Vegetative Reproduction in Metzgeria.

BY

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With sixteen Figures in the Text.

THE organs of vegetative reproduction in *Metzgeria* are so conspicuous that they attracted the attention of observers at a very early date. They consist of thalloid structures, usually but one cell thick throughout, and easily become detached at maturity. Each one arises from a single cell of the parent thallus, either from an alar cell or from one of the cortical cells of the costa. The position of the reproductive bodies on the thallus varies in different species. In some they are always marginal, while in others they are borne on the upper, or antical, surface of the wings. In still other species, where they are produced on strongly specialized branches, their position is much more indefinite, any superficial cell being apparently able to assume the reproductive function. It has been customary to designate these reproductive bodies as 'adventive branches' when they arise from marginal cells of the thallus, and as 'gemmae' or 'bulbils' when they arise elsewhere. It has already been shown, however, by Schostakowitsch ('94, p. 350) and others that there is no essential difference between them, either in their development or in the way in which they become detached from the parent plant. In the present paper, therefore, they will be spoken of as 'gemmae', whatever their position. The term 'adventive' may then be retained for branches which arise from the postical surface of the costa, and in the development of which the internal costal cells take part. Strictly speaking, such branches are not reproductive structures at all, although they may eventually give rise to new individuals through the progressive dying away of the old thallus. The differences between adventive branches of this character and gemmae are usually well marked, but they sometimes become less definite on poorly developed individuals.

Apparently, Hooker ('16, pl. 55) was the first one to describe the gemmae of *Metzgeria* clearly. He studied them in what he called *Jungermannia* [now *Metzgeria*] *furcata γ aeruginosa*, a plant characterized by a peculiar bluish-green colour and by specialized gemmiparous branches. The next writer who added substantially to our knowledge was Nees von

Esenbeck ('38, p. 488), who redescribed Hooker's variety *aeruginosa* under the name *M. furcata* δ *gemmipara* and called attention to the most striking peculiarities of the gemmiparous branches. He also described, as ε *prolifera* and ζ *ulvula*, forms of *M. furcata* in which the gemmae are marginal. A few years later Naegeli ('45) gave a full description of the way in which these marginal gemmae develop, and emphasized the fact that each one arises from a single cell. Further details were added by Hofmeister ('51, p. 22) and by Kny ('64, p. 76), the latter stating that the separation of the gemmae was brought about by the destruction of tissue.

Up to this time the gemmae had been of interest more particularly to students of plant morphology; but Lindberg showed, in his Monographia *Metzgeriae* ('77), that they deserved the attention of taxonomists as well. Unfortunately he failed to emphasize this fact very strongly, although he went far enough to refer different types of gemmae to definite species, and to imply by omission that they did not occur in the other species which he recognized. He stated that marginal gemmae occurred not only in *M. furcata*, but also in his newly described *M. myriopoda*, and that specialized gemmiparous branches were to be observed in *M. conjugata*, var. *violacea*, and *M. furcata*, var. *fruticulosa*, the latter being identical with Hooker's variety *aeruginosa.* He also called attention, apparently for the first time, to those gemmae which arise on the surface of the wings, and noted their occurrence in *M. Liebmanniana*, *M. dichotoma*, *M. crassipilis* (published here as a sub-species of *M. furcata*), and *M. linearis.* According to his statements gemmae of this character are always borne on the postical surface of the wings, but the writer has found them to be invariably antical in origin. Apparently, Lindberg's mistake was due to the fact that gemmae, after becoming separated, often attach themselves to the postical surface of an overlying thallus and begin their germination in this position.

Subsequent references to the gemmae of *Metzgeria* are very much scattered, but describe a few new observations of interest. Miss Boatman ('92), for example, notes the production of marginal gemmae in *M. conjugata*, while Schiffner ('00, p. 60) and Pearson ('02, p. 465) say that they are sometimes to be seen in *M. hamata.* Specialized gemmiparous branches have been studied by Ruge ('93, p. 304) in an unnamed species from Ecuador, and by Goebel in the South American *M. adscendens* ('93, p. 427), as well as in plants which he referred to *M. conjugata* ('98*a*, p. 275). According to Ruge, the gemmiparous branches grow out from the antical surface of the costa, but Goebel states that they are simply the prolongations of ordinary branches of the thallus. Except for a short note by the writer ('09, p. 189) on the antical gemmae of *M. crassipilis*, there are apparently no allusions to reproductive bodies of this type in the recent literature. Stephani, in his revision of the genus ('99), makes no mention whatever of gemmae, and consequently does not connect the specialized branches studied by Ruge and Goebel with processes of reproduction. He attaches but slight importance to these branches (from the standpoint of the taxonomist), and implies that they probably occur in many species where they have not yet been detected. He suggests that their development may perhaps be due to heliotropic stimuli, but makes no further attempt to account for them.

The study of an abundant material of *Metzgeria*, mostly from North America, soon made it evident to the writer that the gemmae showed a much greater variety in form and structure than had been supposed. It also became evident that many of their peculiarities were specific in character, and that they often afforded a convenient means for distinguishing between closely related plants. The individual peculiarities of the gemmae have scarcely been noticed in earlier publications. This, however, is not surprising, because it is only within comparatively recent times that gemmae in other genera of the Bryophytes have been at all adequately described. Perhaps another reason why *Metzgeria* has been especially neglected in this respect is because the gemmae sometimes undergo reversion to a greater or less extent, and under these circumstances may fail to show their normal characteristics. This phenomenon has already been discussed by Goebel ('98 *b*) in the case of *M. furcata*, and allusion will again be made to it in the following pages.

Description of Gemmae.

In the present paper the gemmae of twelve species are described, and fall naturally into three groups according to their position on the thallus. In the first group, including five species, the gemmae are marginal; in the second group, including six species, they arise from the antical surface of the wings; in the third group, including but a single species, they are indefinite in position. The gemmiparous branches in the first and second groups are very similar to normal branches, but in the third group they are much more specialized. In a few other species gemmae have also been noted, but they are not present in sufficient number for careful investigation. The remaining species examined seem to be entirely destitute of gemmae. Since these include both *M. conjugata* and *M. hamata*, where gemmae have been indicated by other observers, it would appear either that their statements were based on incorrect determinations or that the gemmae in these two species required very exceptional conditions for their development. Since several of the gemmiparous species discussed are apparently new, their diagnoses will follow the descriptions of their gemmae.

Metzgeria uncigera, sp. nov.

A gemmiparous branch in this species tends to be narrower than a normal branch and to develop a less highly differentiated costa. When gemmae are produced in abundance the growth of the branch soon comes to an end and the gemmae become crowded in the apical region (Fig. 1). In many cases, however, a branch will develop gemmae for awhile and then continue its growth normally. The gemmae arise in no definite order, large and mature individuals being often scattered among those which have scarcely begun their development. There is no evidence therefore that they are formed in acropetal succession.

When a gemma is to be produced one of the marginal cells projects beyond its neighbours. In doing this the outer wall of the cell is ruptured, but the protruding protoplast is not naked, being covered over by a thick layer of transparent gelatinous substance, which perhaps represents a modification of the inner portion of the original outer wall (Fig. 2, A). The deposition of this substance takes place prior to the rupture of the wall. Upon the inner surface of the gelatinous layer a very thin new wall is soon secreted. The projecting cell thus formed does not represent the mother-cell of the future gemma, except in very rare instances. It almost invariably divides by a periclinal wall into two cells, the outer of which becomes the actual mother-cell. The periclinal wall is sometimes at right angles to the surface of the thallus, but is more likely to be inclined to it in such a way that the mother-cell of the gemma lies partly over the antical surface of the inner cell. The first wall in the mother-cell extends obliquely outwards from about the middle of the periclinal wall. A second oblique wall meets the first (Fig. 2, B) and thus forms at the tip of the young gemma a wedge-shaped cell, which proceeds to function as a two-sided apical cell, and to give rise to two rows of segments in the way so often described for *Metzgeria furcata*. The segments soon undergo further divisions (Fig. 2, C), and usually one of the two cells first cut off from the mother-cell divides as well, thus making the base of the gemma three cells wide (Fig. 2, D). In the early stages the gelatinous substance which covered over the original projecting cell becomes stretched out into a thinner and thinner layer at the apex of the gemma, and before long disappears completely (Fig. 2, C and D).

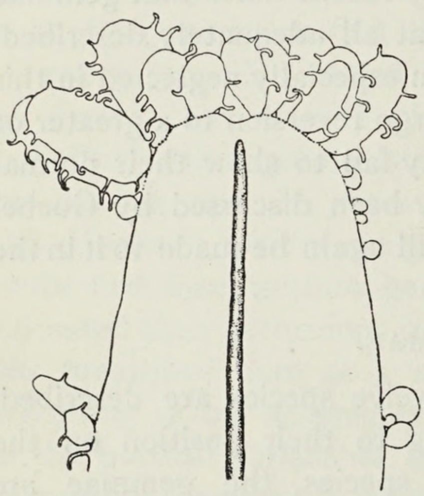

FIG. 1. *M. uncigera*. Apex of a gemmiparous branch. ×40.

The separation of the gemmae is brought about by the splitting of the walls between the two or three basal cells and the cell of the thallus cut off by the original periclinal wall. At the time of separation they vary considerably in length, a condition which is doubtless due to the fact that germination sometimes begins prematurely. What may be considered an average gemma is represented in Fig. 2, E. It consists of a flat strap-shaped thallus about eight cells broad and narrowing somewhat towards the base. At the rounded apex the single apical cell, still active in cutting off segments, can be distinguished. Such a gemma is about 0·6 mm. long and 0·25 mm. wide. Along the margin are scattered hairs, each about twice as long as one of the ordinary cells of the gemma and almost always hooked at the apex. The hairs are often strictly marginal, but in some cases are slightly displaced to one surface. The gemma shows no signs of dorsiventrality; even when the hairs are displaced they appear on either surface indiscriminately. There are also no signs of cell-differentiation except for the marginal hairs.

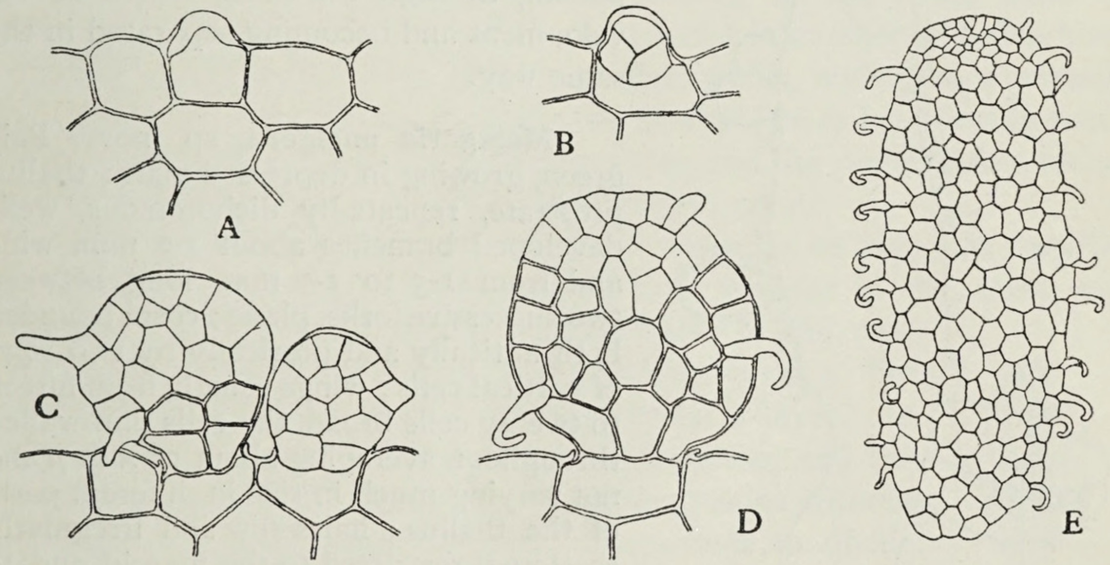

FIG. 2. *M. uncigera.* A–D. Gemmae in various stages of development. ×300. E. A gemma at time of separation. ×80.

