On the Prophases of the Heterotypic Mitosis in the Embryo-sac Mother-cell of *Lilium*.

BY

DAVID M. MOTTIER,

Professor of Botany in Indiana University.

With Plate XXIII.

IN a recent paper, dealing with the development of the heterotypic chromosomes in the pollen mother-cells of *Lilium* and in certain other plants, attention was directed to the fact that the chromatin in the stage just preceding the synaptic contraction appeared as larger and coarser lumps in some cells of the same loculus than in others. On the one hand the chromatin was found to be distributed upon the linin reticulum in the form of relatively large lumps (Mottier, '07, Figs. 17, 22), in which condition the nucleus passed into synapsis; and on the other hand, a readily distinguishable and distinct thread with small and uniform chromatin granules represented the contracting mass (l. c., Figs. 19, 20, 21). It was suggested as a probable explanation that the action of the fixing fluid might have been in a measure responsible for this behaviour of the chromatin, and it was with the view of determining more definitely the effect of the reagents, as well as ascertaining more fully the early development of the heterotypic spirem in the megaspore mother-cell of *Lilium* as compared with that in the pollen mother-cell, that I undertook this investigation. With these two objects chiefly in view, a careful study of the prophases of the heterotypic mitosis was made in the developing megaspore mother-cell of *Lilium*, *L. Martagon*, and *L. candidum* being used.

METHODS.

The same methods of fixing and staining were used as in the study referred to in the preceding. However, before the ovaries were placed in the killing fluid (chrom-osmic acetic acid of the writer's formula), the walls of the ovaries were carefully cut away with the razor on the sides opposite the loculi, so that in some cases only a very thin layer of tissue was left to enclose the cavity; in others the wall was cut away, laying

bare the ovules to the direct contact with the fixing fluid, while in still others, not only were the ovules exposed but a part of their chalazal ends were cut away, as will be seen, for example, from Figs. 1*a* and 2*a*. From this method of preparation, it will be seen that in case the ovule is exposed, or if a portion be cut away from the chalazal region, the fixing fluid will more readily penetrate the large megaspore mother-cell. Long experience with the tissues of higher plants in the use of the three-acid mixture, as well as of other fixing reagents, has shown that cells thus treated present slightly different appearances in certain structural details of cytoplasm and nucleus, and in the readiness with which stains are retained by these structures. If the fixing fluid must first pass through a layer of tissue of considerable thickness before reaching a given cell, the effect of the osmic acid upon that cell, as shown by structure and staining qualities, will be somewhat different than had the fluid a more direct contact with that cell. Experience has demonstrated also that, whenever cells to be studied are embedded any considerable depth in a tissue, there is likewise danger in cutting away too much, assuming that one operates with a fixed strength of the killing fluid. It is always to be understood that when cells show poor or faulty fixation, such preparations are not used as evidence in support of a conclusion. What is good, and what constitutes poor or faulty fixation, are matters to be determined by experience. Practice must also determine how material is to be prepared for any given reagent of known or unknown merit as tested for a similar tissue.

In order that any effect of preconceived ideas of the author may be eliminated in the preparation of the illustrations, he has had the drawings of the nuclei made by an artist who has been thoroughly trained in microscopic observation, and a careful comparison of the preparations and the respective drawings shows that each illustration is a very faithful representation of the object. In this connexion it gives me pleasure to acknowledge my indebtedness to Miss Carolyn A. Black for making the drawings of the nuclei.

OBSERVATIONS.

With the foregoing remarks on methods, we are now ready to present the results of observations. As mentioned in a foregoing paragraph, *Lilium Martagon* and *L. candidum* furnished the material for study. Even before the inner integument of the ovule is apparent, the megaspore mother-cell is conspicuous because of its large size and the density of its contents.

