

MONOGRAPH OF CHROOGOMPHUS (GOMPHIDIACEAE)¹

ORSON K. MILLER, JR.²

(WITH 6 FIGURES)

The study of the interesting agaric family, Gomphidiaceae, was undertaken in 1958. Since that time collections have been made and examined from Idaho, Washington, Oregon, Montana, and the Upper and Lower Peninsulas of Michigan. Collections from New Hampshire failed to yield any specimens in this genus. All but three of the North American species have been studied from fresh material. In addition, the help of Dave Largent in sending fresh material via air mail from California is acknowledged. A large number of collections of dried material were examined at the University of Michigan Herbarium. Notes and photographs at the University of Michigan Herbarium by C. H. Kauffman and A. H. Smith were made available and invaluable assistance was given by Dr. Smith during the course of this study. I am also indebted to the curators of the following herbaria for the loan of or permission to study material which greatly aided in this study: Naturhistoriska Riksmuseet, Stockholm, Sweden; New York State Museum, Albany; New York Botanical Garden; Royal Botanic Gardens, Kew; and the Farlow Herbarium, Harvard University.

Singer (1949, 1951, 1962) includes two genera in the Gomphidiaceae, namely *Gomphidius* and *Cystogomphus*. *Cystogomphus* is a monotypic genus. The remaining species in the family are classified under three subgenera within *Gomphidius*. These are *Chroogomphus*, *Laricogomphus*, and *Gomphidius*. Smith and Dreisinger (1954) found that a number of species in *Gomphidius* contain amyloid (dark blue to violet) tramal hyphae when mounted in Melzer's solution. All of the species examined in *Chroogomphus* were found to contain amyloid tramal tissue in some degree but the species of *Gomphidius* were either dextrinoid (rusty brown to ochraceous) or nonamyloid (hyaline to yellow). In

¹ Adapted from a Ph.D. thesis submitted to the Rackham School of Graduate Study, University of Michigan, May 1963. Partial support for the publication of the figures from the University of Michigan Herbarium.

² Present address: Forestry Sciences Laboratory, Intermountain Forest and Range Experiment Station, Moscow, Idaho.

Laricogomphus, however, one species was found to have amyloid tramal tissue but the other one was weakly dextrinoid to nonamyloid. These facts pointed out the need for a reevaluation of the existing subgenera and a close reexamination of species within the genus *Gomphidius*.

Colors were recorded when possible by comparison with the plates of Ridgway (1912). Throughout this paper, Ridgway colors are indicated in quotation marks, e.g., "ochraceous salmon." Ridgway names not included in quotation marks are used as general color terms.

Measurements were made of all structures by sampling. Ten measurements or more were made and then the mounts were scanned to include exceptionally large or small structures. In the species descriptions, the range of the sample size is given, and if the extremes vary from the sample size they are enclosed in parenthesis, e.g., spores (10-)12-15(-16.5) \times (4-)5-6.2 μ . The collections are all deposited in the University of Michigan Herbarium unless otherwise stated. In the paragraph on material cited only representative collections are cited rather than all of those examined.

It became apparent that the subgenus *Laricogomphus* did not comprise a natural group. Singer (1949) placed *Gomphidius flavipes* Peck and *G. maculatus* (Scop. ex Fr.) Fries in this subgenus. He used the association of the two species with larch and the presence of fascicles of glandulae at the apex of the stipe of both as common characters of species within *Laricogomphus*. Study of dried material verified the findings of Smith and Dreisinger (1954) with regard to the narrow but clear belt of amyloid tissue in the pileus trama of *G. flavipes*. Repeated study of *G. maculatus* revealed only weakly dextrinoid to nonamyloid tissue. In addition, the moist to viscid cuticle of *G. flavipes* contrasted sharply with the glutinous pellicle of *G. maculatus*. In the summer of 1962 *G. flavipes* was collected in the vicinity of Douglas Lake near Pellston, Michigan, in an area where no larch could be found. The combined evidence resulted in the decision to abandon the subgenus *Laricogomphus* and place *G. flavipes* with the amyloid Gomphidii and *G. maculatus* with the dextrinoid to nonamyloid species included under the subgenus *Gomphidius* by Singer (1962). This leaves *Gomphidius* in the sense of Singer with two well-defined subgenera, namely *Chroogomphus* and *Gomphidius*.

Further study of fresh material from these two groups revealed several additional characters which separate them. A study of the mycelium at the base of the buttons of a number of species of *Chroogomphus* and *Gomphidius* met with unexpected results. All of the species examined in the subgenus *Chroogomphus* contained amyloid hyphae and large

clamps, FIG. 6, A-C. Some species also appeared to have a smaller nonamyloid hyphal system with clamps, FIG. 6, A. This is the first report of vegetative amyloid mycelium in the Homobasidiomycetes and certainly within the Agaricales. It is also the first report of regularly occurring clamp connections within the Gomphidiaceae. Previous studies dealt only with the sporophore which apparently has no clamp connections on its hyphae. Study of the vegetative mycelium in species within the subgenus *Gomphidius* revealed dextrinoid to nonamyloid but clamped hyphae, FIG. 6, D. Clamps were then common to the entire genus but the persistent amyloid reaction in *Chroogomphus* was unique and very distinctly different.

Cytological study further strengthened the difference between the two subgenera when it was found that the Feulgen reaction resulted in positively stained chromatic material in the amyloid Gomphidii but no staining reaction could be observed in the nonamyloid species of *Gomphidius*. Species in the two different groups were often collected on the same day, killed from the same bottle of Newcomer's solution, and repeatedly subjected to the same staining procedure but positive results were only obtained with members of *Chroogomphus*.

In addition to the characters described above, *Chroogomphus* is characterized by ochraceous flesh in the pileus trama; a moist to viscid, but never glutinous pellicle; and pinkish ochraceous gills in young caps. *Gomphidius* is characterized by white to pallid flesh in the pileus trama; a glutinous pellicle; and pallid to whitish gills on young caps. In my opinion the characters described above are sufficient to warrant the elevation of the subgenus *Chroogomphus* to the level of a genus in the Gomphidiaceae. In fact, the number of characters used are far greater than those used to separate genera in the Tricholomataceae and in other families within the Agaricales.

The genus *Chroogomphus* as described here consists of two sections: *Floccigomphus* and *Chroogomphus*. *Floccigomphus* is characterized by a dry pileus cuticle of appressed tomentose to fibrillose innate, non-gelatinous hyphae. There are three species, two of which (*C. tomentosus* and *C. leptocystis*) are found almost exclusively in North America, with the exception of a single report of the former by Imai (1938) from Japan. The other, *C. sibiricus*, is known only from the USSR. The section *Chroogomphus* is characterized by a pileus cuticle of appressed, gelatinized hyphae. These hyphae do not form a gelatinous pellicle but unlike members of *Floccigomphus* the cap is viscid to the touch. *Chroogomphus* contains five species, all found in North America. Only one species, *C. rutilus*, has been reported outside North America. It is

widely distributed in Europe and reported from Japan, Siberia, and Asia Minor. In all likelihood *C. ochraceus* is also present in Europe. No member of the genus has been reported in the Southern Hemisphere. *C. jamaicensis* is the only species which has been reported with a southern temperate to subtropical distribution.

