

PHYLOGENY OF AGARICS: PARTIAL SYSTEMATICS SOLUTIONS FOR CORE OMPHALINOID GENERA IN THE AGARICALES (EUAGARICS)

Scott A. Redhead

*Systematic Mycology and Botany
Eastern Cereal and Oilseed Research Centre
Research Branch, Agriculture and Agri-food
Ottawa, Ontario, Canada, K1A 0C6*

and

François Lutzoni, Jean-Marc Moncalvo, and Rytas Vilgalys

*Department of Biology, Duke University
Durham, NC 27708-0338, USA*

Abstract: The taxonomy of species previously assigned to *Omphalina* sensu lato or *Clitocybe* is reevaluated in light of recent molecularly-based phylogenetic hypotheses. Nomenclatural complications involving generic and specific names, lectotypifications and changes to the Code are analysed. *Lichenomphalia* gen. nov. (type *Hygrophorus hudsonianus*, syn. *Omphalina hudsoniana*) is proposed for lichenized former omphalinas. *Ampulloclitocybe* gen. nov. (type *Agaricus clavipes*, syn. *Clitocybe clavipes*) is erected for its type species. *Arrhenia* is emended to include greyish species formerly included in *Omphalina*, but excluding reddish brown species related to *Omphalina pyxidata*, the conserved lectotype for *Omphalina*. The genera *Cantharellula*, *Chrysomphalina*, *Gerronema*, *Glabrocypella*, *Gliophorus*, *Haasiella*, *Hygrophorus*, *Hygrocybe*, *Pseudoarmillariella*, and *Rickenella*, and the generic names *Botrydina*, *Coriscium*, *Leptoglossum*, *Phaeotellus*, *Phytoconis*, and *Semiomphalina* are discussed.

Key words: basidiolichen, *Ampulloclitocybe*, *Arrhenia*, *Lichenomphalia*, *Omphalina*, *Gerronema*.

Introduction

As noted in the accompanying article on omphalinoid mushrooms that may have evolved outside of the Agaricales (Redhead et al. 2002), the omphalinoid and clitocyboid habits represent simple agaric morphologies that presumably arose multiple times. This hypothesis is well-supported by analyses that distantly separate several omphalinoid clades, including a lineage encompassing *Rickenella* Raithelh., possibly outside of the Agaricales (Moncalvo et al. 2000 & 2002; Redhead et al. 2002). In the present paper, we discuss the systematics and biology of several genera with omphalinoid basidiomata, including clades containing the conserved lectotype for the name *Omphalina* Quél., viz. *O. pyxidata* (Pers.: Fr.) Quél. (see Greuter et al. 2000, p. 192; see Kuyper 1995 for authorship), and type species for the names *Arrhenia* Fr., *Leptoglossum* P. Karst., and *Phaeotellus* Kühner & Lamoure, as well as the lichenized omphalinoid taxa previously referred to a lichenized genus for which the rejected names *Phytoconis* Bory, *Botrydina* Bréb., and *Coriscium* Vain. (see Greuter et al. 2000, pgs. 393-395), were applied. The discussion necessarily involves the generic name *Gerronema* Singer (1951a), because Singer (1970, 1986), and those who followed his classification, included the lichenized omphalinoid taxa within the enlarged concept he ultimately adopted for that genus.

Stereotypical omphalinoid species fall into at least five inferred lineages within the greater Agaricales (= euagaric clade) using ITS and LSU data (Lutzoni 1997) and as supported by LSU data alone but using a much larger taxon sampling (Moncalvo et al. 2000 & 2002). These lineages are: (1) *Gerronema* sensu stricto (Singer 1951a, emended by Redhead 1986) non Singer (1986), e.g., *G. strombodes* (Berk. & Mont.) Singer and *G. subclavatum* (Peck) Singer ex Redhead; (2) *Chrysomphalina* Cléménçon sensu stricto (emended by Redhead 1986, Norvell et al. 1994) non Cléménçon (1982), e.g., *C. chrysophylla* (Fr.) Cléménçon and *C. grossula* (Pers.) Norvell et al. (syn. *Omphalina wynniae* (Berk. & Br.) Ito); (3) the primarily bryophilous grey and brownish grey

pigmented *Arrhenia-Phaeotellus-Omphalina epichysium* clade; (4) the lichenized omphalinas (*Botrydina* & *Phytoconis* of Redhead & Kuyper 1987, 1988, Norvell et al. 1994, Kuyper 1995); and (5) the *Omphalina pyxidata* group = *Clitocybe* sect. *Pyxidatae* sensu Bigelow (1974, 1985) and Lamoure (1974) *pro parte*. A distinct omphalinoid lineage, (6) e.g., *Rickenella* and allies (*Cantharellopsis* Kuyper, *Cotylidia* P. Karst., *Loreleia* Redhead et al., *Contumyces* Redhead et al., *Sphagnomphalia* Redhead et al.), which possibly evolved independently outside of the Agaricales (Moncalvo et al. 2000 & 2002), is treated in a separate paper (Redhead et al. 2002).

All 6 lineages were previously supported by the equally weighted parsimony and maximum likelihood analyses of the combined ITS and LSU data set (Lutzoni 1997, figs. 5a, 7). In larger taxon samplings (Moncalvo et al. 2000 & 2002), these clades of omphalinoid agarics often appear separated from each other and interspersed with clades of agarics and other fungi not previously analysed by Lutzoni (1997), some being additional omphalinoid agarics. We reproduce Lutzoni's (1997, fig. 7) as our **Fig. 1**, but with the various clades reclassified and renamed as discussed below.

Taxonomy and nomenclature

Gerronema was originally proposed for lignicolous tropical species (Singer 1951a) that were latter characterized, in part, by the presence of sarcodimitic tissues (Redhead 1986, Norvell et al. 1994). Two such species, *G. strombodes* and *G. subclavatum*, formed a monophyletic unit in the analyses by Lutzoni (1997). Subsequently they were shown to be distantly related to other omphalinas (Moncalvo et al. 2000). In a much larger analysis (Moncalvo et al. 2002), these two species of *Gerronema* cluster with other taxa with sarcodimitic tissues (e.g., with species assigned to *Clitocybula* (Singer) Métrod, *Hydropus* (Kühner) Singer, *Megacollybia* Kotl. & Pouz., cf. Redhead, 1987), which together form a well-supported lineage (to be treated in a separate paper). Hence, neither the lichenized omphalinas nor *Rickenella* and allies are closely related to *Gerronema* *sensu stricto*.

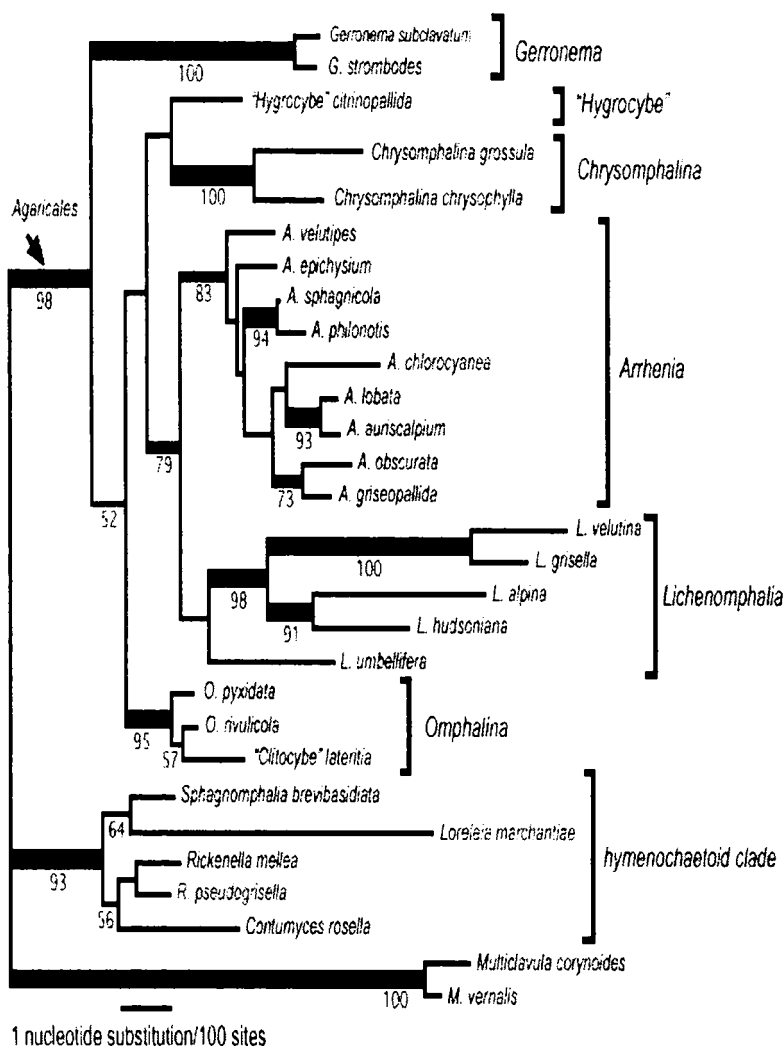


Fig. 1. Most likely phylogenetic tree for Omphalinoid mushrooms based on a combined nuclear LSU and ITS rDNA data set. Adapted from Lutzoni (1997, Fig. 7). Note the revised labelling of the clades proposed here and that "wynniae" and "grossula" are combined as *C. grossula*.

"*Chrysomphalina*" nom. invalid. (Haas, 1962) was coined for two carotenoid forming taxa. The "type" *C. chrysophylla*, was retained in *Chrysomphalina* Cléménçon (1982) when the name was validated, while the other, *Haasiella venustissima* (Fr.) Kotl. & Pouz., was excluded and treated in the genus *Haasiella* Kotlaba & Pouzar (1966); see also Kost (1986) and Chiaffi & Surault (1996). Neither of the two presently recognized *Haasiella* species have been sequenced, but it seems possible that *Chrysomphalina* species might be their closest allies, and if nested among them, the name *Haasiella* would have priority. Following a detailed anatomical study, Kost (1986) however, concluded they were not closely allied.

When *Chrysomphalina* was validated by Cléménçon (1982), he included two species, the type, *C. chrysophylla*, and *Gerronema strombodes*, while excluding *H. venustissima*. As indicated above, *G. strombodes* is unrelated to *C. chrysophylla*. Additionally, the European concept of "*G. strombodes*" represented a misapplication of that name. *Gerronema strombodes* is restricted to eastern North America. The European taxon known to Cléménçon as "*G. strombodes*" represents a different species, *G. xanthophyllum* (Bres.) Norvell et al., also a true *Gerronema* (Norvell et al. 1994; Birrer 2000). As characterized by Norvell et al. (1994), *Chrysomphalina* accommodates lignicolous, clampless, carotenoid forming, omphalinoid taxa with nonamyloid thin-walled spores, pachypodial subhymenia, and monomitic tissues.

Chrysomphalina, as thus defined, appears to be a monophyletic taxon allied firstly to a sister genus *Hygrophorus* Fr. (Moncalvo et al. 2000 & 2002), and possibly allied to other hygrophoroid genera (Lutzoni 1997; Moncalvo et al. 2000 & 2002). The genus *Hygrophorus* sensu stricto (e.g., *H. bakerensis* A.H. Smith & Hesler, *H. sordidus* Peck) is clearly a distinct lineage and genus, distinguished by a presumed obligate ectomycorrhizal symbiosis, absence of carotenoids (pigmented by sundry other pigments, Gill & Steglich 1987), possession of a different chemistry, and clamp connection formation. *Chrysomphalina* species have elongated basidia (Norvell et al. 1994) and because of the pachypodial subhymenium, a somewhat divergent lamellar trama, perhaps homologous to the divergent, slightly differently arranged lamellar tramas characterizing *Hygrophorus* sensu stricto.

