The Development of *Mutinus caninus* (Huds.), Fr.¹

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With Plates XVII and XVIII.

IT is my purpose to trace in the present paper the course of development of *Mutinus caninus*, as shown in a closely connected series of the so-called eggs. Three objects are kept in view :—

1. To determine from the course of development in the youngest stages the relationship, if any, between the Phalleae and the Clathreae—the two principal sections of the Phalloideae.

2. To subject the development of the wall of the receptaculum—the latter consisting of merely a stipe in this species—to a more critical examination than it has hitherto received.

3. To make suitable record, by means of the illustrations, of the most important typical stages of development which could be selected from forty-four fructifications of this species which have been examined, and of which I have permanent preparations.

Although a valuable contribution to our knowledge of the

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Phalloideae has been recently made by A. Möller¹, still, up to the present time, only two of the Phalleae have been described and figured in their youngest stages, on account of the great difficulty of procuring such stages. Both investigations were made by Ed. Fischer. The first of these, published in 1890, was on *Ithyphallus impudicus*², and the second, in 1895, on *Mutinus caninus*³. In both these investigations, however, the supply of material was deficient in important young stages. In the case of *I. impudicus*, this resulted in an erroneous view of the course of development at a point of great importance in determining the relationship between the Phalleae and Clathreae. A more correct view is presented in the recent paper on *M. caninus*, yet here also the lack of closely connected stages compels the author to make the reservation that the course of development outlined in the earlier paper may, after all, be the true one, thus leaving the question still open. But these points, and that in regard to the origin of the gleba, will be treated more explicitly in the following pages.

The material used in my investigation was collected in Somerville, Mass., in July, 1894. In this connexion I desire to express my thanks to Mr. B. M. Duggar and to Mrs. H. A. Ricker for directing me to a locality where this plant—which, in our region, is usually found growing solitary or in clusters of but few individuals—was growing in great luxuriance and abundance in a neglected area.

Through the kindness of Prof. Farlow this material has been compared with authentic specimens of *Corynites Ravenelii*, B. and C., in the Curtis Herbarium, and it is undoubtedly of the same species. There does not seem to be good ground for regarding *C. Ravenelii*, B. and C., as specifically distinct from *Mutinus caninus* (Huds.), Fr.

¹ Brasilische Pilzblumen. Jena, 1895.

² Untersuchungen zur vergleichenden Entwicklungsgeschichte und Systematik der Phalloideen. Denkschr. d. Schweiz. Naturf.-Ges., Bd. XXXII, 1, 1890, p. 22.

³ Die Entwicklung der Fruchtkörper von *Mutinus caninus* (Huds.). Berichte der Deutschen Bot. Ges., 1895, Bd. XIII, p. 128.

METHODS.

In general, alcohol-material as needed for study was stained in the mass for twenty-four hours in P. Mayer's paracarmine—a 70 per cent. alcoholic stain. This penetrated well. After washing and dehydrating, the fructifications were finally brought into pure cedar-oil. After they had sunk to the bottom in this, paraffin was gradually added to saturation. The fructifications were then transferred to the paraffin-bath, and finally imbedded in paraffin melting at 58° C.

The sections were usually cut $6\frac{2}{3} \mu$ thick, with a Minot-microtome, and were attached to the slide with Mayer's albumen-fixative after floating out on the slide in water. The paraffin was removed with xylol. The sections were run down through the grades of alcohol to water, and were then stained on the slide with aqueous solution of safranin for about five minutes.

They were mounted temporarily in water. All the drawings showing hyphal structure were made from preparations in water. They were then permanently mounted in glycerine by running under the cover-glass a mixture of two volumes of concentrated glycerine and one volume of distilled water. After allowing this to concentrate by evaporation from under the edges of the cover-glass, the mounts were cleaned and then sealed with hot glycerine jelly and finished with Bell's cement.

Attempts were made to find staining methods which would give still better results than the one described, but they were unsuccessful in general. With very small fructifications not having the gelatinous layer of the volva differentiated, haematoxylin stains could be used, and the dark colour which they gave to the walls was a great help in the camera lucida work of such medium power drawings as my Figs. 1 and 2. A slight staining of the walls of the hyphae with Ehrlich's haematoxylin, just before using the safranin, may be made with advantage in some cases. The method of employing potassium hydrate with thin unattached sections is described in another place.

FINAL STAGE.

The main features of *M. caninus*, and the chief terms to be employed, may be brought to mind by a brief description of the more familiar mature stage. In this stage a fusiform-cylindrical stipe issues vertically upward through the ruptured apex of a fleshy bag, called the volva or peridium. The apex of the volva is usually near the surface of the ground. The white or reddish stipe is hollow, about 6 to 15 cm. long by 1 cm. in diameter, and has a brittle wall of chambered structure (Figs. 13 and 14). The partition-walls of these chambers consist of a modified hyphal tissue called pseudoparenchyma (*k*, Fig. 15). In the lower part of the stipe the chambers open outward, giving a perforated outer surface.

At the time of elongation of the stipe the upper one-sixth to one-third of its length is covered by a closely adnate, greenish spore-mass called the gleba, which has in some degree the fetid odour characteristic of the Phalloideae. Deliquescence of the gleba, accompanied by the formation of sugars¹, at once sets in, and the gleba soon drips away or is removed by flies and other insects², thus exposing the spore-bearing (i. e. gleba-supporting) part of the stipe. This portion is more highly flesh-coloured than the portion below, and the chambers of its wall open inwards into the main central cavity of the stipe.

The volva consists of three layers: a thin outer layer continuous with the cortical layer of the mycelial strand; a thin inner layer—the inner layer of the peridium—in the plane in which the volva splits away from the gleba at maturity; and a broad middle layer, highly gelatinous in nature, and hence called the gelatinous layer of the volva.

¹ Rathay und Haas: Ueber *Phallus impudicus* (L.) und einige Coprinus-Arten. Sitzungsber. d. Mathem.-Naturwiss. Akad. zu Wien, 1883, Bd. LXXXVII, 1. Abth. p. 18.

² Rathay und Haas, l. c.; Fulton, T. W.: Dispersion of Spores of Fungi by Insects. Annals of Botany, Vol. iii, 1889, p. 207; Gerard, W. R., In Bulletin of Torrey Botanical Club, Vol. vii, 1880, p. 30.

