



*Southern Hemisphere*



# *Cyttaria*: Most Bizarre Mushroom of the Southern Hemisphere

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Photos courtesy of Giuliana Furci

The strange ascomycete *Cyttaria* species are obligate biotrophs of trees in the genus *Nothofagus* (known as “Southern beech” but not closely related to Northern Hemisphere beech; Southern beech are relatives to witch hazel). *Cyttaria* species are restricted to the Southern Hemisphere, inhabiting southern South America (Argentina and Chile) and southeastern Australasia (southeastern Australia including Tasmania, and New Zealand). The relationship of this fungus with its host remains unclear; if truly parasitic, it’s only weakly so—maybe it’s beneficial in some way.

*Cyttaria* species are members of the inoperculate discomycetes; the genus is

comprised of 11 species. Also unclear is the phylogenetic relationship of *Cyttaria* to its closest fungal relatives, which, along with its unusual compound fruit bodies, specialized habit, and *lack of cell wall chitin* (having instead  $\beta$ -1-3-glucan) (Oliva et al., 1986), further obscure its phylogenetic affinities. The strange-looking fungus, with an even stranger growth habit, has long been a mystery to science but recently a number of studies have shed light on the taxonomy and phylogeography of this fungus and its host. But I think I’m getting ahead of myself. Such a noteworthy group of fungi as this need a proper introduction!

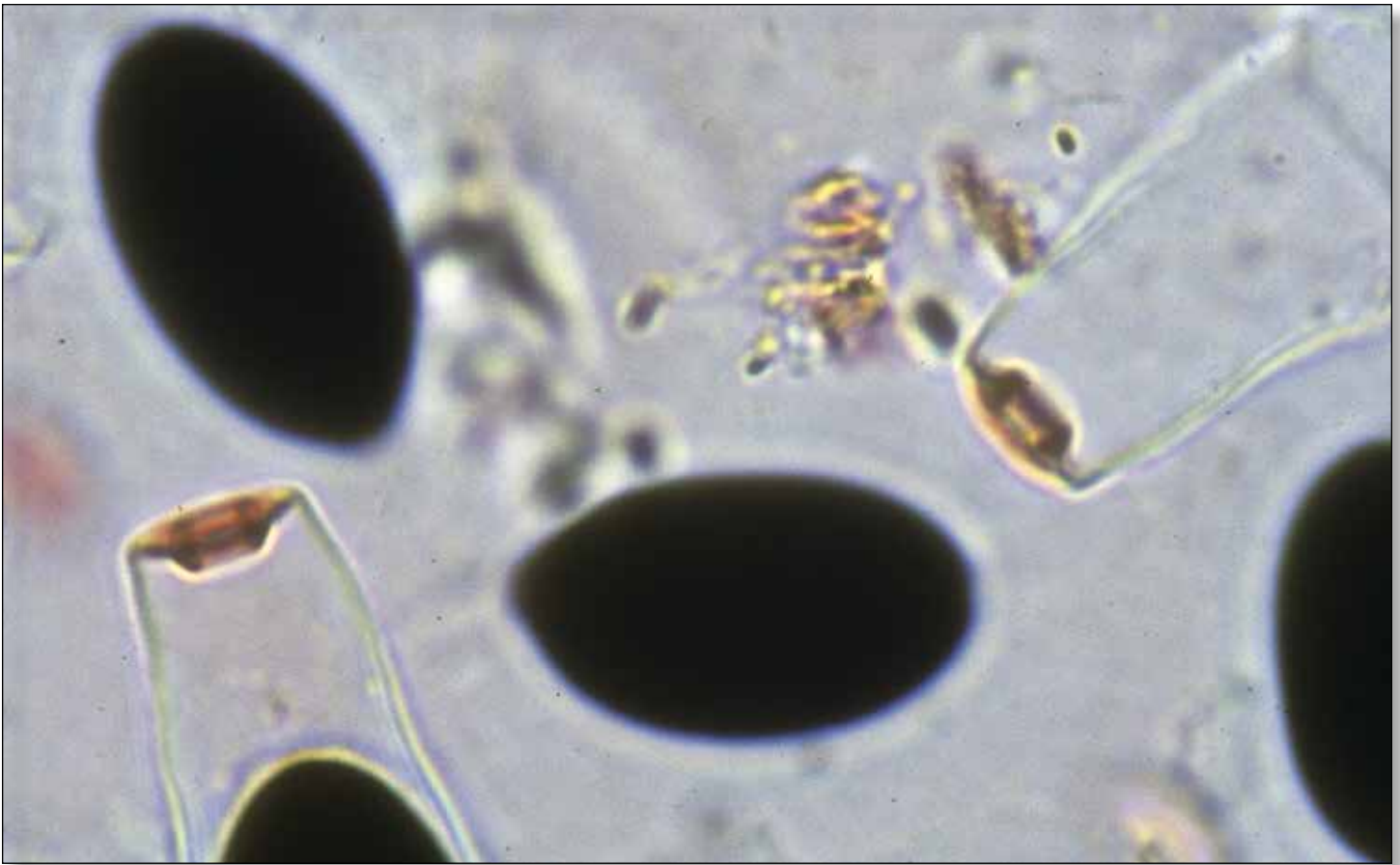
It was Charles Darwin who first brought this peculiar fungus to the mycological world’s attention. He chronicled (1839) and collected fruitbodies from large cankers on Southern beech trees during a stop at the southern tip of South America (Tierra del Fuego), during his voyage on the *Beagle* (for a review, see Schaechter, 2010). Darwin sent his collections to the esteemed mycologist Reverend Miles Berkeley who described the new genus *Cyttaria* (1842). Field notes about the ascocarp fruitbodies noted that the indigenous people there collected them as food.

