

Studies in the basidium

Spore-spacing and the *Boletus* spore

by

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A geometrical analysis of the 4-spored homobasidium is made on the assumption that spore-spacing is determined by sterigmatic spacing on the basidium-apex. Given, then, the values of spore-width and the interval between adjacent spores of the tetrad, other details of the basidium-unit can be worked out except the lengths of the spores, sterigmata and basidium. The relations between the parts are summarised as equations; their values in ratios of spore-width are tabulated in an appendix. Observations on *Mycena illuminans* with subglobose spores are given as a check on the theory.

The smooth *Boletus*-spore is shown to be the unornamented endospore of a subglobose spore with endosporic ornamentation that has suffered compression and reduced spacing through the adaxial displacement of the sterigmata. The spores of *Strobilomyces* and *Phylloboletellus* appear as the more primitive.

The use of this theory is shown by analysis of the cruciform spores of *Marasmius nigricans*.

During the tumultuous years 1942–1945, when Dr Kwan Koriba maintained the scientific status of the Singapore Botanic Gardens, I was permitted to work with him in the upstairs laboratory of the office. We studied trees, their seasons and their reproduction, and I was allowed a more personal investigation, which had long intrigued me, into the construction of the basidiomycete hymenium. Some of this work has been published (Corner 1947, 1948). It has shown that the lengths and widths of basidia, spores and cystidia are bound by specific constants which have generic trends. The dimensions of these parts are usually given independently in taxonomic descriptions, but they are related in consequence of the characteristic of the hypha that produces them. The relations can be displayed as sporographs, basidiographs and so on, as explained in those papers, but their interconnection lies in the dependence of spore-width on that of the basidium. This is the matter that I now take up, and it becomes the problem of spore-spacing on the basidium.

With many detailed observations for such genera as *Amanita*, *Lepiota*, *Hygrophorus*, *Marasmius*, *Russula*, *Entoloma*, *Agaricus* and *Coprinus*, I had intended an extensive survey but the long hours necessary for such a work have never recurred. I take it up for the special case of *Boletus* because in the course of my account of the rich *Boletus*-flora of Malaysia (Corner 1972) the problem has loomed continually and is fundamental to the classification of the species by means of their distinctive spores. My thesis is the geometrical analysis of the position of the spores on the basidium. It is not an explanation of their arrangement by physical means but a guide to understanding how the spore grows to its full size and shape and, indeed, how it may develop its superficial structure. I have set forth this analysis in the simplest terms, step by step, so that it may be followed by mycologists who, like myself, may have lost touch with advanced mathematics.

Most basidiomycetes have four spores on the basidium. There have been several accounts of the development of individual spores (Corner 1948, 1968; Malençon 1958; Perreau-Bertrand 1967). I propose to consider the tetrad as a unit. The four spores are regularly spaced. Their arrangement can be affected by adjacent basidia. The spacing is affected by the contour of the hymenium. Spore-shape results from the way in which spore-volume is contained in this spacing. A prime factor is the width of the basidium. Yet the tetrad of one basidium does not contact that of another; the spores of a tetrad are not in contact; they are separated from the basidium by sterigmata; maturing basidia are separated from each other by immature. To secure this spacing there must be action at a distance. The force appears to be electrostatic repulsion at free surfaces; the whole mechanism collapses when wetted. To prove this, I had intended to grow basidia in an induced electric field, but this has not materialised. I hope, however, that this article will open a new line of enquiry from which some real understanding of the precision of the hymenium will come and better appreciation of the basidiocarp which houses it. The toadstool is essentially an umbrella opened geotropically.

Method

The sporing basidium is a delicate turgid structure that readily shrinks in contact with a fixative. As my object was to make fine measurements of spore-size and the intervals between spores on the basidium, it was necessary to examine undistorted living basidia under high enough magnification to make reasonably large camera lucida drawings. I first used dry mounts of thin strips of hymenium for surface-view and moderately thick sections for side-view, and observed them with an oil-immersion lens. Condensation on the coverslip, however, in the high humidity of Singapore brought failure and I had to resort to aqueous mounts. Thus I learnt that sooner or later, after ten minutes with some species or an hour or two with others, the apex of the wetted basidium collapsed and the sterigmata inclined, even jumped, inwards; to be effective the basidium had to be superficially dry. By dint of perseverance I managed to obtain for subsequent analysis many accurate camera lucida drawings of a great variety of agarics, boleti, polypores, stereums and clavarias. The present article merely summarises these results because names are not available for most of the fungi, and the labour is great; about a thousand measurements are needed for accuracy in any one species.

The two aspects of the basidium, end-view and side-view, need to be combined. From this a geometry of the basidium emerges to relate the shape of the basidium-apex via the sterigmata with the spore-spacing and, thus, with spore-shape. As the spores are borne at the same level above the basidium (though there are exceptions), one can obtain in end-view an optical section of the tetrad. Focussing down, one can see the basidium-outline in its optical section at maximum width and, on then focussing slightly upwards, even the tips of the sterigmata. However, it is easier to see these tips on discharged basidia before they have collapsed. The four spores, as seen in end-view, occupy the corners of a square and one can imagine them to be confined by two spore-circles, an outer circumscribing circle S' (Figure 3) and an inner inscribing circle S''' , to which may be added a third spore-circle S'' passing through the centres of the spores. Then there is the real basidium-circle as the outline of the basidium, which I call w , and for the sterigmata one

can imagine a sterigmatic circle M passing through the tips of the sterigmata. The circles are concentred on the long axis of the basidium. S' exceeds the basidium circle which can often be seen to lie within S'' ; the M circle lies slightly outside or abaxial from S''' . These real and imaginary circles, derived from end-view of the basidium-unit, can be projected on to the basidium apex, as in Figure 3.

Since a basidium cannot be examined both in end-view and side-view, an average must be taken from a set of measures for each. In end-view basidia are often seen to be compressed and ellipsoid in optical section. Such can be avoided but they cannot be recognised in side-view, for which the average is necessary. The figures in the following pages are based on such averages from sets of twenty to one hundred drawings.

Following the system adopted in my previous papers, I continue with this notation: —

n is the spore-number per basidium.

D is spore-length.

d is spore-width; $d \text{ rad}$, when measured in side-view, and $d \text{ tan}$, when measured tangentially or at right angles to $d \text{ rad}$.

E is the ratio D/d .

l is the length of the basidium.

w is the maximum width of the basidium.

M is the diameter of the sterigmatic circle.

m is the diameter of the sterigmatic patch circle.

S' is the diameter of the outer spore-circle.

S'' is the diameter of the middle spore-circle.

S''' is the diameter of the inner spore-circle.

(S') , (S'') , (S''') and (m) refer to the inner spore or endospore when needed to be distinguished.

σ is the ratio of spore-interval to d .

θ is the spore-angle.

δ is the angle subtended by the half-spore on the spore-circle.

α is the angle subtended by the sterigmatic patch at the centre of the curved apex of the basidium.

Evidence of spore-spacing

The following considerations supply the evidence that the spores of a tetrad are regularly spaced.

Elongate spores. A tetrad of elongate spores in end-view appears as four circles equidistant round the basidium-apex (Figure 1; Buller 1924, fig. 84-86, 91; Corner 1964 p. 234). The long axes of the spores are parallel with that of the basidium; the spores face this axis and are not inclined. This is the main evidence for supposing the imaginary circles S' and S''' and the lateral spacing factor ' σ '.

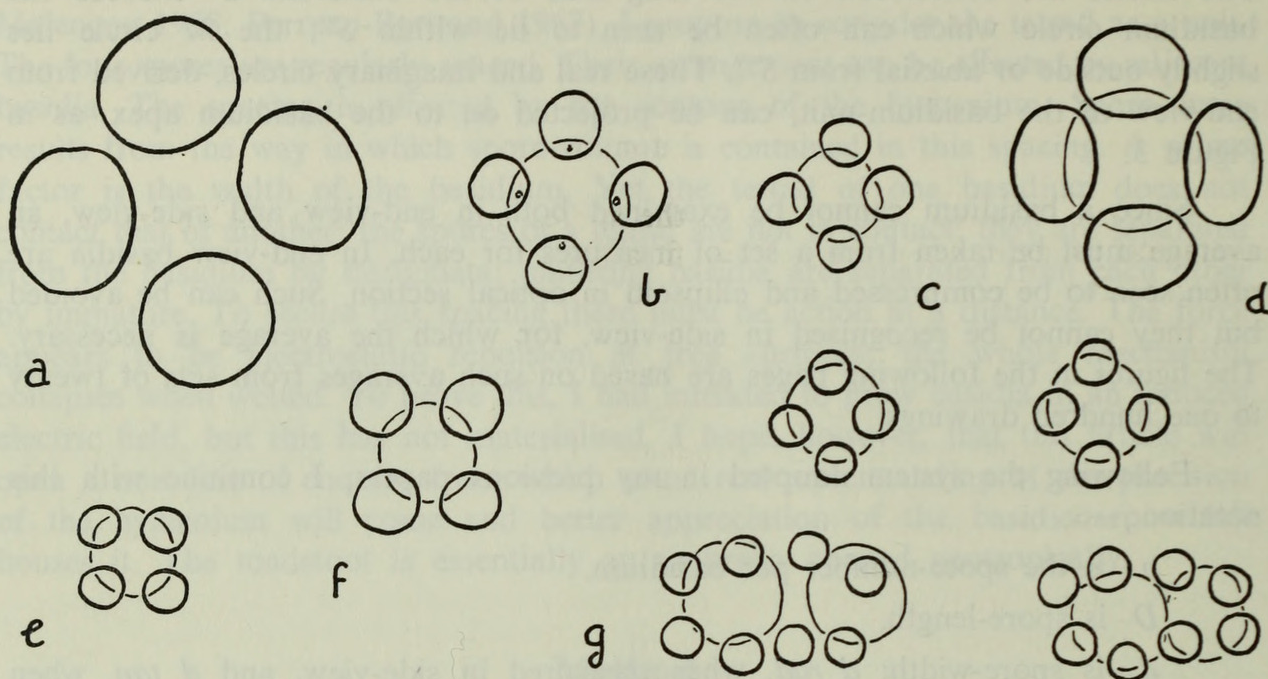


Figure 1. Spore-tetrads in end-view, x 800 (a. x 500); a, *Oudemansiella*; b, f, *Amanita*; c, *Pluteus*; d, *Panaeolus*; e, *Psathyra*; g, *Boletus ravenelii*, with two normal basidia and two pairs of approximated basidia having their eight spores set in an ellipse.

Interfering tetrads. Usually a basidium develops its tetrad freely at some distance from other sporing basidia. New basidia are intercalated and take the place of those that have discharged their spores and become ineffective. Occasionally two basidia mature so close together that their tetrads are distorted and, as seen in end-view, their eight spores are combined into one imaginary ellipse (Figure 1). This re-arrangement shows that sporing basidia act as spacing units and influence their neighbours. Where two S' circles approach or would intersect the adjacent spores of each tetrad are repulsed outwards. The unit has a boundary at S' .

The adaxial patch. In many verrucose or echinulate spores, for which *Russula* and *Thelephora* are good examples (Malençon 1958; Corner 1968), the warts or spines develop all over the spore except in a small area on the adaxial side of the spore just above the apiculus. I call this smooth area the adaxial patch. It is the part of the spore impinging on the inner spore-circle S''' and it shows that this imaginary circle is a boundary defining a central 'dead space' over the basidium-apex where spore-growth is forbidden. It is the sharpest boundary in the tetrad.

Tangentially compressed spores. The tetrads of *Panaeolus* (Figure 1) and some species of *Coprinus* (Buller 1922, fig. 104; 1931, fig. 29-32), show radial or adaxial compression of the spores; d_{rad} is less than d_{tan} . In contrast with globose spores that are strictly confined by the one spacing given by S' and S''' , they bulge laterally; a lateral spacing has to be considered as well as a radial. More spectacular are the trigonous and cruciform spores in various agarics (Figure 12). Evidently there may be variation in the lateral spacing and in the intensity of inhibition from S' (as shown by abaxially echinulate spores), while that of S''' is rigid. Here, however, the exception comes with the *Boletus*-spore.

Reversed spores. Tetrads of homobasidiomycetes do not bear reversed spores; that is, spores do not develop with the apiculus turned abaxially. This may happen with diads in normally tetrasporous species (Corner 1950, fig. 271). In such cases the two spores are evidently so far apart that the sterigmatic spacing by the sterigmatic disc is ineffective; nevertheless, S' and S''' operate from the basidium-apex to maintain the spore-shape, even if σ is also ineffective.

6-8-spored basidia. When n is 3, the spores in end-view fit the angles of an equilateral triangle; when n is 4, they fit a square; when n is 5, they fit a regular pentagon. But, when n is 6 or 8, they do not fit a regular hexagon or octagon; they are disposed in an ellipse, as with interfering tetrads. This ellipse, however, seems not to be plane but to have decurved ends. Four spores occupy the central part of the ellipse and one or two spores at each end lie at a slightly lower level through the obliqueness of their sterigmata. The same effect may be seen in the tetrads of *Russula* and *Lactarius*. I have not succeeded in examining such hexads and octads in any detail. The obvious material is to be found in *Cantharellus*, *Craterellus* and *Pterygellus* (Corner 1966), but the basidia of these fungi are too long for suitable study in end-view. The regular disposition of the spores proves, nevertheless, that spacing factors operate through the ring of 6-8 sterigmata placed peripherally at the basidium-apex with its superimposed dead space.

