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OMPHALINA SENSU LATO IN NORTH AMERICA 1-2.

1: OMPHALINA WYNNIAE AND THE GENUS CHRYSOMPHALINA

2: OMPHALINA SENSU BIGELOW

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ABSTRACT: The four year observation of an Oregon population of *Omphalina wynniae* has facilitated reevaluation of its generic placement and that of other North American omphalinoid agarics. In Part 1, the species is illustrated and described in detail, its nomenclatural history discussed, and the new combination *Chrysomphalina grossula* proposed for it. The genus *Chrysomphalina* is reevaluated: new combinations *C. chrysophylla* var. *salmonispora* and *C. chrysophylla* var. *hoffmanii* are made; *Gerronema strombodes* is removed from *Chrysomphalina* and the new combination *G. xanthophyllum* is made for a vicariant European taxon which has been confused with *G. strombodes*. A key to the known species and varieties of *Chrysomphalina* is presented. In Part 2, the division of *Omphalina* sensu Bigelow and the generic concepts of *Gerronema*, *Haasiella*, *Omphalina*, *Phytoconis*, *Pseudoarmillariella*, and *Rickenella* are discussed. New combinations are *Omphalina hohensis* and *O. marchantiae*, and *Hygrocybe luteo-omphaloides* nom. nov. is proposed for *O. occidentalis*. A key to generic segregates of *Omphalina sensu* Bigelow and expanded generic descriptions are provided.

KEY WORDS: Basidiomycetes, Agaricales, Tricholomataceae, *Camarophyllus*, *Chrysomphalina*, *Clitocybe*, *Gerronema*, *Haasiella*, *Hygrocybe*, *Omphalina*, *Phytoconis*, *Pseudoarmillariella*, *Rickenella*, Pacific Northwest, nomenclature, new combinations, generic key, anatomy, ecology, morphology

Introduction

Since Bigelow's 1970 monograph of the genus *Omphalina* in North America, several revised classifications of the species he treated have been published. One of the species, *O. wynniae* (Berk. & Br.) Ito, is rare, and on this continent is geographically restricted in distribution. Fresh material was not available to Bigelow; however, the availability of living material in Oregon has allowed us to study the species and its generic placement in detail (Part 1), which in turn has prompted reconsideration of the generic concepts of other North American omphalinoid agarics (Part 2).

Methods: Microscopical data were taken either from fresh material, observed in water, or dried basidiomes, rehydrated and mounted in Melzer's reagent or 3% KOH. Capitalized color notations are from Ridgway (1912). Collections cited under 'SPECIMENS EXAMINED' are deposited in the University of Washington Herbarium (WTU) unless otherwise stated. Herbarium abbreviations are from Holmgren et al. (1990). Norvell collection numbers start with initials, year, month, and day, i.e. LLN 92.10.28-3 = *Oct. 28, 1992*, 3rd collection.

Part 1. *OMPHALINA WYNNIAE* AND THE GENUS *CHRYSOMPHALINA*

Weekly monitoring of an Oregon population of *O. wynniae* from 1990 to 1993 facilitated reevaluation of the generic placement of the species, with macroscopic and microscopic features, pigmentation, and biology all supporting its placement into the segregate genus, *Chrysomphalina* Clç. Additionally, a review of the literature revealed the existence of an earlier name, *Agaricus grossulus* Persoon, for the taxon.

A detailed consideration of generic placement follows a complete species description and nomenclatural discussion.

CHRYSOMPHALINA GROSSULA (Pers.) comb. nov.

Figs. 1-7

Basionym: *Agaricus grossulus* Pers. Mycol. Eur. 3: 110. 1828.

- ≡ *Omphalina grossula* (Pers.) Sing. Persoonia 2(1): 29. 1961.
- ≡ *Camarophyllus grossulus* (Pers.) Clç. Beih. Z. Mykol. 4: 55. 1982.
- ≡ *Gerronema grossulum* (Pers.) Sing. Beih. Sydowia 7: 14. 1973.

= *Agaricus umbelliferus* var. *abiegna* Berk. & Br. Ann. Mag. Nat. Hist. Ser. 4, XV: 28, #1143. 1875.

- ≡ *Omphalia abiegna* (Berk. & Br.) J. Lange. Dansk. Bot. Arkiv 6: 13. 1930.
- ≡ *Omphalina abiegna* (Berk. & Br.) Sing. Lilloa 22: 212. 1951.

= *Hygrophorus wynniae* Berk. & Br. Ann. Mag. Nat. Hist. Ser. 5, III: 208, #1781. 1879.

- ≡ *Omphalia wynniae* (Berk. & Br.) Quél. C. R. Assoc. Franc. Av. Sci. (La Rochelle, 1882) p. 390. 1883.
- ≡ *Omphalina wynniae* (Berk. & Br.) Ito. Myc. Fl. Japan 5(2): 128. 1959.

= *Omphalina bibula* Quél. Ench. Fung. p. 44. 1886.

- ≡ *Omphalia bibula* (Quél.) Sacc. Syll. Fung. 5: 324. 1887.

= *Omphalina umbellifera* var. *citrina* Quél. Ench. Fung. p. 44. 1886.

= *Omphalia bibula* var. *citricolor* Rolland. Bull. Soc. Myc. France 7: 94. 1891.

- ≡ *Omphalia bibula* f. *citricolor* (Rolland) Konr. & Maubl. Icon. Sel. Fung. p. 288. 1934.

5/cm at midpoint), arcuate, 1-1.5 (3) mm broad, 0.5-0.8 (1.0) mm thick; often intervenose, lamellulae 1- or 2-tiered, regularly interspersed; edges even; **color** generally yellow to greenish-yellow (Marguerite Yellow, Citron Yellow, Pyrite Yellow, Sulphur Yellow) becoming slightly paler to whitish on exposure or with age. **STIPE:** central, 5-40 (55) mm long, more or less equal 1.5-7 (10) mm at apex, evelate, usually hollow; **surface** appearing glabrous to the naked eye, appearing sparsely minutely pubescent under magnification; **color** overall yellow or greenish-yellow (Massicot Yellow, Citron Yellow) gradually paling toward base with age; **context** pliable, pale yellow (Massicot Yellow). **Odor and taste** not distinctive. **SPORE PRINT** whitish in thin deposits.

SPORES: 5.9 - 9.6 X 3.7-5.5 (6) μm , ellipsoid to subellipsoid with conspicuous obtuse apiculus (Fig. 3); hyaline, smooth, thin-walled, inamyloid, frequently containing one large central oil droplet when fresh and viewed in water or KOH [dried spores older than ten years contain many small droplets]. **BASIDIA:** 33-48 X 5-8 μm , 4-spored (rarely 2-spored), cylindrical to narrowly clavate with sterigmata ranging in length from 3 - 7.4 (10) μm ; packed with the basidioles into a dense hymenial layer (Fig. 4); ratio of basidioles to sterigmate basidia very high. **HYMENIAL CYSTIDIA:** absent. **OLEIFEROUS HYPHAE:** flexuous, with dense, yellowish refractive contents, 4-6 μm diam, occasionally present in all tramal tissues and in the stipitipellis. **CLAMP CONNECTIONS:** absent throughout the basidiome.

PILEIPELLIS: in radial section a cutis of compact parallel to subparallel, broadly cylindrical, repent, frequently septate hyphae (3)-6-13 μm diam; (occasionally branching or fusing with other elements in age); occasional cylindrical to tapered cystidioid elements with rounded apices exerted from the surface (Fig. 6); hyphal walls thin, smooth, neither gelatinized nor with incrustated pigments, and with slight banding from presence of intraparietal pigment; faint brownish-yellow intracellular pigments present when viewed in water. **PILEAL TRAMA:** a loosely radiating mesh-like structure of septate, hyaline, smooth, thin-walled, nongelatinized hyphae, 8-20 (22) μm diam, often ampullaceous at septa, giving many cells a femur (bone-like) shape (Fig. 5).

HYMENOPHORAL TRAMA: mature lamellae in cross section with a relatively wide mediostratum of greatly inflated cells similar to those in the pileal trama bracketed by a thin layer of narrow descending hyphae giving rise to the subhymenium, the latter of perpendicular hyphae branched in a candelabra-like manner which give rise to the basidia (Fig. 4). [In young lamellae the mediostratum is composed of parallel to subparallel hyphae (the parallel alignment being more noticeable in the central portion) which become highly inflated (>12 μm diam) in older lamellae; hyphal walls smooth, thin, neither gelatinized nor incrustated; yellowish intracellular pigment present throughout; bracketing subhymenium of 1-4 individual strands of parallel, narrow, cylindrical, septate hyphae 10 μm diam, with age becoming more sinuous, less regular and obscured by inflated hyphae of the mediostratum (often visible only in squash mounts); perpendicular to these strands, a layer of irregularly shaped di-/ trichotomously branched inflated hyphal elements, 3-5 μm diam, each giving rise to 2-3 basidioles, basidia, or



Fig. 1. *Chrysomphalina grossula* (LLN 92.10.25-4) *in situ*.
Approximately actual size.

