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 apothèces de très petite taille, translucides, blancs ou jaunes, portant des asques 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'asque, (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 asques, 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 Pseudoascoboleae (Kimbrough 1966*b*) 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 multispored 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 Theleboloideae 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* Vel. 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

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these organisms were outlined by Kimbrough (1966*a*). 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). Starback'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 uninucleate at least in those of *C. glaucelleus* 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 1966*a*; 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 uncinate, 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

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), *Tricholoulus zukalii* (Heimerl) Kimbr. (Kimbrough 1966*a*), 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) *Rhyparobius*. The eight-spored forms may resemble species of *Iodophanus*, *Coprobia*, *Peziza*, *Psilopezia*, *Pyronema*, *Octospora* (= *Humaria*), or young specimens of *Thecotheus*. The nonamyloid 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 *Coprobia*, 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 *Rhyparobius*, *Ascozonus* (= *Streptotheca*), 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. glaucelleus*, 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 maturity; *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 biseriate, or irregularly crowded, 8–256 or more per ascus, smooth, elliptical, 6.0–25.0 × 3.5–12.0 μ, thin-walled, some with yellowish contents, most at maturity with a conspicuous de Bary bubble; *paraphyses* filiform, septate, uncinate 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. luteus*
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 × 10–15 μ, ascospores 12–14 × 6.0–8.5 μ ..... *C. aurora*
D. Apothecia yellow, asci 45–55 × 15–18 μ, ascospores 10–13 × 6.5–8.5 μ ..... *C. breviascus*

E. Ascospores 15–18 × 9.0–10.5 μ, asci 110–150 × 12–18 μ, paraphyses slightly inflated ..... *C. ochraceus*
E. Ascospores 17–25 × 11–14 μ, asci 65–100 × 20–28 μ, paraphyses slightly uncinate above ..... *C. vicinus*

F. Asci eight-spored ..... G
F. Asci with more than eight spores ..... M

G. Asci broadly clavate, paraphyses strongly inflated at their apices ..... *C. granuliformis*
G. Asci cylindric, 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 uncinate at their apices ..... *C. glaucellus*
I. Asci longer, paraphyses slightly inflated above ..... J

J. Asci 65–85 × 15–20 μ, marginal cells of excipulum not extremely elongate ..... *C. lacteus*
J. Asci 80–100 × 8–12 μ, marginal cells of excipulum long, flexuous, and capitate ..... *C. marginatus*

K. Spores mostly 14 μ or longer ..... *C. leucopocillum*
K. Spores less than 14 μ long L

L. Spores narrowly ellipsoid, 12–13.5 × 5–8 μ, asci 75–90 × 10–15 μ, apothecia white ..... *C. disculus*
L. Spores broader, 11–13 × 7.5–10 μ, asci 80–125 × 18–24 μ, apothecia with yellowish border ..... *C. dextrinoideus*

M. Asci 16-spored ..... N
M. Asci with more than 16 spores ..... O

N. Ascospores 11–16 × 8–10 μ, asci 85–140 μ long ..... *C. sexdecimsporus*
N. Ascospores 7.5–10 × 4.0–6.5 μ, asci 70–90 μ long ..... *C. duplus*

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.....*C. albidus*
P. Spores more than 13 μ long, asci larger.....*C. rhyparobioides*

