

# What Ever Happened to the Shaggy Parasol?

Else C. Vellinga\*

SHAGGY MANE almost the only species left in *Coprinus*, Shaggy Parasol no longer a *Lepiota* species—what is happening in the mushroom world we took for granted, and why?

The answer lies in a story of molecules, but it indicates clearly that once you know that species are related, based on similarities in their DNA, your eyes open similarities and differences that have long been known in the mushrooms themselves. For instance, that mysterious cord which runs through the central tube of the stem in the Shaggy Mane, *Coprinus comatus*, is absent in *Coprinellus disseminatus*, *C. micaceus*, and *Coprinopsis atramentarius* (to call species that were formerly considered *Coprinus* by their new names). The Shaggy Mane also lacks cells on the gills which keep adjacent gills from bumping into each other—cells which function like ships' fenders to cushion them from damage (Redhead 2000). All the other inky caps have these pleurocystidia. We saw these differences, but discounted them in light of similarities, especially the fact that both the Shaggy Mane and the other inky caps turn into ink as they age. It shouldn't be so surprising that *C. comatus* is now one of only a handful of species left in the genus.

Shaggy Parasols have their own story of changing names and different historical contexts.

In the beginning there was a simple time when all white-spored, free-gilled mushrooms lacking a volva were classified as *Lepiota*. But as numbers grew and members of the group were found to vary considerably in size, shape, colors, texture and many microscopical characters, *Lepiota* was split up into an ever-growing number of smaller and smaller genera. *Leucocoprinus* was the first new genus (in 1888), followed by *Leucoagaricus* and *Macrolepiota* (both in 1948), *Cystolepiota* (1952), *Sericeomyces* (1978), *Echinoderma* (1991) and then *Pulverolepiota* (1993), the youngest kid on the block. Some of these names may be unfamiliar but



Figure 1. Young specimen of *Chlorophyllum brunneum*. Photo by John Lennie.

all these genera are represented in North America.

The Shaggy Parasol migrated from *Lepiota* to *Macrolepiota*, on account of its size (*Macrolepiota* means “big *Lepiota*”) and the scaliness it shares with *Macrolepiota procera*, the prototypical *Macrolepiota* species. Thus *Lepiota rachodes* became *Macrolepiota rachodes*. The species name is preserved in such cases (but might change in ending, when the gender of the new genus differs from that of the old one—a puzzling effect sometimes since these Latin and Greek subtleties are largely forgotten.) Unfortunately, the original spelling was “rachodes,” which is meaningless. Perhaps what the first author had in mind was “rhacodes,” which means “ragged”; it would be an appropriate description, and later some well-intentioned authors used this spelling. But in the first publication the species name is consistently spelled “rachodes,” and that is what counts.

In addition to the white-spored free-gilled mushrooms lacking a volva (those with a volva

\* 861 Keeler Avenue, Berkeley, CA 94708; e-mail [ecvellinga@comcast.net](mailto:ecvellinga@comcast.net).

