Coprinus Pers. and the disposition of *Coprinus* species *sensu lato*

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Summary

Redhead, S. A., Vilgalys, R., Moncalvo, J.-M., Johnson, J. & Hopple, J. S., Jr.: *Coprinus* Pers. and the disposition of *Coprinus* species *sensu lato*. – Taxon 50: 203–241. 2001. – ISSN 0040–0262.

Based upon molecular studies, the genus *Coprinus* Pers. is subdivided into *Coprinus sensu stricto* (*Agaricaceae*), and *Coprinellus* P. Karst., *Coprinopsis* P. Karst., and *Parasola* gen. nov. in the new family *Psathyrellaceae*. The nomenclatural history and typifications of names previously treated as synonyms of *Coprinus* are reviewed. It is demonstrated that taxonomic characters previously considered not to be generically significant gain importance when correlated with molecular evidence. Many new combinations are proposed. A key using anatomical features to molecularly (phylogenetically) recognised coprinoid genera is provided.

Keywords: *Agaricaceae*, *Coprinus*, nomenclature, *Psathyrellaceae*, taxonomy.

Introduction

Molecular phylogenetic research on the genus *Coprinus* Pers. (1797) was initiated by Hopple (1994) for his doctoral dissertation and as part of a growing molecular study of agaric fungi in the mycology laboratory at Duke University. Early results using RFLP data (Hopple & Vilgalys, 1994; Vilgalys & al., 1994) unexpectedly indicated that the type of *Coprinus*, *C. comatus* (O. F. Müll. : Fr.) Pers., did not appear to be monophyletic with other "*Coprini*". Initial separation of *Coprinus comatus* and a close ally, *C. sterquilinus* (Fr. : Fr.) Fr., from virtually all other "*Coprini*" was subsequently and repeatedly supported during increased taxon sampling and by sequence analyses of the nLSU—rDNA region (Hopple & Vilgalys, 1999; Johnson & Vilgalys, 1998; Johnson, 1999; Moncalvo & al., 2000). All results showed that *Coprinus comatus* and *C. sterquilinus* form a clade within *Agaricaceae* together with lepiotaceous genera and *Agaricus* L. : Fr., whereas the other "*Coprini*" (>90%) cluster together near *Psathyrella* (Fr.) Quél. Additional support for this phylogeny for a few taxa using ITS region sequences has been published by Park & al. (1999a, b). In larger samplings (Moncalvo & al., 2000; and unpublished work in progress on >800 taxa) psathyrelloid fungi and the bulk of the "*Coprini*" (but excluding the type) form one large recognisable clade well separated from the distinct and large *Agaricaceae* clade. Clearly, if these clades are to be

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recognised as distinct at the family level, it would appear that the majority of the "*Coprini*" cannot be members of the genus *Coprinus* (as typified by *C. comatus*), and therefore that clade cannot be labelled *Coprinaceae* Overeem, whereas the greatly reduced taxon bearing the name *Coprinaceae* becomes an integral part of the family *Agaricaceae* Chevall., and is reduced to synonymy. Consequently, *Coprinus* s.l., now divided between two families, must be divided into two or more genera, and a new family name must be found.

Hopple & Vilgalys (1999) provided the most detailed analysis of the groupings of coprinoid taxa, but were unable to assign taxa to other genera in part because of the historical baggage (unresolved typifications) that must be overcome to decide on available generic names. Additionally, it is not a frivolous matter to undermine a generic concept that has been well established for over 200 years, one that is usually easily recognized by scientists, naturalists, and laypersons, and concerns species with economic and scientific value (edible and poisonous mushrooms, enzyme production, genetic studies, patents). There exists taxonomic inertia (see Hibbett & Donoghue, 1998) in the face of such major changes in taxonomy in general despite the knowledge that the current classification is grossly incorrect, in part because the new data do not answer all newly posed questions adequately. Despite the fact that for six years it has been known that *Coprinus* s.l. is polyphyletic, it has been nearly impossible to make changes, because answers to where the species are to be assigned have remained elusive. Questions arise as to monophyly of the residual "*Coprini*" (whether to place all in one or more genera), the independence of the coprinoid species from the genus *Psathyrella* (with possible nomenclatural repercussions), and of the possible biological, anatomical, and morphological correlations with molecular data that have been overlooked or considered taxonomically insignificant.

Taxonomy: coprinoid versus psathyrelloid species

Having established that *Coprinus comatus*, together with *C. sterquilinus*, represent the genus *Coprinus* in *Agaricaceae*, we must consider whether or not *Psathyrella* and the residual "*Coprini*" are congeneric. In Moncalvo & al. (2000, Figs. 2, 5), clades labelled "T" represent in our minds a distinct family that includes *Psathyrella*, *Lacrymaria* Pat., and 90% of the former "*Coprini*". We propose (below) to recognise this family as the *Psathyrella*ceae (Singer) Vilgalys & al. The *Psathyrella*ceae are represented in Hopple & Vilgalys (1999, Fig. 3) by the clade bound by the numbered node "16". It is evident from both reports, Moncalvo & al. (2000) and Hopple & Vilgalys (1999), that the coprinoid taxa are not clearly separated from the psathyrelloid taxa in monophyletic lines. If the residual coprinoid taxa were to be retained in a single genus and also separated from *Psathyrella*, then the name *Psathyrella* would cover a paraphyletic taxon, or even a polyphyletic taxon. However, there is internal structure to *Psathyrella*ceae that allows for alternative classifications. A large number of coprinoid species form a single recognisable, presumably monophyletic line, distinguished as node "38" (Hopple & Vilgalys, 1999, Fig. 3), recognised again as the *atramentarius-latisporus* clade (labelled 90% support) in the strict consensus tree (Hopple & Vilgalys, 1999, Fig. 4), the *atramentarius-kimurae* clade in clade "T" (labelled 51% support) in the

Maximum Parsimony tree (Moncalvo & al., 2000, Fig. 2), clade "I" (Park & al., 1999a, Fig. 2), and finally as clade "II" (Park & al., 1999b, Fig. 2). A second, strongly supported presumed monophyletic line (*auricomus-nudiceps* clade) is recognisable from node "36" (Hopple & Vilgalys, 1999, Fig. 3), the *auricomus-nudiceps* clade (100% support) (Hopple & Vilgalys, 1999, Fig. 4), and by a single species, *Coprinus nudiceps* P. D. Orton in Moncalvo & al. (2000) well separated from the *atramentarius-kimurae* clade in "T". It is with the third group of coprinoid species (which includes species such as *C. micaceus* (Bull. : Fr.) Fr., *C. disseminatus* (Pers. : Fr.) Gray, and *Coprinus bisporus* J. E. Lange) that clear separation from psathyrelloid species becomes difficult. Based upon their much more limited analyses, Park & al., (1999a) suggested that "...*Psathyrella* would be better included in genus *Coprinus*...." but it is the reverse which appears to be closer to the truth. Hopple & Vilgalys (1999: 17) suggested that, "The most parsimonious explanation that takes into account the morphological anomalies of the genus while still heeding the phylogenetic hypothesis based upon molecular characters is that both *Psathyrella* and *Lacrymaria* have arisen from within *Coprinus* (clades I and II)". We now believe this conclusion was based upon an under-sampling of psathyrelloid taxa. From the broader generic analyses (Moncalvo & al., 2000), the taxonomically narrower IST-based analyses including *Psathyrella spadiceogrisea* (Schaeff. : Fr.) Maire (Park & al., 1999a, b), and unpublished data available to us including three additional psathyrelloid species from a larger analysis involving approximately 800 agaricoid taxa representing over 50% of all known agaric genera (Moncalvo & Vilgalys, unpubl.), and from the cladograms and data published by Hopple & Vilgalys (1999), it is evident that this third coprinoid clade (if it, in fact proves to be monophyletic) arose from within a clade of psathyrelloid taxa, and indeed, so must have the *atramentarius*-clade, and the *nudiceps*-clade, each independently.

We still believe that *Psathyrella* and psathyrelloid taxa are under-sampled and as a result clear resolution of the generic limits within *Psathyrella*ceae will not be possible until broader sampling is done. For this reason we leave for the time being *Psathyrella* [typified by *P. gracilis* (Fr. : Fr.) Quél.; see discussion below] as a recognised paraphyletic (possibly polyphyletic) taxon, because we cannot reasonably re-align generic limits with the current data. We anticipate that in the future it will be broken into several genera. The genus *Lacrymaria*, represented by *Lacrymaria velutina* (Pers. : Fr.) Konrad & Maublanc [more correctly called *L. lacrymabunda* (Bull. : Fr.) Pat.] appears in various positions within the *Psathyrellaceae* in the difference analyses (Hopple & Vilgalys, 1999, Figs. 3, 4; Moncalvo & al., 2000, Figs. 2, 5; Moncalvo & Vilgalys, unpubl.), usually between two coprinoid clades and mostly near the *auricomus-nudiceps* clade. Anatomically it is quite unlike species in that latter clade. Therefore, we continue to recognise *Lacrymaria* as a distinct genus, with its intermediate position between the coprinoid clades as further evidence of their generic separation.

Philosophically we are opposed to the merging of *Psathyrella* with the residual coprinoid species (and with *Lacrymaria*) because that would reduce all of the members of this "family" to one genus. Additionally it would also lead to many potential homonyms, making publication of many new species epithets necessary, and it eliminates information conveyance at a "generic" level because referring to all

such coprinoid taxa as "*Psathyrella*" would no longer distinguish the primarily deliquescent taxa from the nondeliquescent taxa. Hopple (1994) conducted an anatomical analysis of the species he sequenced, and there is nearly 100% correlation between cuticular types and the strongly supported clades. Furthermore, there is a correlation between ontology and the recognised groups (see Reijnders, 1979). Therefore, we propose to recognise four genera for coprinoid taxa, the genus *Coprinus* itself in *Agaricaceae*, and three other genera in the new family, *Psathyrella*ceae.

Genus **(A),** the *atramentarius-latisporus* clade at 90% bootstrap value (Hopple & Vilgalys, 1999, Fig. 3, node 38) is one such taxon, genus **(B)** the *nudiceps-auricomus* clade at 95% bootstrap value (Hopple & Vilgalys, 1999, Fig. 3, node 36) is another, and genus **(C)** the *curtus-heptemerus* clade (Hopple & Vilgalys, 1999, Fig. 4) is the third, and weakest supported taxon. For the time being we have eliminated the species, *Coprinus cordisporus* Gibbs, from our re-classification, and excluded from consideration *Psathyrella candolleana* (Fr. : Fr.) Maire, a taxon that appears internal to clade "II" [node "19"] in Hopple & Vilgalys (1999, Fig. 3) but appears elsewhere in other cladograms (Hopple & Vilgalys, 1999, Fig. 4; Moncalvo & al., 2000, Figs. 2, 5; Moncalvo & Vilgalys, unpubl. +800 taxa data). We address the unresolved *Coprinus cordisporus* situation further, below.

Assigning generic names to these three coprinoid clades in the *Psathyrella*ceae involves considerable nomenclatural analysis. Rationalising the recognition of these genera based upon data other than molecular data is another exercise and it involves a further discussion of taxonomy. A third intellectual or philosophical exercise is rationalizing the occurrence of coprinoid taxa in two agaric families, again introducing taxonomic concepts. We will deal with each independently.

Nomenclature: typification of *Coprinus* and availability of previous synonyms

Singer (1986) in his last edition of *The Agaricales in Modern Taxonomy*, the worldwide standard reference for generic agaric taxonomy, listed 13 synonymous names for "*Coprinus* (Pers. ex) S. F. Gray" 1821. The typifications of most of these had been discussed by Donk (1949a, b; 1962), Horak (1968), Singer (1951, 1962, 1975), and Singer & Smith (1946). Singer (1986) was not operating under current nomenclatural rules and did not accept the starting point date of 1753 for fungal nomenclature or the concept of sanctioned names. The correct authority and date of publication (i.e., priorability for the generic name) is *Coprinus* Pers. dating from 1797, not "ex S. F. Gray" 1821, an authority interpretation made by Singer when 1821 was the starting date for fungi in earlier versions of the Code. Similarly, the authority for the type of *Coprinus* is not "*C. comatus* (Müller in Fl. Dan. ex Fr.) S. F. Gray" as given by Singer (1986). The combination was made by Persoon (1797) when the generic name was first published, hence the name with authority is *C. comatus* (O. F. Müll. : Fr.) Pers.

Other problems regarding validation dates, lectotypification resulting from different interpretations (with nomenclatural repercussions), and the resulting incorrect authorships abound. Among the synonymous names listed by Singer (1986) are "*Prunulus* Ces. ex S. F. Gray" and "*Annularius* Roussel ex Earle". These (now incorrectly interpreted) authorities resulted from conclusions based upon

earlier Codes. Donk and Singer never agreed upon the typification of *Prunulus,* and as long as it was sunk into synonymy with an older generic name, the unresolved controversy did not particularly matter. Donk (1949a, b, 1962) and Singer (in Singer & Smith, 1946) also disagreed upon typifications for other listed synonymous generic names. However, now that *Coprinus* must be divided into more than one genus, the typifications and authorships for all previously synonymised generic names must be reconsidered in light of current nomenclature and taxonomy. These include not only the 13 names listed by Singer, but also *Xerocoprinus* Maire and *Psathyrella* (Fr.) Quél., as is detailed below.

Nomenclature: generic names assigned to coprinoid taxa (validation dates, typification, authorities)

Coprinus Pers. 1797 [lectotype *Coprinus comatus* (O. F. Müll. : Fr.) Pers.]

Coprinus was first lectotypified by Earle (1909), whose choice was accepted by Clements & Shear (1931) and repeatedly accepted by all subsequent authors (hence validated despite Earle's use of the American Code [see Donk, 1949a, b, 1962]). The basionym is *Agaricus comatus* O. F. Müll. (Müller, 1780: 8).

