

The Stirps Caligata of *Armillaria* in North America

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This group of variants in the genus *Armillaria* of the Friesian system, is interesting in several respects. First, it is not the same as stirps Caligatum (in *Tricholoma*) of SINGER (1975). It is, in a sense more restricted. *Armillaria focalis*, for instance, is not included since in my estimation it is not closely related to *A. caligata*. In addition, the generic concept of *Armillaria* is being reviewed in a separate publication (MITCHEL & SMITH, in press). Also, some features of the veil have been found to indicate a close relationship to *Cystoderma*. In the variant of *A. caligata* which is here regarded as the type variety, a parallel situation as regards veil structure and the chemical reactions of the veil hyphae has been observed (see discussion under var. *caligata*).

The present study is an "interim report" on the group for North America to give direction to future critical studies. I consider it worthwhile to summarize my own investigations of the group even though many studies are incomplete. The final evaluation of diversity in this group cannot be made on the information previously available.

As defined here the stirps features a duplex (2-layered) veil, the outer layer often colored; basidia seldom over 40 μ long and small, spores rarely up to 9 \times 5 μ . The annulus is typically membranous and formed mostly from inner-veil tissue. The species all appear to be mycorrhiza formers.

Key to Species and Varieties

1. Pileus white at first, slowly becoming \pm dull vinaceous brown on the appressed squamules; lamellae staining pinkish cinnamon to vinaceous brown; odor when fresh slight but fruity 1. *A. ponderosa*
1. Pileus \pm colored when young (pale alutaceous to dark vinaceous brown) 2
2. Pileus at first pale buff to pale alutaceous 3
2. Pileus cinnamon brown to vinaceous brown 4
3. Spores 5–6 \times 3.5–4 μ ; cheilocystidia abundant and versiform (crooked and knobbed)..... 2. *A. contorticystis*
3. Spores 6–8 \times 4.5–5.5 μ ; cheilocystidia absent or basidiole-like 3. *A. viscidipes*
4. Odor pungent; taste disagreeable; FeSO₄ vinaceous tan on pilear context 4c. *A. caligata* var. *nardosmia*
4. Not with all the above features 5
5. Lamellae or context developing bluish gray to olive-blue stains by late maturity; FeSO₄ gray in stipe base 4a. *A. caligata* var. *glaucescens*
5. Not as above 6

6. Odor and taste spicy and agreeable; gills (apparently) not readily discoloring; growing under conifers *A. matsutake* (Japan)
6. Not with all the above features 7
7. Growing under conifers, odor spicy, taste disagreeable; lamellae staining slowly to cinnamon; spores $5-6.5 \times 4.5-5 \mu$ 4b. *A. caligata* var. *occidentalis*
7. Growing under hardwoods; spores $6-7.5(8) \times 4.5-5.5 \mu$; taste agreeable .. 8
8. Odor fruity 4. *A. caligata* var. *caligata* f. *caligata*
8. Odor not distinctive 4. *A. caligata* var. *caligata* f. *inodora*

1. *Armillaria ponderosa* (PK.) SACCARDO, Syll. Fungi 5: 78. 1887.

Agaricus ponderosus PECK, Bull. Buff. Soc. Nat. Sci. 1: 42. 1873.

Agaricus magnivelaris PECK, Ann. Rep. N. Y. State Mus. 29: 66. 1878.

Armillaria magnivelaris (PK.) MURRILL, North Amer. Flora 10: 37. 1914.

Armillaria arenicola MURRILL, Mycologia 4: 212. 1912.

Tricholoma murrillianum SINGER, Lloydia 5: 113. 1942.

Tricholoma ponderosum SINGER, Lloydia 5: 114. 1942.

Pileus (5) 10—20 cm broad, obtuse to broadly convex, expanding to plane or the margin becoming broadly uplifted, when wet the surfaces subviscid to tacky (not slimy), soon dry, at first glabrous or nearly so, but soon more appressed-fibrillose, white at first, surface fibrils soon aggregating to form broad appressed spotlike scales and these soon “verona brown” to “warm sepia” (dark reddish brown) over disc, toward margin paler, ground color white, occasionally scales not forming and fibrils of cuticle simply darkening to vinaceous brown, the surface then virgate from colored fibrils; margin inrolled, cottony tomentose, extending beyond the gills. Context 2—3 cm thick, tapered to cap margin, hard, firm, white, unchanging, odor spicy-aromatic to fruity as in *A. caligata* var. *caligata* f. *caligata*; taste perfectly mild.