The fructification, or compound gonidiophore, in the stages before elongation of its stipe has occurred, is commonly called an 'egg.' The eggs usually arise at the ends of fine lateral branches of the mycelial strands, but they are occasionally found sessile laterally on the strands.

YOUNG STAGES.

First egg.—The youngest body that I have been able to recognize from its microscopic structure as an egg, and not the mere vegetative tip of a mycelial strand, is shown in median longitudinal section in Fig. 1. It was a soft, hyphal body having a length of $\frac{2}{3}$ mm. and a transverse diameter of $\frac{1}{5}$ mm. The mycelial strand bearing it had a diameter of $40\ \mu$. A bundle of about half a dozen hyphae *M*, Fig. 1, extends from the medullary portion of the mycelial strand up through the middle of the section into its upper portion. There the bundle branches, forming a dense, sheaf-like head *N* of interlacing and anastomosing hyphal branches very difficult to follow. The rest of the section is a more open structure *C*, consisting of loosely interlacing hyphae curving and branching and crossing in all directions. At the base of the egg, hyphae from the cortical portion of the mycelial strand may be followed up into this tissue *C*, where they branch, curve about, have the characteristic form of the tissue, and soon become lost by leaving the plane of the section. One such hypha is indicated by *e*.

Several eggs in this stage of development have been met with in preparing a complete series of stages. Rarely a hypha from the medullary bundle *M* will send out a branch into the cortical portion *C*, but here it immediately takes on the characters of this portion, and curves in and out among the other hyphae, branching as they do. In the mycelial strand such branches occasionally pass from the medullary into the cortical portion and become a part of it.

Contrary to the idea that has prevailed, these three parts of the egg—*C*, the continuation in the egg of the cortical

system of the mycelial strand; *M*, the continuation of the medullary system of that strand; and *N*, the upper end of *M*—come to play very unequal parts in later development. Of these parts *C* becomes the outermost layer of the volva; *M*, the bundle of medullary tissue connecting the mycelial strand with the base of the stipe; while the sheaf-like head *N* gives rise to all the remaining parts, including stipe, gleba, and gelatinous layer of the volva.

In eggs of this stage stained *in toto* in Delafield's haematoxylin or in P. Mayer's haemalum, the hyphae of the medullary bundle were about 4μ in diameter. They had very thin walls and were divided by extremely thin cross-walls into cells about 20μ long. In most of these cells there could be seen a deeply-stained, opaque, spherical mass about 2μ in diameter—presumably the nucleus. In the sheaf-like head *N*, the tissue was so intricate from the crossing of hyphae in different planes that the cross-septa could not be made out with certainty. The nuclei were, however, very numerous in this portion and not more than 3 or 4μ apart. The hyphae of the cortical portion are from 4 to 5μ in diameter and from 20 to 25μ long.

Ed. Fischer¹ described as young a stage of *Ithyphallus impudicus*, shown in his Fig. 18, which differs from my Fig. 1 chiefly in the greater number of hyphal branches from the medullary bundle (*M* of my Fig. 1) passing out nearly at right angles into the cortical layer. In having more such branches in the cortical layer of its egg than exist in *M. caninus*, the cortical tissue of the egg *I. impudicus* merely shares a character of the cortical system of its mycelial strand, as the latter has been made known by De Bary². On account of the presence of such branches in the egg of *I. impudicus*, Fischer separated the tissue which I have designated by *C* into an outer peripheral zone and an inner mass bordering on the medullary bundle. The inner mass he supposed to be identical with the

¹ L. c., 1890, p. 22.

² Zur Morphologie der Phalloideen. In Beiträge z. Morph. u. Physiol. der Pilze, Abhandl. d. Senkenb. Naturf.-Ges., Bd. V, 1864, p. 204.

intermediate tissue (*Zwischengeflecht*) of later stages. In reality the mass in question and the peripheral zone become only the outermost layer of the volva; hence a distinction between the two ceases to be of importance.

Second egg.—The next stage in the differentiation of the sheaf-like head *N* is shown in Fig. 2, with the same magnification as in the preceding figure. The egg of this stage had a length of about 1 mm. and a transverse diameter of $\frac{1}{2}$ mm. The general arrangement of parts is the same as in Fig. 1. The cortical tissue *C* is continued up from the mycelial strand and forms the outer portion of the egg. The bundle of medullary tissue *M* has about the same position as in Fig. 1, and can be traced as a bundle up to about the centre of the egg, where it branches as in Fig. 1, and becomes lost in the spherical mass *N*, lying in, and almost wholly constituting, the upper half of the egg.

The peripheral portions at the upper end and sides of the head *N* have pushed outward against the cortical layer *C*, and have become differentiated into a more loosely interwoven structure *L*, in which many of the hyphae have a radial position. Many of the hyphae along the inner surface of the cortical layer *C*, pass into, and take part in, the formation of the marginal portion of this more open structure; still the general appearance of the section is such as to indicate that the structure is, on the whole, of medullary nature, arising from *N*. In this stage, two regions may therefore be indicated in the head *N*; the more open portion *L*, just described; and the dense portion *O*, consisting of hyphae intricately interwoven and anastomosing, and with their nuclei at only very short distances apart.

At *m*, Fig. 2, the medullary bundle *M* breaks up and passes into the sheaf-like head *N*. One of the few hyphae of that bundle has chanced to lie in the plane of the section for a portion of its length after leaving the bundle. This hypha is designated by *m*. It passes obliquely upward towards the left, and certainly at two points gives off branches into the open portion *L*, and is also connected on the other side with

the dense portion *O*, by anastomosing branches or processes. There is great significance in the direct connexion of the medullary bundle *M* with the outer portion of the sheaf-like head at its base; for it shows an original direct connexion of the medullary bundle with the base of all parts of the later plant except the outermost layer of the volva.

Third egg.—The egg of this stage is larger, measuring $1\frac{1}{2}$ mm. long by $\frac{4}{5}$ mm. wide. By far the greater part of the increase in growth has been in the sheaf-like part, which now measured 700μ in diameter. Differentiation of the dense portion *O* has now given rise to an axial column of interlacing hyphae, extending upward from the upper end *m* of the medullary bundle of Figs. 1 and 2 (*R*, Fig. 3). In the preparation this column is about 500μ long by 100μ wide; it has taken an orange-red stain, and is thus quite distinct from the surrounding tissue on its sides; a longitudinal direction slightly predominates in the position of its hyphae. This column *R* persists as an axial column of gelatinous tissue until the period of elongation of the stipe.

