

THE SPLITTING

of

Hygrocybe

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The genus *Hygrocybe* probably contains more pretty mushrooms than any other. They provide an unrivalled bright, crisp and colourful delight to the eye—hands down, a photographer's favourite, drawing amateur and professional alike with their beauty. To the inquisitive they also provide an interesting subject for investigation, because, as mentioned in a past [OMPHALINA](#) article, how they make their living has not been elucidated.¹ It seems that they are not saprobes (decayers of organic material), as had long been thought, but what type of partnerships they have established, and with whom, remains unclear.

Recently, with the help of many collaborators, I completed a major study of the phylogeny of the Hygrophoraceae.² For many amateur as well as some professional mycologists the greatest changes are in several groups of species previously classified in the genus *Hygrocybe*. All but one of these evolutionary branches had previously been named as separate genera, so most are not new. Genera made by splitting groups from existing genera, leaving some species behind in the original genus, are called segregate genera. We were able to confirm (in many cases, reconfirm) the phylogenetic basis for these groupings, and to define their limits more accurately than has been the case before. Thus, now these groupings have a solid and well-defined basis, and should find widespread acceptance.

In this article I review the changes to the genus *Hygrocybe*, as they apply to its species identified in Newfoundland and Labrador.

Recognition of some of the segregate genera is optional, but recognizing one segregate and not the others in the same branch of the tree is not—you cannot pick and choose. For example, I notice that in the Foray Newfoundland & Labrador cumulative species list, you recognize *Humidicutis* as a good genus, separate from *Hygrocybe*. If you look at the phylogeny in Fig. 2, you will see that *Humidicutis* appears among several other branches assigned to the genera *Neohygrocybe*, *Porpolomopsis*, and *Gliophorus*, and the bold branch supporting this cluster indicates it is highly supported while the genus *Hygrocybe* in the strict sense appears on a separate, strongly supported branch. There is yet another strongly supported branch that is sister to the others corresponding to *Chromosera citrinopallida* and *C. lilacina* on one side, and species assigned to the new genus *Gloioxanthomyces nitida* and *G. vitellina* on the other side.

The sister relationship of *G. nitida* and *G. vitellina* was unraveled by David Boertmann³ in a previous issue of **OMPHALINA** that included DNA sequences of '*Hygrocybe*' *nitida* from Newfoundland. All of the species above the blue line in Fig. 2 can be referred to the genus *Hygrocybe*, as long as you don't recognize *H. marginata* and *H. pura* as belonging to *Humidicutis* rather than *Hygrocybe*. In other words, you can't recognize a genus that is embedded within another genus—that would make it polyphyletic.

My solution, together with most of my collaborators, is to recognize the segregate genera. Recognizing one genus previously segregated from *Hygrocybe*—*Cuphophyllus*—is inescapable. The molecular phylogeny in Fig. 1 shows that what you've recorded in NL as '*Hygrocybe*' *pratensis* and '*H.*' *borealis* belong to the genus *Cuphophyllus*—one of the basal, early diverging genera in the Hygrophoraceae near the backbone of the agaric fungi, while *Hygrocybe* is a later diverging group at the apex of the family. If one wanted to place these two groups in the same genus, the genus name would have to be *Hygrophorus* as it is the oldest name and the basis of the family name, and the genus would contain species that form lichens (e.g., *Lichenomphalia hudsoniana* and



Figure 1. Upper: Voucher photograph of the *Humidicutis pura* collection from Cape St. Mary's in 2006 (photo: Roger Smith). The smallest mushroom is in the herbarium of David Boertmann and a portion of the largest was sent to D.J. Lodge and then to Bryn Dentinger at the Royal Botanic Gardens Kew for sequencing and deposit. The drawing in Figure 3 comes from the latter. Lower: The habitat, where the collection was made (photo: Michael Burzynski). The yellow cross marks the location, which may explain why there is no in situ photo, just a voucher.

L. umbellifera, which are found in NL), species that form ectomycorrhizal symbioses with tree roots (e.g., *Hygrophorus eburneus*, *H. pudorinus* and *H. russula*, all found in NL), species that grow on wood (e.g., *Chrysomphalina chrysophylla*, found in NL) and species with amyloid spores (*Cantharellula umbonata*, which is in NL, and *Pseudoarmillariella ectypoides*). To avoid that unacceptable solution, everyone needs to recognize the genus *Cuphophyllus*.

