

# HYPOGEOUS CORTINARII

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## SUMMARY

The discovery of four new hypogeous species of *Cortinarius*, *C. wiebeae*, *C. bigelowii*, *C. velatus* and *C. verrucisporus*, which have permanent or long persisting membranous universal veils, are reported. The possible phylogenetic relationships of these species with other agarics and gastromycetes are discussed. *Pholiota magnivelatus* Morse has been found to be a member of this group and is, therefore, transferred to *Cortinarius*.

During the course of collecting Cortinarii in North America over a period of many years we have amassed a great deal of information on the genus, but of all the "new" species encountered those described here deserve some special comment. To us they represent Cortinarii in which the stipe elongates only slightly or not at all. They appear to be of special significance in contributing toward an understanding of the relationships between *Cortinarius* and the genus *Thaxterogaster* (Singer and Smith, 1958), a gastromycete so closely resembling *Cortinarius* in the aspect of the basidiocarps that it is often mistaken for one. The problem of whether *Cortinarius* is the ancestor of *Thaxterogaster* or vice-versa is still a subject of debate. The proper solution of this problem hinges on a complete restudy of all brown-spored hypogeous Hymenogastreales and further field work to ascertain the evolutionary tendencies in *Cortinarius* as these relate to gastromycetous taxa and to other agarics. Singer and Smith (1960), in an elaborate study of the group designated as the Asterosporales Malençon & Heim (or the Astrogastreales series to use a less formal category), concluded that because there were no connections at the agaric level between the Russulaceae and the other families of Agaricales it was logical

to regard the Russulaceae as derived from gastromycetous ancestors. Since the same clear-cut situation does not hold for the Cortinariaceae in relation to other agaric families, to solve the problem one must not only know the agaric genera intimately but the gastromycetous ones as well. Such knowledge has never been brought to bear on this problem. For years the junior author has been working toward making a substantial contribution in this area by studying *Cortinarius* in North America, a life-time's work in itself, and by investigating such related genera as *Galerina* (Smith and Singer, 1964), *Phaeocollybia* (Smith, 1957) and, most recently, *Hymenogaster* (Smith, 1966) and related genera.

The key to the whole relationship appears to us to be concerned with the Cortinari. The odd species described here illustrate one of the situations frequently encountered in the genus, namely arrested basidiocarp development, which is usually not so pronounced as in the present examples. The question in point is whether a detailed "mapping" of the evolutionary tendencies in *Cortinarius*, as can be ascertained from existing species, will give a reasonable answer to the question of which way evolution is progressing—to or away from the gastromycetous forms. Whether or not the results will be conclusive one way or the other remains to be seen, but by the very technique of "mapping" perhaps one can keep his mind free from preconceived ideas and in the end arrive at a conclusion which is relatively unbiased. At the same time a better perspective would be possible in evaluating the gene-pool represented by the taxa studied.

If one proceeds from the general to the specific, the first subject to be considered in regard to the evolutionary problems in *Cortinarius* is the ecology of its species and the overall aspects of the genus. There are about 700 species (estimated) in North America, and they are forest-inhabiting fungi with fewer than a dozen having a lignicolous habitat. None of these is a cause of primary wood decay. Further, by far the majority behave in their fruiting patterns as if they were mycorrhizal-formers. The genera of agarics most closely related to *Cortinarius* show variability in the above noted pattern. *Galerina* (Smith and Singer, 1964) has been shown to connect clearly to *Cortinarius* but its ecology shows a less specialized substrate relationship. The species vary from lignicolous to terrestrial or bryicolous, but apparently few, if any, mycorrhizal-formers exist. *Hebeloma* is almost certainly a mycorrhizal-forming genus but probably *Phaeocollybia* is not. *Gymnopilus* is mostly lignicolous. *Thaxterogaster*, as far as known species are concerned, is apparently mycorrhiza-forming. Thus, the

mycorrhizal habit, central to *Cortinarius* and evident in some of its "satellite" genera, is present in the presumably related gastromycetous genus. A connection from *Thaxterogaster* to *Hymenogaster* on the basis of spore and peridial characters is also well established, and Smith's data (1966) support the conclusion that *Hymenogaster* is a mycorrhiza-forming genus just as are *Cortinarius* and *Thaxterogaster*. In other words, physiological specialization, as well as spore morphology and spore pigmentation, can be traced "to" or "from" the gastromycetes "to" or "from" *Cortinarius*.