CHROOGOMPHUS (Singer) O. K. Miller, stat. nov.

Gomphidius Fr. subgenus *Chroogomphus* Singer, Pap. Mich. Acad. 32: 150. 1948.

Pileus 1-9 cm broad, surface viscid to dry and coarsely fibrillose; bright orange, dark salmon to dark red. Lamellae dull ochraceous to flesh-yellow or pale salmon finally clouded smoky brown from spores in age. Stipe fibrillose to sparsely fibrillose, dry to slightly viscid in some; context mostly concolorous with pileus, whitish, gray, pinkish salmon, ochraceous to wine-red, occasionally light to dark yellow at base. Spores 12-29 × 4.5-8(-9) μ, subfusiform in profile, elliptical in face view, smooth, entire, light to medium gray-brown in KOH, in Melzer's solution ochraceous tawny; smoke-gray to nearly black in deposit in all species. Cystidia 82-255 × 9-26 μ, cylindric, clavate, fusiform; thin- or thick-walled, walls hyaline, yellow-brown to vinaceous in KOH and hyaline to yellowish or blue in Melzer's solution; protruding conspicuously from the hymenial layer as pleurocystidia and cheilocystidia. Veil when present fibrillose. Pileus cuticle of innate to appressed hyphae hyaline, yellowish, dextrinoid to amyloid in Melzer's solution.

Habit, Habitat and Distribution. Species of *Chroogomphus* are terrestrial, solitary to gregarious, especially under members of the genus *Pinus* or in mixed stands containing pines but also under *Larix*, *Picea*, *Tsuga*, *Pseudotsuga* and other conifers. Fruiting from August through late October, late December through April on the Pacific Coast of North America. They are found in North and Central America; Japan (Hokkaido, Honshu); Europe; USSR; and Asia Minor. Members of this genus have been found wherever agarics have been collected extensively under members of the Coniferales in the Northern Hemisphere.

Type: *Chroogomphus rutilus* (Sch. ex Fr.) O. K. Miller.

Observations: The genus *Chroogomphus* is separated from the genus *Cystogomphus* Sing. by its lack of spherocysts in the veil tissue. It is differentiated from the genus *Gomphidius* Fr. by its amyloid pileus trama; colored pileus context pale buff, light salmon, ochraceous to wine-red; pileus cuticle dry, moist to viscid but never glutinous; pinkish ochraceous gills in young caps; and the constant positive Feulgen reac-

tion of the chromatic material in the nucleus. In addition, the hyphae of the mycelium at the base of buttons have clamp connections and are strongly amyloid. In species of *Gomphidius* the clamped hyphae are only weakly dextrinoid to hyaline.

KEY TO SECTIONS OF CHROOGOMPHUS

1. Cuticle of filamentous nongelatinous hyphae; pileus unpolished when dry, subviscid only in wet weather.....Section FLOCCIGOMPHUS
1. Cuticle an appressed layer of gelatinous hyphae; pileus often shiny when dry, viscid when moist.....Section CHROOGOMPHUS

CHROOGOMPHUS section **Floccigomphus** (Imai) O. K. Miller, comb. nov.

Gomphidius sect. *Floccigomphus* Imai, Jour. Fac. Agr. Hokkaido Imperial University 43: 285. 1938.

Cuticle of pileus appressed tomentose to coarsely fibrillose, of innate, nongelatinous hyphae.

Type: *Chroogomphus tomentosus* (Murr.) O. K. Miller.

KEY TO SPECIES OF CHROOGOMPHUS SECT. FLOCCIGOMPHUS

1. Terminal cells of cuticular hyphae broadly obtuse to cystidioid.....*C. sibiricus*
1. Terminal cells cylindrical.....2
 2. Hyphae of cuticle amyloid, mostly 7-9 μ in diameter; cystidia thick-walled.....*C. tomentosus*
 2. Hyphae of pileus cuticle hyaline, not amyloid, and distinctly narrower than tramal hyphae; cystidia thin-walled throughout.....*C. leptocystis*

Chroogomphus sibiricus (Singer) O. K. Miller, comb. nov.³

Gomphidius sibiricus Singer, Revue Mycol. Paris 3: 174. 1938.

Pileus 5-6 cm broad, convex, becoming depressed in center, variegated, disc orange, margin turning fuscus-gray, occasionally cinereous-lilac, dry, entirely squamulose-tomentose of loose floccose hyphae. Taste and odor not distinctive. Lamellae distant, wide (usually about 12 mm), gray. Stipe 55 mm long, 10 mm (5 mm at base) wide, light yellowish-orange near apex, lower part dark pinkish orange, fibrillose from remains of an indistinct veil.

Spores 16-19 \times 5.5-7.5 μ , fusoid. Hymenium: Basidia (40-)42-50(-58) \times 11-15.8 μ , four-spored. Cystidia 100-200 \times 16-22 μ , fusoid, clavate or subcylindric, rarely flask-shaped, numerous, hyaline or rarely fuscus to pallid, apex incrusted on some. Tissues: Cuticle of pileus of

³ Description taken from Singer, Revue Mycol. Paris 3: 174. 1938.



FIG. 1. *Chroogomphus tomentosus* X 1 (Smith 17691). Photo by A. H. Smith.

dry floccose hyphae, *hyphal ends broadly obtuse* and cystidioid, 8–21.5 μ wide. Trama of pileus of hyaline hyphae, partly incrustated and sometimes with a ferruginous pigment to strongly incrustated. Stipe tissue vivid yellow at the base, merging into saturated orange, consistency similar to *C. rutilus*. No clamp connections seen.

Habit and Habitat. Terrestrial, solitary, rare, under *Abies*, *Pinus sibiricus*, often with *Boletus sibiricus*. Fruiting occurs in September.

Distribution. Found on the banks of the Telezken reservoir, Altai Mts., USSR.

Observations. I have not studied this species and have no knowledge of any collections of it other than the type as described by Singer. The squamules on the cap consisting of hyphae with cystidioid end-cells separate this species from *C. tomentosus*. It is assumed on the basis of correlated features that if tested, the hyphae of the cap or of the gill trama would be amyloid, but material was not available to substantiate this. It is quite possible that it will be found along our Pacific Coast, as have other species described from the Altai Mountains.

Chroogomphus tomentosus (Murr.) O. K. Miller, comb. nov. FIG. 1
Gomphidius tomentosus Murr., Mycologia 4: 307. 1912.
(non *Gomphidius tomentosus* Murr., Bull. Soc. Mycol. Fr. 42: 75.
1926.)

Pileus 2–6 cm broad, broadly convex becoming flat, dry, innately appressed tomentose over all, pale to bright ochraceous “light ochraceous buff,” evenly colored, fibrils often with a faint vinaceous tinge. Context orange-yellow “capucine buff,” to near “capucine orange,” Murrill (1912) described it as “ochraceous becoming reddish tinted on drying.” Odor and taste not distinctive. Lamellae moderately distant, decurrent, moderately thick, broad in middle tapering to each end, colored like cap but soon smoky umber from the spores. Stipe 4–17 cm long, 9–14 mm thick, colored like the pileus, sparsely fibrillose, solid, surface showing ochraceous-orange color where handled or where fibrils are removed, base of stipe colored like pileus, and tapering rather abruptly to a root-like projection. Remnants of the fibrillose veil sometimes seen on stipe. Context “ochraceous-orange,” pith paler to pallid.

