CANADA. ONTARIO: Huntsville, on rabbit dung, as *Podospora glutinans* Cain, 6 Sep. 1931 (date dung collected), 17 Nov. 1931 (date fungus developed in laboratory) (TYPE, TRTC 5165). NEW ZEALAND. N. ISLAND: Egmont National Park, on opossum dung, 22 Feb. 1988, *D. Mahoney* (WELTU 601). S. ISLAND: Arthur's Pass, high point of Highway 73, on hare dung, 20 Jan. 1988, *A. Bell and D. Mahoney* (WELTU 602).

Comments. This species has been recorded from New Zealand only three times during this study and once previously (Bell, 1983). The four samples represent widely separated sites on both North and South Islands and include dung from hare (1), rabbit (1) and opossum (2). Worldwide, *P. glutinans* has been reported from Belgium, Canada, Denmark, Finland, France, Ireland, Japan, Mexico, Poland, Spain, Sweden, United Kingdom and the United States (Barrasa and Solans, 1989; Furuya and Udagawa, 1972; Lundqvist, 1972; Mirza and Cain, 1969).

Our records indicate that *P. glutinans*, like *P. aloides*, produces few perithecia on the dung. Both have perithecia whose venters are largely sunken in the dung but the large agglutinated hairs of *P. aloides* make that species easily seen, while the dark protruding necks and inconspicuous agglutinated hairs of *P. glutinans* make that species easily overlooked against a dark dung surface. This may account for our first observations of mature perithecia on the dung varying between 2 and 8 wk, and perhaps also for the scarcity of our recorded sightings.

Our single axenic culture of *P. glutinans* failed to produce perithecia on a wide range of media including CMA (separately supplemented with 1 g/L yeast extract, with 2 g/L glucose and 3 g/L sucrose and with sterile rabbit and opossum dung), PDA, WSH and modified Leonian's agar. Only recently have perithecia appeared in culture (see Characteristics in culture) and there only on one culture, among several replicates, in association with a *Cladosporium* contaminant. The homothallic or heterothallic condition of this species is unknown.

The *Phialophora* anamorph of this species is similar to the anamorphs of other species in the study. Also, its mound-like agglutinated perithecial hairs resemble those of *P. dakotensis*, *P. miniglutinans* and *P. curvuloides*.

6. *Podospora miniglutinans* Mirza & Cain, Canad. J. Bot. 47: 2030. 1969. FIGS. 1, 27, 28, 41, 47, 53

= *Schizothecium miniglutinans* (Mirza & Cain) Lundq., Symb. Bot. Upsal. 20(1): 254. 1972.

Characteristics on dung. Perithecia usually maturing in 2½–4 wk, in one case ripe perithecia first seen after 12 wk, scattered, semi-immersed to superficial, varying in shape from narrowly to broadly pyriform, 360–680 × 170–370 μm; venter semitransparent; neck dark, smooth, ca 100–200 μm long; venter and neck peridia as described for *P. dakotensis*; usually with a low distinct mound-like collar of short agglutinated hairs at the base of the neck, details as given for *P. dakotensis*; small inconspicuous mounds of swollen cells and single inflated cells scattered over the middle to upper venter with long flexuous brown hyphae below. *Interascal tissue* and *jacket paraphyses* as in *P. conica*. *Asci* cylindrical to cylindrically clavate, containing eight ascospores initially arranged uniseriately, often irregularly biseriate with age or in slide mounts; apex simple with a cytoplasmic plug. *Ascospores* with a broadly ellipsoid olivaceous-black cell (19–)21–24(–25) × 13–15(–16) μm and a basal hyaline pedicel 7–8 × 2 μm; germ pore on the slightly umbonate, darker apex of the dark cell; caudae single, long and whip-like, one each over the germ pore and at the end of the pedicel, the former broader with a faint central light region appearing to extend upward from the germ pore, the latter continuous with a thin gelatinous sheath over the pedicel.