PHYLOGENETIC GENERA WITHIN THE FORMER *HYGROCYBE*

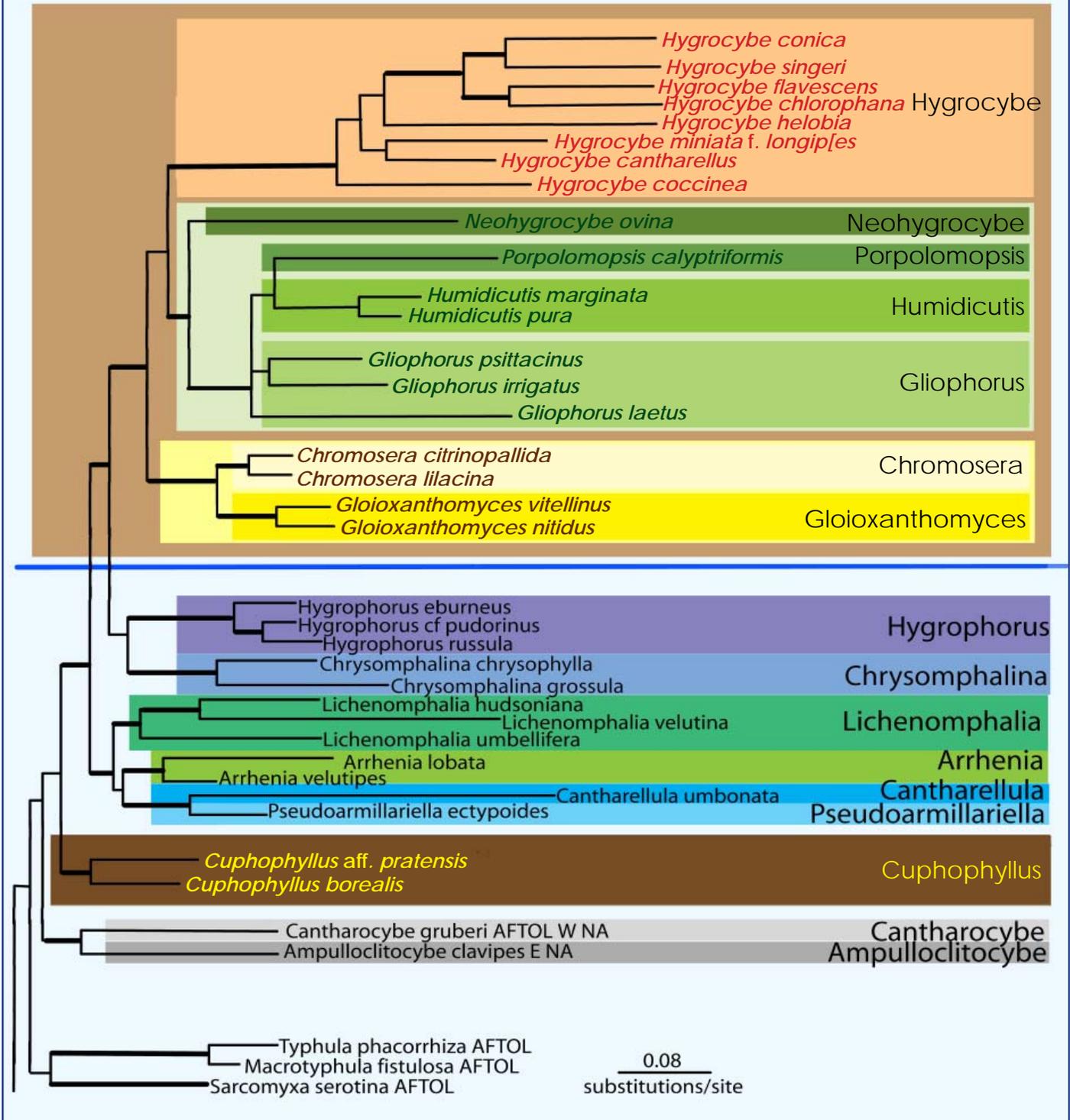
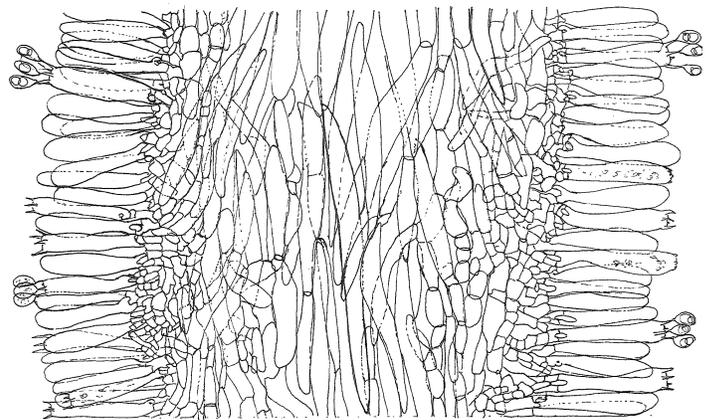