Q. Asci approximately 64-spored.....*C. niveus*
Q. Asci approximately 256-spored.....*C. winteri*

1. *Coprotus albidus* (Boud.) Kimbr. Figs. 1–3
≡ *Rhyparobius albidus* Boudier, Bull. Soc. Mycol. Fr. 4: 49. 1887.
≡ *Coprotus albidus* (Boud.) Kimbrough, Am. J. Bot. 54: 22. 1967.
= *Rhyparobius tenacellus* Phillips, Grevillea, 19: 74. 1891.
= *Rhyparobius mirabilis* Vel., Discom. 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 × 20–30 μ, with a broad operculum; *ascospores* irregularly disposed, 10.0–12.5 × 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 "*Rhyparobius*" belong to *Coprotus*. They are *C. albidus* and *C. rhyparobioides*. 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. Discom. 54. 1847.
= *Ascophanus auranticus* Velen., Monogr. Discom. 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 × 8.0–12.0 μ, with carotenoid pigments; *asci* eight-spored, cylindrical to clavate, 65–90 × 10–15 μ, rounded above, attenuated below; *ascospores* uniseriate to biseriate, broadly ellipsoid, 12.0–14.0 × 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 uncinate, 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). Illincis: 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 uncinate and highly pigmented paraphyses.

3. ***Coprotus breviascus*** (Vel.) comb. nov. Figs. 8, 9
≡ *Ascophanus breviascus* Velenovsky, Monogr. Discom. 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 × 20–28 μ, abruptly attenuated at base; *ascospores* biseriate, 12.0–16.0 × 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, uncinate 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 Höhnel* (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 siccatus. Excipulum e cellulis angularibus vel globosis (textura angulari vel textura globulosa), luteis, cyanophilis compositum. Cellulae marginatae elongatae, 8.0–15.0 × 3.0–6.0 μ. Asci octospori, cylindracei, 80–125 × 18–24 μ, ad apicem late rotundati, ad basem attenuati. Ascosporae late ellipsoideae, uniseriatae, raro biseriatae, 11.0–13.0 × 7.5–10.0 μ, "de Bary bubble" praeditae. Paraphyses filiformes, septatae, valde ramosae, hyalinae, guttulatae.

HOLOTYPUS: In fimo vaccino, Puerto Rico, West Indian 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 × 3.0–6.0 μ; *asci* eight-spored, cylindric, rounded above, attenuated below, 80–125 × 18–24 μ; *ascospores* uniseriate, rarely biseriate, broadly ellipsoid, 11.0–13.0 × 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 × 6–10 μ. Asci octospori (rare quantuorspori), cylindracei, 75–90 × 10–15 μ, ad apicem rotundati, ad basem attenuati. Ascosporae anguste ellipsoideae, uniseriatae, raro biseriatae, 12.0–13.5 × 5.0–8.0 μ, dilute luteae, "de Bary bubble" praeditae. Paraphyses filiformes, septatae, hyalinae, non guttulatae, superne incrassatae usque 4.0 μ diam et leniter uncinatae.

HOLOTYPUS: In fimo cervino, Bergen Swamp, near Rochester, New York, 5 Oct. 1947, *Rogerson* (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 × 6–10 μ; *asci* eight-spored, rarely four-spored; cylindric, 75–90 × 10–15 μ, rounded above, attenuated below; *ascospores* uniseriate, sometimes biseriate, narrowly ellipsoid, 12.0–13.5 × 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 uncinate.

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.: Chaffeys Locks, on deer dung, 28 Sept. 1963, *Luck-Allen* 41256 (TRTC). Oxford Co.: Benwell Swamp, Gobles, on deer dung, 13 Sept. 1943, *Cain* 45718 (TRTC). Quebec: Mt. Albert, Lac Cascapedia, on horse dung, 21 Aug. 1957, *Bigelow* 63011 (DAOM). EUROPE: ITALY (N): Lombardy, on cow dung, 23 Aug. 1907, *Coll*? D6831 (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 × 4–6 μ. Asci sexdecimspori, anguste cylindracei, 70–90 × 10–18 μ. Ascosporae ellipsoideae, biseriatae, leves, hyalinae vel leniter luteae, 7.5–10.0 × 4.6–6.5 μ, "de Bary bubble" praeditae. Paraphyses filiformes, septatae, non ramosae vel rarissimo ramosae, ad basem 1.8–2.0 μ crassae, superne usque 1.8–2.0 μ diam, guttulatae.