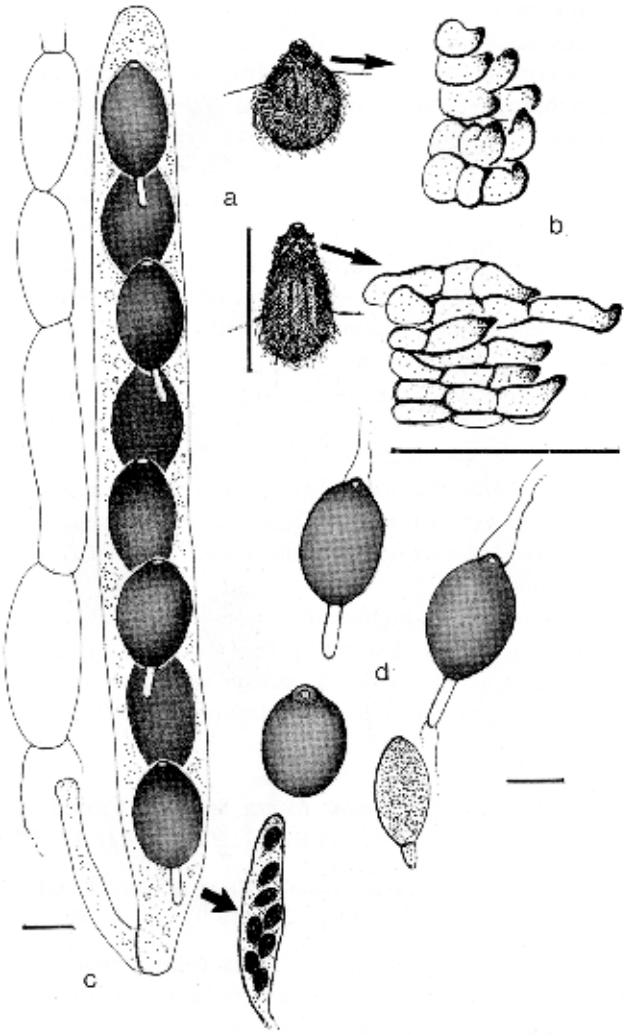


FIG. 53. *Podospora miniglutinans*. a. Two perithecia. b. Agglutinated hairs (arrows) illustrating the variability in morphology. c. Mature asci and jacket paraphysis; small sketch to right illustrating the biseriate arrangement quickly assumed when asci swell in water mounts. d. Three mature ascospores and an immature unpigmented ascospore illustrating early septation. Scale = 0.5 mm for (a), 30 μm for (b), 10 μm for (c) and (d).

Characteristics in culture. Colonies on CMA inoculated and incubated as described for *P. conica*; spreading slowly, ca 40 mm in diam in 4 wk; mycelial growth semitransparent, olivaceous brown, mostly submerged with variable amounts of greyish brown aerial hyphae. *Perithecia* maturing in approximately 3 wk, usually concentrated near the colony center, numerous, semiimmersed to superficial on the agar surface; morphological features as described on dung. *Anamorph* none but with few to many distinctive, solitary, hyaline, smooth, thin-walled, apically rounded, right-angle branches on the surface substrate hyphae (FIG. 47). These branches varying from cylindrical to clavate, usually cylindrical and slightly clavate apically with a basal septum and containing a single large darkly staining cytoplasmic mass (in cotton blue lactophenol); mostly 8–11 μm long × 1.5–2 μm wide basally × 2–2.5 μm wide apically, occasionally shorter and more swollen to 3–3.5 μm wide; function unknown; produced on all of our axenic CMA cultures from four different dung samples.

Homothallic. Colonies inoculated with single germinating ascospores yielding fertile perithecia. Ascospore germination as described for *P. conica*; germination percentage low.

Herbarium specimens examined. AUSTRALIA. NEW SOUTH WALES: 18 km NW of Adaminaby, upper Alum Creek, open Eucalyptus forest, alt. 1260 m, on rabbit (?) dung, as *Schizothecium miniglutinans* (Mirza & Cain) Lundq., 5 Apr. 1981, *Tibell 12094-j* (UPS, WELTU 526). MEXICO. HIDALGO: N. of Zimapan, on burro dung, as *Podospora miniglutinans* Mirza & Cain, 21 Aug. 1961 (TYPE, TRTC 38801). NEW ZEALAND. N. ISLAND: Waikawa Beach, sand dune vegetation, on rabbit dung, 26 Feb. 1992, *D. Mahoney and H. Keena* (WELTU 604). S. ISLAND: Highway 7, E. of Lewis Pass, roadside near Boyle River Lodge, on rabbit dung, 12 May 1990, *A. Bell and D. Mahoney* (WELTU 607); S. of Hillersden, pasture in Wairau Valley, on rabbit dung, 7 May 1990, *A. Bell and D. Mahoney* (WELTU 606); N. of Kaikoura, sand dune vegetation, near mouth of Waima River, on rabbit dung, 2 Apr. 1988, *D. Mahoney* (WELTU 605).