Lying against the column *R*, on its sides and upper end, is the remainder of the dense tissue *O*, which is now—especially in its upper portion—a denser structure than *R*. It is now the region where the nuclei are most numerous and nearest together in the hyphae. The hyphae of this portion still retain their connexion with the column *R*; they are densely interwoven and many of them are arranged radially.

A gelatinous accumulation has set in at *G*, in the open tissue *L*. It is the beginning of the gelatinous layer of the volva. This gelatinous substance is regarded as a transformation-product of the hyphal wall¹. It lies close against the dense portion *O*, in a narrow zone of irregular width—ranging from 20 to 80μ in this preparation. It is stained orange by the safranin employed.

¹ See De Bary, *Beiträge z. Morphologie u. Physiologie der Pilze*, I. Reihe, (1864), p. 195; and also Van Bambeke, *Sur la Morphologie du Phallus impudicus* (L.), Bull. de la Société Royale de Botanique de Belgique, T. XXVIII, 1889, p. 39.

The features of this stage consist in the beginning of—

1. The differentiation of the main central column *R* of the stipe, and
2. The gelatinous accumulation in the layer of that nature in the volva.

Fourth egg.—In the more advanced stage of Fig. 4, the central column *R* is more distinctly set off from the tissue at its sides. Near the column this tissue has become looser (the portion *A*), but still remains dense and with many nuclei in its dome- or bell-shaped peripheral portion. At its upper end, the column *R* has connexion with this dense portion, thus marking out the permanent connexion that exists at the apex of the receptaculum between the column *R* and the tissues of the gleba and gelatinous layer of the volva in Fig. 5, and in those of later stages. In the early stage of Fig. 4 the column is not contracted at this place of connexion, as in Fig. 5, but its hyphae spread apart, forming a mass with an angle of divergence of about 60° between its opposite sides.

This stage shows a great increase in the gelatinous accumulation, which now fills all the loose structure *L*, in the upper part of the egg, and is extending downward in this structure, but keeping close against the cortical layer *C* in its downward course.

Fifth egg.—This stage is intermediate between that of Figs. 4 and 5. The central column spreads out less at its upper end and has thus become cylindrical in form. With the growth of the egg, the dense zone has become still further removed from the column at the sides. Along the inner surface of this zone, differentiation of the hymenium is in progress; this is shown under low magnification by the presence of a dark, narrow, interrupted line lying parallel to the dense zone, and evidently formed from an inner portion of it. Under high magnification this line is found to consist of swollen portions of hyphae and of their branches arranged side by side.

INTERMEDIATE STAGES.

It is convenient to consider as *young* stages all those in which there is not yet any well-marked differentiation of the wall of the receptaculum; as *intermediate* stages, those in which the wall of the receptaculum is present but not yet crowded into folds; and as *advanced* stages those with the walls of the receptaculum folded.

Sixth egg.—The rudiment of each part of the mature plant is now recognizable, occupying the position which it has in the old egg. This is apparent by a glance at Figs. 10 and 5. The latter, Fig. 5, represents a median longitudinal section through an egg about 2 mm. in diameter, drawn under lower magnification than the preceding figures. Comparing this with the general features of those figures, we observe, that the vigorous growth in the sheaf-like head *N*, which has gone on with its rapid differentiation, has greatly changed the relative proportions and apparent positions of the parts of those stages; that the cortical layer *C* forms the outer covering of the egg, and is still present in greatest amount at its lower end; and that the medullary bundle *M* runs upward through this basal mass to the lower end of the central column *R*. With the exception of the cortical layer *C*, and the medullary bundle *M*, all the rest of the egg has been found to arise from the sheaf-like head *N*.

Examining the latter structure more closely, it may be seen that the central column *R* is now slightly contracted at its apex, and is taking on the slightly fusiform outline characteristic of the cavity of the stipe in the mature plant. Just outside the column *R* the rudiment of the wall of the stipe *S* is becoming differentiated from the loose tissue *A*. Following Ed. Fischer, this loose tissue *A* will be called *intermediate tissue* (*Zwischengeflecht*), but this term should not be used for the Clathrae.

In later stages, splitting away of the volva from the gleba and receptaculum occurs through the zone *i* in a plane parallel with the outer surface of the egg. On the peripheral side of

i there is a broad mass of gelatinous tissue, horse-shoe shaped in section; it is the gelatinous layer of the volva, and has already been described as making its way downward in the loose tissue *L* and keeping close to the cortical layer. Now it quite encloses on the top and sides the central mass of tissue, in which important developmental changes are in progress. Although the question must be left unanswered, it may be asked if the function of this gelatinous layer is not protective?

On the opposite side of *i*—at *H*—the young basidia of the hymenium are forming. A cluster of these basidia from near the point indicated by the end of the line from *H* is shown in Fig. 6. As nearly as I could determine, the hyphae which give rise to the basidia are composed of short cells, the cross-septa of which do not show very distinctly, however, in my preparations. From each of these cells an outgrowth occurs which may form one of the swollen basidial cells, or may become septate, like the hypha from which it arises, and then give rise to a cluster of basidia. The latter is more likely to occur when the outgrowth originates at some distance from the palisade-like layer, in which the young basidia stand side by side. The tramal connexions of the basidia are towards the dense zone *i* and the apex of the column *R*.

In Fig. 6, the intermediate tissue *A*, lying between the hymenial layer *H* and the stipe, has been separated from the tramal tissue through the formation of the basidia. In Fig. 5, the tramal tissue and intermediate tissue are in connexion at several points where basidia have not yet formed. In the preceding stage intermediate portions of the hyphae were swollen with protoplasm in the region where the hymenium was developing. The conditions there, taken in connexion with those of the present and with those of later stages to be described, seem to indicate that the ready separation from, and pushing away of, the intermediate tissue *A* by the forming basidia may be favoured by atrophy of the hyphal connexions with that tissue. In a slightly later stage the separation becomes more complete (Fig. 8).