Annularius Roussel 1806 (here lectotypified by *Agaricus typhoides* Bull. = *Coprinus comatus*)

When Donk (1962) attributed the validation of the "devalidated" generic name "*Annularius* Roussel per Earle" to Earle (1909), Donk was following the rules in effect in 1962. Hence he accepted Earle's (1909) designation of "*Coprinus ephemeroides*" as type as if by original designation (which would make it a holotype if the name were truly validated in 1909). However, the previously "devalidated" name *Annularius* must now be considered to be valid from 1806, not 1909, and any type designation by Earle must be considered in light that he was not the validating author. As noted by Donk (1962), Roussel included two taxa, naming one as *Agaricus* "*ephemerus*" Bull. but probably intended to indicate *Agaricus* "*ephemeroides*" Bull. [the name for Fig. 1 on the Bulliard's plate 582, where Bulliard (1793) illustrated an annulate species that Roussel presumably intended to include in his genus *Annularius*]. The second species Roussel listed was *Agaricus typhoides* Bull. It did no harm to accept Earle's flawed "lectotypification" in Donk's mind because *Annularius* simply became a synonym of *Coprinus*. However, if one accepts that "*ephemeroides*" (sensu J. E. Lange, 1915, 1939) is the type, then *Annularius* potentially becomes an available name for a major group of the residual "*Coprini*". However, Roussel did not publish any recombinations under the name *Annularius* (and neither did Earle), and Roussel (perhaps) accidentally used the wrong species name. The rules of nomenclature must be bent to allow the lectotypification of *Annularius* by *Agaricus ephemeroides* Bull. when in fact Roussel named "*ephemerus*", which is the epithet of another species validly published by Bulliard. It would also have the unfortunate consequence of potentially resurrecting the name *Annularius,* which will cause confusion if current, albeit demonstrably incorrect modern applications of the species epithet "*ephemeroides*", are invoked (see details below). Earle's lectotypification of *Annularius* by *Coprinus ephemeroides* (Bull. : Fr.) Fr. was incorrect (he named as lectotype a species name not used by Roussel), and it is rejected by us as not included in the protologue. The

alternative is to name *Agaricus typhoides* Bull. as lectotype, which we do here. *Agaricus typhoides* is readily recognisable from Bulliard's (1793) plate 582 as a synonymous name for *Coprinus comatus* as was accepted by Fries (1821) who listed it as a synonym of the sanctioned name *Agaricus comatus* O. F. Müll: Fries.

It should be noted that the name *Coprinus ephemeroides* is currently misapplied in all modern literature. Bulliard illustrated taxonomically significant features for this species, especially the cottony central strand in the interior of the stipe, an anatomical character that could never form in the minute species to which the name is currently applied. Furthermore, it is a feature that J. E. Lange (1939) admitted he could not find in the species to which he applied the name (and whose concept most modern authors follow). It is here suggested that *Agaricus ephemeroides* Bull. (1793, pl. 582; see also Bulliard & Ventenat, 1809) was actually a small form of *Coprinus sterquilinus* or possibly *C. spadiceisporus* Bogart (see more discussion on this taxonomic feature below). Hence, it is likely that both species Roussel named in his genus *Annularius*, *A. typhoides* and *A. ephemeroides* Bull. sensu Bull., are in fact congeneric (using molecular data as a standard), with the result that typification by either species would have the same taxonomic result, i.e., *Annularius* would be synonymous with *Coprinus* s.str.

Ozonium Link 1809 (holotype *O. auricomium* Link).

This generic name was described for a subiculum-like mycelial structure now associated with "*Coprinus*" species such as *C. domesticus* (Bolton : Fr.) Gray. As a *nomen anamorphosis* it is of restricted priorability (Donk, 1962). The name was sanctioned by Fries (1821).

Prunulus Gray 1821 [lectotype *Prunulus denticulatus* (Bolton) Gray].

Donk (1949, 1962) and Singer (Singer & Smith, 1946; Singer, 1986) consistently disagreed upon the typification of the name *Prunulus*, but both authors intended to reduce it to synonymy under larger genera, viz. "*Mycena* (Pers.) per S. F. Gray" by Donk, *Coprinus* by Singer. While these arguments may seem academic, they now have increased relevance because molecular evidence indicates that both *Mycena* and *Coprinus* are polyphyletic and generic names are required for segregate genera.

Donk (1949a, b) has already commented on the false attribution of the generic name *Prunulus* to Caesalpino by Gray (an attribution repeated by Earle, Murrill, and Singer & Smith). "*Prunulus*" was an ancient "generic" term (i.e., not a formal genus name) used by classical authors such as Hermoläus, Caesalpino, Clusius, etc. (see Fries, 1836: 7; 1874: 66 for a discussion) much as the terms "mycena" and "agaricus" or "boletus" had been used before being formally recognised as genera. Paulet (1790: 22) noted that "prunuli" had been used for a species that commonly came up near *Prunus*, that had a pleasant odour. "*Prunuli Cæsalpina*" and *Agaricus prunulus* Scop. were listed as synonyms of "*Mousserons d'Italie, ou Mousserons gris & blanc*" (Paulet 1790: 526). *Agaricus prunulus* is now called *Clitopilus prunulus* (Scop. : Fr.) P. Kumm. Gray (1821) was the first to actually use *Prunulus* as a generic name with binomial species names, hence it must be attributed to him alone, and he applied it to a different group of species (not including *C. prunulus*).

The name *Prunulus* had been taken up for over 100 species by Murrill (1916), who like Earle (1909) typified *Prunulus* by the first named (and/or illustrated)

species, *P. denticulatus* (Bolt.) Gray, following the American Code. Earle (1909) actually named *Mycena pelianthina* (Fr.) Quél. as type [using Saccardo's (1887) *Sylloge fungorum* nomenclature as was explained by Earle, 1909: 382]. Murrill (1916) treated virtually all of the species currently classified in *Mycena*, in *Prunulus*, and he made many combinations under the latter generic name. Murrill (1917) used the name *Mycena* (Pers.) Roussel (1806) for species now classified as *Bolbitius* Fr. (Fries, 1838), because he and Earle (1909), again following the American Code, considered the type of *Mycena* to be "*Bolbitius conocephalus* (Fries) Gill."

Art. 10.5(b) (Greuter & al., 2000a) indicates that lectotypifications "... based on a largely mechanical method of selection" may be superseded. Singer & Smith (1946) were the first to lectotypify *Prunulus* outside of the American Code, choosing "*P. extinctorius* Bolt. ex Gray" as type because, by being a later synonym of *Coprinus*, they believed it would not endanger established generic names. On the face view it would appear that *P. extinctorius* must be accepted as lectotype. However, there is a question of what that name means, what its authorship is, and ultimately what its type is, and whether or not as ultimately typified, it is in conflict with the protologue for *Prunulus*. Gray (1821) placed no authorities after species binomials in general, but he listed "*Agaricus extinctorius*, Bolt. Fung. 24; Persoon Syn. 417" in synonymy with *P. extinctorius*. Bolton (1788) attributed the name *Agaricus extinctorius* to Linnaeus (1753), but the fungus described and illustrated by Bolton does not exactly match the scant description by Linnaeus, in that Linnaeus described *Agaricus extinctorius* L. on dung ("in fimetis"), whereas Bolton's fungus was on sandy soil. Despite the apparent misapplication of the name, nomenclaturally there remained only one valid name, namely *Agaricus extinctorius* L. Persoon (1801) cited Bolton for an illustration of his concept of *A. extinctorius*, a species on sandy soil, and also cited Linnaeus' (1753) description, but with a question mark. Nomenclaturally, the name was still *A. extinctorius* L. Notably Gray (1821) did not specifically exclude *A. extinctorius* L. in any way, and therefore, his listing of *A. extinctorius* linked to Bolton (1788) who cited Linnaeus, as a synonym of *P. extinctorius*, should be interpreted as having made a new combination, specifically, *Prunulus extinctorius* (L.) Gray (Art. 33.2).

Current application of the epithet "*extinctorius*", as a "*Coprinus*" traces back to Bulliard (1790), through the citation of the authority, e.g., "*C. extinctorius* (Bulliard ex St.Amans) Fries" (Orton & Watling, 1979) or "*C. extinctorius* (Bull. ex St.Amans) Fr." (Singer, 1986). Bulliard (1790) did not cite Linnaeus on the plate where he depicted an initially slightly scaly fungus (basidiocarp), recognisable as a coprinoid fungus. However, Bulliard & Ventenat (1809) later listed *A. extinctorius* L. as a questionable synonym. The name *A. extinctorius* in Bulliard (1790) might debatably be interpreted two ways, either as *A. extinctorius* L., or as an illegitimate later homonym attributable to Bulliard alone. Although Bulliard's fungus was on dung, like Linnaeus' fungus, its pileus was scaly (Linnaeus did not mention scales) and brownish centrally (Linnaeus mentioned "albido"), and its lamellae became blackish (Linnaeus described them only as "niveis"). Evidently Fries (1832) was also puzzled and never accepted (therefore never sanctioned) the name *A. extinctorius*. He indexed the name with three different authorities: (1) "L."—indicating that name was synonymous with "*A. procerus*" [a synonymy that makes

no sense if one compares the two despite Fries' 1874 later indication that *A. extinctorius* L. was *A. procerus* Scop. without an annulus]; (2) "Bull."—synonymising it with "*A. micaceus* d."; and (3) "Bolt."—synonymising it with "*A. plicatus*". Even more confusing is the fact that Fries did not accept the name "Agaricus plicatus", instead alphabetically listing four different authorities for that binomial, each placed in synonymy, and a fifth treated under "*plicatilis* Sow." in the index, apparently as a synonym, and with the authority "*A. plicatus*. Bull". "*A. plicatus* Bull." is not a valid name because Bulliard (1782) attributed the name *Agaricus plicatus* to Schaeffer (1762, tab. 31; 1774, 15), and later when reconsidering Schaeffer's fungus and name, coined a new name for his own fungus, *Agaricus striatus* Bulliard & Ventenat (1809). The listing in Cacialli & al. (1999) of "*extinctorius*" as a sanctioned epithet by their use of ": Fries" is in error.

There remains the question of the identity of *Prunulus extinctorius* (L.) Gray. The only fungi that come remotely close to that described by Linnaeus (contrary to Fries' observations) are *Coprinus*-like fungi, which, if correct, more astute mycological observers (like Fries) would have described with additional details, such as lamellae darkening and dissolving. Nonetheless, Linnaeus' description of a lacerate pileus and growth on dung certainly suggested to Bulliard and others that this name applied to a *Coprinus*-like fungus in the absence of any other type of fungus fully matching the description. Fries (1838) resurrected the epithet "*extinctorius*" as *Coprinus extinctorius*, attributing it to Bulliard. He did not specifically mention *A. extinctorius* L. in this publication, but he did treat *A. procerus* Scop. and he referred to his earlier treatment (Fries, 1821) wherein he had listed *A. extinctorius* L. as a synonym. In a later publication, Fries (1874) treated *Coprinus extinctorius* (linked to Bulliard) separate from *A. procerus* Scop. (specifically listing *A. extinctorius* L. as a synonym). It appears best to consider *Coprinus extinctorius* in Fries (1838) as a new species, hence *C. extinctorius* Fr., centred around Bulliard's concept. If not so interpreted, then a later illegitimate (unsanctioned) homonym, "*Coprinus extinctorius* Fr." (1874), will have been created following publication of "*Coprinus extinctorius* (L.) Fr." (1838). We accept the name as *C. extinctorius* Fr. (1838). Nomenclaturally, this alternative name attained valid status years after Gray (1821) had published the combination *Prunulus extinctorius*, and therefore, it is the status of *Agaricus extinctorius* L., as basionym of *P. extinctorius*, and not *C. extinctorius* Fr., that determines whether or not Singer & Smith's (1946) choice of "*P. extinctorius* Bolt. ex Gray" is a suitable lectotype for *Prunulus* Gray.

Fries (1821, 1874) interpreted *A. extinctorius* L. as being *A. procerus* without an annulus. However, *A. procerus*, now known as either *Lepiota procera* (Scop. : Fr.) Gray or *Macrolepiota procera* (Scop. : Fr.) Singer, is a large brownish fungus, with a prominent annulus, with prominent scales on the pileus and banding on the stipe, and in general not coprophilous (all features not matching Linnaeus' description). Fries' synonymy is unexplainable. Bulliard's concept of "*Agaricus extinctorius*", i.e., that of a *Coprinus*-like fungus (*Coprinus extinctorius* Fr.), is actually a better generic-level match, but appears to have been applied to a different species (with scales, not on dung).

Interpreted as a *Coprinus*-like fungus, "*extinctorius*", be it *Coprinus extinctorius* Fr., *Agaricus extinctorius* L., or *Prunulus extinctorius* (L.) Gray, would be tied to

one or more fungi with autodigesting lamellae, even misapplied as it was by Bolton (1788: 24), where he stated the gills "in decay dissolve in a dark brown liquor." As so typified, the choice of *Prunulus extinctorius*, as type of *Prunulus* is the choice of a type in conflict with Gray's generic protologue. The protologue for *Prunulus* in part reads, "gills persisting"; and the lamellae of the Linnaeus species, if it is to be believed to be a "*Coprinus*"-like taxon, as Singer & Smith (1946) believed *Prunulus extinctorius* to be, autodigest, i.e., they do not "persist" in Gray's terminology. Hence the choice of "*extinctorius*" creates a conflict with Gray's concept of *Prunulus*, and possibly with whatever taxon he misapplied the name *P. extinctorius*. Gray reserved for species with dissolving lamellae, the genus *Coprinus* Pers. His description of that genus in part reads "gills unequal, growing watery..." and in his key to the four genera in subfamily *Pratellideae* Gray, three times he repeated, "gills persistent" for *Pratella* "Pers.", *Cortinaria* "Pers.", and *Prunulus*, versus "gills diffluent" for *Coprinus*. As a misapplied species name, the choice of *Prunulus extinctorius* (L.) Gray as a lectotype for *Prunulus*, may be superseded because the choice is in conflict with the protologue (Art. 10.5a).