The next question pertains to the gross morphology of the fruiting body and the problems of progressing from one type of basidiocarp to the other (gastroid and agaricoid). In the first place it should be kept in mind that in nature the basidiocarps of both are initiated at the line between the mineral soil and the duff. This observation applies especially to the larger *Cortinarii* and not so much to the galerinoid species. In the subgenus *Bulbopodium* it is particularly pronounced, and here we have a special type of agaricoid basidiocarp which, if it remains unexpanded, resembles a gastromycetous type and is "hypogaeous." In the fruitings of *Bulbopodia* which we both have observed it is not at all uncommon to find a few out of a hundred carpophores in one fruiting which do not expand but still shed their spores, the latter accumulating on the unbroken cortina. From this one is tempted to ask if species are known in which the basidiocarps characteristically remain unexpanded, and which show other modifications to indicate that they are not simply freaks of species with normally expanding basidiocarps. The species described in this paper appear to be such species. The veil is either weakly or strongly membranous instead of cobwebby. In some the hymenophore is practically powdery when dried which is a gastromycetous rather than an agaric feature. All species appear to be members of the Agaricales belonging to the genus *Cortinarius* because spore prints have been obtained or at least observed on the cortina. There is a point that needs checking however, and this is: are the spores observed as a deposit on the inner surface of the veil actually discharged from the basidia or are they released as old basidia disintegrate? We have obtained spore deposits from more than one of these species and believe them to be true agarics. The situation, best exemplified by *C. wiebeae*, needs further checking in view of the very small basidia and the tendency for the hymenophore to be powdery to some extent when dry. Here, as in *Hymenogaster* and *Thaxterogaster*, there is a tendency for masses of spores to adhere to the hymenial surface. Yet a deposit of spores was obtained, and de-

posits were observed on the interior surface of the veil. How is one to classify *C. wiebeae* and other similar species? On the basis of the tendency observed in the other species, and by the spores collected as a deposit, it is here described as a *Cortinarius*, but certainly one which shows progressions toward the level of the gastromycetes as represented by *Thaxterogaster*. The overall ecological data support this: all species described here are alpine to subalpine fungi, and in such a habitat even well-known species have stipes tending to be shorter than those of basidiocarps of the same species collected at lower elevations. Because of the somewhat intermediate position of these fungi, it seems worthwhile to present data on them and locate them on the "map" of the Cortinariaceae as somewhat reduced agaric forms. Possibly they are agarics recently derived from *Thaxterogaster*, but we do not subscribe to this. To us who have seen the fungi in question they are Cortinarii in which the stipe elongation has been repressed and the veil considerably strengthened.

***Cortinarius wiebeae* Thiers & Smith, sp. nov.**

Pileus 6–13 cm latus, siccus, albus, convexus demum planus, lamellae ferruginosae, latae, tenuissimae; stipes 40–90 mm longus, ad apicem circa 4 cm latus, deorsum 5 cm latus, siccus, albidus, subannulatus; spores 9–11 × 6–7.5  $\mu$ , verruculosae. Typum legit prope Mt. Hood, Oregon. 8 Juni, 1958. Etna Wiebe. In herbarium University of Michigan conservatum.

Pileus 6–13 cm broad, broadly convex becoming nearly plane or finally slightly depressed, surface dry and silky, with radiating fibrils, white, becoming somewhat tan colored on handling and on drying, margin long remaining inrolled. Context white, firm, confluent with stipe, 3 cm thick near stipe; taste mild; odor faintly radish-like.

Lamellae "hazel" (ferruginous) when fresh and young, dark rusty brown from spores in age, sinuate, broad (up to 13 mm), narrowed toward both extremities, crowded, numerous tiers of lamellulae present, very thin and very fragile, edges eroded.

Stipe 4–9 cm long, 2.4–4 cm at apex, up to 5 cm thick at base, clavate, whitish when fresh within and without, solid, surface dry and coated with white fibrils from the copious veil ending in a submembranous annulus. Veil persistently extending from pileus margin to stipe and only in age shredding radially (hence development of the gills is angiocarpic until the spores mature).

