

PHYLOGENY OF AGARICS: PARTIAL SYSTEMATICS SOLUTIONS FOR BRYOPHILOUS OMPHALINOID AGARICS OUTSIDE OF THE AGARICALES (EUAGARICS)

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Abstract: The taxonomy of several species previously assigned to *Omphalina* sensu lato or *Gerronema* is reevaluated in light of recent molecularly based phylogenetic hypotheses. One surmised clade, herein informally labelled the rickenelloid clade, falls outside of the Agaricales using nLSU data. Analysis of how best to classify these taxa results in the establishment of two new genera, *Loreleia* (type: *Agaricus postii*) and *Sphagnomphalia* (type: *Clitocybe brevibasidiata*), and the renaming of a later homonym, *Jacobia* nom. illeg. as *Contumyces* (type: *Clitocybe rosella*). New combinations are proposed and an interim key to these genera is provided.

Key words: nLSU, *Omphalina*, *Gerronema*, *Rickenella*, *Cantharellopsis*, *Contumyces*, *Loreleia*, *Sphagnomphalia*, *Cotylidia*.

Introduction

An evolutionarily sound classification of omphalinoid and clitocyboid agarics, especially those lacking distinctive or highly developed anatomical features was virtually impossible when based solely on phenotypic characters. It may be assumed that relatively undifferentiated growth forms, such as these, arose multiple times and that taxonomic reliance upon them would result in classifications that would not reflect their phylogenetic history. Historically all such agarics were lumped together in only one or two genera (*Omphalina* Quél., *Clitocybe* (Fr.) Staude), hence the loosely applied terms omphalinoid and clitocyboid (Largent 1977), which merely refer to agarics with decurrent lamellae and either small (omphalinoid) or large (clitocyboid) basidiomata. Species with moderately sized basidiomata were left ambiguously classified. Phylogenetic analyses of nucleotide sequence data from the nuclear large ribosomal subunit RNA gene (nLSU) placed some omphalinoid agarics, e.g., *Rickenella* Raithelh., outside the Agaricales (Moncalvo et al. 2000). A more recent study (Moncalvo et al. in press) suggests that *Rickenella* and other omphalinoid fungi may be classified in an unanticipated lineage of Homobasidiomycetes, the Hymenochaetales (= hymenochaetoid clade, Hibbett & Thorn, 2001). In the present companion article to a larger phylogeny of agaricoid fungi (Moncalvo et al. in press), we conduct a new phylogenetic analysis of nLSU sequences from omphalinoid agarics and representatives of all major homobasidiomycete lineages, outline a new classification, and delimit several lamellate genera that possibly classify in the Hymenochaetales.

Re-investigation of published phylogenetic data

Lutzoni (1997), when investigating lichenized versus nonlichenized omphalinoid agarics using four datasets (ITS1, 5.8S, ITS2, and nLSU), demonstrated that several taxonomically problematic bryophilous taxa [labelled *Gerronema marchantiae* Singer & Cléménçon, *Omphalina brevbasidiata* (Singer) Singer, *O. rosella* (M.M. Moser) M.M. Moser, *Rickenella mellea* (Singer & Cléménçon) Lamoure, and *R. pseudogrisella* (A.H. Sm.) Gulden] clustered together away from the

majority of the other omphalinoid taxa in a limited sampling of agarics (23 species; 1 purported outgroup = *Multiclavula* R.H. Petersen). He pondered whether all five problematic taxa should be considered to be congeneric and named *Rickenella*. Moncalvo et al. (2000) used only the nLSU (25S) data of only 3 representatives of that clade (*O. rosella*, *R. mellea* and *R. pseudogrisella*) and 12 additional species from Lutzoni (1997) as a subsample, but combined these data with a far more diverse taxon data matrix (139 other taxa, mostly agarics). They suggested that these three problematic bryophilous taxa (labelled clade "X" in their fig. 2) formed a monophyletic group outside of the main agaric clade, i.e., outside the Agaricales or euagarics. Subsequently, as the 154-taxon-sized data matrix utilized by Moncalvo et al. (2000) grew in size through the addition of taxa, it was learned serendipitously that *Cotylidia aurantiaca* (Pers.) A.L. Welden clustered with taxa in clade "X", as did *Cantharellopsis prescottii* (Weinm.) Kuyper. The latter species is yet another bryophilous omphalinoid agaric (Redhead 1984; Kuyper 1986; Bigelow 1985), whereas *Cotylidia aurantiaca* is terrestrial and has been considered to be a stipitate stereoid taxon (Reid 1965) in the Podoscyphaceae ("Aphylophorales").