That’s right, those brightly colored fruitbodies are similar to those of morels. Both are apothecia, a sort of cup-shaped ascocarp, with sterile ridges separating the fertile areas. Harvard researchers Kristin R. Peterson and Donald H. Pfister in 2010 published a phylogeny of *Cyttaria* based on a combination of morphological data and DNA sequence analysis. They found evidence for a close relationship between the *Cyttariales* and members of the order *Helotiales* which includes the green stain fungus *Chlorociboria*, as well as *Leotia*, *Ascocoryne*, *Bisporella*, and *Bulgaria* (Wang et al., 2006a; 2006b). Furthermore, three major clades were identified within *Cyttaria*: one in South America hosted by subgenus *Nothofagus*, another in South America hosted by subgenera *Nothofagus* and *Lophozonia*, and a third in South America and Australasia hosted by subgenus *Lophozonia*, thus producing a non-monophyletic clade of South American species and a monophyletic clade of Australasian species, including monophyletic Australian and New Zealand groups. Expanding their investigation to the only hosts of *Cyttaria*









spp. (*Nothofagus* spp.), the researchers found cophylogeny (Peterson et al., 2010b). In other words, the evolutionary trees of the fungus and host tree overlap a great deal. (Some discrepancies are explained by host-jumping, extinctions, and speciation that also has occurred over time.) Thus, as Southern beech migrated around the Southern Hemisphere, the trees took their fungal passengers with them.

What is known about the association between *Cyttaria* species and Southern beech? First off, not all species of *Nothofagus* seem to be associated with the

fungi. Also, the association (parasitism, commensal, mutualistic) has not been clearly determined; it is possible the fungus benefits the tree in some unknown way (Gamundí and Lederkremer, 1989). The symbiosis is readily noticed; infection by the fungus results in visible trunk and branch cankers. A typical mature fruitbody of *Cyttaria* species consists of what may appear to be an orange to very pale, pitted ascoma, somewhat similar to a morel or a deeply dimpled golf ball (though Darwin, Berkeley, and contemporaries would have never

described them that way—golf balls did not get dimples until the 1900s!). Each fruitbody is actually composed of sterile fungal tissue, or stroma, in which apothecia are embedded. According to Peterson et al. (2010) the seemingly otherworldly-looking stromata “typically have a fleshy-gelatinous consistency, but those of some species are gummy or slimy. As the stromata develop, apothecia form beneath a membrane that envelops the fruitbody. At maturity this membranous ectostroma peels away to reveal, depending on the species and the

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## FROM HUMBLE BEGINNINGS TO

# King of Beers

The beginning of agriculture and the domestication of plants and animals are among the most decisive events in human history because they triggered the rise of civilizations and the attendant demographic, technological, and cultural developments. The domestication of barley in the Fertile Crescent led to the emergence of the forebear of modern beer in Sumeria 6,000 years ago. Beer and other alcoholic beverages may have played a pivotal role in cementing human societies through the social act and rituals of drinking and by providing a source of nutrition, medicine, and uncontaminated water. In Europe, brewing gradually evolved during the Middle Ages to produce ale-type beer, a process conducted by *Saccharomyces cerevisiae* ("brewer's yeast"), the same species involved in producing wine and leavened bread. Lager-brewing arose in 15th century Bavaria, gained broad acceptance by the late 19th century, and has since become the most popular technique for producing alcoholic beverages, with over 250 billion dollars of global sales. Unlike most ales and wines, lagers require slow, low temperature fermentations that are carried out by cryotolerant *Saccharomyces pastorianus* (formerly called *S. carlsbergensis*).

stroma, 1–200 apothecia, each lined with asci." Spore print is dark gray to black. As is the case with some other ascomycetes (*Xylaria* comes to mind), prior to sexual spore production, the stromata of some *Cyttaria* species can produce asexual conidia, termed haploid mitospores (Minter et al., 1987).