Spore deposit "Sanford's brown"; spores 9–11 × 6–7.5  $\mu$ , subelliptic in face view, obscurely inequilateral in profile, warty-rugulose. Basidia 4-spored, hyaline in KOH, 17–22 × 5.5–7  $\mu$ . Pleurocystidia none. Cheilocystidia scattered, hyaline, filamentose, 3–4  $\mu$  in diam. Gill

trama of parallel, hyaline, thin-walled, scarcely inflated hyphae  $4-8\ \mu$  in diam. Pileus trama lacking a differentiated cutis, hyphae at surface appressed, all hyphae thin-walled, hyaline, smooth,  $3-12\ \mu$  in diam, some cells inflated, others  $4-9\ \mu$  broad and uninflated. Clamp connections rare and very inconspicuous.

Gregarious and hypogeous under a fir tree, Camas Corral, Mt. Hood, Ore. June 8, 1958. Etna Wiebe collector. Type. (MICH.) Known only from the type collection.

*Observations.*—The ferruginous gills on a white *Inoloma* are practically unique, but the small basidia and heavy veil in addition make the species most unusual. The gills are so thin that when the specimens are dried they powder to some extent, enough so that the package

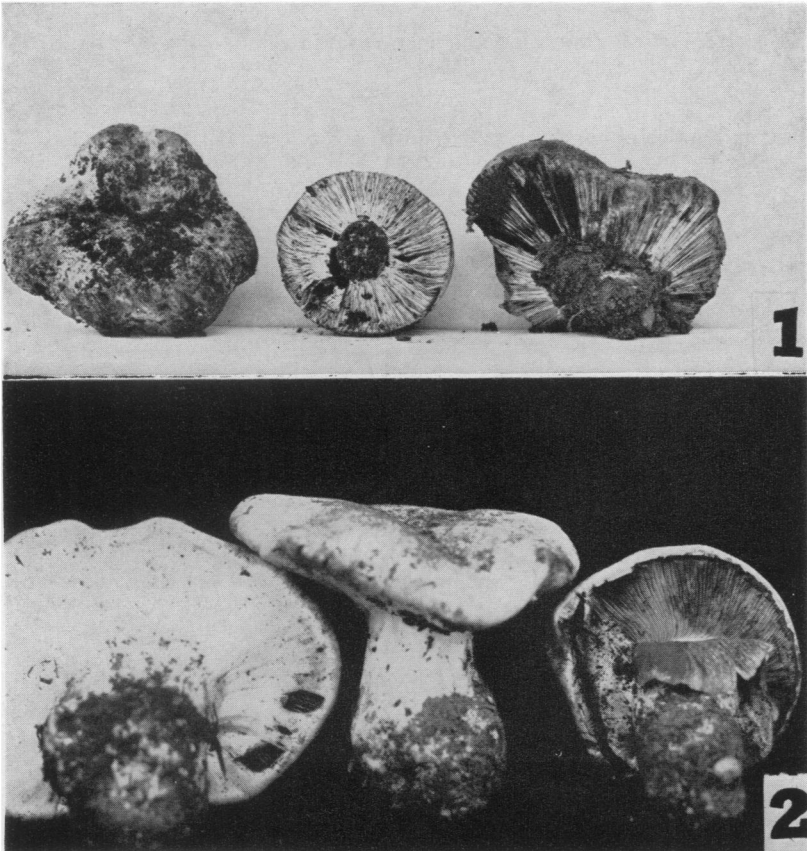


FIG. 1. *Cortinarius bigelowii*,  $\times \frac{1}{2}$ . FIG. 2. *Cortinarius magnivelatus*,  $\times 1$ .

containing the dried specimens was saturated with spore powder as invariably happens with gastromycetes such as *Pisolithus* or various species of *Calvatia*. This, along with the hypogeous habit and size of the basidiocarps, add to the oddity of this fungus. Its relationships, however, appear to us to be with the group of species in *Inoloma* centered around *Cortinarius pinetorum*. We are indebted to Ruth Oswald of Portland, Oregon for the specimens and notes.