Spores 15–25 \times 6–8(–9) μ , subfusiform in profile, elliptical in face view, light gray brown in KOH, light to medium ochraceous tawny in Melzer’s solution but becoming darker after several hours. Hymenium: Basidia 31–48 \times 6–11 μ , clavate, four-spored, hyaline in KOH, in Melzer’s solution yellow containing scattered amyloid granules. Cystidia 118–255 \times 10–21 μ , cylindric to fusiform, the walls 2–4 μ thick in thickest part, occasionally thin-walled, sometimes containing yellow-

brown granules as seen in KOH mounts, the walls faintly amyloid but yellow as seen in crushed mounts, contents hyaline or dingy-brown, apex often encrusted. Tissues: Cuticle of nonviscid, innate hyphae (5-)8-13(-14) μ broad, hyaline in KOH, amyloid throughout becoming light violet with somewhat darker walls in crushed mounts but nevertheless sharply differentiated from the dark purple hyphae of the trama; occasionally narrowly fusiform pilocystidia present. Trama of pileus of interwoven hyphae (5-)7-18(-22) μ in diam, yellow-brown in KOH, in Melzer's solution amyloid with dark amyloid walls but an occasional hypha seen which is yellow-brown. Gill trama of interwoven hyphae, 8-17 μ in diam, yellow brown in KOH, darkly amyloid, when crushed out the walls a darker violet than the contents. No clamp connections seen on hyphae of the carpophore. The hyphae of the mycelium at the base of the stipe and in the surrounding needles amyloid with scattered large clamp connections, FIG. 6 A.

Habit and Habitat. Terrestrial, on needles or in deep moss under conifers. It is most frequently collected under *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Abies grandis*, but *Thuja plicata*, *Pinus monticola*, and *Pinus contorta* have been recorded in mixed stands in the USA where this fungus has been collected. In the western United States it is usually found between 2800 and 4500 ft elevation. Fruiting occurs from late August to late October.

Distribution. Western USA: Oregon, Washington, California, and Idaho. Japan: Hokkaido, Honshu, reported by Imai in 1938.

Observations. For a comparison of *C. leptocystis*, *C. tomentosus*, and *C. sibiricus* see the discussion under *C. leptocystis*. My description is drawn from fresh material (*O. K. Miller 1382, 1383, 1384, 2175, 2215*) and notes on fresh material (*A. H. Smith 2493*). Microscopic characters are from *Murrill 330* (TYPE) (NY).

Material examined. California: UCLA Campus, Ore. Mycol. Soc., Feb. 4, 1945. Idaho: *O. K. Miller 1382, 1383, 1384, 2054, 2175, 2215; Smith 60653*. Oregon: *Smith 24131*. Washington: *Murrill 330* (TYPE) (NY); *Smith 2493*.

Illustrations: Kauffman, *Mycologia* 17: plate 14. 1925.

Chroogomphus leptocystis (Singer) O. K. Miller, comb. nov. FIG. 2
Gomphidius leptocystis Singer, Pap. Mich. Acad. 32: 148. 1948.

Pileus 2.5-9 cm broad, disc with a low broadly conic umbo, intermediate area sloping slightly, margin decurved, surface dry, coarsely fibrillose, over the disc minutely squamulose, toward margin the fibrils grouped into appressed patches; central area tinged dark salmon "ochraceous-salmon," marginal area with more or less drab ground color to



FIG. 2. *Chroogomphus leptocystis* × 1 (Smith 53841). Photo by A. H. Smith.

gray but the tips of the scales showing "ochraceous-salmon." Context thick, near pale orange "capucine-buff" or paler "pale apricot," changing slightly to purplish red along cuticle when cut and around the worm holes. Taste slightly acidulous, odor none. Lamellae up to 13 mm broad, tapered either way, decurrent, subdistant, in three tiers, many of them forked, ground color "clay-color" but dusted darker by spores. Stipe 6-13 cm long, 2-8 cm wide, narrowing downward, solid but often worm riddled and torn, upper part purplish red, remainder flavous, base yellow or sordid ochraceous-brown, surface fibrillose and with a fibrillose ring at apex, flavous but fibrils reddish from handling. Context pale orange (near "capucine buff"), yellow to dingy yellow at the base.

Spores $12-18 \times 6-7 \mu$, subfusiform in profile, elliptical in face view, smooth, light gray brown in KOH, in Melzer's solution medium ochraceous-tawny. Hymenium: Basidia $24-52 \times 6-10 \mu$, four-spored, clavate, orange-red in Melzer's solution turning yellow to hyaline with a bluish tint in crushed mounts, hyaline in KOH. Cystidia $103-187 \times 15-18 \mu$, cylindrical to fusiform, thin-walled ($1-1.5 \mu$), occasionally thick-walled, in Melzer's solution hyaline or with weakly amyloid walls or often amyloid near center or cystidium only, hyaline in KOH. Tissues: Cuticle of pileus of filamentous nonviscid innate hyphae ($4.5-7-9(-10) \mu$ in diam, hyaline in KOH and in Melzer's solution. Trama of pileus of interwoven hyphae ($10-12-16(-18) \mu$, yellow-brown, hyaline to yellow in Melzer's solution with an occasional distinctly amyloid hypha, in KOH yellow-brown. Gill trama of loosely interwoven broad hyphae weakly dextrinoid in Melzer's solution before sections are crushed and hyaline to yellow in crushed mounts; in KOH yellow-brown. No clamp connections seen on hyphae of carpophore, vegetative hyphae not yet examined.

Habit and Habitat. Terrestrial under *Pinus monticola*, *Tsuga heterophylla*, and mixed conifers from about 2500-4000 ft elevation. Fruiting is generally from September through late October.

Distribution. Western United States: Oregon, Washington, and Idaho.

Observations. *C. leptocystis* is differentiated from *C. sibiricus* by its lack of broadly obtuse to cystidioid hyphal end-cells of the epicuticular hyphae of the pileus. The reduced amount of amyloid tissue and the thinner-walled cystidia of *C. leptocystis* clearly differentiate it from *C. tomentosus*. In addition the cuticular hyphae of *C. leptocystis* are narrower than the tramal hyphae beneath them, whereas in *C. tomentosus* they are the same size. Also the spores of *C. tomentosus* are somewhat larger than those of *C. leptocystis*. The weak amyloid reactions of *C. leptocystis* and *C. flavipes* suggest the possibility of a relationship be-

tween them. All other species in *Chroogomphus* have very darkly amyloid context tissue in the pileus and little or no dextrinoid to yellow tissue.

Material examined. USA, Idaho: *Trueblood* 762. Oregon: *Gruber and Smith* 10/20/1944; *Smith* 23971, 24131, 48543. Canada British Columbia: *J. E. Davidson* 222 (TYPE).