Consequently, 2 additional species of *Cotylidia* P. Karst., *C. aurantiaca* var. *alba* Reid and *C. diaphana* (Schw. apud. Berk. & Curt.) Lentz, were added to the expanding taxon matrix for analysis by Moncalvo et al. (in press), in order to test for fidelity of the sequence data at the generic level for the characteristically monomitic genus *Cotylidia*. Additionally, a representative of the dimitic genus *Podoscypha* Pat., *P. parvula* (Lloyd) Reid, was added to the data set to test for taxonomic and phylogenetic relationships that nomenclaturally might affect the use of the names Podoscyphaceae and Podoscyphales. Results showed that *Podoscypha parvula* belongs to a distant clade, which can be called the Polyporales (= polyporoid clade, Hibbett & Thorn 2001) and is also equivalent to outgroup "BB" in Moncalvo et al. (2000). In all current bootstrap and maximum parsimony analyses of LSU sequence data (Moncalvo et al., in press), all three *Cotylidia* mentioned above cluster in close proximity with each other and with *Rickenella* representatives and other allies. It is possible that the genus *Cotylidia* is also bryophilous. Its biology has not been examined in detail. Lammers (1992) reports that *Cotylidia undulata* (Fr.: Fr.) P. Karst. grows among

pioneering vegetation, including the mosses *Bryum argenteum* Hedw. and *Pohlia nutans* (Hedw.) Lindb. and Moncalvo (pers. obs.) collected the sequenced sample of *C. aurantiaca* on mosses on a decaying coconut stump. Curiously, nLSU data (Moncalvo et al., in press) also suggests a relationship of these taxa and the lignicolous taxa *Resinicium bicolor* (Alb. & Schwein.) Parmasto (a corticioid), *Trichaptum abietinum* (Dicks.: Fr.) Ryvarden (a polypore), and *Hyphodontia radula* (Pers.) Langer & Vesterh. (a corticioid). However, there is somewhat conflicting published ITS1-5.8S-ITS2 data suggesting that *Cotylidia diaphana* is related to species of *Phanaerochaete* P. Karst. (Boidin et al. 1998), a genus which LSU data available to us suggests is more closely allied to most *Phlebia* Fr. species, in the polyporoid clade of Hibbett & Thorn (2000). As a result, until resolved by further study, it is difficult to assign either a family or order name for the group that includes the genera *Rickenella* and *Cotylidia*. The Podoscyphaceae does not appear to be appropriate because in all analyses of the nLSU data, the type genus, *Podoscypha*, clusters elsewhere. Based solely on the analysis by Moncalvo et al. (2000) it would be tempting to name a new family for *Rickenella* and allies. However, for classification purposes, we now would include several previously described genera (*Cantharellopsis* Kuyper, *Cotylidia*, *Rickenella*) and tentatively excluding genera such as *Hyphodontia* J. Erikss., *Resinicium* Parmasto, and *Trichaptum* Murrill, while noting that *Phlebia tristis* (Litsch. & S. Lundell) Parmasto possibly has affinity to the group. However, Hibbett et al. (1997) have demonstrated that *Trichaptum abietinum* and *Hyphodontia alutaria* (Burt.) J. Erikss. belong to a clade that Hibbett & Thorn (2001) named the hymenochaetoid clade. That clade included genera traditionally placed in the Hymenochaetaceae (*Coltricia* Gray, *Phellinus* Quéél., *Inonotus* P. Karst.), as well as *Schizopora* Vel. (Schizoporaceae Jülich 1981), *Basidioradulum* Nobles (Hyphodermataceae Jülich 1981), and *Oxyporus* (Bourdot & Galzin) Donk sp. (Rigidiporaceae Jülich 1981). Thus there is no shortage of potential family names in this unresolved large clade for which we adopt the name Hymenochaetales.

Here we conduct a new phylogenetic analysis of nLSU sequences in order to examine in more details the relationships of omphalinoid agarics that classify outside the Agaricales, and further test their possible affinities with hymenochaetoid taxa. To do this, we combined

sequences taken from Moncalvo et al. (2000 and in press) with several hymenochaetoid sequences that have recently been deposited in GenBank by E. Langer. We propose here several new genera and combinations for omphalinoid agarics.

Materials and methods

The data matrix for this study consisted of 47 nLSU sequences representative of the eight major clades of Homobasidiomycetes as determined in Hibbett & Thorn (2001) and Binder & Hibbett (in press). A sequence of *Auricularia polytricha* (Mont.) Sacc. (Heterobasidiomycetes) was used to root the phylogeny. The GenBank accession number of each sequence is given after each taxon name in Fig. 1. Sequences were aligned manually. Phylogenetic analysis was conducted in PAUP* version 4.0b6 (Swofford 1999) using maximum-likelihood (ML) as the optimality criterion. ML settings were determined by likelihood-ratio tests (LRT) in MODELTEST vs. 3.06 (Posada & Crandall, 1998). A heuristic search was conducted with ASIS addition sequence, TBR branch swapping, and MULTREES on. Statistical support for nodes in the phylogeny were evaluated from 500 bootstrap replicates using maximum-parsimony with the following settings: one round of random addition sequence in each replicate, TBR branch swapping, steepest descent not in effect, branch allowed to collapse when maximum branch length was zero (amb = -), MULPARS on, and MAXTREES set to 10 in each replicate.