In his recent paper on *M. caninus*, Ed. Fischer has pointed out the connexion between the masses of tramal and intermediate tissue, and has concluded that the gleba must originate from the differentiation of portions of the intermediate tissue¹. The course of development does not favour this conclusion (see Fig. 4), but shows rather that the intermediate tissue *A* and that of the gleba, although both arising from the sheaf-like head *N*, by the differentiation of originally intimately connected portions, tend to almost wholly lose such connexions through developmental changes, and have nothing further in common in their development. In such further development the glebal tissue, making its tramal connexion with the upper end of the central column *R* of apparently increasing functional importance, takes on the formation of spores; while the intermediate tissue *A*, losing also its connexions with the sides of the column *R*, but retaining those with the basal portions of the egg, goes on to form a receptaculum of varied form for the different genera—a supporting and elevating structure for the spore-mass.

The rudiment of the wall of the stipe is in the stage of Fig. 5, a narrow layer, *S*, of swollen portions of hyphae very irregular in form and very intimately connected with the loose intermediate tissue *A*, of which they form a part. The hyphae of this rudiment lie close against, and often interlock with, the longitudinally running hyphae of the column *R*. The details of this structure are shown in Fig. 7, which represents under higher magnification a portion of the rudiment of the stipe with adjacent tissues at the lower end of the stipe. The exact position of this area in Fig. 5 is indicated by *S*. The hyphae on the left in Fig. 7 belong to the tissue of the central column *R*; those on the right are in the intermediate tissue *A*; the more deeply shaded hyphae between constitute the rudiment of the stipe *S*. The septa of the hyphae did not show distinctly in the preparation, and no attempt at their representation has been made in the figure. The hyphae of

¹ L. c., 1895, p. 136.

this rudiment run in very irregular and zigzag courses in all directions, and give out short lateral processes or branches, but these are probably in part anastomosing connexions which have been cut in sectioning. These hyphae stain deeply. Higher up the stipe the hyphae of the stipe and those of the column *R* are less interlocked than in this figure.

Relationship of Phalleae and Clathreae.

We may here consider the bearing of the facts of early development upon the views held as to the relationship between the Phalleae and Clathreae. As a stage of development has now been reached which is about the same as that illustrated by Ed. Fischer for *I. impudicus*¹, in his Figs. 20 and 21, it becomes possible to compare the actual course of development with the ideas that are prevalent. It should be understood, however, that Fischer's statement of the course of development was advanced tentatively, until a fuller series of stages should be available for study, and that in his late paper on *M. caninus*² he outlines and favours in some important features the course of development which I have presented here, but which I had already worked out independently in my inaugural thesis, before the publication of Fischer's paper. While advancing such newer views, he also states his inability to determine from his preparations whether his earlier scheme of development might not be the true one after all.

In Fischer's earlier account the central column of the intermediate stage was regarded as identical with the medullary bundle *M* of my Fig. 1, although Fischer was not sure that a portion of the upper end of the column might not be formed from a part of the sheaf-like head of *M*. The gelatinous layer *G*, the dense portion *i*, and the tissue of the gleba, were regarded as arising from the sheaf-like head *N*. By a vigorous interstitial growth, and the production of radially arranged

¹ L. c., 1890, p. 22.

² L. c., 1895, p. 130.

hyphae, the sides of the head would be carried farther and farther apart, until finally they would become directed obliquely downward about the sides of the medullary bundle *M*. *N* would thus become a dome resting on the top of the bundle *M*, with its sides extending obliquely downward about that bundle. Throughout this process the point *m* of the youngest stage would be regarded as close underneath and against the closed end of the forming dome, and having in later stages the position of the point *r* in my Fig. 5. The basidia were regarded as arising on the lower surface of the dome from the portions of *N*, which were so recurved as to face towards *M*.

This theory was directly misleading as regards the phylogenetic relationships of the Phalleae. In the Clathreae the hymenial tissue is within the receptaculum, and the free ends of the basidia face towards the periphery; in the Phalleae the hymenial tissue is on the outside of the receptaculum, and the free ends of the basidia face towards the longitudinal axis of the plant, as shown in Figs. 5 and 6. In these two respects the conditions in the Phalleae are exactly the reverse of what they are in the Clathreae. These differences, taken in connexion with the course of development that was accepted, would be reconciled by an origin of the Phalleae from some Anthurus-like member of the Clathreae by a protrusion upward—from the upper end of the rudiment of the receptaculum of that ancestor—of the tissue which was to give rise to the gelatinous layer of the volva and to the hymenium. By spreading out above the receptaculum and then recurving downward about it on the outside, the hymenial structure would have come to have the position on the outside of the receptaculum characteristic of the Phalleae. This would also have given the relative inversion in the direction of the basidia. The basidia, having a position in the young Clathreae close against the inner side of the receptaculum, with their free ends directed toward the periphery of the egg, would, upon coming outside the receptaculum and recurving downward, come to face in the opposite direction, or toward the axis. If

such had been the origin of the Phalleae, there ought to have been intermediate forms left somewhere on the way, but no such form could be found.

The actual course of development has proved to be very different from that presumed. The original medullary bundle *M* does not become the central column *R*; but instead merely connects the lower end of the latter with the mycelial strand. The rudiment of the stipe does not arise from the primitive cortical tissue lying next to the medullary bundle *M*, but from a secondary tissue differentiated in the medullary sheaf-like head *N*. Instead of being originally only connected with the mycelial strand in a roundabout way through the tissue of the central column *R*, there was originally a more direct connexion with the tissue giving rise to the gleba and the gelatinous layer *G* at the lower end of the future stipe—at the point *m*, Figs. 4 and 5. That this primitive condition should become lost, and that an apparently secondary connexion by way of the upper end of the column *R* through anastomosis of hyphae should become of more permanent functional importance, is exceedingly interesting, but no more surprising than the well-known later developmental change, through which the originally free surface of the hymenial or glebal structure becomes so firmly adnate to the receptaculum as to permit the gleba to be torn from its tramal connexions on the opposite side and carried aloft by the elongation of the receptaculum.

Since the original connexion of the tissue giving rise to the gelatinous layer of the volva, to the dense zone *i*, and to the hymenium, was directly connected with the point *m*, the outline first presented as to how the Phalleae might have arisen from the Clathreae becomes plainly contradicted by the facts, which show differences so fundamental as to point rather to independent origins for these two sub-families.

Seventh egg.—This egg was about 4 mm. long by 3 mm. in transverse diameter. On account of the curvature of the parts in the egg, my sections are not median for the full length of the receptaculum. The portion of the figure below

the line *S*, Fig. 8, had to be drawn from another section in the same series. The outer portions of the section have been omitted in the figure.