Selected descriptions and illustrations: NORTH AMERICA: Bigelow (1970, 25-26, Fig. 10 as *Omphalina wynniae*); Phillips (1991, 76-77 as *Omphalina wynniae*); Smith (1937, 481 as *Omphalia abiegna*); EUROPE: Breitenbach & Kränzlin (1991, 100-101 as *Camarophyllus grossulus*); Cléménçon (1982, 58 as *Camarophyllus grossulus*); Cooke (1886, Pl. 905 [911], Fig. A as *Hygrophorus (Hygrocybe) wynniae*); Jossierand (1955: 74-76 as *Omphalia abiegna*); Konrad & Maublanc (1933: Pl. 235, Fig. 2 as *Omphalia wynniae*); Kühner & Romagnesi (1953, 123 as *Omphalia abiegna*); Moser (1983, 98 as *Omphalina grossula*); Persoon (1828, 110, Tab XXVI Fig. 6 (NOT Fig. 2) as *Agaricus grossulus*); Quélet (1886, 44-45 as *Omphalina umbellifera* var. *citrina*); Rolland (1891, 94-95 Pl. VI, Fig. 1 as *Omphalia bibula* var. *citricolor*); Ryman & Holmäsén (1984, 260 as *Omphalina grossula*); AFRICA: Malençon & Bertault (1975: 202-204 as *Omphalina abiegna*); ASIA: Ito (1959, 128 as *Omphalina wynniae*); Kawamura (1929, No. 58 & 1954, 314 (Fig. 311) both as *Hygrophorus wynniae*).

PILEUS: 2-35 (60) mm, convex to plano-convex with incurved margin when young, becoming convexo-umbilicate to uplifted with age; extreme margin even, crenate or occasionally sulcate; **surface** moist, hygrophanous, striate from disc to extreme margin, glabrous; **color** of disc and striations initially yellow to brownish yellow or greenish yellow (Wax Yellow, Citron Yellow, Old Gold, Olive Lake), with age becoming paler (Citrine, Old Gold, Olive Lake) or even whitish, color of margin yellow to greenish yellow (Wax Yellow, Massicot Yellow, Citron Yellow, Pyrite Yellow), with extreme age entire cap almost white; **context** thin (1 mm over gills), pale yellow (near Massicot Yellow). **LAMELLAE:** strongly decurrent, initially ending at the same point on stipe apex, distant (L + l ca. 9/cm at edge and

NORTH AMERICAN SPECIMENS EXAMINED: CALIFORNIA:
Humboldt Co, Arcata -- *XII.18.1986* BLT 606 (HSC). **IDAHO:** **Bonner Co**, Nordman -- *X.6.1956* AHSmith 54126 (MICH); *X.8.1956* AHSmith 54271 (MICH); *X.11.1956* AHSmith 54452 (MICH); *IX.23.1964*, AHSmith 70705 (MICH); Priest Lake -- *IX.10.1966* RWatling 2892 (E); *IX.29.1968* AHSmith 76757 coll. RHPetersen (MICH); **Shoshone Co** -- *IX.21.1966* OKMiller 3351 (E). **OREGON:**
Clackamas Co, Mt. Hood -- *X.3.1946* AHSmith 24026 (MICH); **Lincoln Co**, Van Duzer State Park -- LLN 92.11.10-2; **Multnomah Co**, Portland -- LLN 90.10.20-2; LLN 90.10.28-1,2,3,4,5; LLN 90.11.26-3; LLN 91.04.07-1,2; LLN 91.05.12-1; LLN 91.11.19-1 (DAOM); LLN 91.11.23a-c; LLN 92.01.02-1,2 coll. OLNorvell 3 (DLamoure pers. herb.); LLN 91.01.12-1; LLN 92.01.25-1; LLN 92.01.31-2; LLN 92.02.07-1,2,3,4,5,6; LLN 92.02.29-1; LLN 92.04.19-1; LLN 92.04.28-3,4; LLN 92.05.02; LLN 92.05.03-3; LLN 92.11.10-1 coll. GTNorvell; LLN 93.04.11; LLN 93.04.18-1,2,3,4,5; LLN 93.04.25-1,2. **WASHINGTON:**
Clallam Co, Lake Crescent -- *X.9.1935* AHSmith 3059 (MICH); *X.13.1935* AHSmith 3123 (MICH); **Columbia Co**, Tucannon River -- *IX.22.1984* JFAmmirati 9014; **King Co**, Seattle -- LLN 90.11.26-4 coll. DV Bark; LLN 90.12.11-2 coll. DV Bark; **Lewis Co**, Longmire -- *VIII.1.1948* AHSmith & DEStuntz; **Pierce Co**, Green Lake -- *X.2.1952* AHSmith 40415 (MICH); *X.19.1952* Stuntz 7554 AHSmith; Mt. Rainier Natl Park, Lower Tahoma Creek -- *X.22.1972* JWLennox 1412; **Whatcom Co**, Mt. Baker National Forest, Noisy Creek Preserve -- LLN 92.03.28-1 coll. JFAmmirati.

EXTRALIMITAL SPECIMENS EXAMINED: CZECHOSLOVAKIA: Mt. Boubin Nature Reservation -- *IX.28.1970* RSinger C5205 (F). **SCOTLAND:**
Hanzyll, Ben More Garden -- *IX.6.1963* DMHenderson 7087 (E); **Herefordshire**, Covenhope -- *XI.21.1959* PDOorton 2062 (E); **Invernesshire**, Cullodon Visitor Center -- *X.20.1989* RWatling 21679 (E); **Keltshire**, Black Craig -- *VII.25.1970* RWatling 7618 (E); **Lothenchurch**, Lachane -- *IX.13.1957* RWatling 37C (E); **Perthshire**, Rannoch, Dall -- *X.7.1976* PDOorton 4855 (E); Straloch -- *VIII.18.1978* RWatling 12844 (E); **Skye**, Treaslane -- *X.21.1980* AP & FM Bennell NG 394524 (E). **SWEDEN: Lena Parish**, Storveta -- *IX.28.1937*: SLundell *ex Fungi Exsicc. Suec #517* (BPI); SLundell, det. RSinger 5563 (F); **Småland**, Nassjo Parish, [Stuntamalen] -- *X.9.1945* G Haglund 572 (MICH); **SWITZERLAND: Maschwanden/ZH** Meggenwald -- *X.20.1975* FKränzlin 2010-75 K1 (LU); Obfelden/Oberholz -- *XII.11.1988* JBächler 1112-88BA1 (LU).

Observations and Notes

In 1981 brilliant yellow basidiomes of *Chrysomphalina grossula* were noticed in a forested garden on the outskirts of Portland, Oregon. In September of 1990, the species reappeared. A few basidiomes were found approximately 150 feet away from the original site on a trail leading into a second-growth forest. In both instances the fungus occurred on chipped bark imported to the garden for use as mulch. During the first few months following its reappearance, the current population expanded from its original location along the path for approximately fifteen feet. Subsequently in the summer of 1991 basidiomes extended over 150 feet in large numbers over the entire length of the trail; spread of the original population, now extending over a distance of 700 feet, has continued to the present time.

Observations of individual basidiomes over time have revealed that this species exhibits considerable color variation throughout its development. The basidiomes are long-lived; some specimens have been observed *in situ* for

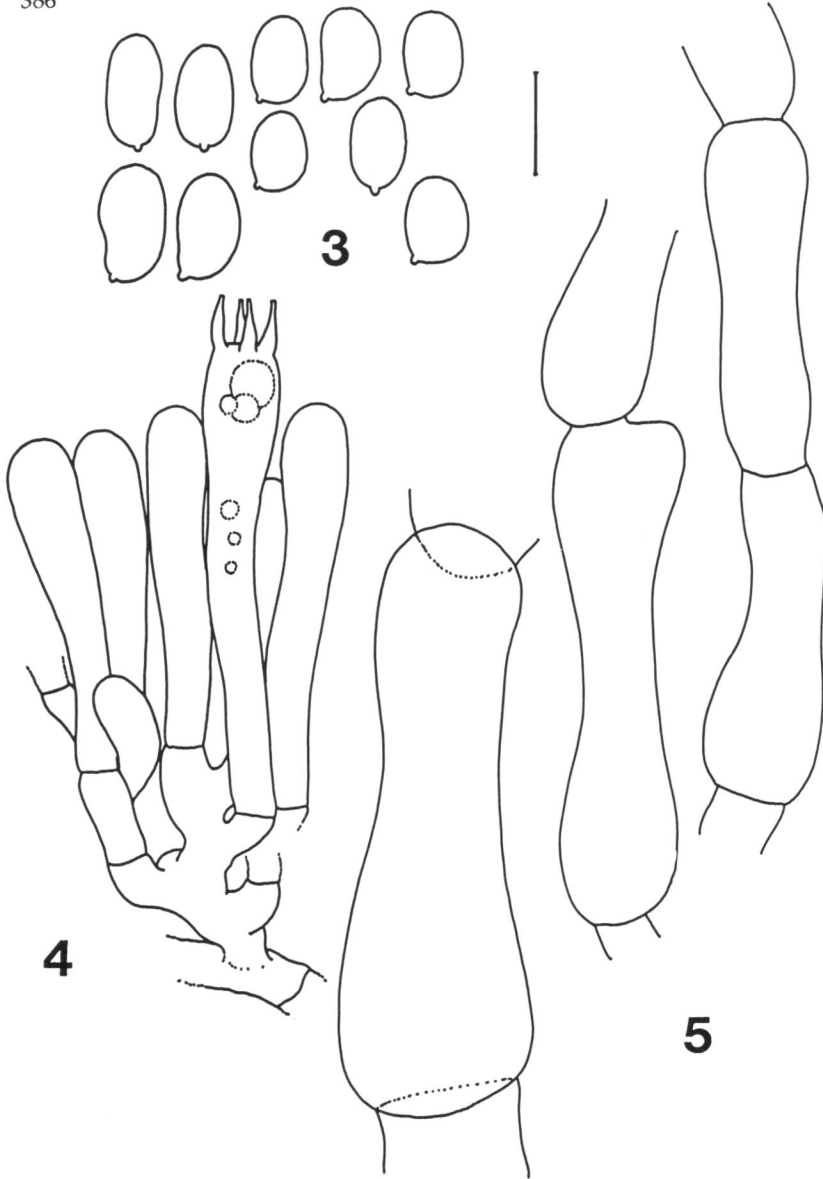
other subhymenial elements; this candelabra-like layer, 20 μm wide in young specimens, with basidia arising from different levels.]

