

North American species of *Coprotus* (Thelebolaceae: Pezizales)¹

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The genus *Coprotus* is a segregate of the coprophilous genus *Ascophanus* Boud. characterized by minute, translucent, white to yellow apothecia, operculate, non-amyloid, eight- to multi-spored asci, and hyaline, smooth, thin-walled ascospores that contain gas bubbles. Species are distinguished by (1) the number of spores per ascus, (2) the presence or absence of pigments in paraphyses and excipular cells, and (3) the relative size and shape of asci, spores, and sterile elements. Five new combinations are made and six new species are proposed. Keys, descriptions and illustrations are provided for the 18 recognized North American species.

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Le genre *Coprotus* est séparé du genre coprophile *Ascophanus* Boud. et est caractérisé par des apothécies de très petite taille, translucides, blancs ou jaunes, portant des ascus operculés non-amyloïdes produisant huit ou plusieurs ascospores lesquelles sont lisses, hyalines, à paroi mince et contiennent des bulbes de gaz. Les espèces se distinguent (1) par le nombre de spores dans l'ascus, (2) par la présence ou l'absence de pigments dans les paraphyses et les cellules de l'excipulum et (3) par la dimension et la forme relatives des ascus, des spores et des éléments stériles. Cinq combinaisons nouvelles sont faites et six nouvelles espèces sont proposées. Des clés, des descriptions, des illustrations sont présentées pour les 18 espèces nord-américaines reconnues.

The genus *Coprotus* was first suggested by Korf (1954) for a segregate of the genus *Ascophanus* Boudier, and was provisionally placed in the tribe Acetabuleae of the Pezizaceae. The limits of *Coprotus* nom. nud. were further clarified by Korf (1958), who recommended transferring to the taxon all species of *Ascophanus* with non-amyloid, eight-spored asci, smooth, hyaline, guttulate ascospores, and strongly hooked paraphyses. A study of the Pseudoscolecaceae (Kimbrough 1966b) supported the recognition of this segregate; however, it was shown that 'spore guttules' were actually gaseous inclusions referred to as de Bary bubbles, that the paraphyses were not always hooked, and that both eight-spored and multi-spored species occurred in this genus. Kimbrough and Korf (1967) validated *Coprotus*, selected *Ascobolus sexdecimsporus* Cr. & Cr. as the holotype, and placed the genus in the tribe Theleboleae of the Pezizaceae. In addition to *A. sexdecimsporus*, five other species were transferred to it.

Coprotus is recognized in the most current treatments of the Pezizales (Rifai 1968; Eckblad 1968). In both of these investigations, the tribe

Theleboleae was elevated to Thelebolaceae (Pezizales). Brummelen (1967), however, recognized only the genus *Ascophanus* and retained it in the subfamily Theleboloidae of the Ascobolaceae. Eckblad (1968) questioned the validity of the name *Coprotus*, suggesting instead the name *Leporina* Velenovsky. According to him, van Brummelen studied Velenovsky's type, *L. multispora*, and found it to be identical with *A. sexdecimsporus*. This implied to him that *Leporina* Vcl. would be the correct name for *Coprotus* Korf and Kimb. In a separate paper (Kimbrough 1970) the nomenclatural problem is discussed in more detail. In view of the multiplicity of organisms that commonly occur on rabbit dung, the discrepancy between Velenovsky's (1947) description and what is present, or might have been present then, it was concluded that *Leporina* should be rejected as a name for this genus.

Subsequent studies of herbarium and fresh collections of coprophilous discomycetes, especially specimens placed in *Ascophanus* and *Ryparobius* sensu Boud., have resulted in the transfer of five more species to *Coprotus* and the discovery of six new ones.

This study is based upon herbarium specimens supplemented whenever possible with fresh collections. Procedures for collecting and culturing

these organisms were outlined by Kimbrough (1966a). Nuclei were stained with acetocarmine (Pincheira and Srb 1969). Measurements were made in distilled water. Frozen sections were prepared according to an agar-block technique described by Sanchez and Korf (1966). Starbuck's system of tissue classification as modified by Korf (1951) was used to describe cell arrangement.

Observations

Macroscopic Features of Apothecia

Apothecia of all species of *Coprotus* appear to develop gymnocarpically or, according to Brummelen (1967), gymnohymenially. In both types, the hymenium is exposed from the beginning until maturation of the asci. Brummelen (1967) subdivided the "gymnohymenial ascoma" into the paragymnohymenial type, in which hyphae of limited growth arch over the ascogonium, and the eugymnohymenial type, which does not exhibit this pattern of growth. This latter type of "ascoma" may or may not have an excipulum. The apothecia are sessile, superficial or slightly immersed, globose at first but soon becoming discoid or pulvinate. They are initially white or translucent; some may become slightly yellowish to bright yellow. Pigmented species grown under reduced light tend to be only faintly colored. They range in size from less than 0.1 mm to almost 3 mm in diameter with the majority of species falling below 1.5 mm. They are frequently overlooked by the unaided eye (Figs. 4, 16, 20, 25).

Excipulum

The excipulum is reduced in all species, and in most, medullary and ectal areas are almost indiscernible. The cells range from a "textura angularis" to a "textura globulosa" and are uniloculate at least in those of *C. glauccellus* and *C. niveus*. Marginal cells may vary from filamentous, hyaline, and thin-walled in some species (Figs. 13, 46) to globose, slightly pigmented, and thick-walled in others (Figs. 7, 26). Species which possess thickened, pigmented walls generally stain intensely blue in lactic acid with cotton blue (cyanophilous) and reddish brown in Melzer's reagent (dextrinoid). The intensity of these color reactions is extremely variable, depending on the age of apothecia, or on the manner in which the specimens have been

preserved and then revived. Often the natural pigmentation of excipular cells can be easily confused with a positive dextrinoid reaction.

Asci

Asci are clavate-cylindrical to broadly clavate, eight- or multi-spored, operculate, non-amyloid, and usually protrude slightly above the hymenium at the time of spore liberation. The young ascus is thick-walled, thinner at apex (Figs. 28, 64). The ascus wall is actually two-layered (Kimbrough 1966a; van Brummelen 1967), the outer one staining in Congo red and the inner staining in acid fuchsin. This is in strong contradiction to that which has been described for "unitunicate" ascomycetes. The asci vary in size from less than 50 μ to more than 150 μ long and from less than 10 μ to more than 50 μ wide. The ascus apex may be dome-shaped (Fig. 62), almost truncate (Fig. 36), to slightly constricted (Fig. 31). The base may be sharply constricted (Fig. 18) to extremely elongate. They all appear to have croziers.

Ascospores

Mature ascospores of all *Coprotus* species usually develop a conspicuous de Bary bubble in several different mounting agents. Immature spores possess slightly thickened walls composed of two distinct layers. The inner layer, especially in young spores, is faintly stained with acid fuchsin in lactic acid and remains unstained in heated cotton blue. It decreases in thickness as the spores mature. The outer layer stains in heated cotton blue and remains thin and smooth. Spore cytoplasm is densely granular, faintly yellow in some species, and usually contains a conspicuous gas bubble. Spores are uninucleate.

Paraphyses

Paraphyses are septate, simple or branched, filamentous to abruptly clavate, straight or strongly uncinately, with or without oil droplets and carotenoids. Cells of the paraphyses are uninucleate.

Cultural Features

Cultural studies for this segregate of *Ascophanus* have been very limited. Dangeard (1907) observed early developmental stages of *A. ochraceus* in which single and chained, multinucleate ascogonia were formed. Numerous ascogenous hyphae were borne from each ascogonium and several ascogonia were involved in

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the production of a single apothecium. However, the interpretation of these observations has been questioned (Gwynne-Vaughan 1922).

Occurrence and Distribution

Species of *Coprotus* have been found on the dung of a wide variety of animals. They are probably cosmopolitan, having been reported in North and South America, Europe, Southeast Asia, Australia, and Africa. They show no seasonal preference, fruiting whenever the temperature remains high enough and moisture is adequate. On dung placed in moist chambers, species of *Coprotus* appear to be one of the last discomycetes to emerge.

Taxonomic Position of *Coprotus*

We are in agreement with both Eckblad (1968) and Rifai (1968) who place *Coprotus* in the Thelebolaceae of the Pezizales. We disagree with van Brummelen (1967) and perhaps others who wish to retain hyaline-spored taxa in the Ascobolaceae. Characters such as small apothecia, broad asci which protrude beyond the hymenium, and a predominantly coprophilous habitat still appear to be the bases for his classification.

The uninucleate nature of the cells of the paraphyses and excipulum is similar to those of *Lasiobolus ciliatus* (Schm. ex Fr.) Boud. (Berthet 1964), *Trichololus zukaii* (Heimerl) Kimbr. (Kimbrough 1966a), and *Thelebolus* spp. (unpublished observations). Sterile structures of the Ascobolaceae appear to be coenocytic. Pigmentation and the cyanophilous reaction of the excipulum suggest a possible relationship to the Aleuriaceae (Arpin 1968). Inadequate living material of such pigmented species as, for example, *C. aurora* has prevented experimental studies for determination and characterization of pigments in *Coprotus*. Cytological and cultural features, correlated with the tendency toward reduction in the number of asci and an increase in the number of ascospores tend to justify retention of the family Thelebolaceae.

