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Materials for a hypogeous mycoflora of the Great Basin and adjacent cordilleras of the Western United States II. Two subemergent species *Cortinarius saxamontanus*, *sp. nov.*, and *C. magnivelatus*, plus comments on their evolution

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Abstract: *Cortinarius magnivelatus* and *C. saxamontanus*, *sp. nov.*, two species of subemergent taxa from the Western United States, are described and illustrated. Two hypotheses on the evolution of these subemergent taxa are also presented. A hypothesis of recent parallel evolution of these taxa is better supported by distribution data and glacial pluvial history of the Great Basin than the alternative hypothesis suggesting present populations are relicts of older widely distributed populations of these taxa.

Key Words: Basidiomycotina, Cortinariaceae, evolution, false-truffle, hypogeous fungi, biogeography, systematics

INTRODUCTION

This is the second in a series containing materials for a hypogeous mycoflora of the Great Basin and adjacent cordilleras (Fogel and Pacioni, 1989). The region has received little attention from mycologists despite its potential for studies of fungal biogeography, evolution, and coevolution. The Great Basin itself is an area of 714 854 square km as defined by Cronquist et al. (1972). Composition of the vegetation and availability of suitable ectomycorrhizal hosts for hypogeous fungi in the region reflects the interaction of environmental optima for species, soil factors, preglacial flora, extent of glacial advance, pluvial lake levels, and subsequent reinvasion from glacial refugia (Wells, 1983). Another significant factor affecting the presence of hypogeous fungi is the efficiency of mycophagous rodents, and perhaps insects, in spore dispersal.

Cortinarius is a large, mostly ectomycorrhizal genus, producing typical epigeous basidiomes releasing ballistospores to the atmosphere. Seven hypogeous taxa have been described, however, that are characterized by having very short stipes and persistent veils. Spores are forcibly discharged but deposited on the inside of

the veil rather than in the air. The basidiomes of these hypogeous taxa are better described as subemergent, rather than hypogeous, because they often betray their presence by creating humps in the duff ca 5 cm high or less, where they have failed to emerge.

The slight morphological differences in the stipe and veil of these subemergent basidiomes raises the question of whether they represent unique species or simply aberrant basidiomes arrested in development by environmental factors. Low light levels, for instance, have been reported to cause aberrant basidiomes in *Flammulina velutipes* (Fr.) Singer (Gruen, 1982), *Panus tigrinus* (Bull. ex Fr.) Singer (Bobbitt and Crang, 1975), and *Psilocybe mutans* McKnight (McKnight, 1955). Drought has been identified as a common factor in all of the habitats producing subemergent *Cortinarius* species (Bougher and Malajczuk, 1986; Thiers and Smith, 1969; Watling, 1980) and has been identified as causing developmental arrest in mushrooms (Savile, 1968). Thiers and Smith (1969) concluded that these fungi are not “freaks” because their extensive observations of *C. bigelowii* Thiers & Smith showed that it has a definite fruiting period in the subalpine white-bark pine zone of Idaho. My observations on *C. saxamontanus* support their conclusion. This species has a large geographic range (Nevada to Colorado), definite fruiting period from late June to late July, and occurs in subalpine and upper montane stands of *Abies* and *Pinus*. In addition, I have collected *C. saxamontanus* from the same locality over a period of several weeks when stipitate mushrooms were fruiting, suggesting subemergent basidiomes are not drought-induced/arrested stages in development, or other mushrooms occurring at the same time would also have been aberrant. In addition, I have observed that stipitate mushrooms failing to emerge produce a spore print on the soil or duff below an expanded cap. Spores are deposited inside the veil of subemergent taxa.