We conducted a search that constrained the omphalinoid agarics to be monophyletic, and compared the resulting constrained trees with unconstrained trees using the Shimodaira-Hasegawa (SH) test in PAUP*. The SH test was performed using 1000 bootstrap replicates for REL and full optimization.

Results and discussion

Phylogenetic analysis

The 48 sequences were unambiguously aligned for 868 positions, of which, 459 were constant, 125 were variable but parsimony-

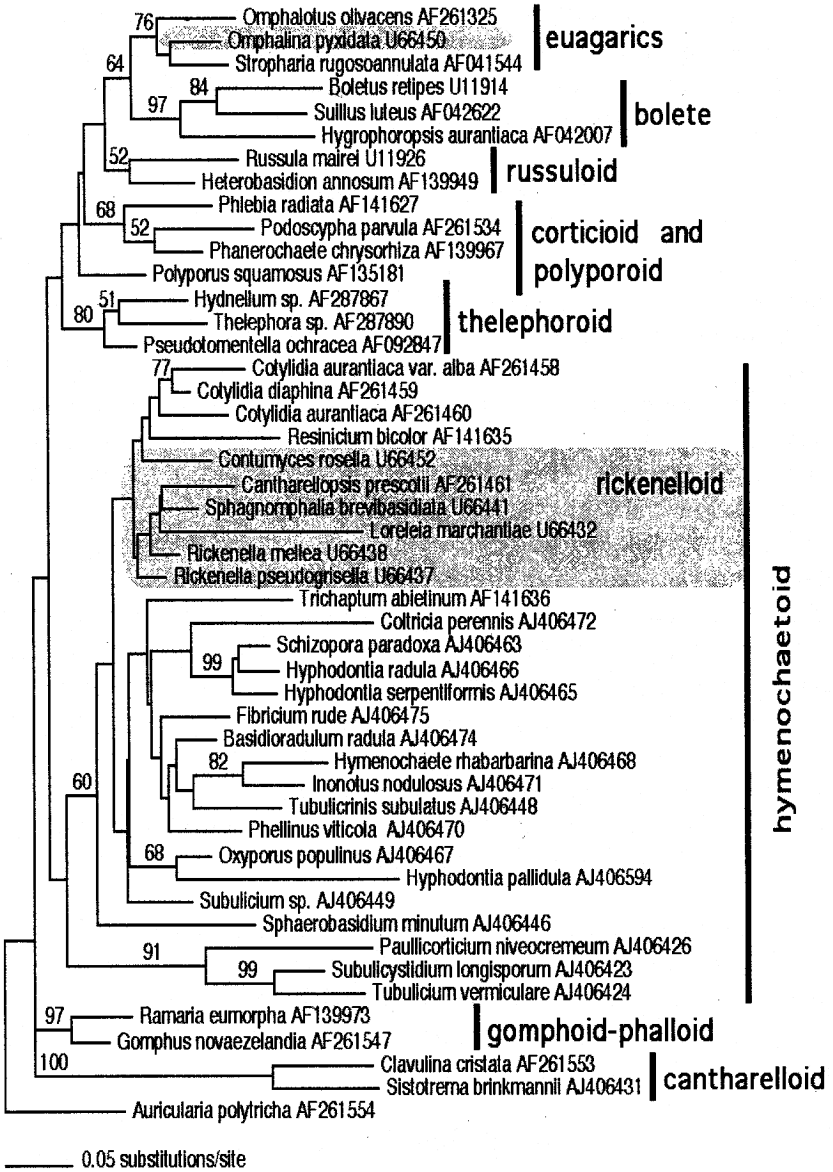


Fig. 1. One of 3 ML trees discussed in text, showing the surmised placement of the rickenelloid fungi in the hymenochaetoid clade and the type species for *Omphalina* in the euagarics clade.

uninformative, and 284 were variable and parsimony-informative. LRT in MODELTEST suggested the use of the TrN+I+G model of evolution for ML analysis, as follows: Base frequencies: A = 0.2654, C = 0.1804, G = 0.2949, and T = 0.2593; substitution model (rate matrix): [A-C] = [A-T] = [G-T] = 1.0000; [A-G] = 3.5597; and [C-T] = 8.1045; proportion of invariable sites = 0.3625; gamma shape parameter for variable sites = 0.5908; and 4 rate categories. With these settings, the ML search produced three trees of score $-\ln = 9604.30157$. One of these three trees is shown in Fig. 1, along with parsimony-based bootstrap statistical support for branches. A search that constrained *O. pyxidata* (Pers.: Fr.) Quéél., type of *Omphalina*, to form a monophyletic group with the omphalinoid taxa nested within the hymenochaetoid clade produced a tree of score $-\ln = 9696.17366$. Based on the SH test, this constrained topology was significantly less-likely than the unconstrained tree ($P < 0.001$), and this hypothesis could therefore be rejected.

The tree depicted in Fig. 1, although produced from partial nLSU sequences, is largely congruent with the phylogeny of Binder & Hibbett (in press) who combined sequence data from 4 ribosomal genes and proposed the recognition of eight major homobasidiomycete lineages (Hibbett & Thorn, 2001).