Cultures deposited. Living CMA cultures from WELTU 604 have been deposited as IMI 361011, ATCC 90646 and CBS 131.94.

Comments. During this study *P. miniglutinans* has been recorded from nine dung samples, including rabbit (7), lagomorph (1) and deer (1), from seven widely separated collection sites on the South Island and two on the North Island. In previous studies, Bell (1983) reported it from cervid and lagomorph dung in New Zealand, Mirza and Cain (1969) from rabbit and burro dung in Mexico and Lundqvist (1972) on rabbit, hare and sheep dung in Scandinavia and on various dungs from other countries. Overall, a preference for lagomorph dung is indicated. It has a widespread occurrence worldwide with records from Canada, Canary Islands, Corsica, Denmark, Hungary, Iraq, Kenya, Mexico, Netherlands, Norway, South Africa, Spain, Sweden and the United States (Abdullah and Rattan, 1978; Lundqvist, 1972; Mirza and Cain, 1969).

Like *P. tetraspora* and *P. dakotensis*, *P. miniglutinans* performs well in CMA culture. Our four cultures of this species continue to produce perithecia after several transfers to fresh media.

Certain features of *P. miniglutinans*, including its perithecial morphology and collar of agglutinated hairs, its ascospore size, shape and number per ascus and its lack of any anamorph suggest relationships with, or

confusion with, *P. dakotensis, P. vesticola* and other species in this group. For further details the reader is referred to the Comments section under *P. dakotensis* and *P. vesticola.*

7. *Podospora tetraspora* (Winter) Cain, Canad. J. Bot. 40: 460. 1962. FIGS. 1, 5, 6, 16, 21–24, 33–35, 54

≡ *Sordaria tetraspora* Winter, Hedwigia 10: 161. 1871.
= *Schizothecium tetrasporum* (Wint.) Lundq., Symb. Bot. Upsal. 20(1): 256. 1972.

Characteristics on dung. Mature *perithecia* usually appearing within the first week of dung incubation, gregarious to scattered, superficial, narrowly ovoid/pyriform, 250–700 × 130–260 μm; venter and neck peridia as in *P. conica*; triangular tufts of agglutinated hairs, to ca 45 μm long, located at the base of the neck, each tuft composed of several hairs, each hair of two to five moderately swollen cells with the end cells bluntly pointed and having a thicker, more pigmented wall. Triangular tufts at the base of the neck grading into smaller tufts on the upper venter, gradually replaced by single inflated cells on the lower regions. *Interascal tissue* and *jacket paraphyses* as in *P. conica. Asci* broadly cylindrical, containing four obliquely uniseriate ascospores; apices simple with a cytoplasmic plug or rarely with a small ring; basal portions seldom seen free of the centrum cluster. *Ascospores* with ellipsoid, olivaceous-black dark cell, 18–23 × 11–13 μm, and hyaline, straight or slightly curved pedicel, 8–12 × 1.5–2 μm; dark cell bilaterally symmetrical to asymmetrical with one side slightly flattened; germ pore at the darker umbonate apex of the dark cell. Caudae single and whip-like at the spore extremities; the upper one slightly broader, the lower one encasing the pedicel, both very fugaceous. A third cauda infrequently seen attached near the base of the pedicel (FIG. 34).

Characteristics in culture. Colony inoculation onto CMA, incubation, growth rate and appearance, as described for *P. conica. Perithecia* numerous, usually concentrated in the colony center; morphological features as described from dung. *Anamorph* a *Phialophora,* sparsely produced in each of the axenic cultures from 12 different dung samples. *Phialides* borne singly, sessile and usually separate from each other on surface substrate or low aerial hyphae, hyaline, smooth, variously shaped but typically pyriform with a flared apical collarette, 6–16 × 3–4 μm. *Phialoconidia* small, hyaline, moderately thin-walled, smooth, broadly obovoid and truncate basally (often appearing globose to subglobose), 2.5–3 × 2–2.5 μm; collecting apically in a glioid mass or occasionally forming short chains of up to 15 conidia. *Aleuriospores* sparse, but in a few cultures more numerous than the anamorph, solitary, sessile on substrate hyphae or terminal on short branches, moderately thin-walled, smooth, hyaline, variable in shape and size from phialoconidia-like to more elongate-obovoid and up to 7 μm long.