HOLOTYPUS: 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 × 4–6 μ; *asci* 16-spored, narrowly cylindric, 70–90 × 10–18 μ, dome-shaped to almost truncate above; *ascospores* biseriate, smooth, hyaline to faintly yellowish, ellipsoid, 7.5–10.0 × 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* 41884 (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, Paradis 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 cylindric 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 × 6.0–8.0 μ below, marginal cells elongated up to 10 μ; *asci* eight-spored, cylindric, rounded above, attenuated below, terminating in a short stalk, 40–55 × 8–12 μ; *ascospores* uniseriate to biseriate, ellipsoid, 7.5–9.0 × 4.5–5.5 μ, each with one de Bary bubble; *paraphyses* hyaline, filiform, septate, strongly uncinate 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. Saseje wun, 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.: Poshkokogan 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 discomycetes. 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.) Kimbr. Figs. 25–29

≡*Ascobolus 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.

=*Ascobolus 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 nonelongated, almost isodiametric, reaching 10–12 μ diam, with cell walls slightly thickened and pigmented with age; *asci* eight-spored, broadly clavate, 40–55 × 15–30 μ, almost truncate above, sharply tapering to a short stalk below; *ascospores* mostly biseriate, broadly ellipsoid, 9.0–15.0 × 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.: Chaffeys 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, *Höhnel* 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. roselus*) (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 × 4–5 μ; *asci* eight-spored, cylindrical to clavate, 65–85 × 15–20 μ, rounded or dome-shaped above, attenuated below; *ascospores* uniseriate to biseriate, smooth, hyaline, ellipsoid, 8.0–10.0 × 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 uncinate 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.: Chaffeys 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 uncinate 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 cellulis (textura angularis vel textura globulosa). Cellulae basilares isodiametricae, 8–15 μ diam. Cellulae marginales elongatae, 5–8 × 12–15 μ leniter dextrinoideae. Asci octospori, late cylindracei, 80–110 × 15–22 μ, inferne in stipitem brevem attenuati. Ascosporae late ellipsoideae biseriatae, 14.0–18.0 × 7.5–11.5 μ, hyalinae vel

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

HOLOTYPUS: 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 × 12–15 μ, sometimes slightly dextrinoid; *asci* eight-spored, broadly cylindric, 80–110 × 15–22 μ, rounded to slightly truncate above, terminating in a short stipe below; *ascospores* broadly ellipsoid, biseriate, 14.0–18.0 × 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 uncinate.

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 cylindric 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 cellulis coloratis (textura angulari vel textura globulosa). Cellulae basilares rotundatae, usque 10–14 μ diam. Cellulae marginales angustae, elongatae, 4–5 × 8–12 μ. Asci octospori, cylindracei, 60–85 × 10–15 μ, superne rotundati, inferne in stipitem brevem attenuati. Ascosporae ellipsoideae, uniseriatae, 8.0–10.5 × 5.0–6.5 μ, tenuiter tunicatae, "de Bary bubble" praeditae. Paraphyses filiformes, septatae, non ramosae vel rare ramosae, guttulatae, superne usque 3.5 μ diam inflatae, leniter uncinatae.

HOLOTYPUS: 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 × 8–12 μ; *asci* eight-spored, cylindric, 60–85 × 10–15 μ, rounded above, terminating in a short stipe; *ascospores* hyaline, thin-walled, mostly uniseriate, ellipsoid, 8.0–10.5 × 5.0–6.5 μ, each with one de Bary bubble; *paraphyses* filiform, septate, simple or sparingly branched, slightly uncinate 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 cylindric 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 exspansa, 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 × 8–12 μ, ad apicem rotundati, inferne in stipitem brevem attenuati. Ascosporae anguste ellipsoideae, uniseriatae, 8.5–10.0 × 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 guttulatae.