Both cell and nucleus now begin their period of rapid growth. At first the rate of growth of cell and nucleus seems to be equal. When the inner integument has begun to grow up about the nucellus (Pl. XXIII,

Fig. 1), the nucleus contains one to three large nucleoli and sometimes several additional smaller ones. The linin is disposed in a very delicate network, with many delicate threads extending radially from the larger nucleoli. The chromatin is distributed upon the linin threads in small granules. Here and there are to be seen larger aggregations of chromatin granules at the angles of the linin meshes (Fig. 1). This is the structure of the typical resting nucleus.

Each figure of the nucleus is accompanied by an outline drawing of the ovule in which the nucleus is found. Certain stages in the development of the ovule correspond rather closely with certain steps in the prophase of mitosis, so that the form of the ovule is helpful in enabling one to determine the correct stage in karyokinesis, especially when there is some variation in the form of the chromatin, due to the reagents or other causes. As will be seen from Fig. 1*a*, the ovule from which Fig. 1 was taken was not only exposed to the direct contact of the fixing fluid, but a little of the ovule itself (only the epidermis in this case) was cut away along the line *x-x*. In this and in neighbouring ovules in the same section, the beginning of the outer integument was just perceptible as a slight bulging out of a few epidermal cells.

In Fig. 2 is shown a nucleus which, judging from the stage of development of the ovule to which it belonged, and from the size and form of the cell, seems to represent the same stage in mitosis as Fig. 1. One very large and two or three small nucleoli are present. The chromatin, however, presents a striking contrast from that of Fig. 1 or of a later stage. Here we have rather large angular lumps of chromatin and a sparse linin reticulum, a condition which, it seems to the writer, may be due to the action of the fixing fluid. In this case the wall of the ovary was only partly cut away, so that the fixing fluid must first pass through a layer of tissue of six or seven cells in thickness before reaching the ovule. In nearly all preparations of this kind, the nucleus reveals a similar disposition of the chromatin, and the writer is of the opinion that the lumpy nature of the chromatin in this nucleus is due partly, if not wholly, to the action of the fixing fluid. Fig. 2*a* is an outline of the section of the ovule containing Fig. 2. Owing to the shape of the ovarian cavities, it sometimes happens that the nucellus of the developing ovules is pressed against the inner wall of the loculus, especially in the ends of the ovary, thereby becoming somewhat truncated as in Fig. 2*a*. In other parts of the loculus the nucellus has more room to elongate and round out at this stage in the development (Fig. 3*a*). With further growth the nucleus increases in size, and the chromatin granules (not the lumps of Fig. 2) not only become larger, but they are more regularly distributed upon the linin framework, whose meshes are now larger (Fig. 3). The change in the nuclear net from that of Fig. 1 to Fig. 3 foreshadows the transformation into a con-

tinuous thread, which is to appear later. In fact one sees now, in Fig. 3, the beginning of such a pre-synaptic thread, although there is not yet a continuous spirem. At this stage one large nucleolus is usually present, with sometimes one or more small ones. However, there may be considerable variation in regard to the number of smaller nucleoli. In preparing the ovary from which Fig. 3 was taken, not only was the outer wall of the loculus but a considerable slice of the chalazal end of the ovule cut away (Fig. 3*a*), so that the killing fluid undoubtedly had a more direct access to the megaspore mother-cell than in the case of Fig. 2. In this ovule the outer integument had just become evident. Both cell and nucleus are elliptical in longitudinal section. Following close upon the stage of Fig. 3 is the beginning of the synaptic contraction (Figs. 4, 5). Sections of the ovules (Figs. 4*a*, 5*a*) to which these nuclei belong show that the stage of mitosis is only slightly in advance of that in Fig. 3. The nucleolus has the form and position frequently seen in this stage of synapsis. That there is a single thread with a single row of chromatin granules cannot be questioned, and that there is no union side by side of two spirems is equally evident. Figures 4 and 5 represent rather thick sections of the nuclei, but they do not include the whole of their respective nuclei. In Fig. 5 the contraction of the thread has progressed further than in Fig. 4. The spirem seems thicker and more definite, whilst the chromomeres or granules are perceptibly larger. In the case of these two ovules, the wall of the ovary was cut away, giving the fixing fluid direct contact with the ovules from the instant the ovaries were thrown into the reagent. In Fig. 6 is shown the compactly balled-up synaptic mass, the stage so frequently observed, and the one almost invariably figured in the literature dealing with the heterotypic mitosis. Here the mass is so dense that little in detail can be made out. It seems, however, that the chromatin granules in this nucleus were much larger and less uniform in size than would result from a compact balling-up of the structure shown in Fig. 5. In preparing the ovary from which Fig. 6 was obtained, the outer wall of the loculus was not entirely cut away; a layer of tissue five cells in thickness remained to be penetrated by the fixing fluid before it reached the ovule. To what extent the fixing fluid was responsible for the denseness of the synaptic mass the writer is unable to say, but that the size and form of the chromatin masses observable in the contracted ball are due in some measure to the reagents is highly probable. The author called attention to precisely similar conditions observed in the pollen mother-cell of *Lilium* (l.c., Figs. 19, 20, 21, 22, and 23). Whether the chromatin thread presented by Fig. 5 normally contracts into a mass as dense as that in Fig. 6 cannot be stated with certainty, but subsequent events indicate the possibility that it may not always do so. The nature of the chromatin thread fol-

