Omphalina sensu lato in North America 3: Chromosera gen. nov.*

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Redhead, S. A., J. F. Ammirati & L. L. Norvell (1995). *Omphalina sensu lato* in North America 3: *Chromosera* gen. nov. – Beih. Sydowia X: 155–167.

Omphalina cyanophylla and Mycena lilacifolia are considered to be synonymous. A new genus Chromosera is described to acccommodate C. cyanophylla. North American specimens are described. Variation in the dextrinoid reaction of the trama is discussed as is the circumscription of the genus Mycena. Peculiar pigment corpuscles are illustrated.

Keywords: Agaricales, amyloid, Basidiomycota, dextrinoid, *Corrugaria*, *Hydropus*, *Mycena*, *Omphalina*, taxonomy.

We have repeatedly collected – and puzzled over – an enigmatic species commonly reported in modern literature under different names: *Mycena lilacifolia* (Peck) Smith in North America (Smith, 1947, 1949; Smith & al., 1979; Pomerleau, 1980; McKnight & McKnight, 1987) or Europe (Horak, 1985) and *Omphalia cyanophylla* (Fr.) Quél. or *Omphalina cyanophylla* (Fr.) Quél. in Europe (Favre, 1960; Kühner & Romagnesi, 1953; Kühner, 1957; Courtecuisse, 1986; Krieglsteiner & Enderle, 1987). The species is well characterized macroscopically. It is lignicolous with an omphalinoid habit, viscid yellow pileus and stipe, and strikingly differently colored lamellae which are either bluish, lilac, or rosy depending upon pigment intensity. Because it is relatively undifferentiated microscopically (discussed below), the species has been the subject of continual taxonomic debate concerning its generic placement.

In older taxonomic works the fungus was considered to be a classical omphalioid species and placed in *Agaricus* (*Omphalia*), *Omphalia*, or *Omphalina* (Fries, 1863; Peck, 1872; 1878; 1892; Quélet, 1872; 1886; Murrill, 1916). Singer, the first contemporary mycologist to reexamine the species using a staining reagent (Melzer's), reported that the basidiospores and hyphae in the trama of the type of *Agaricus lilacifolius* Peck were nonamyloid (Singer, 1942: 105). He considered

 $^{^{\}ast}$ This paper is dedicated to Professor M. Moser on the occasion of his seventieth birthday.

Peck's species comparable to another lignicolous fungus, *Clitocybe violaceifolia* Murrill, and therefore transferred it to *Clitocybe*.

Smith (1947), aware of Singer's disposition of A. lilacifolius in Clitocybe, considered the species more closely allied to lignicolous Mycena species with viscid stipes. He placed Peck's species into Mycena subg. Glutinipes Sect. Caespitosae. Smith confirmed Singer's observations on the basidiospores but contradicted Singer's report that the trama was unreactive. Smith (1947) reported that the trama of his specimens became 'reddish brown to more or less vinaceous brown in iodine.' He further noted, 'This is a rather anomalous species by virtue of its gill color, nonamyloid spores, and deep reddish-brown flesh of the pileus in iodine. The iodine reactions of the flesh of the pileus are not vinaceous as in other members of this group.' Smith (1949) subsequently published an additional description with a stereoscopic colour illustration, reiterating his opinion that the species belonged in Mycena.

In 1951 Singer (p. 353) subsequently accepted Smith's disposition of the species in *Mycena*, writing, 'It is obvious that this species does not belong in *Omphalina* but it has nonamyloid spores and nonamyloid tissue, and it cannot be considered as belonging in *Mycena* unless the genus *Mycena* is emended so as to accommodate species without any positive iodine reaction. If one studies carefully the taxonomy of the small Clitocybes and that of the glutinous and viscid Mycenas, one is led to prefer Smith's solution.' As a result he modified his concept of *Mycena* and has since accepted *M. lilacifolia* in his 'Agaricales in Modern Taxonomy' series (Singer, 1951; 1962; 1975), naming it in the most recent edition as type of a new subsection, *Mycena* sect. Hygrocyboideae subsect. Lilacifolinae (Singer, 1986: 412).