Lamellae close to crowded, about 230 reach the stipe, about two tiers of lamellulae, many forked near the cap margin, narrow but in age finally broad (1.5 cm), \pm equal, rounded-adnexed, white to whitish, staining pinkish to vinaceous brown when bruised and in age at times entirely brown, edges even or becoming wavy to undulating.

Stipe 6—12 (18) cm long, 2—4 cm thick at apex, solid, white within, tapered to a pointed base or \pm equal, lower two thirds sheathed by a soft whitish veil which is somewhat viscid to the touch if moist, white to pallid at first, soon breaking up into large patches which become dull vinaceous brown, veil terminating in a thick soft ring which is white above and often vinaceous brown below; surface above annulus white and obscurely furfuraceous to squamulose.

Spores $5.5-7 \times 4.5-5.5 \mu$, broadly ellipsoid to subglobose, non-amyloid, white in mass. Basidia $30-35 \times 6-8 \mu$, 4-spored. Pleuro- and cheilocystidia none. Gill trama \pm parallel, non-amyloid. Pileus cuticle of \pm radially arranged hyphae $5-10 \mu$ in diam.; clamps: none found.

Habit, habitat and distribution. Scattered to gregarious under pine in the late summer and fall; common during warm wet seasons and widely distributed in the western forested areas.

Observations. This species is often called the "White Matsutake" and is very close to *A. caligata* and *A. matsutake*. It is the best known species in the stirps here in North America. It was described from New York and in addition has been found under pine in the sandy areas of the Great Lakes Region.

2. *Armillaria contorticystis* sp. nov.

Pileus 16 cm latus, late umbonatus, siccus, virgatus, pallide alutaceus; odor subpungens; sapor mitis; lamellae angustae, confertae, depressi-adnatae pallidae, tactu tarde brunescens; stipes 15 cm longus, 4 cm crassus, deorsum attenuatus, peronatus; sporae $5-6 \times 3.5-4$ μ , non-amyloideae; cheilocystidia filamentosi-contorta, $18-30 \times 3-5$ μ . Specimen typicum in Herb. Univ. Mich. conservatum est; legit prope Bay City, Mich., Oct 10, 1975, comm. N. S. WEBER.

Pileus 16 cm broad, the margin slightly uplifted, disc with a low rounded umbo, surface dry and radiately fibrillose-virgate, "cinnamon buff" with a slightly darker disc. Context thick, firm, white, odor \pm pungent-fungoid; taste \pm mild to fungoid, KOH weakly yellow on context, no reaction on cuticle; FeSO_4 no reaction.

Lamellae narrow, crowded, depressed-adnate, pallid ("tilleul buff"), edges staining brownish in age.

Stipe 15 cm long, 4 cm thick, tapered to a narrow base, solid, hard and not brittle, surface booted to above middle by a membranous veil discoloring to alutaceous or darker and leaving a zone below the membranous, ragged-edged annulus, scurfy and slowly becoming \pm cinnamon buff above the annulus.

Spores $5-6 \times 3.5-4$ μ , smooth, ellipsoid, thin-walled, not amyloid or very weakly so (possibly). Basidia 4-spored, clavate, $33-40 \times 6-7$ μ . Pleurocystidia none; cheilocystidia $18-30 \times 3-5$ μ , filamentose-contorted, crooked and variously bulging, abundant. Gill trama with a central area of enlarged cells flanked by parallel tubular hyphae to the inconspicuous subhymenium (no divergence of hyphae observed). Pileus trama of boldly defined interwoven thin-walled hyaline hyphae of enlarged \pm sausage-shaped cells. Pileus cuticle of appressed-interwoven hyphae 4-10 μ wide; at the surface some \pm amorphous as if subgelatinous. Clamps not present.

Habit, habitat and distribution. Brought in from near Bay City to Dr. WEBER's class, Oct. 10, 1975.

Observations. This species is close to *A. viscidipes* but has smaller spores. It lacked any yellow tints, and in this respect differs from Peck's type of *A. viscidipes*. The abundant versiform cheilocystidia and different odor distinguish it from *A. ponderosa* if the latter has discolored somewhat.