The next lectotypification by an author not using the American Code was by that of Donk (1949a, b), who again selected *Agaricus denticulatus*, as had earlier authors using the American Code (Earle, 1909; Murrill, 1916), and as has been accepted by Horak (1968). This lectotypification itself was questioned as possibly being in conflict with the protologue by Singer (1951, 1986) in defence of the earlier attempted lectotypification of *Prunulus* by *P. extinctorius* (Bull. : Fr.) Gray by Singer & Smith (1946). Singer (1951, 1986) noted that *Prunulus denticulatus* had a smooth pileus, whereas Gray (1821) had indicated that the genus *Prunulus* had been described as having a "scaly" cap.

In the generic description for *Prunulus*, Gray (1821: 630) categorised the genus as having a "...cap brittle, scaly, membranous; gills persisting;...." Donk (1949b, 1962) too was puzzled by Gray's use of the descriptor "scaly". However, neither Donk nor Singer appears to have examined Gray's book for patterns in generic description construction, or how the generic description of *Prunulus* compared to other generic descriptions by Gray, of which there are many for fungi, algae, plants, etc. The following example suffices to explain what Gray intended, and it defuses and makes irrelevant the controversy over the word "scaly".

Gray (1821: 378) described the algal genus *Gastridium* Lyngb. as follows: "Thallus threadlike, round, tubular, gelatinous, cartilaginous; tubercles roundish, lateral or terminal; sporidia in the tubercles and also on the twigs". This example of a generic name for a seaweed demonstrates how Gray stated variations in his descriptions in 1821. Sometimes he used the connectives "or" or "and" as in the second and third phrases, and sometimes he merely ran together the various alternatives, as in the first phrase. This did not mean that all included species were threadlike, round, tubular, gelatinous **and** cartilaginous. In this case it meant that they were threadlike, round, tubular, gelatinous **or** cartilaginous. For example, for *G. pinnatifidum* (Huds.) Gray, the thallus was described as "...compressed, cartilaginous, branched....", but it had three varieties, one with roundish thalli and two with compressed thalli. The thallus of *G. obtusum* (Huds.) Gray, was described as "...cartilaginous, cylindrical, threadlike, repeatedly pinnated". That of *Gastridium*

tenuissimum (Gooden.) Gray was described as "Thallus gelatinous, threadlike, cylindrical, pinnatedly branched". while *Gastridium repens* (Lightf.) Gray, had a "... nearly cylindrical, threadlike, solid...." thallus, and *G. articulatum* (Huds.) Gray had a "...cylindrical, threadlike, tubular, contracted throughout as if jointed...." thallus. One has to conclude that the seaweeds in this genus were either cartilaginous or gelatinous, and were sometimes round (sometimes not, i.e., compressed), sometimes tubular (sometimes not, i.e., solid), and only sometimes threadlike. There are many other examples like this in *A natural arrangement of British plants* (Gray, 1821) that can be used to argue that Gray's phraseology and generic descriptions were sufficiently broad and flexible, that concern over the presence of a listed character in such a description must be taken within context rather than in isolation as being literal and exclusive.

The puzzlement by Donk (1949, 1962) over the "mystery" of the inclusion of the word "scaly", and the argument of Singer & Smith (1946) and Singer (1986) to reject "*denticulatus*" as lectotype based upon Gray's description (because *P. denticulatus* had a smooth pileus), are based on a gross misunderstanding and lack of full appreciation of Gray's modus operandi. While Gray's description read "Cap brittle, scaly, membranous...." the included species were not both brittle and membranous (a contradiction) and neither were they all necessarily scaly, just as the seaweeds in *Gastridium* were not all tubular or all cartilaginous. Much more telling of Gray's generic concepts were his keys, and the key quadruplet for the subfamily *Pratellideae* (p. 596) as noted above distinguished *Prunulus* from *Coprinus* as follows: "Cap thin; gills persisting; sporidia in pairs; collar 0..... *Prunulus*" "Cap thin; gills diffluent; sporidia in fours; collar distinct or 0..... *Coprinus*".

Latitude has to be allowed that Gray was just beginning to understand the microscopic features, and he thought the sporidia of both *Pratella* (Pers.) Gray and *Cortinaria* (Pers.) Gray were single, those of *Prunulus* double, and of *Coprinus* in tetrads (he made too many mistakes on microscopic features to take these comments literally). He described the gills as becoming black for subfamily *Pratellideae* (Gray, 1821: 596), but he really meant black when decaying, because the previous two subfamilies, *Agaricideae* and *Mycenadeae* Gray, had gills described as "...decaying without changing colour...." Within the proper context then, it is clear that Gray placed in the genus *Prunulus*, species that had lamellae which darkened upon deterioration (by his observations), and he believed that they persisted in *Prunulus* while they dissolved in *Coprinus*. Therefore, the choice of lectotype by *P. denticulatus* cannot be held to be in conflict with the protologue as was suggested by Singer (1986). We thereby accept and are bound by Donk's (1949, 1962) lectotypification [i.e., we accept *denticulatus*] and not Singer's (1986) choice [i.e., we reject *extinctorius*].

The species related to "*Mycena pelianthina*" (= *Prunulus denticulatus*) currently require a generic name because they form a distinct monophyletic clade. One nomenclatural casualty of accepting *Prunulus denticulatus* as type will be the generic name *Mycenula* P. Karst. (1889), lectotypified by *Mycenula pura* (Pers. : Fr.) P. Karst. by Earle (1909)—a typification accepted by Donk (1962) and Horak (1968)—which has not been recognised as a distinct genus in recent times, but which becomes a taxonomic synonym of *Prunulus* as here lectotypified.

Prunulus is not necessarily a misnomer or inappropriate for the *Mycena pura* group, as the few related species are roseus, vinaceous, or purplish-coloured, i.e., often somewhat plum-coloured, i.e., prunicolour!

Rhacophyllus Berk. & Broome 1871 (holotype *R. lilacinus* Berk. & Broome)

The type of this originally monotypic genus represents an unusual morphological form with a complex taxonomic and nomenclatural history that is discussed separately (Redhead & al., 2000). It is considered to be a *nomen anamorphosis* with limited priority.

Psathyrella (Fr.) Quél. 1872 (type *P. gracilis* (Fr. : Fr.) Quél.—proposed for conservation, cf. Redhead & al., 2001)

≡ *Agaricus* "trib." *Psathyrella* Fr. 1838

Earle (1909), using the American Code, chose as lectotype *Agaricus gracilis* Fr. : Fr., and all modern day authors (Donk, 1949b, 1962; Horak, 1968; Ito, 1959; Pegler, 1983, 1986; Kits van Waveren, 1985; Kühner, 1980; Singer, 1986; Singer & Smith, 1946; Smith, 1972) in the latter half of the century accepted this lectotypification of the name as applied to a large, common genus. Nonetheless, the lectotypification by Earle was superseded by the lectotypification of *Psathyrella* with *P. disseminatus* (Pers. : Fr.) Quél. by Clements & Shear (1931), a lectotypification accepted by Imai (1938). Both species selected as lectotypes were treated by Fries (1838) and Quélet (1872). Although Donk (1949b) preferred to stick with *P. gracilis* because it had never been excluded (whereas *P. disseminatus* had been designated the type of *Pseudocoprinus* Kühner, 1928—see below), and Singer (1986) considered *P. disseminatus* to be a marginal species, neither reason is sufficient to disqualify the lectotypification by Clements & Shear (1931) that superseded Earle's based on the American Code (Art. 10.5b). Nonetheless, virtually all modern taxonomists (Dennis & al., 1960; Horak, 1968; Ito, 1959; Kits van Waveren, 1985; Kühner, 1980; Moser, 1983; Singer, 1986; Singer & Smith, 1946; Smith, 1972, etc.) have excluded *P. disseminatus* from *Psathyrella*, treating it either as a species of *Coprinus* or of *Pseudocoprinus*. It would cause considerable confusion to reverse the general acceptance of *P. gracilis* as lectotype, hence we are proposing (Redhead & al., 2001) conservation of *Agaricus gracilis* as type of Fries' (1838) tribe and Quélet's (1872) genus, *Psathyrella* based on that "tribe".

Onchopus P. Karst. 1879 (lectotype *Coprinus clavatus* Fries = *C. comatus*)

The name was first lectotypified by Earle (1909) whose choice was accepted by Singer & Smith (1946); said to be often considered a synonym of *C. comatus* by the latter. The typification was uncontested by Donk (1962) who nonetheless hinted *Agaricus sterquilinus* Fr. : Fr. might be preferred. *Agaricus sterquilinus* was chosen as lectotype by Horak (1968), but this does not change the generic concept. There seems little reason to disqualify Earle's lectotypification and taxonomically it makes no difference as both species even by molecular standards fall within the same clade. *Onchopus* and *Oncopus* (see below) are synonyms of *Coprinus* s.str.

Oncopus P. Karst. 1882 (alternative spelling, see Donk, 1962).

Pselliophora P. Karst. 1879 (lectotype *Pselliophora atramentaria* (Bull. : Fr.) P. Karst. or *P. comata* [O. F. Müll. : Fr.) P. Karst.].

The name was first lectotypified by Earle (1909) who chose *C. comatus*, but that lectotypification was superseded (Art. 10.5b, e.g., Ex. 7) by the choice of *P. atramentaria* by Singer & Smith (1946), who noted that Fayod (1889) had restricted the use of *Pselliophora*. Their lectotype, *P. atramentaria*, was accepted by Donk (1962) and Horak (1968), neither of whom actually wished to actively use the name. Singer & Smith (1946) did not address Earle's lectotypification (it was not specifically rejected). Instead, they purposely chose a type to place *Pselliophora* into synonymy to prevent it from being used, based their decision on the residue method of typification, and incorrectly concluded that Fayod (1889) had restricted the genus to one species (i.e., an implied lectotypification). In fact Fayod accepted two species. Nevertheless, the acceptance of Singer & Smith's choice by others (Donk, Horak), firmly establishes the superseding lectotypification by *P. atramentaria*. There is considerable debate over the acceptance and merits of lectotypifications enacted under the American Code (see the defeated proposal 79 and its preceding discussion, "*Mechanical typification and the American Code*" by the Special Committee on Lectotypification; Barrie, 1998; cf. Barrie & Greuter, 1999; Greuter & Hawksworth, 1999; Greuter & al., 2000b: 94–99). Combined with the de facto acceptance of American Code lectotypifications (over later superseding lectotypifications) when supportive (witness the widespread acceptance of *P. gracilis* as "lectotype" of *Psathyrella* above), we believe the enforced supersession lectotypification of *Pselliophora* by *P. atramentaria* results in "a disadvantageous nomenclatural change" (Art. 56.1). For taxonomists who accept molecular evidence for re-classifications (in particular the evidence splitting up *Coprinus*), and who opt to use the *Code* (Greuter & al., 2000a) rather than the "*PhyloCode*" (Cantino, 2000; Redhead, 2000), it would become necessary to use the generic name *Pselliophora* for 50% of all former *Coprini*. Among these taxa are the exceedingly well-known *Coprinus atramentarius* (Bull. : Fr.) Fr., the common inky cap, and the even more important *Coprinus cinereus* (Schaeff. : Fr.) Gray, an organism used in numerous patent processes and considerable genetic and growth experiments. Were it not for the supersession of the first lectotype chosen, i.e., *C. comatus*, type of the older name *Coprinus*, *Pselliophora* could be synonymised with *Coprinus*, and the name *Coprinopsis* P. Karst. would become available (see below). The name *Coprinopsis* provides what we believe is an advantageous root word link to the past treatment in *Coprinus* for over 100 years. In as much as none of the authors involved in the lectotypification processes (neither Earle, Singer, Smith, nor Donk) wished to activate the generic name *Pselliophora*, its resurrection now, by strict interpretation of Art. 10.5b is most unfortunate, as is the demise of the name *Psathyrella* if a conservation proposal is not made. We therefore propose that *Pselliophora* (if lectotypified by *P. atramenaria*) be rejected under Art. 56.1, as a "name that would cause a disadvantageous nomenclatural change" (Redhead & al., 2001). The inappropriateness of a generic name is not normally cause for rejecting a name (Art. 51.1), but the exceedingly long history of the link to *Coprinus*, the obscurity of the phonetically dissociated long dead name, *Pselliophora*, and the shear number of significant species makes *Pselliophora* an exceptional case for rejection. Although the generic name *Coprinopsis* P. Karst. has not been in active use for 100 years either, the epithet remained in use as *Coprinus* subg. *Coprinopsis* (P. Karst.) Pat. As

an alternative to our proposal to reject *Pselliophora* under Art. 56.1 (Redhead & al., 2001), we offer a second proposal, to conserve *Coprinopsis* over *Pselliophora*, which achieves virtually the same goal, i.e., to reject *Pselliophora*.

Coprinellus P. Karst. 1879 [lectotype *Coprinellus deliquescens* (Bull. : Fr.) P. Karst.]

Earle (1909) first lectotypified the name and his choice was accepted by Singer & Smith (1946), Donk (1962), and Horak (1968). Donk (1962) noted that *C. deliquescens* was often considered to be a doubtful species, as did Orton & Watling (1979) who rejected the species name. For example Konrad & Maublanc (1924) treated it as a variety of *C. atramentarius*, but Karsten's concept appears to be the same as *Coprinus silvaticus* Peck (Horak, 1968), a rough-spored taxon. The latter interpretation corresponds well to Bulliard's plates and description and as the authority for both *Agaricus atramentarius* Bull. : Fr. and *Agaricus micaceus* Bull. : Fr., he distinguished *A. deliquescens* Bull. : Fr. from both, from the former by colour, from the latter by micaceous granules. Fries (1821) disagreed almost from the onset with Hornemann's (1808) concept of *A. deliquescens*, by citing Flora Danica pl. 1780 (Hornemann, 1808) as an illustration of *A. atramentarius* while recognising *A. deliquescens* as a good species. However, he questioned Bulliard's second plate. Horak (1968) located and illustrated with a full description, a specimen of Karsten's and "lectotypified" the genus *Coprinellus* and the species "*deliquescens*" sensu Karsten by a collection that he determined to be conspecific with *Coprinus silvaticus*. This Karsten collection cannot be considered to be either a lectotype of *Agaricus deliquescens* Bulliard (1792, pl. 437; see also Bulliard & Ventenat, 1809) or of *Coprinellus* (Karsten, 1879), because it was collected in 1881 (Horak, 1968), some years after both were described (Art. 9.9). However, the collection could be considered to be a neotype (or an epitype if Bulliard's plate is selected as lectotype). We accept the specimen illustrated by Horak (1968) as being a neotype for the species name *Agaricus deliquescens* Bulliard, the "lectotype" for the generic name *Coprinellus* P.Karst.