HOLOTYPUS: 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, cylindric, 80–100 × 8–12 μ, rounded above, terminating in a short stalk below; *ascospores* hyaline uniseriate, narrowly ellipsoid, 8.5–10.0 × 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 uncinate 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.)

≡*Rhyparobius 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 roughened 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 × 6–7 μ; *asci* 64-spored, very broadly clavate, 80–130 × 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 × 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 *Rhyparobius 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 *Thelebolus* 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. glaucellus*, *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 velenovskyi* Svrček, Ceska Mycol. 13: 95. 1959. Not. *Ascophanus velenovskyi* 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 × 12–14 μ; walls somewhat thickened, slightly yellowish; *asci* eight-spored, cylindric, 110–150 × 12–18 μ, rounded above, tapering below; *ascospores* uniseriate, broadly ellipsoid, 14.0–18.0 × 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 uncinate.

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, *Wehmeyer* (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. velenovskyi* 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 *Coprobia granulata*. In *Coprobia 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 rhyparobioides* (Heimerl) Kimbr. Figs. 52–54

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

≡*Rhyparobius ascophanoides* Sacc., Syll. Fung. 10: 33. 1892.

≡*Coprotus rhyparobioides* (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 uncinate, 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, *Massee* (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.

≡*Rhyparobius 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 uncinate 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.: Chaffeys Locks, on deer dung, 28 Sept. 1963, *Luck-Allen* 40658 (TRTC). Muskoka Dist.: Germania, on rabbit dung, 27 Aug. 1932, *Cain* 40022 (TRTC). York Co.: Nashville, on horse dung, 17 Nov. 1963, *Cain* 40657 (TRTC). 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 (TRTC). UNITED STATES: Colorado: Larimer Co.: Roosevelt Natl. Forest, Buckhorn, on porcupine dung, 17 Aug. 1957, *Cain* 41614 (TRTC). New York: Delaware Co.: Oneonta, on deer dung, 21 Sept. 1963, *Luck-Allen* 40079 (TRTC). Wyoming: Platte Co.: 12 mi SW of Wheatland, on cow dung, 1 Sept. 1964, *Cain* 42748 (TRTC).

COMMENTS: The presence of 16 spores per ascus led Saccardo (1889) to place this species in *Rhyparobius*. Boudier (1869) and Heimerl (1889) both recognized that there were certain multispored species whose spores differed from those of *Rhyparobius* 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 uncinate 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* biseriate 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

≡*Rhyparobius 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 cylindric, 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, uncinate.

HABITAT: On dung of "damarum" and horse.

TYPE: On dung of "damarum," Tevueren, 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, cylindric 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, × 1000. Fig. 2. Broad operculum of empty ascus, × 1000. Fig. 3. Septate, slightly inflated paraphyses, × 1000. FIGS. 4–7. *Coprotus aurora*. Fig. 4. Mature apothecia on dung, × 30. Fig. 5. An ascus with ascospores, × 800. Fig. 6. Branched, septate, and highly pigmented paraphyses, × 800. Fig. 7. Section of apothecium showing excipulum and young ascus, × 800. FIGS. 8, 9. *Coprotus breviascus*. Fig. 8. Section of apothecium showing excipulum, × 800. Fig. 9. Ascus, ascospores, and paraphyses, × 800. FIGS. 10–12. *Coprotus dextrinoideus*. Fig. 10. Section of apothecium showing excipular cells, × 800. Fig. 11. Paraphyses hyaline, × 800. Fig. 12. Ascus with ascospores, × 1000.