The combined phylogenetic analyses by Lutzoni (1997) sometimes placed *Hygrocybe citrinopallida* (A.H. Smith & Hesler) Kobayasi (another hygrophoroid taxon) in proximity to *Chrysomphalina* (with weak support). The analyses by Moncalvo et al. (2000, fig. 2, clade "K") sometimes shifted it closer (also with weak support) to the lichenized omphalinas ("*Phytoconis*") and *Arrhenia* clade. With the addition of more genera, especially other hygrophoroid taxa, analysis of the most parsimonious trees found from heuristic searches (MP) and the bootstrap 50% majority rule consensus tree (BS) (Moncalvo et al, 2002) continues to support the taxon pair *Chrysomphalina-Hygrophorus*. *Hygrocybe* (Fr.) P. Kumm. (including its type *H. conica* (Schaeff.: Fr.) P. Kumm.) appears to represent a monotypic lineage with two fundamental subgeneric divisions, e.g., *H. cantharellus* (Schw.) Murr. & *H. miniata* (Fr.: Fr.) P. Kumm. [sect. *Coccineae* subsect. *Squamulose*], and *H. spadicea* (Fr.) P. Karst. & *H. conica* [sect. *Hygrocybe* subsect. *Hygrocybe*]. The surmised sister taxon to this monophyletic *Hygrocybe* clade is a well-supported clade (90% BS) with *Chromosera cyanophylla* (Fr.) Redhead et al. and the wayward *Hygrocybe citrinopallida*, also known as *Gliophorus citrinopallidus* (A.H. Smith & Hesler) Kovalenko (1999). *Chromosera* Redhead, Ammirati & Norvell (1995) is a recently described monotypic genus established to account for a species alternately known as *Mycena lilacifolia* (Peck) A.H. Smith in North America and *Omphalina cyanophylla* (Fr.) Qué. in Europe. This lignicolous species was clearly neither an *Omphalina* nor a *Mycena* (Pers.) Roussel, but interestingly enough, Kühner (1980) suggested that it belonged in *Hygrocybe* subg. *Gliophorus*, and called it "*Hygrocybe*" *cyanophylla* nom. inval. (see Redhead et al. 1995).

Both *Gliophorus* Herink and *Chromosera* are characterized by viscid stipes and pilei, and by bright pigments. *Gliophorus* species are terrestrial and their biological status remains uncertain. Another species, *G. laetus* (Pers.) Herink, appears on a largely omphalinoid clade (the *Phytoconis*, *Arrhenia*, and *Cantharellula-Pseudoarmillariella* lineage, discussed below), i.e., separate from *G. citrinopallidus*. Unfortunately, as the type for *Gliophorus*, *G. psittacinus* (Schaeff. Fr.) Herink, has not been included in any of the analyses, application of the generic name is unresolved. The name *Gliophorus* potentially could compete with *Chromosera*, or be applicable to a sister taxon. *Gliophorus psittacinus*

is a terrestrial species with an unestablished biological role (?ectomycorrhizal). In the analyses by Moncalvo et al. (2000, 2002), there is weak bootstrap support linking the *Chromosera-Hygrocye* clade to the *Chrysomphalina-Hygrophorus* clade together with *Humidicutis* (Singer) Singer, a third hygrophoroid genus. Bootstrap analysis (but not MP analyses) support the phylogenetic placement of *Humidicutis marginata* (Peck) Singer (type for that generic name) next to the *Chrysomphalina-Hygrophorus* clade. These results potentially bring into inferred evolutionary proximity, a group of taxa that form muscaflavin based pigments (as surmised from other chemically analyzed *Hygrocye*) and other *Hygrophorus*, known to be able "to induce extradiol cleavage of L-DOPA leading to the formation of muscaflavin" (Gill & Steglich 1987, p. 86). *Humidicutis* is in part defined by the absence of clamp connections and is otherwise different because of pigment characters (see Singer 1986). There are some indications that the core of the hygrophoroid taxa (the classical "Hygrophoraceae"), are basal to the Agaricales (euagaric clade). In the analyses of a portion of the mt LSU rRNA gene by Bruns et al. (1998), representatives of *Hygrophorus* and *Hygrocye* actually appeared outside of the depicted main agaric clade, whereas in the analyses by Hibbett et al. (2000), *Hygrocye conica*, *Humidicutis marginata* (as *Hygrocye marginata* (Peck) Murr.) and the two *Hygrophorus* species analysed by Moncalvo et al. (2000) were shown to be basal to the rest of the euagaric clade. In all analyses, the backbones of all resulting phylogenetic trees are weakly supported, except for those using fewer taxa combined with several genomic regions evolving at different rates (ITS region combined with LSU nuc rDNA in Lutzoni 1997). We regard the Hygrophoraceae s.l. and s.s. (whether or not recognized as a distinct taxon) to be among the Agaricales (euagarics). Future investigation of that traditional family should include *Chrysomphalina*, *Chromosera*, possibly *Haasiella*, and the two omphalinoid lineages "*Phytoconis*" (= *Lichenomphalia*, see below) and *Arrhenia* as emended below.

The primary goal of the study by Lutzoni (1997) was to investigate the phylogeny of lichenized omphalinas and their relationships to non-lichen-forming omphalinoid agarics. Four of the five sampled lichenized species (*Omphalina grisella* (P. Karst.) Moser, *O. hudsoniana* (Jenn.) Bigelow, *O. luteovitellina* (Pilát & Nannf.) M. Lange, and *O. velutina*

(Quél.) Quél.) formed a clearly defined, strongly supported (BS = 92-98%) monophyletic lineage. The fifth, *O. ericetorum* (Pers.: Fr.) Bigelow (see discussion on authorship below and synonymy with "*umbellifera*"), was inferred to be sister to this lineage in all three combined analyses of the ITS region with the LSU nuc rDNA, but the placement received weak support (BS < 50-70%; Lutzoni 1997: figs. 5 & 7). The sister group to the lichenized clade in the 1997 analyses was a nonlichenized, largely bryophilous group of omphalinoid-arrhenoid species, all with dark pigments. This sister relationship was supported by bootstrap support ranging from 70-83% when the ITS region was combined with LSU data (Lutzoni 1997). Deeply nested among the lamellate omphalinoid taxa were the reduced agarics, *Arrhenia auriscalpium* Fr. (type for *Arrhenia*), *Arrhenia lobata* (Pers.: Fr.) Redhead (type for *Dictyolus* Quél.), and *Phaeotellus griseopallidus* (Desm.: Fr.) Kühner & Lamoure. In a larger taxon sampling restricted to the LSU data (Moncalvo et al. 2000), this close relationship between lichen-forming omphalinas and the grey and grey-brown omphalinoid-arrhenoid clade continues to be detectable with even larger datasets (Moncalvo et al. 2002), but the exact relationship of the taxon labelled *O. ericetorum* (= *umbellifera*) became uncertain with regard to these two lineages because of the paucity of characters inherent to a single gene phylogenetic analysis for such a large taxon sampling. In the smaller taxon matrix, a third bryophilous omphalinoid clade identified by Lutzoni (1997; BS = 95-100%, Figs. 5 and 7) and labelled "*Clitocybe*" (i.e., *Omphalina pyxidata*, *O. rivulicola* (J. Favre) Lamoure, *Clitocybe lateritia* J. Favre) appeared to be a sister taxon to the "*Omphalina*"-*Chrysomphalina* clade, with bootstrap support in all combined analyses ranging from 52-83% (Lutzoni 1997, Figs. 5 and 7). However, support weakened when diluted by the addition of far more diverse taxa and when phylogenetic analyses were restricted to LSU (Moncalvo et al. 2000). The *O. pyxidata*-*C. lateritia* clade (in clade "J") no longer groups with any other identifiable former *Omphalina*. MP analysis using a far larger taxon sampling suggests a relationship both to the bryophilous genus *Rimbachia* Pat. (*R. bryophila* (Pers.: Fr.) Redhead) and (less closely) to "*Clitocybe*" *clavipes* (Pers.: Fr.) P. Kumm. (a taxon which remained distantly located in Moncalvo et al. 2000, fig. 2). None of these were close to the core *Clitocybe* (Fr.) Staude (eg. *C. nebularis* (Batsch: Fr.) P. Kumm., *C. dealbata* (Fr.: Fr.) P. Kumm., *Lepista nuda*

(Fr.: Fr.) Cooke), which appear to be far more closely related to the former *Lyophylleae* (Hofstetter et al, in prep.).

The conserved lectotype for the generic name *Omphalina* Quél. is *O. pyxidata* (Greuter et al. 2000, p. 192), hence we will hereafter apply the generic name *Omphalina* to the presumably bryophilous clade centered around the type, *O. pyxidata*, and not refer to it as "*Clitocybe*" as it was tentatively labelled with a question mark by Lutzoni in 1997. Conservation of the lectotype for *Omphalina* ends decades of debate (Bigelow 1970, Donk 1962, Jørgensen & Ryman 1989, 1994, Lange 1981, Redhead & Weresub 1978, Redhead 1993, Redhead & Kuyper 1987, 1988, 1993, Singer 1962, 1975, 1986, Singer & Smith 1946), but with unanticipated repercussions. As thus defined and restricted, *Omphalina* is not congeneric with either the lichenized species or the grey-brown nonlichenized "omphalinas". Biologically, *Omphalina* (sensu conserved lectotype) occupies similar habitats and substrates as species in the *Arrhenia* lineage, but they differ in subtle pigmentation chemistry and topology (the presumed melanins are more reddish brown than grey brown, and the deeper tissues are pigmentless, i.e. whitish). Without sequence data as a guide, these differences would not normally be considered to be generically significant, especially when compared to far more conspicuous morphological differences. Nonetheless, they do appear to correlate with base-pair sequence data generated phylogenies.

A fungus identified as *Omphalina pyxidata* has been linked by Hornby & Ward (1995) to a sclerotium-forming, weak pathogen of turf grass roots. However, they reported unspecified genetic differences between herbarium specimens of *O. pyxidata* and the suspected causal agent; specimens were not retained (Hornby 1995, pers.com.). Additionally the pinkish-purple coloration of the basidiomata (illustrated in color) suggests that another fungus might be involved. Therefore, its generic identification remains ambiguous.

Notwithstanding the above report, *Omphalina pyxidata* has been regarded as a bryophilous fungus (Bigelow 1974, Lamoure 1974). Similarly *O. rivulicola* is bryophilous (Lamoure 1974). Together they form a bryophilous clade (Moncalvo et al., 2002). Sister to this

bryophilous clade was one containing an unidentified *Clitocybe* sp. and *Clitocybe lateritia*. The latter grows with *Dryas* litter in alpine meadows (Lamoure 1972) and presumably is not bryophilous. In common with *O. pyxidata* and *O. rivulicola*, *C. lateritia* produces reddish brown melanin-like pigments, rather than the greyish pigments of the *Arrhenia* clade. We will return to the discussion of the *Omphalina* (*O. pyxidata* clade) further below.

The oldest available generic name for any of the other omphalinoid species that appear on the combined *Arrhenia*-*Phytoconis* clades is *Arrhenia* Fries (1849). *Arrhenia* was first erected for basidiomycetes characterized by nutant basidiomata with cantharelloid hymenia (Corner 1966, Høiland 1976, Pilát & Nannfeldt 1954). Later the genus was expanded to include species with pleurotoid basidiomata, incl. *Leptoglossum* and *Phaeotellus* (Aronsen 1992, Breitenbach & Kränzlin 1991, Courtecuisse 1986, Gulden 1987, Gulden & Torkelsen 1996, Kreisel 1987, Kühner & Lamoure 1972, Moser & Jülich 1997, Redhead 1984, Senn-Irlet 1987, Watling 1988, Watling & Gregory 1989). However, the delimitation from omphalinoid taxa has always been controversial (Gulden 1987, Høiland 1982, Lange 1981, Watling 1988), as has been the delimitation of *Arrhenia* from *Leptoglossum* (Corner 1966, Redhead 1984), including debatably classified species with centrally stipitate basidiomata, and cantharelloid hymenia. There is a complete transitional series of morphological features from gross omphalinoid to cyphelloid habit, and lamellate to meruloid to smooth hymenia. Based upon the deeply nested position of *Arrhenia* within the clade of more typically omphalinoid taxa (Lutzoni 1997, Moncalvo et al. 2000 & 2002) and the gradation of morphological features, we are now prepared to expand the coverage of the name *Arrhenia* to include omphalinoid, pleurotoid, nutant, and cyphelloid forms to this primarily bryophilous/phycophilous lineage with greyish melanized basidiomata. Invasion of dead moss cells has been documented (Hassel & Kost 1998), at least in the instance of the species with the most reduced basidiomata, *A. retiruga* (Bull.: Fr.) Redhead, a cyphelloid taxon and apparent necrotrophic parasite. Although described on old bovine dung, the grey-brown, clampless, cyphelloid fungus, *Glabrocypbella stercoraria* Barrasa, Esteve-Rav. & Sánchez (Barrasa et al. 1998), is best considered to be a species of *Arrhenia* perhaps associated with the algae also

reportedly growing on the dung substrate. Notably, the possibility of microscopic moss protonema was not excluded. For now we are prepared to include the similar species, *Leptoglossum omnivorum* Agerer (1984), in *Arrhenia*, based in part on examination of the type. These cyphelloid and nutant taxa are morphologically terminal groups of the primarily dark grey "omphalinoid" group of species (cf. Lamoure 1975, Singer 1956).

