Published in final edited form as:

Fungal Biol. 2010 January ; 114(1): 57–63. doi:10.1016/j.mycres.2009.10.006.

Why mushrooms form gills: efficiency of the lamellate morphology

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Abstract

Gilled mushrooms are produced by multiple orders within the Agaricomycetes. Some species form a single array of unbranched radial gills beneath their caps, many others produce multiple files of lamellulae between the primary gills, and branched gills are also common. In this largely theoretical study we modeled the effects of different gill arrangements on the total surface area for spore production. Relative to spore production over a flat surface, gills achieve a maximum 20-fold increase in surface area. The branching of gills produces the same increase in surface area as the formation of freestanding lamellulae (short gills). The addition of lamellulae between every second gill would offer a slightly greater increase in surface area in comparison to the addition of lamellulae between every pair of opposing gills, but this morphology does not appear in nature. Analysis of photographs of mushrooms demonstrates an excellent match between natural gill arrangements and configurations predicted by our model.

Keywords

Agaricomycetes; ballistospore; Basidiomycota; basidiospore; convergence; hymenium

Introduction

The agaricoid basidiome, with its spore-producing hymenium organized on the surface of lamellae (or gills), is the predominant type of fruit-body within the Agaricales and Russulales. Basidiomata with similar morphology are also featured within species of Boletales, Polyporales, Gloeophyllales, and Hymenochaetales, and fruit-bodies with gill-like folds occur in the Cantharellales (Hibbett 2007). The patchy distribution of lamellate basidiomata across the phylogeny of the mushroom-forming Agaricomycetes, coupled with the diversity of gill anatomy and development in these species (Moore 1998; Webster and Weber 2008), suggests that this morphology has developed from multiple, independent origins during the evolution of the fungi.

Convergence upon this form is driven, presumably, by the fact that the formation of lamellae greatly increases the surface area for spore production beneath a single mushroom cap. In one of his classic experiments, Buller (1909) removed gills from a variety of mushroom

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species by painstaking dissection and measured their surface area. He found that relative to a flat surface, the formation of gills increased the hymenium surface by a factor of 7.0 (lowest) in *Russula citrina* (Russulales) and 20.0 (highest) in *Agaricus campestris* (Agaricales).

Buller (1909 1922) also recognized the importance of gill spacing for successful release of spores. Spores are propelled horizontally from the gill surface by a mechanism called the surface tension catapult (Turner and Webster 1991). This mechanism was not understood in Buller's time, but was solved by John Webster and colleagues in the 1990s (Money 1998). The horizontal portion of the flight path is halted by air viscosity within one millisecond of the launch and the spores then continue to fall vertically between the gills for a few seconds before reaching the airflow swirling underneath the cap (Fig. 1). The range of the discharge process is critical: spores that are not shot sufficiently far will descend onto the lower surface of the gill from which they originate, and spores shot too far will hit the opposing gill. There must be, therefore, some fine-tuning of the discharge process to match range to taxon-specific variations in gill spacing (Ingold 1992). This postulate has been verified by recent analysis of spore discharge using ultra-high-speed video microscopy: mushroom spores are propelled over distances ranging from 0.1 to 0.6 mm (Stolze-Rybczynski et al. 2009). The efficiency of this system for spore release is evidenced by the astonishing output of spores from lamellate fruit-bodies. Under ideal environmental conditions, a single basidiome of *Agaricus campestris* can release 31,000 spores per second, or 2.7 billion spores per day (Buller 1922).

There is considerable variation in the arrangement of gills among mushroom-forming Agaricomycetes. In some species, the hymenium forms on a single series of unbranched gills that radiate from the central stipe (Fig. 2A). Minimal gill separation occurs at the gill origin next to the stipe. For the reasons detailed above, this distance cannot be smaller than the range of the spore discharge mechanism without incurring spore wastage. Buller (1909) referred to the "margin of safety" in gill separation, beneath which, the increase in surface area for spore production would be offset by spore loss, particularly when the basidiome becomes tilted. The distance between the gills increases toward the periphery of the cap. If the cap radius is sufficiently large, gill separation will be sufficient for the insertion of a second array of partial gills, or lamellulae, between the primary lamellae without spore wastage. This configuration is observed in many mushroom species and additional sets of small tertiary and quaternary gills are also formed in larger fruit-bodies, making use of the gaps produced between the lamellulae (Fig. 2B). An alternative morphology, in which spaces at the pileus periphery are filled by bifurcation of the gills, is also quite common (Fig. 2C). In this paper, we report our analysis of the effects of different gill arrangements upon hymenium surface area, and compare theoretical predictions with morphometric data from photographs of fruit-bodies.