Discussion

The species treated in this paper appear to be congeneric. Each has been treated at one time or other either as belonging to *Ascophanus* and (or) *Rhyarobius*. The eight-spored forms may

resemble species of *Iodophanus*, *Coprobola*, *Peziza*, *Psilopezia*, *Pyronema*, *Octospora* (= *Humaria*), or young specimens of *Thecotheus*. The non-amyloid character of asci in *Coprotus* separates this genus not only from *Peziza* (Pezizaceae), but also from *Iodophanus*, *Thecotheus*, and *Psilopezia*. In the walls of the ascospores in *Coprobola*, there are longitudinal striations which can be demonstrated by testing for cyanophily (Kotlaba and Pouzar 1964); thus, *Coprotus* can easily be distinguished from it. It is difficult to confuse *Coprotus* with *Octospora* since the latter genus is predominantly terrestrial and consists of species with guttulate ascospores. In addition, the species are more brightly colored than in *Coprotus* because of the predominance of carotenoids in the paraphyses and excipular tissue. *Coprotus* is chiefly distinguished from *Pyronema* by its more extensive excipulum and by the de Bary bubbles in its ascospores. Multispored species of *Coprotus* may resemble *Rhyarobius*, *Ascozonus* (= *Streptothea*), or *Thelebolus*; however, operculate asci and the presence of de Bary bubbles in the ascospores will distinguish *Coprotus* from these genera.

It has been difficult to delimit species within *Coprotus*. There appear to be two groups of species based mainly on the presence or absence of carotenoids. *Coprotus aurora*, *C. ochraceus*, *C. vicinus*, and *C. luteus* have variable, but obvious, pigment. In *C. granuliformis*, *C. sexdecimsporus*, *C. glaucellus*, and *C. marginatus*, the pale yellow pigment present in most collections is restricted to the cell walls of the excipulum. The remaining species are translucent to white. Within each group, species are separated by relative size and shape of asci and ascospores—elements which are usually well correlated with structures of the excipulum and features of the paraphyses.

Approximately 120 names have been applied to species placed in the genus *Ascophanus* at one time or other. Many of these have now been segregated and placed in other genera, or in synonymy with existing species of *Coprotus*. Yet, it is apparent from descriptions, illustrations, and personal observations that most of these names are now applied to taxa belonging to *Coprotus*. We could not locate types for certain named species. In a few, it has been difficult to reconcile what is found in the type collection with the author's original description.

Some species have been recognized on the basis of shape and color of apothecia and length of asci. We consider these features too variable and of little taxonomic value.

Although Kimbrough and Korf (1967) provided a generic diagnosis for *Coprotus*, further observations and the addition of other species make the following modifications necessary.

Coprotus Korf and Kimbrough, Am. J. Bot. 54: 21. 1967.

= *Coprotus*, Korf, Rapp. Comm. VIII Congr. Int. Bot. I, 1954(18–20): 80. 1954. nomen nudum.

Apothecia sessile, solitary to gregarious, 0.1–3.0 mm diam, discoid to slightly convex, pallid, white, faintly ochraceous to bright yellow, roughened by protruding asci at matu-

ity; *excipulum* of a *textura angularis* to almost *globulosa*, basal or extending to the ascus apices, marginal cells globose to extremely elongate, dextrinoid and cyanophilous in some; *asci* extremely variable in number, 30–200 μ long, 5–60 μ wide, operculate, non-amyloid, staining uniformly in Congo red; *ascospores* uni- or biserial, or irregularly crowded, 8–256 or more per ascus, smooth, elliptical, 6.0–25.0 \times 3.5–12.0 μ , thin-walled, some with yellowish contents, most at maturity with a conspicuous de Bary bubble; *paraphyses* filiform, septate, uncinately filiform to clavate at the apices, simple or branched, and with or without oil guttules and carotenoids.

HOLOTYPE: *Coprotus sexdecimsporus* (Cr. & Cr.) Kimbrough & Korf, Am. J. Bot. 54: 22. 1967.

A KEY TO NORTH AMERICAN SPECIES OF *Coprotus*

- | | |
|--|--------------------------|
| A. Apothecia yellow to orange, paraphyses with orange granules or guttules, excipulum weakly cyanophilous | B |
| A. Apothecia translucent to white, drying faintly yellowish, paraphyses without pigmented guttules, excipulum sometimes strongly cyanophilous and dextrinoid | F |
| B. Ascospores less than 10 μ long | C. <i>luteus</i> |
| B. Ascospores more than 10 μ long | C |
| C. Ascospores less than 15 μ long | D |
| C. Ascospores more than 15 μ long | E |
| D. Apothecia bright yellow or orange, asci 65–90 \times 10–15 μ , ascospores 12–14 \times 6.0–8.5 μ | C. <i>aurora</i> |
| D. Apothecia yellow, asci 45–55 \times 15–18 μ , ascospores 10–13 \times 6.5–8.5 μ | C. <i>breviascus</i> |
| E. Ascospores 15–18 \times 9.0–10.5 μ , asci 110–150 \times 12–18 μ , paraphyses slightly inflated | C. <i>ochraceus</i> |
| E. Ascospores 17–25 \times 11–14 μ , asci 65–100 \times 20–28 μ , paraphyses slightly uncinately above | C. <i>vicinus</i> |
| F. Asci eight-spored | G |
| F. Asci with more than eight spores | M |
| G. Asci broadly clavate, paraphyses strongly inflated at their apices | C. <i>granuliformis</i> |
| G. Asci cylindrical, paraphyses not strongly inflated | H |
| H. Ascospores less than 10 μ long | I |
| H. Ascospores more than 10 μ | K |
| I. Asci less than 55 μ long, paraphyses filiform and strongly uncinately at their apices | C. <i>glaucellus</i> |
| I. Asci longer, paraphyses slightly inflated above | J |
| J. Asci 65–85 \times 15–20 μ , marginal cells of excipulum not extremely elongate | C. <i>lacteus</i> |
| J. Asci 80–100 \times 8–12 μ , marginal cells of excipulum long, flexuous, and capitate | C. <i>marginatus</i> |
| K. Spores mostly 14 μ or longer | C. <i>leucopocillum</i> |
| K. Spores less than 14 μ long | L |
| L. Spores narrowly ellipsoid, 12–13.5 \times 5–8 μ , asci 75–90 \times 10–15 μ , apothecia white | C. <i>disculus</i> |
| L. Spores broader, 11–13 \times 7.5–10 μ , asci 80–125 \times 18–24 μ , apothecia with yellowish border | C. <i>dextrinoides</i> |
| M. Asci 16-spored | N |
| M. Asci with more than 16 spores | O |
| N. Ascospores 11–16 \times 8–10 μ , asci 85–140 μ long | C. <i>sexdecimsporus</i> |
| N. Ascospores 7.5–10 \times 4.0–6.5 μ , asci 70–90 μ long | C. <i>duplus</i> |

O. Asci with 32 spores.....	P
O. Asci with more than 32 spores.....	Q
P. Spores less than 13 μ long, asci 50-110 μ long.....	<i>C. albidus</i>
P. Spores more than 13 μ long, asci larger.....	<i>C. rhyarobioideus</i>
Q. Asci approximately 64-spored.....	<i>C. niveus</i>
Q. Asci approximately 256-spored.....	<i>C. winteri</i>

1. *Coprotus albidus* (Boud.) Kimbr. Figs. 1-3
= *Rhyarobius albidus* Boudier, Bull. Soc. Mycol. Fr. 4: 49. 1887.

= *Coprotus albidus* (Boud.) Kimbrough, Am. J. Bot. 54: 22. 1967.

= *Rhyarobius tenacellus* Phillips, Grevillea, 19: 74. 1891.

= *Rhyarobius mirabilis* Vel., Disc. Bohem. 364. 1934.

Apothecia sessile, globose to lenticular, 0.2-0.4 mm in diam, white to almost translucent, smooth, hymenium roughened by protruding asci; *excipulum* pseudoparenchymatous in surface view; asci 32-spored, broadly clavate, attenuated at base, 75-100 \times 20-30 μ , with a broad operculum; *ascospores* irregularly disposed, 10.0-12.5 \times 5.0-7.5 μ , smooth, hyaline, each with a de Bary bubble which may be lacking at times; *paraphyses* cylindrical, septate, without apparent oil guttules, enlarged to 5.0-6.0 μ at their apices.

HABITAT: On dung of rabbit and cow.
TYPE: On cow dung, in Forêt de Carnelle, France, March, 1884, Boudier (PC).

SPECIMENS EXAMINED: The type (cited above). On rabbit dung, the Wrekin, Shropshire, Britain, Phillips (NY).

COMMENTS: Two 32-spored species of the old genus "*Rhyarobius*" belong to *Coprotus*. They are *C. albidus* and *C. rhyarobioideus*. Both asci and *ascospores* are considerably smaller in *C. albidus*. Phillips (1891) felt that *R. tenacellus* differed from *R. albidus* in having larger asci and *ascospores*, but an examination of Boudier's type revealed that the asci and spores of *R. albidus* were larger than recorded in the original description.

2. *Coprotus aurora* (Cr. & Cr.) comb. nov. Figs. 4-7

= *Peziza aurora* Crouan & Crouan, Fl. Finist. 53. 1867.

= *Ascophanus aurora* (Cr. & Cr.) Boud., Ann. Sci. Nat. V-10: 248. 1869.

= *Aleuria aurora* (Cr. & Cr.) Gill., Champ. Fr. Disc. 54. 1847.