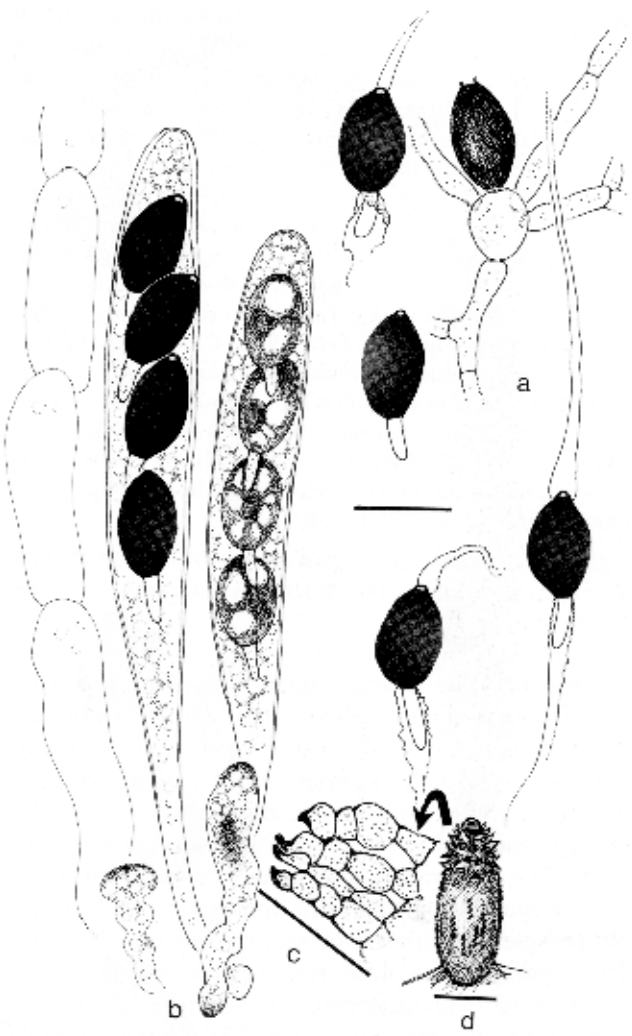


FIG. 54. *Podospora tetraspora.* a. Mature ascospores together with a germinated ascospore. b. Immature and mature asci accompanied by a jacket paraphysis. c, d. Habit sketch of perithecium with details of agglutinated hairs (arrow). Scale = 20 μm for (a) and (b), 45 μm for (c), 0.25 mm for (d).

Homothallic. CMA cultures, inoculated with single germinating ascospores, yielded colonies as described above. Ascospore germination is as described for *P. conica.*

Herbarium specimens examined. CANADA. ONTARIO: Bruce Co., Teeswater, on rabbit dung, as *Podospora tetraspora* (Wint.) Cain, 10 Jul. 1930, *Cain 5451* (TRTC 5206). QUEBEC: Esker, de la riviere George, à l'est 55.09 lat., 19 Jul. 1947, *J. Rousseau s. n.*, det. R. F. Cain (TRTC 32007). GERMANY. Harth bei Leipzig, auf Mäusekoth (= on mouse dung), as *Sordaria*

tetraspora Wint., Feb. 1872, herb. Barbey-Boissier 1529 (NEOTYPE, G). MEXICO. DURANGO: W. of Durango, on rabbit dung, as *Podospora tetraspora* (Wint.) Cain, 14 Aug. 1960, det. J. H. Mirza (TRTC 41107). NEW ZEALAND. N. ISLAND: Hokio Beach, sand dune vegetation, on rabbit dung, 26 Feb. 1992, *D. Mahoney and H. Keena* (WELTU 608); E. slope Ruahine Mts., near Sunrise Hut, tussock-grassland, alt. 1300 m, on hare dung, 14 Apr. 1990, *K. Churchill* (WELTU 609); Waikawa Beach, sand dune vegetation, on rabbit dung, 11 Jul. 1992, *A. Bell and D. Mahoney* (WELTU 610). POLAND. ZIELONA GÓRA: Tamsel, on rabbit dung, as *Sordaria tetraspora* Wint., 16 Feb. 1935, *Cain 6356* (TRTC); Tamsel, on cow dung, as *Podospora tetraspora* (Wint.) Cain, 24 Feb. 1935, *Cain 6526* (TRTC); Tamsel, on field mouse dung, as *Podospora tetraspora* (Wint.) Cain, 27 Feb. 1935, *Cain 6477* (TRTC). SWEDEN. GOTLAND: on rabbit dung, as *Schizothecium tetrasporum* (Wint.) Lundq., 22 Sep. 1990, *Lundq. 18505-d* (S, WELTU 563).