A different opinion has been expressed by Maas Geesteranus (1980), who – uncertain as to where to place *M. lilacifolia* – ultimately specifically excluded Peck's species from *Mycena* (Maas Geesteranus, 1984: 240): 'A species with non-amyloid spores, devoid of cheilocystidia, and with a lamellar trama that remains unchanged in Melzer's reagent is not a member of *Mycena*.' It follows that in his compilation, Maas Geesteranus (1992) did not account for the combination of characteristics found in this species in his key to the sections of *Mycena*, and therefore the species cannot be keyed.

Kühner also excluded the species from *Mycena*. Neither *Omphalia cyanophylla* nor *Mycena lilacifolia* were treated in his *Mycena* monograph (Kühner, 1938). Kühner & Romagnesi (1953: 124) include *Omphalia cyanophylla* in Sect. B of *Omphalia*, and not in *Mycena*. In the notes and observation section (p. 129), the authors – the first to compare *O. cyanophylla* to *M. lilacifolia* – explained why they retained the species in *Omphalia*: 'R. K. a toutefois remarqué, sur

des exemplaires européens d'O. cyanophylla, transmis par J. Favre, que cette réaction brun-rouge des parois des hyphes à l'iode, bien sensible dans toute la région corticale du st., devient ± indistincte dans le chap. et surtout dans les lam.' More recently Kühner (1980: 876) proposed excluding the species from both Mycena and Omphalina (which he recognized in lieu of Omphalia), suggesting instead that it be placed in Hygrocybe subgen. Gliophorus, '...Ag. cyanophyllus est un champignon très différent de toutes les Omphales que nous connaissons par la viscosité de ses revêtements (viscosité particulièrement remarquable sur le stipe), que nous plaçons dans le sous-genre Gliophorus des Hygrocybe.' [Although the combination 'H. cyanophylla' was used on p. 688, it apparently has never been validly published (cf. Index of Fungi)]. Horak (1985) was exceptional among Europeans in adopting the name Mycena lilacifolia.

Others in Europe continued to refer O. cyanophylla to Omphalina (Hirsch, 1978; Krieglsteiner & Enderle, 1987). As Singer (1986) did for M. lilacifolia in Mycena, Courtecuisse (1986: 44) has named O. cyanophylla type of its own subsection, Omphalina sect. Violaceovirides subsect. Cyanophyllinae. Bigelow (1970), when monographing Omphalina for North America, followed Smith (1947) by specifically excluding M. lilacifolia from Omphalina and retaining it in Mycena. Having accepted this decision, he did not treat the species further in his monograph of Clitocybe (Bigelow, 1985), thereby tacitly rejecting Singer's 1942 placement of the species into Clitocybe in accordance with Singer's (1951; 1962; 1975) later treatments.

In summary, modern taxonomic treatments by different authors have placed *Agaricus cyanophyllus* Fries (= *A. lilacifolius* Peck) into *Omphalina*, *Clitocybe*, *Mycena* and *Hygrocybe*.

Tramal reaction in Melzer's Reagent

Central to the various arguments concerning generic affinities has been the perception that there is a negative iodine reaction for the tramal tissues of A. cyanophyllus in Melzer's reagent. Singer (1942) obtained a negative reaction using fragments of the type of A. lilacifolius and later expressed concern about admitting species with nonreactive tissues into Mycena (Singer, 1951). Maas Geesteranus (1984), misinterpreting Smith (1947), included a negative reaction among the itemized features which justified exclusion of M. lilacifolia from Mycena. However – as noted above – neither Smith (1947) nor Kühner & Romagnesi (1953) claimed that the tramal tissues were unreactive in Melzer's reagent. Smith (1947) in fact recorded a positive reaction: a change to reddish brown to more or less vinaceous brown.