= *Ascophanus auranticus* Velen., Monogr. Disc. Bohem. 360. 1934.

Apothecia scattered to gregarious, sessile, at first globose, finally discoid, yellow to bright orange, less than 0.5 mm diam; *excipulum* of a textura globulosa around the base, cells up to 15 μ in diam; marginal cells elongated, 5.0-6.0 \times 8.0-12.0 μ , with carotenoid pigments; *asci* eight-spored, cylindrical to clavate, 65-90 \times 10-15 μ , rounded above, attenuated below; *ascospores* uniseriate to biseriate, broadly ellipsoid, 12.0-14.0 \times 6.0-8.5 μ , hyaline to pale yellow, smooth, with perispore layer thin and slightly cyanophilous, each with a de Bary bubble; *paraphyses* septate, mostly branched, 2.0-2.5 μ below, inflated to 4.0-5.0 μ above, slightly uncinuate, filled with yellow oil guttules.

HABITAT: On dung of various animals.
TYPE: On old cow dung, Finistère, France, 15 Nov. 1866, Crouan & Crouan (observed by Le Gal (1953)).

SPECIMENS EXAMINED: UNITED STATES: Delaware: Faulkland, on cow dung, 24 Oct. 1887, Commons (NY). Illinois: McLean Co.: Funk's Grove, on horse dung, 13 Aug. 1965, Luck-Allen 44788 (TRTC). Wyoming: Park Co.: W of Cody, on porcupine dung, 1 Sept. 1962, Cain 39043 (TRTC). CANADA: Alberta: Jasper Natl. Park, S of Jasper, on moose dung, 8 Aug. 1962, Luck-Allen 40171 (TRTC). Ontario: York Co.: Nashville, on cow dung, 18 Nov. 1962, Cain 38950 (TRTC).

COMMENTS: *Coprotus aurora* is the most brightly colored species of this genus. It can be confused with *C. luteus* but may be distinguished by its larger more elliptic spores and more uncinuate and highly pigmented paraphyses.

3. *Coprotus breviascus* (Vel.) comb. nov. Figs. 8, 9

= *Ascophanus breviascus* Velenovsky, Monogr. Disc. Bohem. 360. 1934.

Apothecia scattered to gregarious, yellowish to orange, discoid to lenticular, 0.2-0.6 mm in diam; *excipulum* slightly pigmented, non-cyanophilous, cells of a textura angularis and elon-

gated at the tips; *asci* eight-spored, broadly clavate, 45-60 \times 20-28 μ , abruptly attenuated at base; *ascospores* biseriate, 12.0-16.0 \times 8.5-12.0 μ , hyaline to pale yellow, smooth, broadly ellipsoid, with perispore layer thin and cyanophilous; *paraphyses* filiform, septate, simple or branched, 1.5-2.0 μ below, slightly inflated, uncinuate at their apices and containing yellowish oil droplets.

TYPE: On cow dung, Radotin, Mnichovice, Czechoslovakia, Velenovsky (PR).

SPECIMENS EXAMINED: EUROPE: AUSTRIA: Sonntagesberg, on cow dung, July, 1906, von Hönlner (FH) (TYPE PR). UNITED STATES: Wyoming: Big Horn Co.: Granite Pass, on sheep dung, 2 Sept. 1962, Luck-Allen 39485 (TRTC).

COMMENTS: *Coprotus breviascus* is morphologically similar to *C. granuliformis* and *C. ochraceus*. The broadly clavate *asci* and broadly ellipsoid *ascospores* are similar to those of *C. granuliformis*, but the latter species can be distinguished by its strongly inflated, hyaline paraphyses and larger, more globose *excipular* cells. *Coprotus ochraceus* has both larger *asci* and *ascospores*. Velenovsky (1934) cites the same figures for *C. breviascus* and *A. bilobus* but the latter appears to be a synonym of *C. ochraceus*. Contrary to the original description, we find oil droplets in the paraphyses of *C. breviascus*.

4. *Coprotus dextrinoideus* sp. nov. Figs. 10-12

Apothecia dispersa, 0.1-0.5 mm in diametro, cupulata vel discoidea; hymenium album; margo subluteus, fuscoluteus siccatu. *Excipulum* e cellulis angularibus vel globosis (textura angulari vel textura globulosa), luteis, cyanophilis compositum. *Cellulae* marginatae elongatae, 8.0-15.0 \times 3.0-6.0 μ . *Asci* octospori, cylindracei, 80-125 \times 18-24 μ , ad apicem late rotundati, ad basem attenuati. *Ascospores* late ellipsoideae, uniseriatae, raro biseriatae, 11.0-13.0 \times 7.5-10.0 μ , "de Bary bubble" praeditae. *Paraphyses* filiformes, septatae, valde ramosae, hyalinae, guttulateae.

HOLOTYPE: In fimo vaccino, Puerto Rico, West India Exploration No. 1, Jan.-Apr., 1923, Seaver and Chardon (NY).

Apothecia scattered, 0.1-0.5 mm in diam, cupulate to discoid, hymenium white, margin yellowish, darker on drying; *excipulum* of a textura angularis to globulosa, cells slightly

thick-walled, yellowish, cyanophilous, marginal cells elongated, 8.0-15.0 \times 3.0-6.0 μ ; *asci* eight-spored, cylindrical, rounded above, attenuated below, 80-125 \times 18-24 μ ; *ascospores* uniseriate, rarely biseriate, broadly ellipsoid, 11.0-13.0 \times 7.5-10.0 μ , each with a conspicuous de Bary bubble; *paraphyses* filiform, septate, mostly branched, hyaline, with a few inconspicuous oil guttules.

HABITAT: On dung of cow, deer, antelope, wapiti, and burro.

SPECIMENS EXAMINED: MEXICO: Durango: N of Durango, on burro dung, 13 Aug. 1960, Cain 36996 (TRTC). PAKISTAN: Sind Area, on cow dung, 1 Sept. 1967, Ahmed F49069 (FLAS). PUERTO RICO: TYPE. UNITED STATES: New York: L. Placid, on cow dung, 4 Sept. 1914, Kauffman and Mains (MICH). Wyoming: Big Horn Co.: Upper Shell Canyon, on wapiti dung, 2 Sept. 1962, Cain 41267 (TRTC); on deer dung, 2 Sept. 1962, Luck-Allen 41793 (TRTC); on antelope dung, 2 Sept. 1962, Luck-Allen 42111 (TRTC). Niobrara Co.: N of Lusk, on cow dung, 2 Sept. 1964, Cain 42598 (TRTC).

COMMENTS: This species may be confused with *Coprotus disculus* on the basis of *ascus* and *ascospore* measurements. The spores of *C. disculus* are more narrowly elliptic and the *asci* are generally 20-25 μ shorter than those of *C. dextrinoideus*. In addition, the *excipular* cells in *C. dextrinoideus* are more pigmented, thicker-walled, and more elongated at the margins. The paraphyses of *C. disculus* are more inflated and without oil guttules.

5. *Coprotus disculus* sp. nov. Figs. 13-15

Apothecia pellucida, alba, deinde lutea, discoidea vel lenticularia, 0.5-1.0 mm diam. *Excipulum* e cellulis hyalinis (textura angulari vel textura globulosa). *Cellulae* basilares globosae, 20 μ diam. *Cellulae* marginales 8.0-12 \times 6-10 μ . *Asci* octospori (rare quantuorspori), cylindracei, 75-90 \times 10-15 μ , ad apicem rotundati, ad basem attenuati. *Ascospores* anguste ellipsoideae, uniseriatae, raro biseriatae, 12.0-13.5 \times 5.0-8.0 μ , dilute luteae, "de Bary bubble" praeditae. *Paraphyses* filiformes, septatae, hyalinae, non guttulateae, superne incrassatae usque 4.0 μ diam et leniter uncinatae.

HOLOTYPE: In fimo cervino, Berger Swamp, near Rochester, New York, 5 Oct. 1947, Roger-son (CUP 37168).

Apothecia translucent to white, becoming yellowish discoid to lenticular, 0.5–1.0 mm in diam; *excipulum* of a textura angularis to globulosa; cells thin-walled, essentially hyaline, basal cells almost globose, up to 20 μ diam, marginal cells 8.0–12 \times 6–10 μ ; *asci* eight-spored, rarely four-spored; cylindrical, 75–90 \times 10–15 μ , rounded above, attenuated below; *ascospores* uniseriate, sometimes biseriate, narrowly ellipsoid, 12.0–13.5 \times 5.0–8.0 μ , faintly yellowish, with one de Bary bubble; *paraphyses* filiform, septate below, hyaline, without oil guttules, with apices inflated 3.0–4.0 μ and slightly uncinata.

HABITAT: On dung of deer, horse, cow, and small rodents.

TYPE: On deer dung, New York: Bergen Swamp, near Rochester, 5 Oct. 1947, *Rogerson* (CUP 37168).