STIPITIPPELLIS: a cutis of repent, subparallel, somewhat inflated, septate hyphae 3.7 - 12.5 (17) μm diam, with occasional exerted cystidioid elements (Fig. 7); pale yellowish intracellular pigment present; walls thin, smooth, neither gelatinized nor pigment-incrusted. **STIPITITRAMA:** composed of inflated, septate, hyaline, thin-walled vesicular hyphae 8-22 μm diam.

ECOLOGY AND DISTRIBUTION: gregarious to caespitose on water-soaked coniferous wood, bark chips, debris (occasionally found on angiosperm wood mixed with colonized coniferous wood) in mixed forests or parks at elevations from 30 m to 1100 m. *Chrysomphalina grossula* (as *Omphalia abiegna*) was first reported in North America from Washington state (Smith, 1937). In North America this species is uncommon, restricted to the *Tsuga heterophylla*/*Pseudotsuga menziesii* zone of the Pacific Northwest where it is normally found in small numbers on coniferous debris. A report from Alberta by Schalkwyk-Barendsen (1991) was based on a collection of *Clitocybe*, sect. *Candicantes* [specimen in DAOM examined].



Fig. 2. Young, more darkly colored *Chrysomphalina grossula* basidiomes exhibiting hollow stipe (LLN 90.10.20-2). Slightly larger than natural size.



Figs. 3-5. *Chrysomphalina grossula*. **Fig. 3.** Basidiospores. (LLN 92.04.19-1). **Fig. 4.** Candelabra-like subhymenium with irregularly shaped di-/trichotomously branched hyphal elements giving rise to a dense hymenial layer with basidioles and basidium. (LLN 93.04.18-1). **Fig. 5.** Femur-like hyphal cells from pileal trama (LLN 93.04.18-1). Scale = 10 μ m.

over a month. The greatest intensity of color, a brilliant greenish-yellow, occurs upon emergence from the substrate. Throughout this period the pileus and stipe base gradually lose pigments. Intense coloration is lost from the more exposed areas; the pilei tend to fade from an intense olive-yellow through greenish-brown or tan to almost white, while more protected areas of the basidiomes, such as the lamellae and stipe apex, retain an intense greenish-yellow hue for a much longer time. Eventually the entire basidiome can become pallid. This developmental color variation is paralleled by differences in innate pigmentation: instances of partial albinism, where yellow pigments are missing from the onset, also have been observed in the Oregon population (LLN 90.10.28-2, LLN 91.11.23c, LLN 93.04.18-1&2.). This variability of the intrinsic color found in different forms of *C. grossula* was noted by Jossierand (1955), who also commented on the occurrence of a double-pigment system: one citrine, the other a bister-fuscous.

The lamellae thicken considerably over the life of the basidiome; as a result the lamellar trama varies from subregular to irregular depending upon the disruption caused by inflation of the hyphae in the mediostratum (Fig. 5). Simultaneously the hymenium thickens slightly. At any given time there are few sterigmate basidia relative to basidioles (Fig.4); this is due to the continual rejuvenation of the hymenium over the extended life-span of the basidiome.

The range in size of the individual basidia in *C. grossula* is similar to that observed in *C. chrysophylla* (Fr.) Clç. In his discussion of subhymenial and basidial development in that fungus, Kühner (1928) remarked "each cell of the subhymenium gives rise to an ascending crooked lateral branch which in turn leads directly to a basidium or to a new subhymenial cell; it follows that the basidia -- arising as they do from extremely variable depths -- are of very different lengths..." (translated by LLN). *C. grossula* also has a candelabra-like subhymenium, but it is not as strongly developed. Jossierand (1955) drew attention to the similar hymenial development in *C. chrysophylla* (as *Omphalia*) and *C. grossula* (as *O. abiegna*). He noted that this developmental pattern led to an abundance of immature elements in the hymenium, resulting in a low level of spore production. These observations explain the difficulty in obtaining satisfactory spore deposits for either species.

Oregon basidiomes of *C. grossula* produced scant spore deposits; a thin deposit on paper is creamy-white; deposits on one microscope slide appeared very slightly greenish. In his descriptions of the species (as *O. wynniae* in 1882 and *O. bibula* in 1888) Quélet described a white or greenish spore print ("*hyaline ou verdâtre*"). After obtaining sufficiently heavy spore deposits (only twice over a 21 year period), Jossierand (1955) noted a very pale ("*trés, très pale*") creamy-greenish color when the print was compared to a very white standard, bicarbonate of soda.

Possibly because of similarity in size, habit, overlapping habitats, and color when faded, *C. grossula* has been confused with another clampless species, *Phytoconis ericetorum* (Fr.) Redhead & Kuyper (also variously known as *Omphalina ericetorum* (Fr.) M. Lange or *Omphalia umbellifera* (Fr.) Kumm.). Older faded forms of both species can be microscopically

Choice of Species Epithet

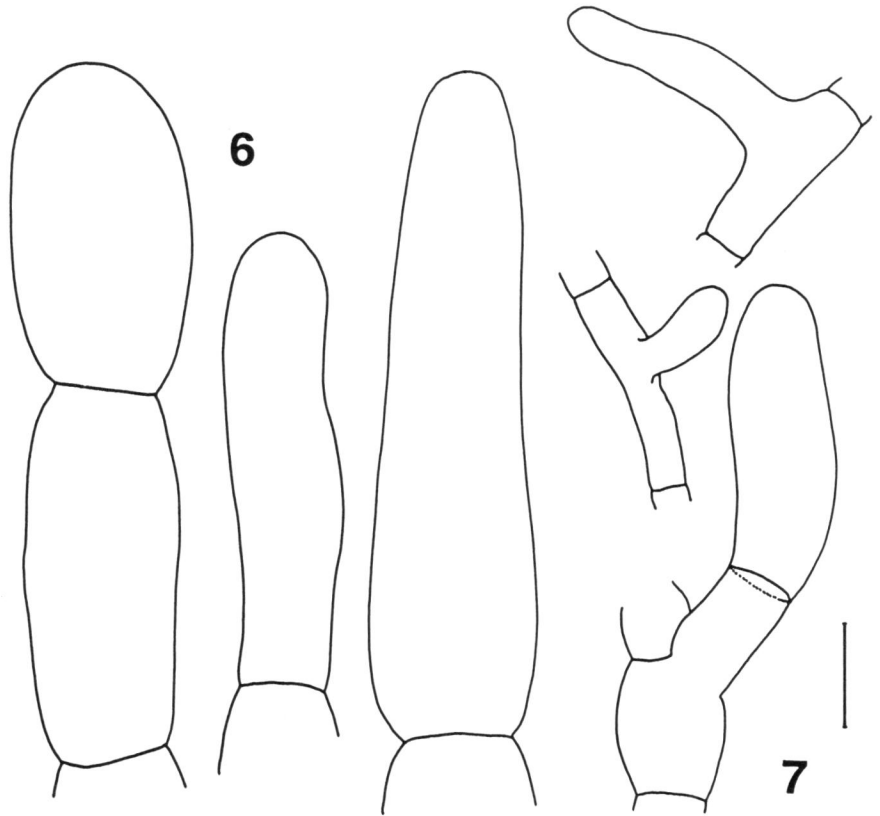
The highly variable coloration and thickening lamellae of *C. grossula* have contributed to the generation of several species epithets. Persoon (1828) named the mushroom *Agaricus grossulus*, selecting a species epithet referring to the gooseberry green coloration. The fungus was later described as a pale yellow variety of *Agaricus umbelliferus* by Berkeley & Broome in 1875 (as var. *abiegnus*), probably based on aged, partially faded specimens; the name "*abiegnus*" refers to its normal substrate, coniferous wood. The species in its lemon-yellow state, a coloration common in *Hygrophorus sensu lato*, was next described as *Hygrophorus wynniae* by Berkeley & Broome in 1879 who named it after the collector, Mrs. Lloyd Wynne. Apparently this assignment to *Hygrophorus* obscured the fact that the authors had earlier described the same agaric as an omphalioid taxon.

Quélet (1886) simultaneously assigned the species two names: *Omphalina umbellifera* var. *citrina* for the more mature lemon-yellow colored form, and *Omphalina bibula*, a reference to its bibulous nature, for the more intense, younger olive-citrine colored form. In 1888 Quélet treated *O. wynniae* as conspecific with *O. bibula*. Rolland (1891) named what he believed to be a new yellow-colored form of the olive-citrine fungus *Omphalia bibula* var. *citricolor*.

Lange (1930) transferred *A. umbelliferus* var. *abiegnus* to *Omphalia* at the species level, treating *H. wynniae*, *Omphalina bibula* and *O. umbellifera* var. *citrina* as synonyms. After examining the type of *A. grossulus*, Singer (1961b) placed both *O. abiegnus* and *O. wynniae* in synonymy with *A. grossulus*, transferring the species to *Omphalina*. Cléménçon (1982) accepted Singer's synonymy but placed the taxon into *Camarophyllus* (q.v.). Both the macroscopic description by Persoon (1828) and the microscopic description of the type by Singer (1961b) are consistent with our concept of the species.