Towards the geometry of the basidium

Certain features of the basidium-unit need more explanation.

Positioning of the spores. They are positioned by the sterigmata. These outgrowths, at first normal to the curved apex of the basidium, become parallel with the basidium-axis and develop at their attenuate tips the sterigmatic discs. From these the spores, inhibited by S''' , develop abaxially to the limit of S' and then elongate within these limits, parallel to the basidium-axis, if they are to become larger. The transverse sterigmatic discs appear to be the initial spacers and the apiculus of the mature spore is the adaxial feeler which indicates, but seldom coincides with, S''' . Careful measurement of the spore- and sterigmatic circles have shown me that, as a general rule, $M = S'' - 0.7d$; for a single spore, that is, the tip of the sterigma is situated external to S''' by a distance of $0.15d$.

If spore-spacing is determined by sterigmatic spacing, the cause of this cannot be discovered by simple observation because it must lie within the basidium. It must be connected with the hyaline cap which forms at the apex of the basidium shortly before the sterigmata emerge (Corner 1948). The substance of this cap forms, evidently, the walls of the sterigmata and those of the spore-rudiments; presumably it becomes electrically charged at the surface. It must be partitioned into four blocks which underlie the sterigmatic patches, or bases of the sterigmata (Corner 1948). I have pursued the geometrical consequences of the projection of this patch on the plane of the spore-circles and its hypothetical function in spore-spacing (p. 169).

Spore-angle. The direction in which the spore grows from the transverse sterigmatic disc was studied by Buller. He concluded that this angle was at 45° to the long axis of the basidium. I have measured the angle on camera lucida drawings and, though it is impossible to be precise with such minute structures, I agree with Buller's conclusion. It is supported by the following argument.

With reference to Figure 3, $\angle MTC$ is the spore-angle θ . If this is 45° , then

$$MC = TC \sin \theta = \frac{d}{2} \sin 45^\circ = 0.35d$$

or, for the whole basidium-unit,

$$M = S'' - 2MC = S'' - 0.70d$$

This is the value of M found by direct measurement of S''' , S' and M . The longitudinal plane of S''' lies adaxially to that of M by this small fraction $0.15d$.

The ratio d/w . The positioning of the sterigmata and that of the spores about the longitudinal axis of the basidium so that the basidium circle (in end-view of the tetrad) lies within S'' imply that there is a close relation between spore-width d and basidium-width w . These are two easy measures and their relation is an important feature of the basidium-unit. For the smooth ellipsoid spores of many homobasidiomycetes from *Amanita* to *Clavaria*, I find that in general $d = 0.6$ to $0.65w$. Large globose spores may increase the ratio to $0.8w$ and narrow spores may decrease it to $0.5w$. These differences may occur within a genus; the latitude in positioning of S' may be the explanation, but specific differences in spore-width generally imply differences in the valve of w . Thus, a basidium 8μ wide will bear spores 5μ wide; one 10μ wide will bear spores 6.3μ wide. Despite records to the contrary, I have not seen a tetrasporous homobasidiomycete in which d equals or exceeds w . The exception among the disporous is *Clavulina* with $d = 1.18w$ (Corner 1948).

No species has basidia of constant width. There is always some variation. Hence I have used as values of w and d either the mean of their variation or, when there have been sufficient measurements, their averages.

Lateral spacing in the tetrad. As a measure of this feature, I take the ratio σ of the spore-interval to spore-width, as seen on the spore-circle. In Figure 3

$$\sigma = \frac{KL}{2CK} = \frac{KL}{d}$$

Measurements of the tetrads of various basidiomycetes with isodiametric spores (d rad equals d tan) show that in general $\sigma = 0.5$.

The spacing can also be expressed by the angle δ (Figure 3), as explained on p. 169.

The basidium-apex. The projection of the spore-circles and other items of the basidium-unit on to the basidium-apex in median longitudinal section implies knowledge of the curvature of the apex, but this is a difficult matter and I can give only an approximation. The clavate basidium, fully grown but without sterigmata, has a hemispherical apex. When the hyaline cap forms, the apex protrudes slightly and in the long basidia of agarics with polymorphic basidia (such as *Coprinus*) this projection is lengthened and becomes almost cylindric with hemispheric apex. The question is whether it is ellipsoid or paraboloid. To test this, I measured the diameter of the basidia with hyaline caps, yet without sterigmata, at certain levels. These were the level of maximum width w and those at $\frac{1}{4}$, $\frac{1}{2}$ and $\frac{3}{4}$ of the vertical distance between the apex of the basidium and the plane of w . I compared these results with those that can be calculated for similar chords of a sphere (or ellipse) and a parabola, as shown in Table 1.

Table 1. Diameter of the basidium-apex, as ratios of w , at successive levels from the apex.

Levels	w	$0.25w$	$0.5w$	$0.75w$
ellipse	1	0.661	0.866	0.968
observed	1	0.687	0.854	0.954
parabola	1	0.438	0.750	0.938

The apex is clearly ellipsoid but, as rounding off of a clavate apex with slight protrusion, it is probably ellipsoid with a small dome of spherical curvature. This is the dome between the sterigmatic bases that struts them and collapses when wetted.

Globose spores. Longitudinal alignment cannot be discerned directly from such spores but, from their positioning on the sterigmata, they clearly obey the dead space defined by S''' . Presumably they have lateral spacing and external limits, defined at least by the total effect of the basidium-unit.

Spore-length. A globose spore fills the space between the limits of S' and S''' . If more protoplasm enters the spore, it elongates within these limits. For a given spore-volume, the closer these limits the longer the spore will be. But spores vary in the way that they grow into and fill this space. Some are globose from the first and then lengthen; others expand gradually as they lengthen and become pip-shaped, obovoid or clavate. None of these factors, however, has prime significance in spore-spacing, though the limits of S' and S''' explain why ellipsoid spores vary much in length though little in width, and conform to a sporograph-locus.

Sterigmatic length. Since the sterigmata become parallel, their length has no immediate effect on spore-spacing. They may lengthen abnormally, however, and remove one or two spores of the tetrad from the spacing effect of the whole, and this may be usual in Tremellaceae, but it is exceptional in homobasidiomycetes and leads to the abortion of the spore. Many exceptional states occur in Gasteromycetes with their variously disorganised basidium-mechanism.

I have been unable to detect any relation between the length of the sterigmata and other features of the basidium-unit. The length seems to depend on the hydrostatic pressure in the basidium and to be related with spore-number. Thus in species with $n = 3$ or 2 or 1, as variations on $n = 4$, the sterigmata are progressively longer. Sterigmatic length can, therefore, be neglected in basidium-geometry.

Basidium-length. With any one kind of basidium as defined by its equation (Corner 1947) w depends on l , but l does not otherwise determine spore-spacing. In all species l varies, but the resulting differences in w are so slight that the shorter basidia bear spores of practically the same shape and size as the longer. Thus, in tetramorphic species of *Coprinus*, there are not four sizes and shapes of spores. Nevertheless, as always, there are exceptions. At least two species of *Hygrophorus* have normally basidia of two sizes, very different in length, and they bear spores of very different size (Corner 1936). For the purpose of spore-spacing, basidium-length can also be ignored.

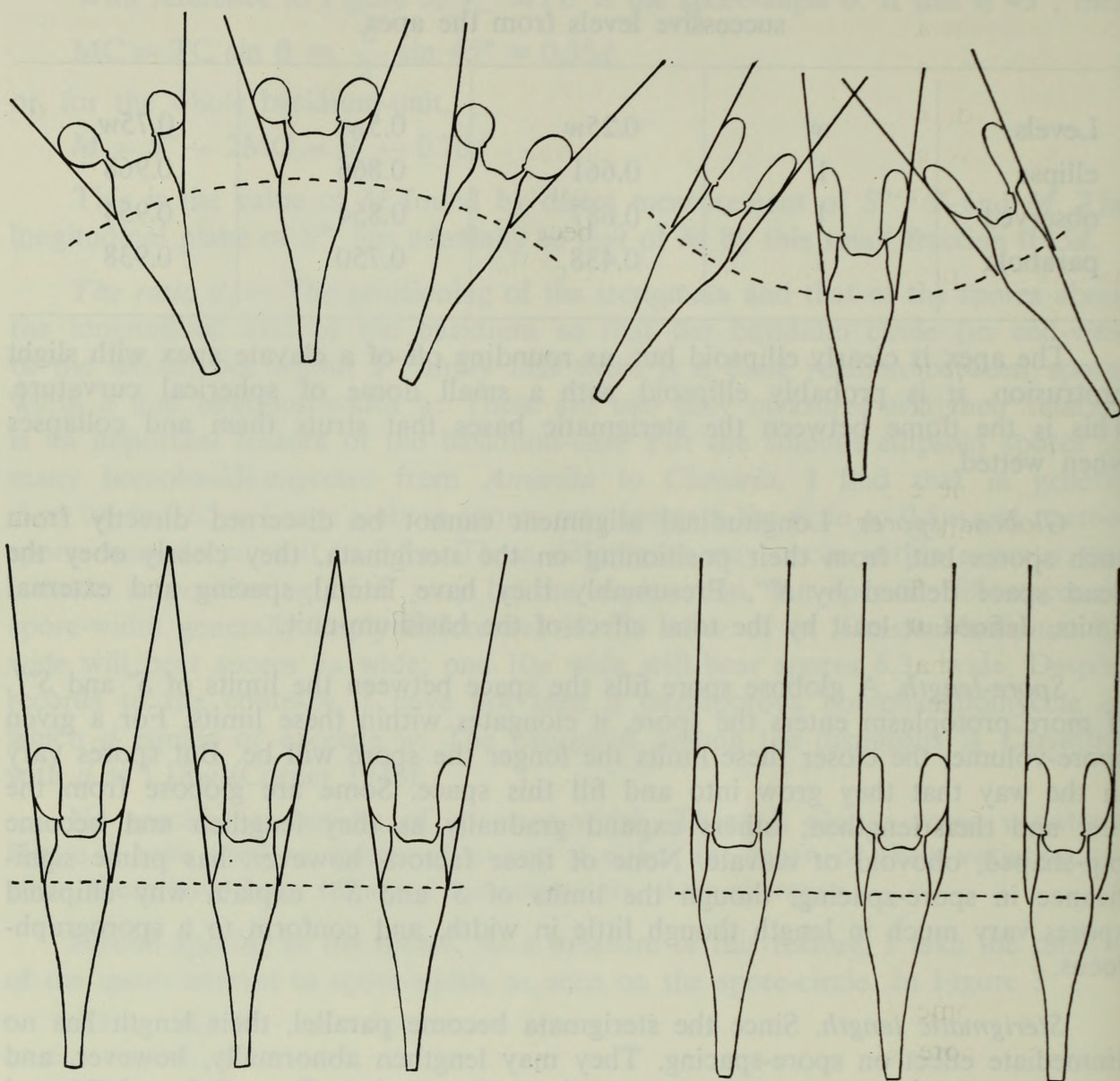


Figure 2. Diagrams of basidium-units, treated as cones, divergent in the convex hymenium (upper left), convergent in the concave hymenium (upper right), and divergent or paraboloid in the plane hymenium (lower figures).

The basidium-unit. The whole basidium with its spores can be regarded as an inverted cone expanding from the base (inverted apex) to the value of S' . Within the cone the unit develops; outside the cone it restrains other basidia. The effect is well seen in clavarioid basidia. Their sterigmata often diverge slightly and their long spores may also diverge and appear in optical section on the spore-circle as short ellipses. I suppose that this divergence is connected with the convex curvature of the hymenium, developed on the outside of the cylindric or clavate fruit-body, and that this curvature makes the basidia slightly divergent (Figure 2). In the agaric hymenium the basidium-unit becomes paraboloid with sterigmata and spores parallel to the long axis of the basidium. But the poroid hymenium is concave, lining tubes; the basidia are convergent and their cone-effects interfere; the outer spore-circles of adjacent units conflict and the whole unit is distally compressed. This is the problem in *Boletus*, many species of which

have long and narrow spores with convex adaxial face, known as the boletoid spore. Superficially this spore may resemble a *Clavaria*-spore; actually it is developed in a more complicated manner because the sterigmatic circle is displaced inwards.

The hydroid hymenium resembles the clavarioid. Its basidia are often small and their divergence may explain the prevalence of globose or subglobose spores. The stereoid hymenium with plane extension resembles that of the agaric but the basidium-units are not strictly aligned because of the thickening hymenium; new basidia may project beyond the influence of the mature and have slightly divergent sterigmata.

Asymmetric basidia. Very occasionally a basidium that has grown aslant develops a typical spore-circle asymmetrically on the exterior side of the apex. Whether or not this is the effect of light, gravity or some other external stimulus on the hyaline cap, the configuration proves that the sterigmatic arrangement is a structural unit.

Measurements. I have relied on my own measurements from living material. The basidium-unit is an inflated, semi-rigid structure prone to collapse, and it is not certain that measurements from dried material or that fixed in alcohol-formalin agree exactly with those from the living. It is tempting to use the published data in descriptions, but I have avoided these not only because they often refer to preserved specimens but because it is clear that immature basidia are often measured and such will give misleading results.