The taxonomic question of whether or not to distinguish the lichenized "*Phytoconis*" generically from nonlichenized *Arrhenia* hinges in part on conveyance of information regarding phylogeny, biological status, and anatomy, and in part on nomenclature. It has previously been argued based upon anatomy and biology that the lichenized omphalinas should be recognized in a distinct genus (Kuyper 1986, 1994, 1995, Norvell et al. 1994, Redhead & Kuyper 1987, 1988). Lutzoni & Vilgalys (1995a) confirmed these results (BS = 75%, Figs. 2A) with a phylogenetic analysis restricted to morphological and anatomical characters. When combined with LSU data, the bootstrap value dropped slightly to 67% (Lutzoni & Vilgalys 1995a, Fig. 7). In the phylogenetic study with the most molecular characters (i.e., ITS region combined with LSU nuclear DNA, Figs. 5 and 7, Lutzoni 1997) the three combined analyses consistently revealed the lichenized omphalinas as a monophyletic entity with bootstrap support as high as 70%. Other studies with broader taxon sampling but restricted to the LSU (Moncalvo et al. 2000, & 2002) did not have sufficient data to provide bootstrap values (< 50%) for the phylogenetic placement of "*Omphalina*" *ericetorum/umbellifera* specifically on this clade; rather it is only placed in proximity. The latter studies do not confirm nor contradict the monophyly of the lichenized omphalinas. Therefore, our best phylogenetic estimates (i.e., those with the highest level of confidence) come from the phylogenetic analyses of morphological data alone (BS = 75%; Lutzoni & Vilgalys, 1995a) and from the phylogenetic analyses with the most molecular data, i.e., combined ITS with LSU data set (BS up to 70%; Lutzoni 1997). Both analyses independently supported the monophyly of the lichen-forming omphalinas. None of the competing phylogenetic relationships for the paraphyly or polyphyly of the lichenized omphalinas received bootstrap support > 50%. We therefore opt to recognize the lichenized omphalinoid agarics as a distinct genus.

Unfortunately, all three applicable validly published generic names – *Phytoconis*, *Botrydina*, and *Coriscium* – have been placed on a list of rejected names (see Gams 1995; Greuter et al. 2000) and hence are unavailable. This regrettable nomenclatural consequence results from not applying the same standards to basidiolichen generic names as is done for ascolichen generic names. To quote from the report of the Committee for Fungi (Gams 1995, p. 413), "By consequence those accepting the lichenized species as a separate genus are instructed to describe and name it as new, based upon holomorphic material, rather than using the anamorph name *Phytoconis* which was taken up by Redhead & Kuyper (in Mycotaxon 31: 321-323. 1988), following the letter (but not the intention) of Art. 59." Therefore, despite the recognition of a distinct wholly lichenized genus and acceptance of the name "*Phytoconis*" by agaricologists (Cléménçon 1997, Collin & Lauron 1994, Grgurinovic 1997, Kuyper 1995, Nezdoininogo 1997, Norvell et al. 1994, Redhead & Kuyper 1987, 1988, Romagnesi 1992, Watling 1988), the name *Phytoconis* is no longer available. We therefore name a "new" genus, *Lichenomphalia* gen. nov. (see below).

Lichenomphalia appears to have evolved from a bryophilous or phycophilous ancestor as suggested by Redhead & Kuyper (1987) and confirmed by Kranner & Lutzoni (1999). Using *Omphalina* as a model system (cf. Lutzoni & Vilgalys 1995a & b, Lutzoni 1997, Lutzoni & Pagel 1997), Kranner & Lutzoni (1999) noted that among analyzed *Lichenomphalia* (as lichenized *Omphalina*) and the non-lichenized sister genus *Arrhenia* (as *Arrhenia*, *Omphalina*, and *Phaeotellus*), *L. umbellifera* comb. nov., *Arrhenia velutipes* comb. nov., and *A. epichysium* comb. nov. (see below), are the most basal and exhibit the slowest evolutionary rate changes in their respective clade. Therefore, they are the closest living phenotypic representations of the common ancestor that the non-lichenized *Arrhenia* and lichenized *Lichenomphalia* share. All three species are bryophilous and/or phycophilous. Kranner & Lutzoni (1999, Fig. 1) identified three major predispositions for a successful transition to a lichenized state: 1) high phenotypic plasticity/broad ecological amplitude, 2) low fungal virulence/high photobiont infection resistance, 3) desiccation and sun irradiation tolerant/efficient DNA repair mechanisms. They further noted that *L. umbellifera* (as *O. ericetorum*) is the most plastic species of the

lichenized *Omphalina* group, as well as the most common, the most broadly distributed, and with the broadest range of substrates. This fulfils the first requirement. The study of predacious fungi lysing colonies of algae, bacteria, pollen, and/or yeasts (Barron 1988, Hutchinson & Barron 1996, 1997a, b) using modified hyphae remarkably similar to those forming the thalli of these and other basidiolichens (Oberwinkler 1970, Redhead & Kuyper 1987), suggests a physical mechanism and chemo-attractant response to algal colonies that provided an opportunity for the lichenization process to begin. It has also been shown that *Coccomyxa icmadophilae* Jaag, the alga entrapped by *Lichenomphalia*, forms cell walls resistant to lysolytic enzymes (Honegger & Brunner 1981). Thus, the combined low-level parasitism and resistance to enzymatic lysing fulfils the second requirement.

Lutzoni & Pagel (1997) outlined phenomena supporting fulfilment of the third requirement, i.e., strong positive selection in the lichenized omphalinas toward replacing one of two adjacent thymines by another nucleotide to prevent thymine dimerization. Given the poikilohydric and heliophylic nature of most lichens, lineages tolerant to oxidative stress caused by desiccation and sun irradiation, and/or with efficient DNA repair mechanisms would be more suited to forming a successful mutualistic association with terrestrial cyanobacteria or green algae. Again, *L. umbellifera* appears to exhibit more ancestral features because its thallic mycelium is broader and not as thick-walled (Redhead & Kuyper 1987, as *Botrydina botryoides* (L.) Redhead & Kuyper) and therefore, presumably less tolerant of radiation and dehydration damage, it occupies wetter habitats on average, and its basidiomata are less protected by strong pigments (either dark melanins or the bright yellow-orange uncharacterized pigments).

We anticipate that the as-yet unsequenced and rare genus, *Semiomphalina* Redhead (1984), a nutant, pale arrhenioid but lichenized basidiomycete (known only from the type collection of *S. leptoglossoides* (Corner) Redhead) will prove to be a sister taxon to *Lichenomphalia*. Its stipe and thallus resemble those of *L. umbellifera*.

Other omphalinoid/clitocyboid genera

In both the final BS and MP trees generated for the Agaricales analyses (Moncalvo et al. 2002), a moderately supported clade (49% BS) bearing *Cantharellula umbonata* (J.F. Gmelin: Fr.) Singer and *Pseudoarmillariella ectypoides* (Peck) Singer (types of their respective generic names) appears together on a weakly supported clade bearing the *Arrhenia* clade (77% BS) and all sampled *Lichenomphalia* as defined above (*L. velutina*, *L. alpina*, *L. hudsoniana* - on one clade with 77% BS; and *L. umbellifera* separately), and also *Gliophorus laetus*. Anatomically, the *Cantharellula*-*Pseudoarmillariella* clade is generically easily distinguished from nonamyloid-spored *Arrhenia*, *Lichenomphalia*, and *Gliophorus laetus* by the formation of amyloid spores.

Pseudoarmillariella ectypoides is lignicolous (a white rot agent ?) and has a scaly, orangish brown pileus. *Cantharellula umbonata* is primarily bryophilous, but occasionally remains in residual populations in young conifer forests with recently, closed canopies where populations of host mosses have died (Redhead & Malloch 1986). Species in both *Pseudoarmillariella* and *Cantharellula* share characters such as forked lamellae, reddish brown bruising reactions of the hymenium, and similarly arranged subhymenial elements, i.e., "subirregularly intermixed-subramose" elements "strongly interlaced-curved in all directions and therefore at times appearing cellular" (Singer 1986 [when comparing *Pseudoarmillariella* to *Cantharellula*]). Previously Singer (1951b) had treated both type species in one genus, *Cantharellula*. The generic name *Pseudoarmillariella* (Singer) Singer was in fact an elevation in status of *Cantharellula* subg. *Pseudoarmillariella* Singer. Interestingly, Bigelow (1982) had transferred *P. ectypoides* to *Omphalina* sensu Bigelow (ca. = *Gerronema* sensu Singer), but he maintained the distinction between it and *Cantharellula* (Bigelow 1975). We maintain the separate generic identities for *Pseudoarmillariella* and *Cantharellula* as proposed by Singer (1956) and outlined by Singer (1986), while still acknowledging the close relationship between them. As noted by Norvell et al. (1994), *Pseudoarmillariella* possesses two pigment classes and forms a thickening hymenium, in addition to being a wood decay fungus.

Clitocybe clavipes, which occurs on a weakly supported clade with *Rimbachia* and *Omphalina* sensu lectotype (Moncalvo et al. 2002, fig. 2), presents a dilemma because it seems to represent a distinct genus, phylogenetically more closely related to the type of *Omphalina* than the type of *Clitocybe* (see discussion below). The sequence data are unlike other traditional clitocyboid taxa, most of which prove to be more closely related to the Lyophylleae (Moncalvo et al. 2002; Hofstetter et al. in prep.). *Clitocybe clavipes* is uniquely characterized among clitocyboid taxa by the formation of coprine-like compounds (Cochran & Cochran 1978, Yamaura et al. 1986) and by ultrastructurally minutely roughened basidiospores (Pegler & Young 1971, Bigelow 1981, 1982) compared to smooth-spored *Clitocybe* or echinate-spored *Lepista* (Fr.) W.G. Smith. *Clitocybe clavipes* also produces a novel class of tyrosine kinase inhibitors, named the clavilactones (Cassinelli et al. 2000). The combination of significantly different sequence data from other "*Clitocybe*", and ultrastructurally distinctive spores suggest that "*C. clavipes*" has been incorrectly classified as a *Clitocybe*. We therefore propose to recognize a distinct genus, *Ampulloclitocybe* (type = *A. clavipes*, see below) for the species. Strict consensus of the 5,000 most parsimonious trees found (MPF) by Moncalvo et al. (2002) place *Ampulloclitocybe clavipes* next to *Rimbachia bryophila*, which in turn is sister to the *Omphalina* (*O. pyxidata*) and *Clitocybe lateritia* clades.