***Agaricus chrysoleucus* Pers.:** Several authors have considered *Agaricus chrysoleucus* Persoon (1801) to be an earlier name for the fungus we call *C. grossula*. We do not accept this synonymy.

Lange (1930) treated *A. chrysoleucus* (as *Omphalia umbellifera* var. *chrysoleuca* Pers.) as a synonym of *O. abiegnus*, although he acknowledged that there was confusion regarding Fries' concept of the latter. Konrad & Maublanc (1934) listed *Omphalia umbellifera* var. *chrysoleuca* Pers. [non Fries] as a synonym of *Omphalia wynniae*. They additionally recognized var. *bresadolae*, listing *O. bresadolae* R. Maire, *Clitocybe xanthophylla* Bres., and *Omphalia hypoxantha* Bres. as synonyms. However, *A. chrysoleucus* as originally described by Persoon in 1801 has more characters in common with the fungus currently named *Gerronema strombodes* in Europe than with *C. grossula*. Persoon's *A. chrysoleucus* was said to be cespitose on conifer trunks in the Harz Mountains. Colors of the pileus, lamellae, and stipe were described as "*albido... distantibus sulphureis... albo*" respectively. *Clitocybe xanthophylla* Bresadola (1881), considered synonymous with *G. strombodes* (Beardslee 1917, Singer 1970, Cléménçon 1982a, Breitenbach & Kränzlin 1991), was also described as cespitose on conifer trunks in the Italian Alps



Figs. 6-7. *Chrysomphalina grossula*. **Fig. 6.** Exserted cystidioid end cells from pileipellis (LLN 93.04.18-1). **Fig. 7.** Exserted cystidioid elements on stipe (LLN 93.04.18-1). Scale = 10 μ m.

differentiated: hyphae in the pileal and lamellar trama of *C. grossula* are markedly inflated (reaching 22 μ m in diameter) and constricted at the septa (cf. Fig. 7) while those of *P. ericetorum* are narrower (4-10 μ m) and not normally swollen at the septa [cf. Bigelow, 1970]. Additionally, *P. ericetorum* is lichenized with the basidiomes surrounded by a thallus composed of small sphaerules. This species, unlike *C. grossula*, frequently develops a fairly conspicuous pubescent vestiture on its stipe.

CHRYSOMPHALINA CLÉMENÇON

Given the anatomical similarities between *Chrysomphalina grossula* and *C. chrysophylla* outlined earlier, we consider the two species to be congeneric. *Chrysomphalina chrysophylla* is the type species for the genus *Chrysomphalina* Clç. (non Haas, see Redhead 1986). Cléménçon (1982a) validated *Chrysomphalina* to accommodate two omphalinoid species, *C. chrysophylla* and *C. strombodes* (Berk. & Mont.) Clç. We interpret the genus differently, restricting *Chrysomphalina* to species having a hymenium which thickens over an extended life-span by the production of basidia of different lengths on short subhymenial cells (see Cléménçon 1982a, Kost 1986a, Kühner 1928). In *C. chrysophylla* the combination of hymenial thickening and short subhymenial cells was so conspicuous that Cléménçon coined the term "pachypodial trama" for it. This tissue is formed, but to a lesser extent, in *C. grossula*. A third species, *C. aurantiaca* (Peck) Redhead, also exhibits this phenomenon; however, here the pachypodial trama is even less well-developed than in *C. grossula*. We consider the development of this type of hymenium to be not only taxonomically significant as emphasized by Cléménçon, but indicative of a possible linkage to the Cantharellaceae, as suggested by Kühner (1928) and Kost (1986b) (See also Arpin & Fiasson 1971 and Tyler 1971). *Chrysomphalina*, as represented by the type species, also shares with *Cantharellus* the presence of intracellular carotenoid pigments (Arpin & Fiasson 1971, Kost 1986b, Kühner 1980). Other important features of the three *Chrysomphalina* species are monomitic tissues, strictly lignicolous habit associated with white rot, and the absence of clamp connections on all tissues.

Included in the genus are five taxa -- the type species *C. chrysophylla* with three varieties [*C. chrysophylla* var. *chrysophylla*, *C. chrysophylla* var. *salmonispora* (Bigelow) comb. nov. (Basionym: *Omphalina chrysophylla* var. *salmonispora* Bigelow. Mycologia 62: 22. 1970.), and *C. chrysophylla* var. *hoffmanii* (Peck) stat. et comb. nov. (Basionym: *Agaricus hoffmanii* Peck, New York State Mus. Rept. 24: 60. 1872.)], *C. aurantiaca*, and *C. grossula*.

Key to *Chrysomphalina* species

1. Basidiomes typically uniformly orange colored (pileipellis and stipitipellis concolorous with context; only bright yellowish to rosy orange pigments present); pileus margin fringed by hair-like concolorous scales, at least when young.....*C. aurantiaca*
1. Basidiomes typically bi-colored (pileipellis typically more darkly colored than context; both an intracellular brownish or greenish fuscous pigment and a yellowish or orange pigment present); pileus either glabrous or subglabrous, or if scaly, with darker scales confined to the central region2
2. Basidiomes bright greenish-yellow when young, becoming yellower or paler with age but not exhibiting orangish hues at any stage; tramal cells frequently femur-like at maturity (cf. Fig. 7); basidiospores with broadly rounded ends (cf. Fig. 3)*C. grossula*

(Bresadola 1881, 1928). Its protologue reads very much like that for *A. chrysoleucus*: Pileus "griseocanus", lamellae "distantes...laete flavae", and stipe "albo-griseus". We believe *A. chrysoleucus* is more likely to be synonymous with *Clitocybe xanthophylla* than with *C. grossula*. However, even this synonymy is questionable (cf. below).

Fries (1818) appears to have misapplied the name *A. chrysoleucus* Pers. to a species having broad yellow lamellae and occurring on bare earth in Sweden, and subsequently (Fries 1821) applied the name *A. chrysoleucus* to yet another species with a deeply umbilicate pileus and narrow lamellae. By 1830 Fries considered *A. chrysoleucus* a dubious species, possibly a form of *Agaricus melizeus*. Later Fries (1832) listed *A. chrysoleucus* twice with two different authorities, "Pers." and "Fr.", in the index to the *Systema Mycologicum*, clearly indicating that he had earlier misapplied the name *A. chrysoleucus* to a different fungus from that described by Persoon. In 1838 Fries no longer synonymized *A. chrysoleucus* Pers. with the hygrophoroid *A. melizeus*, considering the former a yellow-gilled lignicolous form of *A. umbelliferus* [possibly *Phytoconis luteovitellina* (Pilát & Nannfeldt) Redhead & Kuyper]; at this time he recognized *A. chrysoleucus* Fr. as a distinct taxon. The lignicolous yellow-gilled form described by Fries (1838) may have been either a *Gerronema* or *Chrysomphalina*.

Given this history of confusion, we prefer to drop the name *A. chrysoleucus* from usage, considering it a *nomen confusum*.

Generic placement

The taxon under discussion has most often been treated as an omphalinoid species. For instance, Bigelow included *C. grossula* in *Omphalina* as *O. wynniae*, while Singer, after initially (1961b, 1962) placing it in *Omphalina* as *O. grossula*, later incorporated the species in *Gerronema* (Singer 1975, 1986). Bigelow and Singer's differing circumscriptions of *Omphalina* and selected segregate omphalinoid genera will be fully explored in Part 2.

Some authors, however, have emphasized the similarities between *C. grossula* and hygrophoraceous species. Cléménçon (1982b) placed *C. grossula* into *Camarophyllus* subgenus *Aeruginospora* because it appeared to have a highly irregular hymenophoral trama and because the basidiomes sometimes appear slightly greenish, linking it to the putatively green-spored type of the subgenus. As typified by *C. pratensis* (Pers.: Fr.) Kumm., *Camarophyllus* is a typically hygrophoraceous genus with elongated basidia characterized by having a distinctly irregular lamellar trama and a terrestrial habit. Out of the five *Camarophyllus* sections accepted by Singer (1986), only section *Aeruginospora* is characterized by clampless hyphae. Notably all three species included by Singer in this section are not lignicolous, which clearly makes inclusion of the lignicolous *C. grossula* an anomaly. Furthermore, *C. grossula* does not have a typically irregular lamellar trama. In our opinions, the species is not closely allied to *C. pratensis* and does not belong in the Hygrophoraceae. Kuyper (1986) reached a similar conclusion in his cladistic analysis of European omphalinoid genera.

Excluded species: In our classification, *Chrysomphalina strombodes* is not congeneric with *C. chrysophylla*. Microscopical examinations of both North American and European collections (see specimens examined) have revealed that taxa identified as *C. strombodes* on both continents form basidiomes composed of sarcodimitic tissues and therefore should be retained in *Gerronema*. Additionally, they represent two taxa: a North American species with minute dark brown to blackish appressed squamules on the pileus composed of fascicles of clavate to clavate-pedicellate pileocystidia with brown cellular contents (Fig. 14) and a European species with innately radiating fibrils, wholly lacking pileocystidia and resulting squamules. As the name *Gerronema strombodes* applies to the North American species (Fig. 12), originally described from Ohio, another name must be used for the European species (Fig. 13). Given our doubts about the name *A. chrysoleucus*, the next available epithet is *Clitocybe xanthophylla*, for which authentic material has been examined. We therefore propose for the European species the name ***Gerronema xanthophyllum* (Bres.) comb. nov.** [**Basionym** = *Clitocybe xanthophylla* Bres. Fungi Tridenti Vol 1: 8. 1881. **Synonyms** = *Omphalia hypoxantha* Bres. nom. nov. Icon. Mycol. VI. Tab CCLIX 1928. (non *Omphalia xanthophylla* (Berk. & Curt.) Sacc. Syll. Fung. 5: 312. 1887 = *Agaricus (Omphalia) xanthophyllum* Berk. & Curt. Ann. Mag. Nat. Hist. 4. 1859.) = *Omphalia bresadolae* R. Maire nom. nov. Ann. Mycol. 11: 338. 1913.]