SPECIMENS EXAMINED: CANADA: Ontario: Bruce Co.: Inverhuron, on deer dung, 8 Oct. 1961, *Cain* 38739 (TRTC). Leeds Co.: Chaffey's Locks, on deer dung, 28 Sept. 1963, *Luck-Allen* 41256 (TRTC). Oxford Co.: Benwell Swamp, Gables, on deer dung, 13 Sept. 1943, *Cain* 45718 (TRTC). Quebec: Mt. Albert, Lac Cascapedia, on horse dung, 21 Aug. 1937, *Bigelow* 63011 (DAOM). EUROPE: ITALY (N): Lombardy, on cow dung, 23 Aug. 1907, *Colla*? D6331 (CUP, MICH). UNITED STATES: New York: TYPE: Courtland Co.: McLean Bog near Dryden, on deer dung, 5 Sept. 1952, *Cain* 24411 (TRTC); Lyndonville, on cow dung, 1904, *Fairman* D450 (CUP).

COMMENTS: *Coprotus disculus* is close to *C. lacteus*. In fact, specimens of the former have been accessioned in some herbaria under the latter name. *Coprotus lacteus* differs in having shorter *asci* and *ascospores* and narrower *paraphyses*.

6. *Coprotus duplus* sp. nov. Figs. 16–19

Apothecia alba vel leniter lutea, 0.3–0.8 μ diam, cupulata vel discoidea, leves. *Excipulum* ordinibus tribus vel quatuoribus compositum. Cellulae basilares usque 10–12 μ diam, hyalinae vel leniter luteae (textura angulari vel textura globulosa). Cellulae marginales elongatae, 10–12 \times 4–6 μ . *Asci* sexdecimspori, anguste cylindrici, 70–90 \times 10–18 μ . *Ascospores* ellipsoideae, biseriatae, leves, hyalinae vel leniter luteae, 7.5–10.0 \times 4.6–6.5 μ , "de Bary bubble" praec-

ditae. *Paraphyses* filiformes, septatae, non ramosae vel rarissimo ramosae, ad basem 1.8–2.0 μ crassae, superne usque 1.8–2.0 μ diam, guttulate.

HOLOTYPE: In fimo leporino, 5 mi S of Dorset, Haliburton Co., Ontario, 14 Sept. 1931, *Cain* 40026 (TRTC).

Apothecia white to slightly yellowish, cupulate to discoid, smooth, 0.3–0.8 mm in diam; *excipulum* of three to four layers, basal area of a textura angularis to globulosa, cells up to 12 μ in diam, hyaline to slightly yellowish, marginal cells elongated, 10–12 \times 4–6 μ ; *asci* 16-spored, narrowly cylindrical, 70–90 \times 10–18 μ , dome-shaped to almost truncate above; *ascospores* biseriate, smooth, hyaline to faintly yellowish, ellipsoid, 7.5–10.0 \times 4.0–6.5 μ , each with a de Bary bubble; *paraphyses* filiform, septate, simple or sparingly branched, 1.8–2.0 μ below, 2.2–2.5 μ at apices, guttulate, with oil guttules small, few in number.

HABITAT: On the dung of various animals.
TYPE: On rabbit dung, 5 mi S of Dorset, Haliburton Co., Ontario, 14 Sept. 1931, *Cain* 40026 (TRTC).

SPECIMENS EXAMINED: CANADA: Ontario: Bruce Co.: Teeswater, on rabbit dung, 10 July 1932, *Cain* 40024 (TRTC); N of Kincardine, on rabbit dung, 8 Oct. 1961, *Cain* and *Luck-Allen* 41384 (TRTC). Nipissing Dist.: Lake Timagami, on porcupine dung, 19 July 1934, *Cain* 46224 (TRTC); Lake Timagami, Sand Point, on partridge dung, 12 Sept. 1936, *Jackson* 40023 (TRTC); Lake Timagami, Paradise Bay, on deer dung, 22 Aug. 1935, *Cain* 40025 (TRTC). Victoria Co.: Oakwood, on rabbit dung, 15 Sept. 1931, *Cain* 36406 (TRTC). Quebec: Duchesnay, on partridge dung, 27 Aug. 1938, *Cain* 46234 (TRTC).

COMMENTS: *Coprotus duplus* has been confused with *C. sexdecimsporus* but differs in having *apothecia* with less pigment, smaller more cylindrical *asci*, and smaller *ascospores*. This species also resembles *C. glaucellus* except for size of *asci* and *ascospore* number.

7. *Coprotus glaucellus* (Rehm) Kimbrough Figs. 20–24

Ascophanus glaucellus Rehm, in Rab. Krypt. Fl. 1(3): 1086. 1895.

Coprotus glaucellus (Rehm) Kimbrough, Am. J. Bot. 54: 22. 1967.

Apothecia scattered to gregarious, smooth, translucent to white, becoming slightly yellowish on drying, discoid to lenticular, broadly attached, 0.1–1.2 mm in diam; *excipulum* of a textura angularis to textura globulosa; cells hyaline to pale yellow, thin-walled, in two to three layers, lower cells measuring 5.0–6.0 \times 6.0–8.0 μ below, marginal cells elongated up to 10 μ ; *asci* eight-spored, cylindrical, rounded above, attenuated below, terminating in a short stalk, 40–55 \times 8–12 μ ; *ascospores* uniseriate to biseriate, ellipsoid, 7.5–9.0 \times 4.5–5.5 μ , each with one de Bary bubble; *paraphyses* hyaline, filiform, septate, strongly uncinata at apices, 1.5 μ below, slightly broader above, without oil guttules.

HABITAT: On dung of deer, goat, moose, porcupine, and rabbit.

TYPE: On deer dung, Bavarian Alps, Oct. 1906, *Rehm* (Rehm: Ascomyceten 1678, CUP D, MICH).

SPECIMENS EXAMINED: CANADA: Ontario: Muskoka Dist., Purbrook, on rabbit dung, 2 Sept. 1956, *Cain* 32427 (TRTC). Nipissing Dist.: Algonquin Park, Brewer Lake, on porcupine dung, 26 Aug. 1939, *Cain* 36674 (TRTC); Algonquin Park, Norway Lake, on deer dung, 25 Aug. 1939, *Cain* 36620 (TRTC); Algonquin Park, L. Sasejewan, on moose dung, 27 Oct. 1963, *Cain* 41885 (TRTC); Lake Timagami, W Mainland, on porcupine dung, 11 Aug. 1931, *Jackson* 2698 (TRTC). Oxford Co.: Benwell Swamp, on deer dung, 13 Sept. 1943, *Cain* 27407 (TRTC). Thunder Bay Dist.: Poshkogan R., on moose dung, 5 Aug. 1965, *Luck-Allen* 43519 (TRTC). EUROPE: (The TYPE). MEXICO: San Luis Potosi, Ciudad del Maiz, on goat dung, 19 Aug. 1960, *Cain* 41238 (TRTC).

UNITED STATES: Colorado: W of L. George, on deer dung, 4 Aug. 1960, *Cain* 38291 (TRTC). Florida: 3 mi E of Gainesville, on rabbit dung, 4 Feb. 1969, *Kimbrough* F48427 (FLAS). Michigan: Cheboygan Co.: Reese Bog, 23 Aug. 1946, *Kanouse* (MICH). New Jersey: Newfield, on horse dung, 27 Sept. 1879, *Ellis* D4630 (CUP). New York: Allegany State Park, Stoddard Brook, on moose dung, 11 June 1961, *Cain* 37587 (TRTC); Adirondack Mts., Warrensburg, on deer dung, 3 Oct. 1959, *Cain* 38296 (TRTC).

COMMENTS: *Coprotus glaucellus* is one of the most common of the coprophilous discomy-

cetes. It has frequently been confused with *Coprotus lacteus* primarily because of the broad concept many authors had of *C. lacteus*. *Coprotus glaucellus* has the smallest *asci* and *ascospores* of all species of *Coprotus* having translucent *apothecia*. The pale yellow color is largely due to the presence of pigments in the walls of the *excipular* cells.

8. *Coprotus granuliformis* (Cr. & Cr.) Kimbrough Figs. 25–29

Ascophanus granuliformis Crouan & Crouan, Ann. Sci. Nat. IV, 10: 195. 1858.

Ascophanus granuliformis (Cr. & Cr.) Boudier, Ann. Sci. Nat. V, 10: 245. 1869.

Coprotus granuliformis (Cr. & Cr.) Kimbrough, Am. J. Bot. 54: 22. 1967.

Ascophanus argenteus Currey, Trans. Linn. Soc. 24: 496. 1864.

Ascophanus argenteus (Curr.) Boud., Ann. Sci. Nat. V, 10: 245. 1869.

Ascophanus rosellus Starbäck, Bot. Notis. 216. 1898.

Apothecia cupulate to discoid, white to pale yellow, margins darker in color than hymenium, 0.2–0.6 mm in diam; *excipulum* of a textura angularis to globulosa, marginal cells non-elongated, almost isodiametric, reaching 10–12 μ diam, with cell walls slightly thickened and pigmented with age; *asci* eight-spored, broadly clavate, 40–55 \times 15–30 μ , almost truncate above, sharply tapering to a short stalk below; *ascospores* mostly biseriate, broadly ellipsoid, 9.0–15.0 \times 6.5–9.5 μ , each with one large de Bary bubble; *paraphyses* filiform, septate below, inflated at apices to 5.0–8.0 μ , hyaline to slightly pigmented, often with minute oil guttules.

HABITAT: Mostly on cow dung, but also on deer and sheep dung.

TYPE: On cow dung, Brest, Finistère, France, Crouan (examined and figured by Le Gal (1961)).

