

A Fascination with Waxcaps: In Search of the Scarlet Waxcap

By Peter Russell

*Waxcaps can be as attractive as autumn dahlias,
as redolent of antiquity as oil paintings,
and as magical as a glow-worm's midsummer shining
or a nightingale's song. – David Bangs, 2005*

This is a short tale about my fascination with waxcaps, a search for the elusive scarlet waxcap in the Pioneer Valley, a brief introduction to some easily identifiable species, and an attempt to entice people to start recording them.

Unfortunately, this is not a tale of culinary delights as only a small number are collected for eating. Most are too bland or too watery to be of note. I have heard good reports of the edibility of the meadow waxcap (*Cuphophyllus pratensis*) but seeing as I have only ever found two small specimens in our area, I have never been able to verify that!



The meadow waxcap, *Cuphophyllus pratensis*, reportedly a good edible.

But first let's introduce them: they are a group of white-spored mushrooms whose most obvious visible feature is their thick gills which have a waxy feel like soft candle wax when rubbed between the fingers (the Australians refer to these mushrooms as "waxy gills").

I find this waxy gill test a little difficult and I don't usually try it, as it would destroy a small fragile fruiting body. But to explain how to otherwise identify a waxcap in the field is difficult. One learns what a typical waxcap looks like from experience: the thick gills which

are usually widely spaced, with no ring on the stem or remains of a veil on the cap, and with the stem attached to the center of the cap. But there are many waxcaps that do not fit the norm; for example, *Hygrocybe aphylla* has no gills, but luckily that is a South American species and I can ignore it in this tale!

I usually rely on the fact that that many waxcaps are brightly colored so I am always looking for a flash of color on the woodland floor. That does mean I am often fooled into wading through a sphagnum bog or scrambling down a slippery slope only to discover some other type of fungus, such as those shown below. There are also many drab-colored waxcaps that I normally only see in other peoples' baskets!



The cinnabar chanterelle, *Cantharellus cinnabarinus*, a waxcap look-alike from a distance.

Yellow patches,
Amanita flavoconia,
doing its best to look
like brightly colored
waxcaps.



The orange mycena (*Mycena leaiana*), another waxcap look-alike

Waxcaps belong to the Hygrophoraceae family. This used to contain two main groups: the *Hygrophorus* genus, which are woodland species growing in association with the roots of trees, and the *Hygrocybe*

genus. This article is about the waxcaps in the *Hygrocybe* genus, including those that were recently moved into other genera as a result of DNA studies. These are a bit of an enigma in that we don't really know how they live. They were originally thought to be saprobic (living on decaying organic matter) but as they are difficult to cultivate and contain isotope ratios more similar to those in living plant tissue, it is now thought they have at least some association with living plants (biotrophic).

My fascination with waxcaps began when I lived back in the UK. There waxcaps are found on old unimproved grassland. With modern agricultural methods and urbanization this habitat is becoming increasingly rare, and nowadays is more or less restricted to churchyards, old village greens, or small patches of unimproved grassland. One of the best places, if you also have a historical bent, is around the old Roman forts along Hadrian's Wall! They are not the only fungi that are indicative of old grassland. Fairy clubs (Clavarioid), earth tongues (Geoglossaceae), and pink gills (*Entoloma*) are the other three main groups. The richest grassland sites can be a riot of color in Autumn with dozens of these species fruiting, often in a very small area. I used to spend my Autumns searching for the rarer waxcaps and the richest grassland as part of a larger national survey.



Hygrocybe splendidissima growing on an old cricket pitch in the UK.

When I moved to the USA twelve years ago I quickly discovered things were very different. Although I have since found the odd moss covered lawn with some waxcaps, the main habitat is in woodland growing on soil, humus and well decayed logs or sometimes in bogs or sand dunes. In my experience the richest areas tend to be damp and shaded, along the sides of streams or wet boggy areas, on north facing slopes.

One similarity with the waxcap grasslands of Europe is that I often see waxcaps growing near the same unimproved meadow fungi. So I always pause if I see an earth tongue or a fairy club to see if there is a waxcap hiding nearby!

I have found waxcaps on the East Coast from May through leaf fall. But the season doesn't stop there; in

Europe most fruit in late Autumn and can continue through November depending on the advent of frosts. Then from the beginning of December through March the Californian Redwoods are an excellent place to hunt. I guess this is an all year round obsession!



A springtime waxcap, *Hygrocybe flavescens*, fruiting at the same time as the tulip trees flower.

Having spent so long in the UK, trying to master North American waxcaps is difficult and confusing. Although some species are unique to North America, many others are named after European species but they don't look the same (with a few exceptions). For the ones whose DNA I have sequenced, their DNA barcodes seem sufficiently different DNA to be described as separate species.