As in the 877 taxa analysis in Moncalvo et al. (in press), the analyses conducted here placed *Rickenella mellea*, *R. pseudogrisella*, "*Omphalina*" *marchantiae*, "*O.*" *brevibasidiata*, "*O.*" *rosella* and *Cantharellopsis prescottii* in the hymenochaetoid clade, with moderate bootstrap statistical support (60 %, versus 68 % in Moncalvo et al.). These taxa are well separated from the type species of *Omphalina*, *O. pyxidata*. The latter species unequivocally belongs to the euagarics clade (Agaricales), which is moderately well supported as a sister group to the bolete clade (Boletales) (64 % bootstrap support). The latter relationships were first shown convincingly (90 % bootstrap support) in the multi-gene analysis by Binder & Hibbett (in press).

Taxonomy

Among the sampled omphalinoid taxa classified outside the Agaricales,

the number of taxa to be recognized at a generic level is debatable. All of the taxa discussed above fall within a weakly supported clade in the neighbourhood of *Cotylidia* and *Resinicium bicolor*. We draw upon the data published by Lutzoni (1997) and Moncalvo et al. (2000 & in press) for guidance. "*Gerronema*" *marchantiae* exhibited the greatest amount of divergence among the omphalinoid taxa studied by Lutzoni (1997). Throughout his analyses, using pruned and unpruned 25S, ITS1 and ITS2 data, separately or combined (and using equally or unequally weighted parsimony or maximum likelihood methodologies), the placement of *G. marchantiae* was unstable in the resulting tree topologies. We surmise that the species should not be amalgamated with *Rickenella* because of the gross divergence in nucleotide sequence data complemented by anatomical data. *Gerronema marchantiae* and the closely allied species, *Omphalina postii* (Fr.: Fr.) Singer (*Gerronema postii* (Fr.: Fr.) Singer) lack evenly distributed leptocystidia that characteristically cover all surfaces in *Rickenella*. It has already been argued that *Gerronema sensu stricto*, as typified by a lignicolous species with sarcodimitic tissues, is not an appropriate generic disposition (Redhead 1986, Norvell et al. 1994) for *O. marchantiae* (Singer & Cléménçon) Norvell, Redhead & Ammirati and *O. postii*. Representatives of *Gerronema sensu stricto* (*G. strombodes* (Berk. & Mont.) Singer, *G. subclavatum* (Peck) Redhead) in fact cluster elsewhere (Lutzoni 1997, Moncalvo et al. 2000, and in press). Pending phylogenetic studies utilizing DNA sequence data and settlement of the typification of the name *Omphalina*, Norvell et al. (1994) adopted a conservative position and transferred *G. marchantiae* to *Omphalina* rather than create a new genus. The lectotype for the generic name *Omphalina* is now conserved as *O. pyxidata* (Pers.: Fr.) Qué! (Greuter et al. 2000). The placement of *Omphalina pyxidata* well within the Agaricales (euagarics) clade, far removed from *Rickenella* and *Gerronema/Omphalina marchantiae*, is strongly supported (Moncalvo et al. 2000; and in press). In the absence of an appropriate generic name, we propose a new genus, *Loreleia* gen. nov. (see below), for the two nearly identical species, *L. marchantiae* comb. nov. and *L. postii* comb. nov. Both species form clampless, orange basidiomata (pigmented by unknown noncarotenoid parietal pigments, Kühner 1980) and are seemingly obligately associated with living bryophytes (mosses and/or liverworts).

Currently we also prefer not to include "*Omphalina*" *brevibasidiata* in *Loreleia* or to include "*Omphalina*" *rosella* in either *Loreleia* or *Rickenella*. *Omphalina brevibasidiata* in Lutzoni's (1997) combined analyses (his fig. 7) appeared in a clade near *Loreleia marchantiae*, but that inferred relationship is poorly supported by the combined Maximum Likelihood bootstrap analysis (BS = 64%) and was not recovered by his two combined Maximum Parsimony analyses. When additional taxa such as *Cantharellopsis prescotii* are added to LSU analyses of larger taxon data sets, monophyly of a smaller clade combining *Loreleia marchantiae* and "*Omphalina*" *brevibasidiata* is not supported (Moncalvo et al. in press). Additionally, there are slight anatomical and biological differences. *Omphalina/Clitocybe/Gerronema brevibasidiata* is lightly pigmented (not orange), forms clamped hyphae, is sphagnicolous, and lacks well differentiated caulocystidia (Redhead 1985). These differences, albeit subtle, compliment the large base pair divergence, which suggests to us that maintaining separate genera is in actuality a more conservative and prudent option than lumping both taxa together in one genus. Unknown to everyone, including Lutzoni (1997), other taxa such as *Cantharellopsis prescotii* and *Cotylidia* spp. prove to be related and their inclusion affects the approximations of relationships in larger analyses. The even more disparate corticoid and polyporoid taxa skew relationships further. As a solution, we propose the monotypic genus *Sphagnomphalia* gen. nov. for *S. brevibasidiata* comb nov. (see below).