Figure 2. Phylogenetic tree including the genera previously classified in the genus *Hygrocybe* that are found in NL rooted with the coralloid fungi *Typhula phacorhiza* and *Macrotyphula fistulosa*. Note that *Cuphophyllus* is the most basal (diverged from the other agaric fungi earliest), whereas genus *Hygrocybe* diverged relatively late in this phylogenetic tree. The specimen of *Hygrocybe pura* from Cape St. Mary's is shown in its correct position within *Humidicutis*, something we were unable to show at the time of our original publication. Branches that are in bold have at least 70% support.

Hygrocybe The genus with the most species; colourful, red orange or yellow, but may stain black; may be dry or viscid; may be conical, dome shaped or indented; cap often scaly, at least minutely (loupe).	Chromosera Subarctic/subalpine, in heath; small; glutinous; brightly coloured; translucent; hygrophanous; colours fade (lilac to yellow and yellow to white).
<i>Hygrocybe acutoconica</i>	<i>Chromosera citrinopallida</i>
<i>Hygrocybe cantharellus</i>	<i>Chromosera lilacina</i>
<i>Hygrocybe ceracea</i>	Cuphophyllus
<i>Hygrocybe chlorophana</i>	Very broad central umbo or bump; caps often become opaque and chalky as they dry; considerable crossveining of gills, NL species not brightly coloured.
<i>Hygrocybe coccinea</i>	<i>Cuphophyllus borealis</i>
<i>Hygrocybe coccineocrenata</i>	<i>Cuphophyllus cinerellus</i>
<i>Hygrocybe conica</i>	<i>Cuphophyllus colemannianus</i>
<i>Hygrocybe conica</i> var. <i>chloroides</i>	<i>Cuphophyllus lacmus</i>
<i>Hygrocybe conica</i> var. <i>conicopalustris</i>	<i>Cuphophyllus pratensis</i>
<i>Hygrocybe constrictospora</i>	<i>Cuphophyllus radiatus</i>
<i>Hygrocybe flavescens</i>	Gliophorus
<i>Hygrocybe helobia</i>	Very slimy; may have bright colours or somewhat muted; Some coloured green or purple, unusual for mushrooms; colours fade and change over time. Gill edge may be gelatinized; gills often become carrot pink-orange on drying.
<i>Hygrocybe insipida</i>	<i>Gliophorus irrigatus</i>
<i>Hygrocybe miniata</i>	<i>Gliophorus laetus</i>
<i>Hygrocybe miniata</i> var. <i>mollis</i>	<i>Gliophorus psittacinus</i>
<i>Hygrocybe mucronella</i>	Gloioxanthomyces
<i>Hygrocybe phaeococcinea</i>	Gluey, brilliant yellow mushrooms with a thin, dark, slimy gill edge. One species only. Can be distinguished from yellow <i>Gliophorus</i> species by swollen cells, seen microscopically in the gill flesh, and does not develop carrot orange colour on drying.
<i>Hygrocybe punicea</i>	<i>Gloioxanthomyces nitida</i>
<i>Hygrocybe reidii</i>	Humidicutis
<i>Hygrocybe ruber</i>	Acutely conical in youth; cap cracks radially somewhat when expanded; may be brightly colourful, often with pink tint or carrot pinkish-orange in colour, with or without green; moist or viscid.
<i>Hygrocybe singeri</i> var. <i>albifolia</i>	<i>Humidicutis marginata</i>
<i>Hygrocybe</i> sp. nov.	<i>Humidicutis marginata</i> var. <i>olivacea</i>
<i>Hygrocybe splendissima</i>	<i>Humidicutis pura</i>
<i>Hygrocybe squamulosa</i>	
<i>Hygrocybe substrangulata</i> var. <i>rhodophylla</i>	
<i>Hygrocybe turunda</i>	
<i>Hygrocybe turunda</i> var. <i>sphagnophila</i>	