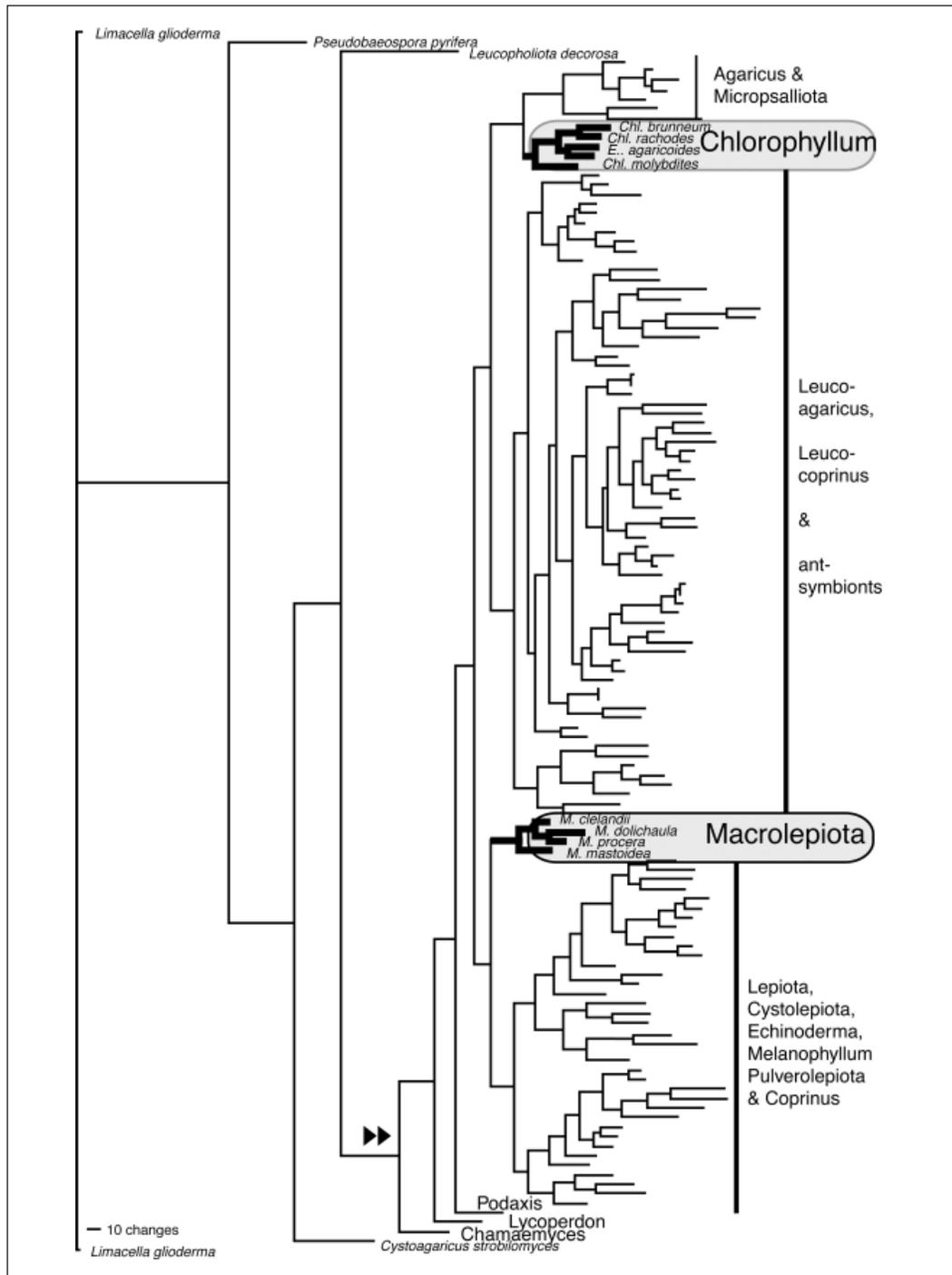


Figure 2. The position of the Shaggy Parasol and Macrolepiota species within the Agaricaceae, based on ITS and LSU sequence analyses. One of 2299 most parsimonious trees is given. *Limacella glioderma* is the outgroup. The origin of the family Agaricaceae is indicated with a double arrow. To keep it legible, names of taxa have been left out, except for the ones in Macrolepiota and Chlorophyllum, and those outside the family Agaricaceae. *Leucoagaricus rubrotinctus*, *L. americanus*, *Leucocoprinus birnbaumii*, *Lepiota roseolivida*, *L. sequoiarum*, and *L. brunnescens* belong to the *Leucoagaricus/Leucocoprinus* group, and species like *Lepiota aspera*, *L. clypeolaria*, and *L. cristata* are in *Lepiota proper*.

are accommodated in *Amanita*), one green-spored mushroom is also free-gilled. In the 19th century, spore color was the primary character to distinguish genera, so this mushroom got its own genus in 1898, viz. *Chlorophyllum*. *Chlorophyllum molybdites* is the well-known Green-spored Parasol, a lawn species in parts of the U.S.A. with hot summers and the cause of more poisonings there than any other mushroom.

The Shaggy Parasol and the Green-spored Parasol look very similar—both have big whitish caps with brown scales, a beautiful fringed ring on a white smooth stem, and they both change to reddish/orangish when scratched on the stem. Even the spores and the cells on the gill edge are very similar, though the spores in the Green-spored Parasol acquire pigment late in life and turn the gills green.