The geometry of the basidium

The geometry, as I have analysed it, is set out in Figure 3. The upper part shows the spore-tetrad, as seen in optical section from the end-view of the basidium, together with the spore-circles S' , S'' , S''' , the basidium-circle w , the sterigmatic circle M , the square joining the spore-centres C , and the tangents from the long axis of the basidium A to the spores. Then there are shown four small circles m on the spore-radii; they are the orthogonal projections of the sterigmatic patches on to this transverse plane. The lower part of the figure shows the longitudinal geometry of the basidium-apex which is drawn as a hemisphere on the base ww of maximum width of the basidium. The right half of the basidium-apex shows the sterigmatic patch (arc Hw) and the angle Haw which it subtends; I call this angle α . The various circles of the upper figure are projected on to the base-line ww . The lower right-hand spore represents a globose spore in side-view as it would fit on to the sterigma which, for clarity, has been omitted. If the upper figure is rotated through 90° , it represents the spore-circles above the basidium.

Many relations of the parts can be derived from this figure. I give merely the more useful that can be reduced to the minimum data d and σ , when $n = 4$. It must be noted that the symbols S' , S'' , S''' , M , w , d and m refer to diameters and not radii.

CC (side of the square) = $d(1 + \sigma)$ (1)
because CC = CK + KL + LC, and by definition KL = $d\sigma$, therefore

$$CC = \frac{d}{2} + d\sigma + \frac{d}{2} = d + d\sigma = d(1 + \sigma)$$

$S'' = \sqrt{2}d(1 + \sigma)$ (2)
because $S'' = 2AC$ and, as S'' (diameter) is hypotenuse to the rt. $\triangle$ triangle with sides CC, then

$$(2AC)^2 = 2(CC)^2$$

$AC = \sqrt{2}CC = \sqrt{2}d(1 + \sigma)$, as from (1)
Obviously $S' = S'' + d$ and $S''' = S'' - d$ (3)

$M = S'' - 0.7d$ (see p. 164) (4)

Now it is convenient to turn these relations into functions of δ . In Figure 3, P is the point where the tangent from A meets the spore.

$$\sin \delta = \frac{PC}{AC} = \frac{d}{2} \times \frac{2}{S''} = \frac{d}{S''} = \frac{1}{\sqrt{2}(1 + \sigma)} \quad \text{..... (5)}$$

$$\text{or } \operatorname{cosec} \delta = \sqrt{2}(1 + \sigma)$$

$$S'' = \frac{d}{\sin \delta} = d \operatorname{cosec} \delta \quad \text{..... (6)}$$

$$S' = S'' + d = \frac{d}{\sin \delta} + d = \frac{d(1 + \sin \delta)}{\sin \delta} = d(+ \operatorname{cosec} \delta) \quad \text{..... (7)}$$

$$\text{or } S' = d[\sqrt{2}(1 + \sigma) + 1]$$

$$S''' = S'' - d = \frac{d}{\sin \delta} - d = \frac{d(1 - \sin \delta)}{\sin \delta} = d(\operatorname{cosec} \delta - 1) \quad \text{..... (8)}$$

$$\text{or } S''' = d[2(1 + \sigma) - 1]$$

$$M = d(\operatorname{cosec} \delta - 0.7) \quad \text{..... (9)}$$

$$\text{or } M = d[\sqrt{2}(1 + \sigma) - 0.7]$$

$$\sigma = \frac{\operatorname{cosec} \delta}{\sqrt{2}} - 1 \quad \text{..... (10)}$$

Sterigmatic patch hypothesis. I assume that the spacing of the sterigmatic patches provides that of the spores by transmission through the sterigmata. The symmetrical partition of the hyaline cap in the basidium-apex into four areas, set as far as apart as possible on the level of w , may be the physical basis. The geometrical consequence must be traced by the projection of the sterigmatic patch on to the transverse plane of the spore-circles. In Figure 3 any circle with centre on AC and inscribing AP will provide the spore-spacing, but the sterigmatic patch implies certain conditions. Its projection must lie within the basidium-circle; it must place the sterigmatic tips on the sterigmatic circle; and it must be related with w (that is the perpendicular ww in Figure 3). For convenience I use m^* for the diameter of the projected circle of the sterigmatic patch and denote the circle accordingly.

The most likely position for the centre of m is C' where AC cuts the S''' circle (in the upper part of Figure 3). This m circle contacts the basidium-circle, as can be seen from the following argument with reference to Figure 4.

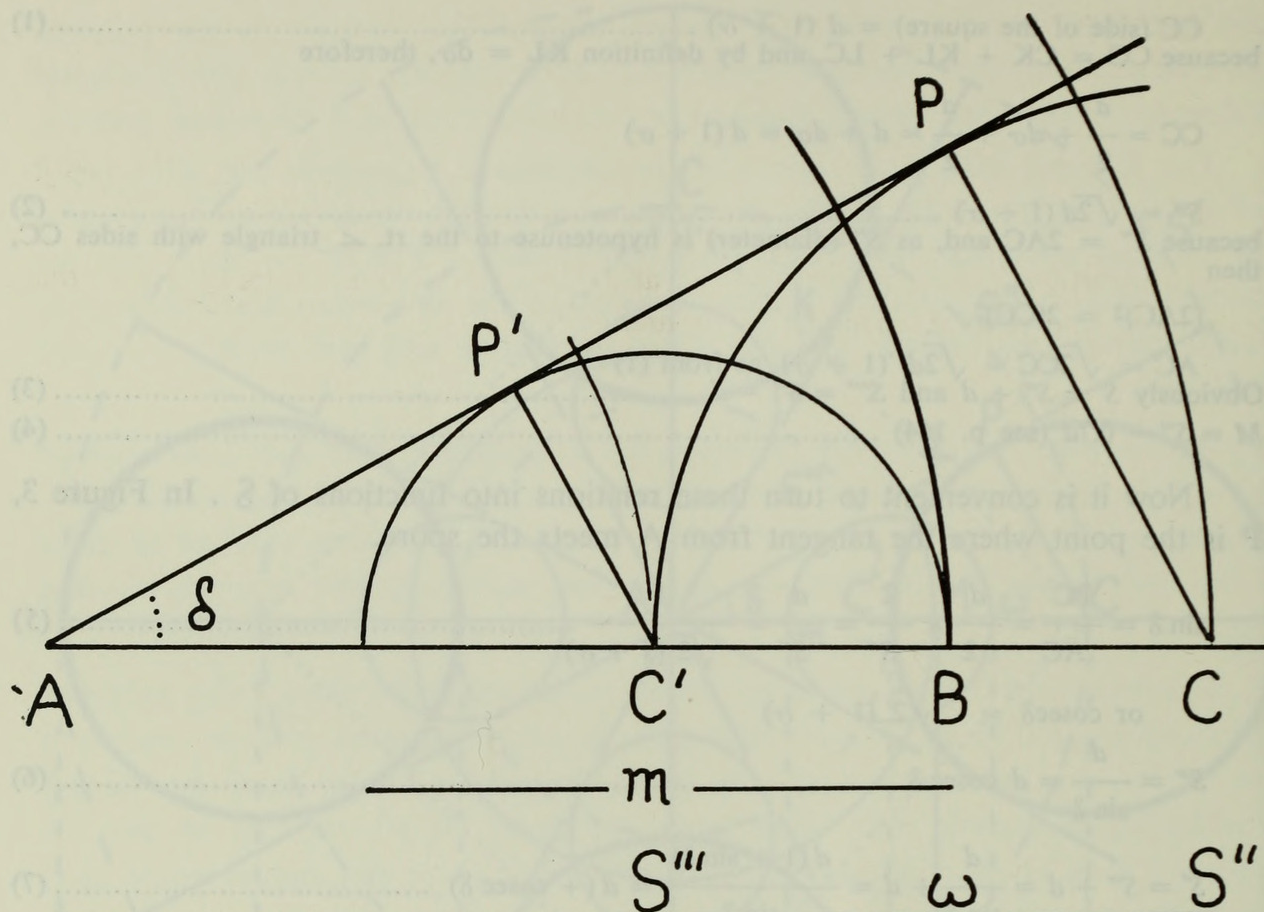


Figure 4. Construction to prove that the m circle with centre C on the S''' circle contacts the basidium circle w .

For a circle with centre on AC and with AP as tangent, then $C'P' = C'B$, as radii of this circle.

$$C'P' = AC' \sin \delta, \text{ or in this case}$$

$$= \frac{S''' \sin \delta}{2} = \frac{d(1 - \sin \delta) \sin \delta}{2 \sin \delta} = \frac{d(1 - \sin \delta)}{2} \text{ from (8)}$$

$$C'B = AB - AC', \text{ or in this case}$$

$$= \frac{1}{2} (W - S''')$$

$$\text{Now } S''' = \frac{d(1 - \sin \delta)}{\sin \delta} \text{ from (8)}$$

$$m = S''' \sin \delta \text{ ex hypothesi}$$

$$w = S''' + m = S''' + S''' \sin \delta = S''' (1 + \sin \delta)$$

Therefore,

$$C'B = \frac{d(1 - \sin \delta)(1 + \sin \delta)}{2 \sin \delta} - \frac{d(1 - \sin \delta)}{2 \sin \delta}$$

$$\frac{2 \sin \delta C'B}{d} = 1 - \sin^2 \delta - 1 + \sin \delta = \sin \delta - \sin^2 \delta$$

$$\text{Therefore } C'B = \frac{d(1 - \sin \delta)}{2} = C'P'$$

The following equations may therefore be added

$m = S''' \sin \delta = d (1 - \sin \delta)$ (11)

$w = S''' + m = S''' (1 + \sin \delta) = \frac{S' S'''}{S''}$ (12)

This curious relation between *w* and the spore-circles follows from that between *w* and *d* as determined by σ and δ . Thus

$w = S''' + m$ and $S''' = S'' - d$

$m = S''' \sin \delta = (S'' - d) \times \frac{d}{S''} = \frac{S'' d - d^2}{S''}$

Therefore $w = (S'' - d) + \frac{S'' d - d^2}{S''}$
 $= \frac{(S'')^2 - S'' d + S'' d - d^2}{S''} = \frac{(S'')^2 - d^2}{S''} = \frac{(S'' + d) (S'' - d)}{S''}$
 $= \frac{S' S'''}{S''}$ from (3)
 $w = S''' (1 + \sin \delta) = d \cos \delta \cot \delta$ (13)

because $S''' (1 + \sin \delta) = \frac{d (1 - \sin \delta)}{\sin \delta} \times (1 + \sin \delta) = \frac{d (1 - \sin^2 \delta)}{\sin \delta}$
 $= \frac{d \cos^2 \delta}{\sin \delta} = d \cot \delta \cos \delta$

The longitudinal relations may now be considered.

Let the sterigmatic patch circle *m* be projected on to the basidium-apex, as in the lower part of Figure 3. It occupies arc Hw and subtends $\angle$ HAw or α . Bisect α and the bisecting radius AF will meet the arc Hw where it is intersected by the projection of the sterigmatic circle *M*. That is, if the centre of the longitudinal sterigmatic arc on the basidium is projected parallel with the long axis of the basidium up to the level at which the spores are developed, it becomes the sterigmatic tip, whence the spores grow abaxially with the spacing initiated on the basidium-apex. This is one of the most remarkable agreements between the geometry of the basidium and the observation of the spore-circles, the sterigmatic circle and the spore-angle. At first there seems to be no reason for the position of the sterigmatic tips, other than structural convenience; now it is seen to be an integral part of the basidium-unit. The tips are eccentric in the sterigmatic patch circle. It would be interesting to compare this construction with the basidium of *Gasteromycetes* with sessile or sessile spores.

By means of the angle α , other relationships in the basidium can be found which have value in checking reconstruction from specific data.

$$M = w \cos \frac{\alpha}{2} \dots\dots\dots (14)$$

$$\cos \alpha = \frac{1 - \sin \delta}{1 + \sin \delta} \dots\dots\dots (15)$$

$$\text{because } \cos \alpha = \frac{Am}{AH} = \frac{2Am}{w} = \frac{2Am}{S''' (1 + \sin \delta)} \quad \text{from (12)}$$

$$Am = \frac{S'''}{2} - \frac{m}{2} = \frac{S'''}{2} - \frac{S''' \sin \delta}{2} = \frac{S''' (1 - \sin \delta)}{2} \quad \text{from (11)}$$

Therefore

$$\cos \alpha = \frac{S''' (1 - \sin \delta)}{2} \times \frac{2}{S''' (1 + \sin \delta)} = \frac{1 - \sin \delta}{1 + \sin \delta}$$

$$\text{Alternatively, } \cos \alpha = \frac{S''' - m}{S''' + m} \dots\dots\dots (16)$$

$$\sin \delta = \frac{1 - \cos \alpha}{1 + \cos \alpha} \quad \text{from (15)} \dots\dots\dots (17)$$

$$\sin \theta = \frac{S'' - m}{d} \dots\dots\dots (18)$$

$$\text{because } \sin \theta = \frac{MC}{TC} = \frac{S'' - M}{2} \times \frac{2}{d} = \frac{S'' - m}{d}$$

$$d = \frac{S'' - M}{\sin \theta} \quad \text{from (18)} \dots\dots\dots (19)$$

$$M = w \sqrt{\frac{1 + \cos \alpha}{2}}, \quad \text{from (14)} \dots\dots\dots (20)$$

$$= w \sqrt{\frac{1}{1 + \sin \delta}} \quad \text{from (15)}$$

$$S''' = \frac{d (1 - \sin \delta)}{\sin \delta} \dots\dots\dots (21)$$

$$\text{because } S''' = S'' - d = \frac{d}{\sin \delta} - d = \frac{d (1 - \sin \delta)}{\sin \delta}$$

$$M = d \cot \delta \cos \delta \sqrt{\frac{1}{1 + \sin \delta}} \quad \text{from (20) and (13)} \dots\dots\dots (22)$$

This, at last, gives M a value in terms of spore-spacing.

$$\sin \theta = \operatorname{cosec} \delta - \cot \delta \cos \delta \sqrt{\frac{1}{1 + \sin \delta}} \dots\dots\dots (23)$$

This, at last, gives θ in terms of spore-spacing. The proof is detailed, thus

$$\sin \theta = \frac{S'' - M}{S'' \sin \delta} \quad \text{from (18), because} \quad \sin \delta = \frac{d}{S''}$$

$$\text{whence} \quad \sin \delta = \frac{S'' - M}{S'' \sin \theta}$$

$$\text{Now for} \quad \frac{S'' - M}{S''} = 1 - \frac{M}{S''} \quad \text{write } k$$

Then $\sin \theta = k \operatorname{cosec} \delta$ and $\sin \delta = k \operatorname{cosec} \theta$, and from (22)

$$k = 1 - \frac{M}{S''} = 1 - \frac{d \cos^2 \delta}{\sin \delta} \sqrt{\frac{1}{1 + \sin \delta}} \times \frac{\sin \delta}{d} = 1 - \cos^2 \delta \sqrt{\frac{1}{1 + \sin \delta}}$$

Therefore

$$\begin{aligned} \sin \sigma &= \operatorname{cosec} \delta \left(1 - \cos^2 \delta \sqrt{\frac{1}{1 + \sin \delta}} \right) \\ &= \operatorname{cosec} \delta - \cot \delta \cos \delta \sqrt{\frac{1}{1 + \sin \delta}} \end{aligned}$$

These equations are summarised in Appendix 1. The values of the various factors are given in Appendix 2. With the three data d , σ and $n = 4$, all other parts of the basidium-unit can be calculated except the lengths of the spores, sterigmata and basidium.