Methods

General considerations

In our models of gill arrangement, lamellae and lamellulae were treated as parallel-sided rather than wedge-shaped leaflets. Wedge-shaped gills are characteristic of the majority of gilled mushrooms, but calculations based on parallel-sided gills were simpler and did not affect the analysis of the *relative* efficiency of various gill arrangements. For the same reason, gills were modeled as rectangular, unless stated otherwise, and it was assumed that spores were produced only on the gill surfaces and not on the interlamellar arches. The following values for gill sizes were used for all of the modeling in this study: gill depth, $d = 1\text{ cm}$; gill thickness, $t = 0.5\text{ mm}$; and minimum gill separation, $s = 0.5\text{ mm}$. These values

were chosen in order to reproduce gill area:cap area ratios consistent with the range of values determined experimentally by Buller (1909).

Modeling gill arrangement

(1) Parallel (Venetian blind) or spiral gills—A flat surface beneath a cap offers the minimum hymenium surface area (πr^2). The increase in surface area achieved by the addition of gills depends upon the depth (height) of the gills, gill thickness, and minimum gill separation. The greatest possible increase in surface area would be obtained by completely filling the available area beneath the pileus with non-radial gills arranged like an open Venetian blind, or by forming a single gill as a spiral that wound from the stipe to the outer edge of the pileus. There would be no wasted space with either morphology assuming that the distance between the gill surfaces was set at a constant minimum value to avoid spore impaction following discharge. Neither arrangement is seen in nature, but these models are useful for the analyses because they establish a theoretical maximum, or benchmark, against which the effects of other gill arrangements can be assessed. An area, A , covered with gills of depth d , gill thickness t , spaced a distance s , apart would produce a total gill area of

$$2A \frac{d}{t+s}$$

Thus, the ratio of gill area:cap area is

$$\frac{2d}{t+s}$$

Eq. 1

(2) Single array of radial gills—For gills arranged radially from a central stipe, the initial number of gills is determined by the circumference of the stipe. The maximum number of gills that would fit around the stipe while maintaining the optimal minimum gill separation is given by

$$\text{Number of gills} = N_0 = \frac{\text{Circumference of stipe}}{\text{Gill thickness} + \text{Gill spacing}} = \frac{2\pi r_s}{t+s}$$

where r_s is the stipe radius. For a cap with radius, r , the surface area of the gills will then be

$$\text{Area of gills} = 2N_0 d (r - r_s)$$

while the area of the underlying cap is given by

$$\text{Area of cap} = \pi(r^2 - r_s^2)$$

The ratio of these areas, then, is

$$\frac{\text{Area of gills}}{\text{Area of cap}} = \frac{2N_0d(r-r_s)}{\pi(r^2-r_s^2)} = 2 \frac{2d}{t+s} \times \frac{\frac{r}{r_s} - 1}{\left(\frac{r}{r_s}\right)^2 - 1}$$

Eq. 2

(3) Addition of lamellulae: doubling model—As gills that are spaced optimally at the stipe radiate outward, wasted space appears between them (Fig 3A). One way to reduce this wastage is to insert lamellulae between each of the primary gills once the space is sufficiently large to allow insertion without incurring spore loss (Fig 3B). Doubling of gill number can occur first at a radius where the cap circumference is twice the circumference at the stipe, or at $r = 2r_s$. After the addition of a first set of lamellulae (or secondary gills), the ratio of gill area:cap area is

$$\begin{aligned} \frac{\text{Area of gills}}{\text{Area of cap}} &= \frac{N_0d(2r_s-r_s)+2N_0d(r-2r_s)}{\pi(r^2-r_s^2)} \\ &= 2 \frac{2d}{t+s} \times \left(\frac{\frac{2r}{r_s} - 3}{\left(\frac{r}{r_s}\right)^2 - 1} \right) \end{aligned}$$