SPECIMENS EXAMINED *Chrysomphalina aurantiaca*: NORTH AMERICA:

CANADA: BRITISH COLUMBIA: Glacier Natl Park, Illecillewaet River -- IX.9.1980 Redhead 3533 (DAOM 184112, **NEOTYPE**). **USA: CALIFORNIA: Mendocino Co, Rockport -- XII.31.1968** JWLennox 150'b. **WASHINGTON: Chelan Co, Rainy Pass -- LLN 93.08.03-3, coll. JFAmmirati & TWKuyper; Clallam Co, Olympic Natl. Pk., Sol Duc Falls -- LLN 92.10.14-4, LLN 92.10.14-7; King Co, Redmond -- XI.24.1979, FVdBogart 3980. Lewis Co, Cispus -- X.22.1972** Stuntz 17500; **San Juan Co, Friday Harbor -- XII.8.1974** SLibonati-Barnes 408; **Yakima Co, White Pass: Clear Lake -- VI.4.1989** JFA 9905 coll. LBaxter.

***Chrysomphalina chrysophylla* var. *chrysophylla*: NORTH AMERICA:**

CANADA: ALBERTA: Kanaskis Valley, Marmot Creek Basin -- VII.13.1972 RMDanielson 308 (DAOM 143591). **BRITISH COLUMBIA: Vancouver Island, Pacific Rim Natl Park, Long Beach -- IX.29.1979** SARedhead 3247 (DAOM 175260). **QUEBEC: L'Islet co, Elgin Rd -- X.19.1949** HACJackson (DAOM 84909). **USA: OREGON: Coos Co, Beaver Hill Forest -- X.24.1986** CArdrey; **IX.4.1989, C. Ardrey 1429; Multnomah Co, Estacada -- LLN 91.12.30-4, coll. LLN & JRogers. WASHINGTON: King Co, Seattle -- XI.12.1956** Stuntz 9776, coll. Bell & Stuntz; **Pierce Co, Mt. Rainier Natl Park, Lower Tahoma Creek -- IX.12.1948** Stuntz 4421, det. AHSmith; **San Juan Co, Friday Harbor -- IX.17.1979** FVdBogart 3920. **WYOMING: Teton Co, Flagstaff Road -- VIII.12.1987** JFAmmirati 9525.

***Chrysomphalina chrysophylla* var. *hoffmanii*: NORTH AMERICA:**

CANADA: BRITISH COLUMBIA: Mt. Revelstoke Natl Park, Illecillewaet Riv. -- IX.27.1980 SARedhead 4124 (DAOM 181086). **USA: WASHINGTON: Ferry Co, White Mountain, HWY 20 -- VII.1.1993, SAR 7700** coll. Ammirati, Norvell, Redhead & Seidl.

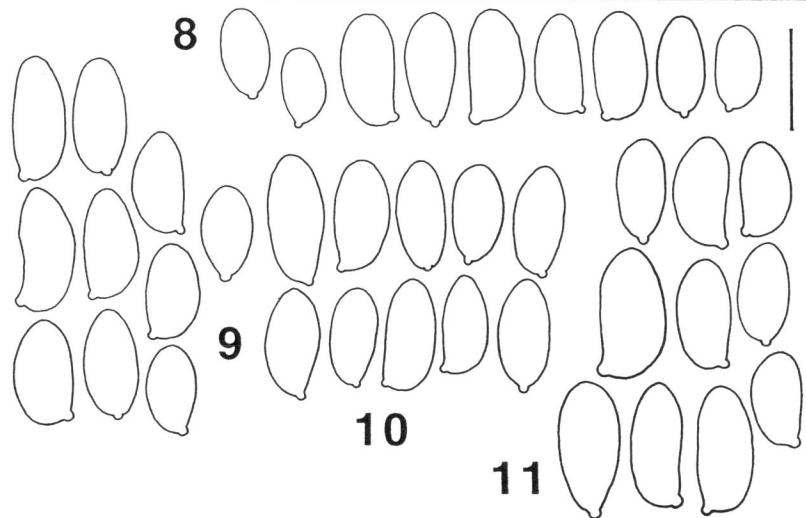
***Chrysomphalina chrysophylla* var. *salmonispora*: NORTH AMERICA:**

USA: WASHINGTON: Chelan Co, Rainy Pass -- LLN 93.08.03-2b, coll. JFAmmirati.

***Chrysomphalina grossula*: See under species description above.**

2. Basidiomes with orange (orange, pinkish orange, or orangish yellow), never greenish tints; tramal cells rarely femur-like; basidiospores elongated, with many slightly tapered toward the apex (cf. Figs. 8-10)3
3. Pileipellis either glabrous or subglabrous, lacking dark scales on disc.....*C. chrysophylla* var. *hoffmanii*
3. Pileipellis with definite dark scales on disc and inner margin.....4
4. Basidiomes with orange or orangish yellow tints, lacking pinkish or salmon tones.....*C. chrysophylla* var. *chrysophylla*
4. Basidiomes with pinkish-orange or salmon tones.....
.....*C. chrysophylla* var. *salmonispora*

We believe *C. chrysophylla* var. *salmonispora* may be a color variant with either different carotenoids or a different mixture of carotenoids from those found in *C. chrysophylla* var. *chrysophylla*. Although *C. chrysophylla* var. *hoffmanii* may be no more than a growth form, it is impossible to tell from current data whether the smooth pilear condition is genetically or environmentally controlled; some collections (e. g. Stuntz 9776) range from the glabrous to the scaly condition. Additionally the spores are virtually identical in all three varieties (Figs. 9-11) and differ subtly from *C. grossula* (Fig. 3) and *C. aurantiaca* (Fig. 8).



Figs. 8-11. Basidiospores. **Fig. 8.** *Chrysomphalina aurantiaca* (LLN 93.08.03-3). **Fig. 9.** *Chrysomphalina chrysophylla* var. *chrysophylla*. (CArdrey 1429). **Fig. 10.** *C. chrysophylla* var. *hoffmanii* (SARedhead 7700). **Fig. 11.** *C. chrysophylla* var. *salmonispora* (LLN 93.08.03-2b). Scale = 10 μ m.

PART 2: *OMPHALINA sensu BIGELOW*

Omphalina was erected by Quélet (1886) for white-spored, centrally stipitate mushrooms with thin umbilicate or tubaeform pilei, decurrent lamellae, and cartilaginous stipes. From this macroscopical circumscription the terms "omphalioid" and "omphalinoid" were derived, i.e. "any mushroom [of small stature \approx 1-2 cm diam.] with decurrent or subdecurrent gills, a cartilaginous stipe, a broadly convex to depressed pileus, a slightly to markedly depressed pileal disc, and lacking an annulus and a volva" (Largent & Baroni 1988).

Microscopical observations, however, suggest that this is a polyphyletic group, with parallel evolution having produced morphologically similar but anatomically distinct taxa. This view is consistent with recent segregations of genera from *Omphalina sensu lato* by taxonomists apparently seeking monophyletic genera within a more natural classification system.

Chrysomphalina, one such segregate genus, has already been outlined above. Other recently described or redefined genera (i.e. *Gerronema*, *Pseudoarmillariella*, *Haasiella*, *Rickenella*, and *Phytoconis*) are discussed below, followed by an evaluation of the genus *Omphalina* itself. A key to the genera as we accept them and expanded generic descriptions follow this discussion.

GERRONEMA Singer: Singer (1951b) erected the genus *Gerronema* to accommodate three tenacious omphalinoid to clitocybeoid species from South America. He later (1964) transferred some species traditionally placed in *Omphalina* to *Gerronema*. Problems have arisen from the different circumscriptions of *Omphalina* by Singer and Bigelow. Virtually all the species recognized in Bigelow's 1970 monograph of *Omphalina* are included in Singer's expanded concept of *Gerronema* (Singer 1986), while Bigelow's concept of *Clitocybe* (Bigelow 1982a&b, 1985) encompassed any species left by Singer (1986) in *Omphalina*. In both classification systems, the primary distinction between the paired genera, either *Omphalina sensu* Singer and *Gerronema sensu* Singer or *Clitocybe sensu* Bigelow and *Omphalina sensu* Bigelow is pigment-based. Singer distinguishes *Omphalina* from *Gerronema* almost solely on the presence of fuscous, intraparietal or incrusting pigments, present in the former and absent in the latter. Bigelow's circumscription of *Omphalina* revolves around the presence or suspected presence of carotenoids in all included species. Neither author analyzed pigments in the species each treated.