The gleba and its relations to the intermediate tissue *A* are of especial interest. The separation of the gleba from the intermediate tissue *A*, in progress in Fig. 5, is now more complete, and has resulted in the formation of a cavernous space, shown in Fig. 8. Some feeble hyphal connexions still remain between the projecting lobes of the gleba *H* and the tissue *A*. In some of the furrows of the former structure, hyphae are seen in a position suggesting their having been pulled away from the tissue *A*, in the movements which brought the portions of the hymenial surface to which they were attached to the bottom of the furrows. The formation of the cavernous space may be due to a very vigorous growth of the dome-shaped gelatinous layer of the volva, which, by becoming a portion of the shell of a sphere of greater diameter, would tend to pull tissues attached to it laterally away from the central axillary core of tissue more firmly attached at top and bottom.

The formation of the folds of the hymenial surface was stated by Ed. Fischer, in his study of *Ithyphallus tenuis*, to be due to the repeated formation of new basidia, which crowd their way to the hymenial surface, pushing in between basidia already lying in that surface¹. The steps leading to such an increase in the hymenial surface are shown in Fig. 6.

The rudiment of the wall of the stipe is thicker and denser than in the preceding stage. A portion of the rudiment from another egg in about the same stage of development as that of Fig. 8 is shown in Fig. 9. Ed. Fischer has found in *I. tenuis*² and in *I. impudicus*³, a loose tissue with numerous spaces between its hyphae, forming a clear zone between the

¹ Ed. Fischer, Zur Entwicklungsgeschichte der Fruchtkörper einiger Phalloideen. Annales du Jardin Botanique de Buitenzorg, Vol. vi, 1887, p. 10.

² L. c. 1887, p. 8, fig. 8.

³ L. c., 1890, p. 25, fig. 22.

central column *R* and the rudiment of the wall *S*. Such a condition does not generally exist; for in *M. caninus* the rudiment of the stipe *S* and the central column *R* are in close contact (Figs. 9 and 11).

The hyphae of the rudiment *S*, Fig. 9, are richer in protoplasm than they are in other portions of the intermediate tissue. This protoplasm does not form a continuous mass distributed uniformly throughout the length of each hypha, but is broken up into short masses, as shown in the figure. It is possible that this appearance of the hyphae is due to their being cross-septate into short cells, but I could not be sure of this.

Eighth egg.—In this more advanced intermediate stage (Fig. 10), the egg has become elongated—measuring 9 by 5 mm.—and its parts have undergone important changes. By the repeated formation of folds and the growing together of such folds where they came into contact, the gleba has become a structure of innumerable closed or labyrinthine chambers lined by the hymenium, the basidia of which now bear spores. There is no longer a cavity between the gleba and the intermediate tissue *A*. Where the lobes of the former have pressed against the latter, the tramal tissue has grown out against the tissue *A*. It is by such growth that the gleba becomes adnate to the stipe in the older stages.

The stipe has become more fusiform, and a chambered structure is beginning to form in its wall. Under a magnification of sixty diameters, the future chambers show as light areas marked out from the more deeply stained portions which become their walls. Under higher magnification (Fig. 11), the transition from the light areas *c, c* to the darker portions is so gradual that one cannot fix upon any point at which the light portion *c* ends and the darker part begins. The tissue composing both the future chambers and their walls was so dense, and the lateral inflations of the hyphae were so irregular in form, as to make it quite impossible in a camera-lucida drawing to follow the hyphae accurately in sections attached to the slide and mounted in

water or glycerine, even though such sections were only $6\frac{2}{3}\mu$ thick. It is, however, possible to treat such thin sections so as to render this practicable.

The steps of the process are as follows:—

1. Do not attach the section to the slide.
2. Remove the paraffin.
3. Carefully run down through the alcohols to water.
4. Treat for about five minutes with 7% solution of potassium hydrate.
5. Wash out the potassium hydrate with water.
6. Stain with aqueous solution of safranin or with Hoffman's blue.
7. Crush out somewhat by careful pressure on the cover glass.

The process is rather long, and very delicate manipulation is required; but in successful preparations the dense tissue opens sufficiently so that it may be drawn, and the hyphae separate from each other slightly so that they may be followed in their course with certainty. Fig. 11 has been drawn from such a preparation. It shows the same intricately interwoven structure that we have seen in the preceding stages of the rudiment of the stipe. This holds true also for the portion of the rudiment lying next to the central column *R*. Ed. Fischer¹ has, however, repeatedly figured and described this portion in quite as early a stage as consisting of swollen hyphal ends extending outwards from the central column *R* at right angles to that column, and forming a continuous palisade-layer along its entire length. I have made a very thorough search in early intermediate stages for such a palisade-layer, but fail to find in the region below the spore-bearing part any structure next to *R* that can be so regarded upon close examination. The arrangement of the protoplasm in the hyphae in block-like masses—which are short cells, perhaps—greatly increases the difficulty of determining the

¹ L. c., 1887, figs. 13 and 17; l. c., 1890, figs. 16 and 24; Neue Untersuch. z. vergleich. Entwicklungsgeschichte u. Systematik d. Phalloideen. Denkschr. d. Schweiz. Naturf.-Ges., Bd. XXXIII, 1, 1893, figs. 61, 62, 72; l. c., 1895, p. 132.

real course of these crowded hyphae in ordinary preparations. Their real courses and arrangement in the region in question have, however, been carefully traced in Figs. 9 and 11.

Hyphae may be seen (Fig. 11) passing through the light areas *c, c* and showing in their different portions the variations in intensity of stain characteristic of the adjacent tissue. I have traced a hypha from one light area through the darker partition-wall into the next light area. The points marked *c, c* in the figure are not the only ones at which crossing of interwoven hyphae occurs, but these marked points are places in which further advancing differentiation ceases, and in which a formation of gelatinous substance sets in. Into these lightly staining areas, channels of a similar nature may lead from the outer surface of the stipe, and thus bring the intermediate tissue *A* into intimate communication with a much greater surface of the pseudoparenchyma of the wall (Fig. 14).