Eq. 3

As the cap radius increases, additional space again appears between each of the gills until the point at which the circumference has grown by a factor of 4, 8, 16, etc., i.e., when $r = 4r_s, 8r_s, 16r_s$, etc. At each of these radii, there is room for an additional set of lamellulae, doubling the number of gills with each insertion (Fig 3C). The expression for the ratio of gill area:cap area for a cap of arbitrary radius, r , becomes quite complicated:

$$\frac{\text{Area of gills}}{\text{Area of cap}} = \left(\frac{2d}{t+s} \right) \frac{\sum_{j=1}^{\text{Floor}\left[\log_2 \frac{r}{r_s}\right]} \left[2^{2j-1} \right] + 2^{\text{Floor}\left[\log_2 \frac{r}{r_s}\right]+1} \left(\frac{r}{r_s} - 2^{\text{Floor}\left[\log_2 \frac{r}{r_s}\right]} \right)}{\left(\frac{r}{r_s} \right)^2 - 1}$$

Eq. 4

This model is shown graphically as the solid curve in Fig. 4. (Note: $\text{Floor}[x]$ represents the greatest integer less than x .)

(4) Addition of lamellulae: alternating model—As an alternative to inserting lamellulae between every pair of primary gills, lamellulae could be produced between every second gill (Fig 3D). This would occur when a pair of adjacent gills occupies enough space for three gills without causing spore wastage. This occurs sooner than the doubling of space required above: new lamellulae can develop at $\frac{3}{2}r_s, \frac{9}{4}r_s, \frac{27}{8}r_s, \dots$ versus $2r_s, 4r_s, 8r_s, \dots$ in model (3) above. In this case, the model yields slightly higher ratios of gill area:cap area. The ratio is given by

$$\frac{\text{Area of gills}}{\text{Area of cap}} = \left(\frac{2d}{t+s} \right) \frac{\sum_{i=1}^{\text{Floor}\left[\text{Log}_{\frac{3}{2}} \frac{r}{r_s}\right]} \left[\left(\frac{3}{2} \right)^{2(i-1)} \right] + \left(2 \left(\frac{3}{2} \right)^{\text{Floor}\left[\text{Log}_{\frac{3}{2}} \frac{r}{r_s}\right]} \right) \left(\frac{r}{r_s} - \left(\frac{3}{2} \right)^{\text{Floor}\left[\text{Log}_{\frac{3}{2}} \frac{r}{r_s}\right]} \right)}{\left(\frac{r}{r_s} \right)^2 - 1} \quad \text{Eq.}$$

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(5) Alteration of gill shape—The treatment of gills as rectangular leaves with parallel sides in the preceding models represents a significant simplification of the structures produced in nature. It allows, however, unambiguous comparisons between the relative effects of different gill arrangements. To begin to explore the effects of different gill shapes, the same analyses were also performed on gills with an adnate morphology (i.e., attached to the stipe; see Fig 6 inset). This shape was chosen arbitrarily from the range of gill shapes found in mushrooms. It allowed us to study the general effects of changing gill shape on gill area:cap area ratio in our models; other gill shapes (e.g., decurrent) would obviously have different specific effects upon gill surface area.

Analysis of basidiome photographs

Images of the underside of mushroom caps from 39 species in 19 genera were examined in Phillips (1991). Measurements were made by superimposing concentric rings of defined radius printed on transparent acetate sheets on the images. The choice of species for analysis was based on the presence of clear images of radially symmetric caps, with centrally placed stipes, and unobscured, unbranched gills. Measurements were not made from fruit-bodies with branched gills, because it was often difficult to discriminate between branching and the addition of free-standing lamellulae in the published photographs. Measurements were scaled by the supplied photographic scale factors (1/2 life-size, 1/3 life-size, etc.) then normalized by the respective stipe radii.

Results and Discussion

Effects of different models for gill arrangement

(1) Parallel (Venetian blind) or spiral gills—As described above, the greatest possible increase in surface area relative to an unconvoluted hymenium is obtained with an artificial (unnatural) Venetian blind gill configuration, or with a single spiral gill. Substituting the chosen parameters for gill depth, thickness, and distance into Eq. 1, these models produce a theoretical maximum gill surface area that is 20-fold larger than the underlying (flat) cap area. In this, and the other models for gill arrangement, substitution of thinner gills and/or reducing spacing between gills boosts the surface area gain, but it is hypothesized that these parameters are limited in nature by the spore loss produced by crowding.

(2) Single array of radial gills—The simplest radial gill arrangement a single set of gills radiating from the stipe to the edge of the cap (Figs 2A, 3A). Because the area of these gills increases linearly with increasing cap radius while the area of the cap itself increases quadratically, the ratio of gill area:cap area falls with increasing cap radius. This is shown as the dashed curve in Fig 4.