A close examination of the asci reveal them to be 8-spored and inoperculate "with *Bulgaria inquinans*-type ascus apices" (Mengoni, 1986) that stain blue in iodine. Ascomycete asci are either operculate or inoperculate. Most Pezizales have operculate asci; the spores are released through a lid-like structure, the operculum, at the tip of the ascus. In contrast, inoperculate asci have no lid, instead these fungi have a pore at the ascus tip and the mature spore squeezes out through that pore. The photo of *Sordaria superba* shows the tips of two inoperculate asci made visible with Congo red stain.

And what of the edibility of this fungus? Elio Schaechter, The Authority on all things microbial, recounted in FUNGI (2014) that Darwin noted the natives of Tierra del Fuego, the Yaganes, ate these mushrooms "although, oddly, they bypassed fresh specimens in favor of older, wizened ones. Some years ago, I came up with a possible explanation. Uniquely among mushrooms, *Cyttaria* have a concentration of fermentable sugars ... could it be that [the Yanage] favored the older specimens undergoing fermentation? These people were surprisingly hardy; they were very scantily dressed, yet living under very harsh climatic conditions. I posited that a little alcohol from fermented *Cyttarias* may have gone a long way towards good cheer." Support of this notion comes from the modern-day people who live in this region and call the fruitbodies that fall from Southern beech *llao-llao*. Besides consuming them outright, the fruitbodies are collected and fermented into a beverage called *chicha de llao-llao*.

But wait there's more. Could *chicha de llao-llao* be the "mother of all beers?" Maybe. Here's why. The wild source of lager yeast has long been sought, and it may have just been found growing on *Cyttaria* fruitbodies (see sidebar). Did I just blow your mind? Firstly, it is important to point out that ale yeasts come from the environment where modern beers were invented: Europe.

And work best at ambient temperatures. Lager yeasts are strange creatures as they work best under cold conditions and, it's been reasoned, must come from cold climates. It was recently shown that *Cyttaria hariatoti* harbors the yeast *Saccharomyces eubayanus* which may be source of cold tolerance in the lager yeast, *S. pastorianus* (= *S. carlsbergensis*) (Libkind et al., 2011). How it found its way to Europe and wound up in a beer tun is still unclear but there have been centuries of trade between South America and Europe, so it's not the most far-fetched facet to this story of the most bizarre mushroom of the Southern Hemisphere.

Strangely, *S. pastorianus* has never been isolated from the wild and depends entirely on humans for its propagation. Weird, huh? I know. So ... how did it arise? Glad you asked. Pour yourself a cold one, get comfy, and I'll tell you. In a paper just published in the journal *Proceedings of the National Academy of Science* a multinational team of researchers led by Diego Libkind and Chris Todd Hittinger have found that, during a global inventory of wild yeasts, *S. pastorianus* was created through the hybridization of a *S. cerevisiae* ale yeast with another, previously unknown cryotolerant (cold tolerant—remember that lager beers are "cold-brewed") *Saccharomyces* species.

In nature, many different yeasts are found in the sap flows that exude from wounds and cracks commonly seen on trees. *Saccharomyces* spp. are associated with oak trees (Fagaceae) in the Northern Hemisphere. Because species of the genus *Nothofagus* (Southern beeches, also members of the Fagales) occupy the oak niche in the colder temperate regions of the Southern Hemisphere, the research team reasoned this may be a good place to look for undiscovered wild lager yeasts. They focused on woodlands containing populations of *Nothofagus antarctica*, *Nothofagus dombeyi*, and *Nothofagus pumilio*, as well as the sugary fruitbodies of *Cyttaria* associated with the trees. In their report, the team documents the isolation of that mystery yeast species and designate it *Saccharomyces eubayanus* because of its resemblance to *S. bayanus* (a complex hybrid of *S. eubayanus*, *S. uvarum*, and *S. cerevisiae* found only in the brewing

environment). Populations of the newly discovered *S. eubayanus* exist in the chilly *Nothofagus* (Southern beech) forests in Patagonia (way down at the southern tip of South America—I know, not the first place you think of when thinking of beer). Still, identifying the wild genetic stock of the cryotolerant yeast *S. pastorianus* is necessary for resolving the taxonomy and systematics of this important species complex, and for understanding the key events that led to the domestication of lager yeast. In contrast to extensive investigation into domestication of crops and livestock, studies of domestication of eukaryotic microbes have been all but nonexistent.

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## Wild Mushrooms

for Casey and Alla

My Polish neighbors invite me to go hunting for wild mushrooms on the slopes of Mt. Evans, though they don't say exactly where. I can't go that day, but I imagine them:

the Sunday drive, the leisurely climb the search beneath conifer duff, maybe not far from Echo Lake. Something they always did in the home country, they say. And now that this is home, they're learning all the places to keep it so. Wild mushroom soup's a delicacy this time of year. In it I can taste the soil, the stone, in each spoonful.

And Alla never spares the cream. These are not the pale fungi neatly boxed and ready at King Soopers (though I don't scorn those).

But here, there, in the baskets, picked by hand a little of the wild consumed. Enough to keep the taste of home in the mouth.

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