We investigated this property using living, recently dried, and older herbarium specimens we had identified as *M. lilacifolia*. Our

observations indicate that tramal cell walls of this species are weakly to moderately strongly dextrinoid. Living material directly mounted in Melzer's reagent, whether at room temperature, heated slightly, or brought just to the boil on a slide, gave negative to inconclusive results in both pileus and stipe. Dried materials, regardless of length of storage, gave positive results of varying degrees when prepared carefully. Materials were soaked in 95% ETOH followed by flooding in water to rehydrate them. Both pilei and stipes were sectioned, with the sections either dipped directly into Melzer's reagent or dipped into weak ammonia solution, blotted, and then dipped into Melzer's reagent. In all cases stipe tissues gave stronger reactions than did those of pilear and lamellar tissues (noted by Kühner & Romagnesi, 1953). Immature specimens and pilear and lamellar tramas of fully expanded pilei gave weaker reactions than did partially expanded pilei. For example, tissues in specimen LLN 93.11.11-7 (Fig. 3) gave stronger reactions than those in specimen SAR 7577 (Fig. 1). The strongest reaction was noted at the base of the stipe in a mass of unoriented hyphae. The next strongest reaction was found in the parallel hyphae of the stipe. The reaction became more and more diffuse from the apex of the stipe out into the pilear trama and down into the lamellae. It was accelerated and intensified by prewashing in ammonia solution but also developed in its absence. Over 24 hours the reaction intensified over time; specimens left soaking in Melzer's reagent overnight were indisputably dextrinoid. In the pileus the dextrinoid reaction was most clearly viewed in sections where the nonreactive, yellowish hymenium offers a clear contrast to the reddish brown to vinaceous brown trama cell walls. Unconvincing results were usually obtained when 'quick' mounts were made of lamellar fragments directly in Melzer's and viewed immediately. Kohn & Korf (1975) demonstrated that positive amyloid reactions using Melzer's reagent on ascus apices could be enhanced or induced by pretreatment in an alkaline solution (KOH), while Morton (1986) showed that the color of the iodine complex in Endogonaceae spore walls could be modified by different mountants and different concentrations of iodine. Considering these types of factors – and the apparent negative results in 'quick' mounts – it is understandable that tramal tissues have been reported as unreactive (neither amyloid nor dextrinoid) in the past.

Smith (1947) compared the iodine reaction of *M. lilacifolia* to other species he placed in sect. Caespitosae. We compared tramal tissues of *Mycena leaiana* (Berk.) Sacc. (Stz. 11339, WTU), now in *Mycena* sect. Hygrocyboideae subsect. Caespitosae (Smith) Singer, and noted that it gave an instantaneous dextrinoid reaction. Vinaceous to violaceous (nearly amyloid) coloration develops in the pileus, while vinaceous to reddish brown tones predominate in the

lamellar trama, the latter tones the same as those found in *O. cyanophylla* stipe tissues after 12 hrs. It was the vinaceous to violaceous coloration in species such as *M. leaiana* that Smith considered to be different from the reaction in *M. lilacifolia*. We agree with his assessment but still consider the reaction to be a positive one.

Weakly dextrinoid reactions have been reported for *Hydropus* species (Singer, 1986). By comparison, pilear tramal tissues were found to be nonreactive in three species of *Hydropus* (Kühner) Singer representing three subsections: *H. kauffmanii* (Smith) Singer (sect. Mycenoides subsect. Anthidepades Singer Stz. 2723, WTU), *H. marginellus* (Pers.: Fr.) Singer (sect. Hydropus subsect. Marginelli Singer - Stz. 1671, WTU) and *H. nigrita* (Berk. & Curt.) Singer (sect. Hydropus subsect. Hydropus - Stz. 2950, WTU). Even after pretreatment in ammonia and soaking in Melzer's reagent over 48 hours, the pilear tissues did not darken, although stipe tissues of *H. kauffmanii* did give a faint dextrinoid reaction. This weak reaction is the sort Singer (1986) described when circumscribing *Hydropus*.