SPECIMENS EXAMINED: CANADA: Ontario: Bruce Co.: Brinkman Corners, on sheep dung, 12 July 1930, *Cain* 39472 (TRTC). Leeds Co.: Chaffey's Locks, on cow dung, 28 Sept. 1963, *Luck-Allen* 40118 (TRTC). Parry Sound Dist.: Byng Inlet, on deer dung, 22 Aug. 1955, *Cain* 41420 (TRTC). Peel Co.: N of Palgrave, on cow dung, 17 Sept. 1946, *Cain* 23399 (TRTC). Saskatchewan: Cypress Hills Prov. Park, W of East Block, on cow dung, 26 July 1962, *Luck-Allen* 41266 (TRTC). EUROPE: AUSTRIA: Northern, on cow dung, Sept.

1902, Höhnelt D11754; Rehm 104b (CUP). Tyrol, in higher Alps, on cow dung, Aug. 1872, Rehm 104 (NY). SWEDEN: Uplandia, on cow dung, Aug. 1895, Starbäck D4591 (as *A. rosehus*) (CUP). UNITED STATES: Colorado: Geneva Creek Canyon, on cow dung, 3 Sept. 1910, Seaver (NY). Oregon: Hood R., on cow dung, 30 Aug. 1932, Kienholz (NY). New York: Hendershot Gorge, Alpine, on deer dung, 28 Sept. 1964, Spevak, Korf 3180 (CUP). McLean, on cow dung, 2 June 1919, Olive 11192 (CUP). Tompkins Co.: Ithaca, on cow dung, 18 July 1904, Kauffman (MICH). Wyoming: Rocky Mt. Natl. Park, on deer dung, 19 Aug. 1952, Cain 41717 (TRTC).

COMMENTS: *Coprotus granuliformis* is easily distinguished from other species of the genus by its short, very broadly clavate asci and by paraphyses which are greatly inflated at their apices.

9. *Coprotus lacteus* (Ck. & Phill.) comb. nov.

Figs. 30-33

= *Ascobolus lacteus* Cooke & Phillips, *Grevillea*, 5: 119. 1876.

= *Ascophanus lacteus* (Ck. & Phill.) Phill., *Man. Brit. Discom.* 306. 1887.

Apothecia smooth, white, becoming yellowish discoid to cupulate, sessile but narrowed below into a minute basal attachment, 0.2-0.5 mm in diam; *excipulum* of a textura angularis to globulosa with cells of the medullary area thin-walled, up to 12 μ diam and with those of the ectal area becoming dextrinoid and cyanophilous; marginal cells elongate, 8-10 \times 4-5 μ ; *asci* eight-spored, cylindrical to clavate, 65-85 \times 15-20 μ , rounded or dome-shaped above, attenuated below; *ascospores* uniseriate to biseriata, smooth, hyaline, ellipsoid, 8.0-10.0 \times 5.0-6.5 μ , each with one de Bary bubble; *paraphyses* filiform, septate, simple or branched, hyaline, 1.5 μ below, slightly inflated and somewhat uncinata at apices.

HABITAT: On dung of various animals.

TYPE: On cow dung, Shrewsbury, England, 1876, Phillips D11141 (CUP).

SPECIMENS EXAMINED: CANADA: Ontario: Bruce Co.: Inverhuron, on deer dung, 8 Oct. 1961, Cain & Luck-Allen 40111 (TRTC). Halton Co.: S of Ballinafad, on porcupine dung, 12 Oct. 1964, Luck-Allen 41777 (TRTC). Leeds Co.: Chaffey's Locks, on deer dung, 28 Sept. 1963, Luck-Allen 40445 (TRTC). EUROPE: ENGLAND:

The TYPE. Halifax, on horse dung, 27 Dec. 1898, Soppett 263 (Crossland Herb., NY). MEXICO: Durango: N of Durango, on rabbit dung, 13 Aug. 1960, Cain 36812 (TRTC); N of Durango, on burro dung, 13 Aug. 1960, Cain 37487 (TRTC). San Luis Potosi: Ciudad del Maiz, Dry Pass, on goat dung, 19 Aug. 1960, Cain 37475 (TRTC). Villa Hidalgo, on goat dung, 18 Aug. 1960, Cain 36931 (TRTC). Tamaulipas: Reynosa, on sheep dung, 20 Aug. 1960, Cain 36717 (TRTC). PUERTO RICO: on cow dung, 24 Jan. - 5 Apr. 1923, Seaver and Chardon 174 (NY). UNITED STATES: Alachua Co.: Gainesville, near Muck Pond, on rabbit dung, 7 July 1965, Kimbrough F48918 (FLAS). Gainesville, San Felasco Hammock, on rabbit dung, 4 Feb. 1970, Kimbrough F48891 (FLAS). New York: Botanical Gardens, on horse dung, 27 Jan. 1915, Seaver (NY).

COMMENTS: Not until after several perplexing observations, was it found that the type collection was a mixture of *C. lacteus* and *C. granuliformis*. In fact, apothecia of *C. granuliformis* were much more abundant. The authors were almost convinced that what Heimerl (1889) and others had described and illustrated as *C. lacteus* was really another fungus and that the type of *C. lacteus* would fall into synonymy with *C. granuliformis*. Phillips (1887), however, had found both species on cow dung from Shrewsbury; consequently this necessitated further critical and more extensive examination of the type collection. This eventually led to the discovery of a second fungus which agreed with the description of *C. lacteus*. *Coprotus lacteus* is close to *C. glaucellus* but may be distinguished by its larger asci and more clavate, less uncinata paraphyses. *Coprotus lacteus* and *C. granuliformis* can be separated on the basis of spore dimensions and on the characters of the ascus.

10. *Coprotus leucopocillum* sp. nov. Figs. 34-36

Apothecia dispersa vel gregaria, alba vel dilute lutea, levia, cupulata vel lenticularia, 0.3-0.5 mm in diametro. *Excipulum* e cellulosa (textura angularis vel textura globulosa). Cellulae basillares isodiametricae, 8-15 μ diam. Cellulae marginales elongatae, 5-8 \times 12-15 μ leniter dextrinoideae. *Asci* octospori, late cylindracei, 80-110 \times 15-22 μ , inferne in stipitem brevem attenuati. *Ascospores* late ellipsoideae biseriatae, 14.0-18.0 \times 7.5-11.5 μ , hyalinae vel

leniter luteae, leves, "de Bary bubble" praeditae. *Paraphyses* non ramosae vel rare ramosae, septatae, hyalinae, non guttulateae, ad basem 1.5 μ diam, superne usque 3.0-4.5 μ diam inflatae, leniter uncinatae.

HOLOTYPE: In fimo vaccino, Bermuda, 29 Nov. - 14 Dec. 1912, Britton and Seaver (NY).

Apothecia scattered to gregarious, white to pale yellow, smooth, cupulate to lenticular, 0.3-0.5 mm in diam; *excipulum* of a textura angularis to globulosa, basal cells almost isodiametric, 8-15 μ in diam, marginal cells elongated, 5-8 \times 12-15 μ , sometimes slightly dextrinoid; *asci* eight-spored, broadly cylindrical, 80-110 \times 15-22 μ , rounded to slightly truncate above, terminating in a short stipe below; *ascospores* broadly ellipsoid, biseriata, 14.0-18.0 \times 7.5-11.5 μ , hyaline to slightly yellowish, smooth, each with one de Bary bubble; *paraphyses* simple, rarely branched, septate, hyaline, without granules or guttules, 1.5 μ below, frequently enlarged to 3.0-4.5 μ at apices and slightly uncinata.

HABITAT: On dung of various animals.

TYPE: On cow dung, Bermuda, 29 Nov. - 14 Dec. 1912, Britton and Seaver (NY).

SPECIMENS EXAMINED: BERMUDA: TYPE. CANADA: Alberta: SW of Beaver Mines, on cow dung, 29 Aug. 1962, Cain 38945 (TRTC). Ontario: Grey Co.: 4 mi SW of Markdale, on cow dung, 30 May 1964, Cain 41765 (TRTC). Nipissing Dist.: L. Timagami, Gull L. Portage, on porcupine dung, 21 Aug. 1933, Cain 41772 (TRTC). York Co.: Nashville, on cow dung, 8 June 1958, Cain 38256 (TRTC). EUROPE: FRANCE: near Boulogne, on cow dung, July 1909, Ludwig (PC). PAKISTAN: N Karachi: on goat dung, 15 Oct. 1966, Ahmed. UNITED STATES: Michigan: Isle Royale: Sargent L. on moose dung, 29 July 1930, Povak (MICH). New York: Courtland Co.: McLean, on cow dung, 5 Sept. 1952, Cain 24271 (TRTC). Wyoming: Big Horn Co.: Upper Shell Canyon: on deer dung, 2 Sept. 1962, Luck-Allen 40653 (TRTC).

COMMENTS: The ascus and ascospore measurements of *C. leucopocillum* approach those of *C. oracheus* but the apothecia of the latter species are usually much larger and more pigmented, the asci are slightly more cylindrical and more abundant, and the paraphyses contain more pigment.