If the values of the factors, as given in Appendix 2, are plotted against those of σ as graphs (which is the easiest method of obtaining intermediate values), it will be found that they form very gradual curves. This stability of form is the character of the homobasidium, which is one of the more constant structures in botany.

The curve $\sin \theta = f \sigma$ has its greatest curvature where $\sigma = 0.73 = \sin \theta$. The curves $\sin \theta = f \sigma$ and $\sin \delta = f \sigma$ intersect at $\sigma = 0.807$ when $\sin \theta = \sin 2 \delta = 0.72$.

When $\sigma = 0.5146$, there is the special case in which the diameter of the basidium equals the circumference of the sterigmatic patch circle; that is, $w = \pi m$. Thus

$$m = S''' \sin \delta \quad \text{and} \quad w = S''' + m = S''' (1 + \sin \delta)$$

$$\begin{aligned} \text{Therefore} \quad \frac{w}{m} &= \frac{1 + \sin \delta}{\sin \delta} = \sqrt{2} (1 + \sigma) + 1 \quad \text{from (5)} \\ &= 2.414 + \sqrt{2} \sigma \end{aligned}$$

If this expression is to give the value of π , then

$$\sqrt{2} \sigma = \pi - 2.414 = 0.7276, \quad \text{and} \quad \sigma = 0.5146.$$

Also, at this value of σ , the length of the arc subtended by ∞ equals $1.004d$, which is practically the value of d . In other words, at the commonly observed value of σ , the longitudinal arc of the sterigmatic patch equals the spore-width, and the diameter of the basidium, if rolled up into a circle, equals the circumference of the sterigmatic patch circle. Here, again, it would seem that the volume of the hyaline cap of the basidium must be the basic cause.

***Mycena illuminans* P. Henn., as a test**

This small luminous agaric, not uncommon in Singapore (Corner 1954), has fairly large, almost globose spores and the sporing basidia are fairly resistant to immersion in water. I used it, therefore, as a test of the theory. However, the basidium is large and the gill-tissue opaque, with the result that I could not obtain the basidium-circle along with the spore-circles; focussing down to the basidium-outline crushed the spore-circles. Therefore I have used average measures. The spore is very slightly wider tangentially than radially and I have kept these measures apart as d_{tan} and d_{rad} . Then, the basidia project to various levels; they are not clearly dimorphic, but those that project most have slightly wider spore-spacing. I have given the average for M as observed; insufficiency of basidia may account for the discrepancy with the calculated value of M .

The measures were taken from camera lucida drawings, averaged, and then used to construct an ideal basidium for the species at a magnification of 10,000. Angles on such a figure could be measured with sufficient accuracy. The figure so closely resembles that in Figure 3 that I limit myself to the comparison between the calculated values and those observed, whether in the original drawings or in the geometric reconstruction. These are given in Tables 2 and 3.

I do not consider any of the slight discrepancies in Table 3 to conflict with the general theory. I would emphasize how the variability of the basidium-unit, constructed from interweaving hyphae, is combined in the hymenium into an average regime. Thus, some basidia were so compressed as to be oblong ellipses in end-view, with diamond-shaped sterigmatic 'square', yet the average of the two diagonals of this diamond was that of the square. Spores vary in size and spacing, yet the averages obtain.

The Boletus-spore

The spores of most boleti are elongate with the smooth and slightly thickened wall brown, ochraceous or pink. The adaxial face bulges slightly, but the abaxial is remarkably straight. Other species, placed in *Strobilomyces*, *Boletellus*, *Heimiella* and *Porphyrellus*, have a verrucose, echinulate, reticulate or striate ornamentation which is also coloured. These spores have recently been studied in great detail by Perreau-Bertrand (1967), who distinguishes five layers in the wall of the ornamented spore. For my present purpose I simplify this complexity into the two layers of customary application, namely the outer colourless and apparently structureless exospore (which is the ectospore and perispore of Perreau-Bertrand) and the coloured endospore with its ornamentation, which I regard as an extension of the endospore into the exospore; the ornaments make the exospore of Perreau-Bertrand. The point is that, as Perreau-Bertrand discovered, these spores have a hyaline outer layer, $0.5-1.5\mu$ thick, within which the coloured layer forms as the endospore. Often this outer layer becomes mucilaginous and is scarcely noticeable in aqueous mounts. The question arises whether the coloured and apparently external wall of the smooth boletoid spore represents the outer hyaline or the inner coloured layer of the wall of the ornamented spore. Perreau-Bertrand found that some smooth boletoid spores had a hyaline mucilage-sheath to suggest that the coloured wall was endospore. I confirm this observation from many Malayan

species and add positive proof that the coloured layer is endospore (see the following observation iii). Evidently the smooth boletoid spore is an endospore; that it is peculiar is shown by the following points.

(i). For most boletoid spores $d = 0.36 w$ to $0.58 w$, instead of the usual $0.6 w$ to $0.65 w$. The spore, therefore, is compressed.

(ii). In the case of the ornamented spores of *Strobilomyces* and other genera, $d = 0.59 w$ to $0.71 w$ but, if the inner spore is taken, then $d = 0.48 w$ to $0.60 w$ as with the smooth boletoid spore. This means that there are two spacing factors, σ' for the outer spore of diameter d' and σ for the inner spore of diameter d . However, some species of *Boletellus* have spores that are merely finely striate and such spores are equivalent only to the endospore of *Boletellus*; and this genus, incidentally, becomes practically inseparable from *Boletus*.

(iii). In some pink-spored species, such as *B. albo-ater* Schw. and *B. nanus* Mass., the spore grows to a size that exceeds the final spore by c. 1μ in length and breadth. This larger spore is hyaline and, very soon, there forms within it a coloured, thickening layer which becomes the outside of the mature spore, while the outer hyaline layer turns mucilaginous and loses its firm limiting membrane. In these cases the larger transient spore has $d = 0.46 w$ to $0.60 w$ and the mature spore has $d = 0.37 w$ to $0.50 w$. This proves that the endospore makes the coloured wall of the boletoid spore and, as corroboration, some of these spores, are extremely finely striate and could be referred to *Boletellus*, except for the spore-colour. I think that this phenomenon of spore-shrinking is widespread among smooth-spored boleti and that the limits of *Boletellus*, as of most segregates from *Boletus*, are unsatisfactory.

(iv). The ornamented spores of *Strobilomyces* and *Porphyrellus* sect. *Graciles* have a small adaxial patch without ornamentation; it is absent from the spores of *Boletellus* and *Heimiella*. The adaxial patch forms where the spore-wall contacts or approximates with S''' and, therefore, in these two genera exospore and endospore must coincide more or less in this area. Radial spacing must be the same for both exospore and endospore, in which respect these spores are less specialised than those of other boleti.

(v). The elongate spores are strictly parallel with the long axis of the basidium and, as already noted, the abaxial side is straight. This is evidence of the compression of the spore-circles which is to be expected from the tubular hymenium.

In order to discover what may be happening in the development of the *Boletus*-spore, I studied in detail several species with a diversity of spores. Table 4 summarises the results. Figures 5-11 show the simplified geometry of the basidia. The reconstruction of such figures I find to be the only satisfactory way to appreciate the intricacy of the basidium-unit. The species which I studied have the following particulars.

Strobilomyces velutipes Cke. et Mass., with purple brown, verrucose, ellipsoid to subglobose spore; adaxial patch present.

Porphyrellus sect. *Graciles*, an undescribed species with imperfect observations; spores purple brown, verrucose but with smooth apex and base, and with a narrow adaxial patch.

TABLE 2
MYCENA ILLUMINANS
Values of the basidium-unit in μ from observation

—	D	$d \tan$	$d \text{ rad}$	$\sigma \tan$	S'	S'''	M	w	l	θ
Average	..	9.00	8.86	3.86	26.88	9.16	10.94	14.07	30.5	50° 85'
Range	..	8.5–10.3	8.0–9.6	2.4–6.6	24.0–30.9	5.3–12.5	8.5–13.5	11.9–16.8	23–39	48.3°–56.5°
Number observed	..	118	103	118	52	52	64	85	30	10
Ratio to $d \tan$	..	1.06	0.98	0.430	—	—	1.22	1.56	—	—
$d \text{ rad}$	..	1.08	1	0.438	3.03	1.03	1.24	1.59	—	—
w	..	—	0.63	—	1.91	0.65	0.78	1	2.17	—

TABLE 3

MYCENA ILLUMINANS

Comparison of observed and calculated values of the basidium-unit in μ

	TANGENTIAL SPACING			RADIAL SPACING			OBSERVED
	σ equations	w equations	observed	σ equations	w equations	observed	
d	..	9.08	9.00	..	9.00	8.86	9.05 and 8.82
σ	..	..	0.430	..	..	0.438	..
S'	27.2	27.44	..	..	27.29	26.88	27.45
S'''	9.2	9.35	..	..	9.3	9.16	8.9
M	11.25	11.35	10.94	11.19	11.36	10.94	11.0
w	13.75	..	13.87	13.67	..	13.87	14.35
m	4.55	4.59	..	4.50	4.57	4.67	..
δ	29° 38'	29° 38'	..	29° 27'	29° 27'	..	29° 30' to 30°
α	70° 13'	70° 12'	69° 14'	70° 5'	70° 4'	69° 14'	..
θ	50° 33'	..	..	50° 26'	..	50° 85'	52° 38'

Boletus emodensis. B. and *B. longicollis*. Ces. with olive brown, striate-costate, ellipsoid spores as in *Boletellus*.

B. retisporus Pat. et Baker with olive brown, reticulate and ellipsoid spore (*Heimiella*).

B. albo-ater Schw., *B. nanus* Mass. and an undescribed species (*Boletus* 18b of my notes), with pink, smooth boletoid spores but with evanescent exospore and very faintly striate endospore.

B. aureomycelinus Pat. et Baker, *B. phaeocephalus* Pat. et Baker, *B. ravenelii* B. et C. and *B. umbilicatus* Mass. with olive brown smooth ellipsoid to boletoid spores. [It is to be noted that *B. phaeocephalus* is the species which I called *B. funerarius* Mass. in my earlier paper (Corner 1947); there is a mixture of type-painting and type-specimen for *B. funerarius*, the former being *B. phaeocephalus*].

Phylloporus cingulatus Corner with smooth, brown ellipsoid spores.

The first point to note from Table 4 is that, except for *Strobilomyces*, the observed values of w exceed those calculated from the spore-circles. The circles are smaller than would be expected. The sterigmata have been approximated by an adaxial shift, upwards along the basidium-axis, and therefore the spore-circles have been narrowed and the spores compressed. The compression is most marked in *B. emodensis* (Figure 11) and *B. phaeocephalus* (Figure 5) in which S'' lies within w .

The point is illustrated by the position of the sterigmatic patch. In all species, if a sterigmatic patch circle is drawn on S''' with radius $S''' w$, it greatly exceeds the arc of the sterigma on the basidium-apex. I have shown two sterigmatic patch circles in the figures, m for σ' spacing and (m) for σ spacing. The (m) circle is the determinant that fits the sterigmatic arc, while the m circle is the unstable, excessive factor. However, the centres of m and (m) vary from S''' to M itself. Thus *B. emodensis* (Figure 11) shows the greatest compression with the centre of (m) on S''' and radius $S''' M$.