Table 1. Species formerly placed in the genus *Hygrocybe* that are found in Newfoundland and Labrador, assigned to their respective segregate genera, with a brief description of each genus. The “parent” *Hygrocybe* on the left, and the segregate and subsegregate genera on the right.

Figure 3. Drawing of cross section of a gill of the *Humidicutis pura* specimen. The basidia are on the outsides, some with sterigmata (prongs where spores are formed), some with developing spores attached. Note especially the bases of some of the basidia – they look like bow-legged cowboys. This form of clamp connection is typical of *Humidicutis*, *Porpolomopsis* and some species of *Gliophorus*. This sporulating layer is supported by the gill trama (flesh of the gill) in the middle. Characteristically, *Humidicutis* has very short hyphae (elongated cells, making “threads”) in the trama of the gill, as shown here, fitting well with *Humidicutis*, whereas the sister genus, *Porpolomopsis*, has long tapered cells.



Review of the FNL list and that of Andrus Voitk over the past 11 collecting seasons reveals 41 taxa that a decade ago would all be considered species of *Hygrocybe*. According to the findings of our study, these same 41 taxa are now divided among six genera: *Chromosera*, *Cuphophyllus*, *Gliophorus*, *Gloioxanthomyces*, *Humidicutis*, and *Hygrocybe*. Table 1 gives a brief description of each genus and places each identified Newfoundland and Labrador taxon into its currently correct genus.

Our work drew on FNL data in two areas. First, it was very helpful for us to have the relationship between the European *Gloioxanthomyces vitellinus* and the North American *G. nitius* determined, as published in *OMPHALINA* (under the names *Hygrocybe vitellina* and *H. nitida*).³ We also had a white conical *Hygrocybe*, collected from Cape St. Mary's sent for examination. It had been examined by two of us, and both agreed that this was *Hygrocybe pura*. Morphologically, this species is very similar to *Porpolomopsis calyptriformis* (the old *Hygrocybe calyptriformis*), so that in the manuscript we assigned it to the genus *Porpolomopsis*, based on its looks. The sequencing results have since been completed, and analysis shows this specimen instead belongs to the sister genus, *Humidicutis*. Figure 1 shows the specimen and its habitat, and Figure 3 shows the microscopic cross section of its gill, revealing the typical short hyphae described for this species and genus. In addition to these direct contacts with your organization, many of the photographs used

in our manuscript were contributed by Renée Lebeuf, one of your Faculty for several years.

There is no need to be unhappy about learning new names for your beautiful waxcap mushrooms, because your own data contributed to the work that led to these discoveries! Moreover, if you study the genus descriptions and consider the listed species, you will probably discover that you have always noted that some *Hygrocybe* species differed from the majority. The pink tint to the orange *Humidicutis marginata* is a good clue to differentiate it from *Hygrocybe*, and it corresponds to a difference in pigment chemistry. Other segregate genera can be separated by the characters you may have noted in the past: copious gluten and lamellae that dry carrot pinkish-orange in *Gliophorus*, duller colours, or several other characters that make them different from the rest. There is an evolutionary basis for some these different characters, providing you with a great opportunity to check for differences with increased attention, in order to place your finds into their correct genus. I hope that this short explanation has given you an understanding why you will soon find some old friends with new names in your lists.

Acknowledgments

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References

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3. Boertmann D: Update on *Hygrocybe nitida*. *OMPHALINA* 3(1):12-13. 2012.

Illustrations

Title banner: Cuphophyllus lacmus, not a Hygrocybe, even if you do not want to accept the other splits of the genus.

Left: Hygrocybe conica, beautiful and common species of such variability that its many varieties and forms should be reassessed and defined.