lowing close upon synapsis is shown in Fig. 7. The spirem has not become completely distributed within the nuclear cavity. It is, moreover, shorter and thicker. A longitudinal fission cannot be made out, although here and there a few chromomeres are seen to be double. The developmental stage of the ovule (Fig. 7*a*) shows that we have a stage in mitosis only a little later than Figs. 5 and 6, since the inner integument has just attained the height of the nucellus. Fig. 8 is a stage slightly older than Fig. 7. In a number of places the longitudinal fission of the chromomeres can be seen, and the whole thread is rapidly approaching the stage of the hollow spirem. The nucleolus, which lies in a neighbouring section, presents the same appearance as in the preceding figure.

The somewhat closely entangled spirem of Fig. 8 soon passes over into the typical hollow spirem. At this stage there enters a phenomenon which has generally led to confusion in the interpretation of subsequent events. Generally speaking, the spirem in this stage in both micro- and megaspore mother-cells is a rather uniform cord more or less regularly and loosely disposed in the nuclear cavity. It may, or may not, reveal the presence of a longitudinal split. Occasionally this longitudinal fission is seen here and there in the cord, where the halves show a tendency to spread apart (Fig. 9), but more frequently no evidence of a fission is apparent. In Fig. 9 only a portion of the chromatin cord is shown. Comparing the ovule containing this nucleus (Fig. 9*a*) with that of the preceding figure (Fig. 8*a*), it will be seen from the height of the integuments that the two nuclei represent very closely related stages in mitosis. It may be well to bear in mind, however, that the author does not regard the form of the ovule as the sole guide in determining the mitotic stage, but it has been found all along that certain steps in the growth of the ovule correspond closely to definite mitotic stages. While the rather uniform chromatin cord, with or without indications of a longitudinal fission, is the rule in the stage of the hollow spirem, yet there are found nuclei in which the spirem is more slender and the longitudinal halves more widely divergent than in Fig. 9,—the phenomenon referred to in the foregoing. A part of such a nucleus is shown in Fig. 10. Here the longitudinal segments diverge, becoming widely separated for relatively long stretches. Where short turns of the divergent halves are cut by the knife, the two pieces appear as two isolated portions lying somewhat parallel. Attention was called by the writer to a similar condition in the pollen mother-cells (Mottier, '07), except in the latter this phenomenon seemed to appear more frequently at a later stage,—that of the looping or 'second contraction'. Whether this divergence of the longitudinal halves occurs as frequently here as in the pollen mother-cell is not known, for in any study it is not possible to observe as many megaspore as pollen mother-cells. That Figs. 9 and 10 represent about the same, or