How many "*Hygrocybe*" species occur in our area is not an easy question to answer. The last comprehensive treatment of North American waxcaps was L. R. Hesler & A. H. Smith's 1963 monograph. If you exclude the *Hygrophorus* genus, they described about 115 species. But if you search online resources such as Mushroom Expert, the Quebec MycoMontreal, or Omphalina you will find many other species have been added that aren't in this monograph, and many of these have European names.

The big problem is that although there has been a recent reclassification of "*Hygrocybes*," this was concerned with the relationships of genera with each other, and there has been no comprehensive treatment of individual *Hygrocybe* species based on DNA studies. This big problem is what makes studying waxcaps so rewarding. As Michael Kuo of Mushroom Expert puts it: "Answering the question 'What are the North American waxy cap species and how do we tell them apart?' will require many years, many studies, many thorough and well-documented collections." This is what I would encourage readers to help with; especially as I do my own DNA barcoding and am

always looking for samples and collaboration!

Here I am considering only brightly colored waxcaps that are scarlet, red, or orange. I will exclude the other colors like yellow, green, blue, or pink, mainly to make this tale shorter and my job easier. The waxcaps with these three colors are mainly found in the modern *Hygrocybe*, *Gliophorus*, or *Humidicutis* genera. The splitting of the old *Hygrocybe* genus into several separate genera based on DNA studies is interesting but a separate tale! As an aside if anybody has any idea why some waxcaps are so brightly colored I would love to know. I can't find any reference to the adaptive significance of these pigments; nor for that matter why some are so viscid and slippery!

Although daunting, many of the brightly colored waxcaps can be identified reasonably easily in the field. One golden rule: only try to identify fresh specimens as the colors and surfaces often change with age; as they also will if soaked by rain. On that note of caution, here are some descriptions of the scarlet, red, or orange species you are likely to find in the Pioneer Valley.

Honey Waxcap – *Hygrocybe reidii*



This little bright orange beauty is one of my favorites. It is quite variable in shape and can even have a scarlet-colored cap but its widely spaced and almost but not quite decurrent gills and a wavy crenulate cap margin sets it aside from similar species. What makes it distinctive is its smell. If you crush a little between your fingers it has a faint but distinctive sweet smell like honey.

This is probably my most often seen waxcap in our area so it surprises me that I rarely see anybody posting pictures of it. I suspect it is being mistaken for the vermilion waxcap, *Hygrocybe miniata*. I am also

surprised it was not originally described in L. R. Hesler & A. H. Smith's 1963 monograph as it is so common!

Collections in our area look and smell similar to the European version but the DNA I have barcoded indicates they are separate species. Interestingly, one collection I have from the Californian Redwoods has an identical barcode to my UK collections.

Bitter Waxcap – *Hygrocybe mucronella*



There are not many waxcaps you can identify by taste but this small red species is an exception. It has very bitter flesh that can usually be detected just by placing the tip of the tongue on the cap (preferably somebody else's tongue!).

It is a small red to orange species that I have only recorded once on the East Coast, this year. It was on the lawn of an old 1812 property in the Berkshires owned by John Wheeler. On my one visit I found several waxcaps, such as *Hygrocybe conica*, *Gliophorus psittacinus*, and *Hygrocybe minutula* and I am sure there are others that just weren't fruiting when I visited; it was so reminiscent of a moss-rich European waxcap grassland.

Lavender Gilled Waxcap – *Hygrocybe purpureofolia*



This one doesn't have the bright colors like many members of its genus and might be overlooked if you are like me and are only attracted to the bright things on the woodland floor. It has a cap that is dark orange to red when young and fades to orange. But it is easily

recognizable once it is turned over as its gills are a distinctive lavender to purplish color.

This is a relatively uncommon *Hygrocybe*, though I have amassed four collections in the last few seasons!

There is another purple-gilled species that was originally described from Massachusetts so it might be in our area. This is *Hygrocybe metaphitica* that has greyish purple gills, a yellowish brown cap and a mephitic odor (foul smelling).

Goblet Waxcaps – *Hygrocybe cantharellus* & *Hygrocybe coccineocrenata*



Hygrocybe cantharellus is normally distinctive with its strongly decurrent gills, scarlet, red, or orange colors, and a distinctly squamulose cap. Even when the gills are not so decurrent it usually has a thin fragile stem.

It is often found on well rotted logs amongst mosses often with the yellow earth tongue

Microglossum rufum (as in the illustration above). It is also found in bogs. It is one of our most common waxcaps and in drier weather is often the only one you can find.

Another identically shaped but much rarer species is *Hygrocybe coccineocrenata* (below). Its distinguishing



feature is that the cap squamules turn black although this may not be obvious (as in the photo above) although this does get more pronounced on drying. I have only found this once despite soaking my boots in many a bog.