The phylogenetic proximity of the fungus, *Ampulloclitocybe clavipes* to a fungus named *Clitocybe lateritia* (Moncalvo et al. 2002), and the phylogenetically distant taxa named *Clitocybe dealbata*, *C. odora* (Bull.: Fr.) P. Kumm., *C. ramigena* Bigelow, *C. connata* (Schum.:Fr.) Gillet (= *Lyophyllum connatum* (Schum.: Fr.) Singer), *C. glacialis* Redhead et al. (= *Lyophyllum montanum* A.H. Smith), *C. nebularis* (= *Lepista nebularis* (Batsch: Fr.) Harmaja), and *C. nuda* (Fr.: Fr.) Bigelow & A.H. Smith (= *Lepista nuda*), begs a question regarding application of the name *Clitocybe* (Fr.) Staude and its lectotypification. The lectotypification of *Clitocybe* has been as heatedly debated as has lectotypification of *Omphalina*, and the topic remains unsettled (Bigelow 1965, Clements & Shear 1931, Donk 1949, 1962, Harmaja 1969, 1974, Horak 1968, Imai 1938, Korf 1988, Kühner 1980, Kuyper 1982, 1995, Rauschert 1986, Singer 1936, 1951b, 1962, 1975, 1986, Singer & Smith 1946). The choice of *C. clavipes* (type of our

Ampulloclitocybe) as lectotype of *Clitocybe* by Bigelow (1965) is noteworthy, but must be dismissed because of the earlier lectotypifications (Greuter et al. 2000, Art. 9.17). The primary division of thought is split between support for *Agaricus nebularis* Batsch: Fr. versus *Agaricus infundibuliformis* Schaeff. (= *Agaricus gibbus* Pers.: Fr. according to Singer 1986; = *Agaricus flaccidus* Sow.: Fr. according to Fries 1821 and Kuyper 1995). Donk (1962) reviewed the various typifications proposed up to 1962. The earliest lectotypification of the generic level name "*Clitocybe*" [with variously attributed authorship all involving Fries and his "tribus" as basionym] choosing *A. nebularis*, was by Earle (1909) followed by Murrill (1916), both following the American Code of Nomenclature. Such choices made using the American Code may be superseded (Greuter et al. 2000, Art. 10.5b). Using a misspelled epithet with incorrect, non-existent authority, Clements & Shear (1931) selected "*C. infundibulis* (Schaeff.) Fr." Despite the errors, their intent was clear, but because there is, in fact, no such species, their lectotypification [for priority purposes] is rejected. Singer (1936) and Singer & Smith (1946) were the next to name a [lecto-]type, namely *Clitocybe infundibuliformis*, but for either *Clitocybe* "Fr." or *Clitocybe* "(Fr.) Quél." However, the names *Agaricus infundibuliformis* Schaeff. and *A. infundibuliformis* Bull., were both treated as synonyms of *Agaricus flaccidus* Sow.:Fr. (an accepted, named species) by Fries (1821). Technically the choice of *A. infundibuliformis* is rejected simply because in the protologue of the basionym for the generic name, i.e. *Agaricus* "tribus" *Clitocybe* Fr. (1821: 78), that particular species binomial was not used for a named, recognized species. The first choice of a recognised, named species – both in Fries' "tribus" and when elevated by generic status (by Staude) – was Donk's (1949) selection of *A. nebularis*. Nonetheless, unless conserved, lectotypification of *Clitocybe* (Fr.) Staude will remain debatable. A proposal to conserve *Clitocybe* (Fr.) Staude with a conserved lectotype, *Agaricus gibbus* Pers.: Fr., by Rauschert (1986) was rejected (Korf 1988) simply because the proposal lacked detail, and unfortunately the proposer had subsequently died. For our purposes, we accept *C. nebularis* (cf. also Kuyper, 1992). The generic taxonomic delimitations (*Clitocybe* versus *Lepista* and various *Lyophylleae*) and precise phylogenetic placement of *Clitocybe* (typified by *C. nebularis*), which is phylogenetically distant from the clade with *Omphalina* (*O. pyxidata*),

"Clitocybe" lateritia, and *Ampulloclitocybe clavipes*, as well as the clade with *Arrhenia* and *Lichenomphalia*, are the subjects of other manuscripts in this series. At this time we lack sufficient confidence and information to assign a different generic name to *Clitocybe lateritia*. Possibly it will be assigned to the reconstructed genus *Omphalina*.

For an interim key to the omphalinoid genera discussed above we refer to the key in Norvell et al. (1994), replacing the name "*Phytoconis*" with *Lichenomphalia*, and replacing couplet #8 (leading to *Omphalina*, *Clitocybe*) with the following couplets.

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 pigments, odor never farinaceous]; reduced forms exhibit hymenial folds and wrinkles, may lack stipes, may be nutant or pendant [see also key to *Arrhenia* by Redhead, 1984] 9
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 or strongly aromatic, many species large and not omphalinoid] 10
9. Coloration of pilei and stipes grey, blackish, or bluish, and brown-grey, with slightly paler but similarly colored hymenia (lamellae or folds), or for some sphagnicolous species pilei scaly centrally with darkly incrusting pigments but pileus tending to be beige or tan and then lamellae are pallid; clamps present or absent, stipes and/or regular lamellae present or absent *Arrhenia*
9. Coloration of pilei and stipes reddish brown (rusty, vinaceous brown, orangish brown) and lamellae contrastingly much paler (i.e. pallid, whitish, pastel), always smooth and not scaly; clamp connections present; lamellae always well-formed *Omphalina*
10. Basidiomata nonhygrophanous, with markedly darkened fleshy pileus and fleshy bulbous-based stipe contrasting with the whitish cream lamellae; clamps present; pigments intracellular; spores smooth (light microscopy) but ultrastructurally rugose (SEM), not cyanophilous or congophilous, white in prints; producing coprine-like poisonings

..... *Ampulloclitocybe*
 10. Not with above combination other unresolved clitocyboid genera.

Note: It should be recognized that the reclassification based upon phylogenetic studies is a work in progress.

New genera and new combinations

Ampulloclitocybe gen. nov.

Basidiomata clitocybiformis. Non lichenisatus. Trama lamellarum bidirectionalis, hyphis fibulatis, cystidia nulla. Sporis albis, microrugosis, acyanophilis, inamyloideis.

Type: *Ampulloclitocybe clavipes* (Pers.: Fr.) comb. nov. Basionym: *Agaricus clavipes* Pers., Syn. meth. Fung. p. 353. 1801. (*A. clavipes* Pers.: Fr., Syst. mycol. 1: 86. 1821)

Lichenomphalia gen. nov.

Basidiomata omphaliformis. Lichenisatus. Trama lamellarum bidirectionalis, hyphis defibulatis, cystidia nulla. Sporis albis, inamyloideis. Type: *L. hudsoniana* (see below).

= *Phytoconis* Bory 1797 nom. rej. (Greuter et al. 2000)

= *Botrydina* Bréb. 1839 nom. rej. (Greuter et al. 2000)

= *Coriscium* Vain. 1890 nom. rej. (Greuter et al. 2000)

= *Omphalina* sect. *Defibulatae* Singer 1975

= *Gerronema* sect. *Phycophila* Cléménçon 1982

= *Clitocybe* subsect. *Defibulatae* (Singer) Bigelow 1985

Lichenomphalia species

L. alpina (Britzelmayr) comb. nov. Basionym: *Agaricus alpinus* Britz., Ber. Naturw. Ver. Augsburg 30: 13. 1890.

Comments: Synonymous names are: *Cantharellus dovreffeldiensis* P. Henn. & Kirschst., *Agaricus umbelliferus* var. *flavus* Sommerf., *Omphalia flava* (Sommerf.) Möller, *Omphalia luteovitellina* Pilát & Nannfeldt (see Jørgensen & Ryman 1989b).

Application and synonym of the name *Agaricus alpinus* has been disputed (Redhead & Kuyper 1987, Jørgensen & Ryman 1989b). The designation of Britzelmayer's plate by Jørgensen & Ryman (1989b) as lectotype did little to resolve the controversy. **Therefore, we hereby designate an epitype for the name *Agaricus alpinus* Britz., i.e. the type for *Omphalia luteovitellina*.** If we do not do so, thereby fixing application of the name to this taxon, then we are forced to adopt *Cantharellus dovreffeldiensis* as the next available name (Jørgensen & Ryman 1989b). We cannot fully explain the subtle discrepancies, such as paler stipe, and perhaps slightly hollowed stipes recorded by Britzelmayer (1890), neither of which is normal for the taxon accepted here. Neither discrepancy appeared to bother Jørgensen & Ryman (1989b), nor the fact the species as accepted here has not been independently documented in the region where Britzelmayer collected in the past century. However, Favre (1955) found this species, reported as *Omphalia flava*, in alpine regions of the Swiss Alps, and therefore it is possible that Britzelmayer had found it in the somewhat nearby Bavarian alpine regions. The synonym proposed by Redhead & Kuyper (1987), i.e. placement of *Agaricus alpinus* Britz. in synonymy with *Endocarpon viride* Ach. (= *Botrydina viridis* (Ach.) Redhead & Kuyper = *Lichenomphalia hudsoniana*), is rescinded simply for convenience and to reach consensus with Jørgensen & Ryman (1989b).

The report of *Omphalina alpina* (Britzelmayer) Bresinsky & Stangl (with *Omphalia luteovitellina* Pilát & Nannfeldt (1954) in synonymy) from Yunnan was based upon a fungus reportedly with clamp connections (Horak 1987: 179). If the presence of clamp connections is true, that fungus cannot be conspecific with any *Lichenomphalia*.

***L. aurantiaca* (Redhead & Kuyper) comb. nov.** Basionym: *Botrydina aurantiaca* Redhead & Kuyper, Arctic & Alpine Mycology II, p. 334. 1987. Plenum Press, NY.

***L. chromacea* (Cleland) comb. nov.** Basionym: *Omphalia chromacea*, Trans. & Proc. Roy. Soc. South Australia 48: 239. 1924.

Comments: An incorrect basionym citation was given by Redhead & Kuyper (1987, 1988) and corrected by May & Wood (1995). Isotype

material at BPI was recorded by Redhead & Kuyper (1988).

***L. grisella* (P. Karst.) comb. nov.** Basionym: *Omphalia grisella* P. Karst., Medd. Soc. Fauna Flora Fennica 16: 92. 1890 [ut "(Weinm.?) n. sp."].

***L. hudsoniana* (Jennings) comb. nov.** Basionym: *Hygrophorus hudsonianus* Jennings, Mem. Carnegie Mus. III, 12: 2. 1936.

Comments: Synonymous names are: *Endocarpon viride* Acharius [thallus only, rejection of this name has been recommended - cf. Gams (1995), and is somewhat listed as such in Appendix IV of the Code (Greuter et al., 2000: 394) as type for the rejected generic name *Coriscium* Vain.], *Verrucaria laetevirens* Borrer [thallus only], *Omphalia luteolilacina* Favre (fide Redhead & Kuyper 1987), but not *Agaricus alpinus* Britz. (see discussion above).

***L. lobata* (Redhead & Kuyper) comb. nov.** Basionym: *Botrydina lobata* Redhead & Kuyper, Arctic & Alpine Mycology II, p. 334. 1987. Plenum Press, NY.

***L. umbellifera* (L.: Fr.) comb. nov.** Basionym: *Agaricus umbelliferus* L., Species plantarum p. 1175. 1753; *Agaricus umbelliferus* L.: Fr., Elenchus fungorum, p. 22. 1828.

Comments: Synonymous names are: *Byssus botryoides* L. [thallus only - see Redhead & Kuyper 1987, Jørgensen et al. 1994], *Botrydina vulgaris* Bréb. [thallus], *Agaricus pseudoandrosaceus* Bull., *Agaricus nothus* Gmelin, *Agaricus ericetorum* Pers.: Fr., *Agaricus valgus* Holmskjöld, *Merulius turfusus* Pers., *Omphalia luteola* Peck, *Omphalia sphagnophila* Peck, *Omphalina fulvopallens* P.D. Orton (see Redhead & Kuyper 1987, 1988, Kuyper 1995, except for their discussion on *A. umbelliferus* as is detailed below).

Following the extensive review of names and types discussed by Redhead & Kuyper (1987), Jørgensen & Ryman (1989a & b, 1994) published nomenclatural reviews of their own and designated several neo- or lectotypes, some placing names in conflict with those adopted or

rejected by Redhead & Kuyper (1987), and others supporting the interpretations by Redhead & Kuyper (1987, 1988). The most contentious and destabilizing conflict revolves around the choice of *Agaricus ericetorum* Pers.: Fr. versus *Agaricus umbelliferus* L.: Fr. Jørgensen & Ryman (1989b) incorrectly claimed (*i*) that Redhead & Kuyper (1987) had overlooked the fact that Fries (1821) "only cites his own Obs. mycol. 1 p. 87" and (*ii*) that Fries did only that. In fact Fries (1821: 509) specifically gives the authority as "*ericetorum* P. A. S." **not** "Fr." as he did for his own named species ("P." = Persoon and "A.S." = Albertini & Schweinitz). These facts were **explicitly** noted by Redhead & Kuyper (1987: 326-327). Notwithstanding all previous arguments published, we note that in the latest Code (Greuter et al. 2000: 30, Art. 15.1 Ex. 1) the two names are cited as "*Agaricus ericetorum* Fr." and "*A. umbelliferus* L." which suggests that "*Agaricus ericetorum* Fr.: Fr." is a quasi-conserved (i.e. unlisted in any appendix of the Code) name with that authority, rather than "*Agaricus ericetorum* Pers.: Fr." This makes the citation of "*Agaricus ericetorum* Fr." in the Code an ambiguous and poor example. We further note that changes in articles and wording of the Code (Greuter et al. 2000) again alter nomenclatural conclusions reached using earlier Codes by various authors. Specifically, Art. 7.5 now states, "Automatic typification does not apply to names sanctioned under Art. 15." Hence, *Agaricus ericetorum* of Fries (1821) would not be automatically typified by the type of *A. pseudoandrosaceus* Bull., as it would have been under the Code in effect (Voss et al. 1983) when Redhead & Kuyper (1987) interpreted the names.