Taxonomic significance of dextrinoid reaction

Relatively few genera of agarics have dextrinoid hyphal walls in the tramal tissues. The most notable genus is Mycena, where species characteristically have strongly dextrinoid tissues in both the pileus and stipe. However, there are Mycena species with weakly dextrinoid or totally nonamyloid tissues. This genus is also characterized by several other features: highly developed cheilocystidia on well-formed lamellae (lacking only in reduced species), amyloid basidiospores for most species, diverticulate pileipellis and/or stipitipellis hyphae on most species, and often the presence of pleurocystidia and/or gelatinous outer tissues. With a dextrinoid trama and gelatinized pileipellis and stipitipellis, *M. lilacifolia* clearly exhibits an alliance to Mycena. In most definitions, Omphalina (particularly as outlined in Norvell & al., 1994) does not include species with a dextrinoid trama in either pileus or stipe. Dextrinoid tramas are also foreign to *Hygrocybe* (as is the ability to decay wood) and *Clitocybe* (which lacks species with both a viscid pileus and stipe). Confirmation of the tissue reaction simultaneously supports Smith's placement of M. lilacifolia in his broad concept of the genus Mycena and weakens arguments for its exclusion based upon the absence of such a reaction.

Yet *M. lilacifolia* remains an enigma even when placed in *Mycena*, the genus with which it is most closely allied. With the exception of minute species with greatly reduced lamellae (resembling folds) and some species assigned to *Mycena* sect. Radiatae Singer (1961), all

Mycena species characteristically form well-developed cheilocystidia and frequently differentiate pleurocystidia as well. Both types of cystidia are absent in M. lilacifolia despite its well-developed lamellae. The lack of both cystidia and diverticulae on any tissue, the presence of nonamyloid basidiospores, and an easily missed weakly dextrinoid reaction of the trama make M. lilacifolia peripheral to Mycena.

All species in Mycena sect. Radiatae differ from M. lilacifolia by having free or nearly free lamellae which permit the pilei of those species to expand in a fan-like manner. As circumscribed by Singer (1986), however, it is the one section where nonamyloid basidiospores, nonamyloid tramal tissues, smooth pileipellis and stipitipellis hyphae, and the absence of cystidia are among the characteristics for the discussed species. The integrity of this section has been questioned. Maas Geesteranus (1985) restricted the section to the type, *M. radiata* (Dennis) Singer ex Maas Geesteranus, specifically excluding M. aosma Singer and M. chlorinosma Singer. Mycena lenta R. Maire, the type species for Leucoinocybe Singer, was transferred to Clitocybula by Malençon & Bertault (1975). Corrugaria viridiflava Métrod (see type study by Horak, 1968), the type of Corrugaria Métrod (1949), and M. radiata also appear to be fundamentally different. Corrugaria viridiflava has a smooth, membranous pileus which is corrugated. The radiating grooves, which correspond to where the pileus is tightly bound above the lamellae, are structural lines of strength. In M. radiata the pileus is not smooth but instead has diffractive/rimose tissues (i.e. conducive to splitting), which give rise to central scales and plicate-striate margins (Dennis, 1952). Because the tissues apparently pull apart above the lamellae, here the grooves represent structural lines of weakness. Although Maas Geesteranus (1985) admitted M. radiata to Mycena, as did Singer in 1986, we continue to have reservations about the generic disposition of *M. radiata*. Its scaly pileus and absence of both diverticulae and dextrinoid tramal tissues indicate it is generically misplaced. The one Mycena-like feature it does possess, aside from size, is an amyloid basidiospore wall, a characteristic found in many other genera. Mycena squamulosa Singer, a macroscopically similar taxon, represents another variation with a dextrinoid trama, amyloid spores and abundant cheilocystidia (Singer, 1961). It is possible that several genera may have been submerged in Mycena sect. Radiatae as circumscribed by Singer. When these taxa are excluded, Mycena becomes characterized by the presence of well-developed cheilocystidia when lamellae are well differentiated.