very closely related, stages is evidenced by the size of the cells and by the developmental stages of the ovules (Figs. 9*a* and 10*a*). There remains to be considered the probable effect of the reagents as being responsible, at least in a measure, for the more slender spirem and the wider divergence of its longitudinal segments,—a suggestion expressed in a preceding paragraph and in the writer's former publication. From the ovary in which Fig. 10 is found, a part of the ovule as well as the wall of the loculus was cut away; consequently the osmic acid of the fixing fluid had freer access to the cell (Fig. 10*a*). While the author is strongly of the opinion that the fineness or coarseness presented by the chromatin granules in the case of the resting nucleus in question (Figs. 1 and 2) is probably due to the fixing fluid, yet he feels that he cannot speak with positive assurance until experiments now in progress are completed. However, this is certain: no matter how widely, or for whatever length, or lengths, the longitudinal halves of the chromatin spirem may separate and diverge from each other at this stage, they soon come together again and adhere or unite so closely that, apart from rare exceptions, the double nature of the cord is quite obscured at the time of the looping or approximation of parallel parts to form the bivalent chromosomes.

Fig. 11 represents the stage of looping and the approximation of parts of the spirem to form the bivalents just before the cross segmentation. The number of loops is not equal to the number of chromosomes, and it has never been contended by the writer that such is the case. The fact that loops frequently occur may have little or no importance theoretically, but that the two members of a bivalent chromosome are brought together side by side by such a looping is conclusive evidence that these two members were placed end to end in the spirem, no matter whether the spirem was continuous, or interrupted, or 'heterogeneous'. In the case of Fig. 11 *a*, the inner integument of the ovule has grown up beyond the end of the nucellus to form the micropyle. In this respect there is some variation, as the nucleus may reach the stage in question while the integuments are shorter. From this time on the segmentation of the spirem and the further behaviour of the bivalents are quite similar to those processes in the pollen mother-cell as described in my former paper, so that a further description and a duplication of illustrations seem unnecessary.

SUMMARY AND CONCLUSIONS.

From the foregoing it will be seen that the heterotypic mitosis in the megaspore mother-cell of *Lilium* agrees essentially with that mitosis in the pollen mother-cell as described by the author in his former publication (Mottier, '07). In the micro-, as well as in the megaspore mother-cell, the chromatin in the resting nucleus, or in an early pre-synaptic stage, was either in the form of fine granules or larger and coarser lumps. It was

suggested that this difference in form presented by the chromatin might be due in part to the effect of the osmic acid in the fixing fluid, or to the action of the fluid as a whole. If the fluid penetrated readily and quickly, a coagulation in finer granules would result, whilst a slower penetration, or one such that the strength of the osmic acid is made weaker by virtue of its having to pass through a thicker layer of tissue, would lead to the coarser lumps of the chromatin. The results obtained by the method of preparing the ovaries for this study seem to favour this view. The writer does not advance this explanation as a theory to explain all similar phenomena, but merely offers it as a suggestion which seems to be in harmony with certain facts. Nor should it be inferred that he regards synapsis as an artifact, when it is suggested that the reagents may be responsible for the greater compactness of the synaptic ball, for it is generally true that the reagents used in this and similar indirect methods of study cause a certain amount of contraction of the material, although this may be very slight.

In both micro- and megaspore mother-cells, there is a *single* spirem developed which passes into synapsis, assuming, of course, that a complete spirem is formed prior to synapsis. This seems nowhere else so beautifully shown as in the megaspore mother-cell of *Lilium*. There is, therefore, no pairing or fusion of spirems in synapsis. The hollow spirem appearing after synapsis is seen to be double, and all facts point to the conclusion that this is due to a real longitudinal fission—a fission as real as in the ordinary, or 'allotypic', mitosis. Occasionally the halves may separate or diverge for considerable lengths, but this divergence or separation of the halves is only temporary, the segments coming together and uniting or adhering closely before complete cross-segmentation of the chromatin cord. It is suggested that this divergence of the halves of the longitudinally split cord may be due in part to the action of the reagents, but this statement is not made with positiveness.