The similarities led Spanish mycologists to consider *Chl. molybdites* a member of *Macrolepiota*. In 1995 the two genera were joined (Moreno et al., 1995), but *molybdites* was still kept in its own section, *Chlorophyllum*, within *Macrolepiota*. Unfortunately, this action was not done according to the rules of mycological naming, which dictate that in such mergers the older genus name has to be retained; of course in this case *Chlorophyllum* is 50 years older than *Macrolepiota*.

In the meantime, it had become apparent that within *Macrolepiota* there were quite striking differences in appearance and this led to several sections being recognized. One section contained *Macrolepiota procera*, another the Shaggy Parasol, and a third a number of species with small scales on the cap.

This was the state of affairs when molecular research sprang into the world of *Lepiota* systematics with an entirely new perspective. Molecular blueprints could now be compared, and the more similar they were, the more closely the mushrooms were related. The similarities enable common ancestors to be inferred and a family tree to be constructed.

Now, several years have passed and the situation has matured. So what do the molecules have to say? Is the division of *Lepiota* really justified, or should we go back to one big, happy *Lepiota* genus? Are Shaggy and Green-spored Parasols as close as siblings, or is the stately *M. procera* the closest kin of the Shaggy Parasol?

The answer to the second question is clear.

Whatever part of the genome is examined, the Shaggy Parasol is sister to *Agaricus* species, and *M. procera* is only a remote cousin (see e.g. Fig. 2).

The old *Lepiota* is neatly divided up into a number of branches (Fig. 2). For the moment, although the sequence of branching or grouping of the branches still cannot be established, it seems best to consider the main branches as separate genera. To be explicit, *Agaricus* is itself one of those branches, and so are *Tulostoma*, *Battarrea* and *Podaxis*, along with *Coprinus comatus*, and *Lycoperdon* and its relatives. Together the branches form the family Agaricaceae. Going back to one big genus *Lepiota* is not an option, unless all genera in the family are merged. A separate family, like the old Lepiotaceae, for the white-spored species is not feasible either. Neither color of the spores nor shape of the fruitbody is a reliable indicator for relationship. Reliable non-molecular characters do exist but they are either more structural ones—like the arrangement of the tissues in the gills and veil, and the makeup of the root-like cords—or developmental characters. The pigmentation of the spores is almost an afterthought in the development of these mushrooms.

The Green-spored Parasol turns out to be just a green-spored Shaggy Parasol, grouping with other species close to “*Macrolepiota*” *nachodes*, and another colored-spored species from Africa (*Chl. globosum*). *Endoptychum agaricoides*, a species adapted to life in steppes and other dry grassy areas, groups here as well.

The type species of *Macrolepiota* is *M. procera*, and the name *Macrolepiota* is kept for that species and its closest relatives, and the species with the small scales on the cap. *Chlorophyllum* becomes the genus name for the Shaggy Parasol. The name was originally used for species with green gills, but it now applies to an assemblage of species characterized by a different set of characters. It is a bit like family names for humans where we don't find anything strange about Ann Johnson, who is the daughter of Robert Johnson, and not John's son.

Do we depend on the molecules, or can we just look at the mushrooms and decide whether they belong with *Chlorophyllum*, like the Shaggy Parasol, or with *Macrolepiota*, like *M. procera*?

*Chlorophyllum* species have smooth stems, whereas the stems of *Macrolepiotas* are covered in a plush-like material which forms bands when the



Figure 3. The base of the stem of *Chlorophyllum rachodes*, showing the gradually widening base. Photo by John Lennie.

stem grows. So the stems can be striped like tigers, but when the material has the same color as the background, the stripes may not be obvious. There are also consistent differences in the structure of the scales on the cap, and in spore shape and the germ pore. In *Macrolepiota* the pore is a real hole, while in *Chlorophyllum* it is more a depression, as if someone had put her thumb on the end of the spore and pushed it in.

Besides the differences in appearance, *Chlorophyllum* and *Macrolepiota* species typically grow in slightly different habitats. *Chlorophyllum* species like it a little bit more disturbed and nutrient rich, which means that they are more commonly encountered in urban areas, including compost heaps and ruderal areas.



Figure 4. The ring of *Chlorophyllum rachodes*, with its double crown. Photo by John Lennie.