Cultures deposited. Living CMA cultures from WELTU 608 have been deposited as IMI 361012, ATCC 90647 and CBS 132.94.

Comments. The type specimen of *Sordaria tetraspora* Winter (1871) on mouse dung, originally held in Berlin, is "most probably lost" (N. Lundqvist, pers. comm.). On the advice of N. Lundqvist and J. Krug we have selected another collection made a year later as the neotype (no. 1529, see Herbarium specimens examined). The substrate is also mouse dung and it originates from a geographically similar area in Europe. No complete perithecia or asci remain on the dung. The accompanying slide, however, reveals part of a fragmented, swollen, agglutinated perithecial hair tuft and some free ascospores which are devoid of pedicels and caudae. Although brief, Winter's description and measurements match this slide material and there appears to be no ambiguity by more recent authors of Winter's species. We have deposited some of our own material of this species (WELTU 608) at the herbarium of Barbey-Boissier in Geneva.

Among the species of *Podospora* treated here, *P. tetraspora* is the most consistent producer of perithecia in CMA axenic culture. Even after repeated transfers to fresh media, only one of our 12 cultures has lost the ability to produce perithecia. The anamorph, although sparse in all cultures, can be observed by adding a drop of cotton blue in lactophenol to the CMA colony surface, applying a coverslip and scanning with the low powers of a compound microscope. The small clusters of stained phialoconidia are then more easily seen.

This species is also unique among this group of New Zealand *Podospora* species in having only four ascospores per ascus. Worth noting, however, is the occasional ascus with three or five ascospores (FIG. 21; Mirza and Cain, 1969, Fig. 56) or more rarely those asci with one, two, or six to eight ascospores. Apart from its four-spored asci and smaller size overall, *P. tetraspora* is very similar to *P. conica*, with which it shares similar triangular groups of agglutinated hairs, other perithecial features and a similar colony appearance. Also, the *Phialophora* anamorph, although sparse by comparison, is virtually indistinguishable from that of *P. conica*. Other species treated here with similar larger or smaller triangular groups of agglutinated hairs and look-alike anamorphs are *P. aloides* and *P. vesticola*, although the small hair groupings of the latter are often reduced or absent.

Thirty dung collections, representing a wide range of habitats on both the North and South Islands, have yielded this species. It has a clear preference for lagomorph dung: rabbit dung (25 samples) and hare dung (5 samples). Lundqvist (1972, p. 256) noted that *Podospora* (= *Schizothecium*) *tetraspora* was "common on various kinds of dung, particularly that of rabbit, hare and small rodents." Among its many reports are those from Algeria, Canada, Germany, Japan, Kenya, Mexico, Poland, Scandinavia, Spain, United Kingdom, United States and Uruguay (Barrasa and Solans, 1989; Furuya and Udagawa, 1972; Garcia-Zorrón, 1973, 1975; Krug and Khan, 1989; Lundqvist, 1972; Mirza and Cain, 1969).

8. *Podospora vesticola* (Berk. & Br.) Mirza & Cain, Canad. J. Bot. 47: 2044. 1969.

FIGS. 1, 12–15, 18, 25, 26, 42, 55

= *Sphaeria vesticola* Berk. & Broome, Ann. Mag. Nat. Hist., Ser. 3, 3: 370. 1859.

= *Schizothecium vesticola* (Berk. & Br.) Lundq., Symb. Bot. Upsal. 20(1): 256. 1972.