The second point is that in the species with a distinct, if evanescent, exospore the value of d (inner spore) gives a better approximation to that of M than does d (outer spore). Reference to the figures or to the table in Appendix 2 will show that the values of M and w to be expected from d are excessive; this means that σ' spacing is too large and gives place to σ spacing. For some physical reason the exospore is more or less unstable and the spore, constructed on σ spacing, is an endospore. It is not clear, however, that there is any geometrical reason for the development of ornamentation; presumably it is a physical reaction of the membrane to the instability of σ' . Comparison with other species in the groups with ornamented spores may reveal some common peculiarity.

In all the species with smooth spores the plane of S'' approaches that of w in evidence of the compression of the spore-circles. However, as noted, *B. emodensis* with striate-costate spore agrees in this respect with the apparently smooth-spored *B. phaeocephalus*, and, hence, this relation cannot be connected with ornamentation. Yet *B. phaeocephalus* is one of the species in which the endospore can be seen to be exceedingly finely striate.

TABLE 4
Spore-measurement in Boletus

			Observed values (μ)					Theoretical values* (μ)		
			d	σ	S''	S'''	M	w	M	w
<i>S. velutipes</i>	..	..	8.00		16.72	8.74	11.8	14.0	10.88	13.20
			6.80		16.60	9.90			11.76	13.95
	ratio to d'	..	1	0.50	2.09	1.09	1.48	1.75	1.36	1.65
	ratio to d (number)	..	1 (120)	0.76 (104)	1.45 (26)	1.75 (26)	2.06 (61)			
<i>B. emodensis</i>	..	..	7.28		13.91	6.63	9.54	14.46	10.3	10.1
			6.08		13.91	7.83			9.38	11.26
	ratio to d'	..	1	0.38		0.91	1.31	1.99	1.42	1.39
	ratio to d (number)	..	1 (152)	0.65 (102)	1.23 (34)	1.57 (34)	2.38 (44)			
<i>B. longicollis</i>	..	..	10.33		17.44	7.11	11.55	14.5	8.97	11.31
			8.70		16.77	8.07			9.95	12.26
	ratio to d'	..	1	0.20		0.69	1.12	1.40	0.87	1.10
	ratio to d (number)	..	1 (80)	0.36 ?	0.93 (24)	1.33 (24)	1.67 (24)			
<i>B. retisporus</i>	..	..	9.18		17.61	8.42	10.58	15.51	10.39	12.81
			7.58		17.61	10.02			11.99	14.33
	ratio to d'	..	1	0.36		0.92	1.15	1.69	1.13	1.40
	ratio to d (number)	..	1 (164)	0.65 (152)	1.32 (38)	1.40 (38)	2.05 (51)			
<i>Boletus</i> 18b	..	..	5.25		11.00	5.75	9.06	10.00	6.98	8.47
			3.90		11.02	7.12			8.28	9.62
	ratio to d'	..	1	0.48		1.10	1.73	1.91	1.33	1.61
	ratio to d (number)	..	1 (364)	1.01 ?	1.83 (86)	2.32 (86)	2.56 (40)			
<i>B. albo-ater</i>	..	..	4.77		10.91	6.14	8.58	10.34	7.34	8.82
			3.97		10.91	6.94			8.11	9.47
	ratio to d'	..	1	0.618		1.29	1.80	2.17	1.54	1.85
	ratio to d (number)	..	1 (142)	0.945 (112)	1.77 (62)	2.16 (62)	2.60 (41)			
<i>B. nanus</i>	..	..	5.38		10.96	5.58	8.35	10.98	6.81	8.32
			4.03		10.96	6.93			8.10	9.48
	ratio to d'	..	1	0.441		1.04	1.55	2.04	1.26	1.54
	ratio to d (number)	..	1 (250)	0.924 (180)	1.72 (46)	2.07 (46)	2.73 (42)			
<i>B. phaeocephalus</i>	..	..	4.55		11.65	7.10	8.68	12.20	8.37	9.87
	ratio to d	..	1	0.810		1.56	1.91	2.68	1.84	2.17
	(number)	..	(102)	(160)	(50)	(50)	(82)	(66)		
<i>B. umbilicatus</i>	..	..	5.37		13.06	7.69	8.86	12.33	9.12	10.85
	ratio to d	..	1	0.720		1.43	1.65	2.30	1.70	2.02
	(number)	..	(56)	(10)	(9)	(9)	(6)	(38)		

Table 4 — continued.

Spore-measurement in Boletus.

				Observed values (μ)				Theoretical values* (μ)	
				d	σ	S''	S'''	M	w
<i>B. ravenelli</i>	..	..	4.21			10.22	6.01	6.81	9.96
ratio to d	..	..	1	0.720		1.43	1.62	2.37	1.70
(number)	..	..	(132)	(92)		(40)	(40)	(22)	(69)
<i>B. aureomycelinus</i>	..	..	4.89			10.89	6.00	7.90	10.47
ratio to d	..	..	1	0.575		1.24	1.62	2.14	1.48
(number)	..	..	(126)	(56)		(28)	(28)	(36)	(64)
<i>P. cingulatus</i>	..	..	5.20			11.98	6.80	8.96	11.63
ratio to d	..	..	1	0.615		1.31	1.72	2.24	1.57
(number)	..	..	(188)	(80)		(40)	(40)	(17)	(73)

* calculated from $M = S''' \sqrt{\frac{S'}{S''}}$ and $w = \frac{S' S'''}{S''}$

d' outer spore, d inner spore.

(number) refers to the number of observations.

Various errors in observation and construction can be imagined to explain the differences in positioning of the sterigmatic patch circles, but without understanding of the physical forces involved I do not think that they help the solution. I mention one possibility because it is a step in the adaxial displacement of the sterigmata. In Figure 5 I have drawn w' w' as the false base of the basidium-apex; it is the base that makes the basidium-apex hemispheric instead of ellipsoid and, as will be seen, it has the effect of shifting the sterigmata upwards and adaxially to compress the spore-circles. The sterigmatic patch, nevertheless, seems to fit not the arc of $\angle HA' w'$ but the upper half of this arc. It appears that the compression of the cone-effect of the basidium-unit in the concave hymenium acts on the sterigmatic patches before emergence of the sterigmata. This is a part of the more general problem of the hymenium-level where some force causes basidia to stop elongating and to mature; thus cystidia are basidia that have exceeded this level, often before it has become established in the developing hymenium, and remain sterile. The hymenium-level is another apparently electrostatic effect of the fruit-body.

B. phaeocephalus (Figure 5). At first sight this appears to be a normal reconstruction but the S'' circle lies within the w circle, a spacing circle on S''' with radius $S''' w$ greatly exceeds the sterigmatic patch, and the observed spacing, whereas a spacing circle on M with radius Mw almost fits the tangent to the spore; and the sterigmatic arc is much shorter than Hw . I detected no exospore but comparison with Figure 6 shows that the spore of *B. phaeocephalus* is an endospore developed from an adaxially displaced sterigmatic patch. This construction probably represents the normal state for the smooth boletoid spore.

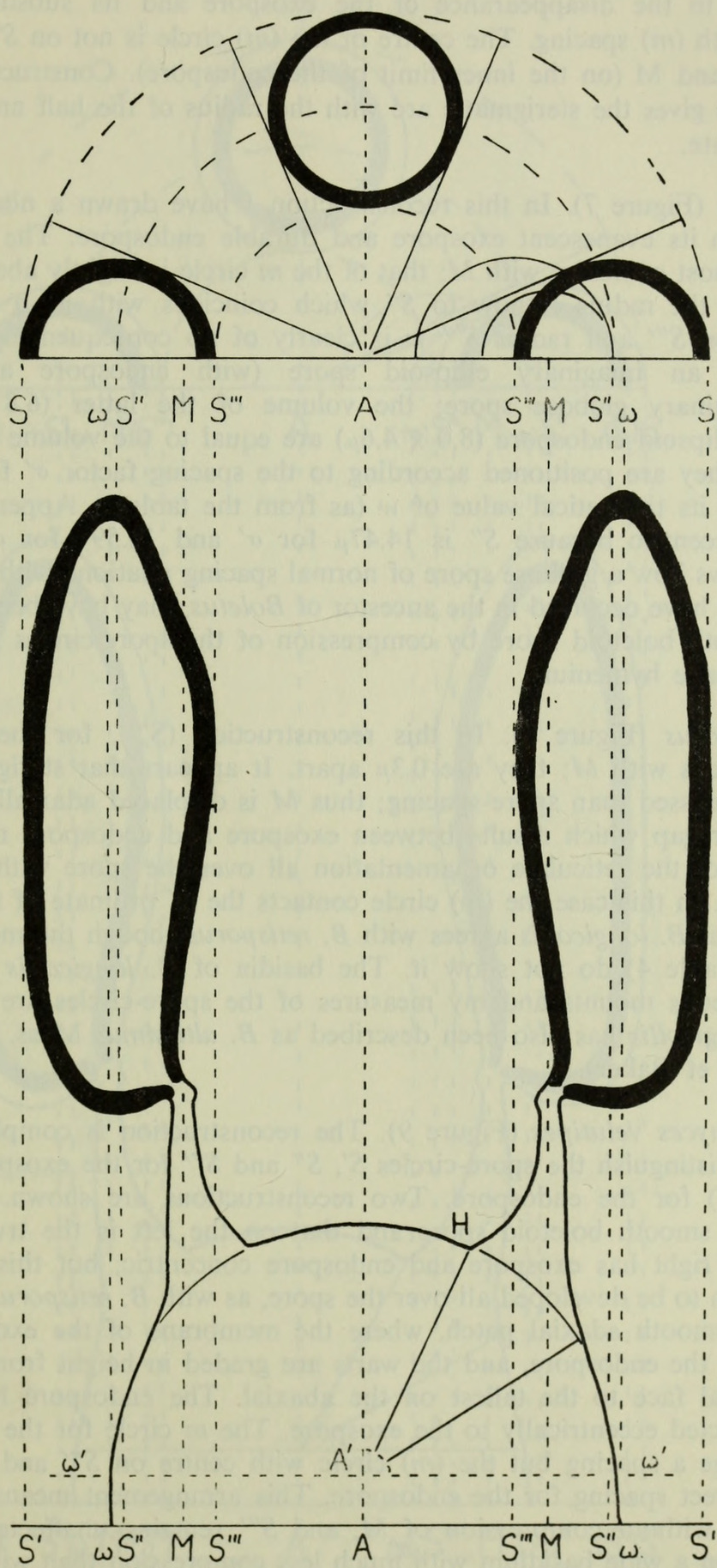


Figure 5. *Boletus phaeocephalus*, with w'w' as the false base of the basidium-apex; x 5000.

B. albo-ater (Figure 6). This reconstruction shows the excessive σ' spacing which leads to the disappearance of the exospore and its substitution by the endospore with (m) spacing. The centre of the (m) circle is not on S''' but midway between S''' and M (on the inner limit of the endospore). Construction of α' on the false base gives the sterigmatic arc with the radius of the half angle contacting the M ordinate.

B. nanus (Figure 7). In this reconstruction I have drawn a normal spore on the right with its evanescent exospore and durable endospore. The centre of the (m) circle almost coincides with M ; that of the m circle is slightly abaxial from S''' , but for both the radius is now to S'' which coincides with w ; a spacing circle with centre on S''' and radius $S''' w$ is clearly of no consequence. On the left I have drawn an imaginary ellipsoid spore (with endospore and exospore) and an imaginary globose spore; the volume of the latter ($6.8 \times 7.1\mu$) and that of the ellipsoid endospore ($8.0 \times 4.6\mu$) are equal to the volume of the normal endospore. They are positioned according to the spacing factor σ' for the normal exospore and its theoretical value of w (as from the table in Appendix 2). These spores are eccentric because S'' is 14.47μ for σ' and 12.59 for σ . The reconstruction shows how a globose spore of normal spacing relations with the basidium, such as might have occurred in the ancestor of *Boletus*, may have been transformed into the smooth boletoid spore by compression of the spore-circles commensurate with the concave hymenium.

B. retisporus (Figure 8). In this reconstruction (S'''), for the inner spore, almost coincides with M ; they are 0.3μ apart. It appears that sterigmatic spacing is more compressed than spore-spacing; thus M is displaced adaxially towards S''' and the wider gap which results between exospore and endospore may allow the development of the reticulate ornamentation all over the spore without a smooth adaxial patch. In this case the (m) circle contacts the w' ordinate of the false base. It is likely that *B. longicollis* agrees with *B. retisporus* though the measures of S''' and M (in Table 4) do not show it. The basidia of *B. longicollis* collapse very easily in aqueous mounts and my measures of the spore-circles are probably too small. (*B. longicollis* has also been described as *B. altissimus* Mass. and *B. singaporensis* Pat. et Baker).

Strobilomyces velutipes (Figure 9). The reconstruction is complicated by the necessity to distinguish the spore-circles S' , S'' and S''' for the exospore from (S'), (S'') and (S''') for the endospore. Two reconstructions are shown. That on the right fits the smooth boletoid spore and that on the left is the true spore. The spore on the right has exospore and endospore concentric, but this would allow ornamentation to be developed all over the spore, as with *B. retisporus*. The normal spore has a smooth adaxial patch, where the membrane of the exospore can be seen to touch the endospore, and the warts are graded in height from the shortest on the adaxial face to the tallest on the abaxial. The endospore has, therefore, to be constructed eccentrically to the exospore. The m circle for the normal spore gives too large a spacing but the (m) circle with centre on S''' and radius $S''' w$ gives the correct spacing for the endospore. This arrangement means compression of S' to (S') without compression of M , and S''' remains unaffected. The spore is produced on a wide basidium with much less compression than with the smooth boletoid spore and is, accordingly, broadly ellipsoid and even subglobose. The whole basidium-unit is the least modified and, presumably, the most primitive among boleti.