CHROOGOMPHUS section CHROOGOMPHUS

Cuticle of pileus of somewhat appressed, gelatinized hyphae, but not forming a distinct gelatinous pellicle, merely viscid to the touch, no distinct gelatinous veil present.

Type: *Chroogomphus rutilus* (Sch. ex Fr.) O. K. Miller.

1. Cystidia thick-walled.....2
 2. Cuticular hyphae 6-7 μ in diam; spores up to 23 μ long; cystidia with somewhat thickened walls in their midportion; distributed throughout North America.....*C. vinicolor*
 2. Cuticular hyphae 2-5 μ in diam; spores not over 20 μ long; cystidia with more evenly thickened walls; southern United States and Jamaica.....*C. jamaicensis*
1. Cystidia thin-walled.....3
 3. Spores 19-28 μ in length.....*C. flavipes*
 3. Spores 14-22 μ in length but never longer4
 4. Pileus dull colored, grayish, ochraceous, vinaceous to dingy vinaceous brown; stipe pale ochraceous, orange-buff to vinaceous red.....*C. rutilus*
 4. Pileus bright colored, bright yellowish orange to bright ochraceous; stipe concolorous with pileus, becoming reddish to magenta near base.....*C. ochraceus*

Chroogomphus vinicolor (Peck) O. K. Miller, comb. nov. FIG. 3
Gomphidius vinicolor Peck, Ann. Rep. New York State Mus. 51:
291. 1898.

Gomphidius vinicolor ssp. *californicus* Singer, Pap. Mich. Acad. 32:
149. 1948.

Pileus 1-8(-12) cm broad, obtuse to convex, in age turbinate to subumbonate, glabrous at first, viscid, marginal area in some obscurely appressed fibrillose, squamulose in age, orange-red, dingy orange-ochraceous, darkening overall to dark yellow-brown "Saccardo's umber" to "bister." Context orange in buttons to very pale buff "pale ochraceous-buff" or pale salmon with an "ochraceous salmon" flush over the disk in age. Odor and taste not distinctive. Lamellae subdistant to



FIG. 3. *Chroogomphus vinicolor* $\times 1$ (Smith 43859). Photo by A. H. Smith (above). *C. vinicolor* $\times \frac{1}{2}$ (Miller 2050) large carpophores from California (below).

distant, decurrent, broad, pale dingy ochraceous, dingy orange, ochraceous, buff or concolorous with the cap, clouded smoky brown with spores in age. Stipe 5–10 cm long, 0.6–2(–6) cm wide narrowing downward, pale ochraceous, orange-buff to vinaceous red in age with an ochraceous fibrillous dry veil which becomes more orange than the ground color in age, mycelium at base “ochraceous-buff.” Context “orange” to “ochraceous-buff” throughout, becoming spongy and vinaceous red where injured.

Spores 17–23 × 4.5–7.5 μ , elliptical in face view, subfusiform in profile, at first gray-brown in KOH fading with time to near hyaline, in Melzer's solution yellow to ochraceous. Hymenium: Basidia 41–57 × 10–15 μ , clavate, hyaline in KOH, in Melzer's solution hyaline to yellowish becoming ochraceous to weakly dextrinoid near subhymenium in crushed mounts. Cystidia 112–164 × 13–19.5 μ , fusoid-ventricose, narrowly clavate to narrowly fusiform, *thick-walled*, (wall reaching 5–7.5 μ at thickest part), thickening toward middle of cystidium, the thickened wall light to dark amyloid in some cystidia but in KOH hyaline to yellow-brown. Caulocystidia absent, scattered or abundant, 60–76 × 12–14.5 μ , narrowly clavate, with somewhat thickened walls, in KOH hyaline, incrustated with dark brown material. Tissues: Cuticle of pileus of appressed, gelatinous, hyaline hyphae 6–7 μ in diam, and light yellow-brown in KOH; scattered weakly amyloid hyphae. Trama of pileus of interwoven hyphae 6–14 μ in diam, darkly amyloid throughout (in crushed mounts light yellow-brown within but with amyloid walls.) Gill trama hyaline flecked with yellow-brown in KOH, the hyphae darkly amyloid, but as observed in crushed mounts with yellow-brown content and amyloid walls. Subhymenium in Melzer's solution ochraceous to weakly dextrinoid, in crushed mounts some hyphae hyaline, others with weakly amyloid walls. No clamp connections seen on hyphae of the carpophores. Amyloid hyphae present around buttons.

Habit and Habitat. Terrestrial, solitary to gregarious or sometimes cespitose, recorded under *Pinus radiata*, *P. taeda*, *P. banksiana*, *P. contorta*, *P. monticola*, *P. murrayana*, *P. resinosa*, *P. rigida*, and *P. virginiana*. Other conifers such as *Tsuga heterophylla*, *Pseudotsuga taxifolia*, *Thuja plicata*, *Picea sp.*, and *Larix laricina* have also been in many habitats. Throughout most of its range fruiting occurs from late August through early October. In northern California, however, it fruits from late July to April. This is the longest fruiting period known for any member of the Gomphidiaceae.

Distribution. Widespread in USA and Canada, from Maine to Washington, south to California, Utah, Texas, Tennessee, Alabama, and North Carolina.

Observations. This is one of two species which have amyloid trama, viscid pileus cuticle, and thick-walled cystidia. It differs from *C. jamaicensis* in having slightly longer spores, somewhat wider cuticular hyphae, and somewhat thicker cystidial walls.

Fresh material of *Chroogomphus vinicolor* Pk. ssp. *californicus* Singer from California has been carefully examined. Aside from the larger size of the carpophore as is well illustrated by comparing the two collections pictured in FIG. 3, the other characters mentioned by Singer (1949) were not substantiated. In particular it was noted that the cystidia, though numerous, varied considerably but were not any more abundant than on very small carpophores (e.g., *O. K. Miller 2083*) collected in northern Montana under *Pinus contorta*. Variation in size is not uncommon in the species of the genus *Chroogomphus* and with no other consistent differences apparent after close macroscopic and microscopic examination, this subspecies has not been retained. The high rainfall and long growing season along the California and Oregon coast is known to produce relatively large carpophores of many species of agarics.

Material examined. California: *Lamphere* Dec. 1960; *O. K. Miller 2050*. Idaho: *Smith 53195, 53773, 59312, 60435, 60649; Trueblood 532*. Montana: *O. K. Miller 2083*. Michigan: *Smith 58124, 60793; Shaffer and Smith 58180*, Oct. 11, 1958. Utah: *McKnight F 909*.

Chroogomphus jamaicensis (Murr.) O. K. Miller, comb. nov.

Gomphidius jamaicensis Murr., *Mycologia* 10: 69-70. 1918.

Gomphidius alachuanus Murr., *Jour. Elisha Mitchell Soc.* 55: 367. 1939.

Gomphidius vinicolor Peck ssp. *jamaicensis* (Murr.) Sing., *Farlowia* 2: 531. 1946.