Note that *Hygrocybe appalachiensis* (not shown) can also have subdecurrent gills and fibrillose cap but the striking colors of a red stem, sometimes purplish-red cap, and yellow gill edges set it apart. It may occur in our area.

Vermilion Waxcaps – *Hygrocybe miniata* & *Hygrocybe squamulosa*



Hygrocybe miniata

These two bright red to orange waxcaps are relatively easy to distinguish as a pair but difficult to tell apart. The important character is the surface of the cap, which starts off smooth but quickly develops a finely hairy appearance (fibrillose) and in the case of *H. squamulosa* small but distinctive scales (squamules). Note also the gills are at most only slightly decurrent.



Hygrocybe squamulosa

This fibrillose/squamulose character can be difficult to see in young or wet specimens and other waxcaps such as the goblet or honey waxcaps also don't have smooth caps, but these species can be separated on other characters.

Hygrocybe squamulosa has a larger thicker cap with distinctive squamules. When looking at populations side by side (as in the illustration) the differences can be striking

but when looking at just one specimen it can be difficult to decide. I am interested to see if DNA barcoding shows these to be distinct species rather than just size variation.

Scarlet Waxcap – *Hygrocybe coccinea*



This is the one waxcap I would love to find here and have been searching for a while. Although it is common back in the UK and appears in most of our North American field guides, the only time I see it is when other people post their finds online!

It is a beautiful scarlet red waxcap. The cap is smooth and the gills are fully attached to the stem (adnate) which is an important character to check (as opposed to partly attached or slightly decurrent). Typical specimens that are scarlet all over are easy to identify but there is some variation and in the Californian Redwoods or back in Europe there are separate more orange colored versions called *Hygrocybe marchii*. The illustration is a collection from the Californian Redwoods.

Hygrocybe minitula



This tiny bright red *Hygrocybe* has a very slimy cap and stipe when fresh; so slimy it is difficult to pick up. It does not have decurrent gills and the cap starts as dome shaped but quickly becomes flat. I have collected it in both grassland and in woodland!

Most of the very slimy waxcaps were moved out of *Hygrocybe* and into the *Gliophorus* genus. Many of these have bright colors, green or purple is common, although these can fade and change over time. Some however, like *H. minitula*, remain in the *Hygrocybe* genus.

Hygrocybe glutinipes is a European species that has been reported as occurring in North America. This has a red version, *H. glutinipes* var. *rubra*, that looks almost identical to *H. minitula* though I have never collected it. There are also other small red waxcaps described in L. R. Hesler & A. H. Smith's 1963 monograph like *H. subminiatus*, though this one has decurrent gills. One sometimes also encounters tiny specimens of normally larger waxcaps.

Spangle Waxcap – *Hygrocybe insipida* (*H. subminitula*?)



Hygrocybe insipida is a small red-orange Waxcap that has a wet stem when fresh. It is a European species. I've included it here because this variant bucks the trend of American species being named using European concepts; this type of *H. insipida* was once described based on an American species!

I've have been collecting and barcoding *Hygrocybe insipida* in the UK for the last few seasons and have found 2 distinct groups that look slightly different. The illustration is one variant that has a persistent red color to the stem and a cap that often fades from red to orange/yellow hues. This variant was collected back in the UK in 1943 (obviously by somebody after my own heart: war in Europe -- but still finding time to look for waxcaps!). It had subsequently been identified as an American species *H. subminitula*!

The book I use on European waxcaps is David Boartmann's *The Genus Hygrocybe*. In several cases the author lumps into one species what other authors have split into separate species on the basis of not seeing any big differences between them. That made my waxcap recording much easier but does mean I missed recording some of the diversity. The author had not recognized this *Hygrocybe subminitula* as a separate species. Now DNA barcoding indicates they actually are separate species, although its DNA does not match that of the American *H. subminitula* so it is something different even though it looks the same. I have never knowingly found *H. subminitula* in our area.

Crimson Waxcap – *Hygrocybe punicea*

Hygrocybe punicea is quite distinctive but several characters need to be considered. Usually its large cap and wide stem shouts *H. punicea* but you can find



scaled down miniature versions!

All the previous examples of waxcaps have caps which are curved (convex) but *Hygrocybe punicea*'s cap is shaped like a cone (conical) when young, although it flattens out with age. The gills are narrowly attached to the stem (which alone should

distinguish it from *H. coccinea*). The stipe does not look smooth but has a fibrillose appearance as if made of tiny strands. The cap is a deep blood red when young but does fade, even to yellow (in which case it might be confused with the golden yellow *H. aurantiosplendens*).