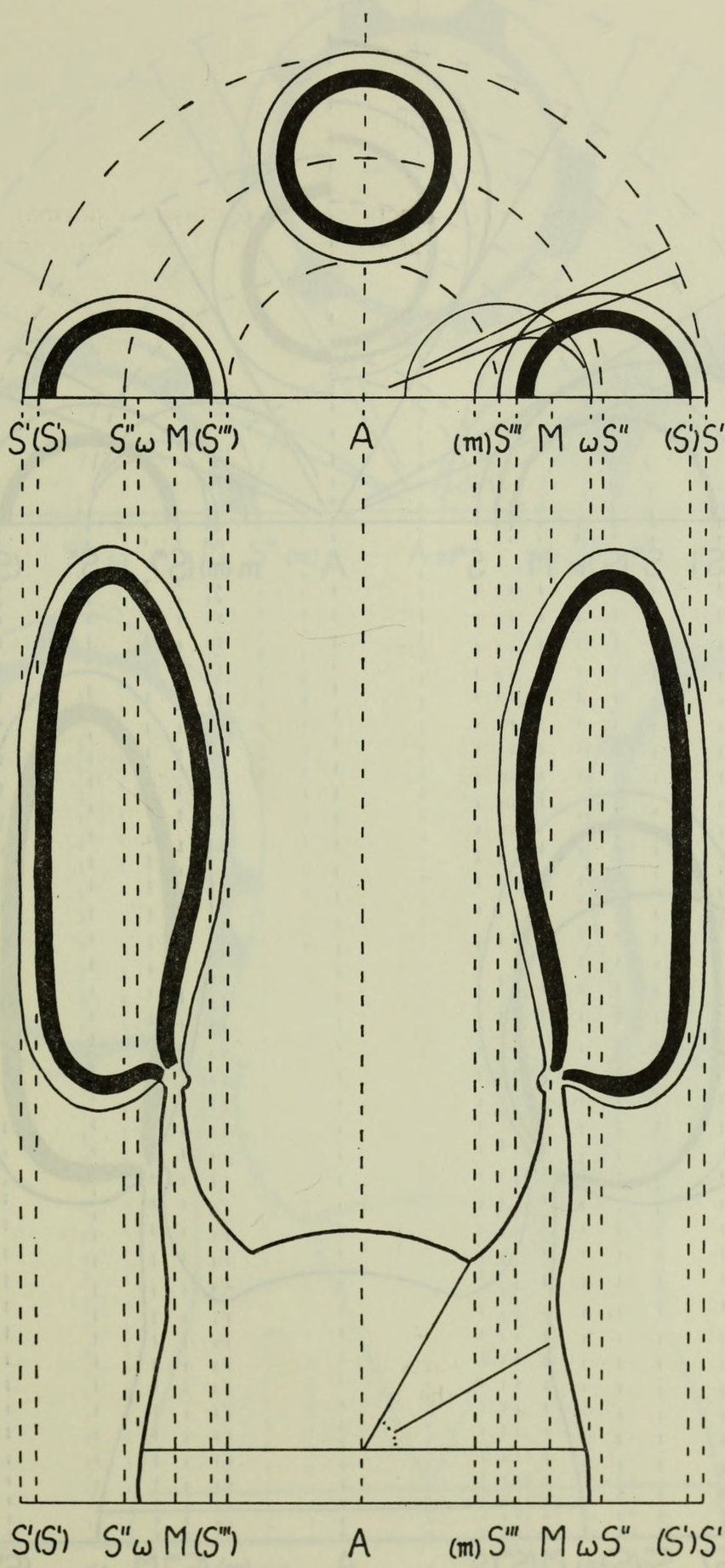


Figure 6. *Boletus albo-ater*, with exospore and endospore; x 5000.

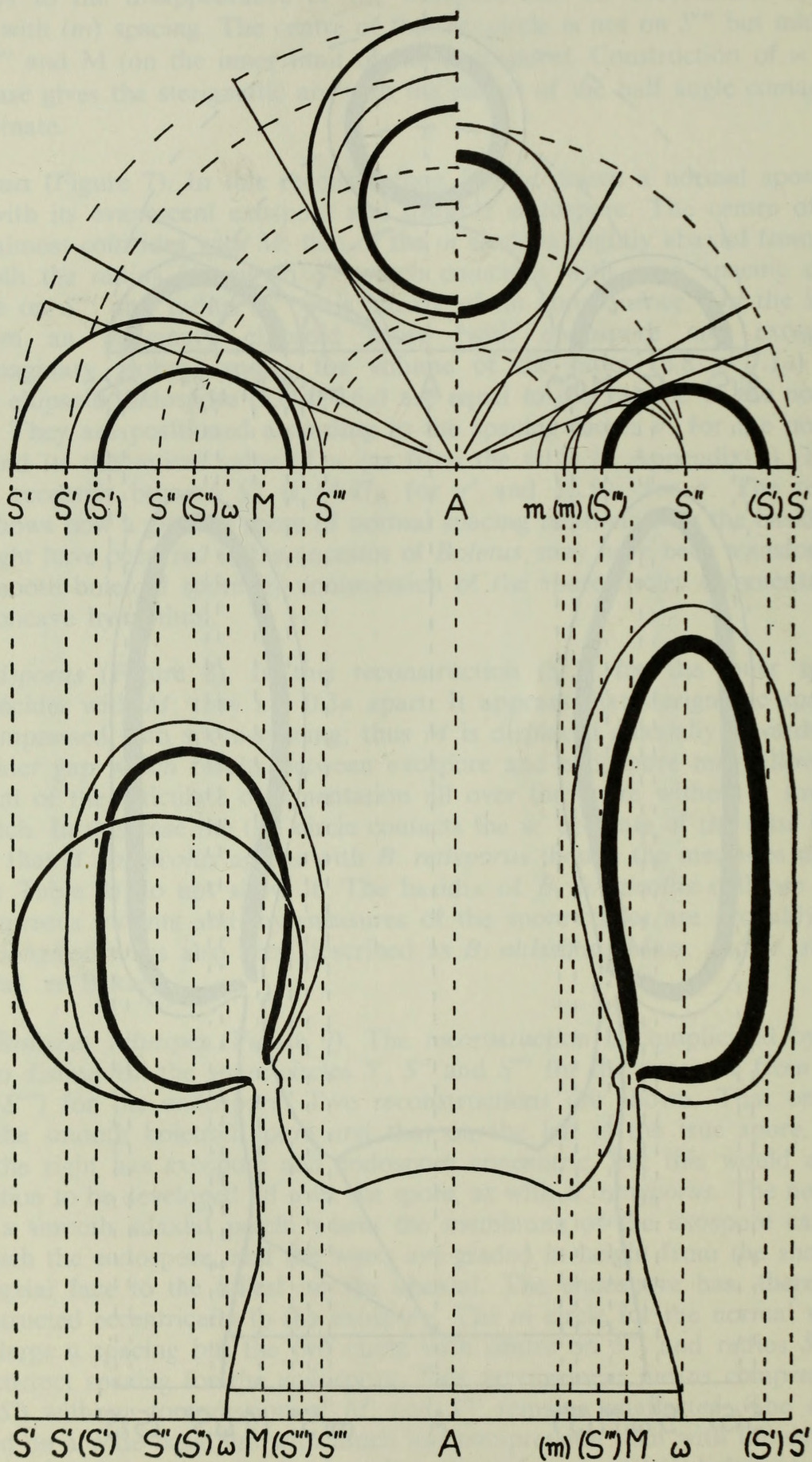


Figure 7. *Boletus nanus* with a normal spore on the right and, on the left, imaginary ellipsoid and globose spores of the same volume as the normal endospore but altered in shape according to the spacing (see text); x 5000.

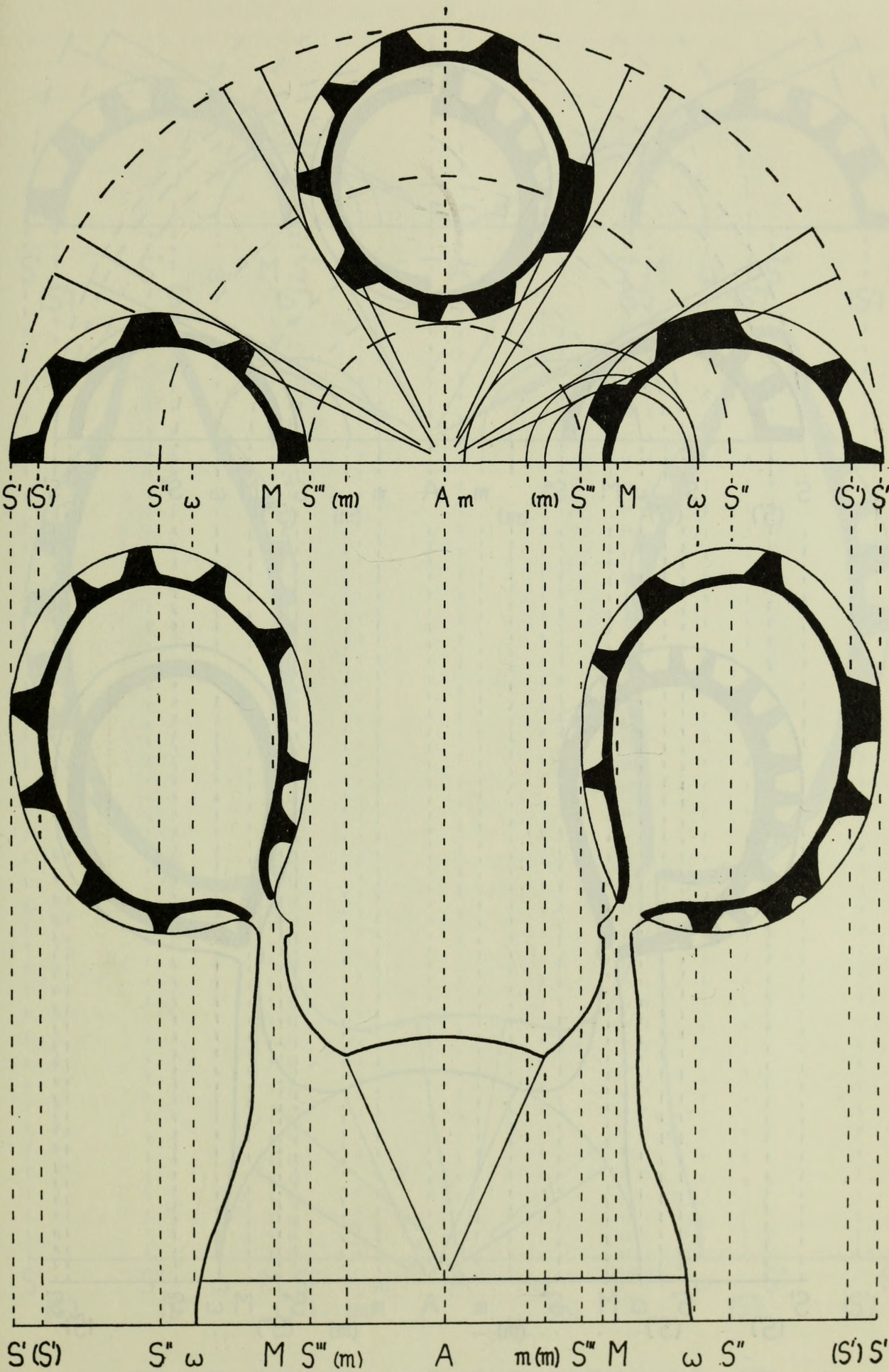


Figure 8. *Boletus (Heimiella) retisporus*; x 4500.