Pileus 2.5-5(-9.8) cm, convex, color dark to pale or bright vinaceous brown, "natal brown," "army brown," or with some areas of "light vinaceous cinnamon" to "Mikado brown,"⁴ with imbricated scales on some sporophores. Context firm, "pale ochraceous salmon," "ochraceous salmon" to "pinkish buff." Odor none, taste not distinctive (according to Murrill, 1918); however, Singer (1946) reports that it is agreeable when young, resembling apples or applesauce. Lamellae subdistant, broad, arcuate, decurrent, dull flesh yellow, pinkish yellow to gray. Stipe 4-8(-10) cm long, 4-8(-15) mm wide, tapering toward the base, solid, fibrillose at apex from remains of veil, remainder glabrous,

⁴ Parts of the description of fresh material are taken from Singer (1946) and Murrill (1918).

smooth, cinnamon, pink to dark wine-red, "light vinaceous cinnamon," "buff pink" to "vinaceous rufous," base cinnamon to light ochraceous, "cinnamon," "light ochraceous-buff," or "ochraceous-buff." Context, upper portion salmon to buff "pale ochraceous-salmon," "ochraceous-salmon" to "cinnamon-buff," base light to dark yellow or clayish "primuline-yellow" with tinges of "yellow-ocher" or "clay-color."

Spores $17-20 \times 4.5-6 \mu$, subfusiform in profile, elliptical in face view, gray in KOH, in Melzer's solution yellowish drab. Hymenium: Basidia $36-50 \times 9-11 \mu$, four-spored, clavate, hyaline in KOH, in Melzer's solution dark yellow. Cystidia $110-165 \times 10-25 \mu$, fusiform to narrowly clavate, thick-walled (reaching $4-5 \mu$ at thickest part), tapering toward apex and base, incrustated and often heavily laden with spores, (indicating a mucilaginous substance over the surface), numerous, hyaline in KOH, occasionally weakly amyloid to amyloid near base, with yellow to hyaline contents. Caulocystidia $80-120 \times 11-12 \mu$, scattered or in loose fascicles, fusiform to narrowly clavate, wall thickened (up to 4μ), some incrustated; occasionally weakly amyloid to amyloid near base, with yellow to hyaline contents; in KOH contents usually yellow-brown. Tissues: Cuticle of pileus of appressed gelatinous hyphae, $2-4.8 \mu$ in diam, hyaline in KOH; in Melzer's solution light ochraceous, in crushed mounts hyaline to yellowish. Trama of pileus of hyphae $7-12 \mu$ in diam, amyloid (inky purple becoming violet when crushed); in KOH hyaline except dingy just under cuticle which is dingy drab to brown in sections. No clamp connections seen on hyphae of carpophore. The vegetative hyphae around fresh buttons have not been studied.

Habit and Habitat. Under two- and three-needle pines from sea level to about 5000 ft elevation.

Distribution. Florida, Alabama, and Cinchona, Jamaica.

Observations. Singer (1949) differentiates *C. vinicolor* as follows: "it differs from ssp. *jamaicensis* in slightly more distant lamellae, slightly larger spores, and the presence, in most specimens, of an umbo; it differs from var. *californicus* in the smaller number of cystidia present and also in the presence of an umbo and more distinct lamellae; all these races differ in their geographic areas and the pine species with which they form mycorrhiza in nature." It appears from this study that there are several characters which separate *C. jamaicensis* sufficiently from *C. vinicolor* to warrant its recognition as a species. *C. jamaicensis* has somewhat shorter spores, narrower cuticular hyphae, and noticeably thinner cystidial walls. In addition, the limited southern distribution of this species may also be significant.

Material examined. Jamaica: Earle 352 (TYPE) (NY).

Illustrations. Singer, Lilloa 22: plate XXVII. 1951.

Chroogomphus flavipes (Pk.) O. K. Miller, comb. nov.

Gomphidius flavipes Peck, Ann. Rep. New York State Mus. 54: 153. 1901.

Pileus 1–4 cm broad, broadly convex with a decurved margin, color vinaceous to pinkish or orange vinaceous or vinaceous-fawn, “pinkish vinaceous” to “orange-vinaceous,” margin usually darker, surface moist but not viscid, fibrillose, striate to radially rimose along margin. Context firm, pallid vinaceous. Odor and taste not distinctive. Lamellae distant, arcuate-decurrent, broad, “pale salmon color” to pallid, becoming grayish from spores. Stipe 3.5–6 cm long, 4–6 mm wide, equal or tapering slightly toward apex, dry to moist but not viscid, lower three-fourths “lemon yellow” and fibrillose-roughened (probably from a dry veil), upper one-third whitish and naked or nearly so, often twisted or bent irregularly. Context firm, pallid vinaceous, lower two-thirds yellow to “wax yellow” at base.

Spores 18–29 × 6–8.5 μ , subfusiform in profile, elliptical in face view, gray brown in KOH becoming darker with age, in Melzer’s solution “ochraceous-tawny” to dextrinoid or darker. Hymenium: Basidia 37–73 × 8–12 μ , clavate, four-spored, hyaline in KOH, with many incrustations; in Melzer’s solution orange at apices to dextrinoid near base, in crushed mounts becoming orange-yellow. Cystidia cylindric to fusiform, 119–249 × 9–26 μ , thin-walled, hyaline in KOH, some incrustated material at or near apex, in Melzer’s solution hyaline with a light bluish tint in crushed mounts. Caulocystidia 140–160 × 9–15 μ , cylindric to fusiform, in small scattered fascicles at the apex of the stipe. Tissues: Cuticle of pileus of appressed gelatinous hyphae (5–)6–12(–18) μ wide, hyaline in KOH, in Melzer’s solution hyaline, when crushed out some hyphae yellow with granular contents. Trama of pileus of hyphae 7.5–18(–24) μ in diam, in Melzer’s solution dextrinoid or in the center of the trama amyloid (best seen in crushed mounts), hyaline to yellow to purple-brown near pileus-surface and near gills; in KOH the hyphae hyaline to yellow-brown toward center of trama. Gill trama of loosely interwoven hyphae 7–14 μ in diam, hyaline in KOH with dark granules adhering to the hyphae, in Melzer’s solution the subhymenium weakly dextrinoid, the rest of tissue dextrinoid with a thin central strand of amyloid hyphae in center, best seen in crushed mounts as scattered but distinctly amyloid hyphae. No clamp connections on hyphae of the carpophore.

Habit and Habitat. Terrestrial, usually solitary or scattered under mixed conifers in bogs especially under *Picea mariana*, *Larix laricina*, and *Thuja occidentalis*. Fruiting occurs from August through early September.

Distribution. In conifer bogs in central and northern Michigan, New York, Maine (Snell 1940), Quebec, and probably throughout the bogs of the boreal forest in the northeastern United States and Canada.