Coprinopsis P. Karst. 1881b [lectotype *Coprinopsis friesii* (Quél.) P. Karst.] non *Coprinopsis* Beeli 1929 (see Donk, 1962).

The original lectotypification by Earle (1909) was adopted by Singer & Smith (1946), Donk (1962), and Horak (1968). By 1889, Karsten had dropped the use of the name *Coprinopsis*, while Patouillard (1887: 126) changed its status to *Coprinus* subg. *Coprinopsis* (P. Karst.) Pat.

Lentispora Fayod 1889 [lectotype *Coprinus tomentosus* (Bull.) Fr.]

First lectotypified by Earle (1909), and followed by Singer & Smith (1946), Donk (1962), and Horak (1968). Orton & Watling (1979) reject the species name as of uncertain application. Konrad & Maublanc (1924) reduced it to a variety of *C. lagopus* (Fr. : Fr.) Fr.Bulliard (1783, pl. 138) certainly depicted a species close to *C. lagopus*. We regard *C. tomentosus* as a species allied to *C. lagopus*, which even if the precise specific application is uncertain, effectively links the generic name *Lentispora* taxonomically to where *C. lagopus* is classified.

Ephemerocybe Fayod 1889 [lectotype *Coprinus ephemerus* (Bull. : Fr.) Fr.]

The first lectotypification by Earle (1909) was accepted by Konrad (1934), Singer & Smith (1946), Donk (1962), and Horak (1968). However, the identity of the species is controversial. M. Lange (1952) and M. Lange & Smith (1953) believed it might be impossible ever to be certain about the identity of *Agaricus ephemerus* Bull. (Bulliard, 1792; Bulliard & Ventenat, 1809), but nonetheless used the species name applied sensu Locquin (1947) for a recognised taxon. Horak (1968), lacking original specimens, illustrated a Favre collection identified as *C. ephemerus*, indicating that it was identical to *C. patouillardii* var. *lipophilus* Heim & Romagnesi. Orton & Watling (1979) treated *C. patouillardii* var. *lipophilus* as a synonym of *C. patouillardii* and separated it from *C. ephemerus* in another stirps. Orton & Watling (1979) followed the concept of M. Lange (1952), as did M. Lange & Smith (1953), in both the latter cases also accepting the concept of Locquin (1947). We use the concept of these last named authors. *Ephemerocybe* would be applicable to the same group of taxa as *Coprinellus* (unless rough-spored taxa are segregated). We consider it to be a synonym of *Coprinellus* until proven otherwise.

Xerocoprinus Maire 1906 [holotype *X. arenarius* (Pat.) Maire = *Coprinus arenarius* Pat. 1892a]

Singer (1986: 856) did not list this name as a synonym of *Coprinus*, rather he treated it as a possible genus of *Gasteromycetes* (hence his exclusion of it from *Coprinus* following his philosophy that the *Agaricales* did not include *Gasteromycetes*). However, other authors disagreed and included the type in the genus *Coprinus*, e.g., Malençon & Bertault (1970). Descriptions of the type specimens were supplied by Patoulliard (1892a, b) and Horak (1968), while additional fresh topotype material of the type, *X. arenarius*, was studied by Malençon & Bertault (1970).

Pseudocoprinus Kühner 1928 [holotype *Pseudocoprinus disseminatus* (Pers. : Fr.) Kühner].

Kühner (1928) segregated this species from *Coprinus* by its lack of deliquescent lamellae. Later he changed his mind about taxonomic separation of *Coprinus* and *Pseudocoprinus*. This same species was selected as lectotype for *Psathyrella* (see above) by Clements & Shear (1931).

"*Coprinellus* (Ricken) J. E. Lange" 1938

This name was considered by Donk (1962) to date from 1936, and to be provisional (which it was in 1936), and hence invalid. However, unbeknownst to Donk in 1962, J. E. Lange (1938: 93) unconditionally took up the name *Coprinellus* and published two combinations in it, viz., *C. disseminatus* and *C. impatiens* (Fr. : Fr.) J. E. Lange. Therefore, the generic name, if based upon a validly published subgeneric name, i.e., "*Coprinus* subg. *Coprinellus* Ricken" (1915: 65), as supposed by Donk, would be valid, and a later illegitimate homonym of *Coprinellus* P. Karst. Donk (1962) selected as type of "*Coprinellus* (Ricken) J. E. Lange", the species "*Psathyrella disseminatus*". J. E. Lange (1936) referred to Quélet with regard to the subgeneric basionym name, but he perhaps intended to say *Coprinarius* Quélet because no reference can be found to Quélet having used "*Coprinellus*" at any taxonomic level. Quélet (1886) placed *Coprinarius disseminatus* (Pers. : Fr.) Quél.

in *Coprinarius* subg. *Psathyrella* (Fr.) Quél. Donk (1962) interpreted the name as "*Coprinellus* (Ricken) J. E. Lange" because of Lange's (1936) reference to Ricken (1915: 65) where the name *Coprinus* subg. *Coprinellus* Ricken was published without attribution to other authors. J. E. Lange's (1938) use of *Coprinellus* (without a Latin diagnosis) was directly linked by him to his 1936 publication, and in that publication (J. E. Lange, 1936: 2), there is a direct link to Ricken (1915), i.e., "Quélet for such reason ["traits in common with certain species of *Coprinus*"] transferred these species ["*P. disseminatus*, *P. impatiens* et al."] to *Coprinus* (*Coprinellus*) (called "Aftertintlinge" by Ricken)". While the reference to Quélet is a lapsus calami, the reference to "Aftertintlinge" by Ricken is clearly a reference to Ricken (1915: 53, 65) where *Coprinus* [unranked] "*Coprinellus*, Aftertintlinge" is described. Ricken (1915) listed Karsten (1879) as a reference consulted for his book, hence it is possible to presume that "*Coprinellus*" of Ricken is a new combination for *Coprinellus* P. Karst. (1879), as *Coprinus* [unranked] *Coprinellus* (P. Karst.) Ricken. If interpreted thus (Art. 33.2), then there is no such generic name as "*Coprinellus* (Ricken) J. E. Lange", because J. E. Lange would simply have been reinstating Karsten's genus back at the generic level. The fact that Ricken (1915) simultaneously treated *Coprinus deliquescens*, the lectotype of *Coprinellus* P. Karst., in a separate subgenus *Coprinus*, may be used to argue that the unranked subgeneric name *Coprinellus* cannot be attributed to Karsten, and therefore must be attributed to Ricken alone (Art. 48.1), but a lectotype is not an "original type". In either event, Art. 55.1, and Art. 55 Exs. 1 and 2 indicate that combinations such as *Coprinellus disseminatus* and *C. impatiens*, made by J. E. Lange, are legitimate, even if they were not made with the legitimate *Coprinellus* P. Karst. (see below). We accept both combinations and consider the name *Coprinellus*, adopted by J. E. Lange, to be *Coprinellus* P. Karst.

Zerovaemyces Gorovoy 1977 (holotype *Z. copriniformis* Gorovoy)

The application of this generic name is linked to the history of *Rhacophyllus*. *Zerovaemyces* is the type for the family name *Zerovaemycetaceae* Gorovoy (1977). It is considered to be a *nomen anamorphosis* (Redhead & al., 2000).

"*Coprinusella*" (Peck) Zerov (1979: 405), nom. inval.

Zerov proposed this new generic status, but failed to cite the basionym, or to indicate where it was published. Hence it is not a validly published generic name. Similarly he failed to cite the places of publication for the basionyms for his three supposed new species combinations, "*Coprinusella phylctidospora* (Romagn.) Zerov", "*C. echinospora* (Bull.) Zerov", and "*C. silvatica* (Peck) Zerov", hence none is a validly published name. To judge from the selected species, Zerov apparently intended to recognise a rough-spored generic taxon with deliquescent lamellae.

Nomenclatural summary

The following *nomina teleomorphosium* are available:

Coprinus Pers. 1797 (synonyms: *Annularius* Roussel 1806, *Onchopus* P. Karst. 1879, *Oncopus* P. Karst. 1882)

Psathyrella (Fr.) Quél. 1872 [but excluded by proposed conservation]

Pselliophora P. Karst. 1879 [but proposed for rejection]

Coprinellus P. Karst. 1879
Coprinopsis P. Karst. 1881
Lentispora Fayod 1889
Ephemerocybe Fayod 1889
Xerocoprinus Maire 1906
Pseudocoprinus Kühner 1928

Nomina anamorphosium with restricted priority are:
Ozonium Link 1809
Rhacophyllus Berk. & Broome 1871 (synonym: *Zerovaemyces* Gorovoy 1977)

Unavailable for coprinoid taxa:
Prunulus Gray 1821 (*Mycenaceae*)

Choice of generic names for coprinoid *Psathyrellaceae*

Coprinopsis: Genus/clade "A" includes the type of *Coprinopsis* P. Karst. (*C. friesii*), the oldest available generic name (after rejection of *Pselliophora*), which is adopted here. It includes other well known species such as *Coprinus lagopus* (Fr. : Fr.) Fr. and *C. cinereus* among others. We consider the generic name *Lentispora* Fayod to be a taxonomic synonym of *Coprinopsis* because its type is clearly related to *C. lagopus*.

Parasola: Genus/clade "B", the *Coprinus auricomus-nudiceps* clade, apparently lacks an available generic name. In reference to their parasol-like appearance we propose a new genus, *Parasola* (see below).

Coprinellus: Genus/clade "C" includes the type of *Pseudocoprinus* (*P. disseminatus*). However, although not sequenced, based upon anatomical similarities, namely a cystoderm and frequently an abundance of pileocystidia, the types of *Coprinellus* P. Karst. and *Ephemerocybe* Fayod would also be placed here. The generic name *Coprinellus* has priority, and is hereby adopted for the clade. Its type, *C. deliquescens*, is anatomically unusual, because it is characterised by rough spores. Otherwise it is somewhat similar to *C. micaceus* (macroscopically) (see J. E. Lange, 1939; pl. 160 F) and *C. heptemerus*, *C. curtus,* or *C. disseminatus* microscopically, i.e., with pilear setules (Orton & Watling, 1979). Therefore, *Coprinellus* is available as a generic name for clade "C", the *C. micaceus* and *C.* (*Pseudocoprinus*) *disseminatus* clade.

Taxonomy: generic features, concepts, and anatomical delimitation

The assumption made by biologists and mycologists for 100 years that deliquescence (autodigestion) of the lamellae is a unique biological and taxonomic feature, and for mycologists in this century that polymorphic basidia, the presence of paraphyses (alternatively known as brachybasidia, pseudoparabasidia, brachycystidia, or pseudoparaphyses), and of synchronous meiotic divisions are all unique and arose only once are brought into question. However, the popular, simplified circumscription of *Coprinus* has not always been as constant as is generally believed. Reijnders (1979: 383–384) referred to *Coprinus* as a "...heteromorphous genus..." and stated, "The question of why this big, polymorphous genus has not been split up can be asked." Given the recent molecular evidence, the classical

features listed above must be re-evaluated, and in doing so the rationale for recognizing genera for various clades must be reconsidered.

Taxonomic features: deliquescens, paraphyses, and inaequihymeniferous development

Not all authors agreed upon inclusion of species such as "*Coprinus*" *disseminatus* in "*Coprinus*". J. E. Lange (1915, 1936) pondered whether to recognise a distinct genus for the non-deliquescent *Coprinus*-like taxa, and ultimately recognised the genus *Coprinellus* (J. E. Lange 1938) for *C. disseminatus* and *C. impatiens*. A. H. Smith (Smith & Hesler, 1946; Smith & al., 1979; Lange & Smith, 1953) and McKnight (McKnight & Allison, 1969; McKnight & McKnight, 1987) persisted in recognising the genus *Pseudocoprinus* for the *P. disseminatus*-group and some members of *Coprinus* sect. *Hemerobii* Fr. (and other odd species, see below after new combinations), because their lamellae do not deliquesce. They adopted the genus *Pseudocoprinus* despite the fact that the original authority for the genus, Kühner (1928, 1980), abandoned it himself. Other authors, in lieu of recognising a distinct genus, allowed for the fact that some "*Coprini*" do not have deliquescent lamellae. Reijnders (1979) noted that *C. heptemerus* M. Lange & A. H. Sm. had non-deliquescent lamellae in culture, and that for both *C. heptemerus* and *C. curtus* Kalchbr., the spores matured over the complete lamellae, rather than from the margins inwards as most deliquescent "*Coprini*" do. Singer (1986: 515) in his key states, "...mostly deliquescent...." and allowed for future taxonomic reorganisation in his discussion of features. Previously, he (Singer, 1951) had accepted the genus *Pseudocoprinus*. Orton & Watling (1979: 5) keyed out *Coprinus* saying "Gills and often also the cap ± deliquescent...." and relied upon other associated features such as the presence of paraphyses to cover the exceptions. Hongo (1960) allowed for the fact that *C. disseminatus* was too close to related "*Coprini*" to be placed separately despite not having deliquescent lamellae.