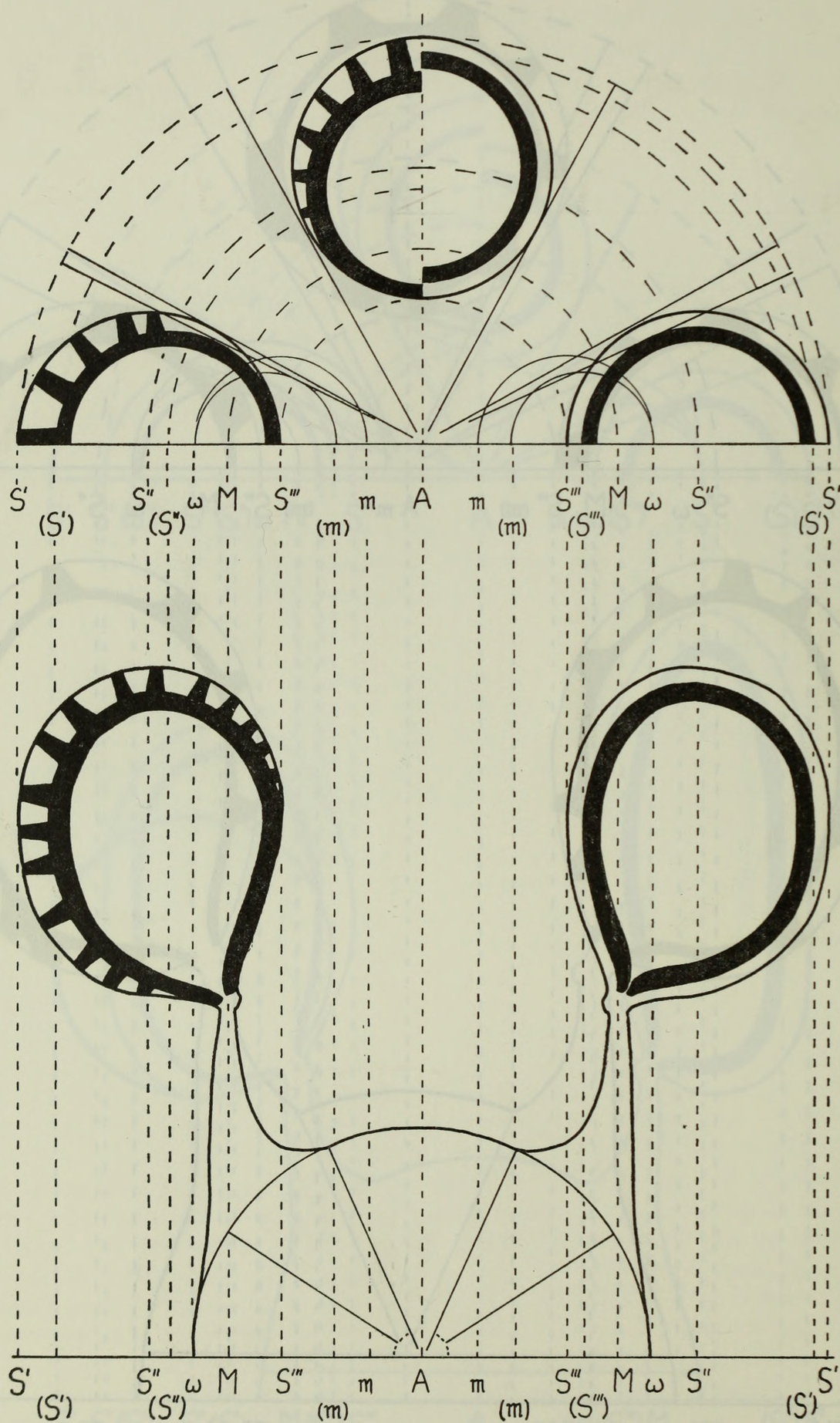


Figure 9. *Strobilomyces velutipes* with a normal spore on the left and an abnormal spore, constructed as a smooth spore, on the right; x 4800.

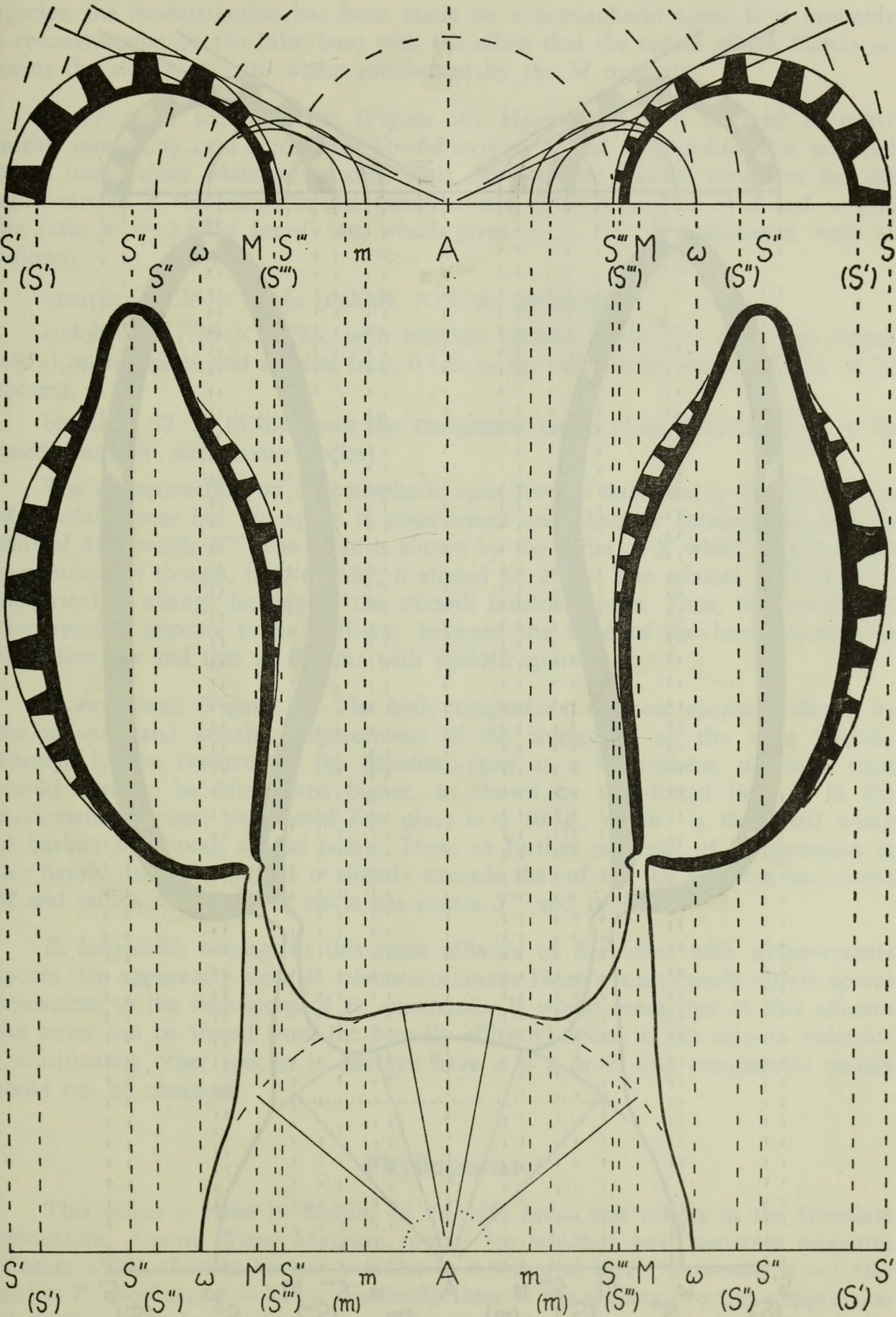


Figure 10. *Porphyrellus* sect. *Graciles* (unidentified species); x 4600.

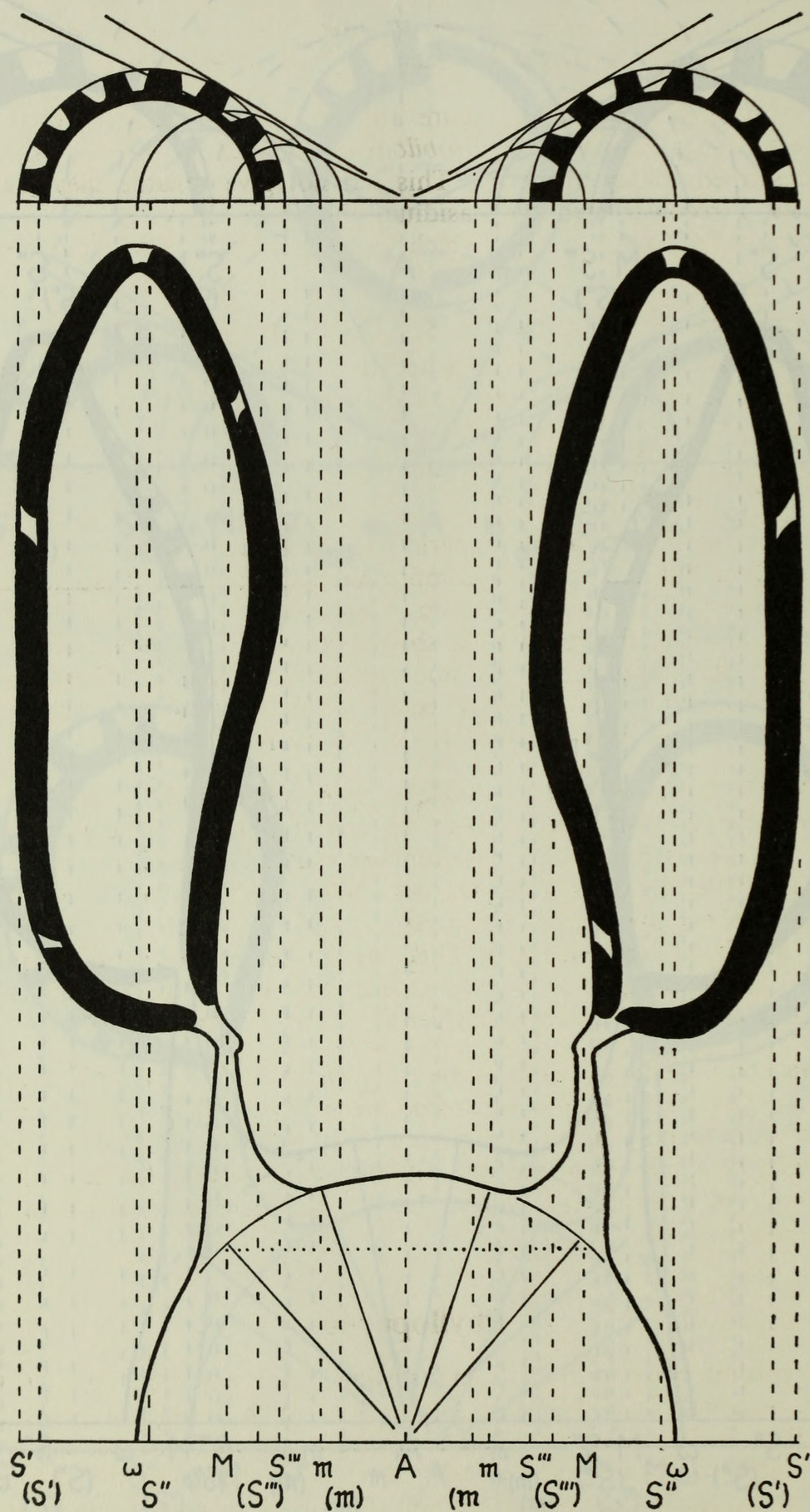


Figure 11. *Boletus emodensis*; x 5000.

Having no detailed analysis of the curvature of the basidium-apex in this species, the reconstruction has been made on a hemispheric apex. It is probably a reconstruction on the false base with the effect that the radius which bisects α meets the sterigmatic arc where intersected by the M ordinate.

Porphyrellus sect. *Graciles* (Figure 10). Having no fresh material to study in this interesting case allied with *Strobilomyces*, I used alcohol-formalin material of an undescribed Malayan species. This did not give reliable measures for the spore-circles. I reconstructed the basidium-unit from measures of d and w and the ratio $w = 1.655d$ for $d' \tan$, which gives $\sigma' = 0.5$. The measures were as follows: —

exospore $17.36 \times 8.41\mu$ (radial), $\times 9.16\mu$ (tangential);

endospore $17.36 \times 7.26\mu$, with truncate conical warts $0.7-1.2\mu$ high (mean 0.95μ) on the sides and abaxial face, $0.1-0.3\mu$ on the adaxial side; (average of 30 spores);

basidium $32 \times 15.16\mu$, with the sterigmatic circle 11.8μ wide (average of 50 basidia and 40 sterigmatic circles).

The reconstruction on a hemispheric apex for the basidium is similar to that of *Strobilomyces* but the spore is compressed and elongate through the adaxial shift of M towards S''' . The point is shown by the value of S' which is 27μ in the reconstruction though, theoretically, it should be 28.6μ . The adaxial shift of M is the principal change leading to the smooth boletoid spore. Thus, this section of *Porphyrellus* appears to be half-way between the state of the basidium-unit in *Strobilomyces* and that in *Boletus* with smooth spore.

B. emodensis (Figure 11). The high compression of these spores is shown by the upward and adaxial displacement of the sterigmata on the wide basidia. Though I have constructed the basidium-apex as a hemisphere, the false base would need to be lifted even higher, as shown by the dotted line, to fit the sterigmatic patches; the dotted line gives $w = 10.1\mu$, which is the usual width of basidia in smooth spored boleti. Then, as further evidence of compression in this figure, the real value of w slightly exceeds that of S'' ; the m circle has centre M and radius Mw ; the (m) circle has centre S''' and radius $S''' M$.

B. longicollis belongs in this same alliance of *Boletellus* with striate-costate spores. So, apparently, does *B. obscurecoccineus* Hoehn. with faintly striate spores equivalent to the endospore of *B. emodensis*. It would seem that in this alliance the series can be traced from the broadly ellipsoid spore to the smooth boletoid. Unfortunately other species in Malaya have $n = 2$ or 3 , and comparable results could not be obtained.

Phylloporus

This genus is close to *Boletus* in its wide sense and differs in the lamellate hymenium. Among fifteen Malayan species for which I have accurate measures (Corner 1970), thirteen have $d = 0.42w$ to $0.56w$, but in *P. borneensis* $d = 0.58w$ and in *P. coccineus* $d = 0.71w$. Evidently there is the tendency to the compression of the spore-circles in this genus without the development of the fully tubular hymenium. I worked out the details for *P. cingulatus* (Table 4); they showed the boletoid features of close agreement between the values of S'' and w and of the location of the M ordinate through the m circle on the false base.