Observations. This is a rare fungus with a rather wide distribution throughout the boreal forest. I have seen fresh material collected both

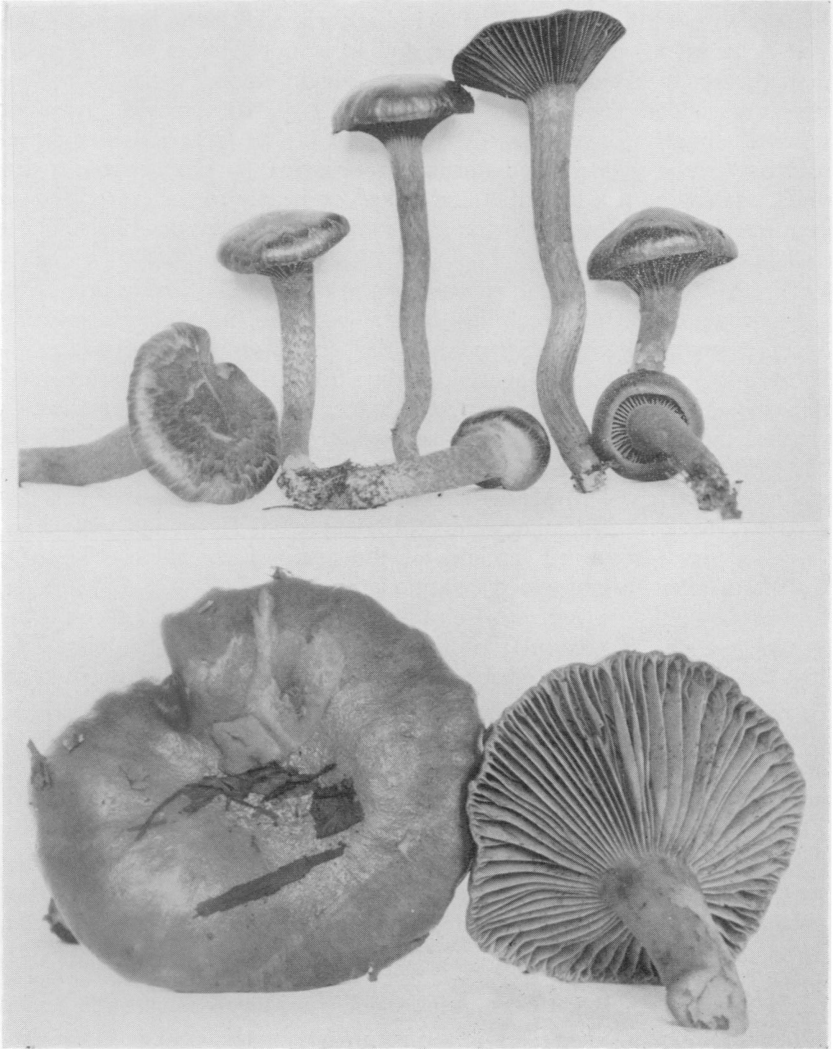


FIG. 4. *Chroogomphus rutilus* $\times 1$ (Smith 1121). Photo by A. H. Smith (above).
C. rutilus $\times 1$ (Smith 55766). Photo by A. H. Smith (below)

in the Upper Peninsula of Michigan and in the northern part of the Lower Peninsula. Notes and color photographs have been taken of fresh material. Sections mounted in Melzer's solution do not show the deep amyloid reactions of species like *C. rutilus*. The amyloid tissue occurs in a narrow zone in the center of the pileus trama. It is, however, clearly an amyloid reaction and has been observed consistently in both fresh and dried material. The diminutive size and the often curved or twisted stipe, combined with the occurrence in boreal bogs, makes this an easily recognizable species. Collections were found near Douglas Lake in Michigan where larch was definitely not in the habitat.

Material examined. Michigan: *Charlton and O. K. Miller 1294; Smith 57515; Smith & Kauffman* Sept. 15, 1929; *Berg & O. K. Miller 1317*. Quebec: *Groves 1941*, (FH).

Illustrations: Peck, C., Ann. Rep. New York State Mus. 54: plate I, fig. 1-4. 1901.

Chroogomphus rutilus (Sch. ex Fr.) O. K. Miller, comb. nov. FIG. 4

Agaricus rutilus Schaeff. ex Fr., Syst. Mycol. 1: 315. 1821.

Cortinaria rutila S. F. Gray, Nat. Arr. Brit. Pl. 2: 629. 1821.

Gomphidius viscidus L. ex Fr., Epicr. Syst. Mycol. 319. 1838.

Gomphidius testaceus (Fr.) Britz., Hymen. Südb. 9: 14. 1893.

Gomphidius litigiosus Britz., Hymen. Südb. 9: 14. 1893.

Gomphidius viscidus var. *columbiana* Kauf., Mycologia 17: 122. 1925.

Gomphidius rutilus var. *pulcher* Killerm., Denkschr. Bayer. Bot. Ges. 21: 58. 1940.

Gomphidius rutilus ssp. *alabamensis* Earle ex Sing., Farlowia 2: 527-567. 1946.

Gomphidius superiorensis Kauffman & Smith, Pap. Mich. Acad. 17: 170. 1933.

Gomphidius ochraceus ssp. *superiorensis* (Kauf. & Smith) Singer, Mycologia 41: 472. 1949.

Gomphidius ochraceus ssp. *muscigenus* Singer, Mycologia 41: 472. 1949.

?*Gomphidius purpurascens* Vassiljeva, Not. Syst. Crypt. Inst. Bot. Acad. Sci. Leningrad USSR 6: 193-194. 1950.

Gomphidius rutilus (Schaeff. ex Fr.) Lundall & Nannfeldt, Fungi Exsic. Suec. 409. 1937.

Pileus 2.5-12 cm broad, obtuse to convex or with an inconspicuously pointed disc, expanding to plane or turbinate or shallow, depressed with an arched margin, surface viscid, ochraceous, vinaceous to dingy umber

or vinaceous brown, "mummy brown," "ochraceous-buff," "ochraceous-tawny," "Saccardo's umber," "tawny-olive," "Dresden's brown" to "Rood's brown," "natal brown, or "Army brown," in age vinaceous red. Context gray to pinkish or rose near cuticle, light salmon, "ochraceous-salmon" to gray or light ochraceous near gills in some, dingy ochraceous to cream color elsewhere. Taste mild, odor none. Lamellae close to subdistant, decurrent, broad in age, pale ochraceous, ochraceous-buff to dingy yellow-brown or dull cinnamon "tawny-olive," "Saccardo's umber" to "sayal brown" when young, many of them forked about one-third to two-thirds of distance to the cap. Stipe 4.7–18 cm long, 0.5–2.5 cm wide, tapering toward base, solid, orange-buff, "capucine-buff," "ochraceous-buff," "orange-rufous," becoming vinaceous in age, with a thin cover of fibrils from fibrillose veil near apex, surface moist but not viscid, mycelium and base of stipe cream color, buff or yellow. Context ochraceous "ochraceous-orange," "orange-buff," "ochraceous salmon," "capucine-yellow," more yellowish near middle portion and correspondingly light yellowish near stipe cuticle, base of stipe light yellow to very light ochraceous.