Characteristics on dung. Perithecia usually maturing within the first 3 wk of dung incubation, gregarious to scattered, pyriform (often narrowly so), mostly superficial, 350–650 × 140–300 μm; venter and neck peridia as in *P. conica*; agglutinated hairs in small triangular groupings, to 30 μm long, usually evenly distributed over the upper ⅔'s of the venter, rarely forming a slight collar near the base of the neck; individual groupings with only a few hairs, each hair only a few cells long, or groupings reduced to single inflated protruding cells with slightly darkened, often thickened, acuminate tips. *Interascal tissue* and *jacket paraphyses* as in *P. conica*. *Asci* cylindrical, containing eight obliquely uniseriate, or occasionally biseriate, ascospores; apices simple with a cytoplasmic plug. *Ascospores* consisting of a narrowly ellipsoid, olivaceous-black cell 17–20 (–22) × 10–12 μm and a basal, hyaline, cylindrical pedicel 5–7(–8) × 2 μm (2.5–3 μm at its attachment to the dark cell); germ pore at the darker umbonate apex of the dark cell; caudae single, long and whip-

like, one at the apex of the pedicel and continuous with a thin gelatinous sheath over the pedicel, the other slightly broader, arising over the germ pore and sometimes with a central light region which appears to extend upward from the germ pore.

Characteristics in culture. *Colonies* inoculated onto CMA; incubation conditions, growth rates and colony appearances as described for *P. conica*. *Perithecia* present only in some colonies from each of the seven dung samples cultured, usually concentrated in the colony center; morphological features as described from dung. *Anamorph* a *Phialophora*, produced in abundance throughout the colony on all colonies. *Phialides, phialoconidia* and *aleuriospores* not significantly different from those described for *P. conica* and *P. tetraspora*.

Ascospore germination as described for *P. conica*.

Herbarium specimens examined. NEW ZEALAND. N. ISLAND: Otaki Beach, sand dune vegetation, on rabbit dung, 2 Sep. 1987, *A. Bell and D. Mahoney* (WELTU 612); inland from Waikanae, summit of Akatarawa Mts., on sheep (?) dung, 11 Mar. 1990, *A. Bell and D. Mahoney* (WELTU 489). S. ISLAND: Banks Peninsula, 8.2 km S. of Diamond Harbour, Mt. Herbert Forest, on sheep dung, as *Schizothecium minutum* (Fckl.) Lundq., 6 Nov. 1980, *Tibell 9386-b* (UPS, WELTU 391); S. of Hillersden, pasture in the Wairau Valley, on rabbit dung, 7 May 1990, *A. Bell and D. Mahoney* (WELTU 611). UNITED KINGDOM. ENGLAND: Somerset, Batheaston, on old table cloth, as *Sphaeria vesticola* Berk. & Br., 24 Dec. 1858, herb. Broome 370 (LECTOTYPE, K).

Cultures deposited. Living CMA cultures from WELTU 611 have been deposited as IMI 361013, ATCC 90648 and CBS 133.94.

Comments. This species is well represented on diverse herbivore dungs from a wide range of habitats throughout New Zealand. In this study we have recorded it from 33 dung samples including sheep (5), goat (2), sheep/opossum? (1), goat/deer? (1), opossum (2), deer (2), rabbit (16), hare (2), lagomorph (1) and horse (1). In Sweden, it is also reported on "various kinds of dung" (Lundqvist, 1972, p. 256) but there, instead of rabbit, it is common "particularly on cow and horse." A selection of other countries from which it is recorded includes Algeria, Canada, Germany, India, Iraq, Japan, Libya, Mexico, Morocco, Pakistan, United Kingdom and the United States (Abdullah and Rattan, 1978; Barrasa and Solans, 1989; Lundqvist, 1972; Mirza and Cain, 1969; Rao and Varghese, 1989).

On rabbit dung *P. vesticola* frequently grows alongside *P. miniglutinans* with whose perithecia it is easily confused at lower magnifications. Slide mounts reveal, however, that although the agglutinated hairs are of similar sizes, those of *P. vesticola* are better developed and more evenly scattered over the perithecium, whereas those of *P. miniglutinans* are typically confined to the region immediately below the neck where