11. *Coprotus luteus* sp. nov. Figs. 37-40

Apothecia dispersa, lutea vel ochracea, 0.2-0.8 mm diametro, discoidea vel cupulata. *Hymenium* minore pigmento praeditum. *Excipulum* e cellulosa coloratis (textura angulari vel textura globulosa). Cellulae basillares rotundatae, usque 10-14 μ diam. Cellulae marginales angustae, elongatae, 4-5 \times 8-12 μ . *Asci* octospori, cylindracei, 60-85 \times 10-15 μ , superne rotundati, inferne in stipitem brevem attenuati. *Ascospores* ellipsoideae, uniseriatae, 8.0-10.5 \times 5.0-6.5 μ , tenuiter tunicatae, "de Bary bubble" praeditae. *Paraphyses* filiformes, septatae, non ramosae vel rare ramosae, guttulateae, superne usque 3.5 μ diam inflatae, leniter uncinatae.

HOLOTYPE: In fimo vaccino, Phelps Woods, Canandaigua, New York, 7 July 1903, Durand D2306 (CUP).

Apothecia scattered, yellow to orange, 0.2-0.8 mm in diam, discoid to cupulate, margins more pigmented than hymenium; *excipulum* of textura angularis to globulosa, cells pigmented, somewhat thick-walled, basal cells rounded, up to 14 μ diam, marginal cells narrow and elongated, 4-5 \times 8-12 μ ; *asci* eight-spored, cylindrical, 60-85 \times 10-15 μ , rounded above, terminating in a short stipe; *ascospores* hyaline, thin-walled, mostly uniseriate, ellipsoid, 8.0-10.5 \times 5.0-6.5 μ , each with one de Bary bubble; *paraphyses* filiform, septate, simple or sparingly branched, slightly uncinata above, enlarged to 3.5 μ , filled with numerous small yellow guttules.

HABITAT: On the dung of various animals.

TYPE: On cow dung, Phelps Woods, Canandaigua, New York, 7 July 1903, Durand D2306 (CUP).

SPECIMENS EXAMINED: CANADA: Alberta: Miette Hot Springs, on moose dung, 4 Aug. 1962, Luck-Allen 39477 (TRTC). British Columbia: Ghita Creek: W of Yellowhead Pass, on moose dung, 7 Aug. 1962, Luck-Allen 39211 (TRTC). Ontario: York Co.: Nashville, on cow dung, 21 June 1953, Cain 24594 (TRTC); on cow dung, 8 July 1961, Cain 37917 (TRTC). MEXICO: Durango: Rt. 45, N of Durango, on deer dung, 13 Aug. 1960, Cain 37045 (TRTC). Nuevo Leon: China, on goat dung, 20 Aug. 1960, Cain 37458 (TRTC). UNITED STATES: Montana: Park Co.: Springdale, on cow dung, 3 Sept. 1957, Cain 42134 (TRTC). New York: Canandaigua (TYPE).

South Dakota: Meade Co.: S of Wall, on cow dung, 3 Sept. 1962, *Cain* and *Luck-Allen* 39483 (TRTC). Wyoming: Yellowstone Natl. Park, Lower Geyser Basin, on horse dung, 1 Sept. 1962, *Cain* 42343 (TRTC).

COMMENTS: This species is similar to *Coprotus aurora*. It is common and is collected by various workers, but generally identified as *C. aurora* primarily because of its yellow to orange color. *Coprotus luteus* can be separated from *C. aurora* chiefly by its more cylindrical asci and smaller ascospores. Typically, the apothecia of *C. luteus* are less pigmented and 2.0–3.0 mm larger. The paraphyses of *C. aurora* are more branched and more deeply pigmented than those of *C. luteus*.

12. *Coprotus marginatus* sp. nov. Figs. 41–44

Apothecia alba vel lutea, levia, discoidea vel lenticularia, patellariformiter expansa, 1.0–1.6 mm in diametro. Excipulum basilare e cellulis 12–15 μ diam, pallide luteis compositum (textura globulosa). Cellulae marginatae valde elongatae, usque 100 μ longae, ad apicem tenuiter inflatae. Asci octospori, cylindracei, 80–100 \times 8–12 μ , ad apicem rotundati, inferne in stipitem brevem attenuati. Ascospores anguste ellipsoideae, uniseriatae, 8.5–10.0 \times 4.0–5.0 μ , hyalinae, "de Bary bubble" praeditae. Paraphyses filiformes, septatae, inferne 2 μ diam, superne usque 3.0 μ diam inflatae, leniter uncinatae, non guttulate.

HOLOTYPE: In fimo vaccino, near Santa Cruz, Costa Rica, 14 Sept. 1964, *Carroll* F49064 (FLAS).

Apothecia smooth, white to yellowish, discoid to lenticular, broadly attached to the substrate, 1.0–1.6 mm in diam, margins somewhat inrolled; excipulum of a textura globulosa below, cells 12–15 μ in diam, pale yellow, marginal cells slightly inflated apically, scarcely distinguishable from paraphyses, more than 100 μ long; asci eight-spored, cylindrical, 80–100 \times 8–12 μ , rounded above, terminating in a short stalk below; ascospores hyaline uniseriate, narrowly ellipsoid, 8.5–10.0 \times 4.0–5.0 μ , each with a de Bary bubble; paraphyses filiform, septate, 2.0 μ below, inflated to 3.0 μ and very slightly uncinuate at their apices, without oil guttules.

HABITAT: On dung.

TYPE: On cow dung, near Santa Cruz, Costa Rica, 14 Sept. 1964, *Carroll* F49064 (FLAS).

SPECIMENS EXAMINED: COSTA RICA: TYPE. PANAMA: El Valle, on horse dung, 1 April 1945, *Meyer* (NY). UNITED STATES: Florida: Sebring, Highlands Hammock, on rabbit dung, 29 June 1970, *Kimbrough* F49068 (FLAS).

COMMENTS: This species is distinguished by the narrowly ellipsoid ascospores and the long flexuous cells of the ectal excipulum.

13. *Coprotus niveus* (Fuckel) comb. nov.

Figs. 45–47

= *Ascobolus niveus* Fuckel, Hedwigia, 5: 4. 1866. (non *Ascobolus niveus* Quel., Ass. Fr. Avanc. Sci. (Congr. Reims, 1880), 9: 674. 1881.)

= *Rhyarobolus niveus* (Fckl.) Sacc., Syll. Fung. 8: 544. 1889.

= *Ascozonus niveus* (Fckl.) Boud., His. Class. Discom. Eur. 79. 1907.

Apothecia translucent to white, drying slightly yellowish, 0.2–0.5 mm diam, sessile, cupulate to discoid, hymenia rounded off by protruding asci; excipulum in the medullary and basal areas of a textura globulosa to angularis, cells slightly cyanophilous, becoming elongated along the margins, 12–15 \times 6–7 μ ; asci 64-spored, very broadly clavate, 80–130 \times 30–60 μ dome-shaped above, terminating in a short stalk below, operculum prominent; ascospores hyaline, thin-walled, irregularly arranged, ellipsoid, 8.0–12.0 \times 4.0–7.0 μ , each with one de Bary bubble; paraphyses filiform, septate, hyaline, simple or branched, 2.0 μ below, enlarged to 2.5 μ at apices, without oil guttules.

HABITAT: On dung of various animals.

TYPE: On dog dung, Mt. Rabenkopf, Germany, winter 1866, *Fuckel* (based on *Fuckel's* (1866) description and illustration).

SPECIMENS EXAMINED: CANADA: Alberta: Hinton, on horse dung, 2 Aug. 1962, *Cain* 39029 (TRTC). Ontario: Muskoka Dist.: Uffington, on cow dung, 27 Aug. 1932, *Cain* 40014 (TRTC). Nipissing Dist.: L. Timagami, on porcupine dung, 21 Aug. 1933, *Cain* 40013 (TRTC). Peel Co.: Palgrave, on rabbit dung, 7 Oct. 1962, *Cain* 41629 (TRTC). Quebec: L. St. Joseph, Pine R., on cow dung, 26 Aug. 1938, *Cain* 46235 (TRTC). EUROPE: ITALY (North): Lombardi, Sante Sofia, near Papian, on cow dung, autumn?, *Cavara* (MICH). MEXICO: Oaxaca: Matias Romero, on cow dung, 16 Aug. 1961, *Cain* 46209 (TRTC).

UNITED STATES: Florida: Gainesville: on cow dung, 10 Oct. 1970, *Kimbrough* F48957 (FLAS); on rabbit dung, 1 Feb. 1970, *Kimbrough* F48893 (FLAS); near Newman's Lake, on rabbit dung, 17 Feb. 1969, *Kimbrough* F48439 (FLAS). Nebraska: Lancaster Co.: Lincoln, University of Nebraska, on horse dung, 8 Apr. 1934, *Walker* (NY).

COMMENTS: Considerable confusion has surrounded this species. The majority of the collections thus far examined have been placed either in *Rhyarobolus crustaceus* (Fckl.) Rehm or *Ascozonus niveus* (Fckl.) Boud. It is clear from *Fuckel's* (1866) description that *R. crustaceus*, with its dark brown apothecia and its apparent lack of opercula in the asci, is a member of the genus *Thielebolus* sensu *Kimbrough* & *Korf* (1967), which will be treated in a later paper. It is also quite evident that *Ascobolus niveus* (*Fuckel*, 1866), with a clearly distinguishable operculum, is not a species of *Ascozonus*. The presence of an operculum, de Bary bubbles in the ascospores, and the morphological and chemical nature of the asci and excipulum are identical with those of *C. glauccellus*, *C. sexdecimsporus*, and other species of this genus.

14. *Coprotus ochraceus* (Cr. & Cr.) Larsen

Figs. 48–51

= *Ascobolus ochraceus* *Crouan* & *Crouan*, Fl. Finist. 57. 1867.