3. *Armillaria viscidipes* PECK, N. Y. State Mus. Rep. 44: 16. 1891.

Pileus 6.5–13.5 cm broad, broadly convex to plane, broadly subumbonate at times, margin incurved at first, finally upturned in age, even, surface dry (when collected — but probably viscid in wet weather — Bigelow), somewhat shining, innately fibrillose, in places diffracted scaly, in age at times cracked or pitted, color a sordid buff; context thick, white, tough, odor pungent, taste mild.

Lamellae adnexed at first, becoming rounded or slightly sinuate, narrow to moderately broad (up to 1 cm), close or crowded, forked at times, whitish becoming cream-color, dingy in age, edges even to slightly undulating.

Stipe 5–11 cm long, apex 1.5–3.4 cm thick, equal or base ventricose up to 4 cm thick, abruptly tapered in the substrate, solid, white within and continuous with pilear context; apex white, fibrillose to somewhat scabrous (about one fourth of the stipe length), partial veil thin and soon collapsed, central portion and base viscid, brownish stained when slime has dried, rather shiny and \pm zoned or appressed-fibrillose to scaly.

Spores $6-8 \times 4-5.5 \mu$, ellipsoid to broadly ellipsoid, smooth, not amyloid, white in deposit. Basidia $31-44 \times 6-8 \mu$, 4-spored. Cystidia not differentiated. Pileus surface with a very thin ixocutis, the hyphae (2) $4-12 \mu$ thick; tramal hyphae cylindric to inflated, $7.5-18(22) \mu$ in diam., walls often \pm thickened. Hymenophoral trama hyphae slightly diverging near the subhymenium, the hyphae cylindric, $2.5-5(8.5) \mu$. Clamps absent.

Habit, habitat and distribution. Gregarious on mossy hummocks near stream through open hemlock.

Observations. Our description is taken from BIGELOW (1969, p. 178). PECK (l. c.) stated it was well known by its white and yellowish hues and penetrating almost alkaline odor. He described the stipe as slightly tinged yellow below the annulus. This species has been reported from Colorado (KAUFFMAN 1921). BIGELOW's observation of divergence in the gill trama is interesting, and in view of the non-amyloid to almost non-amyloid spores and lack of clamp connections, some interesting problems relative to generic concepts in this area of the Tricholomataceae are suggested. The closest species appears to be *A. ponderosa*.

4. *Armillaria caligata* VIV., I Funghi D'Italia p. 40; pl. 35. var. *caligata* f. *caligata*

Pileus 5–12 cm broad, convex with the margin at times elevated finally, the edge often decorated with veil remnants, surface dry and cuticle cinnamon brown to dull vinaceous brown (\pm "Verona brown"), cuticle breaking up into broad patches or appressed squamules

exposing the pallid ground color. Context firm, white, slowly changing to brownish in time where exposed, odor fruity (spicy), taste mild to nutty (pleasant).

Lamellae adnate to sinuate-adnate with a tooth, narrow to (finally) moderately broad, numerous tiers of lamellulae, white or slightly (finally) with brownish stains.

Stipe 4–10 cm long, 2–3 cm thick, \pm equal, solid, white within, white and scurfy above the annulus, \pm glabrescent, below the annulus sheathed by a veil concolorous with cuticle of pileus and finally separating into zones and patches, annulus flaring, membranous, relatively persistent, on underside colored as in pileus cuticle.

Spore deposit white. Spores 6–7.5 (8) \times 4.5–5.5 μ , broadly ellipsoid, smooth, thin-walled, non-amyloid. Basidia 4-spored, clavate, 28–34 \times 7–9 μ . Cystidia none observed on faces or edges. Gill trama regular (\pm parallel), no sign of diverging hyphae as revived in KOH, tissue \pm hyaline in KOH. Pileus trama interwoven hyphae 6–15 μ wide, the cells tubular to \pm inflated, yellowish-hyaline as revived in KOH. Pileus cuticle of “dry” hyphae 7–15 (20) μ broad, cells tubular to inflated, walls thickened slightly and smooth, in MELZER’s the walls dark reddish brown, in KOH quickly dark reddish brown but fading and becoming paler but the surface hyphae remaining vinaceous brown (\pm as in some species of *Cystoderma*). Clamps none. Microscopic characters from SMITH 32–329.