Pigmentation evidently either carried more weight than other taxonomic characters or appeared to be the strongest taxonomically important feature in the absence of other observed characters. However, *Gerronema sensu* Singer (1961a, 1964, 1975, 1986) is considered by many authors to be heterogeneous (i.e. Cléménçon 1982, Moser 1983, Kuyper 1986), and several attempts have been made to reduce it to a more natural group. We agree *Gerronema sensu* Singer is heterogeneous and believe that *Omphalina sensu* Singer (1986) is also heterogeneous, but to a lesser extent. Lange's (1981. See also 1992) expansion of *Omphalina* to include *Gerronema*, *Haasiella*,

Gerronema strobodes: NORTH AMERICA: USA: CONNECTICUT: New London Co, Pachaug St. Forest. -- VIII.4.1988 coll. unknown [N.E. Mycol. Foray] (DAOM 199314). NORTH CAROLINA: Swain Co, Great Smoky Mtns. Natl. Park -- VII.19.1988 D.E. Desjardin 4616 (DAOM 199312).

Gerronema xanthophyllum: EUROPE: ITALY: --1901 JBresadola (ex herb Bresadola, NY). SWITZERLAND: Lucerne Cn: Ruswil, Rotbachtobel -- VI.15.1981 JBächler 1506-81 BA 5 (LU); Adlingenswil, Meggerwald -- VII.13.1989 FKränzlin 1307-89 K 1 (LU).

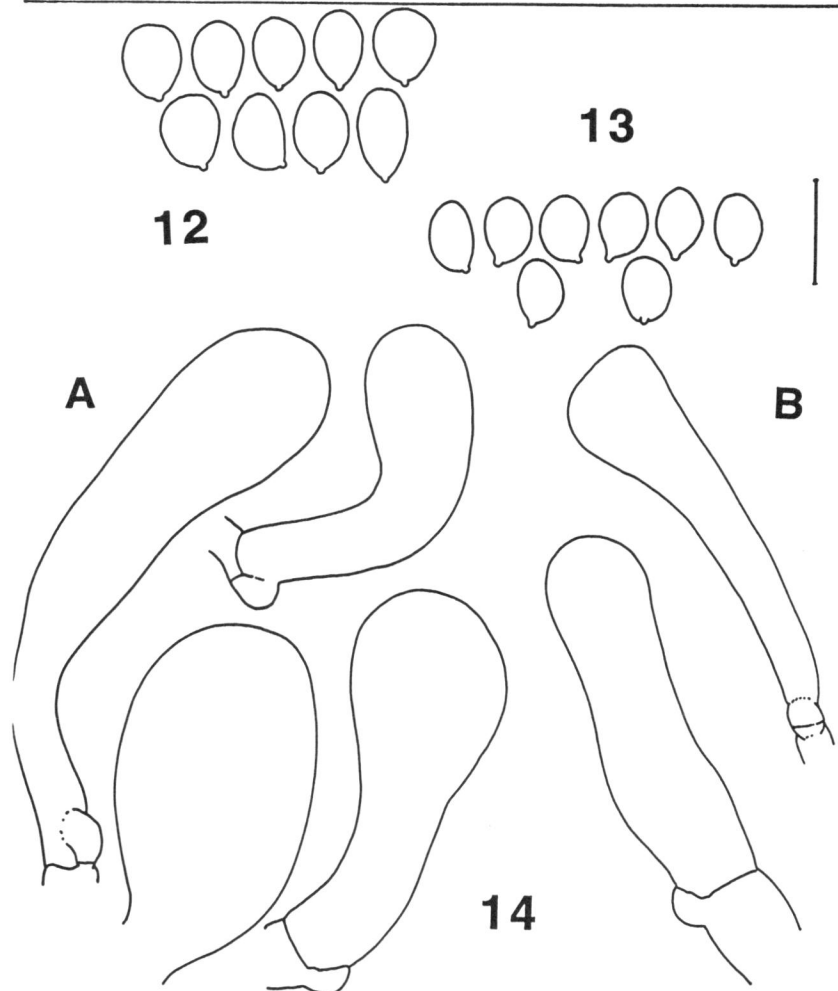


Fig. 12. *Gerronema strobodes*. Basidiospores.(DAOM 199314). **Fig. 13.** *Gerronema xanthophyllum* Basidiospores. (LU FK 1307-89 K1). **Fig. 14.** Pileocystidia in *Gerronema strobodes*. **A.** (DAOM 199314). **B.** (DAOM 199312). Scale = 10 μ m.

PSEUDOARMILLARIELLA (Singer) Singer: Bigelow (1982a) transferred *Agaricus ectypoides* Peck, the type for *Pseudoarmillariella*, to the genus *Omphalina*. By including *A. ectypoides* in *Omphalina*, he radically modified his 1970 concept of the genus which excluded species with amyloid spores. Although he did not so specify in published articles, Bigelow stated to Redhead in 1985 that he based this transfer upon the many similarities between *P. ectypoides* and *C. chrysophylla*.

The monotypic genus *Pseudoarmillariella* is characterized by the production of a thickened hymenium and subhymenium (Singer 1956). Its subhymenium is said to be "subirregularly intermixed-subramose, its elements short, strongly interlaced-curved in all directions and therefore at times appearing cellular (much like the subhymenium of *Cantharellula*)" (Singer 1986). *Pseudoarmillariella ectypoides* differs from all *Chrysomphalina* species by the production of incrusting pileal pigments, amyloid spores and the formation of clamp connections. This indicates a sufficient hiatus to recognize *Pseudoarmillariella* as distinct from *Chrysomphalina*.

HAASIELLA Kotlaba & Pouzar: *Haasiella venustissima* (Fr.) Kotl. & Pouzar (1966), the type of the genus, and *Chrysomphalina chrysophylla* were originally considered to be congeneric by Haas who invalidly proposed the genus "*Chrysomphalina* Haas" in 1962. Clemençon (1982a) excluded *H. venustissima* from *Chrysomphalina* Clç. when he validated the genus.

Like *Chrysomphalina* and *Cantharellus*, *Haasiella* possesses carotenoid pigments (Arpin & Fiasson 1971). However, it differs from *Chrysomphalina* by the formation of thick, metachromatic basidiospore walls (Kotlaba & Pouzar 1966) and a slightly gelatinized pileipellis (Kost 1986b). Both recognized species of *Haasiella* are distinctly terrestrial in contrast to the lignicolous *Chrysomphalina* species, and one, *H. splendidissima* Kotl. & Pouz., forms clamp connections.

Singer (1986) recognized *Haasiella*, but only as a section of *Gerronema*. However, since basidiomes of both species in his section are composed of monomitic tissues, the species are excluded from *Gerronema* in our classification. *Haasiella* is only known from Europe and was not treated by Bigelow (1970) in his North American monograph. Lange (1981) includes this genus in *Omphalina sensu lato*.

RICKENELLA Raithelhüber: Although not accepted in *Omphalina* by Bigelow, he questioned generic placement of the type species, *R. fibula* (Bull. : Fr.) Raithelh. (Bigelow 1970). *Rickenella* was distinguished from *Gerronema sensu lato* by Raithelhüber (1973) based on the presence of prominent characteristically shaped leptocystidia abundantly covering the pileus, stipe, and hymenial surface. These same features serve to distinguish *Rickenella* from *Omphalina*. *Rickenella* has been widely accepted by European and North American agaricologists (notably Kost 1984, Lamoure 1979) and we accept the genus as presently circumscribed.

All *Rickenella* species are small, omphalinoid, and bryophilous; the species are known to colonize either mosses or liverworts (Redhead 1981, Kost

Rickenella, and *Phaeotellus*, thus reflecting the historical basis of *Omphalina*, is appealing because of its simplicity, but clearly, it also represents a polyphyletic grouping.

In the case of *Omphalina sensu* Singer (1986), emphasizing pigmentation based primarily upon a generalized pathway leading to melanization (see Ellis & Griffith 1974; Hegnauer et al. 1985; Swan 1974) appears to us to result in an artificial classification. Notably, there are many genera in the Agaricales *sensu* Singer and in the Cantharellaceae that include species with more than one pigment group. In our opinion, dependence upon the presence or absence of especially common pigment groups, such as melanin, to define genera is perhaps unwise; in this case, pigmentation should be used judiciously or in conjunction with other taxonomic features. We believe that a combination of anatomical and biological characters clearly requiring a series of complex genetic expressions are of greater importance. Molecular analyses of DNA, such as that being conducted by Lutzoni and Vilgalys (1993), would be even more instructive.

The fact that the basic structural tissue forming the basidiomes of certain genera is sarcodimitic -- in contrast to monomitic, dimitic, or trimitic -- is of fundamental taxonomic importance, because the formation of sarcodimitic tissues is a complex series of processes requiring the expression of many genes. However, the extent to which sarcodimitic tissue formation can be used as an important taxonomic indicator of different evolutionary pathways lies somewhere between the extremes at the generic (i. e. *Trogia*, cf. Corner 1966, 1991) or family (i.e. Xerulaceae, cf. Redhead 1987) levels and

schemes in which the presence of sarcodimitic tissue is not taken into account, ignored, or dismissed (Singer 1986, Reijnders 1993). Sarcodimitic tissue formation can be used to help define genera or generic groupings (Vilgalys & Rehner 1993).



Redhead (1986) restricted the genus *Gerronema* to species having sarcodimitic tissues. Subsequent confirmation of sarcodimitic construction in *G. melanomphax* Sing. (the type of the genus) was made by Redhead from an isotype (Singer T-1094 at MICH; Fig. 15). Species lacking sarcodimitic tissues and transferred to *Gerronema* after its inception are thereby excluded. By further delimiting the genus in this way, a more natural group is defined.

Fig. 15. *Gerronema melanomphax* (Isotype Singer T-1094 (MICH). Basidium, basidiolate, and, basidiospores. Scale = 10 μ m.