Subemergent taxa may result from a small number of mutations occurring early in development with a profound effect on subsequent development and morphology. Takemaru and Kamada (1969) have described an elongationless mutant of *Coprinus cinereus* (Schaeff ex Fr.) S. F. Gray produced by chemical mutagenesis in which cap expansion and spore development are normal, but stipe elongation is arrested. An expansionless mutant is also described by the same authors

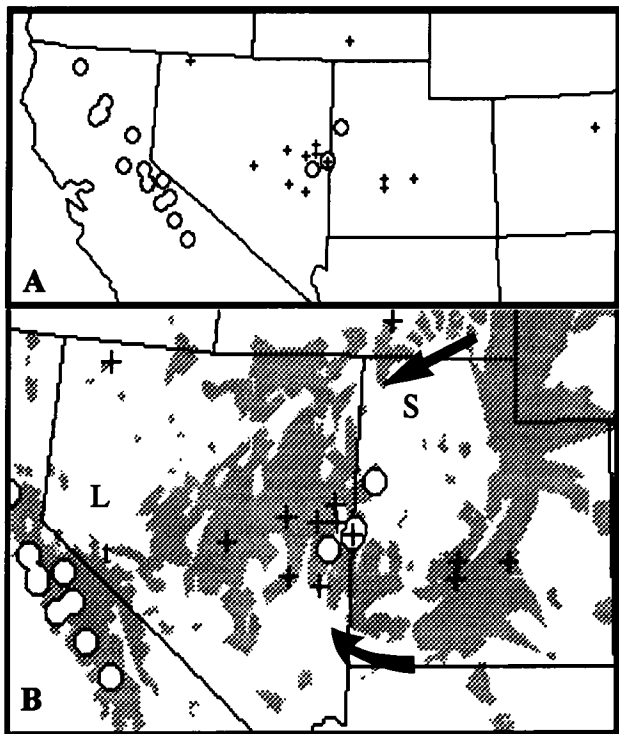


FIG. 1A, B. Distribution of *Cortinarius magnivelatus* (o) and *C. saxamontanus* (+). A. Distribution of examined material. Note the generally western distribution of *C. magnivelatus* and the eastern distribution of *C. saxamontanus* with overlap of the ranges in eastern Nevada. B. Intermountain Region between the Sierra Nevada and Wasatch Range with elevations higher than 1820 m shaded. Arrows indicate invasion routes along forest islands for conifers (Wells, 1983), mycophagous rodents, and hypogeous fungi around Pleistocene Lake Bonneville Basin (S) into the central Great Basin from the East. Dispersal from the Sierra Nevada to the east is blocked by a low elevation trough (t) of the Pleistocene Lake Lahontan Basin (L).

in which stipe elongation is normal, but cap development is arrested. I am unaware of any described veil mutants and cannot predict whether the thickened and/or membranaceous veil present in subemergent taxa is due to developmental effects, i.e., decreased stipe elongation and/or cap expansion prolonging time for veil development, or gene mutation.

Subemergent *Cortinarius* taxa may represent an early step in the morphological reduction series found in a number of basidiomycete families with morphologies grading from stipitate, through secotioid, to hypogeous forms (Thiers, 1984). The rate of morphological reduction in one clade has been shown to be rapid relative to molecular change, suggesting selection is heavy against forms intermediate in morphology (Bruns et al., 1989).

Distribution data for the taxa described here (FIG. 1) suggest two hypotheses for their evolution. *Corti-*

narius magnivelatus is found in the Sierra Nevada and Siskiyou Mountains of California and in the Snake and Schell Creek Ranges of Eastern Nevada. *Cortinarius saxamontanus* is also found in Central and Eastern Nevada, but its range extends east across Utah to the Front Range of the Central Colorado Rocky Mountains. The first hypothesis addressing the origin of subemergent basidiomes in the Great Basin is based on the assumption that the present subemergent populations are relicts of an older widely distributed subemergent population associated with similarly widely distributed ectomycorrhizal trees. The close relationship of present day floras of isolated Nevada mountain ranges to the Rocky Mountain flora, rather than to the Sierra Nevada, indicates that the host ranges, and consequently the ranges of their associated subemergent taxa, have not been contiguous for some time (Harper et al., 1978). In fact, the separation of tree populations has been sufficiently long for the evolution of vicariant subspecies pairs of five ectomycorrhizal conifers in the Rocky Mountains and Sierra Nevada. Evidence from packrat midden analysis suggests isolation of the parent conifers occurred ≤ 2.5 million years ago in the early Pleistocene (Thompson and Mead, 1982).