Anatomically, because of the abundance of leptocystidia, *Omphalina rosella* exhibits the greatest affinity to *Rickenella* as noted by Redhead et al. (1995), and corroborated by ITS and LSU data (Lutzoni 1997), but the circumscription of the latter genus would require alteration to accommodate *O. rosella*, even while it remains uncertain that *O. rosella* is the closest relative to *Rickenella* (BS = 56% with combined ML analyses in Fig. 7 of Lutzoni 1997). To lesser extent than *Loreleia marchantiae*, *O. rosella* drifts in the various analyses (Lutzoni 1994, Moncalvo et al. 2000, and in press). Contu (1997) erected the genus, *Jacobia* Contu typified by *O. rosella*, basing separation of the genus on the irregular lamellar trama. He included two other species which have yet to be molecularly analysed, *J. brunneolilacina* (Contu, M. Bon & L. Curreli) Contu and *J. vesuviana* (Briganti) Contu. Unfortunately the

name *Jacobia* Contu is a later homonym of *Jacobeae* Thunb. 1801 (Asteraceae), and possibly of *Jacobaea* P. Miller 1754 and *Jacobaea* Gärtn. 1791. Therefore, we propose the nomen novum *Contumyces* for *Jacobia* Contu, typified by *C. rosella* comb. nov.

Interim key to terrestrial pileate genera of the hymenochaetoid clade (all nonamyloid, smooth, white-spored fungi)

1. Lamellae present as discrete plates or forked well-formed ridges; bryophilous; clamp connections present or absent 2
1. Lamellae absent, or hymenium merely rugose; bryophilous or possibly merely terrestrial; clamp connections absent 6
 2. Clamp connections absent; pleurocystidia absent 3
 2. Clamp connections present; pleurocystidia present or absent 4
3. Basidiomata bright orange, hymenium clearly lamellate (only occasionally forked once) *Loreleia*
3. Basidiomata nearly white, with tan colored center; hymenium cantharelloid (a series of repeatedly forked folds) . . *Cantharellopsis*
 4. Pileo-, caulo- and cheilocystidia abundant, similar to each other, well differentiated, and projecting conspicuously; basidiomata (esp. pileus and stipes) strongly pigmented (brightly colored [orange, pink, violet] or honey brown over all); not on living *Sphagnum* 5
 4. Pileo- and cheilocystidia absent and caulocystidia restricted to a few clavate ends near the stipe apex; basidiomata (esp. lamellae and stipes) pallid to whitish, pigment restricted to a yellowish-brown disc area; on living *Sphagnum* *Sphagnomphalia*
5. Pileo-, caulo-, cheilo- and pleurocystidia abundant and evenly spaced over each surface (or somewhat grouped on stipes), lacking crystalline deposits of vinaceous pigment on the caulocystidia and elsewhere; lamellar trama regular *Rickenella*
5. Pileo- and caulocystidia initially in solid turfs, on the pileus remaining aggregated into small clusters collapsing on the surface, on the stipe becoming scattered but many remaining in clusters (minute scales); the type bearing rosy to vinaceous crystalline deposits forming on scales on stipes [deposits easily dislodged, tending to

dissolve in KOH or alcohol solutions]; lamellar trama irregular becoming bidirectional *Contumyces*

6. Basidiomata stipitate, pallid to brightly pigmented; fleshy from inflated context hyphae; terrestrial usually on mineral soils but often among mosses; hymenial cystidia often secondarily septate *Cotylidia*

6. Basidiomata stipeless or only vaguely pseudostipitate via a lateral fold; usually fruiting directly on mosses (often Polytrichaceae), or adjacent mineral soil on exposed soil banks; basidiomata membranous and easily obliterated (hyphae tending not to be inflated) *Cyphellostereum*
(presumed relationship, sequence data not available)

New genera and new combinations

Contumyces gen. et nom nov. (f.)

Basionym (Latin diagnosis): *Jacobia* Contu, Bollettino del Gruppo Micologico G. Bresadola N.S. 40(2-3): 170. 1997. Nom. illeg. (ICBN Art. 53.3) non *Jacobea* Thunb. (Asteraceae), Nov. gen. XIII p. 169. 1801.

Etyymology: Named after Marco Contu, in recognition of his work on this genus.

Typus: *Contumyces rosella* (Moser) comb. nov. Basionym: *Clitocybe rosella* Moser, Sydowia 4: 100. 1950. *Nom. nov. ut "Clitocybe rosella* (Lange) Moser comb. nov." (ICBN 58.1, ex 1) for *Omphalia rosella* J. Lange, Dansk. Bot. Ark. 6: 14. 1930, *nom. illeg. non Omphalia rosella* (Batsch) S.F. Gray, Nat. Arrang. Brit. Pl. 1: 813. 1821.