Spores 14–22 × 6–7.5 μ , subfusiform in profile, elliptical in face view, light gray-brown in KOH, in Melzer's solution light to medium ochraceous tawny. Hymenium: Basidia 44–55 × 8–14 μ , clavate, four-spored, hyaline in KOH; in Melzer's solution hyaline with weakly amyloid or weakly dextrinoid walls. Cystidia 82–178 × 13–22 μ , narrowly fusiform, fusiform, narrowly clavate to cylindrical, thin-walled, hyaline in KOH with scattered incrustations, hyaline in Melzer's solution but in crushed mounts light yellow-brown. Tissues. Cuticle of pileus a pellicle of gelatinized hyphae, (2.4–)5–7.5(–8.4) μ in diam, hyaline in KOH, hyaline in Melzer's solution, in crushed mounts hyaline to yellow with many yellow granules within. Trama of pileus of interwoven hyphae, (3.5–)12–14(–22) μ in diam, hyaline in KOH; darkly amyloid (tissue dark violet), in crushed mounts with both the wall and the content amyloid but the wall darker than the content. Gill trama and subhymenium hyaline in KOH; deep orange to dextrinoid in Melzer's solution, subhymenium containing some amyloid hyphae with darker amyloid walls in crushed mounts. Clamp connections present on amyloid mycelium around base of fruiting body (FIG. 6 C) and rare to absent in mature fruiting bodies.

Habit and Habitat. Terrestrial, solitary to scattered, occasionally gregarious, under various species of conifers especially in the genus *Pinus* at a wide range of elevations. Fruiting occurs from August to November.

Distribution. North America, England, Europe, Japan (Hokkaido, Honshu), Siberia, and Asia Minor.

Observations. A great deal of confusion exists in regard to the taxonomy of variants in the *C. rutilus*-*C. ochraceus* complex. This stems from attempts to base subspecies and varieties on assumed limited association with certain conifers and supposedly correlated slight differences in color. The color differences of the subspecies and varieties overlap to the point where they are no longer useful in the recognition of these taxa. No constant morphological differences have been established for any of the subspecies or varieties which I have personally studied. In addition, the variation ascribed to different subspecies and varieties does not seem greater than that found in large fruitings of *Chroogomphus rutilus* which I studied.

In the fall of 1959, a very large fruiting of *C. rutilus* occurred under a pure stand of *Pinus strobus* at Stinchfield Woods near the University of Michigan. Several hundred sporophores of *C. rutilus* were collected and the variation in color, size, and the umbonate condition of the cap were carefully noted. The range of coloration of the pileus and stipe was great enough to eliminate these features as characters in recognizing infraspecific taxa. It was observed that none of the sporophores had the zinc-orange "deep-chrome," "light vinaceous-drab" or "ochraceous-orange" pileus of *Chroogomphus ochraceus*. Observations of smaller fruitings in the western United States have verified these findings. In addition, the description of *Gomphidius rutilus* var. *fulmineus* Maire (Maire et al. 1933) from Spain is exactly that of *Chroogomphus ochraceus*. On the basis of Maire's data, I regard his variety as typical *C. ochraceus*. The recognition of *C. ochraceus* as occurring in Europe may aid in the clarification of the concept of *C. rutilus* in Europe.

After a careful search to find constant characters to further subdivide *Chroogomphus rutilus* and *Chroogomphus ochraceus*, I have concluded that no genetically constant features are known on which to base infraspecific categories for either one.

Material examined. California: *Paul Collett* Dec. 13, 1947. Idaho: *Smith* 46977, 59021, 59232, 59233, 59319, 59336, 59668, 59669, 59805, 59852, 59853, 59900, 59929, 60102, 60220, 60512, 60646, 60748. O. K. *Miller* 773, 1295, 1378, 1379, 1421, 2168, 2180, 2265. *Trueblood* 992. Maryland: *J. R. Morse* Oct. 6, 1919. Michigan: *O. K. Miller* 615, 620, 621, 2127, *Pellston*, Oct. 16, 1960. *Smith* 50244, 57661, 58109. Oregon: *Smith* 55766. Tennessee: *Hesler & Sharp*, U. of Tenn. 10986. Sweden: *Romell* 10708 (S). Switzerland: *Singer* Aug. 1950.

Illustrations. *Kauffman & Smith*, Pap. Mich. Acad. 17: plate XXX. 1933. *Schaeffer*, J. C., *Fungorum qui in Bavaria*, Tom. 1, Tab. LV. 1770. *Singer*, *Lilloa* 22: plate XXVII. 1951.

Chroogomphus ochraceus (Kauf.) O. K. Miller, comb. nov. FIG. 5*Gomphidius ochraceus* Kauf., Mycologia 17: 119. 1925.*Gomphidius rutilus* var. *fulmineus* Heim., Treb. Mus. Cienc. Nat.

15: 68. 1934.

Pileus 1.5–3(–5) cm broad, plane to slightly umbonate or rarely distinctly umbonate, margin incurved at first, disc slightly depressed around the umbo, surface viscid, glabrous, shiny, bright yellowish orange to ochraceous, “deep chrome,” “light vinaceous-drab,” “zinc orange,”



FIG. 5. *Chroogomphus ochraceus* × 1 (Smith 5053). Photo by A. H. Smith.

“ochraceous-orange” to faintly “Hay’s russet,” center clouded with gray in age and finally a dull vinaceous, shiny when dry. Context ochraceous “light ochraceous-buff” abruptly changing to wine-red “acajou red” to “vandyke red” at lamellae, gradually changing to vinaceous “orange-vinaceous” at the base of the stipe. Lamellae close to subdistant, two tiers of lamellules, decurrent, broad, salmon “ochraceous-salmon” to smoky ochraceous, finally red “acajou red” near stipe, edges even. Stipe 3–6 cm long, 4–8(–10) mm wide, tapered downward, lower two-thirds sometimes viscid from veil remnants, concolorous with pileus

yellowish orange to ochraceous with tints of red to vinaceous brown or magenta, near base deep pinkish red "pompeian red" to sordid and soon vinaceous where handled. Context concolorous with pileus context

