Observations on the Methods of Stipe-formation in Stemonitis and Comatricha

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During the course of the writer's observations on myxomycete plasmodia, it has become apparent that many generic as well as specific behavior differences are to be expected. By behavior is meant the various conformations and color changes that are passed through in the development of sporangia from plasmodia; the time required to complete fructification is also taken into account, although it is less likely to be a fixed character. Myxomycete fructifications¹ are of three types: aethalioid, plasmodiocarpous, and sporangiate; the last may be either sessile or stiped. Naturally the behavior of the plasmodium of a plasmodiocarpous species would differ from that of either a sporangiate or an aethalioid type. In addition to such differences, however, there occur differences between forms which possess the same general type of fructification; this is shown particularly well by members of the genera Stemonitis and Comatricha.

Stemonitis and Comatricha are closely-allied genera belonging to the family Stemonitaceae, and mature forms of members of the two genera, when examined macroscopically, show many resemblances-so many, in fact, that at one time the representatives of both genera were included in the same genus. Plasmodia of Stemonitis and Comatricha characteristically inhabit the interior of rotten wood, emerging only for fruiting: in the majority of known cases, the typical plasmodial color is white. A general feature in sporangia of both genera is the presence of a long central columella, which is simply an elongation of the stipe. Observations on species of both genera show that the process by which the stipe and columella are developed in Stemonitis differs somewhat from that process in Comatricha. It is hardly to be expected that stipe- and columella-formation of all the species of Comatricha would be uniform; this is also to be said for species of Stemonitis, since there are forms which may be considered more or less border-line species between the two genera.

A review of the literature yields but few references to the subject of stipe- and columella-formation. DeBary (1884) presented some observations concerning this process in *Stemonitis axifera* (Bull.) Macbr. (*S. ferruginea* of Ehrenberg), but his method of viewing the fruiting bodies was to harden them with alcohol and then render the protoplasm transparent with glycerine. By this method, according to deBary's figures (Figs. 2a and 2b), it may be shown that formation of the stipe and columella begins at an early stage in the development of the fruiting body. Bisby (1914), working on the development of the capillitium

¹Macbride and Martin (1934) define these as follows: *aethalium*: a fructification in which all or a considerable part of a given plasmodium is involved and in which differentiation has not proceeded to the delimination of separate sporangia: plasmodiocarp: a fructification which has the interior structure of a sporangium, but which retains the netted form and outline of the plasmodium; this type is formed by the aggregation of protoplasm into a few of the larger veins of the plasmodium as it rests upon the surface of the substratum; *sporangium*: typically an erect fructification of definite form and structure for a given plasmodium.

in *Stemonitis fusca* Roth, included some material on the formation of the columella; his investigations, however, were largely cytological. Details of the development of *S. fusca*, from plasmodium to sporangia, were described by the writer (Gray, 1936); in this description no figures of the developing sporangia were presented. Jahn (1931) gave an account, accompanied by excellent photographs, of various stages in the development of *Comatricha nigra* (Pers.) Schroet.; he had previously published (1899) on this same species, incorrectly designated *C. obtusata* Preuss.

Were it possible to grow members of this family at will, the matter of observing the development of all species would be simplified; at present, however, one must rely upon finding plasmodia in their native haunts, removing them to the laboratory, and there observing them during the fruiting process. It has been the experience of the writer ordinarily to find emerging plasmodia of these two genera in the afternoon or evening; this is by no means, however, a set rule. The following summaries and the accompanying diagrams will serve, in a measure, to point out the main features of the stipe-forming and other developmental processes observed in the two genera. Figs. 1, 2, and 3 (with the exception of 2a and 2b) are diagrams of species observed by the writer; Figure 4 is redrawn from photographs by Jahn.

Stemonitis fusca Roth. (Fig. 1, *a-e*) Plasmodium pearly-white, relatively large.

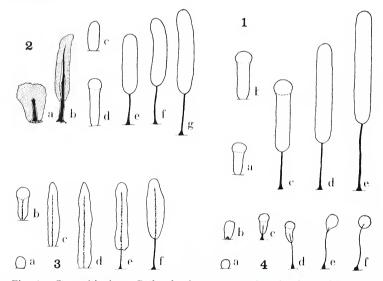


Fig. 1. Stemonitis fusca Roth, showing a sporangium in the various stages of development; a, $17\frac{1}{2}$ hrs. after emergence; b, $19\frac{1}{2}$ hrs.; c, $21\frac{1}{2}$ hrs.; d, $26\frac{1}{2}$ hrs.; e, $36\frac{1}{2}$ hrs.; Fig. 2. Stemonitis axifera (Bull.) Macbr. a and b (redrawn from deBary), longitudinal sections of young sporangia: c-q, a sporangium in the various stages of development; c, $3\frac{1}{4}$ hrs. after emergence; d, 8 hrs.; e, 12 hrs.; f, 17 hrs; g, 19 hrs. Fig. 3. Comatricha typhoides (Bull.) Rost. a, sporangium 8 hrs. after emergence; b, 10 hrs.; c, 11 hrs; d, 13\frac{1}{4} hrs.; e, $13\frac{3}{4}$ hrs.; f, $14\frac{1}{4}$ hrs. Fig. 4. Comatricha nigra (Pers.) Schroet. (redrawn from Jahn's photographs); a, sporangium shortly after emergence; the times listed for the following figures representing hours advanced past the stage shown in Fig. 4a; b, 2 hrs., 47 min.; c, 4 hrs., 43 min.; d, 7 hrs., 22 min.; e, 8 hrs., 55 min.; f, 9 hrs., 38 min. Magnification x4, except 2a and 2b, which are x6 and x7\frac{1}{2} negocitively.