What, then, are the lectotypes for the names *Agaricus umbelliferus* and *Agaricus ericetorum*, how many names with different authorities are there, and – as ultimately typified – are they taxonomic synonyms? Or in other words, how many homonymic names called *Agaricus ericetorum* are there, and which is sanctioned by Fries' (1821) usage of that binomial?

Agaricus ericetorum Pers. (1796) was first introduced as a binomial citing the earlier named *Agaricus pseudo-androsaceus* Bull. pl. 276 (Bulliard 1786) in synonymy. *Agaricus ericetorum* Pers. is therefore illegitimate (Art. 52.1), unless it is considered sanctioned (Art. 15) or conserved (Art. 14). The concepts of both Bulliard (1786) and Persoon

(1796) were broad and as currently recognized included more than one species. Redhead & Kuyper (1987: 329) lectotypified *Agaricus ericetorum* Pers. and *Agaricus pseudo-androsaceus* Bull. by designating the same illustration on Bulliard plate no. 276, specifically choosing the central figure of pale, rather than greyish agarics depicted on a moss cushion, and thus exclude the greyish forms. This typification of *Agaricus pseudo-androsaceus* Bull. was uncontested and accepted by Jørgensen & Ryman (1989a: 140). All authors agreed it was applicable to the species represented by Lundell & Nannfeldt, *Fungi exsicc.* Suec. No. 1753.

Singer (1961: 23) had previously selected a specimen of *A. ericetorum* from Persoon's herbarium in Leiden (L 910.256-1888) as "lectotype" for *Agaricus ericetorum* "Pers. ex Fr.", but it can at best be considered to be an epitype (or neotype) because there is no date on the specimen and it was not seen by Bulliard who coined the earlier included synonym, *A. pseudo-androsaceus*. Furthermore, unless *Agaricus ericetorum* Pers. is considered sanctioned, Art. 7.5 dictates that such illegitimate names are to be "...automatically typified by the type of the name which ought to have been adopted under the rules...." if the author did not designate a type (which Persoon did not do). Therefore, the type of *Agaricus ericetorum* Pers. (1796) is automatically the type of *Agaricus pseudo-androsaceus* Bull., specifically the central figure on Bulliard's (1786) plate 276. Lange (1981: 693) also dismissed Singer's (1961) typification because, "Singer's notes on the specimen do, however, not indicate that it has the qualities of a lectotype." We suppose this refers to the lack of a date. Lange (1981), however, did not offer an alternative type for the name *Agaricus ericetorum* Pers. Instead he sought to typify *Agaricus ericetorum* "Fries" as distinct from *Agaricus ericetorum* Pers. This is illogical if the type method is followed, but understandable given the confusion and broad application of the name to several species. Singer (1962) identified Persoon's specimen (L 910.256-1888, proposed as type of *A. ericetorum* Pers.) with the well known, common, palely pigmented species he called *Omphalina ericetorum*, even while placing the name *O. umbellifera* in synonymy. Jørgensen & Ryman (1989a: 140) concurred with the taxonomic identification. The Persoon specimen and the lectotype for both *A. pseudo-androsaceus* Bull. and *A. ericetorum* Pers. are considered to be conspecific.

However, drawing upon work later reported by Singer & Cléménçon (1973), Singer (1975) re-interpreted the type for *Omphalina* Quélet as being *Omphalina umbellifera* sensu Quélet, and therefore initiated a schism of the treatment of *Omphalina* in the literature wherein *Agaricus ericetorum* "Fr. ex Fr." ended up in his genus *Gerronema*, but *Agarius ericetorum* "Pers." was treated as synonymous with both "*O. rustica*" and "*O. umbellifera* (L. ex Fr.) Quél." as well as with "*O. pseudoandrosaceous*". This contrasted with his earlier assertion the Persoon specimen was typical *O. umbellifera*, which all other authors considered to be synonymous with the species he was then calling *Gerronema ericetorum*. In his 3rd edition of **The Agaricales in Modern Taxonomy**, Singer (1975) proposed retention of the generic name *Omphalina* Quél. after having moved its type (as he accepted it in the 2nd edition, Singer 1962) to *Gerronema* (see also Singer 1970). This massive confusion caused by Singer's flip-flop application of the epithet "*umbelliferus*" and the lack of any single overlapping species between *Omphalina* sensu Singer (1970, 1975) and *Omphalina* sensu Bigelow (1970) led Redhead & Weresub (1978) to try to disentangle the synonymy and typifications of *Omphalina*. Together these publications precipitated the discussion by Lange (1981).

In the absence of conserved types for any of the species names, despite long debate, the typifications must again be reconsidered in light of revised wording of the Code (Greuter et al., 2000). Art. 7.8 currently states, "The typification of names adopted in one of the works specified in Art. 13.1(d), and thereby sanctioned (Art. 15), may be effected in the light of anything associated with the name in that work." Lange (1981: 695) sought to neotypify *Agaricus ericetorum* "Fr. ex Fr." with Lundell & Nannfeldt, Fungi exsicc. Suec. No. 1753 (C). Jørgensen & Ryman (1989a) noted that the specimen could not be a neotype because original material existed, namely illustrations cited by Fries (1821). They later (Jørgensen & Ryman 1994: 254) selected Tab. 1015, *ut "Agaricus niveus"* (Vahl 1790), as lectotype, formally epitypifying it by a specimen Lundell & Nannfeldt, Fungi exsicc. Suec. No. 1753 in herbarium **UPS** (rather than in **C** as was suggested by Lange 1981). The species represented by this specimen (to judge by all accounts on portions in other herbaria, e.g., **C** & **DAOM**), is conspecific with the species represented by the lectotype of *A. ericetorum* Pers. They are the same if

the type method is followed. If they are the same, it cannot be argued that there is both an *Agaricus ericetorum* Pers. and an *Agaricus ericetorum* "Fr." If they are conspecific, and the one name is based on the other name, logically and nomenclaturally they must have the same lectotype. Fries (1821: 509) himself attributed the name to Persoon. Redhead & Kuyper (1987: 329) had selected the earliest lectotype for *Agaricus ericetorum* of Fries (1821) as well as of *Agaricus ericetorum* Pers. and *A. pseudo-androsaceus* Bull. This predates the selection of lectotype by Jørgensen & Ryman (1989a). The selection of an epitype by Jørgensen & Ryman (1994), however, is uncontested. It clearly is applicable to the name *Agaricus ericetorum* Pers.: Fr.

Controversy continued to dog the typification of *Agaricus umbelliferus* L. and *Omphalina* Quélet (Jørgensen & Ryman 1989a, b, Lange 1981, Redhead 1993, Redhead & Kuyper 1987, 1988, 1993, Singer 1986). We note that subsequent changes in the Code now allow different interpretations from those allowed in the 1980's. In particular, Art. 13.(d) does not disallow lichenized fungi from having sanctioned names, and as noted above Art. 7.8 state, "The typification of names adopted in one of the works specified in Art. 13.1(d), and thereby sanctioned (Art. 15), may be effected in the light of anything associated with the name in that work." This would allow for the rejection of the proposed lectotype of *Agaricus umbelliferus* L. by Redhead & Kuyper (1987, 1993), by the fact that Fries (1821) placed that proposed "lectotype" in another species. This in turn allows us to accept the lectotypification proposed by Jørgensen & Ryman (1989a), namely an unpublished original illustration by Rudbeck in the year 1695, apparently available to Linnaeus, which has been posthumously reproduced and published (Rudbeck 1987). A change in the wording of Art. 9.2 (Note 2) regarding "original material" nullifies the nomenclatural argument put forward by Redhead & Kuyper (1993) against this typification. We also accept the same epitype as that for the name *Agaricus ericetorum* Pers.: Fr., proposed by Jørgensen & Ryman (1994), i.e., Lundell & Nannfeldt, Fungi exsicc. Suec. No. 1753, herb. UPS. These lecto- and epitypifications effectively make *Agaricus umbelliferus* L.: Fr. synonymous with *Agaricus ericetorum* Pers.: Fr. It is hoped that this compromise resolves and ends the 250-year old controversy over these names. Among sanctioned names, *Agaricus umbelliferus* has priority (Gams &

Kuyper 1984) and its lichenized status no longer nomenclaturally affects its availability.

***L. velutina* (Quél.) comb. nov.** Basionym: *Omphalia velutina* Quél., C.R. Ass. franç. Av. Sci. (Grenoble, 1885) 14: 445. 1886.

Comments: The following names represent taxa in a species complex, characterized by greyish basidiomata with incrusting pigments, clampless hyphae, velutinous stipes, elongated basidiospores, and a thallus consisting of numerous loose globose *Phytoconis*-like "goniocysts (cf. Serusiaux 1985)" linked by characteristically very narrow hyphae (1-)2(-3) μm diam (see Redhead & Kuyper 1987). They are considered to be synonymous at a species level, although a phylogenetic study by Lutzoni (1997) suggests that more than one species might be recognized molecularly in this complex, hence our recognition of *L. grisella*:

?= *Omphalina oreades* Singer and its nom. nov. *Clitocybe albimontana* Bigelow (see discussion in Redhead & Kuyper 1987).

?= *Omphalina pararustica* Cléménçon (fide Kuyper 1995). Note: said to differ from *L. velutina* by presence of 4-spored basidia.

?= *Clitocybe borealis* Bigelow and its nom. nov. *Clitocybe kemptonii* Bigelow [Holotype at MICH examined by SAR and thalli confirmed; V. Wells & P. Kempton #2298, 13 Jul 1966, Eklutina L., Alaska, USA; also examined were specimens cited by Bigelow (1985), i.e. Wells & Kempton #2410, Alaska, conspecific; A.H. Smith # 55960, California, conspecific; and a specimen identified as *C. kemptonii* by H.E. Bigelow at MICH but not cited by him, i.e. A.H. Smith #80399, 31 Aug 1971, alpine meadow, Davos-Platz, Switzerland].

Excluded from "*C. kemptonii*": Wells & Kempton #2409, Alaska - a clamped, nonlichenized omphalinoid *Arrhenia* cited by Bigelow (1985) as *C. kemptonii*.

?= *Omphalina defibulata* Singer 1952 [Isotype at MICH examined by SAR and thalli confirmed; R. Singer M355, 10 Feb 1950, Tierra

del Fuego, Rio Grande, Estancia, Nueva, Argentina]

?= *Clitocybe solumophila* Bigelow 1983 [Holotype at MICH examined by SAR and thalli confirmed; A.H. Smith #8501, 6 Nov 1937, Siskiyou Natl. Forest, Siskiyou, California, USA]

?= *Clitocybe payettensis* Bigelow 1983 [Holotype at MICH examined by SAR and thalli confirmed; A.H. Smith #44296, 28 June 1954, Lake Fork Creek, Valley Co., Idaho, USA]

?= *Omphalina meridionalis* Contu & La Rocca, Fungi non delineati 9: 32-33. 1999. [Holotype re-examined and reinterpreted as a clampless species by Barrasa & Esteve-Raventós 2000. Confirmation of the clampless state was made on a later collection kindly collected, identified and supplied by Marco Contu for deposit in DAOM (#229481), Italy, Sardinia, Trinita, d'Agultu, loc. Vignola, 18 Feb. 2001. However, this sample has zebra-striped, finely incrustated pigments contrary to the smoothly pigmented hyphae reported by Barrasa & Esteve-Raventós (2000). It also has the narrower thallic hyphae typical for the *L. velutina* complex. It remains debatable as whether or not and how to distinguish this taxon from *L. velutina* or other named 'species' in the complex. The other *Lichenomphalia* species (*L. umbellifera*, *L. alpina*, *L. hudsoniana*) all exhibit variations in pigmentation throughout their geographic ranges (Redhead & Kuyper 1987).]