This is the waxcap that got me interested in DNA barcoding. When I first saw one at a COMA foray I was stumped; it looked nothing like the crimson waxcap I was used to back in the UK. Indeed their barcodes are different. Note there is a crimson waxcap that grows in the Californian Redwoods which looks a lot more like the European version but I have not collected that yet.

Witches Hat – *Hygrocybe conica*

There are several different *Hygrocybes* that have the distinguishing characteristics of an acutely conical cap that turns black with age. But determining which species they are is more difficult, and most people lump them into *Hygrocybe conica*.

Hygrocybe conica typically has a slightly viscid cap when moist and is variable in color from red to orange and sometimes yellow. *H. atro-*

olivacea has an olive brown cap color rather than the usual orange-red and the dune waxcap, *H. conicoides*, has red to salmon-colored gills and grows on sand dunes.

Hygrocybe conica itself is very variable. One variety is called the blood red witch hat (var. *atrosanguineus*), with a slightly viscid dark strawberry-colored cap and a strongly aromatic smell. DNA studies in the UK have shown *Hygrocybe conica* to be a cryptic species



(composed of several similar looking species that have different DNA).

Hygrocybe acutoconica



The best way to describe *Hygrocybe acutoconica* is it's a witches hat that does not blacken. Its conical cap is slimy and ranges in colour from yellow to orange. It has a paler fibrillose stalk.

Ones with a brilliant red cap are *Hygrocybe cuspidata*, but the red quickly fades to orange as illustrated and they end up looking exactly like *H. acutoconica*.

Golden Orange Waxcap – *Hygrocybe flavescens* & Butter Waxcap – *Hygrocybe ceracea*



Hygrocybe flavescens

This common medium sized *Hygrocybe flavescens* is reasonably easy to identify. It's cap is golden yellow, convex to flattened and viscid, and its stem is dry (if the cap has dried out it is possible to apply the upper lip test. If it sticks to the lip it was very likely viscid).

As the cap is not conical, it should easily be separated from the other species with golden yellow viscid caps (e.g., *Hygrocybe acutoconica*).

Hygrocybe flavescens is quite variable in color and it is not uncommon to find yellow capped collections. A separate species, *Hygrocybe chlorophona*, has a lemon yellow viscid cap but this has a distinctly viscid stalk. I have never found the latter species!

Hygrocybe flavescens has gills that are not fully attached to the stem. The smaller more delicate *Hygrocybe ceracea* (below) has gills that are fully



attached or slightly decurrent. That is the easiest way to differentiate the two species although in truth they have a very different look and feel. *Hygrocybe ceracea* is quite common in the UK but I have only seen it once in our area.

Orange Gilled Waxcap – *Humidicutis marginata* and varieties



Humidicutis marginata var. *marginata* (left) and var. *olivacea* (right)

The *Humidicutis* genus contains waxcaps having caps that are acutely conical when young and which crack radially when expanded, and are often colorful. The caps are moist to viscid. There are two species of *Humidicutis* I have recorded in our area: the all-white *H. pura* and *H. marginata*.

Humidicutis marginata has three varieties that can be found in our area: the very distinctive var. *marginata* that has bright orange gills, var. *concolor* which is all yellow, and var. *olivacea* that has orange gills but a cap with olive brown to deep brown colors in the center.

The *Gliophorus* genus

The members of the *Gliophorus* genus are very slimy. They are often difficult to pick up without them slipping through your fingers. Many have bright colors although these often fade with age. The gills often become carrot pink-orange on drying.



Gliophorus perplexus (above) colors are variable from orange brown to pinkish brown or brownish orange to reddish orange when young.

An unknown *Gliophorus* is also illustrated (below). Its DNA barcode has no close match in Unite (an on-line central repository of fungi DNA sequences).



The above covers most of the red or orange waxcaps you are likely to find in the Pioneer Valley, but there are undoubtedly others. For example there are European species that have been reported as being in America, species such as *Hygrocybe insipida*, *Hygrocybe*

glutinipes, or *Hygrocybe constrictospora*, and these might be present. But I hope you will find these illustrations and descriptions useful. One last note of caution: like many other fungi, waxcaps sometimes don't read the descriptions!

Here's how you can help with the waxcap project

By Peter Russell

I collect waxcap specimens from the U.K. and the East and West Coasts of the U.S. and barcode their DNA. I am interested in any sites readers could recommend that are rich in waxcaps (and might be prepared to show me next season!). I am also interested in sightings of any waxcap.

Hygrocybe coccinea (the scarlet waxcap) is one species I am particularly interested in as I have not found it here in the Pioneer Valley, but anything in the *Hygrocybe*, *Neohygrocybe*, *Gliophorus*, and *Cuphophyllus* genera are extremely welcome. If anybody is interested in making collections or showing me some great collecting sites, please contact me at pjrthe1st@yahoo.com.