For all the reasons discussed above, we recognise a distinct genus for *M. lilacifolia* in the *Mycenae*.

Chromosera Redhead, Ammirati & Norvell, gen. nov.

Lignicola, omphalinoidea. Pileus et stipes vivide tincti, viscidi, putrescentes. Lamellae decurrentes. Basidiosporae hyalinae, tenuiter tunicatae, leves, inamyloideae. Cystidia nulla. Hyphae tramales inflatae, obscure dextrinoideae, fibulatae. Pileipellis stipitipellisque hyphae leves, fibulatae, in muco inclusae.

Lignicolous, omphalinoid. Pileus and stipe brightly coloured, viscid, putrescent. Lamellae decurrent. Basidiospores hyaline, thinwalled, smooth, nonamyloid. Cystidia absent. Tramal hyphae inflated, faintly dextrinoid, clamped. Pileipellis and stipitipellis hyphae smooth, clamped, embedded in mucilage.

Typus - Chromosera cyanophylla.

Etymology - Named in honour of Prof. Meinhard Moser while simultaneously alluding to its beautiful coloration, 'chromos'

Chromosera cyanophylla (Fr.) Redhead, Ammirati & Norvell, comb. nov. – Figs. 1–5.

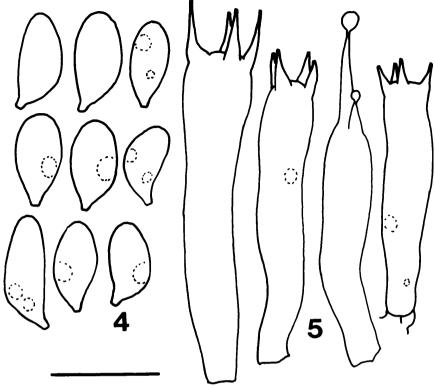
- = Agaricus cyanophyllus Fries, Monogr. Hymen. Sueciae 2: 293. 1863. (basionym)
 - *Omphalia cyanophylla* (Fr.) Quélet, Les Champignons du Jura et des Vosges p. 99. 1872.
 - = *Omphalina cyanophylla* (Fr.) Quélet, Enchir. Fung. p. 45. 1886.
 - = *Omphalina cyanophylla* (Fr.) Courtecuisse & Bon, Docum. mycol. 15 (Fasc. 62): 42. 1986. (superfluous combination)
- = Agaricus lilacinus Peck, Ann. Rept. N.Y. State Mus. 24: 63. 1872. (non A. lilacinus Mont. 1856 = Pluteus lilacinus (Mont.) Singer)
 - = Agaricus lilacifolius Peck, Ann. Rept. N.Y. State Mus. 29: 66. 1878. (nom. nov. for A. lilacinus)
 - = Omphalia lilacifolia (Peck) Peck, Ann. Rept. N.Y. State Mus. 45: 94, 1892.
 - = *Omphalina lilacifolia* (Peck) Murrill, North Amer. Flora 9: 346. 1916.
 - = Clitocybe lilacifolia (Peck) Singer, Lloydia 5: 105. 1942.
 - Mycena lilacifolia (Peck) Smith, North Amer. Species of Mycena p. 414. 1947



Figs. 1–3. – Chromosera cyanophylla. – 1. Basidiomes, SAR 7577 (Scale = 1 cm). – 2. Pigment corpuscle from subpellar region, LLN 93.11.11-7 (Scale = 5 μ m). – 3. Basidiomes, LLN 93.11.11-7 (Scale = 1 cm).