**Cortinarius bigelowii** Thiers & Smith, sp. nov.

FIG. 1

Pileus 3–6 cm latus, convexus vel late convexus, demum irregularis, viscidus, demum siccus, pallide alutaceus; lamellae “avellaneus,” confertae, adnatae, angustae; stipes circa 1 cm longus, 7–10 mm crassus, marginato-bulbosus; sporae 9–11 × 6–7  $\mu$ , verruculosae. Typum legit prope Hell’s Canyon, 7-Devils Mts., Idaho. 26 July, 1954. H. E. Bigelow. In herbarium University of Michigan conservatum.

Pileus 3–6 cm broad, convex becoming nearly plane but very irregular in outline, surface often dry when collected but viscid when young and fresh, color pale alutaceous but often with a thin mycelial coating causing a hoary appearance. Context white, unchanging when bruised; odor and taste none.

Lamellae “avellaneus” (grayish brown) becoming pallid brownish with a liliaceous reflection, finally dull cinnamon from spores, close, adnate, narrow to moderately broad.

Stipe about 1 cm high and 6–10 mm thick above the bulb, marginate-bulbous and bulb 2–3 cm broad at first; veil copious, pallid, seldom breaking, typically remaining as a thin but dense layer of radial fibrils covering the gill cavity.

Spores 9–11 × 6–7  $\mu$ , inequilateral in profile, ovate in face view, rather coarsely verrucose-rugulose, fulvous in KOH, brighter rusty brown in Melzer’s. Basidia 4-spored, 30–38 × 7–9  $\mu$ , hyaline in KOH. Pleurocystidia none. Cheilocystidia basidium-like. Gill trama hyaline in KOH, subparallel, becoming somewhat interwoven. Pileus trama homogeneous and hyaline beneath a gelatinous pellicle of brownish (in KOH) narrow appressed hyphae. Clamp connections present.

Cespitose to scattered under the duff or just breaking through, under conifers, Heaven’s Gate Ridge, 7-Devils Mts. near Hell’s Canyon, Idaho. July 26, 1954. H. E. Bigelow collector (Smith-45385 Type) (MICH). Known also from numerous collections made in the vicinity of McCall, Stanley, Priest River and 7-Devil’s Mts. in Idaho.

*Observations.*—This species is characterized by being extremely flattened, and in producing copious spores which are deposited on the inner side of the veil even though the specimens never become exposed. Extensive observations have been made, and there is no reason to con-



sider the fungus a freak. It occurs in the white-bark pine zone, and has a definite fruiting period. The gills may be quite crisped and are fused at times, but a lacunose “gleba” was not present. The basidiocarps develop at the line between the duff and the mineral soil, and most of the time are “gastroid” except that spore deposits can be obtained from them if one cuts off the stipe and sets up the cap in a normal manner.

**Cortinarius velatus** Thiers & Smith, sp. nov.

Pileus 3–5 cm latus, siccus, planus demum depressus, subvinaceus vel subpurpureus; lamellae decurrentes, brunneae, tenues, fragiles, confertae; stipes 2–3 cm longus, 1–1.5 cm crassus apice, siccus, vinaceus, tomentosus, aequalis; velum eumorphum, permanens, vinaceum; sporae  $9.5\text{--}12.8 \times 5.6\text{--}6.5 \mu$ , subtiliter punctatae; cystidia nulla. Typum legit prope Huntington Lake, California. 6 October, 1965. H. D. Thiers 13414. In herbarium San Francisco State College conservatum.

Pileus 3–5 cm broad at maturity; when young plane becoming shallowly depressed to highly irregular in outline with age; surface dry although considerable debris is often attached; glabrous to finely pubescent to subtomentose; more or less evenly colored near “pale vinaceous drab” to “pale purple drab” (lilac to pale lavender) to occasionally as dark as “light purple drab,” unchanging or becoming slightly paler toward the margin with age; margin incurved, attached to the stipe by a permanent, well-developed, universal veil during all stages of development.

Context up to 1 cm thick, white, unchanging when exposed; firm; taste mild, odor very pungent.

Lamellae decurrent during all stages of development, covered by partial veil or its fragments during all stages of development, thin, fragile, whitish to pallid when young, becoming near “amber brown” (bright brown) at maturity; margin entire, concolorous with gill face.

Stipe 2–3 cm long, 1–1.5 cm broad at the apex; concolorous with the pileus or slightly paler; surface dry, tomentose; equal, solid, flesh concolorous with that of the pileus, unchanging; partial veil permanently covering the lamellae but somewhat thin and arachnoid, becoming shredded and lacerate with age, concolorous with the surface of the pileus.