However, this is not the end of the story because the Shaggy Parasol comes in different shapes and colors. One with a big bulbous base and big scales has had several names applied to it, including var. *hortensis* and var. *bohemica* (see e.g. Arora, 1986). Alas, these names were not published following the rules. More importantly, the characters used to distinguish these varieties do not quite hold up—big bulbous bases and



Figure 5. The cap of *Chlorophyllum olivieri*, with non-contrasting scales. Photo by John Lennie.

big scales do not always go together, nor as was claimed does the width of the germ pore suffice to distinguish big-scaled or wide-bulbous specimens. However, with the help of the molecules, it became clear that there are good characters that consistently differentiate three species in the temperate parts of North America and Europe. Species #1 has a sudden abrupt bulb at the base of the stem, and narrow cells on the gill edge. A second has a gradual bulb at the base of the stem and relatively broad cells on the gill edge. The third has relatively small spores and hardly any difference in color between the scales on the cap and the background. For the first one the name “*brunneum*,” based on a species described by Farlow and Burt (1929) in the beautiful *Icones Farlowianae*, appeared to be appropriate (Vellinga 2003) (Fig. 1). The second keeps the name *Chl. rachodes* (Figs 3 and 4). The third is *Chl. olivieri* (Fig. 5), and Table 1 lists the three species with their most characteristic features.

In the literature there are many conflicting interpretations of the different names. Some are listed in Table 2 with the names most likely to be

correct, as judged from the illustrations.

All three species occur in the Pacific North West (Sieger, 2003, but see also Table 2), and the first two are regular sights in California, with *Chl. brunneum* the more common. The occurrence and distribution in the rest of North America is not adequately understood.

A fourth species is found in Florida. It was described originally by Murrill, as *Chl. subrhacodes*, and it looks like a smaller version of *Chl. brunneum*, but differing in microscopical characters (Murrill, 1943; Vellinga, 2003). At this time no molecular data are known.

Three other species round out the genus as it is known in the U.S.A. The most infamous, of course, is *Chl. molybdites*, with its green spores; then there is *Chlorophyllum hortense*, formerly known either as *Leucoagaricus hortensis* or as *Lepiota humei*, characterized by a pale yellow central patch on the cap, a strong reddening reaction of the stem, and spores without a germ pore; and lastly *Chl. agaricoides*, with secotioid fruitbodies which do not look like gilled mushrooms at all (this species was formerly known as *Endoptychum agaricoides*).

Many *Chlorophyllum* species have a wide distribution. Thus *Chl. brunneum* is known from Europe, North America, and Australia. Some records of *Chl. rachodes* from Africa probably also refer to the species. Whether this is its natural distribution area, or whether it followed human culture or was actively introduced by people, we do not know. *Chlorophyllum rachodes* and *Chl. olivieri* are known from Europe and North America. *Chlorophyllum molybdites* has been reported from all over the globe. In colder regions it does not occur outdoors though it has been found in planters in shopping malls, and in tropical swimming "paradises" (Watling, 1991; Vellinga, 1990). As it is such a widespread species, it has been described many times under different names.

The same is true for *Chlorophyllum hortense*. Murrill himself even described it several times (Akers & Sundberg, 1997); it is known as *L. bisporus* in Africa, and as *M. alborubescens* in Japan. It occurs widely throughout the world, again avoiding the cooler regions, but is still unknown in Europe. In the U.S.A. it has been reported from the southeast, and as far north as southern Illinois (Akers et al., 1999).

The secotioid *Chlorophyllum agaricoides*, in which the cap does not open and the imprisoned

gills form a tangled mass, is found in dry and grassy places all over the Northern Hemisphere.

Among *Chlorophyllum* species *Chl. subrhacodes* seems to be an exception with a restricted distribution, as it is so far only known from Florida.

*Macrolepiota* species on the other hand are not widespread, and there are many local species, with limited distributions. One example is *M. procera* which was once thought to be widespread, and recorded all over the world. Now, the Australian species is called *M. clelandii*, the one in South and Central America *M. colombiana*; the Japanese one is close to the European one, but slightly different; and the North American one is also a different species, yet to be described (it might even be several . . .). The real *M. procera* is now only known from Europe, and its eastern extent is still not known.