North American material

Pileus 3-25 mm diam., convex with a flattened to depressed center, glabrous, transluscent-striate, darkest centrally, pale luteous to amber or honey or olivaceous buff, 'Cream color' to 'Naples yellow', with faint rosy vinaceous tints on larger pilei or buttons, viscid to lubricous, edges even to scalloped, context amber coloured. -Lamellae arcuate decurrent, pale vinaceous, pale rosy vinaceous, rosy vinaceous or 'Pale Lilac', fading with age, edges conclorous, neither crowded nor distant, with 1-2 tiers of lamellulae. - Stipe 10-30(-45) mm long, 1-2.5 mm diam., equal above a slightly swollen base, cartilaginous, fistulose, viscid, amber with a grayish rose to vinaceous tinted apex and often with vinaceous to lilac tints at base. – Odor not distinctive (adapted in part from Smith, 1947 and from notes on fresh material). - Pileipellis a thin, collapsed ixotrichoderm, hyphae 3-5 µm diam., hyaline, nonamyloid, smooth, thin-walled, clamped, embedded in a thin slime which easily disperses, sparsely covered with scattered, roundish, small, yellowish, refractive pigment globules 1.5-2 μm diam. - Subpellis poorly differentiated from the trama except for increased concentrations of extracellular and possibly intercellular pigment globules, many of which form scattered pigment corpuscles 6-7 µm diam. consisting of radially arranged globules around a colorless core (Fig. 2). -Pigment bodies present only in relatively recent collections noted up to 1 yr. after drying, but apparently volatizing or degrading in herbarium specimens hence lacking in older material – subhyaline to faintly yellow in water, becoming bright yellow in dilute NH4OH sol., dissolving in 10 % KOH sol. but not in weak NH4OH sol. or Melzer's reagent. - Pilear tramal hyphae mostly 5-15 μm diam, thin-walled and loosely packed, hence many collapsed in rehydrated material, hyaline except for scattered pigment globules and corpuscles, walls weakly to moderately dextrinoid as described in text. - Lamellar trama more or less regular but becoming slightly disorganised with age, hyphae mostly 5-10 µm diam., similar to those of the pilear trama, mixed with fewer pigment corpuscles, dextrinoid like the pilear tramal hyphae. - Basidiospores (Fig. 4) $6.5-9(-11) \times 3.5-4.5$ µm, amygdaliform to ellipsoid with a prominent tapered apiculus, thin-walled, hyaline, smooth, nonamyloid, not cyanophilous. – B a s i d i a (Fig. 5) $20-25(-29) \times 4-5(-6.5) \mu m$, clavate, 4-sterigmate, lacking siderophilous granules. - Pleurocystidia and cheilocystidia absent. - Stipitipellis similar to pileipellis. – Stipititramal hyphae 5-27 μm diam. most 10-15 μm



Figs. 4–5. Chromosera cyanophylla (LLN 93.11.11-7). – 4. Basidiospores. 5. Basidia. – Scale = $10 \mu m$.

diam, more or less parallel, clamped, hyaline, dextrinoid (see text), with scattered pigment globules and corpuscles.

Habit and Habitat. – Omphalinoid, solitary, scattered, or caespitose on exposed white-rotted wet conferous wood (often cut ends and sides of logs or branches) on the forest floor.