I have stated that the hyphae of the dark partition-walls may extend into, or may issue from, the areas *c, c*. They may arise directly from the intermediate tissue *A* and be traced for considerable distances in the dark walls, crossing and becoming intertangled with the other hyphae of those walls. In these darker portions between the light areas *c, c*, and between these areas and the central column *R* on the one side, and the tissue *A* on the other, rapid growth and further differentiation into pseudoparenchyma occurs in later stages. The inflations of the hyphae become greater, and short branches are formed. The development of pseudoparenchyma is most active along the surfaces where the partition-walls are in contact with the gelatinous tissue of the future chambers *c, c*, with that of the column *R*, or with the intermediate tissue *A*. As a result of such growth, the partition-walls become more and more compact along their surfaces and more open in structure further in (Figs. 14 and 15).

Hyphal knots.—Ed. Fischer¹ accounts for the wall of the

¹ L. c., 1887, pp. 17 and 18.

receptaculum, and for the dense shell of pseudoparenchyma about each chamber, and next to the central column *R*, and next to the intermediate tissue, by stating—

1. That in early development the tissue of the rudiment of the stipe differentiates into a series of isolated dense hyphal knots, which are separated from the central column *R*, from each other, and from the tissue *A*, by narrow open spaces ;

2. That an outgrowth of swollen hyphal ends—pseudoparenchyma—then takes place into these spaces from the isolated knots of hyphae, from the central column *R*, and from the tissue *A* ;

3. That these approaching plates of pseudoparenchyma become loosely grown together later ;

4. That the central portions of the hyphal knots become constantly looser and more gelatinous, finally forming the chamber-cavities of the wall.

There are important features in the above that need modification. It seems probable that Fischer's hyphal knots are the portions *c, c*, Fig. 11, which stain lighter in my preparations ; but these portions are certainly not isolated from each other by open spaces as he states and figures¹. On the contrary, the light-staining portions are closely connected together from their first appearance by a densely interwoven tissue of which they are only portions. These connexions are retained in the various preparations which I have seen. It is quite true that branches from the tissue of the light portions—the chambers later—crowd their way into the plates and become pseudoparenchyma, thus increasing the area of these plates : pseudoparenchymatous hyphae, favourably situated in the partition-wall, also branch and help to augment the same surfaces.

Nature of the 'pits' in the 'spore-bearing' part of the wall.—In the mature plant pits are found opening from the wall of the stipe into its main central cavity. These pits are in the upper portion of the stipe—in its spore-bearing portion,

¹ L. c., 1887, figs. 13, 17, 18.

They are shown in section in Figs. 10 and 13. The identity of such pits with chambers in the lower part of the wall has recently been pointed out by A. Möller in the case of a Brazilian *Mutinus*¹. After stating that the formation of the chambers in the wall of the stipe is from below upward, and hence that they may be more or less incompletely formed at the top of the stipe, he adds further that the deep pits in the wall opening into the central cavity near its upper end must be regarded as chambers lacking a wall on the side next to the main central cavity.

Before reading Möller's work I had reached the same conclusion in regard to the pits of *M. caninus*, but through different evidence. That these pits are of the same nature as the chambers lower down in the stipe, and that they differ from such chambers merely in the absence of a wall on the side towards the cavity of the stipe, becomes very probable when one splits a mature plant lengthwise, and views the chambers and pits from the side of the main central cavity of the stipe. Near the upper end, deep pits, somewhat hexagonal in cross-section, occur; towards the lower end, the chambers are found, each covered by a thin membranous wall, which is so puffed out as to readily show that the form of the chamber is like that of the pit. The change from chambers to pits occurs rather abruptly, yet between the two regions there is a narrow zone within which it is possible to find all intermediate conditions between the two extremes. In some cases the membrane almost closes the chamber, but thins out towards the middle, leaving a minute opening into the chamber-cavity. In other cases the membrane does not cover more than half of the side of the pit, and in others it is a mere border about the pit. Fig. 13 shows some of these intermediate stages in section, but they are best seen by looking against the inner surface of the stipe.

The mode of origin of the pits may be seen by examination of suitable sections from an egg in the stage of Fig. 10. Fig. 12 shows a section through one of the pits in that stage.

¹ L. c., 1895, p. 93.

In passing up the wall, the band of pseudoparenchymatous tissue between the light portions *c, c* and the central column *R* (Fig. 11) becomes narrower, until finally the light portion is in contact with the central column. At points where the light portions are merely tangent to the central column, deeply stained pseudoparenchymatous hyphae may be found running upward from below in the zone next to the column, then crossing through the surface of contact and passing into the dark zone above. The portion of the hypha lying in the light area shows the colour characters of that area. Treatment of the sections by the potash method already described is advisable.

It is unusual to find hyphae which can be traced for as long a distance as is necessary in crossing the pore, but many hyphae may be found which pass from the intermediate tissue *A* through the deeply staining portions—where they show the irregular lateral inflations of pseudoparenchymatous hyphae—and then into the light area *c* (Fig. 11). Of course the greater number of hyphae in a thin section can be followed for only a portion of such a course, when they pass out from the plane of the section. The relations of the intermediate tissue *A* to that of the light portion *c* of a pit are exhibited in Fig. 12, which is a section from an egg in a slightly different stage of development from that of Fig. 11. This light portion was in the upper part of the intermediate zone, and would probably have formed a pit with a narrow membrane about its mouth. Scattered hyphae may be seen passing into *c*, Fig. 12, from the column *R*, but I have been unable to trace them on into the partition-wall *k*. The general connexion of the tissue of the pit *c* with the tissue *A* shows that it should be classed with that tissue—as are the chambers lower down the stipe—rather than with the column *R*. In older stages, when the growth of the pseudoparenchymatous walls increases the size of the other chambers, it also increases the capacity of these chambers or pits, and numerous hyphae from the central column *R* may be seen passing into them and occupying all available space.

Ninth egg.—The following stages in the development of the egg are better known, and can be treated more briefly. A section through the stipe and adjoining parts of an egg 13 mm. long is shown in Fig. 13. The section is median at the upper and lower ends of the stipe, but is slightly oblique about midway between the ends on account of the curvature of the stipe. This gives a somewhat irregular outline to the wall on its inner side in that region.

In its lower portion, the wall of the stipe contains but a single layer of chambers, and these have thin walls; near the middle, the wall is thicker, and its chambers are more numerous and more irregular in form; higher up, the pits have become swollen with tissue from the column *R*, and the wall has become very massive. This massive portion is not thrown into folds in the advanced stages of the eggs. It is the portion upon which the gleba rests. Can it have become massive in order to give a more rigid support for the gleba in its development?