Reports on edibility and on toxicity of *Chlorophyllum* species abound in the literature. Severe problems are caused by the Green-spored Parasol, and by the Japanese *Chl. neomastoideum*; stomach upsets, vomiting, pain, diarrhea are the symptoms. Surprisingly, one of the older names for the species is "esculentum" which means "edible," and indeed a close relative, *Chl. globosum* from Africa, is sold on the markets in Cameroun. Shaggy Parasols are widely eaten, but reports of occasional unpleasant reactions in people who are accustomed to eating them are not uncommon. For *Chl. agaricoides* there are again reports on edibility (Liu, 1984 who also listed its medicinal properties), and on toxicity (especially in animals) (Desjardin, pers. comm.).

Macrolepiotas do not seem to cause any discomfort and can be safely eaten. Some species are even cultivated. Unfortunately, they are much rarer than the Chlorophyllums and are virtually absent from large parts of the U.S.A.

Now we can answer the question in the title of this paper: the Shaggy Parasol is a complex of several species, each with a wide distribution, and all accommodated in the genus *Chlorophyllum*. Its wanderings epitomize the turbulence in the *Lepiota* world as a whole.

Sorting out its classification has prepared us for other genera which contain species with different spore colors—another example is the black-spored *Melanomphalia*, which fits well with white-spored *Omphalina*-like species (Aime et al. 2005). We have also learned not to be surprised

**Table 1.**  
Overview of the characters of *Chlorophyllum brunneum*,  
*Chl. olivieri*, and *Chl. rachodes*.

Species	Diagnostic characters
<i>brunneum</i>	<ul style="list-style-type: none"> <li>◆ Cap with brown scales on whitish background (Fig. 1)</li> <li>◆ Stem with abrupt often marginate bulb</li> <li>◆ Cystidia on gill edge relatively slender</li> </ul>
<i>olivieri</i>	<ul style="list-style-type: none"> <li>◆ Cap with brown or dingy scales on dingy or brownish background (Fig. 5)</li> <li>◆ Stem with rounded bulb or none at base</li> <li>◆ Spores relatively small</li> <li>◆ Cystidia on gill edge broadly club-shaped</li> </ul>
<i>rachodes</i>	<ul style="list-style-type: none"> <li>◆ Cap with brown scales on whitish background</li> <li>◆ Stem with rounded bulb (Fig. 3)</li> <li>◆ Cystidia on gill edge broadly club-shaped</li> </ul>

**Table 2.**  
Overview of the diverse interpretation of names in the group of *Chlorophyllum*  
*rachodes*, and the names now accepted, as judged by the illustrations.

This overview focuses on American authors, but does not pretend to be complete.

Old name	Interpretation	Accepted name
<i>bohemica</i>	Candusso & Lanzoni, 1990 Sieger, 2003	<i>brunneum</i> <i>rachodes</i>
<i>brunnea</i>	Bartelli & Smith, 1964	<i>rachodes</i>
<i>hortensis</i>	Arora, 1986 Breitenbach & Kränzlin, 1995 Phillips, 1981 Phillips, 1991 Sieger, 2003	<i>brunneum</i> <i>rachodes</i> <i>brunneum</i> <i>olivieri</i> or <i>rachodes</i> <i>brunneum</i>
<i>rachodes</i>	Arora, 1986: pl. 69 Breitenbach & Kränzlin, 1995 Huffman et al., 1989 Lincoff, 1981 McKnight & McKnight Miller, 1972 Phillips, 1981 Sieger, 2003 Smith & Smith Weber, 1980 Thomas & Heerkens, 2003	<i>rachodes</i> <i>olivieri</i> <i>Leucoagaricus americanus</i> <i>rachodes</i> and <i>brunneum</i> <i>rachodes</i> <i>Leucoagaricus americanus</i> <i>olivieri</i> <i>olivieri</i> most likely <i>rachodes</i> <i>olivieri</i>

by secotioid species in genera with normally formed gills and forcibly discharged spores—yes, that is now commonplace. For example, the secotioid *Endoptychum depressum*, *Longula texensis* and *Gyrophragmium dunallii* are all incorporated in *Agaricus* (Vellinga et al., 2003; Geml et al., 2004), while *Lactarius rubriviridis* is a truffle that is closely related to the gilled mushrooms *L. rubrilacteus* and *L. deliciosus* (Desjardin, 2003).

Big changes? Perhaps, but they expand our horizons, and our fascination with mushrooms keeps growing!

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