Specimens Examined - CANADA: British Columbia: Glacier Natl. Park, Beaver R. Valley at Connaught Cr., Sept. 19, 1980, SA Redhead 3928 (DAOM 178126). Manitoba: Riding Mt. Natl. Park, Moon L., Aug. 21, 1979, SAR 2951 (DAOM 189958). New Brunswick: Kouchibouguac Natl. Park, UTM Grid 511870, Aug. 18, 1977, RL Millikin (DAOM 169627). Ontario: Algonquin Prov. Park, Found L., July 30, 1975, JF Ammirati 7115 (WTU), Rosepond L., June 1, 1987, RG Thorn 870601/13 (DAOM); Lake Timagami, Aug. 8, 1936, RF Cain (DAOM 80625); Petawawa For. Exp. Stn., Sept. 19, 1945, JW Groves (DAOM 16454); Shaw Woodlot Conservation Area near Eganville, Sept. 2, 1986, SAR 5247 (DAOM 196066). Québec: Burnet, July 28, 1938, JWG (DAOM 8659). – U.S.A. California: Tehama Co., Lassen Natl. Park, June 6, 1965, DT Kowalski 1480 (DAOM 128229). Michigan: Ree's Bog, July 13, 1947, AH Smith & DE Stuntz 2744 (WTU); upper Tahquamenon

Falls State Park, July 10, 1959, DES 11156 (WTU). Oregon: Umatilla Co., Umatilla Natl. For., Mt. Emily, May 29, 1993, SAR (7577) & LL Norvell (WTU). Washington: Clallam Co., Olympic Natl. Park, N side L. Crescent on Spruce Rail Trail, Oct. 28, 1992, LLN (92.10.28-3), SAR & E Fox (WTU); Island Co., Whidbey I., N of Coupeville, Nov. 2, 1947, DES 3403 (WTU); Kitittas Co., Cle Elum pine flats, May 26, 1962, W Issacs 1725 (WTU); Pierce Co., Mt. Rainier Natl. Park: Mazama Ridge, July 30, 1948, DES 3768 (WTU); Ipsut Cr., Nov. 11, 1993, LLN (93.11.11-7) & SAR (WTU); Snohomish Co., Barlow Pass, S. fork of Sauk R., Oct. 13, 1991, G Walker (91.10.13-4) & JFA (WTU); Whatcom Co., Mt. Baker, Mar. 28, 1992, LLN (92.03.28-9) & JFA (WTU).

In North America Chromosera cyanophylla has previously been reported from both the U.S.A. [TN, NY, MI, WA, OR] and Canada [NS. ON, PQ] (Peck, 1872; Murrill, 1916; Kauffman, 1918; Hesler, 1945; Smith, 1947; 1949; Groves & Macrae, 1963; Gourley, 1982). In Europe it is known from France, Germany, Sweden, and Switzerland (Favre, 1960; Fries, 1863; Hirsch, 1978; Horak, 1985; Krieglsteiner & Enderle, 1987; Kühner, 1957; Quélet, 1888). Evidently the species is quite rare in Europe but in North America it is not uncommon, especially in the Pacific Northwest of the United States. Comparison of recent European descriptions (including detailed notes and illustrations on Swiss and German collections provided by E. Horak, pers. comm. in 1994) and the colour illustration by Krieglsteiner & Enderle (1987) convincingly demonstrate the conspecificity of the North American and European taxa. Additionally, the pigment bodies (Fig. 3) are distinctive. Kühner (1957) was the first to note their presence using European material. Further investigation may lead to the recognition of this feature as a generic character but no attempt was made to survey additional brightly colored taxa in Mycena or other genera for their formation. The feature is unstable in herbarium materials and requires investigation on fresh or recently collected, dried material.

Acknowledgments

We thank the Daniel E. Stuntz Memorial Foundation for assistance towards the one year sabbatical for SAR, the Mycological Society of America for a Graduate Fellowship stipend to LLN, and a U.S.D.A. Forest Service - Research Joint Venture Agreement FP-92-1723 to JFA. We also thank Dr. D. P Rogers for translating the Latin diagnoses, Dr. Thomas Kuyper for helpful discussions, and Prof. Dr. Egon Horak for providing additional information.

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(Manuscript accepted 22nd June 1994)

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Zeitschrift/Journal: Sydowia Beihefte

Jahr/Year: 1995

Band/Volume: 10

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L.

Artikel/Article: Omphalina sensu lato in North America 3:

Chromosera gen. nov. 155-164