Note: The selection of names and typification of *Lichenomphalia* listed above bring into conformity the species epithets adopted for *Omphalina* by M. Lange in **Nordic Macromycetes Vol. 2** (Hansen & Knudsen 1992) and by Senn-Irlet et al. (1990). We hesitate to transfer to *Lichenomphalia* the sterile lichen, *Omphalina foliacea* Jørgensen (1989), which remarkably was described as an *Omphalina* despite the lack of known basidiomata (or ascomata), or any proof, other than suspicion, that it represents a Basidiomycete.

***Arrhenia* Fries, Summa Veget. p. 312. 1849.**

= *Boehmia* Raddi 1807 nom. rej. (Greuter et al. 2000)

- = *Corniola* Gray 1821 non *Corniola* Adans. 1763
- = *Leptotus* P. Karst. 1879
- = *Leptoglossum* P. Karst. 1879
- = *Dictyolus* Quél. 1886
- = *Geotus* Pilát & Svrček 1953
- = *Phaeotellus* Kühner & Lamoure 1972
- = *Arrhenia* subg. *Phaeotellus* (Kühner & Lamoure) Kühner 1980
- = *Clitocybe* subg. *Atroviridae* Bigelow 1982
- = *Omphalina* sect. *Atroviridae* (Bigelow) Redhead 1986
- = *Leptoglossum* subg. *Phaeotellus* (Kühner & Lamoure) Singer 1986

Previously transferred and accepted species of cyphelloid, nutant, or cantharelloid taxa:

- A. acerosa* (Fr.) Kühner (1980: 893 & 992) (type for *Phaeotellus* Kühner & Lamoure 1972)
? = *A. latispora* (Favre) Bon & Courtecuisse (1987: 37)
- A. alnetorum* (Singer) Redhead (1984: 875) Note: correction of epithet, genitive plural of *alnetum*, i.e. alder wood), supplied by J.A. Nannfeldt (pers. comm. 1984).
- A. auriscalpium* (Fr.) Fr. (1849:) (lectotype for *Arrhenia* Fr. 1849)
- A. australis* (Cleb.) Grgurinovic (1997: 318)
- A. fissa* (Leys.) Redhead (1984: 875)
- A. griseopallida* (Desm.) Watling (1988: 553)
- A. lobata* (Pers.: Fr.) Kühner & Lamoure ex Redhead (1984: 871) (lectotype for *Dictyolus* Quél. 1886)
- A. retiruga* (Bull.: Fr.) Redhead (1984: 873) (lectotype for *Leptotus* P. Karst. 1879)
- A. rickenii* (Hora) Watling (1988: 553)
- A. salina* (Høiland) Bon & Courtecuisse (1987: 37) [superfl. comb. by Gulden 1988]
- A. spathulata* (Fr.) Redhead (1984: 876) (= *Cantharellus muscigenus* (Bull.: Fr.) Fr. lectotype for *Leptoglossum* P. Karst. 1879; non *Arrhenia muscigena* (Pers.: Fr.) Quél. 1888 = *Cyphellostereum laeve* (Fr.) Reid, see Redhead 1984: 876)

Required new combinations:

Arrhenia andina (Corner) **comb. nov.**, Basionym: *Leptoglossum andinum* Corner, Monogr. Cantharelloid Fungi, p. 140. 1966.

Arrhenia antarctica (Singer) **comb. nov.** Basionym: *Omphalina antarctica* Singer, Beih. Sydowia 1: 16. 1956.

Arrhenia baeospora (Singer) **comb. nov.**, Basionym: *Omphalina baeospora* Singer, Z. Pilzk. 43: 120. 1977.

Arrhenia chilensis (Mont.) **comb. nov.** Basionym: *Agaricus chilensis* Mont., Ann. Sc. Nat. II, 8: 368. 1837.

Arrhenia chlorocyanea (Pat.) **comb. nov.** Basionym: *Agaricus chlorocyaneus* Pat., Tab. anal. Fung. 4: 145. 1885.

Comments: The taxonomic concept adopted here is that of Redhead (1986) under the name *Omphalina viridis* (Hornem.) Kuyper (= *Agaricus ericetorum* var. *viridis* Hornem., incorrectly listed as "*Agaricus umbelliferus* var. *viridis* Hornem." by Kuyper 1995 as a synonym of *Omphalina chlorocyanea* (Pat.) Singer). *Clitocybe atroviridis* Bigelow (1982) was treated as a synonym by both Redhead (1986) and Kuyper (1995). Bigelow (1985: 413-414), defended publication of his new species, but agreed that European collections that he had earlier reported to lack clamp connections (Bigelow 1982), in fact had clamp connections. He then noted that a North American collection (A.H. Smith 70705, MICH) representing "*Omphalina umbellifera* var. *viridis*" lacked clamp connections. However, that collection was later examined by SAR and redetermined as *Chrysomphalina grossula* (Pers.) Norvell et al., a clampless, much paler species lacking bluish green coloration (Norvell et al. 1994). Nonetheless, Bigelow's (1982) name, *Clitocybe atroviridis*, is the only uncontroversial name linked to the vernal species represented by extant specimens because of the availability of Bigelow's type specimen. Having established that reports of a clampless species similar to the currently recognized one were either false or based upon a wholly different species and genus, there remains only the presence of hairs on the stipes, as depicted by Patouillard (1885) as a barrier to acceptance of Patouillard's earlier name. Specimens identified as *A. chlorocyaneus* that might have served as type, are absent from Patouillard's herbarium in the Farlow herbarium, as confirmed by the late H.E. Bigelow (pers. comm. to SAR), and by L.L. Norvell & D. Pfister more recently (pers. com. to SAR). Almost all collections, of the

bluish green omphalinoid taxon cited by Redhead (1986) and Bigelow (1982) have glabrous stipes, but on some there are projecting hyphal ends, sometimes drawn into wisps (e.g., DAOM 188208). Environmental conditions, if not genetic variability, may well explain the occasional occurrence of minutely pubescent stipes. In the absence of the discovery of another vernal bluish green species in France, and the predominantly spring fruitings of the species as we know it in both Europe and North America, we adopt here the epithet published by Patouillard.

***Arrhenia epichysium* (Pers.: Fr.) comb. nov.** Basionym: *Agaricus epichysium* Pers. Syn. Meth. Fung. p. 462. 1801. [*Agaricus epichysium* Pers.: Fr., Syst. Mycol. 1: 169. 1821.]

***Arrhenia elegans* (Pers.) comb. nov.** Basionym: *Merulius elegans* Pers., Syn. Meth. Fung. p. 481. 1801.

***Arrhenia hohensis* (A.H. Smith) comb. nov.** Basionym: *Omphalia hohensis* A.H. Smith, Contr. Univ. Mich. Herb. 5: 27. 1941.

***Arrhenia lundellii* (Pilát) comb. nov.,** Basionym: *Omphalia lundellii* Pilát, Friesii 5: 26-28. 1954.

***Arrhenia obatra* (Favre) comb. nov.** Basionym: *Omphalia obatra* Favre, Les Champignons supérieurs de la zone alpine du Parc National Suisse. Résultats des recherches scientifiques entreprises au Parc National suisse. 5 (N.S.): 46, 199. 1955 [see Lamoure 1975].

***Arrhenia obscurata* (D. Reid) comb. nov.,** Basionym: *Omphalina obscurata* D. Reid, Trans. Brit. Mycol. Soc. 41: 419. 1958. [Note: = *Clitocybe atrobrunnea* Bigelow 1985, nom. nov.].

***Arrhenia omnivora* (Agerer) comb. nov.** Basionym: *Leptoglossum omnivorum* Agerer, Trans. Brit. Mycol. Soc. 82: 184. 1984. [Holotype at K examined by SAR; the assumption is made here that the subtle membranal pigments are indications of affinities with other *Arrhenia* species, rather than with *Rimbachia*].

***Arrhenia onisca* (Fr.: Fr.) comb. nov.** Basionym: *Agaricus oniscus* Fr., Obs. Mycol. 2: 209. 1818. [*Agaricus oniscus* Fr.: Fr., Syst. mycol. 1: 172. 1821].

***Arrhenia parvivelutina* (Cléménçon & Irlet) comb. nov.,** Basionym: *Omphalina parvivelutina* Cléménçon & Irlet, Schw. Z. Pilzk. 1982A Sondernummer 123 (Mycologia Helvetica): 15. 1982.

***Arrhenia pauxilla* (Cléménçon) comb. nov.,** Basionym: *Omphalina*

pauilla Cléménçon, Z. Mykol. 48: 213. 1982.

***Arrhenia peltigerina* (Peck) comb. nov.** Basionym: *Agaricus peltigerinus* Peck, Rep. New York State Mus. (for 1876) 30: 38. 1878.

***Arrhenia philonotis* (Lasch) comb. nov.** Basionym: *Agaricus philonotis* Lasch, Linnaea 3: 394. 1828.

***Arrhenia pubescentipes* (Bigelow) comb. nov.** Basionym: *Clitocybe pubescentipes* Bigelow, Beih. Nova Hedw. 81: 389. 1985.

***Arrhenia rainierensis* (Bigelow) comb. nov.** Basionym: *Clitocybe rainierensis* Bigelow, Beih. Nova Hedw. 81: 390. 1985.

***Arrhenia rigidipes* (Lamoure) comb. nov.** Basionym: *Omphalina rigidipes* Lamoure, Arctic & Alpine Mycol. (First Intl. Symp. Arcto-Alpine Mycology) p. 207. 1982.

***Arrhenia rustica* (Fr.) comb. nov.** Basionym: *Agaricus rusticus* Fr., Epicr. Syst. Mycol. p. 126, 1838. Note: see Jørgensen & Ryman 1989b: 141 for typification.

***Arrhenia sphaerospora* (Lamoure) comb. nov.** Basionym: *Omphalina sphaerospora* Lamoure, Trav. Sci. Parc Natl. Vanoise 6: 164. 1975.

***Arrhenia sphagnicola* (Berk.) comb. nov.** Basionym: *Agaricus sphagnicola* Berk., British Fungi, English Flora 5(2): 67. 1836. (Note: see Redhead & Kuyper 1987 for comments on types).

***Arrhenia stercoraria* (Barrasa, Esteve-Rav. & Sánchez) comb. nov.** Basionym: *Glabrocypbella stercoraria* Barrasa, Esteve-Rav. & Sánchez Mycol. Res. 102: 1265. 1998.

***Arrhenia subglobispora* (Moreno, Heykoop & Horak) comb. nov.** Basionym: *Omphalina subglobispora* Moreno, Heykoop & Horak, Mycotaxon 77: 366. 2001.

***Arrhenia subobscura* (Singer) comb. nov.** Basionym: *Omphalina subobscura* Singer, Flora Neotropica 3: 21. 1970.

***Arrhenia subumbratilis* (Singer) comb. nov.** Basionym: *Omphalina subumbratilis* Singer, Flora Neotropica 3: 23. 1970.

***Arrhenia trigonospora* (Lamoure) comb. nov.** Basionym: *Omphalina trigonospora* Lamoure, Trav. Sci. Parc Natl. Vanoise 6: 157. 1975.

***Arrhenia umbratilis* (Fr.: Fr.) comb. nov.** Basionym: *Agaricus umbratilis* Fr.:Fr. Syst. Mycol. 1: 157. 1821.

***Arrhenia velutipes* (P.D. Orton) comb. nov.** Basionym: *Omphalina*

velutipes P.D. Orton, Trans. Brit. Mycol. Soc. 43: 337. 1960.

Arrhenia viridimammata (Pilát) comb. nov. Basionym: *Omphalia viridimammata* Pilát, Friesii 5: 25-26. 1954.

Arrhenia volkertii (Murr.) comb. nov. Basionym: *Omphalia volkertii* Murrill, Mycologia 3: 98. 1911. [see Bigelow 1985 for type study].

Acknowledgements

This work was supported in part by NSF grants DEB-0076023 and DEB-9708035. SAR thanks the past and present curators of the Michigan herbarium (MICH) and Kew Gardens herbarium (K) for the loan of type materials, and Marco Contu (Italy) for supplying a specimen of *O. meridionalis*. We thank Keith Seifert, Robert Shoemaker and Lorelei L. Norvell for presubmission reviews. SAR also acknowledges the assistance of the late H.E. Bigelow and J.A. Nannfeldt on nomenclature and/or taxonomy.