Wells (1983) summarizes packrat midden data showing that the ranges of the putative ectomycorrhizal hosts have changed dramatically in response to glaciation. He proposes that as the climate cooled tree distributions were displaced downward and that habitats suitable for lower montane conifers (Douglas-fir, pinyon pine, ponderosa pine, white fir) were covered by pluvial lakes. At maximum downward displacement the ranges of the upper montane conifers were dissected by the pluvial lakes, blocking dispersal of spores by mycophagous rodents. The presently greatly dissected ranges of ectomycorrhizal host trees seriously impedes overland dispersal via mycophagous rodents between California and Colorado. Lower montane conifers have slowly reinvaded the Central Great Basin from the NE and SE along two corridors represented by forest islands today (FIG. 1). Insufficient time has elapsed for *C. saxamontanus* to reach the Central Great Basin from either the Front Range in Colorado, or the closer Wasatch-Uinta Mountains complex in Utah through spore dispersal by mycophagous rodents. Present populations then must be relictual implying that these taxa evolved millions of years ago even though their close morphological similarity to mushrooms produced by *Cortinarius* indicates a recent origin.

The second hypothesis, recent parallel origin, assumes that the ancestral mushroom taxa were widely distributed as is typical of wind-dispersed taxa. The prevailing Westerlies across the Great Basin favor wind

dispersal of spores from West to East. After being widely disseminated by wind, the range of the ancestral mushroom producing species and their ectomycorrhizal tree associates was fragmented by elevational lowering of vegetation zones and flooding of lower montane habitats during glaciation, perhaps as recently as the last pleniglacial 12 500 to 20 000 yr BP (Wells, 1983). Regional drought resulting from the warming climate of the Holocene (8000–10 000 yr BP) selected against the mushroom producing ancestors, favoring individuals with a very similar, or the same, subemergent morphology (developmental mutants) in the isolated populations. The result was parallel evolution of the "same" taxon more or less simultaneously from the same or very similar parental genotypes in response to identical environmental selection. The Eastern Nevada records of *C. magnivelatus* support the hypothesis that its mushroom ancestor was widely distributed as wind-borne spores by Westerlies since the dispersal of its tree hosts and rodents is blocked from the west by an extension of the pluvial Lake Lahontan basin, a long, wide trough at 600–1500 m elevation. The distribution of *C. saxamontanus* is also most easily explained by wind dispersal of its mushroom ancestor followed by parallel evolution given the circuitous route created by the distribution of its ectomycorrhizal tree associates between the Central Great Basin and the Front Range of Colorado (FIG. 1). In addition, the isolated population in northwestern Nevada supports wind dispersal over dispersal by mycophagous rodents.

A test of the two different hypotheses on the age of the subemergent *Cortinarius* taxa awaits a molecular clock study comparing rates of evolution of subemergent, secotiid, and hypogeous taxa in the same clade.

MATERIALS AND METHODS

Methods of collection and study of the morphological and anatomical features are essentially those of Smith (Smith and Zeller, 1966). Spores were measured in freehand sections mounted in Melzer's reagent. Lengths and widths of 20 basidiospores randomly selected from a mature basidiome in each collection were measured for statistical comparisons. Color names are given as the ISCC-NBS names (Kelly and Judd, 1965). Herbarium names are abbreviated according to Holmgren et al. (1990).

Distribution maps were created by overlaying coordinates of localities on a digitized base map using C-map Geographic Information System personal computer software (Center for Remote Sensing, Michigan State University). Photostyler (Aldus Corp.) was used to shade contour polygons.

TAXONOMIC TREATMENT

Cortinarius magnivelatus Dearness *ex* Fogel, *sp. nov.*
FIGS. 1–3

Earlier references.—*Pholiota magnivelata* Dearness in Morse, *Mycologia* 33: 367. 1941. (nomen nudum, Art. 36.1). *Cortinarius magnivelatus* (Dearness in Morse) Thiers & Smith, *Mycologia* 61: 534. 1969. (nomen nudum, Art. 36.1).

Illustrations.—*Mycologia* 33: 368. 1941, Figs. 1–7 (as *Pholiota magnivelata*); *Mycologia* 61: 530. 1969, Fig. 2 (as *Cortinarius magnivelatus*).