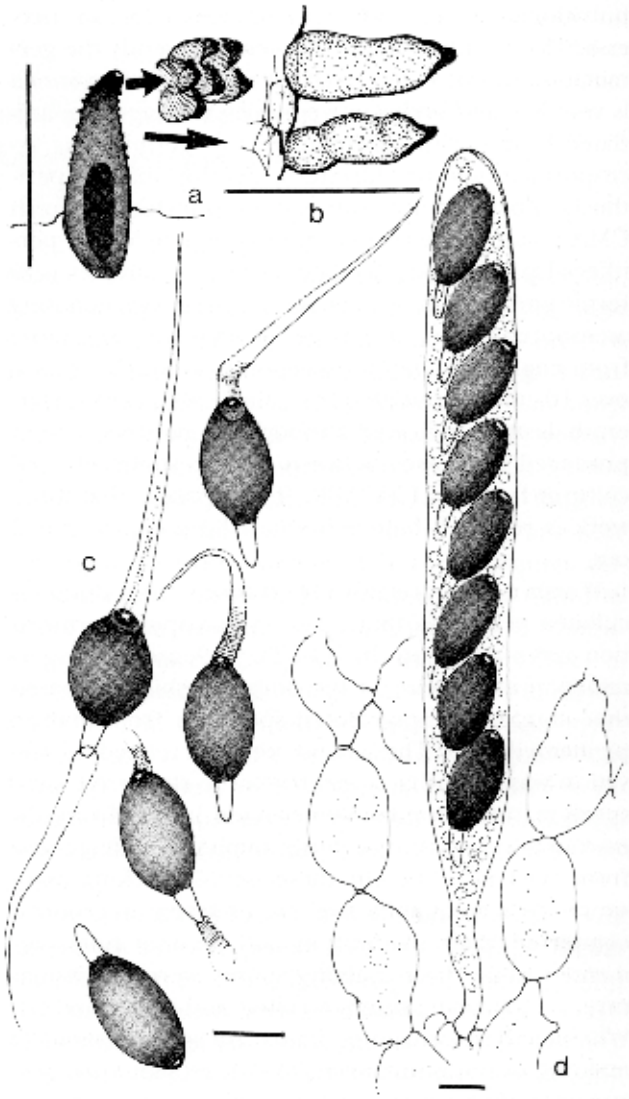


FIG. 55. *Podospora vesticola*. a, b. Habit sketch of perithecium together with details of neck cells (arrow) and agglutinated hairs (arrow). c. Mature ascospores. d. Mature ascus showing uniseriate ascospore arrangement and jacket paraphyses. Scale = 0.5 mm for (a), 15 μm for (b), 10 μm for (c) and (d).

they form a collar. Also the ascospores of *P. vesticola* are usually shorter and always narrower, 10–12 μm versus 13–15 μm. Culturally, there is no problem as *P. vesticola* has a *Phialophora* anamorph and *P. miniglutinans* no anamorph at all.

Podospora aloides, P. conica and *P. tetraspora* appear to be closely related to *P. vesticola*. They share a look-alike *Phialophora* anamorph and similar, although larger, triangular groupings of agglutinated hairs.

Culturally, this species has created more questions than answers. As with *P. conica* and several other species in this group, more information is needed on the requirements for ascospore germination and on the

nutritional, genetic and environmental factors necessary for perithecial development. Presently the germination of untreated fresh ascospores in *P. vesticola* is very low and only some colonies, among many initiated from perithecial fragments or germinating ascospores (single or clustered), develop mature perithecia. Furthermore, subsequent transfers to fresh CMA result in the reduction or complete loss of perithecial production. To date all of our cultures with fertile perithecia have been initiated from germinating ascospore clusters or perithecial fragments and none from single germinating ascospores, although we have over 10 cultures initiated from single ascospores. Heterothallism is indicated although no perithecia were produced in crosses between six ascospore-initiated cultures from WELTU 489. It is apparent that more work is required before homothallism can be ruled out.

Worth noting are two observations from dung-incubated perithecia that relate to ascospore germination and maturation. In WELTU 489, ascospore germination may occur, in the normal fashion, from either immature unpigmented spores or from mature pigmented ones. The second, perhaps related, observation was that what appeared to be staggered ascospore maturity commonly occurred in asci from numerous perithecia of two dung samples, including those from WELTU 489. On these occasions, four ascospores, less frequently five, six or seven ascospores, completed their maturation and became fully pigmented while the remaining spores were still immature, i.e., smaller, thinner-walled and unpigmented. Whether these remaining immature spores gradually matured or not is unknown. The aforementioned germination of unpigmented ascospores were ascospores forced from asci onto the agar surface rather than any that may have been naturally discharged. Whether natural ascospore discharge occurs before all spores are mature was not investigated. The above observations may also apply to ascospores of cultured perithecia but we saw only mature spores there.

ACKNOWLEDGMENTS

We wish to extend sincere thanks to all those individuals and institutions who helped us with this research, to various herbaria who loaned us valuable material, to Nils Lundqvist for his expertise and long correspondence, to Gerry Keating and Stan Carstensen for help with the photography and to John Krug, Nils Lundqvist and Gary Samuels for reviewing the manuscript.

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