The germination of a gemma is a comparatively simple process, although its course is liable to be affected by external changes. The apical cell of the gemma begins to function at once as the apical cell of the young thallus. In fact it is quite impossible to discern where the gemma merges into the young plant to which it gives rise. As development proceeds the young thallus gradually becomes broader and the new hairs formed tend to be straight instead of hooked and to act as rhizoids. Before long the median cells of the thallus become arranged in two longitudinal rows and begin to divide by walls parallel to the surface, thus giving rise to a rudimentary costa. With the appearance of the costa the evidences of dorsiventrality become more distinct. The marginal hairs, for example, when displaced from the margin, always appear on the lower, or postical, surface; the costa itself begins to give off hairs, most of which function as rhizoids; and slime papillae make their appearance in the region of the growing point, always on the postical surface. With the further development of the costa the differentiation of the thallus becomes complete, and the characteristic branching by forking soon begins. The young plant is strongly subject to the phenomenon of reversion. Even after the costa has become distinct it is not unusual for a thallus to continue its development as a simple layer of cells. It is also very prone to develop secondary gemmae (Fig. 3), and it sometimes does this before it has begun to show any signs of differentiation. In fact, secondary gemmae sometimes arise on a primary gemma which is still attached to the parent thallus. The secondary gemmae are essentially like the primary, passing through the same course of development and becoming separated in the same way.

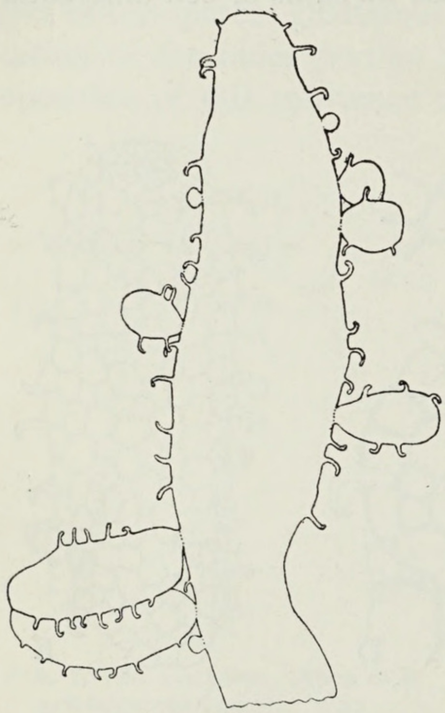

FIG. 3. *M. uncigera*. Apical portion of a thallus developed from a gemma and bearing new gemmae along its margin. × 40.

Metzgeria uncigera, sp. nov. Pale green, growing in depressed mats: thallus prostrate, repeatedly dichotomous, well-developed branches about 1·2 mm. wide and from 1·5 to 2·5 mm. long between two successive forks, plane; costa bounded both antically and postically by two rows of cortical cells; wings usually from fifteen to twenty cells broad, the cells thin-walled throughout, averaging about 28 x 21 μ and not varying much in size in different parts of the thallus; hairs few and irregularly scattered, restricted to the margin and to the postical surface of the costa, the marginal hairs averaging about 70 μ in length, usually straight but sometimes hooked at the apex, occurring singly, sometimes truly marginal, but often slightly displaced to the postical surface: inflorescence dioicous: ♀ branch broadly orbicular-obovate, about 0·15 mm. long, with scattered marginal hairs: gemmae marginal, ligulate, one cell thick throughout, without a distinct stalk, apical cell single, hairs marginal or slightly displaced to one surface, hooked at the tip: remaining parts not seen.

On trunks of trees. Porto Rico: Mount Morales, near Utuado, March 19, 1906 (Howe, No. 1128).

The present species is closely related to *M. furcata*, although the costa has only two rows of cortical cells on the postical surface instead of four. It is distinguished by its smaller cells and by the absence of surface hairs on the wings of the thallus. Its gemmae, also, are less differentiated and fail to show a costa even when large and well developed. The relationship of *M. uncigera* to *M. hamata*, where the costa is built up on essentially the same plan, is much more remote. In this species the thallus is strongly convex, the marginal hairs are longer and occur in pairs, while the leaf-cells are considerably larger, averaging about $57 \times 37\ \mu$.

Metzgeria furcata, (L.) Dumort.

The gemmiparous material examined of this common and widely distributed species came from the following localities:—Zurich, Switzerland (Foerster); Cumberland, Maine (Chamberlain, No. 904); Jackson, New Hampshire (A. W. E.); Onteora Mountain, New York (Miss Vail, No. 26). The plants which develop the gemmae are usually more slender and less highly differentiated than normal plants. The hairs, for example, are less numerous and are sometimes absent altogether, the cortical cells along the postical surface of the costa are often reduced to two rows, while the elongated internal cells of the costa are reduced in number and sometimes not developed at all. The thallus, in other words, undergoes a reversion to a more or less juvenile condition, as Goebel ('98 *b*) has already noted. The gemmae are borne without definite order, and the gemmiparous branch usually continues its growth for a considerable period.

The early development of a gemma is similar to that just described for *M. uncigera*. One of the marginal cells projects in the same way, secretes a gelatinous substance on the inside of the projecting wall, ruptures the outer wall, and then forms a thin new wall on the inner surface of the gelatinous layer. In contrast to *M. uncigera*, however, the projecting cell becomes at once the mother-cell of the future gemma without undergoing a preliminary division. It proceeds to divide in the characteristic way, already described in detail by Naegeli ('45) and other observers. With regard to the separation of the gemmae at maturity, this is doubtless brought about in some instances by a rupture across the base, in the way described by Kny. But this method of separation is often premature and is apparently abnormal. In normal cases the basal cells simply split away from the adjacent thallus cells, and the process is unaccompanied by any destruction of tissue. The remains of the ruptured wall of the original projecting cell may often be distinguished after the gemma has been set free (Fig. 4).

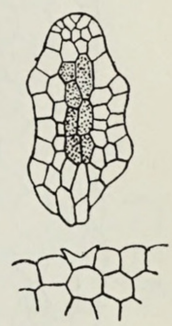

FIG. 4. *M. furcata.* A small gemma just separated from the parent thallus. ×80.

At the time of separation the gemmae vary greatly in length, but are usually more highly differentiated than in the other known members of the genus. They quickly form the beginnings of a costa, even the basal cells often dividing by walls parallel with the surface. The existence of dorsiventrality is also shown very early by the development of slime papillae on one surface of the gemma, the first papilla sometimes appearing only a few cells away from the base. Except for these papillae the gemmae are usually destitute of appendages, but in some cases hairs are produced early, and even the first ones commonly show a slight displacement to the postical surface in the way characteristic for the mature thallus. The gemmae just described may be considered typical, but reversions to a more embryonic condition are likely to occur in a greater or less degree. Under these circumstances a gemma, as fully described by Goebel, may be simply a cell-row or a cell-layer variable in width, and frequently shows no signs either of differentiation or dorsiventrality. The germination of a gemma, so far as observed, exhibits no features of especial interest. It simply gives rise to a thallus, which gradually becomes wider and more differentiated as its growth proceeds, and there is no line of demarcation between the gemma and the thallus. The production of new gemmae on the young plant sometimes begins very early, especially in the var. *ulvula*.

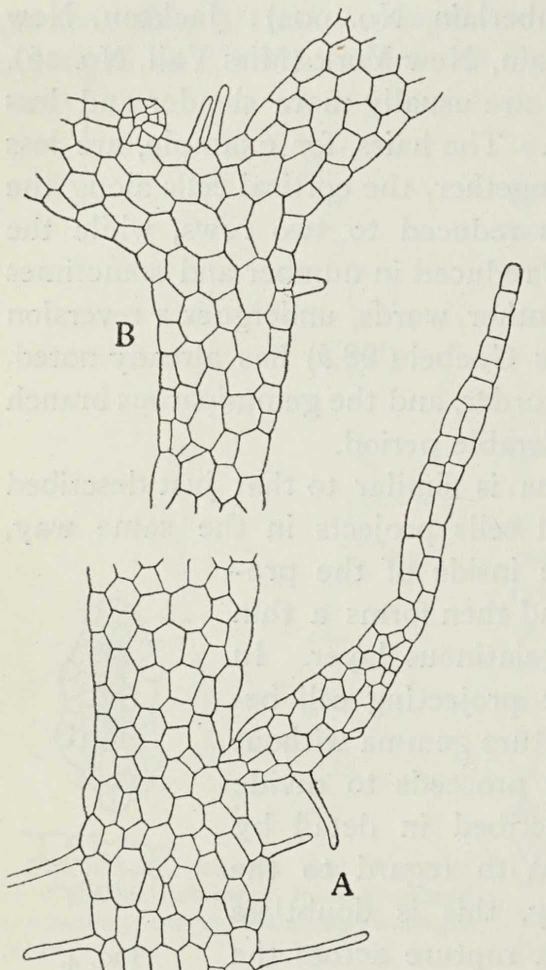

FIG. 5. *M. quadriseriata*. A. Portion of a thallus developed from a gemma; the new gemma on the right shows marked indications of reversion. × 80. B. Another portion of the same thallus, showing dichotomous branching. × 80.

Metzgeria quadriseriata, Evans.

This species is still known from a single locality in Japan, Ioki-mura, Tosa, where it was collected in 1903 by Yoshinaga.[1] The gemmiparous branches are more slender than normal branches, but show no further differences. The gemmae are usually sparingly produced and arise without definite order. They bear considerable resemblance to the gemmae of *M. furcata*, but show no signs of a costa and tend to be much narrower. Occasionally, they bear a very few short and straight marginal hairs, but they are more frequently quite undifferentiated. Although their width, through reversion, may be reduced to only one or two cells (Fig. 5, A), they are normally from six to eight cells wide. Their length, however, varies within wide limits at the time of separation. When a gemma germinates the thallus to which it gives rise usually continues narrow and

[1] Cf. Evans: Proc. Wash. Acad. Sci., viii, 142, pl. 6, figs. 1–5, 1906.

undifferentiated for a long distance. It may even show a branching, by dichotomy, while it still consists of a single layer of cells, a condition which has not been observed in either of the preceding species (Fig. 5, B). It may also give rise to new gemmae at a very early stage. Except for the difference in position the distinction between gemmae and adventive branches is not always clearly marked in *M. quadriseriata.* In typical cases the branches show a definite costa from the beginning, but they are sometimes in the form of narrow band-like structures only one cell thick throughout. Such a branch takes its origin from a single cortical cell of the costa, and is perhaps to be considered an example of regeneration rather than a true adventive branch. The close connexion between regeneration and the production of gemmae will be discussed later.