Habit, habitat and distribution. Scattered to gregarious under oak, late summer and fall, central and eastern United States. Not common.

Observations. The cuticular hyphae of the pileus in this species, especially their reaction with KOH, strongly resemble the color reaction featured by the cuticular hyphae of many species of *Cystoderma*, and the inflation of many of the cells is also suggestive particularly when one recalls that the veil in *Cystoderma* contains many elements that are not, literally, sphaerocysts. However, since a re-evaluation of the status of *Armillaria* is the subject of a paper (MITCHEL & SMITH, in press), it will not be discussed further here. The type variety (as we have accepted it) of *A. caligata* has the deep colors of *A. matsutake* and *A. caligata* var. *occidentalis*. VIVIANI originally described the cap as viscid. When wet the most that can be said of the North American material is that the cap surface is slightly tacky.

As to the odorless form (SMITH 1934) of var. *caligata*, no taxonomic emphasis in the form of a description is given it here. The odor in the “type variety” with us, is not detectable on all basidiocarps.

4a. *Armillaria caligata* var. *glauescens* var. nov.

Pileus 6–8 cm latus, demum late convexus, siccus, fibrillosus, vinaceofulvus vel triste vinaceo-brunneus; contextu pallide tarde griseo-caeruleus; sapor



amarus. Specimen typicum in Herb. Univ. Mich. conservatum est; legit prope Pinckney, Mich., Sep 26, 1975, SMITH 86761.

Pileus 6—8 cm broad, obtuse to convex, expanding to broadly convex, slightly umbonate or plane, cuticle dry, fibrillose or near margin streaked with fibrils, around disc at times \pm appressed squamulose, at times rather ragged in appearance; colors “cinnamon drab” to “Rood’s brown” (dull dark vinaceous brown), fulvous as dried; margin (edge) thinly cottony, near margin stained bluish gray in places. Context white, soft, when cut slowly becoming bluish gray to bluish green, odor slight, taste bitter to sharply disagreeable; KOH on cuticle weakly olive-yellow to no reaction; FeSO_4 gray in stipe base, negative elsewhere.

Lamellae dull creamy white, slowly brownish where bruised and finally in places stained bluish gray, close, narrow, adnate, edges even.

Stipe 5—7 cm long, 7—17 mm thick, \pm equal or narrowed to base, solid, pallid within but slowly becoming pale vinaceous cinnamon in basal area and in time going to olive-gray; surface pallid to brownish above the annulus, floccose fibrillose to \pm silky; below the ring coated with fibrillose veil remnants as a sheath colored like the fibrils of the pileus cuticle, the layer breaking into zones and patches; annulus membranous, ample persistent, 2-layered, upper layer \pm “vinaceous buff” then grayish finally, lower layer of dull vinaceous brown fibrils like those of the pileus.

Spores deposit whitish (on debris around basidiocarp); spores 7—8 \times 4.5—5 μ , ellipsoid, smooth, thin-walled, non-amyloid. Basidia 32—40 \times 7—9 μ , clavate, 4-spored. Pleurocystidia and cheilocystidia none found. Gill trama regular (parallel-interwoven), hyphae tubular near subhymenium, inflated to 15—20 μ in the central strand; subhymenium a very thin (scarcely discernible) layer of hyphae 2—4 μ broad. Pileus trama of interwoven hyphae 5—12 μ broad with some greatly inflated cells, thin-walled and smooth, merely yellowish in MELZER’S. Pileus cuticle of \pm radial hyphae 5—12 μ wide, the walls thin but brownish as revived in KOH, dull reddish brown in MELZER’S, the cells elongate and mostly tabular.

Habit, habitat and distribution. Scattered under *Vaccinium* bushes in low oak woods, Island Lake Area, Pinckney Rec. Area, September and October, 1975, SMITH 86684 & 86761 (type).

Observations. The bluish gray to bluish green stains are peculiar to say the least, and, along with the disagreeable taste, distinguish this variant in stirps *Caligata*.

4b. *Armillaria caligata* var. *occidentalis* var. nov. Fig. 1.