The presence of inflated sterile cells, paraphyses (brachybasidia or pseudoparabasidia) between basidia in *Coprinus* is usually cited as a linked feature, but these are also known to occur in "*Psathyrella*" (Smith, 1972) as were illustrated for *P. typhae* (Kalchbr.) A. Pearson & Dennis by Redhead (1979), and they occur as well-developed pavement-stone-like formation in *Leucocoprinus* Pat. [Buller, 1924 —as *Lepiota cepaestipes* sensu Buller = *Leucocoprinus luteus* (Bolt.) Locq.], *Bolbitius* Fr. (Buller, 1922), and in less well developed forms in *Stropharia* (Fr.) Quél., *Agaricus* [as *Psalliota* (Fr.) P. Kumm.], etc. (Buller, 1922). It is noteworthy that *Bolbitius* not only can have well developed paraphyses, but that it also autodigests its lamellae like the *C. plicatilis*-group, a fact known to Fries (1838). Fries who was notoriously conservative regarding generic names for agarics recognised only a few genera as distinct from *Agaricus* with its many subgenera. Both *Coprinus* and *Bolbitius* were among them, the latter because it was intermediate between *Coprinus* and *Agaricus*, having liquescent lamellae (Fries, 1838). Yet another example of apparent deliquescence is the anomalus *Coprinopsis ealaensis* Beeli (1929), type for the illegitimate generic name *Coprinopsis* Beeli (1929). This species (genus) had white spores, an annulus, and the entire basidiome

liquified rapidly at maturity, hence the generic name. Whatever genus it is in reality, it represents a white-spored deliquescent agaric.

Repeated reference to the strong link between "*Psathyrella*" and some "*Coprini*" is found in many publications, e.g., Buller (1924), Lange & Smith (1953), Smith (1972, 1973). Buller (1924) argued for the exclusion of *P. disseminatus* from *Coprinus* because of its non-deliquescent, geotropic lamellae, but later (Buller, 1931) allowed the inclusion of *C. plicatilis* (Curtis : Fr.) Fr. into *Coprinus* despite its non-deliquescent lamellae. McKnight & Allison (1969) transferred several "*Coprini*" related to *C. plicatilis* to *Pseudocoprinus* because of their non-deliquescent lamellae but inexplicably treated *C. plicatilis* in *Coprinus*. Given such taxonomically transitional and anomalous taxa, it is not surprising to find molecular evidence indicating that some sections of *Coprinus* s.l. are intimately linked with sections of *Psathyrella*, or to see the presence or absence of autodigestion of lamellae as a common but inconsistent feature of taxa nested together. Autodigestion has obviously arisen several times in the *Psathyrella* clade and possibly also lost as a biological function. Buller (1931) noted that one species, *C. curtus*, had lamellae which deliquesced only up to the "V" part of the plicate pileus and lamellae cross section in an otherwise "Y-shaped" tangential pilear section, i.e., the tail of the "Y" lysed. He also noted that genera like *Bolbitius* also deliquesced, but only after sporulation (Buller 1924). Hence, deliquescence of lamellae and/or the pileus occurs in noncoprinoid taxa, and it varies greatly in timing and extent among those taxa which have been placed in *Coprinus* by one or more authors. Massee (1896) also drew attention that like *Coprinus*, wet digestion of basidia also takes place in puffballs (*Lycoperdon* Pers., *Calvatia* Fr.), and molecular evidence now places these genera in the *Agaricaceae*. Reijnders (1979: 422) stated, "Closer scrutiny of these smaller species [*C. curtus*, *C. disseminatus*, *C. heptemerus*] could demonstrate that certain opinions concerning the genus *Coprinus* are generalisations". The same can be said of the larger species, *C. comatus*, *C. atramentarius* and *C. micaceus* (Bull. : Fr.) Fr.

In summary, paraphyses, inaequihymeniferous development, and autolysis of tissues evolved independently several times in the *Agaricales*. Recognition from molecular analysis that the genus *Coprinus* s.str. should be restricted to a very small group of species centred around the type, *C. comatus*, in the *Agaricaceae*, while >90% of all "*Coprini*" belong to another family is not only plausible, it now appears to be reasonable. Whereas many of the "*Coprini*" related to *C. ephemerus* and *C. disseminatus* share many psathyrelloid features, *Coprinus comatus* and its close morphological, anatomical, and molecular ally, *C. sterquilinus*, share features in common with other *Agaricaceae* taxa and differ from other large "*Coprini*".

Hollow stipes with internally suspended yarn-like strand

Bulliard & Ventenat (1809) drew attention to the fact that Bulliard knew of only three species of mushrooms which formed a central, elastic, cottony, extractable cord suspended in the hollow tubular stipes, i.e., his *Agaricus typhoides* (Bulliard, 1781, pl. 16; 1793, pl. 582, Fig. 2), *A. ephemeroides* (Bulliard, 1793, pl. 582, Fig. 1), and *A. colubrinus* Bull. The first is still clearly recognisable as a synonym of *C.*

comatus (and was so treated by Fries, 1821), the second is now consistently misapplied to the wrong species, but in its original sense (= *C. sterquilinus* or possibly *C. spadiceisporus,* see details below), and the third is a synonym of *Macrolepiota procera* (Scop. : Fr.) Singer, all now in *Agaricaceae*. None of the other "*Coprini*" possess this feature. Buller (1924: 184, photo of *C. sterquilinus*; 1931: 73, photo of *C. comatus*) specifically drew attention to the characteristic and constant presence of this strand in both species, known to him only in these two. Fries (1821) knew *A. ephemeroides* only from Bulliard's icones and specifically mentioned the cottony strand in that species. J. E. Lange (1939) when taking up the name seemingly has misapplied it to a different, unrelated much smaller species, specifically stating he could not confirm Fries' observations (actually Bulliard's) of a cord. "*Coprinus ephemeroides*" sensu J. E. Lange is not sensu Bulliard. Bulliard's is most likely conspecific with *C. sterquilinus*. Confirmation of the presence of this strand has been made repeatedly by us on fresh specimens of *C. comatus*. The yarn-like central strand in the stipes of *C. comatus* and allies was used as a taxonomic feature by Bogart (1976) in his key to species. Its unique presence in these "*Coprini*" was used by us to predict correctly its presence in the hollow stipes of *Montagnea arenaria* (DC.) Zeller (e.g., DAOM 208748), a species that is one of the molecularly closest generic and specific allies to *Coprinus* s.str. (Johnson & Vilgalys, 1998; Moncalvo & Vilgalys, unpubl.). Johnson & Vilgalys (1998, Fig. 1) noted that inclusion of secotioid taxa in "*Agaricaceae*" could result in nomenclatural complications, and hesitated to formally transfer such taxa to the family. However, it is not the formal transfer of the genus to the family that is a problem. For example, the type of *Montagnea* Fr. was originally described as an agaric, *Agaricus arenarius* DC., and the genus when circumscribed was first considered to be an agaric genus near *Coprinus* by Fries (1836), while *Montagnites* Fr. (a later illegitimate substitute for *Montagnea*) was included in *Agaricaceae* by Patouillard (1887) and *Montagnea* was again included in *Coprinaceae* by Smith (1973). It is the transfer of species to combined genera that blurs generic (family and order) circumscriptions and also leads to the potential creation of homonyms, that creates problems.

Agaricus and *Lepiota*-like reddening of tissues and pleurocystidia

Coprinus comatus and *C. sterquilinus* are unusual (almost unique) in that their lamellae become pinkish from pinkish cellular contents, prior to darkening from overlying melanising spores. Similar pinkish colouration is a common feature in the *Agaricaceae* clade, in *Agaricus* specifically linked to red quinones and pathways linked to melanin formation (Butler & Day, 1998; Gill & Steglich, 1987).

Among the large and medium-sized "*Coprini*" both *C. comatus* and *C. sterquilinus* are unique in lacking pleurocystidia (species like *C. atramentarius* and *C. micaceus* employ cystidia as structural (physical) barriers to keep the tightly packed lamellae apart; Micheli, 1729; Buller, 1909, 1922, 1924, 1931]; instead, they employ flaring flanges along the lamellar edges. It is noteworthy that *C. arachnoideus* Bogart, which was separated by Bogart (1976) in his key by the lack of a strand in the stipe, forms pleurocystidia and therefore, the conclusion can be drawn that it was misplaced in *Coprinus* sect. *Coprinus*. Among the species Bogart

(1976) included in section *Coprinus*, several matching the profile for *Coprinus* s.str. have reddening lamellae and/or stipes.

In general, in *Agaricaceae*, there is a general paucity of the presence of pleurocystidia in any genus or species, reddening of tissues is common, melanisation of spores has occurred several times, deliquescence of basidia has evolved several times, and large paraphyses and inaequihymeniferous hymenia have arisen in at least one other internal sub-*Agaricaceae* clade. Therefore, the fact that *Coprinus comatus* is nested within the "*Agaricaceae*" clade is not surprising. In retrospect it can be reasoned that taxonomists have been misled by conspicuous features (blackish spores, autodigestion of lamellae) when in fact more subtle differences more closely correlate with phylogenetic groupings. *Coprinus* s.str. can be circumscribed in such a way as to be recognisable morphologically and anatomically in the field or laboratory.

Secotioid versus agaricoid

For the purpose of this paper we are confining our discussion to *Coprinus* and its immediate allies (far broader issues are left for a separate publication). The immediate issue is the potential synonymising of *Montagnea* with *Coprinus* s.str. *Coprinus* is the older name of the two, which means that *Montagnea* species would need to be transferred to *Coprinus*. Based upon a single region sequence data (LSU) *Montagnea* "appears" to be basal to *Coprinus*. However, *Coprinus* produces ballistic basidiospores, and there is no strong evidence that once lost, this basic biological function has ever been regained (despite a long history of arguments and counter arguments). Hence, it must be assumed that all ancestral forms to both *Montagnea* and *Coprinus* have been lost, because a fungus with a *Montagnea* type of morphology could not have given arise to *Coprinus*. Nonetheless, *Montagnea* and *Coprinus* share many features, and it is conceivable that loss of ballistic basidiospores has occurred after divergence. If *Montagnea* and *Coprinus* were synonymised it would entail a change of species epithet for *Montagnea arenaria* (DC.) Zeller because of the earlier name *Coprinus arenarius* Pat. *Montagnites candollei* Fr. would not be available because it was an illegitimate renaming of *Agaricus arenarius* DC., and therefore one would need to transfer *Montagnites argentina* Speg. to *Coprinus* (see Reid & Eicker, 1991; Zeller, 1943). However, there is insufficient evidence to force synonymy, and as it serves little purpose in combining the two genera, we retain both for now.

Another genus to consider is *Xerocoprinus* Maire (1906), based upon *Coprinus arenarius* Patouillard (1892a, b), as was mentioned above. *Xerocoprinus arenarius* is anatomically intermediate between *Montagnea arenaria*, with which it shares the same desert habitats, and *Coprinus comatus*. *Xerocoprinus arenarius* lacks pleurocystidia as does *C. comatus*, and it forms a distinct free annulus similar to *C. comatus*. Unlike both *M. arenaria* and *C. comatus*, apparently *X. arenarius* forms solid stipes (Patouillard, 1892a, b; Horak, 1968; Malençon & Bertault, 1970), and unlike *C. comatus* it is not inaequihymeniferous. Based upon known morphological features (it has not been sequenced), it seems closest to *Coprinus* s.str. (*C. comatus*-*C. sterquilinus*) and *M. arenaria*, rather than any genus in *Psathyrella*ceae.

Unresolved issues

The analyses by Hopple & Vilgalys (1999) placed *Coprinus cordisporus* next to *C. curtus*. These results are anomalous from an anatomical viewpoint and this taxonomic anomaly was discussed several times in that paper. Hopple (1994) had earlier noted that the species was phylogenetically interesting because of this discrepancy, noting that there is a single morphological feature, the presence of setule-like cells among the cheilocystidia, that linked *C. cordisporus* with other species related to *C. curtus*. It is noteworthy that *C. cordisporus* is on a particularly long branch (Hopple & Vilgalys, 1999, Fig. 3). Even more noteworthy is that in the analyses based upon over 800 taxa (Moncalvo & Vilgalys, unpubl.), *Coprinus cordisporus* is not strongly linked to *C. curtus* and *Psathyrella candolleana* nests between *Coprinellus* and *Coprinus cordisporus*. As in the case of *Psathyrella* s.l., we believe there are insufficient data available to resolve where *C. cordisporus* should be placed generically. It may represent yet another coprinoid lineage, or it may merge with existing taxa. Uljé & Noordeloos (1993) monographed *Coprinus* subsection *Nivei* Citerin that included *C. cordisporus*. *Coprinus latisporus* P. D. Orton was synonymised with *C. niveus* (Pers. : Fr.) Fr. by them, and *C. latisporus* was molecularly characterised by Hopple (Hopple, 1994; Hopple & Vilgalys, 1999), where it was placed solidly in the *Coprinopsis* clade in contrast with *C. cordisporus*. Because of these unresolved issues, we prefer not to transfer *C. cordisporus* to either *Coprinopsis* or *Coprinellus*, and to refrain from transferring anatomically similar species (although *C. niveus* and its closest allies are transferred by us to *Coprinopsis*).

Other unresolved dispositions—*Coprinus castaneus* Berk. & Broome as described by Pegler (1986) [hymeniform pileipellis, scant veil of filamentous hyphae, possibly non-deliquescent], *Coprinus elongatipes* A.H.Smith & Hesler (1946) [nonplicate pileus wholly deliquescent after spore discharge, no pleurocystidia, but abundant pilear setae and a hymeniform pileipellis], and *Pseudocoprinus venustus* McKnight & Allison (1969) [plicate non-deliquescent pileus covered with scales composed of swollen cells, sparse pleurocystidia] do not fit well with our anatomically arranged scheme and molecular data are lacking to guide us.

Artificial key to phylogenetically separated *Coprinus*-like genera (not recommended for standard identifications)

Coprinoid species defined as: *hymenium inaequihymeniferous* (basidia di-, tri-, or tetramorphic), brachybasidioles (paraphyses) well-developed (pavement stone-like), spores darkly pigmented, lamellae parallel- to subparallel-sided, deliquescent or half-deliquescent during sporulation, or entire basidiome post-sporulation deliquescent, lamellae ageotropic typically.