Pileus 30–65 mm latus, bombycinus ad tomentosus, albus demum fuscus ochrofulvus, depressus demum umbonatus, ad marginem cortina crassa alba pertinace junctus. Lamellae albus demum ochrofulvus, tenuissimae. Stipes 20–60 × 10–30 mm, ad bases bulbosus vel cylindricus. Basidiosporae 9–14 × 6–8 μm, verrucosus ad regulosae. TYPUS: California, General Grant National Park (fide label) Jul. 1927, E. E. Morse (UC 638890).

Pileus 30–65 mm broad, convex becoming plano-convex expanding with undulate outline, sometimes becoming shallowly depressed to umbonate; surface moist to dry; usually appearing glabrous when young, occasionally silky-appressed fibrillose, becoming innately fibrillose to somewhat tomentose, white when young, becoming pale yellow (89) to moderate yellow (87), then moderate orange yellow (71) to dark orange yellow (72) with age or bruising; margin incurved to strongly decurved; attached to the stipe by a membranaceous veil during all stages of development. *Lamellae* adnate to shallowly depressed; white to light orange yellow (70) in young basidiomes becoming near brownish orange (54) to strong yellowish brown (74) or finally strong yellowish brown (74) when mature, unchanging when bruised; thin, not fragile, even when dry; several tiers of lamellae present at margin; abundantly forked near and at the stipe; margin entire becoming locally eroded at maturity, entirely covered by veil. *Veil* persistent as a heavy, thick membrane, becoming somewhat radially shredded at the pileus margin on drying, remaining attached to the stipe, satiny-white, spores deposited inside. *Stipe* 15–60 × 10–30 mm broad at apex, typically somewhat bulbous at base, occasionally equal to tapering slightly, context white, unchanging. *Taste* and *odor* not distinctive.

Basidiospores 8.5–11 (–14) × 5–8 μm (FIG. 2), grand mean length of 700 spores 9.9 ± 0.6 μm, grand mean width 6.1 ± 0.3 μm, grand mean length to width ratio 1.63 ± 0.01 , inequilateral in profile with laterally placed hilar apex, ellipsoid in face view, minutely verrucose to rugulose, light orange yellow (70), immature spores dextrinoid, spore wall ≤ 0.5 μm thick (FIG. 3). *Basidia* four-spored, 27–40 × 7–10 μm, clavate, hy-

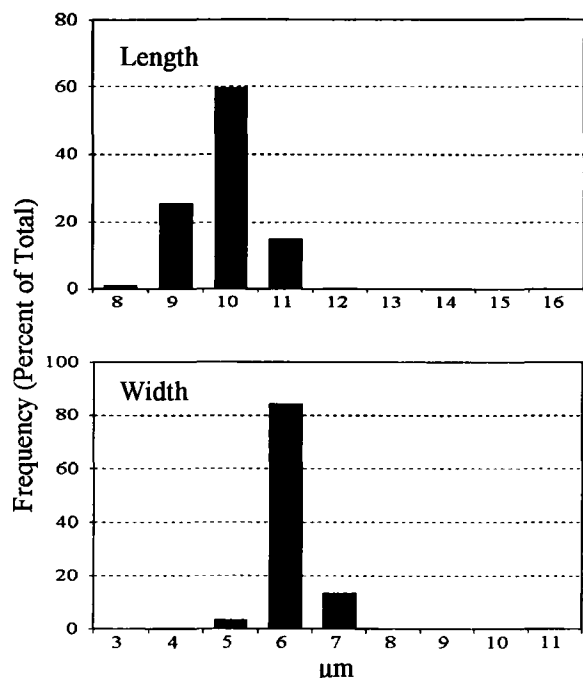


FIG. 2. Distributions of *Cortinarius magnivelatus* spore lengths and widths. Grand mean length of 35 collections = 9.9 ± 0.06 μm . Grand mean of spore width = 6.1 ± 0.03 μm .

aline, thin-walled, base truncate, lacking clamp connection. Sterigmata 2–4 \times 1.5–2 μm , conical, straight to slightly curved. Pleurocystidia not seen; cheilocystidia reviving poorly, 18–23 \times 4–6 μm hyaline, thin-walled, cylindric, ventricose or nearly filamentous.