Metzgeria myriopoda, Lindb.

This species, although first described in 1874, is still incompletely known. It has been collected in several of the Southern States and also in Brazil and Argentina. The gemmiparous material studied came from Sanford, Florida (Rapp, No. 8), and from Opelousas, Louisiana (Langlois); it agrees closely with the specimens distributed by Drummond and by Sullivant, both of which are quoted by Lindberg. The branches which bear the gemmae are a little narrower than normal branches, but are otherwise scarcely modified. The gemmae are irregularly scattered and are sometimes abundant, but their development does not seem to affect the growth of the branch in any marked degree. The early stages in the development of a gemma are similar to those described for *M. furcata,* the original projecting cell becoming at once the mother-cell of the gemma. In most cases the gemmae maintain a width of six cells (about 0·12 mm.), but they may be still narrower or even a little broader (Fig. 6, A). Their length varies greatly and sometimes attains 1·5 mm. before separation takes place. The gemmae are usually but one cell thick throughout, but in rare cases a few of the cells at the base undergo a division parallel to the surface, thus forming an exceedingly rudimentary costa, which may or may not bear a very few postical hairs. This condition, however, apparently never persists, and the gemma as it continues its growth quickly becomes reduced to a simple cell-plate. Marginal hairs make their appearance very early, but usually remain short. Although some of them are truly marginal, the majority are slightly displaced to one surface, thus showing the first

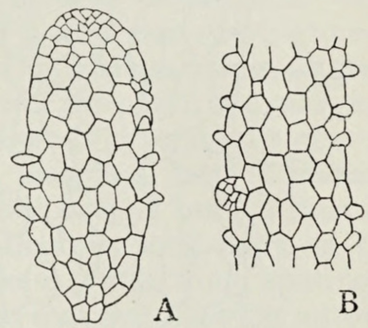

FIG. 6. *M. myriopoda.* A. A young gemma. × 80. B. Portion of a longer gemma, still attached to the gemmiparous branch, but showing a secondary gemma at the left. × 80.

indications of dorsi-ventrality. The gemmae often give rise to secondary gemmae while still attached (Fig. 6, B), and their method of separation from the parent plant is similar to that described for *M. furcata.* The germination of the gemmae has not been observed.

Metzgeria oligotricha, sp. nov.

The gemmae in this species are rather sparingly produced and are borne without definite sequence on normal vegetative branches. In the majority of cases their occurrence is intimately associated with the death of the apex of the branch, or else with the passage of the apical cell and the youngest segments into permanent tissue; under the latter circumstances the growth of the branch is limited even if its cells remain alive. Here again, as in *M. furcata*, the original marginal cell, which projects, becomes at once the mother-cell of the gemma. The gemmae are exceeding variable, not only in size, but also in the degree of differentiation which they show, in the length of time during which their apical cells continue functional, and in the number of secondary gemmae which they produce. A typical gemma is a flat and broad thallus, abruptly broadening out from the two basal cells. It is about ten cells (or 0·4 mm.) wide and usually from two to four times as long, and develops a variable number of long straight marginal hairs (Fig. 7). In some cases the hairs appear as mere rudiments and they may even be absent altogether. Although a gemma is usually but one cell thick, a rudimentary costa occasionally begins its development close to the base. The presence of such a costa, however, does not necessarily indicate dorsiventrality because it rarely develops either postical hairs or slime papillae.

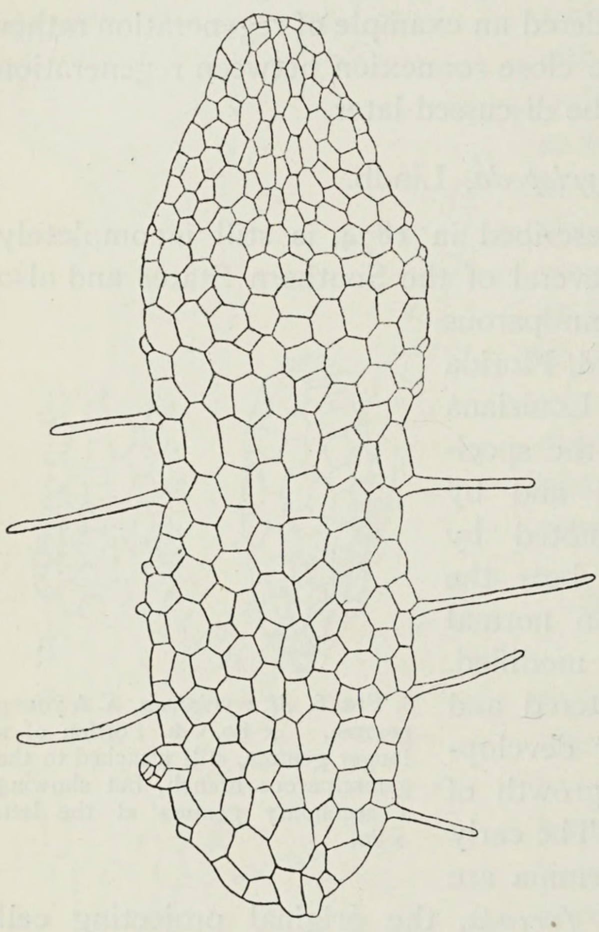

FIG. 7. *M. oligotricha.* A gemma about ready to separate, showing a secondary gemma at the left. × 80.

The germination of a gemma seems to follow a normal course under favourable circumstances. It gives rise at once to a thallus which gradually becomes broader, the costa appears or increases in complexity, postical hairs and slime papillae are formed, and the differentiated thallus soon shows the normal branching by dichotomy. The course of development, however, is usually affected by two tendencies, both of which seem to be especially potent in the present species. One of these is the tendency towards reversion, which has already been discussed under some of the preceding species; the other is the tendency which the apical region shows of acquiring the characteristics of permanent tissue, thus bringing the growth of the young thallus to an end. The cessation of growth and division in the apical cell may take place in any stage of differentiation, and is apparently associated with an early development of secondary gemmae.

Metzgeria oligotricha, sp. nov. Pale green, growing in depressed mats: thallus prostrate, repeatedly dichotomous and frequently giving off adventive branches from the postical surface of the costa, well-developed branches about 1·5 mm. wide, up to 4·5 mm. long between the forks, plane or nearly so; costa bounded both antically and postically by two rows of cortical cells; wings usually from ten to fifteen cells broad, the cells thin-walled throughout, averaging about $55 \times 37\ \mu$ and not varying much in size in different parts of the thallus; hairs few and irregularly scattered, restricted to the margin and to the postical surface of the costa, the marginal hairs often from 150 to 300 μ long, slender, straight or irregularly curved, but never hooked at the apex, usually truly marginal, but sometimes displaced to the postical surface: inflorescence dioicous: ♀ branch broadly orbicular-obovate, about 0·23 mm. long, with numerous long hairs on the margin and postical surface; calyptra clavate, about 1 mm. long, sparingly pilose: ♂ branch not seen: sporophyte (not quite mature) showing an oval capsule about $35 \times 28\ \mu$ and a stalk about 30 μ long: gemmae marginal, broadly ligulate, usually one cell thick throughout, stalk distinct, apical cell single, hairs marginal, not displaced, scattered, long and straight.

On trunks of trees. Cuba: without definite locality (Wright, Hep. Cubenses, distributed as *M. furcata*, mixed with *Dendroceros Breutelii* and other Bryophytes). Jamaica: Morce's Gap, July 12, 1903 (A. W. E., No. 37, mixed with *M. hamata*). Porto Rico: Mount Morales, near Utuado, March 19, 1906 (Howe, No. 1118). The specimens from Jamaica may be considered the type.

In the structure of its costa *M. oligotricha* agrees with both *M. uncigera* and *M. hamata*. It differs from *M. uncigera* in its larger size and larger alar cells, and in its longer marginal hairs which are never hooked at the apex even on the gemmae. The latter are also distinguished by their early development, the original projecting cell not undergoing a preliminary division before functioning as the mother-cell of the gemma. It differs from *M. hamata* in its plane thallus and in its sparse marginal hairs which are never geminate. From *M. furcata*, with which it is also allied, it differs in the structure of the costa, which is bounded postically by two instead of by four cortical cells. It differs further in its larger alar cells, in its longer marginal hairs which are slightly, or not at all, displaced to the postical surface, in its lack of postical hairs on the wings, and in its broader and less differentiated gemmae.

Metzgeria crassipilis, (Lindb.) Evans.

The antical gemmae found in *M. crassipilis* and its allies are on the whole more highly specialized than the marginal gemmae just described. Although they are sometimes borne in great abundance many of the plants fail to produce them altogether. The range of *M. crassipilis*, so far as known, extends from Vermont to North Carolina and Tennessee. The present study is based almost entirely on material collected by J. K. Small, on Blowing Rock Mountain, North Carolina, in 1892 (No. 31). The same material has served for the accompanying figures. The gemmiparous branches differ very slightly from ordinary branches and show no marked indications of having their growth limited. The only important modification which they show is an increase in the number of cortical cells along the antical surface of the costa. On normal branches these cells are arranged in two rows; on gemmiparous branches the number of rows varies from two to four (Fig. 8, A and B). The gemmae are not developed in definite order and sometimes occur so close together that they overlap as their size increases. Each one arises from a single alar cell which first of all projects above the surface of the thallus. In this process the protoplast of the cell

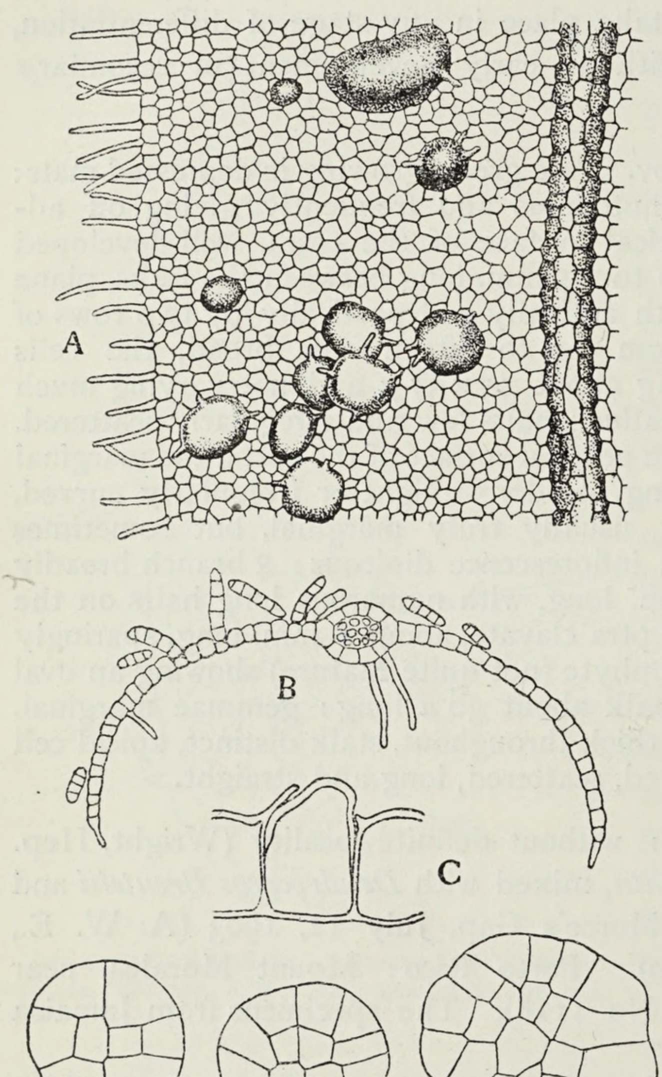

FIG. 8. *M. crassipilis*. A. Portion of a gemmiparous branch. × 50. B. Cross section of a gemmiparous branch. × 50. C–F. Early stages in the development of gemmae. × 300.

