Mushrooms:
Endless Variations in Size and Shape

Hans Halbwachs

What are fungal characteristics good for? Well, for identifying fungi, of course! Field mycologists all over the world are living encyclopedias when it comes to fungal traits. Even the most subtle differences in spore size or cap coloration have their place in identifying mushrooms and other fungi. Quite many mycologists are intrigued by the endless variations, for instance of fruit bodies (Fig. 1).

Moreover, the variability of spore traits is bewildering (as was discussed by Else Vellinga in the previous issue of FUNGI). Size, ornamentation, and pigmentation occur in all combinations (Fig. 2). These are the visible characteristics which may be grouped in (1) morphological (shape, size) and (2) physiological (pigments, taste, smell, toxicity, etc.). A third, more mysterious trait, is the phenology of fruit bodies. Some do it in spring, some even in winter. It has been speculated that this may be a strategy to avoid predators (Halbwachs et al., 2016), though this would imply investment, e.g., into antifreeze substances and producing relatively small fruit bodies, as in *Flammulina velutipes* or *Hygrophorus hypothejus*. Generally, species fruiting in late autumn seem to have larger fruit bodies, at least in *Cortinarius* (Halbwachs, 2018).

Figure 1. Examples of basidiomycete fruit body shapes and colors. From left to right top: *Amanita flavoconia* (courtesy J. Veitch), *Lactarius indigo* (courtesy A. Rockefeller), *Butyriboletus frostii* (courtesy D. Molter); bottom: *Calostoma cinnabarinum* (courtesy D. Molter), *Tricholomopsis decora* (courtesy W. Sturgeon), *Mycena adonis* (courtesy D. Molter). creativecommons.org/licenses/by-sa/3.0/deed.en.

Knockin' on Evolution's Door

Although some ideas are circulating about the functionality of fungal traits, mycologists want to know more about their ecological implications. Why are Porcini so much fatter than some of their cousins? Why is one Brittle Gill bright red and hot as hell, while another tastes mild and has a greenish cap? Do ornamented spores show a higher drag than smooth ones, and are therefore carried farther away by wind? Similar questions have been asked for many years by ecologists for plants (Shipley et al., 2016), be it seed size, flower color, or essential oil contents.

In mycology, trait-based ecology has been put on the screen only during recent years (Aguilar-Trigueros et al., 2015; Pringle et al., 2015). To date, only a few hard facts are available. In some cases, statistical methods are used to trace possible correlations between reproductive traits and resource availability, for instance (Bässler et al., 2016; Halbwachs et al., 2017). Sometimes a new angle of view can come up with rather simple but seminal conclusions. We once looked into the relationship between spore size and spore volume per mm^2 of the hymenium. Intuitively one would assume that it does not matter whether you have many small spores or fewer thick ones. But see for yourself (Fig. 3). This finding suggests that large-spored mushrooms represent a trade-off between relatively few spores and increased survival, while small-spored species have a short lifespan but a high dispersal rate.

Depending on biotic or abiotic circumstances, one or the other strategy may be successful, regarding reproduction and dispersal. You may sense that I remain vague about the specificities of "circumstances." Frankly, I can only speculate. So that's what we did in some recent papers (Halbwachs and Bässler, 2015; Halbwachs et al., 2016). Only that such speculations—particularly when largely plausible—may trigger further research.

Mission Impossible

Fungi are notoriously difficult creatures when it comes to coaxing information out of them about the meaning of their characteristics. Experimental approaches would be ideal, but meet methodological obstacles, especially when considering fungus-animal interaction. Take for example the "warning colors" (aposematism) of the Fly Agaric. Does this mushroom really "inform" fungivores about its toxicity? Then, why is the closely related Destroying Angel boringly whitish? How do many insects cope with fungal toxins, as those in the Fly Agaric (Tuno et al.,