Some chambers in the wall of the stipe are closed, their tissue having no connexion with the intermediate tissue *A* except through pseudoparenchyma. A portion of the wall, showing many places of direct connexion of the intermediate tissue with that of the chambers, is shown in Fig. 14 under low magnification. Such passages into the chambers become the pores or perforations which are found in the outer surface of the stipe after its elongation. The figure shows also by the darker shading the denser structure of the wall of pseudoparenchyma along the surfaces. Perhaps the more favourable conditions for the development of that tissue in those surfaces may be due to proximity to a tissue containing available food.

*Mode of thickening the wall in the spore-bearing part*¹.—In the upper part of the wall of the stipe in Fig. 8, the pseudoparenchymatous hyphae form a single narrow zone bounding the pits, and so forming a very irregular outline for that

¹ Compare also Ed. Fischer on this topic in his already cited paper of 1895, p. 135, figs. 5–8.

part of the stipe. The two opposite sides of this zone are parallel, as shown in Fig. 12. The undifferentiated tissue *A* is thus separated from the tissue *c* of the pits by only a single layer or plate of pseudoparenchymatous nature, and extends in the opposite direction to the gleba. Ed. Fischer has described such a condition of this part of the wall and of the tissue *A* as the permanent condition in *Mutinus Müllerii*¹.

Such a condition is not permanent, however, in *M. caninus*. The two surfaces of the wall in this region are no longer parallel in the older stage of Fig. 13. The section of the outer surface has become nearly a straight line. This has resulted from the formation of a second plate of pseudoparenchyma just outside the first one. It has not conformed to the first plate, but extends more directly from prominence to prominence of that plate. The hyphae of the tissue *A*, which are shown in Fig. 12 directly connected with the first plate *k*, and those in the angles between the pits became pseudoparenchymatous also when the second plate was formed, and may be seen connecting the two plates in Fig. 15. I desire to call attention to this point, for although the two plates of the partition-wall between the rest of the tissue *A* and the pits *c* are not formed simultaneously, in other respects the mode of formation of this partition-wall is the same as that which I have described in connexion with the chambers lower down the stipe.

The differentiation of the second plate began at the outer surface of the wall in the region below the pits, and then advanced upwards; hence this plate cannot be regarded as homologous with the veil or pileus of other genera of the Phalleae.

ADVANCED STAGES.

As already stated, the advanced stages may be regarded as those in which the walls have become folded. In these stages the cell-like bodies of pseudoparenchyma, which constitute

¹ L. c., 1890, p. 32, fig. 25.

the walls of the chambers, increase greatly in size, and it becomes difficult to conceive of their having originated by lateral inflation of hyphae. The growth of the walls is more rapid than that of the tissue of the chambers, and, as a result, the even-surfaced chamber-walls of Fig. 11 are thrown into a series of folds like those of a Chinese lantern, to use the old illustration. As the growth in length of the stipe after the folding of the chamber-walls still continues to be more rapid than the growth in length of the egg, the wall of the stipe as a whole becomes thrown into a series of folds in this species.

In these changes the intermediate tissue *A* and the tissue of the chambers become torn, the latter tissue and that of the central column become more highly gelatinous, and the gleba splits away from the volva in the plane of the inner layer of the latter. During this last change, the volva is burst open at its apex by the receptaculum, which gradually pushes its way up through the opening by the straightening out of its folded walls. It is now believed that the straightening out of the folded walls and consequent elongation of the stipe is due to changes in the form of the cells situated at the inner and outer surfaces of each angle of each fold. At the inner surface of the angle, the cells are wedge-shaped as though by compression; on the outer surface, they are elongated and flattened as though by a pull longitudinally. Both of these sets of cells become more spherical in form during elongation of the stipe. Such a change in the form of the cells at the inner surface of the angle must tend to lengthen that surface and so straighten out the fold; the change in form of the cells on the outer surface of the angle must tend to shorten that surface and so help straighten the fold. The changes in form of the cells on both surfaces of each cell therefore work together in straightening the fold. In Errera's paper taking up this subject, the change in form of the cells at the angles of the folds is regarded as due to a true process of growth¹.

¹ L. Errera, Sur le glycogène chez les Basidiomycetes. Mémoires de l'Acad. roy. de Belgique, t. XXXVII, (1885), p. 52 of reprint.

Ed. Fischer's paper of two years later treats the process as one of turgescence ¹.

SUMMARY.

In its earliest recognizable stage, the egg consists of the cortical and medullary tissues of the mycelial strand, continued directly upward from the strand. Of these tissues, the medullary bundle spreads out at its upper end and forms a dense sheaf-like head by repeated branching and anastomosing.

The cortical layer of tissue becomes the outer wall of the volva; the sheaf-like head gradually differentiates into all the other parts of the older egg.

In such differentiation the central column *R* is the first to be set off, arising from the axial tissue of the head and from below upward.

Formation of the gelatinous layer *G* of the volva now begins in the periphery of the head. The dense portion between the peripheral zone and the central column *R* becomes looser in its inner and lower parts about the column, there forming the intermediate tissue *A*, but remains dense in its upper and outer portions, forming a compact dome-shaped mass. In these changes the direct connexions from the original medullary bundle *N* to the dense dome-shaped mass and to the lateral portions of the sheaf-like head disappear, while indirect connexions by way of the central column *R* are retained, and become of apparently great functional importance.

Along the inner surface of the dense zone and next to the intermediate tissue *A*, the rudiment of the gleba *H* arises from the clustered swollen ends of lateral branches of the tramal tissue. These hyphal ends take position in a palisade-layer facing the intermediate tissue. By the crowding in

¹ Bemerkungen über den Streckungsvorgang des Phalloideenreceptaculums. Mittheil. d. Naturf.-Ges. in Bern, 1887, p. 142.

of new hyphal ends (basidia) into this layer, its surface becomes greatly enlarged and the layer is thrown into folds. During this process it becomes torn from the intermediate tissue.

The rudiment of the stipe arises in the intermediate tissue *A*, lying next to the central column *R*, by the formation of a zone of deeply staining tissue rich in protoplasm.

Somewhat later, masses of tissue in the dense and intricately interwoven rudiment of the stipe show a tendency towards gelatinization. These masses mark the position of the later chamber-cavities in the wall. Towards the upper end of the stipe, such masses are in contact with the central column *R*, and they mark the position of the 'pits' which open into the main central cavity of the stipe in mature stages of *M. caninus*.