Spores ellipsoid to subovoid, slightly inequilateral in side view, very finely punctate and appearing smooth except when seen under oil,  $9.5\text{--}12.8 \times 5.6\text{--}6.5 \mu$ ; pleurocystidia and cheilocystidia apparently not present; hymenium pale brown in KOH; basidia 4-spored, hyaline in KOH, clavate,  $18\text{--}24 \times 5\text{--}6 \mu$ ; gill trama hyaline in KOH, regular to slightly interwoven, occasional lactifers irregularly distributed, hyphae  $2\text{--}4 \mu$  in diam; pileus trama interwoven, homogeneous, hyaline in KOH;

cuticle differentiated as a layer of radially arranged hyphae, colored pale vinaceous, unchanging in KOH, not gelatinous in KOH, hyphae 3–5  $\mu$  in diam; clamp connections present, abundant in the veil tissue.

Scattered in soil under conifers. Huntington Lake, Fresno Co., California. October 6, 1965. Thiers 13414 type (SFSC). Additional collections made in vicinity of Pinecrest, Stanislaus Co., California.

*Observations.*—The two most distinctive features of this species are the definitely purple to lavender color of the pileus and the spores that have punctuations which are very poorly developed. They often can be detected only when viewed under an oil immersion lens.

So far this has been the only species exhibiting any strong pigment development. Such a feature is not surprising, however, when one recalls that many Cortinarii are highly pigmented. As a matter of fact, these lavender or purple colors are commonly observed in many more “normal” appearing species. An indication of the range of spore ornamentation in the group can be gained when *C. velatus* having only obscurely roughened spores is compared with *C. verrucisporus* in which the spores are strongly warty or verrucose.

**Cortinarius verrucisporus** Thiers & Smith, sp. nov.

Pileus 3–6 cm latus, convexus demum planus vel depressus, albus demum flavus, siccus, fibrillosus; lamellae subdecurrentes, confertae vel subdistantes, brunneae; stipes 1–1.5 cm longus, 1–1.5 cm crassus apice, aequalis vel bulbosus, siccus, obsitus cum veli elementis, flavus; sporae crassae verrucosae, ovoideae, 10.5–13.0  $\times$  6.5–8.0  $\mu$ . Typum legit prope Silver Lake, Amador Co., California. 9 Juni, 1966. H. D. Thiers 16919. In herbarium San Francisco State College conservatum.

Pileus 3–6 cm broad at maturity; convex when young, becoming plane to plano-convex to plane to shallowly depressed with age, frequently highly irregular and undulating in outline; surface dry to moist, innately fibrillose to subtomentose when young, unchanging or becoming glabrous to obscurely fibrillose with age; when very young white to “light buff” (tan), very soon becoming “ochraceous tawny” (rusty brown) with some areas colored near “sulfur yellow” to “chamois” to “clay color”; margin strongly incurved, attached to the stipe by a tenacious permanent veil during all stages of development.

Flesh up to 1 cm thick, yellow, unchanging when exposed, firm; taste and odor not distinctive.

Lamellae subdecurrent to adnate, close to subdistant, pallid to “pale olive buff” when young becoming “amber brown” as spores mature, thin, becoming noticeably crisped when dry, fragile; several tiers of lamellulae present; somewhat ventricose; margin entire, concolorous.



Stipe poorly developed and somewhat obscure, 1–1.5 cm long, 1–1.5 cm broad at the apex, equal to slightly bulbous; concolorous with the pileus; covered with partial veil during all stages of development; solid, flesh yellow, unchanging when exposed; partial veil permanent, tough, fibrous, concolorous with the surface of the pileus.

Spores ovoid, noticeably thick-walled, conspicuously verrucose-roughened with large, coarse warts which often unite to form short reticulations,  $10.5\text{--}13.0 \times 6.5\text{--}8.0 \mu$ ; basidia hyaline in KOH, clavate, 4-spored,  $27\text{--}30 \times 7\text{--}9 \mu$ ; pleurocystidia and cheilocystidia apparently absent; gill trama subregular, hyaline, hyphae  $3\text{--}5 \mu$  in diam; pileus trama homogeneous, interwoven, hyaline in KOH; cuticle differentiated as a layer of appressed hyphae which stain vinaceous in KOH, walls subgelatinous in KOH; clamp connections present throughout, abundant in the veil tissue.