Pileus 4—8 cm latus, late convexus, siccus, fibrillosus demum \pm fibrilloso-squamulosus, triste vinaceo-brunneus, sapor subamarus, odor fragrans; lamellae albiae tactu brunnescens; stipes 4—9 cm longus, 1—2 cm crassus; annulus

duplex; sporae $5-6.5 \times 4.5-5 \mu$. Specimen typicum in Herb. Univ. Mich. conservatum est; legit prope Government Creek, Payette National Forest, Idaho, Aug 23, 1958, SMITH 60431.

Pileus 4—8 cm broad, broadly convex, margin inrolled, expanding to plane and often the margin finally wavy, disc at times retaining a slight umbo, surface dry, of appressed fibrils and at times with fibrillose squamules, as cuticle fibrils become separated by expansion of pileus patch-like scales are formed, color “burnt umber” to “Rood’s brown” (very dark vinaceous brown), finally paler over margin, ground color pallid. Context white, unchanging, odor distinctly of cinnamon, taste somewhat disagreeable to bitterish, FeSO_4 — no reaction; KOH no reaction.

Lamellae close, moderately broad, adnate to short decurrent, white at first, edges staining cinnamon to vinaceous brown and becoming eroded.

Stipe 4—9 cm long, 1—2 cm thick at apex, equal or nearly so, solid, white within; surface whitish and scurfy above the annulus or finally \pm pinkish cinnamon, below annulus with a sheath of fibrils concolor with those of pileus, these also present on lower side of annulus, the layer breacking into zones and patches. Annulus membranous, collapsing on the stipe.

Spores $5-6.5 \times 4-5 \mu$, broadly ellipsoid to ellipsoid, smooth. thin-walled, non-amyloid. Basidia 4-spored, clavate, $30-37 \times 6-7 \mu$, Cystidia none found on sides or edges of lamellae. Gill trama of \pm a parallel strand of hyphae becoming \pm interwoven in central portion and the cells there often inflated; subhymenium indistinct. Pileus trama of interwoven hyphae $5-12 \mu$ wide, the cells \pm tubular but crooked and curved, walls thin and hyaline. Pileus cuticle of \pm radial hyphae with thin smooth brownish walls in KOH, in MELZER’s dark reddish brown, cells $\pm 5-12 \mu$ broad and most of them tubular. Clamps none.

Habit, habitat and distribution. Solitary to gregarious in spruce-fir zone of our western mountains and along the west coast, Washington, Oregon, Idaho and Colorado. The description is from SMITH 60431 with data added from SMITH 85890 collected above West Village, Aspen, Colorado.

Observations. This variant is distinguished by its habitat in conifer forests of various conifers but mostly in spruce and fir. The very dark colored pileus, the fragrant-cinnamon odor resembling that of *A. ponderosa*, the \pm disagreeable taste of the raw flesh, the staining gill edges, and lack of distinctive KOH and FeSO_4 reactions, distinguish it. *A. matsutake* is very close, but the taste of the raw context should distinguish them. This variant is, truly, an intermediate between the type variety of *A. caligata* and *A. matsutake*.

4c. *Armillaria caligata* var. *nardosmia* (ELLIS) comb. nov.

Agaricus nardosmius ELLIS, Bull. Torrey Bot. Club 8: 75. 1876.

Armillaria caligata f. *nardosmia* (ELLIS) SMITH, Pap. Mich. Acad. Sci. 19: 205—216. 1934.

Pileus 4—15 cm broad, convex, expanded to plane or with a low umbo, rarely finally slightly depressed; surface typically dry but tacky to touch when wet, color “cinnamon brown” fresh and near russet as dried; fibrils of cuticle separating near margin to expose the pallid context, cuticle becoming \pm broken up at times to form appressed patches or small scales; margin often ragged. Context white, yellowing in apex of stipe when cut, odor pungent (not fruity), taste bitterish-fungoid; KOH in cortex of stipe and above gills yellow becoming dingy buff; FeSO₄ pale vinaceous tan on context.

Lamellae crowded, narrow to moderately broad, adnate-decurrent, white becoming dingy brown in age but typically not staining readily where injured, edges even and concolor with faces.

Stipe 3—9 cm long, 1—2.5 cm thick, solid, fibrous, equal or narrowed below, white within except in cortex (as noted) where it yellows tissue slightly; surface white to pallid above annulus, coated with fibrils the color of those of the pileus below and on underside of the ample persistent membranous annulus.