FIGS. 13–15. *Coprotus disculus*. Fig. 13. Section of apothecium showing excipular cells and a young ascus, × 800. Fig. 14. An ascus with ascospores, × 800. Fig. 15. Hyaline, slightly inflated paraphyses, × 800. FIGS. 16–19. *Coprotus duplus*. Fig. 16. Mature apothecia on dung, × 30. Fig. 17. Filiform, uncinate paraphyses, × 800. Fig. 18. Sixteen-spored ascus, × 800. Fig. 19. Slightly cyanophilous excipulum, × 800. FIGS. 20–24. *Coprotus glaucellus*. Fig. 20. Mature apothecia on dung, × 30. Fig. 21. Asci with ascospores, × 1000. Fig. 22. Section of apothecium showing excipulum and young ascus, × 800. Fig. 23. Filiform, uncinate paraphysis, × 800. Fig. 24. Excipulum, surface view, × 800. FIGS. 25–29. *Coprotus granuliformis*. Fig. 25. Apothecia on dung, × 30. Fig. 26. Section of apothecium showing globose excipular cells, × 800. Fig. 27. Ascus with ascospores, × 800. Fig. 28. Young ascus with thick-walled spores, × 800. Fig. 29. Strongly inflated paraphyses, × 800.

FIGS. 30–33. *Coprotus lacteus*. Fig. 30. Cyanophilous excipulum in cotton blue, × 800. Fig. 31. Mature ascus with ascospores, × 100. Fig. 32. A two-spored ascus, × 1250. Fig. 33. Inflated, slightly uncinate paraphysis, × 800. FIGS. 34–36. *Coprotus leucopocillum*. Fig. 34. Filiform, septate paraphyses, × 800. Fig. 35. Section of apothecium showing excipulum, × 800. Fig. 36. Mature ascus with ascospores, × 800. FIGS. 37–40. *Coprotus luteus*. Fig. 37. Ectal excipulum, × 800. Fig. 38. Guttulate, filiform, paraphyses, × 800. Fig. 39. Young, gymnocarpic apothecium, × 400. Fig. 40. Ascus, ascospores, and paraphyses, × 800. FIGS. 41–44. *Coprotus marginatus*. Fig. 41. Section of apothecium with elongated marginal excipular cells and globose medullary cells, × 800. FIG. 42. Section of apothecium showing broad, lenticular habit, × 100. Fig. 43. Mature ascus with narrowly cylindric spores, × 1000. Fig. 44. Hyaline, slightly uncinate paraphyses, × 1000.

FIGS. 45–47. *Coprotus niveus*. Fig. 45. Young apothecium on dung, × 30. Fig. 46. Section of apothecium showing elongated excipular cells, × 800. Fig. 47. A mature 64-spored ascus, × 800. FIGS. 48–51. *Coprotus ochraceus*. Fig. 48. Section of apothecium showing excipulum, × 800. Fig. 49. Paraphysis with oil guttules, × 800. Fig. 50. A mature ascus with ascospores, × 800. Fig. 51. Young ascus with thick-walled ascospores, × 800. FIGS. 52–54. *Coprotus rhyparobioides*. Fig. 52. Section of apothecium with excipulum and ascus, × 400. Fig. 53. Hyaline, slightly inflated paraphyses, × 800. Fig. 54. A mature ascus with 32 spores, × 800. FIGS. 55–58. *Coprotus sexdecimsporus*. Fig. 55. Apothecia on dung, × 30. Fig. 56. Paraphyses with tiny oil guttules, × 800. Fig. 57. A mature ascus with ascospores, × 800. Fig. 58. Section of apothecium showing excipulum and young ascus, × 800.

FIGS. 59–60. *Coprotus vicinus*. Fig. 59. Young, thick-walled asci, young ascospores, and paraphyses, × 800. Fig. 60. Mature ascus, with ascospores, × 800. FIGS. 61–65. *Coprotus winteri*. Fig. 61. Section through excipulum, × 250. Fig. 62. Squash mount of apothecium showing young and mature asci, × 400. Fig. 63. Filiform, septate paraphyses, × 800. Fig. 64. Young, thick-walled ascus, × 800. Fig. 65. Apex of mature ascus showing line of dehiscence for operculum (arrows), × 800.

NOTE: Figs. 1–65 follow.

PLATE I