1. Pileus with floccose (often recurved) scales, notably with scale bases firmly attached to tramal tissues as if consisting of matted fibrous ends of tramal filaments, white or whitish with only a tan coloured disc area, ellipsoid becoming uplifted, lacerate and deliquescent; stipe containing a central extractable cottony yarn-like string attached at both ends inside its tubular shaft virtually unattached laterally or suspended by arachnoid filaments, often bulbous at base; veil always

present, leaving a conspicuous thick cottony annulus which is either loose or more unusually stuck basally like a pseudovolva; lamellae lacking pleurocystidia, white, then often pinkish, then covered by blackish spores, margins bifurcate-flanged prior to deliquescence, sides subtly subparallel; basidia consistently dimorphic; [one large species (the "Shaggy Mane", *C. comatus*) on buried debris and smaller species (*C. sterquilinus* and allies) on dung] ..... ***Coprinus*** s.str. (*Agaricaceae*)

[Secotioid desert forms referable to *Montagnea* and *Xerocoprinus* belong here but are not keyed]

1. Pileus either glabrous, minutely pubescent from cystidioid (or setoid) hairs, and/or covered with loose granules or micaceous flecks, or if scaly, the scales either mounds of swollen cells or ephemeral cottony-floccose scales or hybrids of these, easily dislodged (not tenacious-rooted in the trama as above), often partially washed or abraded off in nature leaving a bald surface (or if tenacious then merely consisting of flat appressed adhering patches), white or conspicuously pigmented (grey, orange, beige, rusty), ovoid to ellipsoid, becoming uplifted, lacerate and deliquescent, or remaining convex (campanulate to plano-convex), deliquescing or not; stipe never containing a central cottony extractable loose cord, bulbous or not at base; veil absent or fugacious or sometimes leaving an annulus, basal flange or scales; lamellae in large deliquescent species always with large, projecting, conspicuous pleurocystidia (visible with a hand lens) (but pleurocystidia may be absent or sparse in small deliquescent species or medium sized non-deliquescent species), white then blackish or dusky, rarely with pinkish intermediate tints, deliquescent or more rarely not, only rarely flanged, sides strictly parallel or more rarely subtly subparallel; basidia di-, tri- or tetramorphic [coprophilous, lignicolous, or terrestrial on soil or detritus or burns] [if pleurocystidia present or if pileocystidia or setules are present or if sphaerocysts are present in the veil take this choice] 2

2. Pileipellis a cutis of primarily radially arranged elongated (often filamentous) cells which may be short and swollen but are not organised in a palisade and not a sheet of primarily subglobose cells (i.e., not a hymeniderm, not a cystoderm), pileocystidia (both setulae and setae) absent; veil tissue present (usually floccose) and consisting of filamentous or swollen (sometimes globose) cells or mixtures, often leaving shaggy scales or broad membranous patches on pileus; lamellae always deliquescent while sporulating and pileus becoming lacerate (from torn deliquescent margins) often uplifted as remnants, especially in smaller species, or pendant in larger species; basidia dimorphic [ozonium absent, but many coprophilous species with pseudorhizae represented; allies of *atramentaria, lagopus, narcotica, friesii, insignis*, etc.] ..... ***Coprinopsis*** (*Psathyrellaceae*)

2. Pileipellis either a hymeniderm or a cystoderm, with or without pileocystidia; veil absent or when present always containing swollen cystiform cells; lamellae fully, partially, or non-deliquescent; pileus ranging from deliquescent to non-deliquescent during sporulation; ozonium present or absent 3

3. Veil completely absent, not even a few scattered globose superficial cells present; pileipellis a smooth hymeniform palisade forming a membranous layer, lacking superficial lageniform to bulbous-based filament-bearing cells (setulae) converted into secretory round-tipped pileocystidia (but some with nonsecretory, conspicuously projecting, brown setae in disc area); lamellae and pileus non-deliquescent during sporulation and pleurocystidia always present; pileus remaining membranous, always strongly plicate, diaphanous, and intact until post sporulation, post mortem collapse of the entire basidiome; basidia irregularly di- to trimorphic; [terrestrial, frequently on lawns, in gardens, along forest trails; ozonium absent; allies of *plicatilis, auricoma*] ..... ***Parasola*** (*Psathyrellaceae*)

3. Veil (usually of globular cells) present and/or bearing superficial lageniform to bulbous-based filament-bearing cells (setulae) converted into secretory round-tipped pileocystidia; lamellae and pileus fully, partially, or non-deliquescent during sporulation, if non-deliquescent some have geotropic lamellae, otherwise lamellae ageotropic; pleurocystidia present or absent, sometimes concentrated towards margins; pileus membranous or fleshy or very fragile; basidia di-, tri-, tetramorphic; [lignicolous, terrestrial, or coprophilous species; ozonium present or absent; allies of *micaceus, disseminatus, curtus, domesticus*] ..... ***Coprinellus*** (*Psathyrellaceae*)

The following redisposition of coprinoid taxa and resulting new combinations are based upon several taxonomic criteria:

[1]Anatomy combined with LSU data published by Hopple & Vilgalys (1999) and earlier papers.

[2]Anatomy combined with ITS data published by Park & al. (1999a, b).

[3]Anatomy and analogy to the pattern detected using molecular data along with historical linkages. We have drawn heavily upon the following publications where either detailed anatomical studies are available for coprinoid taxa, types were studied, or nomenclature was researched: Bender & Enderle (1988), Bender & al., (1984), Bogart (1976, 1979a, b), Cacialli, Caroti & Doveri (1999), Enderle & Bender (1990), Enderle & al. (1986), Krieglsteiner & al. (1982), Malençon & Bertault (1970), McKnight & Allison (1969), Orton & Watling (1979), Patrick (1977, 1979), Pegler (1977, 1983, 1986), Redhead & Smith (1981), Redhead & Traquair (1981), Richter & Bender (1998), Schulz-Weddigen (1985), Smith & Hesler (1946), Uljé (1988, 1992), Uljé & al. (1998a,b), Uljé & Bas (1988, 1991, 1993), Uljé & Bender (1997), Uljé & Noordeloos (1993, 1997).

[4]LSU data (Johnson & Vilgalys, 1998) combined with morphological and anatomical data.

The list is not exhaustive and a few taxa (not recombined or confirmed) cannot be placed with any confidence at present. Additionally, although we believe these are now more correctly classified, we fully acknowledge that there may be adjustments in the future, and that some assignments may prove to be incorrect, or that generic level taxa may yet be further fragmented or merged. However, it is only by accepting this classification to the extent that we commit to new combinations that we can demonstrate our belief that the molecular evidence is correct. We do not

expect to be followed by everyone for many reasons. The evidence may be questioned and only time and further testing will tell. It may not be practicable in many cases. There are 200 years of tradition to consider. By making the combinations available here, we hope to encourage a serious debate, and to enable us and others to use generic names that apply to monophyletic groups.

Agaricaceae

Coprinus

[1, 2] *Coprinus comatus* (O. F. Müll. : Fr.) Pers., Tentamen Disp. Meth. Fungorum, p. 62. 1797.

[1] *Coprinus sterquilinus* (Fr. : Fr.) Fr., Epicr. Syst. Mycol. p. 242. 1838.

[3] *Coprinus spadiceisporus* Bogart, Mycotaxon 4: 245. 1976.

Montagnea

[4] *Montagnea arenaria* (DC.) Zeller, Mycologia 35: 418. 1943.

Xerocoprinus

[3] *Xerocoprinus arenarius* (Pat.) Maire, Bull. Soc. Bot. France 53: CCXIV. 1953.

Psathyrellaceae (Singer) Vilgalys, Moncalvo & Redhead, **stat. nov.**
Basionym: *Coprinaceae* subfam. *Psathyrelloideae* Singer, Sydowia 15: 67. 1961.

Note: Connected to the family *Coprinaceae* Overeem (1924) [as *Coprinaceae* Roz —a bibliographic error] by Singer (1962: 523).

Syn. *Zerovaemycetaceae* Gorovoy (1977), *nomen anamorphosis*, restricted priority.

Coprinopsis (f.)

[1] ***Coprinopsis acuminata*** (Romagn.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus atramentarius* var. *acuminatus* Romagnesi, Rev. Mycol. (Paris) 16: 120, 127. 1951.

[3] ***Coprinopsis africana*** (Pegler) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus africanus* Pegler, Persoonia 4: 82. 1966.

[3] ***Coprinopsis alutaceivelata*** (Bogart) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus alutaceivelatus* Bogart, Mycotaxon 8: 270–272. 1979.

[3] ***Coprinopsis ammophilae*** (Courtec.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus ammophilae* Courtecuisse, Doc. Mycol. 18(72): 76. 1988.

[3] ***Coprinopsis argentea*** (P. D. Orton) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus argenteus* P. D. Orton, Notes Roy. Bot. Gard. Edinburgh 32: 139. 1972.

[1, 2] ***Coprinopsis atramentaria*** (Bull. : Fr.) Redhead, Vilgalys & Moncalvo **comb. nov.** Basionym: *Agaricus atramentarius* Bulliard, Herb. France, pl. 164 [text on plate]. 1784.

[3] ***Coprinopsis austrofriesii*** (Redhead & Pegler) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus austrofriesii* Redhead & Pegler in Redhead & Traquair, Mycotaxon 13: 392. 1981.

[3] ***Coprinopsis bicornis*** (Uljé & Horvers) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus bicornis* Uljé & Horvers in Uljé & Noordeloos, Persoonia 17: 170. 1999.

[3] ***Coprinopsis brunneistragulata*** (Bogart) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus brunneistragulatus* Bogart, Mycotaxon 8: 246. 1979.

[3] ***Coprinopsis brunneofibrillosa*** (Dennis) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus brunneofibrillosus* Dennis, Kew Bull. 15: 118. 1961.

[3] ***Coprinopsis bubalina*** (Bogart) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus bubalinus* Bogart, Mycotaxon 8: 266. 1979.

[3] ***Coprinopsis burkii*** (A. H. Sm.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus* burkii A. H. Smith in Smith & Hesler, J. Elisha Mitchell Sci. Soc. 62: 178. 1946.

[3] ***Coprinopsis calospora*** (Bas & Uljé) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus calosporus* Bas & Uljé in Uljé & Bas, Persoonia 15: 359. 1993.

[3] ***Coprinopsis caribaea*** (Pegler) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus caribaeus* Pegler, Kew Bull. addit. ser. 9: 466. 1983.

[3] ***Coprinopsis cinchonensis*** (Murrill) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus cinchonensis* Murrill, Mycologia 10: 85. 1918.

[1, 2] ***Coprinopsis cinerea*** (Schaeff. : Fr.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Agaricus cinereus* Schaeffer, Fungorum qui in Bavaria et Palatinato circa Ratisbonam nascentur. Vol. 4: 43. 1774.

[3] ***Coprinopsis cinereofloccosa*** (P. D. Orton) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus cinereofloccosus* P. D. Orton, Trans. Brit. Mycol. Soc. 43: 198–199. 1960.

[3] ***Coprinopsis clastophylla*** (Maniotis) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus clastophyllus* Maniotis, Amer. J. Bot. 51: 491. 1964.

Anamorph: *Rhacophyllus lilacinus* Berkeley & Broome, J. Linn. Soc., Bot. 11: 559. 1871.

[3] ***Coprinopsis coniophora*** (Romagn.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus coniophorus* Romagnesi, Rev. Mycol. (Paris) 6: 126–127. 1941.

[1] ***Coprinopsis cothurnata*** (Godey) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus cothurnatus* Godey in Gillet, Les Hyménomycètes, ou description de tous les champignons (fungi) qui croissent en France.... p. 605. 1878.

[3] ***Coprinopsis cubensis*** (Berk. & Curtis) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus cubensis* Berkeley & Curtis, J. Linn. Soc., Bot. 10: 293. 1869.

[3] ***Coprinopsis depressiceps*** (Bogart) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus depressiceps* Bogart, Mycotaxon 10: 165. 1979.

[2] ***Coprinopsis echinospora*** (Buller) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus echinosporus* Buller, Trans. Brit. Mycol. Soc. 6: 363. 1920.

[3] ***Coprinopsis epichloea*** (Uljé & Noordeloos) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus epichloeus* Uljé & Noordeloos, Persoonia 16: 300. 1997.

[3] ***Coprinopsis episcopalis*** (P. D. Orton) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus episcopalis* P. D. Orton, Trans. Brit. Mycol. Soc. 40: 270. 1957.

[1] ***Coprinopsis erythrocephala*** (Lév.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Agaricus erythrocephalus* Léveillé, Ann. Sci. Nat. Bot., sér. 2, XVI: 237. 1841.

[3] ***Coprinopsis extinctoria*** (Fr.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus extinctorius* Fries, Epicrisis p. 245. 1838 (see explanation on authorship in the discussion under *Prunulus* above). Non *Agaricus extinctorius* L. (1753).

[3] ***Coprinopsis fibrillosa*** (Berk. & Broome) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus fibrillosus* Berkeley & Broome, J. Linn. Soc., Bot. 11: 560. 1871.

[3] ***Coprinopsis filamentifer*** (Kühner) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus filamentifer* Kühner, Bull. Soc. Naturalistes Oyonnax 10–11 (suppl.): 64. 1957.

[3] ***Coprinopsis fluvialis*** (Lanconelli & Uljé) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus fluvialis* Lanconelli & Uljé in Uljé & Noordeloos, Persoonia 16: 297. 1997.

[1] *Coprinopsis friesii* (Quél.) P. Karsten, Acta Soc. Fauna Fl. Fenn. 2(1): 27. 1881.

[3] ***Coprinopsis geesterani*** (Uljé) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus geesterani* Uljé, Persoonia 14: 565. 1992.