secretes a gelatinous layer, just as in *M. uncigera*, and this is followed by a rupture of the outer wall (Fig. 8, C). The projecting cell then divides by a wall approximately parallel to the surface of the thallus, and the upper cell thus cut off becomes the mother-cell of the future gemma. In some cases the projecting cell divides first by a perpendicular wall, and then, when the horizontal wall is formed, the rudiment of the gemma consists of two cells. Even when it consists of a single mother-cell, a condition which seems to be the more typical, it is quickly divided by a longitudinal wall

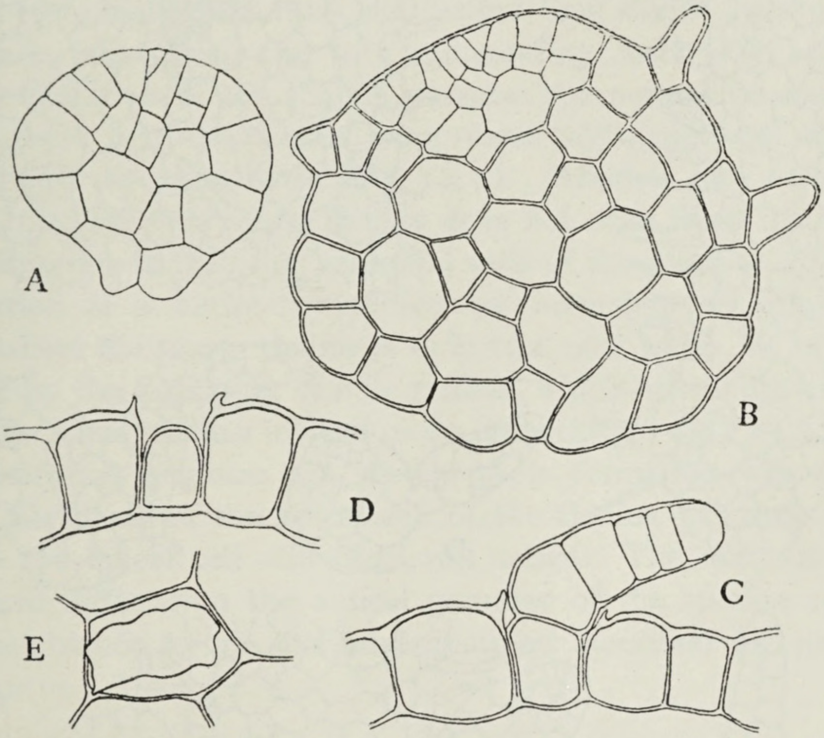

FIG. 9. *M. crassipilis*. A. A very young gemma with two apical cells. × 300. B. A typical gemma about ready to separate. × 300. C. Section through a young gemma and adjacent cells of thallus. × 300. D. Section through a similar region after the gemma has escaped. × 300. E. Surface view of a ruptured cell. × 400.

into two cells. Beyond the two-celled stage the development of the gemma is subject to further variation. The two cells first divide two or three times by cross walls, thus giving rise to a rounded structure composed of two rows of cells side by side. Some of these cells then divide by periclinal walls (Fig. 8, D and E), and before long one or two cells acting as two-sided apical cells make their appearance (Figs. 8, F, and 9, A). The apical cells are derived from the terminal cells of the original two rows, and it usually happens, even when two are formed, that only one continues to function. The result is that the mature gemma, except in very rare instances, has a single apical cell. At the time of separation the gemmae vary considerably in size, but the example represented in Fig. 9, B, may be regarded as fairly typical. Such a gemma is in the form of an orbicular and flat plate of cells, averaging about 0·15 mm. in diameter and measuring from six to eight cells across. Along the margin are scattered a few rudimentary hairs. The gemmae are set free by a splitting of the walls at the base (Fig. 9, C), leaving behind the single cell (or the two cells) cut off by the original

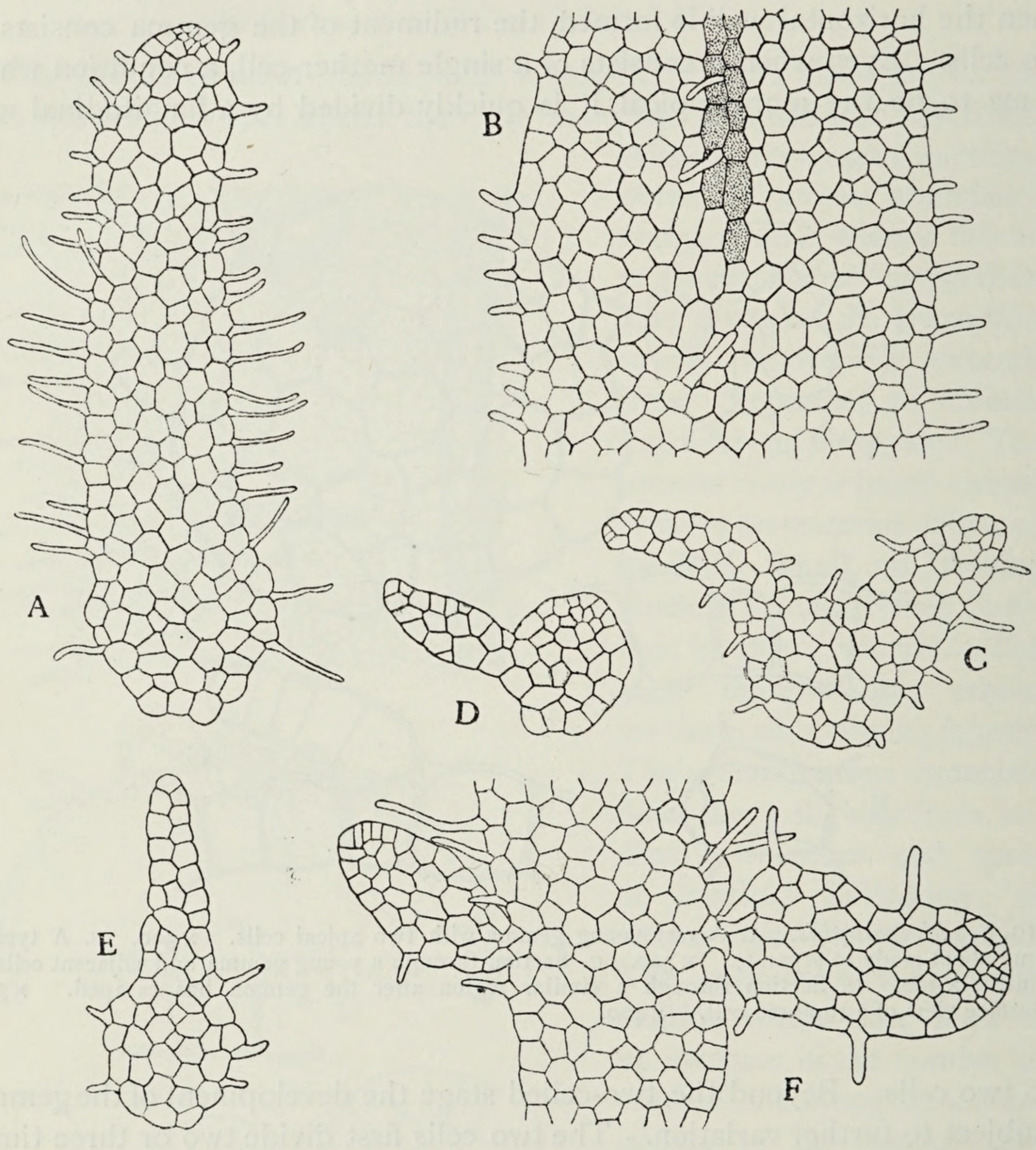

FIG. 10. *M. crassipilis.* A. A germinating gemma. × 80. B. Portion of a young thallus developed from a gemma, showing the first indications of a costa. × 80. C. Germination of a gemma with two apical cells. × 80. D. A germinating gemma, showing the young thallus developed from the margin instead of from the apex. × 80. E. A germinating gemma, the young thallus showing indications of reversion. × 80. F. Portion of a young thallus with new marginal gemmae. × 80.

horizontal wall. The cell thus left is lower than the neighbouring thallus cells, and the remains of the ruptured wall of the original projecting cell may often be demonstrated (Fig. 9, D and E). The two or three basal cells of the gemma become rounded off after separation and can usually be distinguished from the other marginal cells.

In rare cases the germination of the gemmae begins while they are still attached to the parent thallus, but the process is usually deferred until they have become separated. In normal cases, such as the one represented in Fig. 10, A, the apical cell of the gemma renews or continues its activities, and gives rise to a strap-shaped thallus which is at first but a single cell thick and about six cells wide. The margin bears numerous scattered hairs, but the young plant shows no further evidences of cell-differentiation and no signs of dorsiventrality. As its growth proceeds scattered hairs appear on one surface (destined to become the postical), the median cells become arranged in two longitudinal rows, and before long divide by walls parallel to the surface, thus giving rise to a rudimentary costa (Fig. 10, B). The further differentiation of the thallus pursues the normal course. In the rare cases where two apical cells are present and functional the gemma gives rise to two diverging thalli (Fig. 10, C). Another rare case is shown in Fig. 10, D, where the young thallus does not arise from the apical cell at all, but from one of the other marginal cells of the gemma. The process of germination is sometimes modified by reversion, as illustrated in Fig. 10, E, where the young thallus is only two cells wide. It may also be complicated by the formation of new gemma, which invariably arise on the margin of the young thallus instead of on its surface. In Fig. 10, F, where two such marginal gemmae are shown, their formation was apparently induced by the death of the apical cell of the thallus, but they sometimes occur while the apical cell still continues active. The marginal gemmae thus produced differ from the antical gemmae of the species, and bear a marked resemblance to the marginal gemmae described for some of the preceding forms.

Metzgeria vivipara, sp. nov.

The gemmae, as in *M. crassipilis*, are borne upon branches which show few or no signs of specialization. When they are produced in great abundance the growth of the gemmiparous branch tends to be limited, but this tendency is not very apparent and seems to be easily overcome. The projecting alar cell which is to form a gemma first divides by several longitudinal walls before the transverse walls which mark off the young gemma make their appearance. As a result of this the gemma upon separating leaves behind a patch of three to five small thallus cells instead of a single larger cell. The mature gemmae are very similar to the marginal gemmae of *M. uncigera*. Each one is a flat strap-shaped thallus with a single apical cell and numerous hooked marginal hairs (Fig. 11, A). It measures about 0·6 mm. in length by 0·15 mm. in width and is usually from six to eight cells across. Towards the base there is a gradual tapering, and the three to five basal cells, which form a short and poorly defined stalk, are commonly arranged in two layers. Sometimes the two-layered condition persists for a short distance in the basal region (Fig. 11, B), but except for this the gemma is only one cell thick throughout its entire extent. The hooked hairs are sometimes truly marginal, but are more likely to be displaced to either surface. They usually occur singly, but are occasionally found in pairs. The gemmae show no evident indications of dorsiventrality.