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Since the sporangia of this species occur in large clusters, the developing sporangia are intimately associated. Figure 1, a represents a single sporangium $17\frac{1}{2}$ hours after the emergence of the plasmodium; at this point, the sporangium consists solely of a white, protoplasmic column, tipped with a bulbous enlargement. Figure 1, *b* is essentially the same as Figure 1, *a*, being a slightly more advanced stage. Figures 1, *c*, 1, *d*, and 1, *e* represent still further advanced stages in which the development of the stipe may be seen. The approximate time for completion of the fructification was 89 hours.

Stemonitis axifera (Bull.) Macbr. (Fig. 2, *a-g.*) Plasmodium pearlywhite, developing into closely-associated sporangia as in *S. fusca*.

On the whole, plasmodia of this species are inclined to be more active upon emergence than are plasmodia of *S. fusca*. As may be seen from the diagrams (Fig. 2, c-g), development in the two species follows the same general lines, and, at certain stages, the species cannot be determined with certainty; however, there is a time variance, *S. axifera* requiring only 19 hours as compared to 89 hours required by *S. fusca*.¹ The two species pass through approximately the same color changes, white, pink, lavender, and finally brown, although the final shade of brown differs between the two species.

It is to be noted that in neither species of Stemonitis is there any external evidence of the existence of a columella. The sporangia are formed first, then the stipes are developed, appearing simply to lift the sporangia up from the substratum. Of course, the stipe is formed within the protoplasmic column, but obviously does not assume its final form and shining black color until it is exposed. Apparently this change in color takes place as the stipe is exposed. DeBary (1884) has shown that the formation of the stipe and columella begins in the very early stages in the development of *S. axifera*; this is not apparent to the observer, however, unless the immature sporangia are fixed and sectioned. Figures 2, *a* and 2, *b* are redrawn from deBary's figures of longitudinal sections of young sporangia of *S. axifera*.

Comatricha typhoides (Bull.) Rost. (Fig. 3, a-f.) Plasmodium white, but appearing somewhat finely granular and not of the same shining, pearly quality of whiteness exhibited by the two preceding species; rather active and inclined to divide into several smaller plasmodia, from some of which only one sporangium is developed; sporangia not closely aggregated.

Figure 3, a represents a sporangium in the very early stages (eight hours after the emergence of the plasmodium). Figure 3, b is the same sporangium two hours later; it is to be noted that a bulbous enlargement such as is shown by both species of Stemonitis is evident. The development of the stipe and columella has begun; they are dark in color, and their outlines show through the white protoplasmic mass. In Figure 3, c (11 hours after emergence), the protoplasmic column has elongated; dark stipe and columella are quite evident. This protoplasmic column continues to elongate until it has reached the maximum height of the fructification (Fig. 3, d), then the protoplasm contracts

¹Further observations may show that the exact time requirements vary within a species.

upward along the central axis and thus exposes the already apparent stipe at the base of the fructification. Color changes are as follows: white, pale lavender, dark lavender, brownish-purple, and finally dark brown.

Comatricha nigra (Pers.) Schroet. (Fig. 4, a-f.) No observations on this species were made by the writer; diagrams drawn from Jahn's photographs have been introduced for the purpose of comparison. Figure 4, a represents a sporangium shortly after emergence, and Figure 4, b, the same sporangium two hours and forty-seven minutes later. At this stage may be seen the darkened central portion near the base, which marks the beginning of the formation of stipe and columella. Figure 4, c shows this sporangium about four hours and 43 minutes after emergence; the dark central portion, representing stipe and columella, has elongated; a portion of the stipe is already exposed. The stipe continues to elongate, and eventually the cylindrical protoplasmic column contracts along the stipe to form a more or less spherical sporangium about nine hours and 38 minutes after emergence (Fig. 4, f).

Species	Approximate Time Required	Color Changes in Order	Final Shape
S. fusca	89 hrs.	pearly-white pink pale lavender dark brown dark chocolate brown	cylindrical
S. axifera	19 hrs.	pearly-white pink pale lavender dark brown wood brown	cylindrical
C. typhoides	23 hrs.	granular white pale lavender dark lavender purple dark brown	cylindrical
C. nigra	?	watery white ? ? ferruginous or dark brown	spherical or oval

TABLE I. DEVELOPMENTAL FEATURES

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C. nigra differs from *C. typhoides* in that the stipe of the former continues to elongate after the basal portion is exposed. The early and obvious development of the stipe and columella is common to both species of Comatricha as is the contraction of the protoplasmic column along the central axis. On the contrary, at no time in the development of the two species of Stemonitis is the columella apparent. Known developmental features of the four species under discussion are summarized in Table I.

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