= *Ascophanus ochraceus* (Cr. & Cr.) *Boudier*, Ann. Sci. Nat. V, 10: 247. 1869.

= *Coprotus ochraceus* (Cr. & Cr.) *Larsen*, Dan. Bot. Tidsskr. 66: 1–32. 1971.

= *Ascophanus subgranuliformis* *Rehm*, In *Voss*, Verh. Zool.-Bot. Ges. Wien, 37: 224. 1887.

= *Ascophanus violascens* var. *falcatus* *Velenovsky*, Monogr. Discom. Bohem. 360. 1934.

= *Ascophanus bilobus* *Velenovsky*, Monogr. Discom. Bohem. 360. 1934.

= *Ascophanus velenovskij* *Svrček*, Ceska Mycol. 13: 95. 1959. Not. *Ascophanus velenovskij* *Kanouse* 1947.

= *Ascophanus hyalino-niveus* *Svrček*, Ceska Mycol. 26: 29. 1972.

Apothecia pale yellow to orange, at first cupulate later becoming discoid, sessile, 0.5–1.5 mm diam; excipulum of a textura angularis to globulosa, medullary area of thin-walled cells 25–30 μ diam, marginal cells elongated, 6.0–8.0 \times 12–14 μ ; walls somewhat thickened,

slightly yellowish; asci eight-spored, cylindrical, 110–150 \times 12–18 μ , rounded above, tapering below; ascospores uniseriate, broadly ellipsoid, 14.0–18.0 \times 9.0–11.0 μ , smooth, hyaline to slightly yellowish, each with one de Bary bubble; paraphyses filiform, septate, with numerous yellowish oil guttules in the cytoplasm, 1.5 μ diam below, inflated at apices to 4–5 μ and slightly uncinuate.

HABITAT: On dung of various animals.

TYPE: On cow dung, Finistère, France, *Crouan* A2411 (CONC). (Le Gal (1961), examined the type and noted that 4 July 1857 was penciled on the package.) *Van Brummelen* (1967) stated that the type specimen was destroyed by insects (CONC-A2411).

SPECIMENS EXAMINED: BERMUDA: Hungary Bay, on dung, 14 Jan. 1926, *Seaver* and *Whetzel* (NY). BRAZIL: State of Bahia: S of Canudos, on cow dung, 18 July 1962, *Eiten* and *Eiten* (NY). CANADA: Nova Scotia: Colchester Co.: Upper Brookside, on cow dung, 3 July 1931, *Welsh* (MICH). Quebec: Gaspé-Sud: Bonaventure Is., on cow dung, 15 Aug. 1959, *Cain* 36427 (TRTC). EUROPE: FRANCE: on cow dung, July 1913, *Lorton*, *Boudier* Herb. (PC). CZECHOSLOVAKIA: Bohemia: Mnichovice, Aug. 1928, *Velenovsky*, as *A. bilobus* (PR). Mnichovice, *Velenovsky*, as *A. lacteus* sensu *Vel.* = *A. velenovskij* *Svrček* (PR). PAKISTAN: Karachi, near Hub R. Dam, on camel dung, 28 Dec. 1966, *Ahmed*. PUERTO RICO: Westshore, on cow dung, 24 Jan. 1923, *Seaver* and *Chardon* (NY). UNITED STATES: California: Catalina Is., on dung, Mar. 1904, *Baker* (NY). Idaho: Seven Devils Mts., Heaven's Gate, on cow dung, 21 July 1954, *Smith* (MICH). Iowa: Iowa City, on cow dung, Aug. 1915, (NY). Oregon: Rhododendron, on cow dung, 4 Oct. 1944, *Smith* (MICH).

COMMENTS: *Coprotus ochraceus* has frequently been confused with *Coprobria granulata*. In *Coprobria granulata*, the cells of the excipulum are larger than those of *Coprotus ochraceus* and are cyanophilous as well. In addition, the walls of the ascospores in *C. granulata* possess longitudinal cyanophilous striations, a feature which is absent in *C. ochraceus*. When grown under subdued light, the apothecia of *C. ochraceus* often appear less pigmented than when grown under more intense light. *Velenovsky* (1934) included the very faintly pigmented form in *Coprotus lacteus* despite the larger size of the ascospores.

15. *Coprotus rhyarobiooides* (Heimerl) Kimbr.

Figs. 52-54

≡ *Ascophanus rhyarobiooides* Heimerl, *Jahr. k.k. Ober-Realisch. Bezirke Sechshaus*, Wien, 15: 22. 1889.

≡ *Rhyarobius ascophanooides* Sacc., *Syll. Fung.* 10: 33. 1892.

≡ *Coprotus rhyarobiooides* (Heimerl) Kimbr., *Am. J. Bot.* 54: 22. 1967.

Apothecia smooth, white, discoid, sessile, roughened by protruding asci, 0.1-0.3 mm diam; *excipulum* composed of two to four layers, of a *textura angularis* to *globulosa* in lower part, cells around margins hyaline, thin-walled, elongated, 3-4 × 8-10 μ; *asci* usually 32-spored (sometimes slightly more), typically 10-15 per apothecium, 120-175 × 50-75 μ, apices dome-shaped, each with a broad operculum, attenuated below, walls 3.0-4.0 μ in thickness; *ascospores* hyaline, smooth, irregularly arranged, ellipsoid, 13.5-17.5 × 7.0-8.0 μ, each with one de Bary bubble; *paraphyses* numerous, filiform, septate, without oil guttules, 1.8-2.0 μ diam below, slightly uncinuate, and frequently branched toward apices.

HABITAT: On deer and rabbit dung.

TYPE: On deer dung, Pressbaum, Austria, winter 1888, Heimerl.

SPECIMENS EXAMINED: EUROPE: ENGLAND: Kew, on rabbit dung, Dec. 1900, *Masse* (NY). UNITED STATES: Florida: Gainesville, San Felasco Hammock, on rabbit dung, 21 Mar. 1969, Kimbrough F48559 (FLAS).

16. *Coprotus sexdecimsporus* (Cr. & Cr.) Kimbr.

Figs. 55-58

≡ *Ascobolus sexdecimsporus* Crouan & Crouan, *Ann. Sci. Nat.* IV, 10: 195. 1858.

≡ *Ascophanus sexdecimsporus* (Cr. & Cr.) Boud., *Ann. Sci. Nat.* V, 10: 247. 1869.

≡ *Rhyarobius sexdecimsporus* (Cr. & Cr.) Sacc., *Syll. Fung.* 8: 541. 1889.

≡ *Coprotus sexdecimsporus* (Cr. & Cr.) Kimbrough, *Am. J. Bot.* 54: 22. 1967.

Apothecia smooth, sessile, globose to cupulate, eventually discoid, translucent to white, drying yellowish, 0.5-1.0 mm diam; *excipulum* of a *textura angularis* to *globulosa*, basal cells up to 12 μ in length, marginal cells of five or six layers, slightly elongated, 10-12 × 5-6 μ; *asci* 16-spored, broadly clavate, 85-140 × 20-30 μ, rounded above, with a broad operculum,

attenuated below; *ascospores* smooth, hyaline to slightly yellowish, broadly ellipsoid, 11.0-16.0 × 8.0-10.0 μ, each with one de Bary bubble; *paraphyses* filiform, septate, 1.5 μ below, inflated to 2.0-2.2 μ and strongly uncinuate at apices, provided with a variable number of oil guttules.

HABITAT: On dung of animals.

TYPE: Non-existent. Originally on cow dung, Brest, Finistère, France, Crouan Bros. (Le Gal (1961) redescribed the fungus after examining two collections in the Crouan Herbarium.)

SPECIMENS EXAMINED: CANADA: Ontario: Leeds Co.: Chaffey's Locks, on deer dung, 28 Sept. 1963, *Luck-Allen* 40658 (TRIC). Muskoka Dist.: Germania, on rabbit dung, 27 Aug. 1932, *Cain* 40022 (TRIC). York Co.: Nashville, on horse dung, 17 Nov. 1963, *Cain* 40657 (TRIC). EUROPE: FRANCE: Toulon: Fenouillet, on sheep dung, Apr. 1927, *Grelet* (PC). ENGLAND: Bristol, on horse dung, *Broome*, *Rab. Fung. Eur.* 781, D4626 (CUP). MEXICO: Hidalgo, N of Zimapan, on burro dung, 21 Aug. 1961, *Cain* 38799 (TRIC). UNITED STATES: Colorado: Larimer Co.: Roosevelt Natl. Forest, Buckhorn, on porcupine dung, 17 Aug. 1957, *Cain* 41614 (TRIC). New York: Delaware Co.: Oneonta, on deer dung, 21 Sept. 1963, *Luck-Allen* 40079 (TRIC). Wyoming: Platte Co.: 12 mi SW of Wheatland, on cow dung, 1 Sept. 1964, *Cain* 42748 (TRIC).

COMMENTS: The presence of 16 spores per ascus led Saccardo (1889) to place this species in *Rhyarobius*. Boudier (1869) and Heimerl (1889) both recognized that there were certain multisporous species whose spores differed from those of *Rhyarobius* and they placed them in *Ascophanus*. *Coprotus sexdecimsporus* is morphologically similar to *C. ochraceus* with the exception of ascus size and spore number. *Coprotus duplus* sp. nov. also possesses 16 spores but may be distinguished from *C. sexdecimsporus* by its smaller asci and ascospores, its more uncinuate paraphyses, and generally less pigmented apothecia.