(3) Addition of lamellulae: doubling model—Gill spacing, which is optimal at the stipe, becomes inefficient at larger radii. When the space between gills grows large enough,

additional lamellulae can be produced without impinging on the minimum gill spacing required to avoid spore wastage. In the doubling model, lamellulae form when there is enough space between each existing pair of opposing gills. This doubling of the number of gills dramatically improves the gill area:cap area ratio over the case with no lamellulae (solid curve of Fig 4). The addition of each successive set of lamellulae increases the ratio. The ratio does not increase indefinitely with cap radius because the area beneath the cap still grows in proportion to r^2 whereas the area of this expanded set of gills only grows linearly. Averaging over all cap sizes, measured in units of stipe radii, the doubling model produces an average gill ratio:cap ratio of 15 using the chosen parameters, which is 75% of the theoretical maximum.

(4) Addition of lamellulae: alternating model—The alternating model offers a slight increase in surface area relative to the doubling model (Fig 3D). Because new gills are added when two gills take up the space available for three gills, the first addition of lamellulae occurs at a smaller radius than in the doubling model, i.e., at $\frac{3}{2}r_s$ rather than at $2r_s$. This improvement can be seen in Fig 5B. Averaging over all cap radii yields an average gill area:cap area ratio of 17, or 85% of the theoretical maximum.

(5) Alteration of gill shape—Any gill shape other than the “ideal” rectangular shape reduces area per gill and will limit the gill area:cap area ratio. The absence of rectangular gills in nature is a constraint imposed by the curved surfaces underneath mushroom caps that develop during the expansion of spheroidal primordia (Moore 1998). To begin to explore the effects of natural gill shapes, we ran our models using an adnate gill shape. As expected, the ratio of gill area:cap area decreased in both models (Fig 6) relative to the rectangular cases (Fig 5). In the doubling model, the average ratio fell from 15 to 11 (55% of the theoretical maximum). In the alternating model, the average ratio dropped from 17 to 12 (60% of the theoretical maximum). It is interesting that the increase in surface area obtained by this structure continues to exceed the performance of the doubling model for the adnate gill shape. This difference between arrangements is likely to apply to other natural gill shapes.

In his 1909 study of gill arrangement, Buller measured a maximum 20-fold increase in surface area in *Agaricus campestris*. This species produces several tiers of free lamellulae according to the doubling model. The measured surface area was higher than that predicted in our doubling model because the *Agaricus* gills are thinner and more closely-packed than the arrangement chosen for our model. The average 15-fold increase in surface area calculated with the model is close to Buller's measurement from *Clitocybe saeva* (Agaricales), the field blewit.

Analysis of basidiome photographs

Measurements of the position of the first two sets of lamellulae from photographs of the lower surface of mushroom caps showed an excellent agreement with their predicted placement according to the doubling model (Table 1). The first set of lamellulae appear at a mean distance of 1.1 radii from the circumference of the stipe, or 2.1 radii from the center of the stipe, approximating the 2.0-radii predicted by the model. Secondary lamellulae develop at a mean 3.8 radii from the center of the stipe, agreeing with the predicted 4.0 radii. Tertiary lamellulae form at 6.5 radii versus the predicted 8.0 radii. The reason for this difference is not understood. It is interesting that mean cap radius for the species that formed very short tertiary lamellulae was equal to 7.4-times the stipe radius, which is, theoretically, too small to allow for their formation without infringing upon the margin of error for limiting spore loss. In terms of optimizing dispersal, the release of spores from this additional array of tiny lamellulae may exceed the concomitant wastage due to impaction on the gills at the edge of the cap. Relationships between fruit-body morphology and spore production are further

complicated by variations in the numbers of spores discharged per unit area of hymenium surface.

Conclusions and future studies

The increase in hymenium surface area according to the doubling and alternating models are achieved either by the addition of free-standing lamellulae or branching of existing primary gills (with the alternating model producing a slightly greater increase in area). Gill doubling by bifurcation of primary gills and by insertion of free-standing lamellulae is widespread among the Agaricomycetes, but the alternating arrangement of gills is not seen in nature. Its absence may reflect developmental mechanisms that operate in all (or many) of the gilled Agaricomycetes that situate lamellulae wherever sufficient space develops between existing pairs of gills (or gill primordia; Moore 1998). This morphogenetic “rule” would prohibit an alternating arrangement. It is less surprising that the Venetian blind morphology and the single spiral gill are not seen in mushrooms, because neither arrangement is consistent with the radial symmetry of the fruit-body cap.