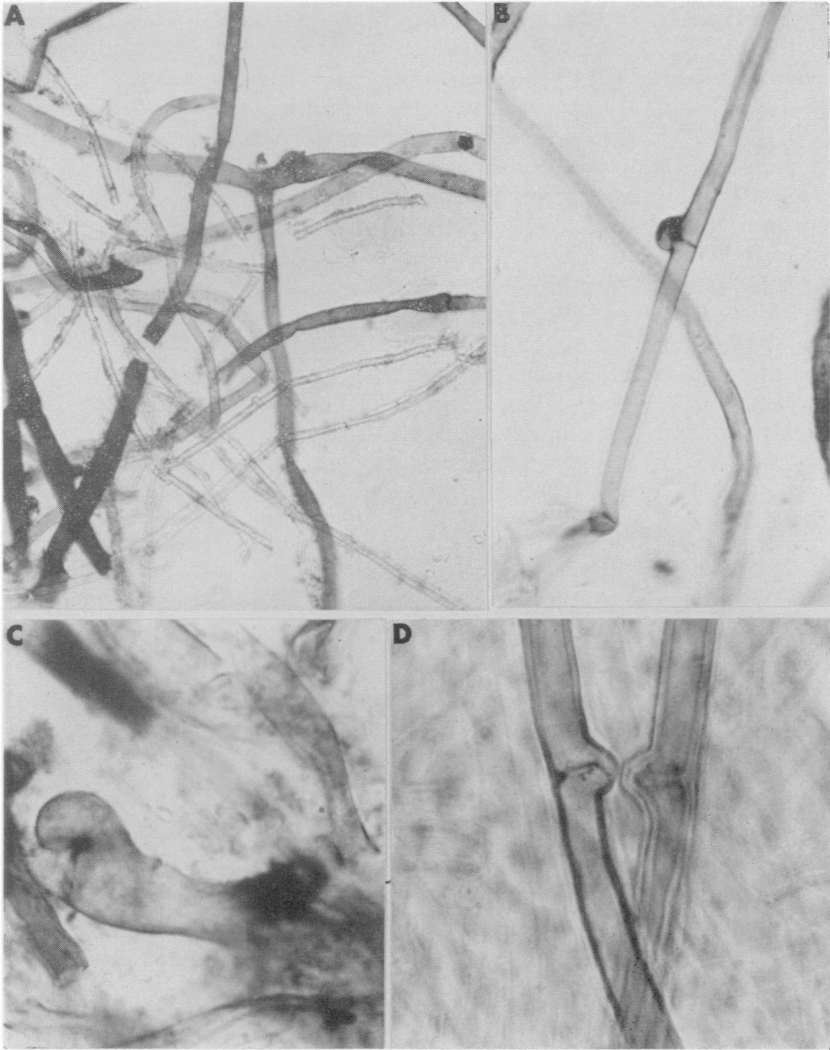


FIG. 6. A. *Chroogomphus tomentosus*, clamp connections on large amyloid and small nonamyloid mycelium at base of button. B. *C. ochraceus*, clamp connection on amyloid hypha at base of button. C. *C. rutilus*, clamp connection on amyloid hypha in mycelium surrounding a button. D. *Gomphidius glutinosus*, two clamps on dextrinoid hyphae at base of button ($\times 900$).

near apex gradually changing to "orange-vinaceous" or light ochraceous at base.

Spores $14-20 \times 4.5-7 \mu$, subfusiform in profile, elliptical in face view, ochraceous in Melzer's solution, in KOH light gray-brown to near hyaline. Hymenium: Basidia $30-41 \times 6-8 \mu$, clavate, yellow-brown in KOH, in Melzer's solution ochraceous to weakly dextrinoid, in crushed mounts becoming light yellow and containing many granules. Cystidia $81-160 \times 12-20 \mu$, narrowly clavate to cylindric, thin-walled, hyaline in KOH but often with yellow-brown to rusty-brown incrusting material; in Melzer's solution yellowish with dingy yellow incrusting material, in crushed mounts with rusty brown incrustations. Tissues: Cuticle of pileus of filamentous hyphae $3-6 \mu$ in diam, hyaline or with purplish walls in KOH; in Melzer's solution mostly hyaline but some hyphae amyloid (grayish purple), in crushed mounts with yellowish contents and light purple walls. Trama of pileus of interwoven hyphae, $(6-8-14(-16) \mu$, dingy brown in KOH, darkly amyloid (dark grayish purple obscuring all detail), somewhat lighter in crushed mounts but strongly amyloid. Gill trama of interwoven hyphae, dingy brown in KOH, darkly amyloid (dark grayish purple) becoming lighter grayish purple in crushed mounts. Clamp connections were found at the base of buttons on the amyloid vegetative mycelium but not on the carpophores, FIG. 6 B.

Habit and Habitat. Terrestrial in needles and moss under conifers, usually solitary to scattered, never abundant. Various members of the genus *Pinus* are usually present, e.g., *P. monticola* and *P. strobus*. Fruiting occurs from late August through November.

Distribution. North America and Europe; in North America particularly the Pacific Northwest, Lake States, Northeast, and Canada; in Europe known only from Spain.

Observations. In the fresh condition it is easily differentiated from *C. rutilus* by the bright color of the pileus and stipe, and the differently colored context as well as the smaller stature of the fruiting body. Microscopically the differences are less distinct. The purple gray walls and scattered appearance of purple gray within the hyphae of the cuticle are in contrast to the usually yellowish to hyaline nonamyloid cuticular hyphae of *C. rutilus*. The pileus of *C. ochraceus* is also mostly broadly convex to only faintly umbonate in the majority of sporophores.

Gomphidius rutilus var. *fulmineus* Heim on the basis of Maire's et al. (1933) description cannot be distinguished from *Chroogomphus ochraceus*. Maire et al. (1933) state that it differs from typical *C. rutilus* by three characteristic aspects: it is smaller, more vividly colored, and has a rosy colored flesh. Orange, apricot to violet-red colors are

indicated for the pileus. These differences used by Maire et al. to differentiate variety *fulmineus* from typical *C. rutilus*, are the same characters used by Kauffman (1925) to describe *C. ochraceus*. Without actually examining fresh material for additional differentiating characters there seems no other course open than to regard variety *fulmineus* as actually *C. ochraceus*. A critical restudy of this group in Europe from fresh material would be desirable since it is quite possible that *C. ochraceus* occurs extensively on that continent.

Material examined. Idaho: O. K. Miller 1365, 2008, 2176, 2195, 2221, 2266; Smith 40478. Michigan: O. K. Miller 1363; Smith 5053. Oregon: Kauffman (TYPE) Sept. 22, 1922; Smith 19120.

LITERATURE CITED

- Imai, Sanshi.** 1938. Studies on the Agaricaceae of Hokkaido. II. Jour. Fac. Agr. Hokkaido Imperial University **43**: 179-378; 2 pls.
- Kauffman, C. H.** 1925. The Genus *Gomphidius* in the United States. Mycologia **17**: 113-125; pls. 12-14.
- , and **A. H. Smith.** 1933. Agarics collected in the vicinity of Rock River, Michigan in 1929. Pap. Mich. Acad. **17**: 153-200; pls. XXLII-XXXIII.
- Maire, R., R. J. Codina, and P. Font-Quer.** 1933. Fungi Catalaunici. Contributions a l'etude de la Flore Mycologique de la Catalogne. Treballs del Museu de Ciencies Naturals de Barcelona **15**: 1-120.
- Murrill, W. A.** 1912. The Agaricaceae of the Pacific Coast III. Mycologia **4**: 294-308.
- . 1918. The Agaricaceae of tropical North America VIII. Mycologia **10**: 62-85.
- Ridgway, R.** 1912. Color Standards and Color Nomenclature, Washington, D. C. Pp. 44; Pls. I-LIII.
- Singer, Rolf.** 1946. The Boletinae of Florida with notes on extralimital species. IV. The lamellate families (Gomphidiaceae, Paxillaceae, and Jugasporaceae). Revue Mycol. N.S. Paris **2**: 527-567.
- . 1949. The genus *Gomphidius* Fries in North America. Mycologia **41**: 462-489.
- . 1951. The Agaricales (mushrooms) in modern taxonomy. Lilloa **22**: 1-832; 29 pls.
- . 1962. The Agaricales in Modern Taxonomy. 2nd ed. 915 p., 72 pls.
- Smith, A. H., and B. R. Dreisinger.** 1954. Further notes on amyloid tramal hyphae in *Gomphidius*. Mycologia **46**: 484-487.
- Snell, Walter.** 1940. Mycological Society of America. Report on the 1940 foray. Mycologia **34**: 226-234.