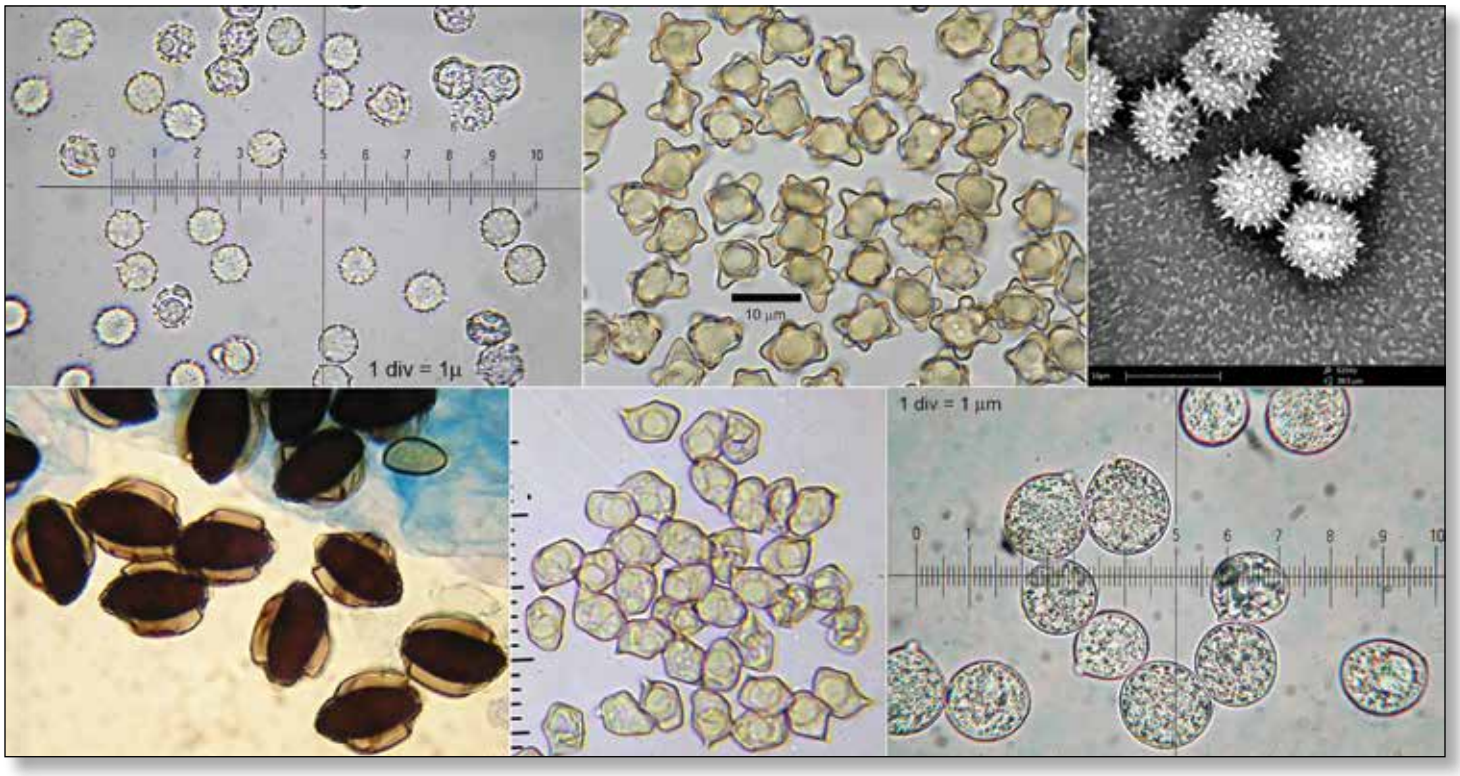

Figure 2. Various basidiospores. From left to right top: *Lactarius volemus* (courtesy A. Trnkoczy), *Inocybe straminipes* (courtesy L. Kudzma), *Laccaria amethystina* (courtesy Annabel); bottom: *Coprinopsis semitalis* (courtesy A. Gminder), *Entocybe haastii* (courtesy M. Inski), *Mucidula mucida* (courtesy A. Trnkoczy). creativecommons.org/licenses/by-sa/3.0/deed.en.