The germination of a gemma exhibits no unusual features. It gives rise to a flat thallus which gradually becomes broader, the new marginal

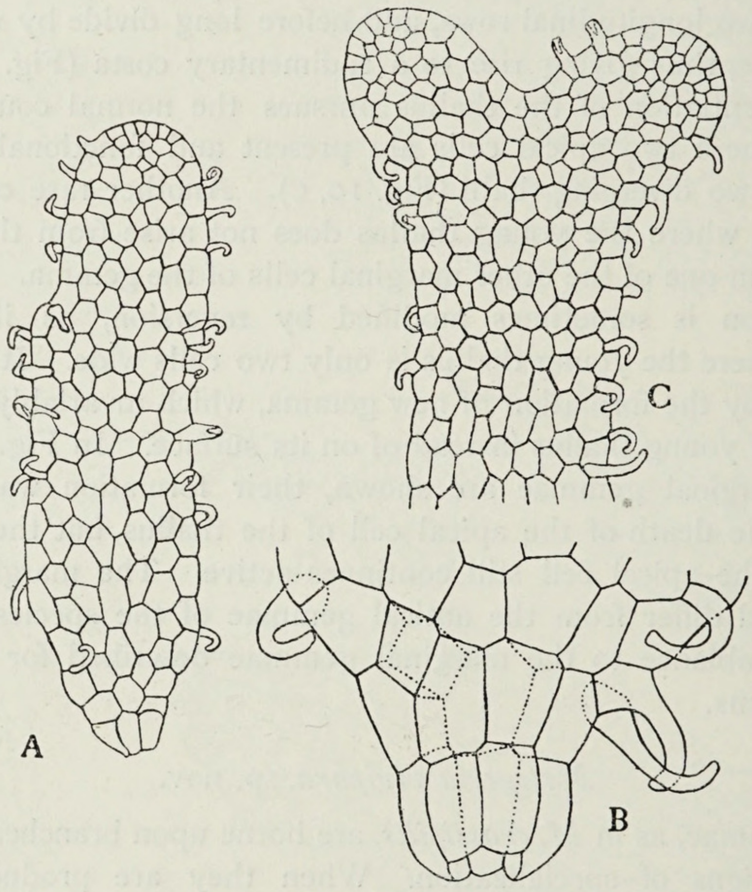

FIG. 11. *M. vivipara*. A. A gemma about ready to separate. × 80. B. Base of a gemma. × 300. C. Portion of a young thallus developed from a gemma, showing dichotomous branching. × 80.

hairs tend to be straight instead of hooked, and many become displaced to what may now be considered the postical surface, other hairs arise on the same surface at some distance from the margin, and finally the costa appears and increases more and more in complexity. In some cases the development of postical surface hairs is deferred until the rudiments of the costa have become evident. A tendency to dichotomy frequently becomes manifest, not only in the gemma itself, but also in the young thallus while it still consists of a single layer of cells (Fig. 11, C). A similar dichotomy has already been described in *M. quadriseriata*, where, however, it occurs as a rather unusual exception. Both the gemmae and the young plants which develop from them are subject to reversion. The production of new gemmae on a young and undifferentiated thallus is very unusual. When they do occur they are invariably marginal.

Metzgeria vivipara, sp. nov. Yellowish or brownish green, growing in depressed mats: thallus prostrate, repeatedly dichotomous, well-developed branches about 1·5 mm. wide and from 1·5 to 3·5 mm. long between the forks, plane or nearly so; costa bounded above by two rows of cortical cells and below by four rows (rarely only two or three); wings mostly from twenty to twenty-five cells broad, the cells thin-walled throughout or with very minute trigones, averaging about $35 \times 25\,\mu$, slightly smaller towards the margin; hairs restricted to the margin and to the postical surface of both wings and costa, the marginal hairs often absent altogether, when present usually few and scattered, up to $150\,\mu$ long, straight or nearly so, sometimes truly marginal, but often slightly displaced to the postical surface, alar surface hairs and costal hairs usually more numerous than the marginal hairs, but sometimes more sparingly developed: inflorescence dioicous: ♀ branch orbicular-obovate, about 0·25 mm. long, sparingly pilose on margin and postical surface: ♂ inflorescence and sporophyte not seen: gemmae numerous, arising from the antical surface of the wings, ligulate, one cell thick except at the very base, stalk poorly defined, apical cell single, hairs marginal, short, hooked at the apex, usually single, but occasionally twinned, sometimes displaced to one surface.

On trunks of trees. Porto Rico: Barceloneta, April 19, 1887 (Sintenis, No. 144, distributed as *M. furcata*); Utuado to Adjuntas, March 21, 1906 (Britton and Cowell, No. 1242). The second specimens may be considered the type.

In its vegetative structure, *M. vivipara* shows a close relationship to *M. furcata*, the costa being built up according to a similar plan and the distribution of the hairs being much the same. It may be at once distinguished, however, by its antical gemmae with their slight cell-differentiation and hooked marginal hairs. Among other species with antical gemmae its closest ally is apparently *M. crassipilis*, which has a similar costa, and also bears hairs on the postical surface of the wings. The gemmae will serve at once to separate the two species; in *M. vivipara* these are ligulate and bear hooked hairs, while in *M. crassipilis* they are orbicular and the hairs are straight.

Metzgeria Liebmanniana, Lindenb. & Gottsche.

According to Stephani the range of this species extends from Mexico to Chile and eastward into Brazil. The specimens here described were collected in Contreras, Mexico, on October 15, 1908, by Barnes and Land (No. 430). They bear gemmae in great abundance. The gemmiparous branches, as in the two preceding species, are very slightly modified. In some cases a tendency towards a decrease in the number of cortical cells along the antical surface of the costa becomes apparent. On normal branches, for example, these cells are arranged in from four to six rows, while on gemmiparous branches there are often only two rows present. An opposite tendency has already been noted in *M. crassipilis*, where the number of rows is often increased from two to three or four. It is possible, however, that this difference between the two species is not of very great significance, because it may be due to factors which are not concerned in the production of the gemmae. The development of the gemmae in *M. Liebmanniana* is very much the same as in *M. crassipilis*. Their structure at the time of separation is also similar, except that they are usually less differentiated. A mature gemma is in the form of a flat or concave plate of cells, orbicular in form and measuring about 0·12 mm. across (Fig. 12, A). It consists throughout of a single layer of cells and does not have a stalk, although the two basal cells can usually be distinguished. Very young gemmae sometimes show two apical cells, but it is exceedingly rare for more than one to persist. Marginal hairs are sometimes absent altogether and sometimes appear, in very small numbers, as short rudiments. If the gemma is plane it shows absolutely no indications of dorsiventrality ; if it is not plane the concave surface represents what is morphologically the postical surface. Even here, however, the dorsiventrality is probably not stable at the beginning.

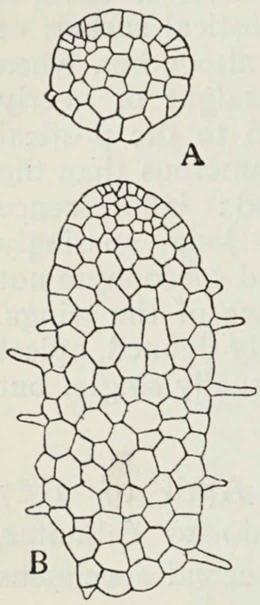

FIG. 12. *M. Liebmanniana*. A. A gemma about ready to separate. ×80. B. A germinating gemma. ×80.

In germination (Fig. 12, B) the rudimentary hairs develop further and assume the function of rhizoids. New marginal hairs also make their appearance and tend to be slightly displaced to one surface. In cases where the gemma is concave, the hairs are always displaced to the concave surface, thus emphasizing its postical nature. The apex of the gemma soon gives rise to a new thallus which consists at first of a strap-shaped plate of cells bearing a few marginal hairs. Since these are truly marginal, the young plant is quite without evidences of dorsiventrality, even if the gemma from which it grew was concave. It is only later, as the differentiation of the thallus proceeds, that the dorsiventrality again becomes apparent. The steps of the process are essentially the same as in previously described cases. In rare cases the young thallus forks while it still consists of a single layer of cells.

Metzgeria dichotoma, (Swartz) Nees.

The present species was originally collected in Jamaica by Swartz and is apparently not uncommon in the Blue Mountains. Lindberg records it also from Cuba, Mexico, and Brazil. The gemmiparous material described below was collected on Mount Morales, near Utuado, Porto Rico, on March 15, 1906, by E. G. Britton and D. W. Marble (No. 498). Its determination as *M. dichotoma* must be considered somewhat doubtful, since the Jamaican specimens examined by the writer are entirely destitute of gemmae. Lindberg, however, notes the occurrence of surface gemmae in this species although he fails to mention any of their peculiarities. The gemmiparous branches in the Porto Rican plants are scarcely if at all modified, and there seems to be no marked tendency for their growth to be limited. The gemmae arise in considerable abundance, but without definite order. An alar cell which is to give rise to a gemma first bulges in the

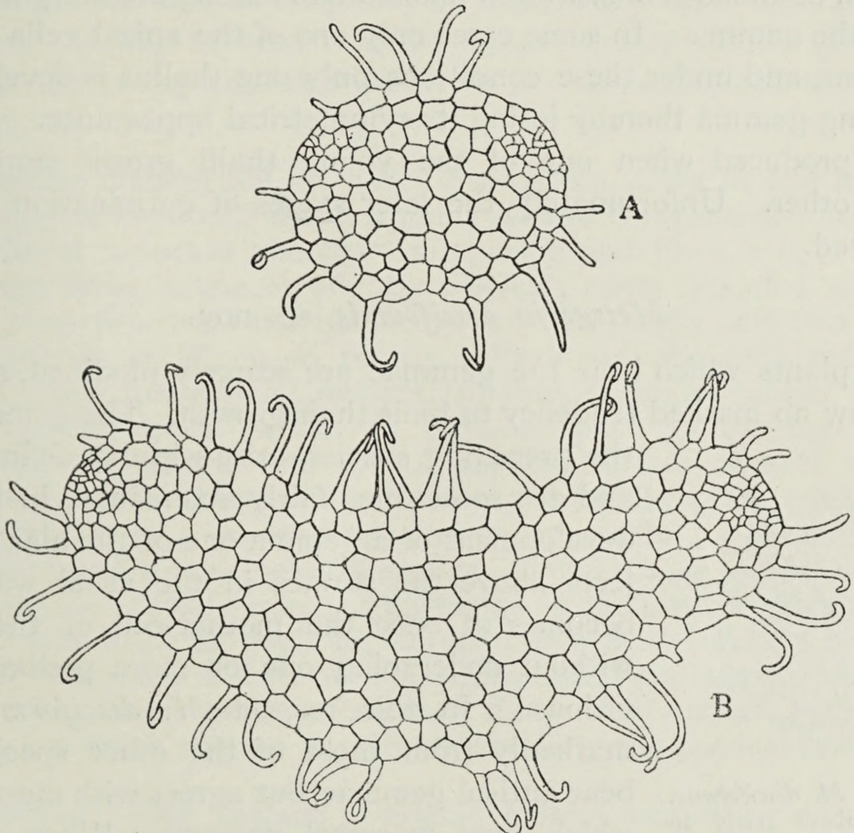

FIG. 13. *M. dichotoma.* A. A gemma at time of separation. × 80. B. A germinating gemma showing the two young thalli. × 80.

usual way and then divides by a longitudinal wall before forming the transverse wall which marks off the future gemma. The result is that the gemma leaves behind two small thallus cells when it becomes separated. The gemmae are very remarkable from the fact that each of the two cells, of which the young rudiment consists, develops regularly an apical cell after a few divisions, and the two apical cells persist and continue their activities until the gemma is ready to separate. The gemma is accordingly symmetrically developed, and the condition which is found in *M. crassipilis* as a rare exception is here the rule. A mature gemma (Fig. 13, A) is a circular or reniform plate of cells, perfectly plane and showing no indications of dorsi-ventrality. Where the two basal cells are situated the margin is either truncate or more or less retuse. The numerous hairs are all truly marginal and always occur singly. They are about three times as long as the cells of the gemma and are hooked at the apex. The two apical cells are situated in the outer portions of the symmetrical halves. A typical gemma is about 0·2 mm. long at the time of separation and measures about eight cells across the middle.