The formation of fertile slats, or tangential cross-bridges, between adjacent gills is a naturally- occurring mechanism that increases the spore-producing surface. This structure is found in a number of taxa, including *Lentinus tigrinus* (Polyporales), and has been viewed as a transitional form between lamellate and poroid basidiomata (Ingold 1971; Hibbett 2007). Calculations show that poroid configurations of the hymenium produce larger increases in surface area, relative to the gill arrangements considered in the present study. For example, a poroid cap with 1.0 cm long $\times$ 0.5 mm diameter tubes, separated from one another by 0.5 mm, has an 18-fold larger hymenium area relative to a flat surface, and narrower tubes (0.2 mm diameter with 0.2 mm spacing) increase the ratio to 45 (data not shown). The poroid morphology, and other basidome types, will be considered in detail in a separate study.

A recent study by Kauserud et al. (2008) suggested that polypore species with large fruit-bodies tend to produce larger spores, which may reflect differences in life histories between these parasitic and saprobic fungi. It would be interesting to explore these morphometric associations further by considering the mechanics of spore discharge. Recent high-speed video analysis suggests that the size and shape of basidiospores affects discharge distance (Stolze-Rybczynski et al. 2009). This link between morphology and mechanics is important, because differences in discharge distance must be congruent with tube radii and distances between gills.

Acknowledgments

This research was supported by grants from the National Science Foundation (0743074) and the National Institutes of Health Health/NIEHS (1R15 ES016425, ARRA Supplement). The authors thank Diana Davis for insightful discussions, and Roger Phillips and Michael Kuo for sharing their photographs of fruit-bodies.

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Fig 1. Spore flight paths in *Bolbitius vitellinus* (Agaricales) from Buller (1924). In this illustration, the pileus of the mushroom has been sliced vertically along a chord to show its gills (primary gills and lamellulae) in transverse section.

Fig 2.

Different arrangements of gills. (A), Single array of gills in *Marasmius rotula* (Agaricales). (B), Primary, secondary, tertiary, and quaternary gills (lamellae and lamellulae) in *Lactarius subplinthogalus* (Russulales). (C), Forked gills in *Cantharellus cibarius* (Cantharellales). Photographs courtesy of Michael Kuo (www.mushroomexpert.com).

Fig 2 Different arrangements of gills. (A), Single array of gills in *Marasmius siccus* (Agaricales). (B), Primary, secondary, tertiary, and quaternary gills (lamellae and lamellulae) in *Lactarius subplinthogalus* (Russulales). (C), Forked gills in *Lactarius hygrophoroides* (Russulales). Photographs courtesy of Michael Kuo (www.mushroomexpert.com).

Fig 3. Schematic representation of radial lamellate morphology. (A), Single set of primary gills; gills are separated at the stipe to allow horizontal spore discharge with minimal spore loss and spread farther apart toward the circumference of the cap. (B), The addition of secondary gills, or lamellulae, makes use of the additional space between the primary gills. (C), Tertiary gills appear in the spaces that develops between the secondary gills. (D), alternating model with bifurcation of gills.

Fig 4.

Ratio of the area of the gill surfaces to the area of the underlying cap surface as a function of cap radius (expressed in units of stipe-radii). Dashed curve shows the ratio of gill area:cap area in the case of a single set of primary gills (illustrated in Figs 2A and 3A). The solid curve shows the ratio of gill area:cap area with the insertion of secondary (Fig. 3B), tertiary (Fig 3C), and quaternary gills (Fig 2B). In all cases, gill depth, thickness, and spacing were assumed to be 1 cm, 0.5 mm, and 0.5 mm, respectively, and gills were modeled as rectangular and parallel-sided. Furthermore, it was assumed that spores were produced only on the gill surfaces and not on the interlamellar arches.

Fig 5.

Comparison of different models for gill arrangement. Ratio of gill area:cap area as a function of cap radius (measured in units of stipe radii) for (A) theoretical optimal arrangement of parallel or Venetian blind gills, or of a single spiral gill; (B) alternating model in which lamellulae are inserted between every other gill, and (C) doubling model in which lamellulae are inserted between every existing gill. Gill depth, thickness, and spacing as stated in Fig 4 legend.