Selected literature: Candusso et al. (1994- *Omphalina rosella*), Cléménçon (1982- *Omphalina rosella*), Bas et al. (1995- *Marasmiellus rosellus*), Contu (1997- *Jacobia rosella*), Kuyper (1986- *Marasmiellus rosellus*), Lutzoni (1997- *O. rosella* [phylogeny]), Lutzoni & Pagel (1997- *O. rosella* [evolutionary biology]), Redhead et al. (1995- *Omphalina rosella*), Robich (1998- *Omphalina rosella*).

Other species (fide M. Contu, 1997):

***C. brunneolilacina* (Contu, M. Bon & L. Curreli) comb. nov.**

Basionym: *Rickenella brunneolilacina* Contu, M. Bon & L. Curreli, *Micol. e Veget. Mediterr.* 4: 58. 1989.

Selected literature: Contu (1997 - *Jacobia brunneolilacina*)

***C. vesuviana* (Briganti) comb. nov.** Basionym: *Agaricus vesuvianus* Briganti, *Hist. Fung. Regni Neapol.* p. 115. 1848.

Selected literature: Contu (1997- *Jacobia vesuviana*), Malençon & Bertault (1975- *Omphalina vesuviana*).

***Loreleia* gen. nov. (f.)**

Basidiomata omphaliforma, aurantiaca. Non lichenisata. Muscicola vel hepaticola. Trama lamellarum bidirectionalis; hyphis inamyloideus, defibulatis; cystidia nulla. Sporis albis, inamyloideus.
Etyymology: Named in honor of Lorelei L. Norvell for work on omphalinoid agarics.

Type: ***Loreleia postii* (Fr.) comb. nov.** Basionym: *Agaricus postii* Fries, *Monogr. Hymenomyc. Sueciae* 2: 291. 1863.

Selected literature: Cléménçon (1982- *Gerronema postii*), Klán (1992 - *G. postii* - ecology, descriptions), Senn-Irlet et al. (1990- *G. postii*), Wark (1997 - *G. postii* - ecology)

Other species: ***L. marchantiae* (Singer & Cléménçon) comb. nov.**
Basionym: *Gerronema marchantiae* Singer & Cléménçon, *Schweiz. Z. Pilzk.* 49: 119.1972.

Selected literature: Cléménçon (1982- *Gerronema marchantiae*, *G. daamsii*), Klán (1992 - *G. marchantiae*), Lutzoni (1997- *G. marchantiae* [phylogeny]), Lutzoni & Pagel (1997- *G. marchantiae* [evolutionary biology]), Senn-Irlet et al. (1990- *G. marchantiae*), Watling (1988- *G. marchantiae*).

***L. roseopallida* (Contu) comb. nov.** Basionym: *Gerronema roseopallidum* Contu, *Mycol. Helvetica* 3(2): 216-217. 1988.

Described as being pale orange centrally but otherwise pale pinkish, lacking clamp connections, lacking cystidia, and growing in xeric habitats on acidic soils. The presence of bryophytes was not mentioned. Additionally it lacks sarcodimitic tissues (Contu 1990).

***Sphagnomphalia* gen. nov. (f.)**

Basidiomata omphaliforma, straminea vel pallida. Non

lichenisata. Sphagnicola. Trama lamellarum bidirectionalis; hyphis fibulatis, inamyloideus; cystidia nulla. Sporis albis, inamyloideus.

Etyomology: Named for its habitat (*Sphagnum*) and its omphalinoid habit, and deliberately spelled in this abbreviated manner.

Type: *Sphagnomphalia brevbisidiata* (Singer) comb. nov.

Basionym: *Clitocybe brevbisidiata* Singer, Ann. Mycol. 41: 45-46. 1951.

Selected literature: Clémençon (1982- *Gerronema brevbisidiatum*), Kubička (1956- *Omphalia cincta*), Lutzoni (1997- *Omphalina brevbisidiata* [phylogeny]), Lutzoni & Pagel (1997- *O. brevbisidiata* [evolutionary biology]), Redhead (1985- *Omphalina brevbisidiata*).

Notes on other genera

Cantharellopsis Kuyper, specifically *C. prescotii* (Weinm.) Kuyper (1986).

Selected literature: Bigelow (1985 - as misapplied name *Hygrophoropsis albida*), Clémençon (1982- *Gerronema albidum*), Corner (1966- as misapplied name *Hygrophoropsis albida*), Horak (1987- *Cantharellus prescotii*), Kuyper (1986), Ohenoja & Vare (1994 - as *Gerronema prescotii* (Wienm.) Redhead - ecology), Redhead (1984- as *G. prescotii*, Watling & Turnbull (1998- as *G. prescotii*).