When a gemma germinates normally each of the apical regions develops a strap-shaped thallus one cell thick and about eight cells wide (Fig. 13, B). These two thalli diverge at a wide angle, and continue to produce an abundance of scattered hooked hairs along the margin similar to those on the gemma. In some cases only one of the apical cells continues its divisions, and under these conditions only one thallus is developed, the germinating gemma thereby losing its symmetrical appearance. A similar result is produced when one of the young thalli grows more rapidly than the other. Unfortunately, the later stages of germination could not be observed.

Metzgeria disciformis, sp. nov.

The plants which bear the gemmae are scarcely modified, and apparently show no marked tendency to limit their growth. The gemmae, as in the preceding species, arise without definite order, and are sometimes fairly abundant. In the early development of a gemma one of the alar cells projects above the surface in the usual way, but it becomes at once the mother-cell of the gemma without undergoing one or more preliminary divisions. In this respect *M. disciformis* differs markedly from most of the other species which bear antical gemmae, but agrees with most of those which bear marginal gemmae. When a gemma separates it leaves behind an empty cell which appears like a perforation of the thallus. The gemmae are often more or less strongly tinged with blue, especially when young, a condition which seems to be due to a pigmentation of the cell-walls. A mature gemma (Fig. 14) is in the form of a concave and circular plate of cells, about 0·2 mm. in diameter and measuring about twelve cells across. In the basal region it shows a short but distinct stalk, composed of two or three cells, and the single apical cell is also clearly apparent. As in *M. Liebmanniana*, the concave surface of the gemma represents the postical surface, and the dorsiventrality of the structure is even better marked. All around the margin are numerous short and straight hairs, some of which are truly marginal, although the majority are slightly displaced to

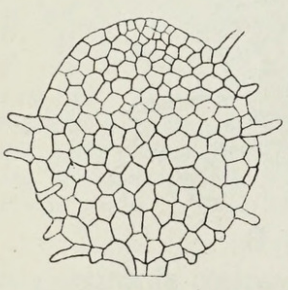

FIG. 14. *M. disciformis*. A gemma about ready to separate, postical view. ×80.

the postical surface. The hairs sometimes spread, but are more likely to be at right angles to the surface of the gemma. The convex antical surface is occasionally destitute of hairs, but usually bears a few near the centre, and these antical hairs are considerably longer than the marginal.

The germination of a gemma was observed in a single instance. The marginal hairs had grown longer, and assumed the function of rhizoids, holding the gemma firmly to the surface of a leaf. The apical end of the gemma had grown out into a short thalloid structure which had produced a number of scattered postical hairs also acting as rhizoids. The majority of these hairs were situated close to the margin. Further differentiation of the thallus had also taken place, a rudimentary costa having made its appearance. It will be seen that the dorsiventrality of the gemma here persists in the young thallus, whereas in *M. Liebmanniana* it apparently disappears.

Metzgeria disciformis, sp. nov. Pale green, more or less tinged with blue, growing in depressed mats : thallus prostrate, repeatedly dichotomous, well-developed branches about 1·2 mm. wide and from 1 to 2 mm. long between the forks, plane or slightly convex ; costa bounded antically by two rows of cortical cells and below by four rows (rarely only two or three) ; wings mostly from fifteen to twenty cells broad, the cells with slightly thickened walls, but without evident trigones, averaging about $25 \times 21\ \mu$, and not varying much in size in different parts of the thallus ; hairs restricted to the margin and to the postical surface of both wings and costa, sometimes few, but usually abundant along the costa, marginal hairs averaging about $90\ \mu$ in length, straight or nearly so, occurring singly, slightly displaced to the postical surface : inflorescence not seen : gemmae arising from the antical surface of the wings, in the form of circular concave disks, one cell thick throughout, abruptly contracted at the base into a short stalk composed of two or three cells, apical cell single, antical hairs few or wanting, borne near the centre of the convex surface, marginal hairs numerous, but much shorter, usually displaced to the postical surface.

On leaves. New Zealand : without definite locality or date (Colenso, No. 1997). The specimens were communicated to the writer under the name *M. australis*, Steph., a species which is now considered a synonym of *M. nitida*, Mitt. They differ, however, very markedly from this species.

Except for its small cells and peculiar colour the present species agrees pretty closely with *M. furcata* in its vegetative structure, the costa being built up according to the same plan, and the distribution of the hairs being much the same. The antical gemmae will at once serve to distinguish it. Their marked dorsiventrality is perhaps their most striking characteristic. It should also be noted that the antical surface of the thallus bears a few scattered hairs in rare instances, a condition which should doubtless be regarded as abnormal.

Metzgeria linearis, (Swartz) Aust.

The original material of this peculiar species was collected by Swartz on the island of Santo Domingo. It has since been found in Cuba by Wright and in Jamaica by E. G. Britton. The account of the gemmae is largely based on Wright's specimens, which have also served for the figures. *M. linearis* is distinguished from the other known species of the genus by the fact that the marginal cells are much elongated and have strongly thickened walls, thus forming a distinct border to the thallus (Fig. 15, A). The marginal hairs also have thickened walls, except when they assume the function of rhizoids, and are frequently sharp-pointed. The gemmiparous branches tend to be a little narrower than usual, and to be more or less tinged with blue. In other respects they are essentially like normal branches, and show no marked indications of being limited in their growth. The gemmae arise in no definite order. Each one begins as a single projecting alar cell, which becomes at once the mother-cell of the gemma, thus agreeing with *M. disciformis*. At the time of separation the gemma consists of an oval or circular plate of cells (Fig. 15, B), which is plane or nearly so. It averages about 0·12 mm., or six cells, wide. At the base of the gemma two stalk-cells, usually lying in a different plane, may be distinguished (Fig. 15, C), while the opposite end, with its single apical cell, is often narrowed to a very blunt point. The hairs produced are short, thin-walled, and few. They are sometimes truly marginal, but are more likely to be displaced to either surface indiscriminately. Under these circumstances they are often situated at the inner edge of the marginal cells, and thus appear at some little distance from the margin. Occasionally, in fact, some of the internal cells give rise to hairs. The gemmae present no evidences of dorsiventrality.

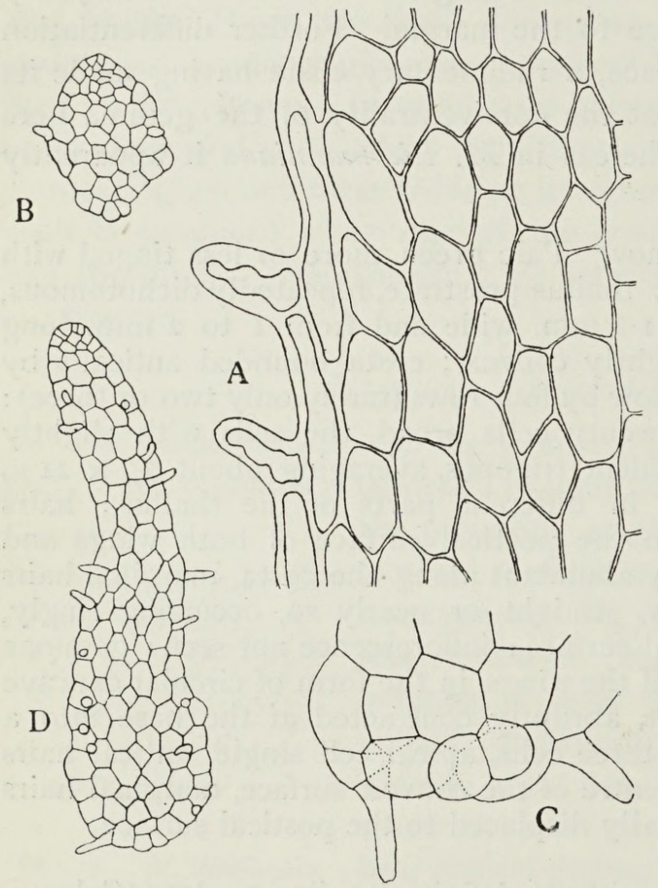

FIG. 15. *M. linearis*. A. Portion of a normal thallus, showing the differentiated margin. × 300. B. A gemma at time of separation. × 80. C. Base of a gemma, showing the two stalk-cells in a different plane. × 300. D. A germinating gemma. × 80.

The germination has been observed only in the early stages, and agrees essentially with what has been described for most of the preceding species. The young thallus, which results from the activity of the apical cell, is usually narrower than the gemma (Fig. 15, D), although the change from one to the other is often gradual. The narrow condition persists for a variable distance, and then the young thallus becomes broader again. Scattered hairs, like those on the gemma, continue to be produced, and a forking of the thallus is sometimes to be observed. Although in some cases the young thalli had attained a length of a millimetre or more, no further differentiation and no evidences whatever of dorsiventrality had become apparent. In all probability the peculiar marginal cells and hairs of the mature thallus mark a very late stage of development.

Metzgeria fruticulosa, (Dicks.) comb. nov.

Since most recent writers have considered *M. fruticulosa* to be nothing more than a form or variety of *M. furcata* its geographical distribution is very incompletely known. It has been recorded in Europe from a number of scattered localities, but the only American station which the writer can quote at the present time is near Aberdeen, Washington, where the plant was collected on February 18, 1909, by Foster (No. 944). The description of the gemmiparous branches (with the accompanying figures) is drawn largely from these specimens, which were kindly supplied by Miss Haynes. Material from Salem in Baden, Germany, collected by Jack (Hep. Europ. No. 357), and from Cherbourg, France, collected by Corbière, has been used for comparison. In contrast to the species already described *M. fruticulosa* has strongly specialized gemmiparous branches. Other species with similar branches have already been alluded to in the introduction, but unfortunately none of these have been available in sufficient quantity for detailed study.

The normal branches in *M. fruticulosa* are prostrate and divide by forking. The costa is usually bounded both antically and postically by two rows of cells (Fig. 16, A), although the number of postical rows is sometimes three or even four. The number of internal costal cells averages about ten in cross section. The wings are plane or slightly convex and attain a width of perhaps ten cells. On the postical surface of the costa and along the margin are numerous straight hairs which often act as rhizoids. Scattered hairs on the postical surface of the wings are sometimes present as well. Most of the marginal hairs occur singly, but they are sometimes geminate. They are apparently never displaced to the postical surface. In the vicinity of the apex slime papillae of the usual type may be demonstrated. According to most writers the fresh plants are green, but they often become tinged with blue after being dried.