17. *Coprotus vicinus* (Boud.) comb. nov.

Figs. 59, 60

≡ *Ascophanus vicinus* Boudier, *Ann. Sci. Nat.* V, 10: 246. 1869.

≡ *Ascophanus violascens* Velenovsky, *Monogr. Discom.* Bohem. 360. 1934.

Apothecia sessile, smooth, cream to yellowish, globose to discoid, 0.3-0.7 mm diam; *excipulum* of three or four layers, of a *textura angularis* to *globulosa* below, cells up to 14 μ, thin-walled and slightly yellowish, marginal cells elongated, 8.0-11.0 × 6.0-8.0 μ; *asci* eight-spored, broadly clavate, 65-100 × 20-28 μ, rounded to almost truncate above, terminating in a short stalk below; *ascospores* biseriolate or crowded toward the apex, broadly ellipsoid 17.0-25.0 × 11.0-14.0 μ, hyaline to pale yellow, each with one de Bary bubble; *paraphyses* filiform, septate, hyaline to yellowish, sparingly branched, inflated at the apices to 5 μ, provided with yellowish guttules.

HABITAT: On dung of various animals.

TYPE: On cow dung, Forêt de Carnelle, Montmorency, 1869, Boudier (PC).

SPECIMENS EXAMINED: EUROPE: CZECHOSLOVAKIA: Bohemia: Mnichovice, on cow dung, 1926, Velenovsky (PR). FRANCE: TYPE.

COMMENTS: This species appears to be intermediate between *C. granuliformis* and *C. ochraceus* with respect to ascus size and morphology; however, the spores in *C. vicinus* are larger than those in the two species mentioned above. A number of collections of *Coprobia*, *Iodophanus*, and immature *Ascobolus* species have at various times been identified as *A. vicinus*.

18. *Coprotus winteri* (Marchal) Kimbr.

Figs. 61-65

≡ *Rhyarobius winteri* Marchal, *Mem. Soc. Roy. Bot. Belg.* 24: 71. 1885.

≡ *Coprotus winteri* (March.) Kimbr., *Am. J. Bot.* 54: 22. 1967.

Apothecia scattered to gregarious, globose to cupulate, translucent to white, glabrous, 0.4-0.5 mm diam, hymenium roughened by protruding asci; *excipulum* of three or four layers, of a *textura angularis* to *globulosa*, marginal cells hyaline, thin-walled, elongated, 10-12 × 4.0-5.0 μ; *asci* approximately 256-spored, broadly cylindrical, 160-210 × 45-55 μ, rounded above, attenuated below; *ascospores* irregularly crowded, ellipsoid, 10.0-11.0 × 5.0-6.0 μ each with a de Bary bubble; *paraphyses* hyaline, filiform, septate, branched above, 1.0-2.0 μ in width below, slightly larger at apices, uncinuate.

HABITAT: On dung of "damarum" and horse.

TYPE: On dung of "damarum," Teuveren, Belgium, autumn 1885, Marchal (not examined),

based upon Marchal's (1885) descriptions and Pl. IV, Figs. 1-7.

SPECIMEN EXAMINED: UNITED STATES: Colorado, on horse dung, 24 Aug. 1910, *Seaver & Bethel* (NY).

COMMENTS: It is clear from Marchal's (1885) description and illustrations that *R. winteri* belongs to the genus *Coprotus*. The white, cylindrical apothecia, operculate asci, numerous paraphyses, and the de Bary bubble in each ascospore (referred to by him as a "distinct nucleus") are features that exclude it from other coprophilous genera.

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EXPLANATION OF FIGS. 1-65

- FIGS. 1-3. *Coprotus albidus*. Fig. 1. An ascus with 32 young spores, $\times 1000$. Fig. 2. Broad operculum of empty ascus, $\times 1000$. Fig. 3. Septate, slightly inflated paraphyses, $\times 1000$. FIGS. 4-7. *Coprotus aurora*. Fig. 4. Mature apothecia on dung, $\times 30$. Fig. 5. An ascus with ascospores, $\times 800$. Fig. 6. Branched, septate, and highly pigmented paraphyses, $\times 800$. Fig. 7. Section of apothecium showing excipulum and young ascus, $\times 800$. FIGS. 8, 9. *Coprotus breviscicus*. Fig. 8. Section of apothecium showing excipulum, $\times 800$. Fig. 9. Ascus, ascospores, and paraphyses, $\times 800$. FIGS. 10-12. *Coprotus destrinoideus*. Fig. 10. Section of apothecium showing excipular cells, $\times 800$. Fig. 11. Paraphyses hyaline, $\times 800$. Fig. 12. Ascus with ascospores, $\times 1000$.
- FIGS. 13-15. *Coprotus disculus*. Fig. 13. Section of apothecium showing excipular cells and a young ascus, $\times 800$. Fig. 14. An ascus with ascospores, $\times 800$. Fig. 15. Hyaline, slightly inflated paraphyses, $\times 800$.
- FIGS. 16-19. *Coprotus doplus*. Fig. 16. Mature apothecia on dung, $\times 30$. Fig. 17. Filiform, uncinuate paraphyses, $\times 800$. Fig. 18. Sixteen-spored ascus, $\times 800$. Fig. 19. Slightly cyanophilous excipulum, $\times 800$. FIGS. 20-24. *Coprotus glaucellus*. Fig. 20. Mature apothecia on dung, $\times 30$. Fig. 21. Asci with ascospores, $\times 1000$. Fig. 22. Section of apothecium showing excipulum and young ascus, $\times 800$. Fig. 23. Filiform, uncinuate paraphyses, $\times 800$. Fig. 24. Excipulum, surface view, $\times 800$. FIGS. 25-29. *Coprotus granuliformis*. Fig. 25. Apothecia on dung, $\times 30$. Fig. 26. Section of apothecium showing globose excipular cells, $\times 800$. Fig. 27. Ascus with ascospores, $\times 800$. Fig. 28. Young ascus with thick-walled spores, $\times 800$. Fig. 29. Strongly inflated paraphyses, $\times 800$.
- FIGS. 30-33. *Coprotus lacteus*. Fig. 30. Cyanophilous excipulum in cotton blue, $\times 800$. Fig. 31. Mature ascus with ascospores, $\times 100$. Fig. 32. A two-spored ascus, $\times 1250$. Fig. 33. Inflated, slightly uncinuate paraphyses, $\times 800$. FIGS. 34-36. *Coprotus leucopocillum*. Fig. 34. Filiform, septate paraphyses, $\times 800$. Fig. 35. Section of apothecium showing excipulum, $\times 800$. Fig. 36. Mature ascus with ascospores, $\times 800$. FIGS. 37-40. *Coprotus luteus*. Fig. 37. Ectal excipulum, $\times 800$. Fig. 38. Guttulate, filiform, paraphyses, $\times 800$. Fig. 39. Young, gymnocarpic apothecium, $\times 400$. Fig. 40. Ascus, ascospores, and paraphyses, $\times 800$. FIGS. 41-44. *Coprotus marginatus*. Fig. 41. Section of apothecium with elongated marginal excipular cells and globose medullary cells, $\times 800$. Fig. 42. Section of apothecium showing broad, lenticular habit, $\times 100$. Fig. 43. Mature ascus with narrowly cylindrical spores, $\times 1000$. Fig. 44. Hyaline, slightly uncinuate paraphyses, $\times 1000$.
- FIGS. 45-47. *Coprotus niveus*. Fig. 45. Young apothecium on dung, $\times 30$. Fig. 46. Section of apothecium showing elongated excipular cells, $\times 800$. Fig. 47. A mature 64-spored ascus, $\times 800$. FIGS. 48-51. *Coprotus ochraceus*. Fig. 48. Section of apothecium showing excipulum, $\times 800$. Fig. 49. Paraphysis with oil guttules, $\times 800$. Fig. 50. A mature ascus with ascospores, $\times 800$. Fig. 51. Young ascus with thick-walled ascospores, $\times 800$. FIGS. 52-54. *Coprotus rhyarobloides*. Fig. 52. Section of apothecium with excipulum and ascus, $\times 400$. Fig. 53. Hyaline, slightly inflated paraphyses, $\times 800$. Fig. 54. A mature ascus with 32 spores, $\times 800$. FIGS. 55-58. *Coprotus sexdecimsporus*. Fig. 55. Apothecia on dung, $\times 30$. Fig. 56. Paraphyses with tiny oil guttules, $\times 800$. Fig. 57. A mature ascus with ascospores, $\times 800$. Fig. 58. Section of apothecium showing excipulum and young ascus, $\times 800$.
- FIGS. 59-60. *Coprotus vicinus*. Fig. 59. Young, thick-walled asci, young ascospores, and paraphyses, $\times 800$. Fig. 60. Mature ascus, with ascospores, $\times 800$. FIGS. 61-65. *Coprotus winteri*. Fig. 61. Section through excipulum, $\times 250$. Fig. 62. Squash mount of apothecium showing young and mature asci, $\times 400$. Fig. 63. Filiform, septate paraphyses, $\times 800$. Fig. 64. Young, thick-walled ascus, $\times 800$. Fig. 65. Apex of mature ascus showing line of dehiscence for operculum (arrows), $\times 800$.

NOTE: Figs. 1-65 follow.