[1] ***Coprinopsis gonophylla*** (Quél.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus gonophyllus* Quélet in Guillaud, Forquignon & Merlet, Ann. Sci. Nat. de Bordeaux et du Sud-Ouest 3: 42. 1882.

[3] ***Coprinopsis goudensis*** (Uljé) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus goudensis* Uljé in Uljé & Bas, Persoonia 15: 362. 1993.

[3] ***Coprinopsis herbivora*** (Singer) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus herbivorus* Singer, Beih. Sydowia 7: 70. 1973.

[3] ***Coprinopsis herinkii*** (Pilát & Svrček) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus herinkii* Pilát & Svrček, Česká Mykol. 21: 137–138. 1967.

[3] ***Coprinopsis heterocoma*** (Malençon) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus heterocomus* Malençon, in Malençon & Bertault, Flore des Champignons superieurs du Maroc. Tome 1: 237–239. 1970.

[3] ***Coprinopsis insignis*** (Peck) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus insignis* Peck, Bull. Buffalo Soc. Nat. Sci. 1(2): 54. 1873.

[3] ***Coprinopsis jamaicensis*** (Murrill) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus jamaicensis* Murrill, Mycologia 10: 84. 1918.

[1, 3] ***Coprinopsis jonesii*** (Peck) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus jonesii* Peck, Bull. Torrey Bot. Club 22: 206. 1895.

Molecular data cited as [1]*Coprinus lagopides*, apparently a misapplied name for *C. phlyctidosporus* (see Uljé & Noordeloos, 1999, for details).

[1] ***Coprinopsis kimurae*** (Hongo & Aoki) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus kimurae* Hongo & Aoki in Aoki & Hongo, Trans. Mycol. Soc. Japan 7: 16. 1966.

[3] ***Coprinopsis krieglsteineri*** (Bender) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus krieglsteineri* Bender, Beitr. Kennt. Pilze Mitteleur., Schw. Gmund 3: 218. 1987.

[3] ***Coprinopsis kubickae*** (Pilát & Svrček) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus kubickae* Pilát & Svrček, Česká Mykol. 21: 142–143. 1967.

[3] ***Coprinopsis laanii*** (Kits van Wav.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus laanii* Kits van Waveren, Persoonia 5: 146. 1968.

[1] ***Coprinopsis lagopides*** (P. Karst.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus lagopides* P. Karsten, Bidrag Kännedom Finlands Natur Folk 32: 535. 1879; also Meddeland. Soc. Fauna Fl. Fenn. 5: 37. 1879.

[1] ***Coprinopsis lagopus*** (Fr. : Fr.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Agaricus lagopus* Fries, Syst. Mycol. 1: 312. 1821.

[1] ***Coprinopsis luteocephala*** (Watling) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus luteocephalus* Watling, Notes Roy. Bot. Gard. Edinburgh 31: 359. 1972.

[1] ***Coprinopsis macrocephala*** (Berk.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Agaricus macrocephalus* Berkeley, British Fungi, English Flora 5(2): 122. 1836.

[3] ***Coprinopsis macropus*** (Berk. & Broome) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus* macropus Berkeley & Broome, J. Linn. Soc., Bot. 11: 560. 1871.

[3] ***Coprinopsis marcida*** (Bogart) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus marcidus* Bogart, Mycotaxon 8: 262–264. 1979.

[3] ***Coprinopsis martinii*** (P. D. Orton) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus martinii* P. D. Orton, Trans. Brit. Mycol. Soc. 43: 201. 1960.

[3] ***Coprinopsis maysoidispora*** (Redhead & Traquair) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus maysoidisporus* Redhead & Traquair, Mycotaxon 13: 381. 1981.

[3] ***Coprinopsis mexicana*** (Murrill) Redhead, Vilgalys & Moncalvo, comb. nov. Basionym: *Coprinus mexicanus* Murrill, Mycologia 10: 84. 1918.

[3] ***Coprinopsis myceliocephala*** (M. Lange) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus myceliocephalus* M. Lange, Mycologia 40: 742. 1948.

[1] ***Coprinopsis narcotica*** (Batsch : Fr.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Agaricus narcoticus* Batsch, Elenchi Fungorum. Continuatio Prima. column #79 (species LXXVII). 1786.

[3] ***Coprinopsis neolagopus*** (Hongo & Sagara) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus neolagopus* Hongo & Sagara, Trans. Mycol. Soc. Japan 8: 17. 1967.

[3] ***Coprinopsis neotropica*** (Redhead & Pegler) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus neotropicus* Redhead & Pegler in Redhead & Traquair, Mycotaxon 13: 394. 1981.

[1] ***Coprinopsis nivea*** (Pers. : Fr.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Agaricus niveus* Persoon, Syn. meth. Fung. p. 400. 1801.

Molecular data (Hopple & Vilgalys, 1999) reported under the name *Coprinus latisporus* P. D. Orton (see Uljé & Noordeloos, 1993 for synonymy).

[3] ***Coprinopsis ochraceolanata*** (Bas) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus ochraceolanatus* Bas in Uljé & Bas, Persoonia 15: 362. 1993.

[3] ***Coprinopsis pachyderma*** (Bogart) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus pachydermus* Bogart, Mycotaxon 8: 274. 1979.

[3] ***Coprinopsis pachysperma*** (P. D. Orton) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus pachyspermus* P. D. Orton, Notes Roy. Bot. Gard. Edinburgh 32: 144–145. 1972.

[3] ***Coprinopsis paleotropica*** (Redhead & Pegler) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus paleotropicus* Redhead & Pegler in Redhead & Traquair, Mycotaxon 13: 394. 1981.

[3] ***Coprinopsis papagoensis*** (Lindsey & G. L. Gilb.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus papagoensis* Lindsey & G. L. Gilbertson, Mycotaxon 2: 96. 1975.

[3] ***Coprinopsis phaeospora*** (P. Karst.) P. Karsten, Acta Soc. Fauna Fl. Fenn. 2(1): 27. 1881. *ut* "*phaeosporus*".

[3] ***Coprinopsis phlyctidos*spora** (Romagn.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus phlyctidosporus* Romagnesi, Rev. Mycol. (Paris) 10: 88–89. 1945.

[3] ***Coprinopsis picacea*** (Bull. : Fr.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Agaricus picaceus* Bulliard, Herb. France pl. 206. 1785.

[3] ***Coprinopsis piepenbroekii*** (Uljé & Bas) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus piepenbroekii* Uljé & Bas, Persoonia 15: 365. 1993.

[3] ***Coprinopsis pinguispora*** (Bogart) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus pinguisporus* Bogart, Mycotaxon 10: 161–164. 1979.

[3] ***Coprinopsis pseudofriesii*** (Pilát & Svrček) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus pseudofriesii* Pilát & Svrček, Česká Mykol. 21: 140–141. 1967.

[3] ***Coprinopsis pseudonivea*** (Bender & Uljé) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus pseudoniveus* Bender & Uljé in Uljé & Noordeloos, Persoonia 15: 270. 1993.

[3] ***Coprinopsis pseudoradiata*** (Watling) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus pseudoradiatus* Watling in P. D. Orton, Notes Roy. Bot. Gard. Edinburgh 35: 154. 1976.

[3] ***Coprinopsis psychromorbida*** (Redhead & Traquair) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus psychromorbidus* Redhead & Traquair, Mycotaxon 13: 382. 1981.

[1] ***Coprinopsis radiata*** (Bolton) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Agaricus radiatus* Bolton, An History of Fungusses, growing about Halifax, vol. 1: 39. 1788.

[3] ***Coprinopsis radicans*** (Romagn.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus radicans* Romagnesi, Rev. Mycol. (Paris) 16: 122–124. 1951.

[1] ***Coprinopsis romagnesiana*** (Singer) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus romagnesianus* Singer, Lilloa 22: 459. 1951 [1949]

[3] ***Coprinopsis rugosobispora*** (Geesink & Imler) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus rugosobisporus* Geesink & Imler, Sterbeeckia 12: 9. 1979.

[1] ***Coprinopsis sclerotiger*** (Watling) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus sclerotiger* Watling, Notes Roy. Bot. Gard. Edinburgh 32: 130. 1972.

[3] ***Coprinopsis sclerotiorum*** (Horvers & de Cock) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus sclerotiorum* Horvers & de Cock in Uljé & Noordeloos, Persoonia 16: 283. 1997.

[1, 3] ***Coprinopsis scobicola*** (P. D. Orton) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus scobicola* P. D. Orton, Notes Roy. Bot. Gard. Edinburgh 32: 147. 1972.

Note: This species appears in the cladogram by Hopple & Vilgalys (1999) as "*C. bilanatus*" an invalid name (see below).

[1] ***Coprinopsis semitalis*** (P. D. Orton) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus semitalis* P. D. Orton, Notes Roy. Bot. Gard. Edinburgh 32: 147. 1972.

[3] ***Coprinopsis spelaiophila*** (Bas & Uljé) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus spelaiophilus* Bas & Uljé in Uljé & Noordeloos, Persoonia 17: 179. 1999.

[3] ***Coprinopsis spilospora*** (Romagn.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus spilosporus* Romagnesi, Rev. Mycol. (Paris) 16: 127. 1951.

[3] ***Coprinopsis stangliana*** (Enderle, Bender & Gröger) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus stanglianus* Enderle, Bender & Gröger in Bender & Enderle, Z. Mykol. 54: 57–62. 1988.

[3] ***Coprinopsis stercorea*** (Fr.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus stercoreus* Fries, Epicr. Syst. Mycol. p. 251. 1838.

[3] ***Coprinopsis striata*** (Bogart) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus striatus* Bogart, Mycotaxon 10: 158. 1979.

[2, 3] ***Coprinopsis strossmayeri*** (Schulzer) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus strossmayeri* Schulzer, Verh. Zool.-Bot. Ges. Wien. 28: 430. 1879.

(Molecular data reported as [2]*Coprinus rhizophorus* Hongo & Yokoyama; see Uljé & Noordeloos, 1997, for synonymy)

[3] ***Coprinopsis subtigrinella*** (Dennis) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus subtigrinellus* Dennis, Kew Bull. 15: 122–123. 1961.

[3] ***Coprinopsis sylvicola*** (Bogart) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus sylvicola* Bogart, Mycotaxon 8: 257. 1979.

[3] ***Coprinopsis tectispora*** (Bogart) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus tectisporus* Bogart, Mycotaxon 8: 276. 1979.

[3] ***Coprinopsis tigrina*** (Pat.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Psathyra tigrina* Patouillard, Bull. Soc. Mycol. France 15: 197. 1899.

[3] ***Coprinopsis tigrinella*** (Boud.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus tigrinellus* Boudier, Bull. Soc. Bot. France 32: 283–284. 1885.

[1] ***Coprinopsis trispora*** (Kemp & Watling) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus trisporus* Kemp & Watling in Watling, Notes Roy. Bot. Gard. Edinburgh 32: 128. 1972.

[3] ***Coprinopsis undulata*** (Bogart) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus undulatus* Bogart, Mycotaxon 8: 250. 1979.

[3] ***Coprinopsis urticicola*** (Berk. & Broome) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Agaricus "urticaecola"* Berkeley & Broome, Ann. Mag. Nat. Hist. ser. 3, 7: 376–371. 1861.

[3] ***Coprinopsis utrifer*** (Watling) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus utrifer* Watling, Notes Roy. Bot. Gad. Edinburgh 31: 362. 1972.

[3] ***Coprinopsis variegata*** (Peck) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus variegatus* Peck, Bull. Buffalo Soc. Nat. Sci. 1: 54. 1873.

[1] ***Coprinopsis vermiculifer*** (Dennis) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus vermiculifer* Dennis, Kew Bull. 19: 112. 1964

[3] ***Coprinopsis verticillata*** (Schulz-Weddigen) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus verticillatus* Schulz-Weddigen, Mycologia 77: 154. 1985.

[3] ***Coprinopsis xantholepis*** (P. D. Orton) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus xantholepis* P. D. Orton, Notes Roy. Bot. Gard. Edinburgh 32: 150. 1972.

[1] ***Coprinopsis xenobia*** (P. D. Orton) Redhead, Vilgalys & Moncalvo, **comb. nov. Basionym**: *Coprinus xenobius* P. D. Orton, Notes Roy. Bot. Gard. Edinburgh 35: 148. 1976.

The following "species" that appear in the cladogram by Hopple & Vilgalys (1999) would belong to *Coprinopsis*, however the names used are invalid provisional names lacking formal Latin descriptions:

"*Coprinus dictyocalyptratus*" Van de Bogart, *nom. invalid.* in thesis.

"*Coprinus americanus*" Patrick, *nom. invalid.* in thesis, and in Weber & Smith, A Field Guide to Southern Mushrooms, p. 231–232. 1985.

"*Coprinus bilanatus*" Kemp. *nom. invalid.* in Trans. Brit. Mycol. Soc. 65: 379. 1975. = *Coprinopsis scobicola* (see Uljé & Noordeloos, 1999).

"*Coprinus pseudoochraceovelatus*" Hopple, *nom. prov. invalid.* in thesis.

Coprinellus (m.)

[3] ***Coprinellus amphithallus*** (M. Lange & A. H. Sm.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus amphithallus* M. Lange & A. H. Smith, Mycologia 45: 774. 1953.

[3] ***Coprinellus angulatus*** (Peck) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus angulatus* Peck, Bull. Buffalo Soc. Nat. Sci. 1: 54. 1873.

[1] ***Coprinellus aokii*** (Hongo) Vilgalys, Hopple & Johnson, **comb. nov.** Basionym: *Coprinus aokii* Hongo, Jap. J. Bot. 41: 167. 1966.

[3] ***Coprinellus aureogranulatus*** (Uljé & Aptroot) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus aureogranulatus* Uljé & Aptroot in Uljé, Aptroot & van Iperen, Persoonia 16: 549. 1998.

[3] ***Coprinellus bisporiger*** (P. D. Orton) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus bisporiger* P. D. Orton, Notes Roy. Bot. Gard. Edinburgh 35: 147. 1976.