Fig 6. Effects of natural gill shape on models of gill arrangement. Gill shape used for this model is illustrated in the inset. Plots show ratio of gill area:cap area as a function of cap radius (measured in units of stipe radii) for (A) alternating model in which lamellulae are added between every other gill, and (B) doubling model in which lamellulae are inserted between every existing gill. Gill thickness and spacing as stated in Fig 4 legend.

Table 1

Analysis of gill arrangements in 39 species of Agaricomycetes. Data show position of lamellulae normalized to the radius of the stipe in each species and are given in units of stipe-radii. Cap radius (last column) also normalized to stipe dimensions. Predicted radii for gill insertion based on the doubling model (see text).

Species	Primary lamellulae	Secondary lamellulae	Tertiary lamellulae	Cap
<i>Agaricus andrewii</i>	2.0	3.0	--	3.5
<i>Cortinarius anomalous</i>	2.0	4.0	6.0	7.0
<i>Cortinarius armillatus</i>	2.0	3.5	--	4.2
<i>Cortinarius collinitus</i>	1.9	3.1	--	4.0
<i>Cortinarius trivialis</i>	2.0	3.5	5.0	6.0
<i>Cortinarius volvatus</i>	2.0	3.0	--	3.5
<i>Entoloma alboubonatum</i>	2.0	4.0	5.0	6.0
<i>Hygrophorus bakerensis</i>	2.0	2.9	--	3.7
<i>Hygrophorus lawrencei</i>	2.0	3.3	--	5.0
<i>Hygrophorus reai</i>	2.5	6.5	--	7.0
<i>Hypholoma elongatipes</i>	2.0	4.0	6.0	6.5
<i>Laccaria amethysto-occidentalis</i>	2.0	--	--	2.9
<i>Laccaria nobilis</i>	2.9	6.5	8.8	9.4
<i>Lactarius caespitosus</i>	2.0	4.0	--	4.4
<i>Lactarius corrugis</i>	2.0	3.1	4.0	4.3
<i>Lactarius hygrophoroides</i>	2.0	2.3	--	2.5
<i>Lactarius luculentus</i> var. <i>laetus</i>	2.3	4.0	--	5.0
<i>Lactarius peckii</i>	1.9	3.1	--	3.5
<i>Lactarius pseudomucidus</i>	2.0	3.0	--	3.6
<i>Lepista nuda</i>	2.5	3.8	--	5.0
<i>Lyophyllum montanum</i>	2.4	4.0	6.0	7.2
<i>Mycena haematopus</i>	1.7	3.0	--	3.3
<i>Phaeocollybia christinae</i>	2.0	5.3	--	6.7
<i>Phaeolepiota aurea</i>	1.7	2.3	--	3.0
<i>Pholiota limonella</i>	2.0	3.6	--	4.2
<i>Psilocybe atrobunnea</i>	2.0	6.0	12.0	14.0
<i>Psilocybe squamosa</i> var. <i>thrausta</i>	2.1	4.6	5.7	6.7
<i>Russula earlei</i>	2.7	4.3	--	5.0
<i>Russula frarantissima</i>	--	--	--	2.6
<i>Russula polyphylla</i>	2.5	--	--	2.8
<i>Russula pulchra</i>	2.0	--	--	3.0
<i>Stropharia hornemannii</i>	2.3	4.3	--	4.7
<i>Tricholoma columbetta</i>	2.0	4.0	--	4.5
<i>Tricholoma flavissima</i>	2.0	3.3	--	4.7
<i>Tricholoma flavovirens</i>	2.0	--	--	2.9

Species	Primary lamellulae	Secondary lamellulae	Tertiary lamellulae	Cap
<i>Tricholoma fulvum</i>	--	--	--	1.7
<i>Tricholomopsis decora</i>	2.0	3.7	--	5.1
<i>Xerula furfuracea</i>	2.0	4.0	6.3	6.8
<i>Xerula megalospora</i>	2.0	3.5	--	4.0
Mean values ^a	2.1	3.8	6.5	4.9/7.4
Predicted position of insertion	2	4	8	

^a Mean radius for all caps was 4.9 stipe radii. Mean radius for caps with at least tertiary lamellulae was 7.4 stipe radii. This was smaller than the radius at which we predicted the appearance of tertiary gills, namely, at 8 stipe radii.