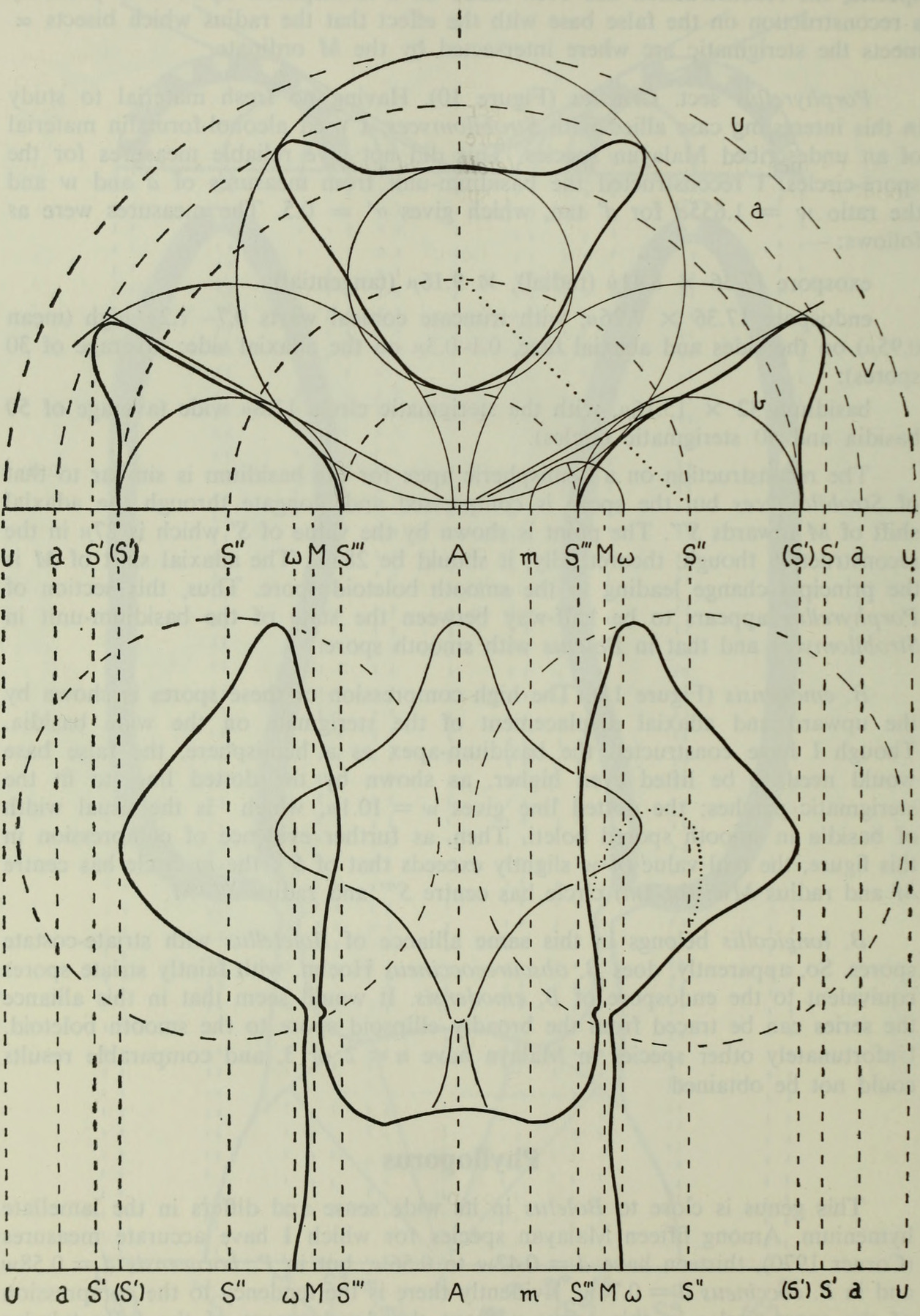


Figure 12. *Marasmius nigripes*; x 5000.

If, as I consider, the poroid *Boletus* has been derived from a lamellate agaric of *Paxillus-Phylloporus* affinity, then it seems that the characteristic of the *Boletus*-spore was developed in this ancestor, but both *Paxillus* and *Phylloporus* have smooth spores. This conflicts with the idea, put forward in previous pages, that the primitive *Boletus* had an ornamented endospore. Therefore the monotypic South American *Phylloboletellus* Singer stands out because it has the phylloporoid hymenium and the striate-costate spore of *Boletellus* (Singer 1964). According to Singer's measurements, in *Phylloboletellus chloephorus* $d = 0.78w$ and this implies both σ' and σ spacing. Certainly it suggests a primitive boletoid fungus, though apparently without adaxial patch. This is supplied by *Gloeocantharellus* with ornamented spores and apparently no exospore. For three of its five species $d = 0.59$ to $0.65w$ (Corner 1969). There appears to be a single spacing factor with external ornamentation, as in *Russula* and without any of the elaboration of the boletoid spore.

Marasmius nigripes Schw.

The remarkable spores of this fungus illustrate the use of geometrical analysis (Figure 12). In adaxial and abaxial view the spores are cruciform; in side-view they are trigonous and in end-view crescentic. They develop from the spore-rudiment into a shortly clavate form ($6 \times 3\mu$), typical of many species of *Marasmius*; this form is shown in dotted outline in the figure. Then shoulders develop to extend laterally and abaxially while the apex lengthens into the third arm and the spore-body swells to full size. There are no radial arms against the boundaries of S' and S''' . Figure 12 is based on averages from ten basidia in side-view and ten in end-view; the basidium apex is drawn as semicircular.

On this reconstruction I then drew (i) the radial tangents to the spore-body and spore-arm; (ii) the sterigmatic patch circle (centre S''' , radius $S''' w$); (iii) a spore-body circle b inscribed on S'' between S''' and S' , and found to my surprise that it fitted the tangent to the spore-arm; (iv) a spore-arm circle v (centre S'' , radius S'' to the apex of the arm), and found to my surprise that it contacted adjacent spore-bodies and almost reached the long axis of the basidium; (v) an outer spore-circle a (centre A, circumscribing the spore-arms); (vi) an outermost circle u circumscribing the v circles, as the outermost limit of the basidium-unit.

This figure leads to the following conclusions:—

(i) the m circle may be the prime spacing circle for the spores; that it does not contact the tangent in the drawing may be due to the difficulty in locating the exact tangent in this region where the curvature of the spore is changing.

(ii) the m circle gives $\sigma = 0.42$ or $w = 1.51d$, which corresponds with $w = 1.52d$ for average measures of spores ($9.12 \times 8.11\mu$) and basidia ($25.32 \times 8.10\mu$).

(iii) the b circle, contacting the spore-arm tangent, gives $\sigma = 0.44$ or $w = 1.55d$.

(iv) the actual spore-body (with radius measured along the dotted line joining adjacent spore-centres in Figure 12) gives $\sigma = 0.61$ or $w = 1.84d$.

(v) the spore starts with theoretical spacing of σ for the mature basidium; it then reduces this to σ' , grows radially to the allowance of σ' , but this extension occurs only about the mid-length of the spore; the spore-body is itself compressed tangentially to a value between σ' and σ .

(vi) in final form, as shown by the v circles, the spore comes to fulfil by some physical means the whole spore-sector.

The compression of the spore-body, mentioned in (v), may bear on the nature of the long, narrowly clavate spores of many species of *Marasmius*, as another instance of spore-compression, similar to that of *Boletus*. I have seen a fine mucilage sheath round many *Marasmius* spores. On germination of the spore of *M. nigripes*, it is only the spore-body that swells.

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Appendix 1

Summary of the relations between the spores and the basidium ($n = 4$) d = spore-width; m = diameter of the sterigmatic patch circle; w = basidium-width; M = diameter of the sterigmatic circle; S' , S'' , S''' = diameters of the outer, middle and inner spore-circles respectively.

α = the sterigmatic patch angle; δ = half the spore-subtending angle; θ = the spore angle; σ = the spore-spacing factor.

Text reference

$$\text{Side of square inscribed in } S'' = d(1 + \sigma) \dots\dots\dots (1)$$

$$S'' = d\sqrt{2}(1 + \sigma) = d \operatorname{cosec} \delta = \frac{d}{\sin \delta} \dots\dots\dots (2), (6)$$

$$S' = S'' + d = d\sqrt{2}(1 + \sigma) + d = \frac{d(1 + \sin \delta)}{\sin \delta} = d(1 + \operatorname{cosec} \delta) = S''' \sec \alpha \dots\dots\dots (7)$$

$$S''' = S'' - d = d\sqrt{2}(1 + \sigma) - d = \frac{d(1 - \sin \delta)}{\sin \delta} = d(\operatorname{cosec} \delta - 1) \dots\dots\dots (8)$$

$$S' + S''' = 2S'' \text{ and } S' - S''' = 2d$$

$$\frac{S'}{S''} = 1 + \sin \delta \quad \frac{S'''}{S''} = 1 - \sin \delta \quad \frac{S'''}{S'} = \cos \alpha \quad \frac{S' S'''}{S''} = w$$

$$M = \frac{w \cos \alpha}{2} = w \sqrt{\frac{1}{1 + \sin \delta}} = w \sqrt{\frac{S''}{S'}} = S''' \sqrt{\frac{S'}{S''}} \dots\dots\dots (14)$$

$$M = d \cot \delta \cos \delta \sqrt{\frac{1}{1 + \sin \delta}} \dots\dots\dots (22)$$

$$M = S'' - 0.7d = d(\operatorname{cosec} \delta - 0.7) = d[\sqrt{2}(1 + \sigma) - 0.7] \dots\dots\dots (9)$$

$$\sigma = \frac{S''}{d\sqrt{2}} - 1 = \frac{\operatorname{cosec} \delta}{\sqrt{2}} - 1 \dots\dots\dots (10)$$

$$\sigma = \frac{1 + \cos \alpha}{\sqrt{2}(1 - \cos \alpha)} - 1 \dots\dots\dots (15)$$

$$m = S''' \sin \delta = d(1 - \sin \delta) \dots\dots\dots (11)$$

$$w = S''' + m = S'''(1 + \sin \delta) = \frac{S' S'''}{S''} = d \cos \delta \cot \delta \dots\dots\dots (12) (13)$$

$$\sin \delta = \frac{d}{S''} = \frac{1}{\sqrt{2}(1 + \sigma)} = \frac{S'' - M}{S'' \sin \theta} = \frac{1 - \cos \alpha}{1 + \cos \alpha} \dots\dots\dots (17)$$

$$\cos \alpha = \frac{S''' - m}{S''' + m} = \frac{1 - \sin \delta}{1 + \sin \delta} = \frac{S'''}{S'} \dots\dots\dots (15)$$

$$\cos \frac{\alpha}{2} = \sqrt{\frac{1 + \cos \alpha}{2}} = \sqrt{\frac{1}{1 + \sin \delta}} = \sqrt{\frac{S''}{S'}}$$

$$\sin \theta = \frac{S'' - M}{d} = \frac{S'' - M}{S'' \sin \delta} = \operatorname{cosec} \delta - \cot \delta \cos \delta \sqrt{\frac{1}{1 + \sin \delta}} \dots\dots\dots (18), (23)$$

$$d = \frac{S'' - M}{\sin \theta}$$

APPENDIX 2

Variations in the parts of the basidium-unit with variations in σ

σ	S'	S''	S'''	M	m	w	2δ	θ	α	$\sin \delta$	$\sin \theta$	$\cos \alpha$
0	2.414d	1.414d	0.414d	0.5413d	0.2929d	0.7069d	90°	60° 47'	80° 7'	.7071	.8728	.1715
.1	2.555d	1.555d	0.555d	0.7106d	0.3569d	0.9119d	80° 3'	57° 33'	77° 27'	.6431	.8439	.2172
.2	2.697d	1.697d	0.697d	0.878d	0.4109d	1.1079d	72° 10'	54° 48'	75° 1'	.5891	.8172	.2584
.3	2.838d	1.838d	0.838d	1.042d	0.4559d	1.2939d	65° 56'	52° 52'	72° 50'	.5441	.7972	.2952
.4	2.980d	1.980d	0.980d	1.203d	0.4949d	1.4749d	60° 41'	51° 3'	70° 48'	.5051	.7776	.3289
.5	3.121d	2.121d	1.121d	1.360d	0.5286d	1.6496d	56° 14'	49° 33'	68° 57'	.4714	.7610	.3591
.6	3.262d	2.262d	1.262d	1.516d	0.5579d	1.8199d	52° 28'	48° 15'	67° 14'	.4421	.7460	.3869
.7	3.404d	2.404d	1.404d	1.671d	0.5840d	1.9880d	49° 10'	47° 13'	65° 39'	.4160	.7338	.4124
.8	3.545d	2.545d	1.545d	1.824d	0.6071d	2.1521d	46° 16'	46° 8'	64° 10'	.3929	.7210	.4358
.9	3.687d	2.687d	1.687d	1.976d	0.6270d	2.3149d	43° 42'	45° 17'	62° 46'	.3721	.7106	.4576
1.0	3.828d	2.828d	1.828d	2.126d	0.6464d	2.4744d	41° 24'	44° 30'	61° 29'	.3536	.7010	.4775
1.5	4.535d	3.535d	2.535d	2.872d	0.7171d	3.2521d	32° 52'	41° 32'	56° 1'	.2829	.6630	.5590
2.0	5.242d	4.242d	3.242d	3.603d	0.7643d	4.0063d	27° 16'	39° 43'	51° 48'	.2357	.6390	.6184
2.5	5.950d	4.950d	3.950d	4.330d	0.7980d	4.7480d	23° 18'	38° 19'	48° 24'	.2020	.6200	.6639
3.0	6.656d	5.656d	4.656d	5.051d	0.8232d	5.4792d	20° 22'	37° 14'	45° 36'	.1768	.6050	.6997



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