When a branch becomes gemmiparous, it gradually curves away from the substratum, and may in time assume a position at right angles to it. The hairs become fewer and fewer, and before long cease to be developed at all, and the slime papillae also fail to appear. The wings become strongly convex, and at the same time grow more and more narrow until in some cases the thallus becomes reduced to the costa. The first change to be noted in the costa is a reduction in the number of internal cells (Fig. 16, B). As growth continues the number of these cells again becomes larger (Fig. 16, C). With their increase in number they also increase in size, thus approaching in appearance the cortical cells, but they can always be

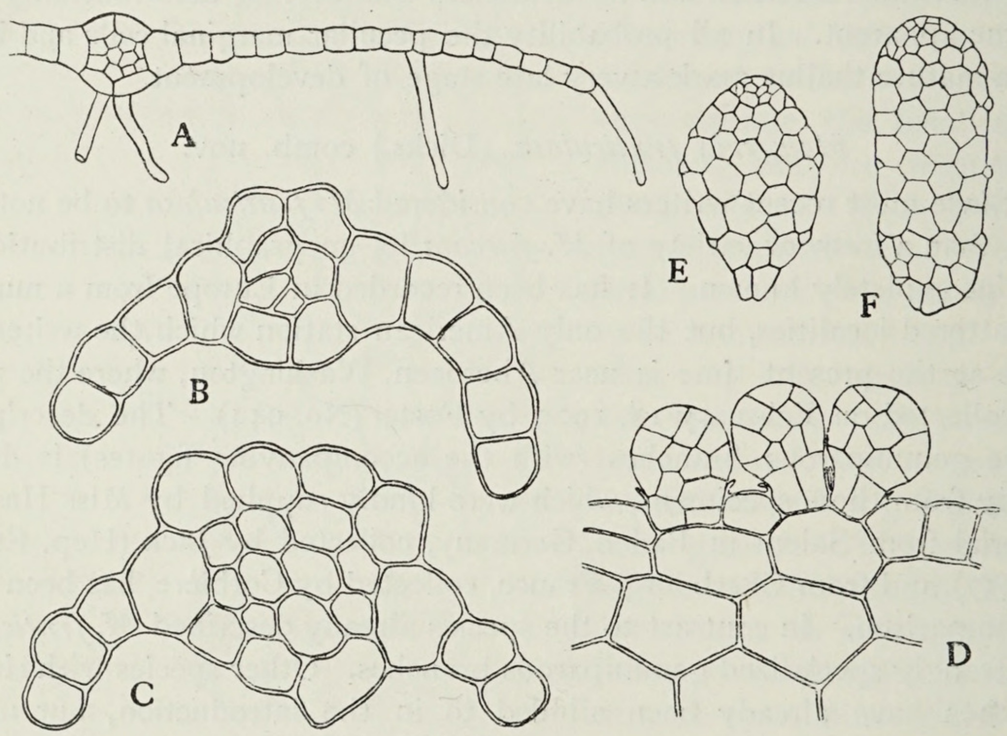

FIG. 16. *M. fruticulosa.* A. Cross section of a normal thallus. × 80. B. Section through the lower portion of a gemmiparous branch. × 300. C. Section through the upper portion of a gemmiparous branch. × 300. D. Young gemmae. × 300. E, F. Gemmae about ready to separate. × 80.

distinguished by their somewhat greater length. The cortical cells first remain in four rows, but are more bulging than in a normal costa. Later on they become more numerous, forming perhaps four rows both antically and postically, but as they increase in number their arrangement becomes irregular so that the rows are no longer distinct. If the wings become reduced to the cells which bound the internal tissues of the costa laterally, then the gemmiparous axis exhibits a condition of radial symmetry, as Goebel ('98 *a*, p. 275) has described for *M. conjugata.* The radial portion of the shoot is always very short because its growth comes to an end soon after extreme specialization has been reached. Very often, in fact, the growth stops before the radial condition has been attained.

The first gemmae formed are marginal in position. Sometimes they appear on branches which are just beginning to show signs of specialization, and under these circumstances the branch may recover, as it were, and continue its growth normally. In most cases, however, the formation of gemmae does not begin until the modification of the branch is well under way. They become more numerous as the growth of the branch continues, and before long arise not only from the alar cells, but from the cortical cells as well. When the thallus ceases to develop wings, any surface cell seems to have the power of producing a gemma. When a gemma is to be formed, whatever its position, the projecting cell becomes at once the mother-cell of the gemma (Fig. 16, D). At the time of separation the gemmae are small circular to oblong plates of cells about 0·12 mm. wide (Fig. 16, E and F). They taper more or less distinctly towards the basal end and show a rounded apex with a single apical cell. Except for the scattered rudiments of marginal hairs they are quite undifferentiated. They also show no distinct signs of dorsiventrality, although they are sometimes slightly concave. It will be seen that these gemmae are among the simplest that have been described.

The germination of a gemma, when following a normal course, shows few peculiar features. The marginal rudiments of hairs become elongated and assume the function of rhizoids. The apical region then grows out into a thallus which gradually becomes broader. Although consisting at first of a single layer of cells it soon produces marginal and surface hairs. The latter are restricted to the surface turned towards the substratum, which at the same time becomes concave, so that the dorsi-ventrality of the young plant is established at an early stage. The marginal hairs usually occur singly, but occasionally appear in pairs as differentiation proceeds. They may be truly marginal or slightly displaced to the postical surface, a condition which tends to become less and less frequent. With the differentiation of the costa, which takes place in the usual way, the postical hairs become more numerous along its course and less numerous on the postical surface of the wings. Forking occasionally takes place before the costa has made its appearance.

The germination, however, often follows an aberrant course. This is sometimes due to reversion, by means of which the thallus becomes narrower or less differentiated as it advances in length. But it is much more frequently due to the development of new gemmae and to the modifications associated with their production. The new gemmae may arise on the original gemma itself or on the young thallus in any stage of its differentiation. When the production of gemmae is abundant the growth of the gemmiparous axis soon comes to an end, and this may take place while the young plant still consists of a single layer of cells. If the costa is already differentiated before the new gemmae appear the axis acquires the form and structure of the specialized gemmiparous branches described above. Except under the last conditions the new gemmae are always marginal and show no peculiar features.

It follows from the above description that the development of gemmae in *M. fruticulosa* is often associated with a more or less incomplete differentiation of the gemmiparous plant ; in other words, that the growth of the plant is concluded while it is still in an embryonic or juvenile condition. Even the prostrate thallus, which has been spoken of as normal, presents certain juvenile features, and apparently never reaches the stage of development in which sexual branches can be produced. These facts naturally bring the validity of the plant, as a species, into question, and it seems possible that it may simply represent an immature stage of some other member of the genus. If the known range of *M. fruticulosa* is taken into consideration, it will be seen that three other species, *M. pubescens*, *M. furcata*, and *M. conjugata*, have a very similar distribution. With the very distinct *M. pubescens* it can hardly have any close connexion, but with the other two species it shares numerous characters in common. In *M. furcata*, var. *ulvula*, however, another plant is met with in which the thallus usually fails to develop beyond a certain stage. Since this variety *ulvula* is entirely different from *M. fruticulosa* in appearance and method of growth, it is scarcely probable that they can both represent juvenile conditions of the same species. The fact that the marginal hairs are not displaced, and that they are occasionally geminate, indicates an approach to *M. conjugata*, but its identity with this species could only be proved by culture experiments. It should be noted, however, that the gemmiparous plants which Goebel ('98 *a*, p. 275) refers to *M. conjugata* are apparently what is here described as *M. fruticulosa*, but Goebel does not state that he demonstrated the connexion between his plants and undoubted *M. conjugata*. Until this is done it seems allowable to keep the two species distinct. If it becomes necessary to unite them in the future the plant should still bear the name *fruticulosa*, since this has a priority of over eighty years. The history of *M. fruticulosa* and the various views which writers have held concerning it are clearly shown by the following synonymy, taken mostly from Lindberg's Monograph:—

Metzgeria fruticulosa, (Dicks.) comb. nov.

Riccia fruticulosa, Dicks., Pl. Crypt. Brit., i, 8. 1785.

Jungermannia fruticulosa Smith, Engl. Bot., xxxv, pl. 2514. 1813.

Jungermannia furcata, var. *aeruginosa*, Hook., Brit. Jung., pl. 55. 1816.

Fasciola violacea, Dumort., Comm. Bot., 114. 1822 (not *Jungermannia violacea,* Ach.).

Echinogyna violacea, Dumort., Syll. Jung. Eur., 84. 1831.

Echinomitrium violaceum, Corda, Deutschl. Jung. (in Sturm's Flora), 81, pl. 22. 1832.

Metzgeria violacea, Dumort., Recueil d'Obs. sur les Jung., 26. 1835.

Metzgeria furcata, var. *gemmifera*, Nees, Naturg. der europ. Leberm., iii, 488. 1838.

Metzgeria furcata, var. *violacea*, Dumort., Hep. Europ., 139. 1874.

Metzgeria furcata, var. *aeruginosa*, Moore, Proc. Irish Acad., 2nd Ser., ii, 665. 1876.

Metzgeria furcata, var. *fruticulosa*, Lindb., Acta Soc. Faun. Fl. Fenn., i, 40. 1877.

By some of the earlier writers *M. fruticulosa* was supposed to be identical with *Jungermannia violacea*, Ach.,[1] a species based on specimens collected at Dusky Bay, New Zealand, in 1773, by Sparrman. These specimens were examined by Lindberg, who pointed out that they were distinct from the European plant. He referred them to *Metzgeria conjugata*, as a variety *violacea*, although he knew the typical *M. conjugata* only from the Northern Hemisphere. Judging from Lindberg's description the variety *violacea* bears specialized gemmiparous shoots and is deserving of further study. In Stephani's monograph of the genus *Metzgeria* neither *M. fruticulosa* nor *M. violacea* is mentioned.

Gemmae of Metzgeria and of other Bryophytes compared.

Vegetative reproduction by means of gemmae is a phenomenon of widespread occurrence among the Bryophytes, and has been observed in all the orders except the Sphagnales and the Andreaeales. The various types of gemmae which have been found in the Bryales are fully discussed by Correns ('99), and the gemmae of the Hepaticae have been similarly, but more briefly, treated by Cavers ('03). According to Correns (p. 446) the power to produce gemmae (and similar reproductive bodies) is inherent in certain species, but absent from others, so that it ought to be regarded as a definite specific character. In most of the gemmiparous species of the Jungermanniales the gemmae are in the form of minute unicellular or bicellular bodies, but in the remaining species they are multicellular and sometimes show a greater or less degree of cell-differentiation. In a few cases such gemmae form solid masses of cells, as in *Blasia* and *Cavicularia*, but it is much more usual for them to be in the form of flattened thalloid structures, similar to those just described for *Metzgeria.* Gemmae of this type are by no means confined to genera in which the adult plant is a leafless thallus. They occur also in a number of leafy genera belonging to the Porelleae, Raduleae, and Jubuleae. In all of these sub-orders, however, as Goebel ('89, p. 16) and others have pointed out, the spore in germinating first gives rise to a thallus, upon which the leafy shoot after-

[1] In Weber and Mohr's Beiträge zur Naturkunde, i, 76, pl. 1, figs. 1–3, 1805.

wards develops, so that the gemmae here, as in *Metzgeria*, show certain of the characteristics of embryonic plants.