2009; for a review, see Bunyard, 2017)?

We may here come across a phenomenon which has been adopted by ecologists from Lewis Carroll's *Through the Looking-Glass*, the Red Queen who had to keep running to stay in the same place. Fungi continuously change their chemical defenses to hold the pace of predator adaption (Kempken and Rohlfs, 2010). Guevara and Dirzo (1999) concluded that coloration of fruit bodies is probably unrelated to fungivory.

One thing is clear: pigments come at a cost to fungi (Halbwachs et al., 2016), which does not really answer the question about aposematism. Plant ecologists struggle to find explanations, too. Lev-Yadun (2016), a botanist at the University of Haifa, conceded in his book about defensive coloration in land plants: "It is … a manifesto representing my current understanding on defensive plant coloration … The book is not the final word in anything, but rather the beginning of many things."

Let us come back to fungal aposematism: Weird though, artificially-colored button mushrooms could bring us a step further by exposing them to fungus gnats under controlled conditions. In the latter "detail" you find the proverbial devil because you need to control growth conditions, genetic uniformity of prey and predator, pigment composition and spectral characteristics as well as reliability of infestation measurement, to name a few. To make things even more complicated, confounding factors like the effects of fungal volatile compounds need to be taken into consideration. No wonder that relevant but painstaking studies are rare, DNA-sequencing technology is nowadays a more easy-going springboard for research-hungry scientists. Other traits, such as hymenial architecture, are less demanding to interpret. Still, hard-core studies about the ecological implications of morphological characteristics are hard to find.

The Meaningless Search for Meaning

It is, of course, good for the inquisitive mind to seek explanations of natural phenomena or attributes of organisms. In the wake of Darwin's theory of evolution not only scientists thought that each and every peculiarity must bear a biological sense. However, evolution is a tinkerer, sometimes a lousy one. Jacob (1977) stated an example: "We need not marvel at the sting of the bee causing the bee's own death." I have an inkling that this is also the case with some fungal traits. Think of cap umbos as in *Psilocybe makarorae* or constricted spores as in *Hygrocybe quieta*. So, the quest of the Holy Grail of trait functions is treacherous and may lead us sometimes into dead end streets. In the vein of Clint Eastwood's "Dirty Harry" in *Magnum Force* let us stick to the wisdom "a mycologist must know his limitations."

Reality Bites

Finally, allow me a flashback to the significance of fungal traits for identification. Most of us have encountered discrepancies between descriptions of the same species in different fungi. Fruit body and spore sizes, coloration, smells, etc. may significantly differ. Moreover, it sometimes happens when trying to identify a mushroom that all traits fit a description, except that the spores are somewhat larger. I recently analyzed fruit body and spore sizes of a few larger basidiomycetes that occur worldwide by comparing data from 16 fungi.