Omphalina species generally lack distinctive hymenial cystidia and highly differentiated cuticles (but exceptionally can have cystidioid end cells or scales, *i.e.* *O. sphagnicola* (Berk.) Moser). *Omphalinas* have smooth, thin-walled, inamyloid spores. Anatomically *Omphalina* differs from both *Chrysomphalina* and *Phytoconis* by the relatively narrow, compact subhymenium composed of short basidia-bearing cells; this tissue, which binds the hymenium more tightly than does the subhymenium of *Phytoconis*, is best observed in squash mounts. Therefore, basidia and basidioles in *Phytoconis* species tend to spread out relatively easily while those of *Omphalina* tend to spread out in rafts or sections of hymenium. We include in *Omphalina* several species groups largely separated by differences in pigmentation. We do not restrict the genus to species with darkly melanized incrustations or intraparietal pigments as does Singer (1986). Examples of differently pigmented species are: *O. postii* (Fr.) Singer (orangish intraparietal pigments), *O. viridis* (Hornem.) Kuyper (blue-green/blackish incrusting pigments), *O. pyxidata* (brownish incrusting pigment) and *Omphalina hohensis* (Smith) *comb. nov.** (greyish black incrusting pigments) *Basionym = *Omphalia hohensis* A.H. Smith, Contr. Univ. Mich. Herb. 5: 27. 1941. Delimitation from *Arrhenia* Fries (including *Phaeotellus* Kühner & Lamoure and *Leptoglossum* Karst. cf. Redhead 1984) is open to reevaluation using molecular analysis.

DISPOSITION OF *OMPHALINA SENSU* BIGELOW 1970

Most of the twelve species and one variety Bigelow (1970) included in *Omphalina* are placed elsewhere following the generic classification for omphalinoid agarics outlined above.

As discussed in Part 1, five taxa belong in *Chrysomphalina*: *O. chrysophylla* (Fr.) Murrill var. *chrysophylla* = *C. chrysophylla* var. *chrysophylla*, *O. chrysophylla* var. *salmonispora* = *C. chrysophylla* var. *salmonispora*, *O. hoffmanii* = *C. chrysophylla* var. *hoffmanii*, *O. luteicolor* Murrill = *C. aurantiaca* (Redhead 1986), and *O. wynniae* = *C. grossula*.

Four other species were transferred to *Phytoconis* by Redhead & Kuyper (1987, 1988): *O. ericetorum* = *P. ericetorum*, *O. luteovitellina* (Pilát. & Nannf.) M.Lange = *P. luteovitellina*, *O. hudsoniana* (Jenn.) Bigelow = *P. viridis*, and *O. sphagnophila* (Peck) Bigelow = *P. ericetorum*.

Omphalina subclavata (Peck) Murr. is now *Gerronema subclavatum* (Peck) Redhead (Redhead 1986).

Of the remaining three species treated by Bigelow, *Omphalina postii* (Fr.) Sing. remains in the genus *Omphalina*. We do not consider the tissues in the stipes of *O. postii* or the related species *Omphalina marchantiae* (Sing. & Clç.) *comb. nov.* (Basionym = *Gerronema marchantiae* Sing. & Clç. Schweiz. Zeitschr. Pilzk. 49: 118. 1971.) to be sarcodimitic as suggested by Senn-Irlet et al. (1990). *Omphalina marchantiae* has been reported from Alaska (Laursen & Ammirati 1982, Laursen & Chmielewski 1982) and British Columbia (Kroeger 1989) in North America since Bigelow's 1970 monograph.

1984) and pure isolates form distinctive slow-growing colonies (Lamoure 1979). This complex of features amply characterizes the genus. Additionally Kost (1984) has drawn attention to the physalomic nature of the tramal tissues in this genus (physalomic hyphae = conspicuously inflated hyphae deeply indented at the septa, see Clémenton 1982a).

Taxa now assigned to *Rickenella* have been placed into various genera by different authors attempting to create a natural classification. The two most common species, *R. fibula* (Bull.: Fr.) Raitheh. and *R. swartzii* (Fr.) Kuyp., were included in *Omphalina* at its inception (Quélet 1886), and Lange again accepted this generic placement in 1981. However, Kühner (1938), Smith (1947), and Bigelow (1970) included *Rickenella* species in the genus *Mycena*. In 1943 Singer treated them in his genus *Hemimycena*, but by 1951 he considered *Hemimycena* congeneric with *Marasmiellus*, including its cystidiate species in *Marasmiellus*, sect. *Fibulae*. Subsequently Singer (1961) transferred the species in section *Fibulae* to the genus *Gerronema*. When Singer (1962) resurrected *Hemimycena* as a distinct genus, he left section *Fibulae* in *Gerronema*. We recognize this section as the genus *Rickenella*.

PHYTOCONIS Bory de St. Vincent: As circumscribed by Redhead & Kuyper (1987, 1988), *Phytoconis* is comprised of species previously treated in *Gerronema* and *Omphalina* (Singer 1986). *Phytoconis* was delimited primarily on the basis of lichenization and secondarily by the presence of a leptomic hyphal system (used by Kuyper, 1986). Molecular analysis of the 25S rRNA gene of these lichenized species indicates that *Phytoconis* is a monophyletic genus linked to *Omphalina* (Lutzoni & Vilgalys 1993).

Notably, the genus includes both species with intracellular bright pigments and species with intraparietal and incrusting melanized pigments. The complex, unique, and characteristic nature of the fungal sheaths formed by these species (as detailed by Redhead & Kuyper, 1987) offers ample evidence of the close relationship among them. Additionally the subhymenium in *Phytoconis* species is loosely structured due to the elongated subhymenial cells and lack of clamp connections. In this regard *Phytoconis* differs from *Omphalina sensu stricto*.

OMPHALINA Quélet: Although this generic name is central to the discussion of omphalinoid genera, its usage is the most controversial and unstable. A major problem lies in the typification of the name. The first lectotype was *Omphalina hydrogramma* (Fr.) Quél., selected by Earle (1909); however, this typification could be superseded by *O. umbellifera* (Fr.: Fr.) Quél. (proposed by Singer & Smith, 1946; Jørgensen & Ryman, 1989), by *O. epichysium* (Pers.: Fr.) Quél. (proposed by Redhead & Weresub, 1978; Redhead & Kuyper, 1993), or by *O. pyxidata* (Pers.: Fr.) Quél. (submitted as an alternative by Redhead, 1993).

We have provisionally adopted *O. pyxidata* as type of the genus since it has to date received the strongest support in the Committee for Fungi and Lichens of the International Association for Plant Taxonomists. We restrict *Omphalina* to a primarily bryophilous group of species centered around *O. pyxidata*.

3. Context of pileus and/or stipe composed of typical sarcodimitic tissues [*spores thin-walled, lignicolous, (primarily found in sub-tropical/tropical regions)*]......**Gerronema**
3. Context of neither stipe nor pileus composed of sarcodimitic tissues [*other features variable*]......**4**
4. Spore walls conspicuously thickened and metachromatic in cresyl blue [*basidiomes orange, possessing carotenoids, terrestrial. EXTRALIMITAL -- European*]......**Haasiella**
4. Spore walls thin, not metachromatic [*other features variable*]......**5**
5. Thalli lichenized, composed of minute sphaerules or squamules while superficially appearing to be terrestrial, bryophilous or lignicolous; walls of hyphae which connect sphaerules or irregular granules and basal mycelium noticeably thickened from slight to > 0.5 um [*clamp connections lacking, context of basidiomes leptomitc, subhymenial layer a loose structure not forming a sealed compact membrane*]**Phytoconis**
5. Thalli not lichenized, typically mycelial and mostly embedded in substrate (terrestrial, bryophilous, lignicolous); walls of basal mycelium not thickened [*other features variable*]**6**
6. Basidia of +/- conspicuously unequal lengths with the subhymenium +/- developing into a pachypodium, hymenium thickening with age [*basidiomes brightly coloured by carotenoids {yellow, orange, yellow mixed with green}, lignicolous, clamps lacking*]**Chrysomphalina**
6. Basidia more or less terminating at the same level, subhymenium a thin layer; hymenium not thickening in age [*other features variable*]......**7**
7. Basidiomes brightly pigmented and pileipellis gelatinized to subgelatinized with a thin but distinct cutis [*pileus minute, clamp connections present, bryophilous*]......**Hygrocybe luteo-omphaloides**
7. Basidiomes not both brightly pigmented and with a gelatinized pileipellis [*other features variable*]**8**
8. Bryophilous or phycophilous (sometimes appearing terrestrial or lignicolous due to sparse growth of associated algae or bryophytes), never on sound clean wood or conspicuously causing white or brown wood rots [*with incrusting or intraparietal pigments, odor never farinaceous, subhymenium a compact dense thin layer totally sealing in the lamellar trama from the hymenium*]......**Omphalina**

Two species of *Omphalina sensu* Bigelow -- *O. occidentalis* (A.H.Sm.) Big. and *O. olivaria* (Peck) Sing. -- remain, both of uncertain status.