Literature Cited

- Agerer, R. 1984. *Leptoglossum omnivorum* sp. nov. from Antarctica. Trans. Brit. Mycol. Soc. 82: 184-186.
- Aronsen, A. 1992. *Hemimycena subglobispora*, spec. nov., and *Arrhenia acerosa* var. *tenella*, comb. nov., from wetlands in southern Norway. Persoonia 14: 425-429.
- Barrasa, J.M., Esteve-Raventós, F., Sánchez, C., Bodensteiner, P. & Agerer, R. 1998. *Glabrocyphella stercoraria*, a new cyphellaceous fungus from Spain. Mycol. Res. 102: 1265-1268.
- Barrasa, J.M. & Esteve-Raventós, F. 2000. A redescription of *Omphalina meridionalis*, based on material collected in Spain. Mycotaxon 75: 273-280.
- Barron, G.L. 1988. Microcolonies of bacteria as a nutrient source for lignicolous and other fungi. Canad. J. Bot. 66: 2505-2510.
- Bigelow, H.E. 1965. The genus *Clitocybe* (Fries) Kummer in North America. Section *Clitocybe*. Lloydia 28: 139-180.
- Bigelow, H.E. 1970. *Omphalina* in North America. Mycologia 62: 1-32.
- Bigelow, H.E. 1974. The *Clitocybe pyxidata* group. Pp. 39-46 in Travaux mycologiques dédiés à R. Kühner. Numéro spécial du Bulletin de la Société Linnéenne de Lyon.
- Bigelow, H.E. 1975. Studies in the Tricholomataceae: *Hygrophoropsis*, *Cantharellula*, *Myxomphalia*, *Omphaliaster*. Beih. Nova Hedwigia 51: 61-77.
- Bigelow, H.E. 1981. Spore ornamentation in the Tricholomataceae I. Mycologia

73: 128-140.

- Bigelow, H.E. 1982. North American species of *Clitocybe*. Part I. Beih. Nova Hedw. 72: 1-280.
- Bigelow, H.E. 1983. Some clampless species of *Clitocybe*. Cryptog. Mycol. 4: 93-98.
- Bigelow, H.E. 1985. North American species of *Clitocybe*. Part II. Beih. Nova Hedw. 81: 281-471. J. Cramer, Berlin & Stuttgart.
- Birrer, H. 2000. *Gerronema xanthophyllum*. Schw. Zeit. f. Pilzk. 78(6): 270-275.
- Bon, M. & Courtecuisse, R. 1987. Espèces ou combinaisons nouvelles et validations de taxons. Doc. Mycol. XVIII (fasc. 69): 37-38.
- Breitenbach, J. & Kränzlin, F. 1991. Fungi of Switzerland. Vol. 3. Boletes and agarics 1st part. Strobilomycetaceae and Boletaceae, Paxillaceae, Gomphidiaceae, Hygrophoraceae, Tricholomataceae, Polyporaceae (lamellate). Mykologia, Lucerne.
- Britzelmayer, M. 1890. Hymenomyceten aus Sudbayren. Teil VI. Boleti, Cortinari, Dermi, Hydnei, Hyporhodii, Leucospori, Melanospori. Berlin.
- Bruns, T.D., Szaro, T.M., Gardes, M., Cullings, K.W., Pan, J.J., Taylor, D.L., Horton, T.R., Kretzer, A., Garbelotto, M. & Li, Y. 1998. A sequence database for the identification of ectomycorrhizal basidiomycetes by phylogenetic analysis. Mol. Ecol. 7: 257-272.
- Bulliard, J.B.F. 1786. Herbar de la France. Vol. 6 Fasc. 65-72. Pls. 256-288. Paris.
- Cassinelli, G., Lanzi, C., Pensa, T., Gambetta, R. A., Nasini, G., Cuccuru, G., Cassinis, M., Pratesi, G., Polizzi, D., Tortoreto, M., & Zunino, F. 2000. Clavilactones, a novel class of tyrosine kinase inhibitors of fungal origin. Biochemical-Pharmacology 59 (12): 1539-1547.
- Chiaffi, M. & Surault, J.-L. 1996. Une espèce rare et remarquable, *Haasiella venustissima* (Fr.) Kotl. & Pouz. Bull. Soc. Mycol. France 112: 127-135.
- Cléménçon, H. 1982. Kompendium de Blätterpilze Europäische omphalinoide Tricholomataceae. Z. Mykol. 48: 195-237.
- Cléménçon, H. 1997. Anatomie der Hymenomyceten. Eine Einführung in die Cytologie und Plectologie der Krustenpilze, Porlinge, Keulenpilze, Leistlinge, Blätterpilze und Röhrlinge. F. Flück-Wirth, Teufen.
- Clements, F.E. & Shear, C.L. 1931. The genera of fungi. H.W. Wilson Co., New York.
- Cochran, K.W. & Cochran, M.W. 1978. *Clitocybe clavipes*: antabuse-like reaction to alcohol. Mycologia 70: 1124-1126.
- Collin, P. & Lauron, A. 1994. *Omphalina peltigerina* (Peck) P. Collin,

- champignon lichenicole nouveau pour la France. Bull. Soc. Mycol. France 110: 11-16.
- Corner, E.J.H. 1966. A monograph of Cantharelloid fungi. Oxford Univ. Press, London.
- Courtecuisse, R. 1986. Contribution à la connaissance de la flore fongique du Morbihan et de quelques départements voisins-I. Doc. Mycol. 16(fasc. 62): 1-22
- Donk, M.A. 1949. Nomenclatural notes on generic names of agarics (fungi: Agaricales). Bull. Jard. Bot. Buitenzorg, Sér. 3, 18: 271-402.
- Donk, M.A. 1962. The generic names proposed for Agaricaceae. Beih. Nova Hedwigia 5: 1-320.
- Earle, F.S. 1909. The genera of the North American gill fungi. Bull. New York Bot. Gard. 5: 373-451.
- Favre, J. 1955. Les Champignons supérieurs de la zone alpine du Parc National Suisse. Résultats des recherches scientifiques entreprises au Parc National suisse. 5 (N.S.): 1-212.
- Fries, E.M. 1821. Systema Mycologicum. I. Gryphiswaldiae.
- Fries, E.M. 1849. Summa vegetabilium Scandinaviae. II. Typographica Academica, Uppsala. pp. 259-572.
- Gams, W. 1995. Report of the Committee for Fungi: 5. Taxon 44: 411-414.
- Gams, W. & Kuyper, T.W. 1984. Problems involved in the sanction of fungal names. Mycotaxon 20: 619-631.
- Gill, M. & Steglich, W. 1987. Pigments of fungi (Macromycetes). Progress in the chemistry of organic natural products. Vol. 51: 1-317. Springer-Verlag, Wien.
- Greuter, W., McNeill, J., Barrie, F. R., Burdet, H. M., Demoulin, V., Filgueiras, T. S., Nicolson, D. H., Silva, P. C., Skog, J. E., Trehane, P., Turland, N. J. & Hawksworth, D. L. (eds.). 2000. International Code of Botanical Nomenclature (Saint Louis Code). Adopted by the Sixteenth International Botanical Congress St. Louis, Missouri, July-August 1999. (Regnum Veg. 138). Koeltz Scientific Books, Königstein, Germany. xviii + 474 pp.
- Grgurinovic, C.A. 1997. Larger fungi of South Australia. Botanical Garden of Adelaide and State Herbarium and Flora and Fauna of South Australia Handbooks Committee. Adelaide.
- Gulden, G. 1987. Studies in the agarics of Svalbard. 1. New species and combinations (Tricholomataceae). Sydowia 40: 51-59.
- Gulden, G. & Torkelsen, A.-E. 1996. Part 3. Fungi I. Basidiomycota: Agaricales, Gasteromycetales, Aphyllophorales, Exobasidiales, Dacrymycetales and Tremellales. Pp. 173-206 in Elvebakk, A. & Prestrud, P. (eds.): A catalogue of Svalbard plants, fungi, algae and

cyanobacteria. Norsk Polarinstitutt Skrifter 198.

- Haas, H. 1962. Die systematische Stellung von *Clitocybe venustissima* Fries. Z. Pilzk. 28: 12-13.
- Hansen, L. & Knudsen, H. [eds.] 1992. Nordic Macromycetes Vol. 2. Polyporales, Boletales, Agaricales, Russulales. Nordsvamp, Copenhagen.
- Harmaja, H. 1969. The genus *Clitocybe* (Agaricales) in Fennoscandia. Karstenia 10: 5-121.
- Harmaja, H. 1974. A revision of the generic limit between *Clitocybe* and *Lepista*. Karstenia 14: 82-92.
- Hassel, A. & Kost, G. 1998. Untersuchungen zur Interaktion von *Leptoglossum retirugum* (Tricholomataceae, Basidiomycetes) mit *Brachthecium rutabulum* (Brachytheciaceae, Musci). Z. Mykol. 64: 207-215.
- Hibbett, D.S., Gilbert, L.-B., & Donoghue, M.J. 2000. Evolutionary instability of ectomycorrhizal symbioses in basidiomycetes. Nature 407: 506-508.
- Høiland, K. 1976. The genera *Leptoglossum*, *Arrhenia*, *Phaeotellus* and *Cyphellostereum* in Norway and Svalbard. Norw. J. Bot. 23: 201-212.
- Høiland, K. 1982. Fjære-mosekantarell, *Leptoglossum salinum*, en sopp med eiendommelig økologi. Blyttia 40: 41-44.
- Honegger, R. & Brunner, U. 1981. Sporopollenin in the cell walls of *Coccomyxa* and *Myrmecia* phycobionts of various lichens: an ultrastructural and chemical investigation. Canad. J. Bot. 59: 2713-2734.
- Horak, E. 1968. Synopsis generum Agaricalium (Die Gattungstypen der Agaricales). Beitr. Kryptogam. Schweiz 13: 1-741.
- Horak, E. 1987. Agaricales from Yunnan, China I. Trans. Mycol. Soc. Japan 28: 171-188.
- Hornby, D. & Ward, E. 1995. Wanted: *Omphalina pyxidata*. Mycologist 9 (1) 36.
- Hutchinson, L.J. & Barron, G.L. 1996. Parasitism of yeasts by lignicolous Basidiomycota and other fungi. Canad. J. Bot. 74: 735-742.
- Hutchinson, L.J. & Barron, G.L. 1997a. Parasitism of pollen as a nutritional source for lignicolous Basidiomycota and other fungi. Mycol. Res. 101: 191-194.
- Hutchinson, L.J. & Barron, G.L. 1997b. Parasitism of algae by lignicolous Basidiomycota and other fungi. Canad. J. Bot. 75: 1006-1011.
- Imai, S. 1938. Studies on the Agaricaceae of Hokkaido. II. J. Fac. Agric. Hokkaido Univ. 43: 179-378.
- Jørgensen, P.M. 1989. *Omphalina foliacea*, a new basidiolichen from America. Nord. J. Bot. 9: 89-95.