Pileus cuticle differentiated only as a narrow layer of compactly interwoven hyphae 4–5 (–8) μm in diam obscured by organic debris. Not reviving well in older herbarium specimens. Context composed of interwoven, hyaline 4–10 (–15) μm diam hyphae. Stipe composed of dextrinoid, appressed parallel hyphae 3–5 μm in diam., a few 10 μm in diam, clamp connections common, no cystidia reviving. Veil composed of hyaline, dextrinoid, thin-walled, appressed, parallel hyphae 3–6 μm in diam. Clamp connections abundant.

Putative mycorrhizal hosts.—*Abies concolor* (Gord. & Glend.) Lindl., *A. bifolia* A. Murray, *A. magnifica* A. Murr., *Picea engelmannii* Parry, *Pinus lambertiana* Dougl., *P. ponderosa* Laws.

Phenology.—Fruiting from May to August at elevations above ca 1525 m in California, 2380 m in Nevada (FIG. 1).

Material examined.—USA. CALIFORNIA: General Grant National Park (as cited on label, now a part of Sequoia National Park), July 1927, *H. Bailey* (UC 659990); Sequoia National Park, 18 Jun. 1931, *H. E. Parks* (UC 64993); Amador Co., *H. D. Thiers* 17250 (SFSU); Butte

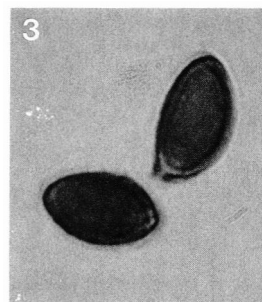


FIG. 3. Basidiospores of *Cortinarius magnivelatus* (Fogel F2280) stained in Melzer's reagent, \times 1600.

Co., 7 Jul. 1943, *E. B. Copeland* (MICH), 24 Jun. 1944 (UC 695913), 6 Jun. 1936, *H. F. Copeland* (UC 640656); 7 Aug. 1938 (UC 638886), 9 Jul. 1953 (UC 977177, MICH); Calaveras Co., *H. D. Thiers* 16744 (SFSU); El Dorado Co., 5 May 1940, *F. Taylor* (UC 652842); Fresno Co., *H. D. Thiers* 13357, 35016, 46091 (all SFSU); Mariposa Co., *R. Halling* 1392 (SFSU); Shasta Co., Lassen Volcanic National Park, *Showers* 4414 (all SFSU); Sierra Co., *D. E. Desjardin* 3363 (SFSU), *R. Halling* 4381, 4392, 4655, 5289, 5333, 6478 (all NY), *H. Saylor* 1928, 1929, 3170 (all SFSU), *H. D. Thiers* 47708, 49855, 52183 (all SFSU); Siskiyou Co., *W. B. Cooke* 50434 (SFSU, UC 1463207); Stanislaus Co., *H. D. Thiers* 17109 (SFSU); Tehama Co., *H. D. Thiers* 51695 (SFSU); Tuolumne Co., Jun. 1945, *C. R. Quick* (UC 695618), *H. D. Thiers* 10466, 11239, 12653, 16920, 19809 (all SFSU). NEVADA: White Pine Co., *Fogel* F2280, F3782, F4343, F4357 (all MICH). UTAH: Juab Co., *Fogel* F4442 (MICH).

Cortinarius magnivelatus and *C. wiebeae* Thiers & Smith are similar in having white basidiomes, a white membranous veil, and becoming darker on handling. Thiers and Smith (1969) state that *C. magnivelatus* is distinguished from *C. wiebeae* by having white to very pallid lamellae when young, not hazel; firm, resistant lamellae rather than fragile and eroded; and an annulus that is tough and persistent, never becoming free. They also noted that *C. magnivelatus* has slightly larger spores, differently shaped cheilocystidia, and forking of the lamellae.