When Smith (1941) first described *Omphalia occidentalis*, he compared it with both *Mycena* and *Hygrophorus*, noting its ambiguous taxonomic affinities. Bigelow (1970) also felt that *O. occidentalis* was poorly delimited from *Hygrocybe* and arbitrarily retained it in *Omphalina*. It appears to us that this species may be closely allied to species such as *Hygrocybe parvula* (Peck) Murr. and *Hygrophorus* (section *Hygrocybe*) *mycenoides* A.H.Sm. & Hesl., both of which have small yellow basidiomes with length:width basidia ratios that overlap those for *O. occidentalis* (cf. Hesler & Smith 1963). The presence of clamp connections and a thin ixocutis in *O. occidentalis*, both present in *H. parvula* and *H. mycenoides*, are features more consistent with *Hygrocybe* than with the omphalinoid genera. Bas (1988) noted that strict application of length-width ratios does not apply for many *Hygrocybe* species, and reliance must be made on other features such as bright colors and viscid pileal surfaces, features particularly evident in *O. occidentalis*. Thus, we propose the name ***Hygrocybe luteo-omphaloides* nom. nov.*** for this fungus. ***Basionym** = *Omphalia occidentalis* A.H. Smith, Contr. Univ. Mich. Herb. 5: 28. 1941 **nec** *Hygrocybe occidentalis* (Dennis) Pegler in Pegler & Fiard, Kew Bull. 32(2):310. 1978. **nec** *Hygrophorus occidentalis* Sm. & Hesl. Lloydia 2:18. 1939

The type of *Omphalina olivaria* possesses incrusting pigments in the pileipellis and may in fact be a small *Clitocybe* as suggested by Bigelow (1970). It is known only from the type collected over 100 years ago from a burn in New York State. The name is retained in *Omphalina* on the assumption it was associated with pyrophilous mosses. Bigelow (1970) has already recorded the fact that other reports of *O. olivaria* are based on misdeterminations.

KEY TO SELECTED OMPHALINOID GENERA

1. Cystidia present, densely and evenly distributed over pileipellis, hymenial surfaces, and stiptipellis, visible under a hand lens as small hyaline hairs, usually capitate, not fasciculate [*bryophilous, lacking incrusting pigments, spores inamyloid and thin-walled*]***Rickenella***
1. Cystidia lacking in most species; if present, more limited in distribution, often inconspicuous or poorly differentiated, not capitate, sometimes fasciculate in small squamules [*other features variable*]**2**
2. Spores amyloid [*both incrusting pigments and non-incrusting pigments present simultaneously, lamellar trama complex with thick dense lateral subhymenial zones, hymenium thickening and basidia of different lengths, lignicolous*].....***Pseudoarmillariella***
2. Spores inamyloid [*other features variable*].....**3**

HAASIELLA Kotl. & Pouz.

Basidiomes fleshy, pileus convex, slightly umbilicate; lamellae decurrent, cantharelloid; stipe central and somewhat cartilaginous; spores yellow to salmon rose in mass, lacking a germ pore, walls thickened (double walls present), smooth, inamyloid, hyaline, red metachromatic in Cresyl Blue.

Pileipellis a layer of gelatinized, leptomitoc hyphae often with swollen hyphal ends; containing intracellular carotenoid pigments in the tissues; tramal hyphae thin- to somewhat thick-walled, inamyloid, +/- gelatinized, with or without clamp connections; hymenophoral trama irregular, possibly bidirectional; subhymenium continually producing basidia; hymenium thickening; lacking hymenial cystidia.

Terrestrial.

Type species: *H. venustissima* (Fr.) Kotl. & Pouz.

OMPHALINA Quél.

Basidiomes membranous to fleshy, pileus convex to infundibuliform or umbilicate; lamellae decurrent, regular to cantharelloid; stipe central to eccentric but not lateral, cartilaginous, most often glabrous; spores white in mass, lacking a germ pore, walls thin, smooth, inamyloid, hyaline, and not metachromatic in Cresyl Blue.

Pileipellis relatively undifferentiated from the monomitoc tramal tissue in most species, sometimes with aggregated hyphal ends forming small scales usually restricted to the pileal disc, rarely abundant enough to form an interrupted turf of fasciculate cystidioid elements; often pigmented with dark or brightly colored intraparietal, incrusting, or intracellular pigments; tramal hyphae thin-walled, inamyloid, nongelatinized, usually with but some species without clamp connections; hymenophoral trama bidirectional to irregular; basidia not varying in length; hymenium not appreciably thickening; subhymenium a relatively thin, compact dense layer; poorly differentiated hymenial cystidia present in at least one species concentrated near the lamellar edge; caulocystidia, when present, generally poorly differentiated and ranging from sparse to aggregated in small squamules.

Either bryophilous or lignicolous.

Type species: *O. pyxidata* (Pers: Fr.) Quél. subject to conservation.

PHYTOCONIS Bory

Basidiomes fleshy to membranous, pileus convex, usually umbilicate; lamellae decurrent; stipe central, cartilaginous to tough, usually pubescent; spores white in mass, lacking germ pore, walls thin, smooth, inamyloid, hyaline, and not metachromatic in Cresyl Blue.

Pileipellis relatively undifferentiated from the leptomitoc tramal tissue; hyphae thin to somewhat thickened, inamyloid, nongelatinized, with either fuscous intraparietal pigments or brightly colored intrahyphal pigments; without clamp connections; hymenophoral trama sub-irregular; basidia in older specimens varying in length; hymenium usually slightly thickening with a loose subhymenial structure; lacking cystidia on the pileus and in the hymenium; frequently with cystidioid or hair-like hyphal ends on the stipe.

{A completely pigmentless species associated with algal films on silty soil is *Hemimycena ignobilis* (Josserand) Singer, of debatable generic disposition}

8. Terrestrial or lignicolous, not dependent on living algae or bryophytes; if on wood mycelium clearly penetrating and decaying wood [*easily cultured on standard general media from spores, odor sometimes farinaceous, many species large and not omphalinoid*].....*Clitocybe*

GENERIC CIRCUMSCRIPTIONS

CHRYSOMPHALINA Clç.

Basidiomes fleshy, pileus convex, usually umbilicate; lamellae decurrent, occasionally forking; stipe central and cartilaginous to fleshy; spores white to slightly pigmented in mass, lacking a germ pore, walls thin, smooth, inamyloid, hyaline, and not metachromatic in Cresyl Blue.

Pileipellis relatively undifferentiated from the monomitic tramal tissues, often with projecting loose undifferentiated hyphal ends +/- aggregated into small scales; often containing intracellular darkish pigments in addition to cytoplasmic carotenoids in the tissues; tramal hyphae thin- to somewhat thick-walled, inamyloid, nongelatinized, without clamp connections; hymenophoral trama bidirectional; hymenium thickening, basidia in older specimens conspicuously varying in length, subhymenium a thick layer forming a dense band of tissue in age; lacking hymenial cystidia; sometimes with scattered relatively undifferentiated cystidioid elements on the stipe

Lignicolous.

Type species: *C. chrysophylla* (Fr.) Clç

GERRONEMA Sing.

Basidiomes membranous to elastic, pileus convex to infundibuliform or umbilicate; lamellae decurrent; stipe central, elastic to fleshy or cartilaginous; spores white in mass, lacking a germ pore, walls thin, smooth, inamyloid, hyaline, and not metachromatic in Cresyl Blue.

Pileipellis poorly differentiated, monomitic, often with intracellular pigments differing from those in the trama or hymenium, occasionally with scattered cystidioid elements on the disc; tramal tissue sarcodimitic (hyphae basically of two types: elongated fusoid cells bonded by filamentous branched hyphae, most easily observed in the stipe), inamyloid, +/- gelatinized, and lacking dark intraparietal or incrusting pigments, with or without clamp connections; hymenophoral trama sarcodimitic; hymenium not conspicuously thickening.

Lignicolous.

Type species: *G. melanomphax* Sing.

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Lichenized, characterized by thalli totally enveloping *Coccomyxa* algal cells in non-perforated sheaths of polygon-shaped cells, forming either scattered sphaerules or irregular granules typically less than 1 mm in diameter or flattened/lobed thalli typically less than 1 cm in diameter connected by filamentous hyphae.

On soils, mosses, peat, or decayed conifer wood.

Type species: *P. botryoides* (L.) Bory = *P. ericetorum* (Fr.) Redhead & Kuyper.

***PSEUDOARMILLARIELLA* Sing.**

Basidiomes fleshy, pileus convex, usually umbilicate; lamellae decurrent, often forked; stipe central and cartilaginous to fleshy; spores white to slightly pigmented in mass, lacking a germ pore, walls thin, smooth, amyloid, hyaline, and not metachromatic in Cresyl Blue.

Pileipellis relatively undifferentiated from the monomitic tramal tissues; with incrusting pigments and non-incrusting cytoplasmic pigments simultaneously present; tramal hyphae inamyloid, +/- gelatinized, thin- to somewhat thick-walled, with clamp connections; hymenophoral trama subirregular; hymenium thickening, basidia in older specimens conspicuously varying in length, subhymenium a dense layer with short, intermixed subramose, strongly interlaced elements, curved in all directions; lacking hymenial cystidia; stipe densely covered with thin-walled hair-like hyphal ends.

Lignicolous.

Type species: *P. ectypoides* (Peck) Sing.

***RICKENELLA* Raitelh.**

Basidiomes fleshy, pileus convex, usually umbilicate; lamellae decurrent; stipe central and cartilaginous; spores white in mass, lacking a germ pore, walls thin, smooth, inamyloid, hyaline, and not metachromatic in Cresyl Blue.

Pileipellis relatively undifferentiated from the physalomic tramal tissue; hyphae thin-walled, inamyloid, nongelatinized, and lacking dark intraparietal or incrusting pigments, with or without clamp connections; hymenophoral trama regular; hymenium not thickening; characterized by abundant capitate to non-capitate refractive-walled evenly scattered leptocystidia on the pileus, hymenial surfaces, and stipe.

Bryophilous.

Type species: *R. fibula* (Bull.: Fr.) Raitelh.

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