There is a question regarding the generic and specific identity of another bryophilous taxon, *Pterygellus polycephalus* (Bres.) Redhead. Some European collections identified as either *Cantharellus polycephalus* Bres. or *Leptoglossum polycephalum* (Bres.) M. M. Moser are undoubtedly *C. prescotii* (Redhead 1984), but the type of *C. polycephalus* had a tougher consistency composed of thicker-walled hyphae with acyanophilous walls and they formed pyxidately pileate basidiomata with tomentose stipes (Redhead 1984). The differences in cyanophily of the thicker walled hyphae was believed to be significant and the two taxa were kept generically separated by Redhead (1984). Horak (1987) synonymized the two species, which begs the question regarding possibly synonymy of *Cantharellopsis* Kuyper (1986) with *Pterygellus* Corner (1966).

Horak (1987) overlooked comments on the cyanophily of the hyphal walls, hence his synonymy of the two taxa is still questionable. It is conceivable that *P. polycephalus* is an older growth form of *C. prescottii*, in which the stipes become overgrown (tomentose), the hyphal walls thicken by deposition of acyanophilous materials, and there is rejuvenation and regrowth of the pilei marginally on older pilei (i.e., pyxidately). Further studies of living populations and/or DNA studies are suggested to resolve the identities of these intriguing fungi. Additionally, although *Cantharellus polycephalus* was transferred to *Pterygellus*, the delimitation of that genus and its biological status also requires investigation. The question of whether or not some *Pterygellus* are mycorrhizal (with *Euphoria*) has been raised (Verbeken 1999).

***Cotylidia* P. Karst.**

Selected literature: Lammers (1992 [ecology]), Reid (1965 [type studies, ecology]).

***Cyphellostereum* D. Reid**

Selected literature: Corner (1966- *Leptoglossum laeve*), Høiland (1976), Keizer & Arnolds (1994 [ecology]), Kuyper in Bas et al. (1995), Redhead (1984 [type studies, ecology]), Reid (1965 [type studies, ecology]), Watling & Gregory (1989).

***Rickenella* Raithelh.**

Selected literature: Cléménçon (1982), Gulden et al. (1985), Kost (1984 [parasitism demonstrated], 1986 [parasitism demonstrated]), Kuyper in Bas et al. (1995), Lamoure (1979 [cultures]), Lutzoni (1997), Lutzoni & Pagel (1997), Norvell et al. (1994), Redhead (1980 [parasitism demonstrated as *Gerronema*], 1981 [parasitism demonstrated as *Gerronema*], 1986), Senn-Irlet et al. (1990), Treu & Agerer (1990 [cultures]).

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Literature Cited

- Bas, C., Kuyper, T.W., Noordeloos, M.E. & Vellinga, E.C. 1995. Flora Agaricina Neerlandica Vol. 3. A.A. Balkema, Rotterdam.
- Bigelow, H.E. 1985. North American species of *Clitocybe*. Part II. Beih. Nova Hedw. 81: 281-471. J. Cramer, Berlin & Stuttgart.
- Binder, M., & Hibbett, D. S. (in press). Higher level phylogenetic relationships of homobasidiomycetes (mushroom-forming fungi) inferred from four rDNA regions. Mol. Phylogenet. Evol.
- Boidin, J., Mugnier, J. & Canales, R. 1998. Molecular taxonomy of the Aphyllophorales. Mycotaxon 66: 445-491.
- Candusso, M., Gennari, A. & Ayala, N. 1994. Agaricales of Baja California - Mexico. Mycotaxon 50: 175-189.
- Cléménçon, H. 1982. Kompendium de Blätterpilze Europäische omphalinoide Tricholomataceae. Z. Mykol. 48: 195-237.
- Contu, M. 1988. Una nuova specie Mediterranea del genere *Gerronema*: *G. pallidum* spec. nov. Mycol. Helvet. 3(2): 215-219.
- Contu, M. 1990. Nuovi taxa di Agaricales (Basidiomycetes) dalla Sardegna. Bol. Soc. Brot., Sér. 2, 63: 379-386.
- Contu, M. 1997. *Jacobia*, un nuovo genere di Tricholomataceae omfalinoidei. Boll. Gruppo Micol. G. Bresadola N.S. 40(2-3): 169-173.
- Contu, M., Bon, M. & Curreli, L. 1989. *Rickenella brunneolilacina* sp. nov., con note sul genere *Rickenella* in Sardegna. Micol. e Veget. Mediterr. 4: 57-62.
- Corner, E.J.H. 1966. A monograph of Cantharelloid fungi. Oxford Univ. Press, London.
- 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.
- Gulden, G., Jensen, K.M. & Stordal, J. 1985. Arctic and alpine fungi-1. Soppkonsulentent, Oslo.
- Hibbett, D.S., Pine, E.M., Langer, E., Langer, G. & Donoghue, M.J. 1997. Evolution of gilled mushrooms and puffballs inferred from ribosomal DNA sequences. Proc. Natl. Acad. Sci. USA 94: 12002-12006.
- Hibbett, D.S. & Thorn, R.G. 2001. Basidiomycota: Homobasidiomycetes. Pgs. 121-168. In *The Mycota VII Part B Systematics and Evolution*. Eds. McLaughlin, McLaughlin & Lemke. Springer-Verlag, Berlin.