The lamellae and cheilocystidia characters are difficult to verify in dried material and I found the previously reported differences in spore size to be insignificant. The size of basidia is a much more useful character for separating the two taxa. *Cortinarius magnivelatus* has larger basidia (27–40 \times 7–10 μm) than *C. wiebeae* (17–22 \times 6–8 μm).

Cortinarius saxamontanus* Fogel, *sp. nov. FIGS. 1, 4–7

Pileus 32–100 mm latus, siccus, glabellus, testaceus ad umbrinus, convexus demum planus, ad marginem cortina

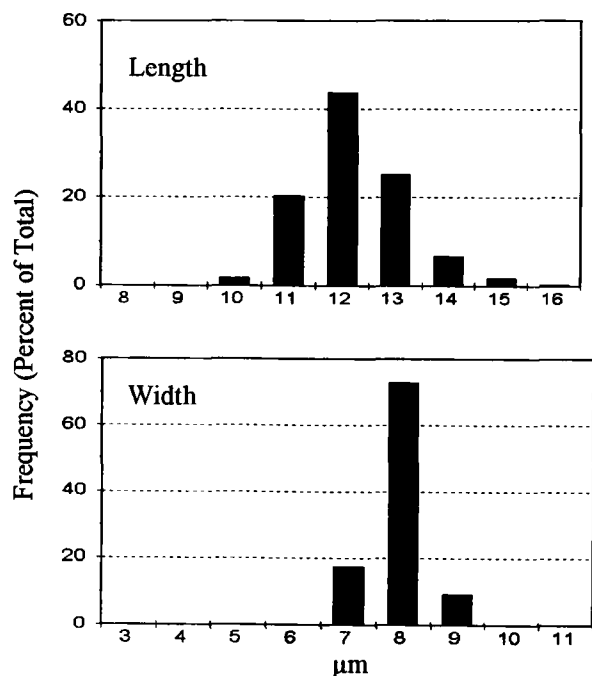


FIG. 4. Distributions of *C. saxamontanus* spore lengths and widths. Grand mean length of 23 collections = 12.2 ± 0.1 μm . Grand mean of spore width = 7.9 ± 0.1 μm .

crassa fibrosus aureus pertinae junctus. Lamellae testaceous ad umbrinus, tenuissimae fragilis. Stipes 15–75 \times 9–25 mm, aureus, bases bulbosus, 15–45 mm latus. Basidiosporae (10–) 11–3 (–15) \times 7–9 μm , tuberculato–rugosae. TYPUS: NEVADA: White Pine Co., Wheeler Peak Campground, Humboldt National Forest (now Great Basin National Park), W of Baker, 38°59'N Lat., 114°20'W Long., elevation 10 200 ft (3080 m), 30 June 1981, R. Fogel F2535 (MICH).

Pileus (FIGS. 6, 7) 22–100 mm broad, flat to convex, expanding with undulate outline, surface apparently dry, glabrous, margin light yellow (86), occasionally light greenish yellow (101), disk brownish orange (54), pale yellow (89), light orange yellow (70), or strong brown (55), not changing color on handling or exposure; margin recurved, attached to a tough, thickened, fibrillar, light yellow (86) cortina which stretches from the pileus to the stipe and is persistent even in the fully expanded basidiome. Cortina rupturing during drying, fragments remaining attached to stipe. *Lamellae* normally developed, brownish orange (54) or strong yellow brown (74) to strong brown (55), unchanging when bruised, thin, brittle, 7–10 mm deep, appearing decurrent in small basidiomes, free in large basidiomes, several tiers of lamellulae present entirely covered by tough veil. *Veil* persistent as a dense layer of radial fibrils, light yellow (86), spores deposited on inner surface of veil. *Stipe* 15–75 \times 9–25 mm, short, glabrous, light yellow (86), context white becoming very pale violet (213) to very light purple (221), not

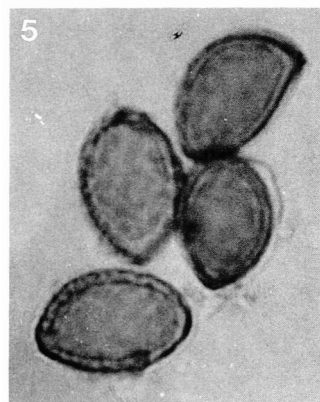


FIG. 5. Basidiospores of *C. saxamontanus* (Fogel F3600) stained in Melzer's reagent, \times 1600.

changing in larger basidiomes. Base bulbous, 15–45 mm broad. *Odor* fungoid, not distinctive. *Taste* not noted.