The tissue of the rudiment of the partition-walls, situated about and between the gelatinous masses, continues its development into pseudoparenchyma, which, with conditions for its development most favourable where it is in contact with the gelatinous tissues and the presumably food-supplying tissue *A*, becomes relatively more and more dense next to those surfaces, and more open, by contrast, between those surfaces. In later stages, before folding of the wall has gone too far, this gives to the partition-wall the appearance of being composed of two plates rather loosely connected together.

At no stage in the course of development was the rudiment of the stipe found to consist of hyphal knots isolated from each other and from the surrounding tissues by narrow open spaces.

The chamber-walls are thrown into folds through a more rapid growth of the pseudoparenchyma than that of other parts of the egg.

Final elongation of the stipe and elevation of the gleba is brought about through the straightening out of the folds in the chamber-walls.

GENERAL CONCLUSIONS.

Although the receptaculum and the gleba are both differentiated from the early sheaf-like head of medullary tissue, still the pseudoparenchymatous walls of the former seem to have nothing more immediately in common with the hymenium either in origin or in mode of formation. There is no good reason for considering the two structures homologous.

The steps by which the lower and lateral portions of the sheaf-like head—those portions bearing the future hymenium—lose their original direct connexion with the medullary bundle *M* and become split away, as it were, from the stipe from below, have no parallel in the Clathreae, and remind one rather of the changes that occur in the formation of the pileus in some of the Agaricineae.

Medullary tissue gives rise to both the tissue of the chambers of the wall and to the pseudoparenchyma of its partition-walls, and one portion of a hypha may undergo the modification characteristic of a chamber, while another portion differentiates into pseudoparenchyma. In the Clathreae, as pointed out in my paper on *Anthurus borealis*¹, cortical tissue continued upward from the mycelial strand forms the pseudoparenchyma, while the tissue of the chambers is of medullary origin, and not connected with that of the partition-walls.

Such fundamental differences must signify that the Phalleae and the Clathreae are not directly related; although they may properly be regarded as two parallel series of forms, on account of their general features of resemblance in spore characters and external form.

This investigation was carried on in the Cryptogamic Laboratory of Harvard University in the winter of 1894-95, under the direction of Professor W. G. Farlow. I desire to express my sincere thanks to Professor Farlow, and also to Professor Thaxter, for helpful suggestion and criticism received in the

¹ A North American *Anthurus*—its Structure and Development. Memoirs of the Boston Society of Natural History, Vol. iii, No. XIV, 1894.

course of the investigation, and for the use of papers which would otherwise have been inaccessible to me. My thanks are also due to Mr. H. M. Richards and to Mr. H. L. Jones, Assistants in the Botanical Laboratories, for numerous favours which have facilitated my work.

EXPLANATION OF FIGURES IN PLATES XVII AND XVIII.

Illustrating Dr. Burt's paper on the development of *Mutinus caninus* (Huds.), Fr.

Note.—All figures were drawn with an Abbé camera-lucida.

Lettering common to all the figures.

M, medullary bundle of young stages; *N*, sheaf-like head of *M*; *C*, cortical layer; *G*, gelatinous layer of the volva; *Gl.*, gleba; *H*, hymenium; *L*, outer and more open portion of *N*; *O*, dense portion of *N*; *R*, central column; *S*, stipe; *c*, tissue of chambers and pits; *i*, region of innermost layer of volva; *k*, partition-wall of pseudoparenchyma; *m*, point at which sheaf-like head *N* arises from medullary bundle *M*.

Figs. 1-4. Median longitudinal sections through eggs in successive young stages, showing the course of differentiation of the several parts from the sheaf-like head *N*. At *m*, Fig. 2, the medullary bundle *M* has direct lateral connexion with the lower part of the region in which the gelatinous layer of volva, innermost layer of volva, and the gleba arise later. Figs. 1 and 2 are magnified 106, Figs. 3 and 4, 66.

Fig. 5. Median longitudinal section through an egg in an early intermediate stage. Differentiation of *O* has given rise to the central column *R*, the intermediate tissue *A*, and the zone *i*. The rudiment of the stipe *S* is differentiating in one side of *A*, and that of the hymenium *H* at the other side. × 36.

Fig. 6. Cluster of young basidia from the point *H*, Fig. 5. × 670.

Fig. 7. Rudiment of the stipe at its base, with adjacent tissues. From Fig. 5 at *S*. × 325.

Fig. 8. An older stage than Fig. 6 with the outer portions omitted. On account of a curvature of the stipe, the lower part of the figure—the part below *S*—had to be drawn from another section in the same series. The crowding in of basidia into the hymenial surface has thrown the latter into folds; separation of the gleba from the intermediate tissue *A* is now almost completed. × 36.

Fig. 9. Portion of the rudiment of the stipe *S* of Fig. 6 more highly magnified. × 325.

Fig. 10. Median longitudinal section through an egg in which the rudiment of the stipe is differentiating into chamber-tissue and that of partition-walls. The lower part of the figure is from another section in the same series. $\times 8\frac{1}{2}$.

Fig. 11. Portion of rudiment of the stipe in about the stage of Fig. 10, showing the chamber-tissue *c, c* and the portions between and about these which become partitions of pseudoparenchyma later. $\times 325$.

Fig. 12. Portion of the upper part of the fundament of the stipe of Fig. 10, showing a 'pit' and the tissues in its vicinity. $\times 325$.

Fig. 13. Median longitudinal section of the stipe and adjacent parts of an egg in a late intermediate stage. $\times 9$.

Fig. 14. Portion of Fig. 13 showing wall of stipe just below the 'spore-bearing' part, showing the connexion of the tissue *A* with the tissue *c* of chambers through passages which are perforations or openings in the external surface of the stipe after its elongation. (*Corynites Ravenelii*, B. & C., with specimens of which my material agrees, was supposed to differ chiefly from *Mutinus caninus* (Huds.) in this portion of the stipe. Comparison of this figure with Ed. Fischer's (1895) Fig. 9 of European *M. caninus* in a somewhat older stage shows no essential structural difference.)

Fig. 15. Longitudinal radial section through the wall in the 'spore-bearing' part of the stipe. Comparison with Fig. 12 shows the thickening of the wall in this part to be by the formation of a later zone of pseudoparenchyma *k* from the intermediate tissue *A*. A 'pit' *c* is on the right. $\times 325$.

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BURT. — MUTINUS CANINUS.

University Press, Oxford.

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