Solitary in humus under conifers, Silver Lake (7,000 ft elevation), Amador Co., California. June 9, 1966. Thiers 16919 type (SFSC). Known only from the type collection.

*Observations.*—There are two major characteristics of this *Cortinarius* which readily distinguish it from other hypogeous species. The presence of the bright yellow stains on the pileus has not been observed on any of the others. The most distinctive feature, however, is the very strong development of the warts on the spores. These ornamentations are, by far, more conspicuous in this species than in any of the others described here. Another feature pertinent to the evolution of the group as a whole is the relatively poorly developed stipe which is usually enveloped by the veil.

***Cortinarius magnivelatus*** (Morse) Thiers & Smith, comb. nov. FIG. 2

*Pholiota magnivelatus* Morse. Mycologia 33: 368. 1941.

(Basionym.)

Pileus 3–6 cm broad at maturity; convex to broadly convex when young, with age typically becoming undulating and irregular in outline, sometimes remaining plano-convex or becoming shallowly depressed to umbonate; surface moist to dry; usually appearing glabrous when young, occasionally silky-appressed fibrillose, when older innately fibrillose to somewhat tomentose; when young white, when older or when bruised typically darkening to “warm buff” to “antimony yellow” to as dark as “ochraceous tawny”; margin incurved to strongly decurved during all stages of development; typically remaining attached to the stipe by a tenacious veil during all stages of development.

Context up to 1 cm thick, white to "pale olive buff," unchanging when exposed, tough, firm; taste and odor not distinctive.

Lamellae adnate to shallowly depressed; white to "pale olive buff" when young becoming colored near "Sanford's brown" to "buckthorn brown" to "ochraceous tawny" when mature, unchanging when bruised; broad, thin, not fragile, even when dry; several tiers of lamellulae present; abundantly forked near and at the stipe; margin entire, becoming somewhat eroded in places at maturity, concolorous with faces.

Stipe 4–6 cm long, 1–3 cm broad at apex, typically somewhat bulbous at the base, occasionally equal to tapering slightly toward the base; white, staining as in the pileus; surface dry, typically appearing peronate or with white fibrils over the entire surface; solid; flesh white, unchanging; veil very heavy, thick, tough, membranous; typically covering lamellae chamber throughout the life of the basidiocarp, sometimes becoming somewhat shredded with age, satiny-white, unchanging or darkening slightly with age.

Spores  $9.5\text{--}14 \times 6\text{--}8 \mu$ , ellipsoid, somewhat inequilateral in side view, verrucose to rugulose; basidia hyaline, 4-spored, clavate,  $27\text{--}32 \times 8\text{--}10 \mu$ ; pleurocystidia not seen; cheilocystidia present, difficult to locate, hyaline, cylindric to ventricose to nearly filamentous, thin-walled,  $18\text{--}23 \times 4\text{--}6 \mu$ ; gill trama regular to nearly so, hyaline, hyphae  $5\text{--}7 \mu$  in diam; pileus trama interwoven, homogeneous, hyaline in KOH; cuticle differentiated only as a narrow layer of compactly interwoven hyphae; clamp connections present, abundant in the veil tissue.

Gregarious to solitary in humus under conifers (sugar pine, red fir and ponderosa pine). Known from throughout the Sierra Nevada of California at elevations approximately 5,000 ft or above. Typically fruiting during June and July.

*Observations.*—This species appears to be related to *C. wiebeae* but is readily distinguished by the following features: the lamellae of *C. magnivelatus* are white to very pallid when young, not hazel as in *C. wiebeae*; in addition, they are firm and resistant rather than fragile and eroded; the annulus in *C. magnivelatus* is very tough and persistent, and never becomes free. There are numerous clamp connections in the veil tissue. Additional differences noted are the slightly larger spores, differently shaped cheilocystidia, and forking of the lamellae. Like *C. wiebeae* it appears to be in the *Inoloma* section and is likewise perhaps closely related to *C. pinetorum*.

*C. magnivelatus* is by far the most common species in the mountainous regions of California. The type of *Pholiota magnivelatus* Morse has been examined and there appears little doubt that, in the present concept, it properly belongs in *Cortinarius* rather than *Pholiota*.

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