Spores 5.5—6.5 \times 4.5—5.5 μ , subglobose to broadly ellipsoid, smooth, thin-walled, non-amyloid. Basidia 4-spored, 28—35 \times 5—8 μ , clavate. Pleuro- and cheilocystidia none found. Gill trama of \pm parallel hyphae, cells of central region \pm inflated (up to 15 μ \pm), thin-walled, smooth; subhymenium of narrow \pm parallel hyphae. Pileus trama of hyphae 6—20 μ diam., intricately interwoven, hyaline in KOH, yellowish in Melzer's. Cuticle of pileus of radial hyphae 5—12 μ wide, mostly tubular, in Melzer's weakly reddish brown on dark colored caps, color in the wall. Clamps none.

Habit, habitat and distribution. Scattered to gregarious under hardwoods, summer and fall, rather rare.

Observations. This variant differs from var. *glaucescens* in lacking the slow change to grayish or greenish blue, in having a pale vinaceous tan color change in the pilear context with FeSO₄, in fulvous rather than vinaceous brown hues of the pileus, and in the pungent (not fruity) odor.

Excluded Species

Armillaria subcaligata SMITH & REA, Mycologia 34: 128. 1944.

Pileus 5—11 cm broad, broadly convex, expanding to nearly plane but not becoming umbonate, surface dry, covered with large subpyramidal innate scales about 5 mm wide; scales pinkish brown with darker tips, toward the margin the scales more fibrillose and

appressed; ground color whitish between scales; margin incurved and exceeding the lamellae by 3—4 mm, inner surface striate from contact with the lamellae. Context pure white, unchanging, compact but soft, 13 mm thick near stipe, \pm 2 mm near margin; odor none.

Lamellae very broad (15—18 mm), subventricose, rounded behind and definitely adnexed but seceding, leaving decurrent lines on stipe, thin, white with faintly yellowish-waxy tinge, subdistant, unequal, not forking, edges eroded.

Stipe 6—10.5 cm long, 2 cm thick at apex, narrowed downward; white and glabrous above the annulus, below annulus sheathed by the thin yellowish brown outer veil which breaks up leaving sub-concentric brown zones and/or scales, solid, white within; veil before breaking \pm 1 mm thick, white and smooth, lower (under) surface of annulus cottony-floccose and with scales like those of pileus but soon collapsing and inconspicuous.

Spores $9.6-12 \times 7.8-9.6 \mu$, ellipsoid, amyloid, smooth. Basidia $50-60 \times 10-12 \mu$, 4-spored, widest between middle and apex. Pleuro- and cheilocystidia not differentiated. Gill trama with a central strand of more or less parallel hyphae with other hyphae diverging from it, the cells of the latter finally greatly inflated, not amyloid. Pileus trama homogeneous, hyphae with mostly inflated cells, at surface the hyphae grouped into fascicles to form scales. Clamps present but rare.

Habit, habitat and distribution. Near Santa Barbara, Calif. (P. & M. Rea 994 — type), on a dry lawn near shrubbery, Aug 7, 1941.

Observations. Upon restudying the type over 30 years after describing this species, it became evident to me at once that the resemblance of it to *A. caligata* was superficial. Microscopically the species more closely resembles an *Amanita*. In well revived sections the divergent hyphae of the gills have greatly inflated cells, a common occurrence in *Amanita*. The basidia are large and widest below the apex — as in *Amanita*. The spores are also distinctly the type (and size) found in *Amanita*. The dried context of the pileus is soft and delicate — not as in the species here placed in stirps *Caligata*. The adnexed gills, the feature which Dr. Rea emphasized in writing of the species as an *Armillaria* is not a definitive feature here since a number of large *Amanitas* have slightly attached lamellae and leave slight gill lines on the stipe when the lamellae secede. It is clear to me now that the species does not belong in the Tricholomataceae, but more than likely belongs in *Amanita*. It will take considerable study to properly place it to species in the latter genus.

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Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Sydowia Beihefte](#)

Jahr/Year: 1977

Band/Volume: [8](#)

Autor(en)/Author(s): Smith Alexander H.

Artikel/Article: [The Stirps Caligata of Armillaria in North America 368-377](#)