- Jørgensen, P.M., James, P.W. & Jarvis, C.E. 1994. Linnaean lichen names and their typification. *Bot. J. Linnean Soc.* 115: 261-405.
- Jørgensen, P. M. & Ryman, S. 1989a. (927) Proposal to conserve *Omphalina* Quélet over *Phytoconis* Bory and *Botrydina* Brébisson (Basidiomycetes). *Taxon* 38: 305-308.
- Jørgensen, P. M. & Ryman, S. 1989b. The correct names of the lichenized *Omphalina* species in Scandinavia. *Graphis Scripta* 3: 138-143.
- Jørgensen, P. M. & Ryman, S. 1994. On the typification of *Omphalina umbellifera* (L.: Fr.) Quél. (Fungi, Agaricales). *Taxon* 43: 253-255.
- Korf, R.P. 1988. Report (N.S. 1) of the Committee for Fungi and Lichens on proposals to conserve and/or reject names. *Taxon* 37: 450-463.
- Kost, G. 1986. Morphologie, Anatomie und Systematik carotinoidhaltiger Blätterpilze. *Ber. Deutsch. Bot. Ges.* 99(1-2): 43-58.
- Kotlaba, F. & Pouzar, Z. 1966. *Haasiella*, a new agaric genus and *H. splendidissima* sp. nov. *Česká Mykol.* 20: 135-140.
- Kovalenko, A. E. 1999. The arctic-subarctic and alpine-subalpine component in the Hygrophoraceae of Russia. *Kew Bull.* 54: 695-704.
- Kranner, I. & Lutzoni, F. 1999. Evolutionary consequences of transition to a lichen symbiotic state and physiological adaptation to oxidative damage associated with poikilohydry. Pp. 591-628. In Lerner, H.R. [Ed.] *Plant responses to environmental stresses*. Marcel Dekker, New York.
- Kreisel, H. 1987. *Handbuch für Pilzfreunde. Vol. 3. Blätterpilze - Hellblättler und Leistlinge*. VEB Gustav Fischer Verlag, Jena.
- Kühner, R. 1980. Les Hyménomycètes agaricoïdes (Agaricales, Tricholomatales, Pluteales, Russulales). Étude générale et classification. Numéro spécial du Bulletin de la Société Linnéenne de Lyon. 49^e 1-1027.
- Kühner, R. & Lamoure, D. 1972. Agaricales de la zone alpine. *Pleurotacées. Botaniste* 55: 7-37.
- Kuyper, T.W. 1986. Generic delimitation in European omphalinoid Tricholomataceae. La Famiglia delle Tricholomataceae. Atti del Convegno Internazionale del 10-15 settembre 1984. Borgo Val di Taro - Italy. Atti del Centro Studi per la Flora Mediterranea 6: 83-104.
- Kuyper, T.W. 1992. Aantekeningen over *Clitocybe* III. *Coolia* 25(2): 39-47.
- Kuyper, T.W. 1994. Genera in the Agaricales: advances and retreats in the search for a natural system. *Mycol. Helvetica* 6: 141-159.
- Kuyper, T.W. 1995. *Clitocybe* (Fr.) Staude, Schwämme Mitteledeutschl.: XXVII, 122. 1857, IN Bas, C., Kuyper, T.W., Noordeloos, M.E. & Vellings, E.C. [eds.]. *Flora Agaricina Neerlandica Vol. 3.* A.A. Balkema, Rotterdam.
- Lamoure, D. 1972. Agaricales de la zone alpine. Genre *Clitocybe*. *Travaux*

- Scientifiques du Parc National de la Vanoise 2: 107-152.
- Lamoure, D. 1974. Agaricales de la zone alpine. Genre *Omphalina*. 1^{ère} partie. Travaux Scientifiques du Parc National de la Vanoise 5: 149-164.
- Lamoure, D. 1975. Agaricales de la zone alpine. Genre *Omphalina*. 2^e partie. Travaux Scientifiques du Parc National de la Vanoise 6: 153-166.
- Lange, M. 1981. Typification and delimitation of *Omphalina* Quél. Nordic J. Bot. 1: 691-696.
- Lutzoni, F.M. 1997. Phylogeny of lichen- and non-lichen-forming omphalinoid mushrooms and the utility of testing for compatibility among multiple data sets. Syst. Biol. 46: 373-406.
- Lutzoni, F.M. & Pagel, M. 1997. Accelerated evolution as a consequence of transitions to mutualism. Proc. Natl. Acad. Sci. USA 94: 11422-11427.
- Lutzoni, F.M. & Vilgalys, R. 1995a. Integration of morphological and molecular data sets in estimating fungal phylogenies. Can. J. Bot. 73(Suppl. 1): S649-S659.
- Lutzoni, F.M. & Vilgalys, R. 1995b. *Omphalina* (Basidiomycota, Agaricales) as a model system for the study of coevolution in lichenized fungi. Crypt. Bot. 5:82-97.
- May, T.W. & Wood, A.E. 1995. Nomenclatural notes on Australian macrofungi. Mycotaxon 54: 147-150.
- Moncalvo, J.-M., Lutzoni, F.M., Rehner, S.A., Johnson, J. & Vilgalys, R. 2000. Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. Syst. Biol. 49: 278-305.
- Moncalvo, J.-M., Vilgalys, R., Redhead, S.A., Johnson, J.E., James, T.J., Hofstetter, V., Verduin, S., Larsen, E., Baroni, T.J., Thorn, R.G., Jacobsson, S., Cléménçon, H. & Miller, O.K. [2002, in press]. One hundred and seventeen clades of euagarics. Molecular Phylogenetics and Evolution. <http://www.biology.duke.edu/fungi/mycolab/publications/117clades.html>
<http://www.biology.duke.edu/fungi/mycolab/publications/agaric877fig2.html>
- Moser, M. & Jülich, W. 1997. Farbatlas der Basidiomyceten. Lieferung 15. *Arrhenia* Fr. Gustav Fischer Verlag.
- Murrill, W.A. 1916. *Omphalina*. North American Flora 9: 344-352.
- Nezdoiminogo, E.L. 1997. [Macromycetes of Kola Peninsula tundras]. Mikologia i Fitopatologia 31: 28-30.
- Norvell, L.L., Redhead, S.A. & Ammirati, J.F. 1994. *Omphalina* sensu lato in North America. 1-2. 1: *Omphalina wynniae* and the genus

Chrysomphalina. 2: *Omphalina* sensu Bigelow. Mycotaxon 50: 379-407.

- Oberwinkler, F. 1970. Die Gattungen der Basidiolichenen. Dtsch. Bot. Ges., Neue Folge 4: 139-169.
- Patouillard, N. 1885. Tabulae Analytique Fungorum. Fasc. IV. No. 301-400. p. 137-180. Jule Gindre, Pologny.
- Pegler, D.N. & Young, T.W.K. 1971. Basidiospore morphology in the Agaricales. Beih. Nova Hedw. 35: 1-210.
- Persoon, C.H. 1796. Observationes Mycologica, I. Leipzig.
- Persoon, C.H. 1801. Synopsis methodica fungorum. Gottingen.
- Pilát, A. & Nannfeldt, J.A. 1954. Notulae ad cognitionem Hymenomycetum Lapponiae Tornensis (Sueciae). Friesia 5: 6-38.
- Rauschert, S. 1986. Proposal to conserve *Clitocybe* (*Fungi caeteri*: Agaricales) with a conserved type. Taxon 35: 736-737.
- Redhead, S.A. 1984. *Arrhenia* and *Rimbachia*, expanded generic concepts and a reevaluation of *Leptoglossum* with emphasis on muscicolous North American taxa. Can. J. Bot. 62: 865-892.
- Redhead, S.A. 1986. Mycological observations: 17-20, nomenclatural notes on some omphaloid genera in Canada: *Chrysomphalina*, *Rickenella*, *Gerronema*, *Omphalina*. Acta Mycologica Sinica Suppl. 1: 297-304.
- Redhead, S.A. 1987. The Xerulaceae (Basidiomycetes), a family with sarcodimitic tissues. Can. J. Bot. 65: 1551-1562.
- Redhead, S.A. 1993. Proposal to conserve *Omphalina* with *O. pyxidata* as conserved type -- an alternative to Proposals (927) and (1068). Taxon 42: 452.
- Redhead, S.A., Ammirati, J.F. & Norvell, L.L. 1995. *Omphalina* sensu lato in North America 3: *Chromosera* gen. nov. Beih. Sydowia 10: 155-167.
- Redhead, S.A. & Kuyper, T.W. 1987. Lichenized Agarics: Taxonomic and Nomenclatural Riddles. Pgs. 319-348 IN: Arctic and Alpine Mycology II. Eds. Laursen, G.A., Ammirati, J.F. & Redhead, S.A. Plenum Press, New York.
- Redhead, S.A. & Kuyper, T.W. 1988. *Phytoconis*, the correct generic name for the basidiolichen *Botrydina*. Mycotaxon 31: 221-223.
- Redhead, S.A. & Kuyper, T.W. 1993. (1068) Proposal to conserve *Omphalina* with *O. epichysium* as conserved type - an alternative to: (927). Taxon 42: 447-451.
- Redhead, S.A. & Malloch, D.W. 1986. *Cantharellula umbonata*. Fungi Canadensis No. 301. Agriculture Canada, Ottawa.
- Redhead, S.A., Moncalvo, J.-M., Vilgalys, R. & Lutzoni, F. 2002. Phylogeny of agarics: partial systematics solutions for bryophilous omphaloid agarics outside of the Agaricales (euagarics). Mycotaxon 82: 151-168.

- Redhead, S.A. & Weresub, L.K. 1978. On *Omphalia* and *Omphalina*. *Mycologia* 70: 556-568.
- Romagnesi, H. 1992. Prodrômes à une Flore Analytique des Agaricomycetes. *Bull. Soc. Mycol. France* 108: 1-15.
- Rudbeck, O. 1987. Iter lapponicum. Skissboken från resan till Lappland 1695. Stockholm. [published posthumously]
- Senn-Irlet, B. 1987. Pilze eines subalpinen Weidengebüsches. In Pätzold, W. (ed.) "Festschrift 25 Jahre Schwarzwälder Pilzlehrschau": 61-71.
- Senn-Irlet, B., Jenssen, K.M. & Gulden, G. 1990. Arctic and alpine fungi-3. Soppkonsulenten, Oslo.
- Serussiaux, E. 1985. Goniocysts, goniocystangia and *Opegrapha lambinonii* and related species. *Lichenologist* 17: 1-26.
- Singer, R. 1936. Das System der Agaricales. I. *Ann. Mycol. (Berlin)* 34: 286-378.
- Singer, R. 1951a. New genera of fungi.V. *Mycologia* 43: 598-604.
- Singer, R. 1951b. [1949] The Agaricales (mushrooms) in modern taxonomy. *Lilloa* 22: 1-832.
- Singer, R. 1952. The agarics of the Argentine sector of Tierra del Fuego and limitrophous regions of the Magallanes area I. White and pink spored groups. *Sydowia* 6: 165-226.
- Singer, R. 1956. A fungus collected in the Antarctic. *Beih. Sydowia* 1: 16-23.
- Singer, R. 1961. Type studies on Basidiomycetes. X. *Persoonia* 2: 1-62.
- Singer, R. 1962. The Agaricales in modern taxonomy. 2nd ed. J. Cramer, Weinheim.
- Singer, R. 1970. A monograph of the subtribe Omphalinae. *Flora Neotropica* 3: 2-84.
- Singer, R. 1975. The Agaricales in modern taxonomy. 3rd ed. J. Cramer, Vaduz.
- Singer, R. 1986. The Agaricales in modern taxonomy. 4th ed. Koeltz Scientific Books, Koenigstein.
- Singer, R. & Cléménçon, H. 1973 [1972]. Notes on some leucosporous and rhodosporous European agarics. *Nova Hedwigia* 23: 305-351.
- Singer, R. & Smith, A.H. 1946. Proposals concerning the nomenclature of the gill fungi including a list of proposed lectotypes and genera conservanda. *Mycologia* 38: 240-299.
- Vahl, M. 1790. *Flora Danica*. Vol. 6. Fasc. 18. Pls. 961-1020. Kobenhavn.
- Voss, E. G., Burdet, H. M., Chaloner, W. G., Demoulin, V., Hiepko, P., McNeill, J., Meikle, R. D., Nicolson, D. H., Rollins, R. C., Silva, P. C., & Greuter, W.(eds.). 1983. International Code of Botanical Nomenclature Adopted by the Thirteenth International Botanical Congress, Sydney, August 1981. (*Regnum veg.* 111). Bohn, Scheltma & Holkema, Utrech/Antwerpen. xv + 472 pp.

- Watling, R. 1988. Some British omphalinoid and pleurotoid agarics. Notes Roy. Bot. Gard. Edinburgh 45(3): 549-558.
- Watling, R. & Gregory, N.M. 1989. British Fungus Flora. Agarics and Boleti 6: Crepidotaceae, Pleurotaceae and other pleurotoid agarics. Royal Bot. Gard. Edinburgh.
- Yamaura, Y., Fukuhara, M., Kawamata, S., Satsumabayashi, H., Takabatake, E., & Hashimoto, T. 1986. Effects of *Clitocybe clavipes* extract on the components and enzymes related to ethanol metabolism in mice. J. Food Hygenic Soc. Japan 27(5): 522-527.