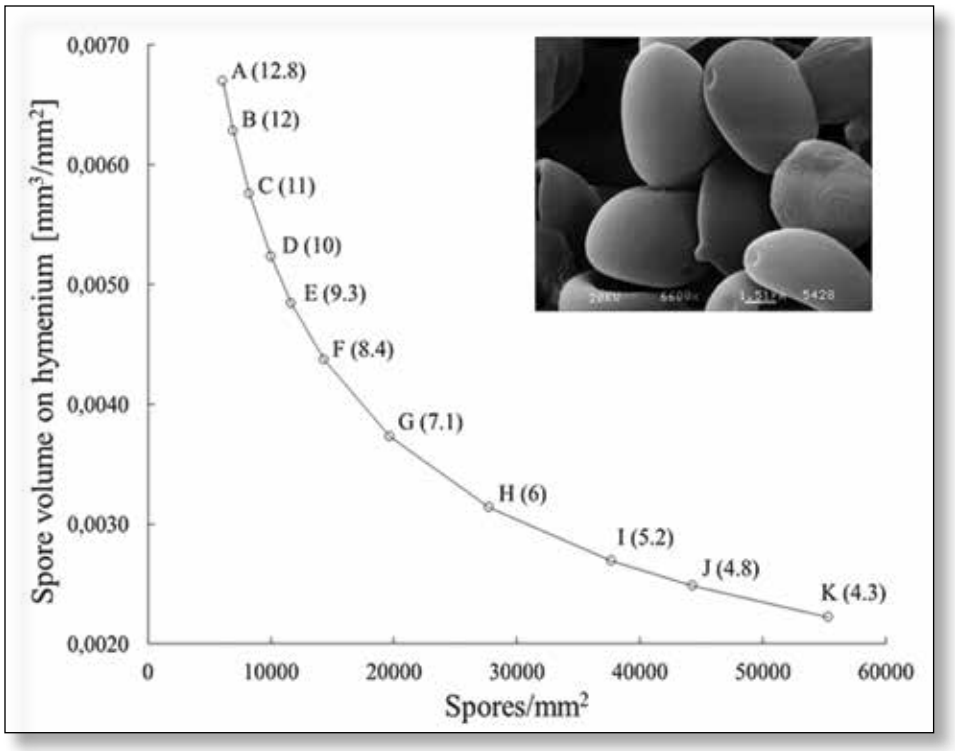

Figure 3. Correlation between spore size and spore volume per hymenial surface unit (Halbwachs et al., 2018). Agaricales show a cubic function between spore diameter (µm in brackets) and spore volume. A. *Laccaria tortilis*. B. *Amanita submembranacea*. C. *Entoloma saundersii*. D. *Fayodia bisphaerigera*. E. *Mycena clavularis*. F. *Coprinopsis spilospora*. G. *Lactarius picinus*. H. *Hydropus floccipes*. I. *Lyophyllum paelochroum*. J. *Camarophyllopsis micacea*. K. *Clitocybe globispora* (Species names according to IndexFungorum.org). The insert shows *Psilocybe* spores, densely packed on the hymenium. creativecommons.org/licenses/by-sa/3.0/deed.en.

Measures differed on average by 16%, the most extreme variations were in *Schizophyllum commune* (Fig. 4).

Closing the Gaps

Dear reader, finally I would like to point to the fact that this text is peppered with questions. The meaning is quite clear: we frequently encounter gaps in our knowledge about the function of fungal traits. Amateurs and professional mycologists need to face this fact and contribute to answering such questions by closely and rigorously recording observations in the field that reach beyond fungal identification. In my view, extra interest should be directed to fungus-animal interactions, because they shed some special light on the functioning of ecosystems.