Thalloid gemmae are now known in nine genera of the leafy Jungermanniales, and have been carefully studied in *Radula*, *Cololejeunea*, *Metzgeriopsis*, and *Cyclolejeunea*.[1] They usually arise on the leaves themselves, but are occasionally borne on the margins of other gemmae or on young plants which are still in the thalloid condition. In all the known cases the gemmae are but one cell thick throughout. Each one takes its origin in a single cell, just as in *Metzgeria*, and in all cases that have been described the cell first projects and then divides into two cells by a wall perpendicular to its long axis. The outer cell thus formed represents the mother-cell of the future gemma, while the inner cell may be regarded as a poorly defined stalk. The conditions are essentially the same as in *M. uncigera* and *M. crassipilis*. The separation of the gemma is schizolytic, and is brought about by a splitting of the walls between its basal cells and the stalk-cell. Although the gemmae in all of these leafy genera are very similar to those described for *Metzgeria*, the resemblance is especially close in the tropical genus *Cyclolejeunea*, of which about six species are at present known. In this genus there are two types of gemmae, one with a single apical cell (which does not always persist until maturity) and the other with two. The first type is apparently the more frequent, the second being known in the single species *C. angulistipa*. Gemmae of the first type are essentially like those of *Metzgeria crassipilis*, *M. linearis*, &c., while those of the second type are duplicated in *M. dichotoma*. The resemblance is made still more striking by the presence of hairs, formed by the elongation of small cells. These hairs sometimes function as rhizoids, but often fail to do so, the true rhizoids being independently produced.

According to Lindberg ('75) the marked similarity between the various thalloid gemmae indicates a true genetic relationship, and in his classification of the Hepaticae he separates *Metzgeria* from the other thallose Jungermanniales and includes it in his group Anomogamae, to which he refers also *Frullania*, *Lejeunea* (in its broad sense), *Radula*, *Porella*, and *Pleurozia*. His views on the subject, however, have not met with much favour, most writers preferring to retain *Metzgeria* in the group to which the other thallose genera are referred. It should be remembered in this connexion that the species producing thalloid gemmae all grow in places where it is difficult for young plants to gain a foothold, such, for example, as rocks, the bark of trees, or the surface of living leaves. The thalloid form is especially effective in enabling the gemmae (as well as the young plants developing from spores) to hold themselves in place. It seems perfectly reasonable, therefore, to associate the similarity in the gemmae with the similarity in environment.

[1] Cf. Goebel ('87), Schiffner ('93), and Evans ('04).

Among the thallose Jungermanniales the closest relative of *Metzgeria* is apparently *Riccardia* (*Aneura*), and this is the only genus in which the gemmae are at all similar. Even here the resemblance is much less striking than in the leafy forms just described, largely because the gemmae are still very rudimentary structures at the time of their separation. They are wholly undifferentiated and are in the form of minute oval bodies, each consisting usually of only two cells. Each gemma arises from one of the surface cells of the thallus, which becomes at once the mother-cell of the gemma without undergoing a preliminary division. The contents of the cell separate from the wall, surround themselves by a new wall of cellulose, and then divide. The free outer wall of the mother-cell is then ruptured and the gemma escapes. According to Goebel ('82, p. 338), the escape is effected by a swelling of the inner layers of the wall of the mother-cell. This process is comparable with the deposition of the gelatinous layer in the projecting cell of *Metzgeria* which is to give rise to a gemma, except that in the latter case the gelatinous substance does not completely enclose the protoplast of the cell, but only that portion of it which would have been exposed upon the rupture of the outer wall. In *Riccardia* further development is deferred until after the gemma is set free, while in *Metzgeria* the development is continued until a multicellular gemma is formed. In other respects the conditions are much the same in the two genera, as Goebel ('98 *a*, p. 275) has already emphasized.

The large and complicated gemmae in the Marchantiales, known only in *Marchantia* and *Lunularia*, are totally distinct from the gemmae of *Metzgeria*, while the gemmae of the Anthocerotales are still too incompletely known to make comparison profitable. The gemmae in the Bryales, which have been so thoroughly studied by Correns ('99), are almost always set free by a rhexolytic process, in which a specialized stalk-cell, or tmema, is torn across. Among those in which the separation is schizolytic the only ones which at all resemble the gemmae of *Metzgeria* are found in *Tortula papillosa* and *T. latifolia*, both of which grow on the trunks of trees. In these two species the gemmae are irregular oval bodies, each consisting of about twelve cells and showing only a slight differentiation. A single leaf-cell gives rise to a number of these gemmae in succession, and when they germinate they first develop a branched protonema as in all other mosses.

Conditions under which Gemmae are produced.

The gemmiparous species of *Metzgeria* do not produce gemmae under all circumstances, and the same is true of other Bryophytes. Apparently the conditions which induce the formation of gemmae are similar to those which induce regeneration. As Goebel (cf. '98 *a*, p. 277) has pointed out more than once almost any liverwort cell has the power of regenerating, that is, of giving rise to an entire new plant. In doing this, if it has acquired the characteristics of maturity, it first goes back into an embryonic condition, and then undergoes the necessary cell divisions. The new plant formed in this way does not at first show the peculiarities of an adult individual, but begins its life in one of the juvenile or embryonic stages of the species. In those Lejeuneae, for example, where the mature plant is a leafy shoot with underleaves, the regenerated plant is very often a leafy shoot without underleaves or even a thallus, upon which a leafy shoot subsequently develops. Under conditions which are considered normal for the growth of a species, the mature cells are in some way prevented from exercising their latent power of division, and regeneration does not take place. This is apparently due to a kind of antagonism which exists between the apical region and the other parts of the plant. In other words, the apical region, where active growth is normally going on, exerts an inhibitory influence upon the other cells, preventing or making difficult their independent development. It is probable that this influence is connected with nutritive processes in such a way that all the food available for growth passes to the apical region, leaving none for the other cells.

The influence just described can easily be removed by dissecting off a leaf or a mature piece of a thallus. If the leaf or thallus fragment is then placed under conditions favourable for growth, regeneration ought to be induced. Among those who have carried on successful experiments along this line, Vöchting ('85) and Schostakowitsch ('94) may be especially mentioned. Vöchting confined his attention to *Marchantia* and *Lunularia*, but Schostakowitsch selected his material from all groups of the Hepaticae. Regeneration is sometimes brought about in nature by a very similar process. In certain leafy species, for example, the separation of some of the leaves from the axis may be considered a perfectly normal occurrence. This is seen especially well in various tropical Lejeuneae, such as *Cheilolejeunea decidua* and the species of *Rectolejeunea* recently described and figured by the writer ('06). The deciduous leaves, under suitable conditions for growth, give rise to new plants by regeneration.

In some of the gemmiparous species of *Metzgeria*, a similar antagonism between the apical region and the cells capable of developing gemmae is evident. When this is the case no gemmae are produced so long as the apical growth continues vigorous. It is only when the apical cell dies or when its activities are lessened or stopped altogether that the formation of gemmae begins. The death of the apical cell apparently takes place regularly in *M. oligotricha*, and brings about not only the production of gemmae, but also the formation of postical adventive branches, which seem to require similar conditions for their development. The gradual diminution in the divisions of the apical cell, leading eventually to complete suppression, is a regular process in the specialized gemmiparous thalli of *M. fruticulosa*, but it also takes place in gemmiparous branches which are not specialized, such as those described for *M. uncigera.* In all these cases the inhibitory influence of the apical region is either destroyed completely or else diminished to such an extent that the thallus cells are able to overcome it and develop gemmae. In other words, some or all of the food available for growth is distributed among the cells capable of forming gemmae.

A similar connexion between the limitation of growth in the gemmiparous shoot and the production of gemmae may also be observed in many of the leafy Hepaticae. It is especially marked in species with unicellular or bicellular gemmae, such as *Odontoschisma denudatum*, *Sphenolobus Hellerianus*, and *Calypogeia Trichomanis.* In these species the gemmiparous shoots curve upwards until they are erect instead of prostrate, their leaves diminish more and more in size, and the shoot as a whole becomes more and more nearly radial. The gemmae are at first limited to the leaf-margins, but eventually, when growth in length has come to an end, the whole apex of the shoot becomes a mass of gemmae. In species with discoid gemmae the connexion is rarely so marked, but in *Cyclolejeunea convexistipa* the gemmae are frequently borne on short branches with reduced and specialized leaves. The modifications exhibited by these gemmiparous shoots with limited growth are comparable with those seen in *Metzgeria fruticulosa.*

Just why the normal activities of the apical region are lessened in these cases and finally brought to an end is by no means clear. In some instances the result is perhaps due to poor nutrition, bringing about an enfeeblement of the whole plant, but this cannot be the effective cause in all cases, because a limitation of growth often takes place in plants which are robust. Under these circumstances the plant is probably able to control the apical growth, perhaps by diverting the currents of food to other regions. Apparently something of the same sort takes place in such species as *M. dichotoma*, where the growth of the gemmiparous branch continues for an indefinite period. The power of the plant to regulate the distribution of the nutritive materials, and thus to weaken or destroy the inhibitory influence exerted by the apical region upon the cells capable of producing gemmae, may be considered a specific characteristic.

In certain species of *Metzgeria*, notably in *M. fruticulosa*, the strength of the inhibitory influence seems to increase as the plant grows more differentiated. In other words, a plant which is passing through an embryonic or juvenile stage is more likely to produce gemmae, and to have its growth brought to an end, than a plant with well-differentiated wings and costa. The same tendency is also strongly marked in *M. furcata*, especially in the variety *ulvula*, and may be observed in a less degree in several of the other species. As the thallus of *M. furcata* becomes more and more differentiated, the apical growth gains so strong a supremacy that its influence can only be overcome with difficulty. The result is that a robust and mature thallus usually produces no gemmae whatever. Whether the species in which gemmae are unknown are able to produce them before they have completed their embryonic life is an interesting problem which can only be solved by experiment. It has already been suggested that *M. fruticulosa* may perhaps represent a juvenile stage of *M. conjugata*. If this is proved to be the case, then the influence of the apical region in this remarkable plant must be regularly overcome before the complete differentiation of the thallus has been reached.

Some writers recognize a second antagonism between the production of gemmae and the development of sexual organs, based on the fact that gemmae are usually more abundant on sterile individuals. Correns ('99, p. 449) has shown, however, that this antagonism is more apparent than real in the Bryales, and the same thing seems to be true of other Bryophytes. The development of sexual organs, as he notes, is associated with a late stage in the differentiation of the gametophyte, while gemmae, as has just been shown, are often produced before the late stages are reached, and sometimes cease to be formed afterwards. It follows from these observations that the sexual organs make greater or more special demands upon the gametophyte than the gemmae. The sterility of gemmiparous plants is therefore due to the fact that they often fail to reach the stage of development which can meet the requirements necessary for the development of sexual organs. The occasional occurrence of both gemmae and sexual organs on the same individual also indicates that there can be no strong antagonism between them.

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