Basidiospores (10–) 11–13 (–15) \times 7–9 μm (FIG. 4), grand mean length of 460 spores 12.2 ± 0.1 μm , grand mean width 7.9 ± 0.1 μm , grand mean length/width ratio 1.56 ± 0.02 , inequilateral in profile with laterally placed hilar apex, subellipsoid to broadly ellipsoid in face-view ($L/W = 1.47$); tuberculate–rugose, some warts anastomosing to appear as short lines, deep orange (51), immature spores dextrinoid, spore wall ≤ 0.5 μm thick (FIG. 5). *Basidia* four-spored, 33–37 \times 6–11 μm , clavate, hyaline, thin-walled, base truncate lacking clamp connection. Sterigmata 3–4 \times 2 μm , conical, straight to slightly curved. Cystidia lacking, although sterile basidioles present 25–30 \times 10 μm , clavate, hyaline, thin-walled.

Pileus lacking a clearly differentiated cutis, hyphae at surface appressed, periclinal, thin-walled, hyaline and 4–6 μm in diam. Diffuse deep pink (6) to deep reddish orange (38) pigment present in KOH. Hyphae in some areas of the surface dextrinoid. Apparently foreign hyphae present on surface due to contact with duff. No cystidia reviving. Context composed of hyaline, thin-walled 7–9 μm diam hyphae; cells becoming inflated to 35–50 \times 20–25 μm . Clamp connections absent. *Stipe* composed of parallel, dextrinoid, thin-walled 5–6 μm diam hyphae lacking clamp connections. No cystidia reviving. *Veil* composed of hyaline, thick-walled, 4–5 μm diam hyphae aggregated into tough strands. Clamp connections frequent, pronounced.

Putative mycorrhizal hosts.—*Pinus* and *Abies* species; host records include: *Abies bifolia*, *A. concolor*, *A. lasiocarpa* (Hook.) Nutt., *Pinus contorta* Dougl., *P. flexilis* James, and *P. longaeva* D. K. Bailey.

Phenology.—Fruiting from late June to late July at



FIG. 6, 7. Photographs of fresh *Cortinarius saxamontanus* basidiomes. 6. Forest litter removed to show heavy veil on basidiome and litter adhering to cap (Fogel F2242). Veil partly damaged in removing litter. Bulbous base damaged by mycetophilid fly larvae. Heavy spore deposit present inside veil. Bar = 20 mm. 7. Veil of larger sporocarp removed to show gills. Longitudinal section of smaller sporocarp shows bulbous base and short stipe (Fogel F2252). Bar = 20 mm.

2500–3050 m elevation in Colorado, Nevada, and Utah (FIG. 1). Subemergent, pushing duff up ca 5 cm (FIG. 6).

Material examined.—USA. COLORADO: Boulder Co., Fogel F2242, F2252. IDAHO: Cassia Co., Fogel F3922. NEVADA: Humboldt Co., Fogel F4507; Lincoln Co., Fogel F3745, F3746, F3747; Nye Co., Fogel F3456, F3943; White Pine Co., Fogel F2535, F2578, F3534, F3600, F3777, F3783, F4355, F4375, F4408. UTAH: Beaver Co., Fogel F2554, F2556, F3717; Juab Co., Fogel F3364; Piute Co., Fogel F3686; Wayne Co., Fogel F3875, F3876 (all MICH).

Notes.—*Cortinarius saxamontanus* and *C. bigelowii* both

have coarse, fibrous veils, but differ macroscopically. *Cortinarius bigelowii* is light brown, has a white unchanging context, and very short (10 mm), bulbous stipe. *Cortinarius saxamontanus* is light yellow with a brownish orange to strong brown disk, a white context that often changes to very pale violet in the stipe in young basidiomes, and a longer (15–55 mm), bulbous stipe. Spore size is also a useful microscopic character for separating these taxa.

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