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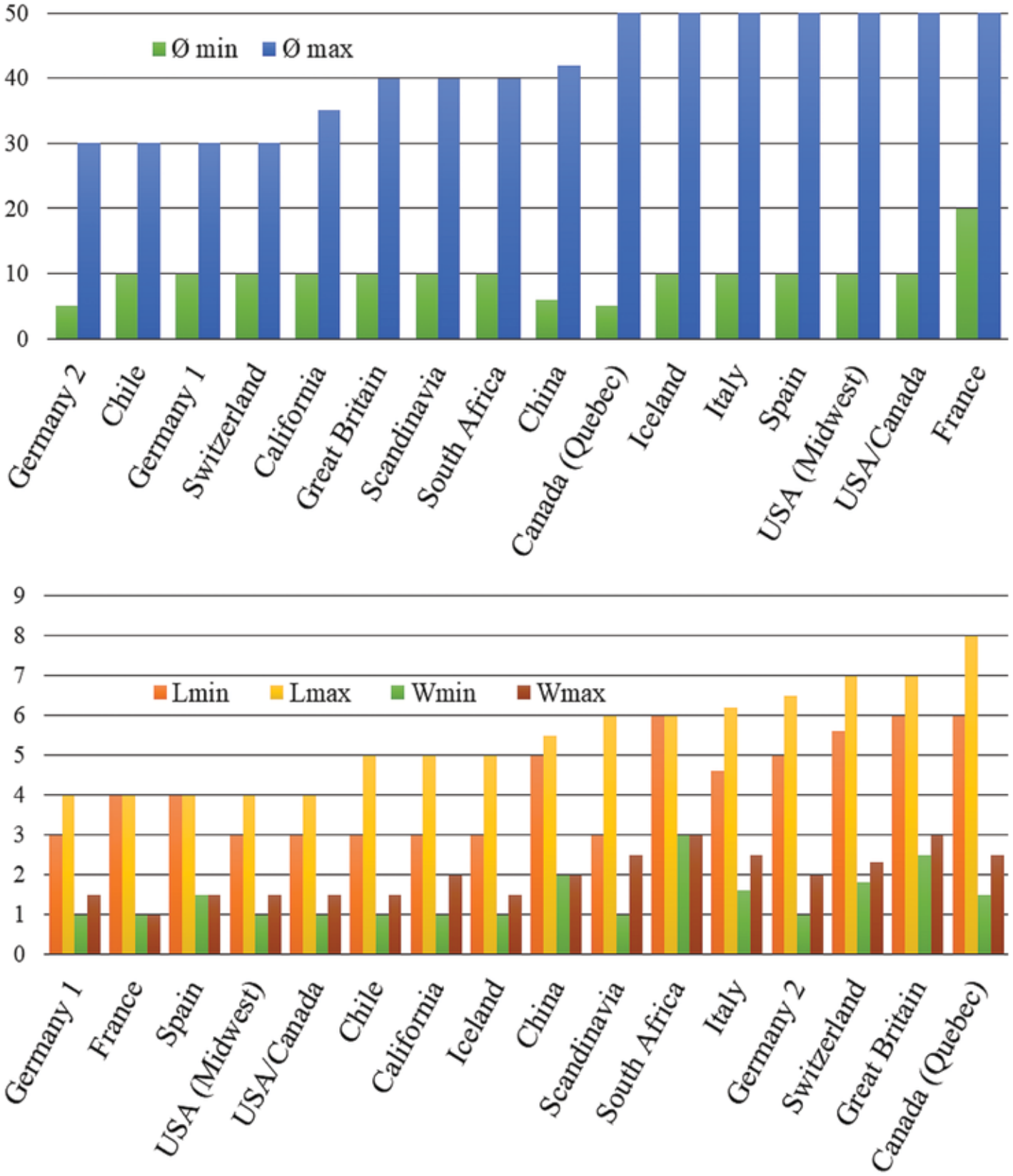

Figure 4. The columns represent smallest and largest cap diameters (mm) (top graph) and spore sizes (L – length, W – width, µm) (bottom graph) of *Schizophyllum commune* in the geographical areas examined (x-axis). Measurements varied on average almost by 30%.

Variations like in *S. commune* signal that even the keenest mycologist needs to keep a critical distance to his own and foreign measurements. To identify a mushroom or to describe a new species, all traits must be taken into account. If in the slightest doubt, DNA barcoding should be considered which – nowadays – is within the financial reach of amateurs. creativecommons.org/licenses/by-sa/3.0/deed.en.

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Hans Halbwachs is a Research Scientist with the Bavarian Forest National Park, and affiliated with both the German Mycological Society and Bavarian Mycological Society.

Strobilomyces

He belongs on that damp forest floor
where I first found him, dark
like the earth itself.
Camouflaged among the leaf litter,
I could have crushed his bearded skull
with one serendipitous boot heel.

A scent remains of the sacred
that comes with the ancient,
the smell of secrets burned and left to the rains.

No way to know if time
has eviscerated all value
without slicing straight through him
from cap to ground
and watching his blood turn black.

If I were only a chef,
with my flashing knife
I'd know how to deal with that old man
of the woods.

J. W. Narkevic