- Høiland, K. 1976. The genera *Leptoglossum*, *Arrhenia*, *Phaeotellus* and *Cyphellostereum* in Norway and Svalbard. *Norw. J. Bot.* 23: 201-212.
- 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.
- Jülich, W. 1981. Higher taxa of Basidiomycetes. *Biblioth. Mycol.* 85: 1-485.
- Keizer, P.-J. & Arnolds, E. 1994. Taxonomical notes on macrofungi in roadside verges planted with trees in Drenthe (the Netherlands)-I. *Persoonia* 15: 489-524.
- Klán, J. 1992. Two *Gerronema* species growing on *Marchantia* thalli: 1. *Gerronema marchantiae* Sing. and Clém.: *Gerronema postii* (Fr.) Sing. *Česká Mykol.* 46: 121-125.
- Kost, G. 1984. Moosbewohnende Basidiomyzeten I. Morphologie, Anatomie und Ökologie von Arten der Gattung *Rickenella* Raithelth.: *Rickenella fibula* (Bull.: Fr.) Raithelth., *R. aulacomniophila* nov. spec., *R. swartzii* (Fr.: Fr.) Kuyp. *Zeit. f. Mykol.* 50: 215-240.
- Kost, G. 1986. Morphology, anatomy and biology of species of the genus *Rickenella*. *Atti del Convegno Internazionale del 10-15 settembre 1984. Borgo Val di Taro - Italy. Atti del Centro Studi per la Flora Mediterranea* 6: 63-81.
- Kubička, J. 1956. *Omphalia cincta* Favre - kalichovcka blatní v Tatrách. *Česká Mykol.* 10: 159-161.
- Kühner, R. 1980. Les Hyménomycètes agaricoïdes (Agaricales, Tricholomatales, Pluteales, Russulales). *Etude générale et classification. Numéro spécial du Bulletin de la Société Linnéenne de Lyon.* 49^e 1-1027.
- Kuypers, 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.
- Lammers, H. 1992. Een merkwaardige afwijking van *Cotylidia undulata*. *Coolia* 35: 91-94.
- Lamoure, D. 1979. Caractères morphologiques, caryologiques et culturaux mycélium de trois espèces de *Rickenella* (Agaricales). *Beih. Sydowia* 8: 251-254.
- Largent, D. L. 1977. How to identify mushrooms to genus I: Macroscopic features. *Mad River Press, Eureka.* 86 p.
- 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.
- Malençon, G. & Bertault, R. 1970. Flore des champignons de Maroc. Tome II. *Trav. Inst. Sci. Chérifien, Sér. Bot. Biol. Vég.* 33: 1-540.
- 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. *Mol. Phylogenet. Evol.* [in press]. One hundred and seventeen clades of euagarics.
- 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.
- Ohenoja, E. & Vare, H. 1994. Larger fungi of the Suvanto area along the river Kitinen, Central Lapland. *Me. Soc. Fauna Flora Fennica* 69: 87-96.
- Posada, D. & Crandall, K.A. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817-818.
- Redhead, S.A. 1980. Fungi Canadenses No. 170. *Gerronema pseudogrisellum*.
- Redhead, S.A. 1981. Parasitism of bryophytes by agarics. *Can. J. Bot.* 59: 63-67.
- 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. 1985. Fungi Canadenses No. 294. *Omphalina brevibasidiata*.
- 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., Walker, G.R., Ammirati, J.F. & Norvell, L.L. 1995. *Omphalina* sensu lato in North America 4: *O. rosella*. *Mycologia* 87: 880-885.
- Reid, D.A. 1965. A monograph of the stipitate stereoid fung. *Beih. Nova Hedw.* 18: 1-[484].

- Robich, G. 1998. Una graziosa specie della Catalogna: *Omphalina rosella* (J.E. Lange) Moser. *Rivista Micol.* 41(1): 47-51.
- Senn-Irlet, B., Jenssen, K.M. & Gulden, G. 1990. Arctic and alpine fungi-3. Soppkonsulenten, Oslo.
- Swofford, D. L. 1999. PAUP*: Phylogenetic Analysis Using Parsimony (and other methods). Sinauer Associates, Sunderland, MA.
- Treu, R. & Agerer, R. 1990. Culture characteristics of some *Mycena* species. *Mycotaxon* 38: 279-309.
- Verbeke, A. 1999. Is *Pterygellus* mycorrhizal with a euphorbia? *Mycologist* 13: 37.
- Wark, M. C. 1997. Regeneration of some forest and gully communities in the Angahook-Lorne State Park (north-eastern Otway Ranges) 1-10 years after the wildfire of February 1983. *Proc. Roy. Soc. Victoria* 109: 7-36.
- 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.
- Watling, R. & Turnbull, E. 1998. British Fungus Flora. Agarics and Boleti 8. Cantharellaceae, Gomphaceae and amyloid-spored and xeruloid members of Tricholomataceae (excl. *Mycena*). Royal Bot. Gard. Edinburgh.