[1] ***Coprinellus bisporus*** (J. E. Lange) Vilgalys, Hopple & Johnson, **comb. nov.** Basionym: *Coprinus bisporus* J. E. Lange, Dansk Bot. Arkiv. 2(3): 50. 1915.

[3] ***Coprinellus brevisetulosus*** (Arnolds) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus brevisetulosus* Arnolds, Biblioth. Mycol. 90: 309. 1982 (= *Coprinus* stellatus Buller sensu M. Lange).

[1] ***Coprinellus callinus*** (M. Lange & A. H. Sm.) Vilgalys, Hopple & Johnson, **comb. nov.** Basionym: *Coprinus callinus* M. Lange & A. H. Smith, Mycologia 45: 770. 1953.

[1] *Coprinellus congregatus* (Bull. : Fr.) P. Karsten, Bidrag Kännedom Finlands Natur Folk 32: 543.1879.

[1] ***Coprinellus curtus*** (Kalchbr.) Vilgalys, Hopple & Johnson, **comb. nov.** Basionym: *Coprinus curtus* Kalchbrenner in Thümen, Flora 59: 424. 1876.

[3] *Coprinellus deliquescens* (Bull.) P. Karsten, Bidrag Kännedom Finlands Natur Folk 32: 542. 1879. Better known as *Coprinus silvaticus Peck* (see above and Horak 1968)

[3] ***Coprinellus dilectus*** (Fr.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus dilectus* Fries, Epicr. Syst. Mycol. p. 250. 1838.

[1, 2] *Coprinellus disseminatus* (Pers. : Fr.) J. E. Lange, Dansk Bot. Ark. 9(6): 93. 1938. *ut "disseminata"*.

[1] ***Coprinellus domesticus*** (Bolton : Fr.) Vilgalys, Hopple & Johnson, **comb. nov.** Basionym: *Agaricus domesticus* Bolton, An History of Fungusses, growing about Halifax, p. 26. 1788.

[3] ***Coprinellus ellisii*** (P. D. Orton) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus ellisii* P. D. Orton,Trans. Brit. Mycol. Soc. 43: 199–200. 1960.

[3] ***Coprinellus ephemerus*** (Bull. : Fr.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Agaricus ephemerus* Bull., Herb. France 12: pl. 542. 1792. [without a description but valid when ICBN Art. 42.3 is applied; otherwise published as *A. ephemerus* DC. in de Candolle & de Lamarck, Flore Française, Ed 3, t. 2: 149. 1805].

[3] ***Coprinellus eurysporus*** (M. Lange & A. H. Sm.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus eurysporus* M. Lange & A. H. Smith., Mycologia 45: 773. 1953.

[3] ***Coprinellus fallax*** (M. Lange & A. H. Sm.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus fallax* M. Lange & A. H. Smith, Mycologia 45: 765. 1953.

[3] ***Coprinellus fimbriatus*** (Berk. & Broome) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus fimbriatus* Berkeley & Broome, J. Linn. Soc., Bot. 11: 561. 1871.

[1] ***Coprinellus flocculosus*** (DC.) Vilgalys, Hopple & Johnson, **comb. nov.** Basionym: *Agaricus flocculosus* De Candolle, Flore Française, Ed. 3, t. 5: 45. 1815.

[3] ***Coprinellus furfurellus*** (Berk. & Broome) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Agaricus furfurellus* Berkeley & Broome, J. Linn. Soc., Bot. 11: 559. 1871.

[1] ***Coprinellus heptemerus*** (M. Lange & A. H. Sm.) Vilgalys, Hopple & Johnson, **comb. nov.** Basionym: *Coprinus heptemerus* M. Lange & A. H. Smith, Mycologia 45: 751–752. 1953.

[1] ***Coprinellus heterosetulosus*** (Watling) Vilgalys, Hopple & Johnson, **comb. nov.** Basionym: *Coprinus heterosetulosus* Watling in Orton, Notes Roy. Bot. Gard. Edinburgh 35: 153. 1976.

[3] ***Coprinellus heterothrix*** (Kühner) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus heterothrix* Kühner, Bull. Soc. Naturalistes Oyonnax 10–11(suppl.): 3. 1957.

[3] ***Coprinellus hiascens*** (Fr. : Fr.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Agaricus hiascens* Fries, Syst. Mycol. 1: 303. 1821.

[3] *Coprinellus impatiens* (Fr. : Fr.) J. E. Lange, Dansk Bot. Ark. 9(6): 93. 1938.

[3] ***Coprinellus marculentus*** (Britzelm.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus marculentus* Britzelmayr, Bot. Centralbl. 54(3) [16]: 70. 1893. [also in a separate published in 1893 as Bot. Centralbl. 15/17: 13]

[1, 2] ***Coprinellus micaceus*** (Bull.: Fr.) Vilgalys, Hopple & Johnson, **comb. nov.** Basionym: *Agaricus micaceus* Bulliard, Herb. France pl. 246 [text on plate]. 1786.

[3] ***Coprinellus pellucidus*** (P. Karst.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus pellucidus* P. Karsten, Bidrag Kännedom Finlands Natur Folk 37: 236. 1882.

[3] ***Coprinellus plagioporus*** (Romagn.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus plagioporus* Romagnesi, Rev. Mycol. (Paris) 6: 121–124. 1941.

[3] ***Coprinellus pyrrhanthes*** (Romagn.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus pyrrhanthes* Romagnesi, Rev. Mycol. (Paris) 16: 128. 1951.

[1, 2] ***Coprinellus radians*** (Desm.) Vilgalys, Hopple & Johnson, **comb. nov.** Basionym: *Agaricus radians* Desmazières, Ann. Sci. Nat. (Paris) XIII: tab. 10, fig. 1. 1828.

[3] ***Coprinellus sassii*** (M. ange & A. H. Sm.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus* sassii M. Lange & A. H. Smith, Mycologia 45: 755. 1953.

[1] ***Coprinellus sclerocystidiosus*** (M. Lange & A. H. Sm.) Vilgalys, Hopple & Johnson, **comb. nov.** Basionym: *Coprinus sclerocystidiosus* M. Lange & A. H. Smith, Mycologia 45: 769. 1953.

[3] ***Coprinellus singularis*** (Uljé) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus singularis* Uljé, Persoonia 13: 486. 1988.

[3] ***Coprinellus subdisseminatus*** (M. Lange) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus subdisseminatus* M. Lange in M. Lange & A. H. Smith, Mycologia 45: 777–778. 1953.

[3] ***Coprinellus subimpatiens*** (M. Lange & A. H. Sm.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus subimpatiens* M. Lange & A. H. Smith, Mycologia 45: 772. 1953.

[3] ***Coprinellus subpurpureus*** (A. H. Sm.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus subpurpureus* A. H. Smith, Mycologia 40: 684. 1948.

[3] ***Coprinellus truncorum*** (Scop. : Fr.) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Agaricus truncorum* Scopoli, Flora Carniolica (ed. 2), vol. 2: 426. 1772. [Often incorrectly attributed to Schaeffer who himself cited Scopoli].

[3] ***Coprinellus velatopruinatus*** (Bender) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus velatopruinatus* Bender, Beitr. Kenntn. Pilze Mitteleur. 5: 80. 1989.

[3] ***Coprinellus verrucispermus*** (Joss. & Enderle) Redhead, Vilgalys & Moncalvo, **comb. nov.** Basionym: *Coprinus verrucispermus* Josserand & Enderle in Bender & Enderle, Z. Mykol. 54: 67. 1988.

[1] ***Coprinellus xanthothrix*** (Romagn.) Vilgalys, Hopple & Johnson, **comb. nov.** Basionym: *Coprinus xanthothrix* Romagnesi, Rev. Mycol. (Paris) 6: 127. 1941.

For information purposes only, we note the following binomials (new combination, new species) were previously published in *Coprinellus* by Karsten, although not all (e.g., *C. hemerobius, C. schroeteri*) would currently be classified in the genus: *Coprinellus digitalis* (Batsch) P. Karsten (1879: 542), *C. tardus* (P. Karst.) P. Karsten (1879: 543), *C. hemerobius* (Fr.) P. Karsten (1879: 543), *C. schroeteri* (P. Karst.) P. Karsten (1879: 543), *C. proximellus* (P. Karst.) P. Karsten (1879: 544), *C. phyllophilus* (P. Karst.) P. Karsten (1879: 544), *C. rapidus* (Fr.) P. Karsten (1879: 544), *C. velaris* (Fr.) P. Karsten (1879: 545), *C. sceptrum* (Jungh.) P. Karsten (1879: 545), *C. sororius* P. Karsten (1881a: 9).

Parasola Redhead, Vilgalys & Hopple, **gen. nov.** (f.)

Basidiomata ephemera, terrestria. Pileus plicatus, membranaceus, glaber vel setosus, eglandulatus. Velum nullum. Lamellae deliquescentes in senectute. Pleurocystidia praesentia. Stipites centrales, friabiles. Basidiosporae atrae.

Typus: [2] ***Parasola plicatilis*** (Curtis : Fr.) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Agaricus plicatilis* Curtis : Fries, Flora Londinensis, tab. 200. 1778; Systema Mycologicum Vol. 1: 312. 1821.

[1] ***Parasola auricoma*** (Pat.) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Coprinus auricomus* Patouillard, Tabulae Analyticae Fungorum 5: 200. 1886.

[3] ***Parasola besseyi*** (A. H. Sm.) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Pseudocoprinus besseyi* A. H. Smith in Smith & Hesler, J. Elisha Mitchell Sci. Soc. 62: 189. 1946.

[3] ***Parasola brunneola*** (McKnight & Allison) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Pseudocoprinus brunneolus* McKnight & Allison, Morris Arbor. Bull. 20: 73–74. 1969.

[3] ***Parasola galericuliformis*** (Watling) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Coprinus galericuliformis* Watling, Notes Roy. Bot. Gard. Edinburgh 28: 42. 1966.

[3] ***Parasola hemerobia*** (Fr.) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Coprinus hemerobius* Fries, Epicr. Syst. Mycol. p. 253. 1838.

[3] ***Parasola hercules*** (Uljé & Bas) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Coprinus hercules* Uljé & Bas, Persoonia 12: 483. 1985.

[3] ***Parasola kuehneri*** (Uljé & Bas) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Coprinus kuehneri* Uljé & Bas, Persoonia 13: 438. 1988.

[3] ***Parasola lactea*** (A. H. Sm.) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Pseudocoprinus lacteus* A. H. Smith in Smith & Hesler, J. Elisha Mitchell Sci. Soc. 62: 191. 1946.

[3] ***Parasola leiocephala*** (P. D. Orton) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Coprinus leiocephalus* P. D. Orton, Notes Roy. Bot. Gard. Edinburgh 29: 88–90. 1969

[3] ***Parasola lilatincta*** (Bender & Uljé) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Coprinus lilatinctus* Bender & Uljé in Uljé & Bender, Persoonia 16: 373. 1997.

[1] ***Parasola megasperma*** (P. D. Orton) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Coprinus megaspermus* P. D. Orton, Notes Roy. Bot. Gard. Edinburgh 32: 141. 1972.

[3] ***Parasola mirabilis*** (Mont.) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Coprinus mirabilis* Montagne, Ann. Sci. Nat. Bot., sér. 4, 1: 106. 1854.

[3] ***Parasola miser*** (P. Karst.) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Coprinus miser* P. Karsten, Bidrag Kännedom Finlands Natur Folk 37: 236. 1882.

[1] ***Parasola nudiceps*** (P. D. Orton) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Coprinus nudiceps* P.D. Orton, Notes Roy. Bot. Gard. Edinburgh 32: 142–144. 1972.

[3] ***Parasola pachytera*** (Berk. & Broome) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Coprinus pachyterus* Berkeley & Broome, J. Linn. Soc., Bot. 11: 561. 1871.

[3] ***Parasola schroeteri*** (P. Karst.) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Coprinus schroeteri* P. Karsten, Meddeland. Soc. Fauna Fl. Fenn. 5: 34. 1879.

[3] ***Parasola setulosa*** (Berk. & Broome) Redhead, Vilgalys & Hopple, **comb. nov.** Basionym: *Coprinus setulosus* Berkeley & Broome, J. Linn. Soc., Bot. 11: 561. 1871.

Mycenaceae van Overeem, Icones Fungorum Malayensium Heft XIV–XV: 4. 1926.

Full citation is given here because the family name has been overlooked in all modern literature, including conservation articles to protect *Tricholomataceae* R. Heim ex Pouzar (*nom. cons.*) as listed in the *Code* (Greuter & al., 2000a).

Prunulus Gray

Although the name *Prunulus* was used by Murrill (1916) for the majority of mycenoid fungi, and therefore most combinations are available for the appropriate restricted group, the currently accepted species epithet for the type species was not recombined because Murrill and Gray used the oldest name available, viz. *Agaricus denticulatus* Bolton. However, current nomenclature requires us to use names sanctioned by Fries (1821), hence the following combination is required:

Prunulus pelianthinus (Fr. : Fr.) James E. Johnson, Vilgalys & Redhead, **comb. nov.** Basionym: *Agaricus pelianthinus* Fries, Syst. Mycol. 1: 112. 1821.

Acknowledgements

This research was supported by a grant (DEB-9708035) from the U.S.A. National Science Foundation to Vilgalys and Moncalvo. We thank Drs. Robert A. Shoemaker and Michael Corlett for presubmission reviews, Dr. John McNeill for valuable post submission review and changes, and Dr. Lorelei L. Norvell for transliterating and translating Ukranian. We also thank Dr. James E. Johnson for assistance with the larger agaric phylogeny project and for discussions regarding *Mycenaceae*. Thanks also go to Dr. Francesco Doveri for greatly improving the accuracy of citations and the Latin diagnosis via his review and for tolerance of our diverging taxonomies. The authors accept responsibility for taxonomic decisions which were not necessarily accepted by all reviewers.

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