The somatic chromosomes (assuming the individuality of the chromosomes) are arranged end to end in the spirem, and two members of each bivalent chromosome, whenever they lie side by side in their final position, are brought to that position by a looping or other manner of approximation. A very striking proof of the end-to-end arrangement of the somatic chromosomes in the spirem is seen in *Oenothera*, according to the results of Gates ('08). Here, in nuclei uncut by the knife, the majority of chromosomes (l. c., Figs. 26, 27, and 28) can be seen adhering end to end in the segmenting spirem. In *Oenothera* there is likewise no union of spirems side by side in synapsis, as only a single thread is present prior to synapsis. Of the species studied by me, *Tradescantia* more closely resembles *Oenothera*. In *Peperomia* the recent investigations of Brown ('08) have shown that a single spirem passes into synapsis, and that the chromosomes are arranged end to end in the spirem, the members of the bivalents being

brought side by side by a looping or other form of approximation. Substantially the same history of the origin of the bivalent chromosomes has been observed by Lewis ('08) for *Pinus* and *Thuja*.

In a recent number of this journal, Overton ('09) has published the results of his latest observations on the heterotypic mitosis in the pollen mother-cells of *Thalictrum purpurescens*, *Calycanthus floridus*, and *Richardia africana*. All of his data are interpreted in the light of the prochromosome theory and of the lateral union of two spirems prior to or during synapsis. In the pre-synaptic as well as post-synaptic stages he sees bivalent 'heterogeneous' spirems, and the line of longitudinal fission of the post-synaptic spirem is regarded as the line of approximation of two spirems. I shall not discuss his data nor his deductions at this writing, except in so far as they pertain to *Helleborus foetidus* and *Podophyllum peltatum*. In his last, as in his preceding paper ('05), he cites *Helleborus foetidus* as revealing prochromosomes and a bivalent spirem in pre-synaptic nuclei (see his Figs. 39 to 43 for *Helleborus*, and Figs. 53 and 54 for *Podophyllum* (l.c., '05); also pp. 39 and 47 (l.c., '09). From a study of my numerous preparations of *Helleborus*, made from material fixed in several of the well-known fixing fluids, I may say with positive assurance that the pre-synaptic stages in the pollen mother-cells of this plant are quite similar to those described and figured by me for the pollen mother-cells of both *Podophyllum* and *Lilium* (Mottier, '07). In fact, my Figs. 1, 2, and 4 of *Podophyllum*, and Figs. 16, 17, 34, 19, and 20 of *Lilium*, are precisely like the corresponding stages in *Helleborus*, and might be readily substituted as illustrating the same conditions in the latter plant. In the very early stages of *Helleborus*, as in *Podophyllum* and in *Lilium*, there is no definite spirem, but a network or reticulum, consisting of chromatin lumps or granules of varying sizes and shapes connected by delicate linin strands. The number of these lumps always exceeds the number of somatic chromosomes. Some of these lumps are paired, as well as some of the linin strands; but there are also clusters of three or more lumps, as well as three or more parallel linin strands connecting different lumps. There are also linin strands radiating or extending in several directions from some of the lumps. Just prior to synapsis in *Helleborus*, a definite slender spirem may be developed precisely as figured for *Lilium Martagon* (l.c., Figs. 19 and 20). As already stated for *Podophyllum*, in one end of the anther of *Helleborus* nuclei may show the structure of my Figs. 1 and 2 (l.c., '07), while in the other end of the same locus the chromatin is much more finely divided, as in Fig. 4 (l.c., '07).

Judging from Overton's figures of the pre-synaptic stages which he gives in his recent paper (l.c. '09), it seems to me that he has failed to distinguish between a network and a spirem. The structure shown in his Figs. 1, 2, 3, 4, 5, 6, and 7 of Pl. I, and Figs. 1, 2, 3, and 8 of Pl. II, for

example, would not be regarded by the writer as spirems, much less as bivalent spirems, but merely as a network—a number of scattered chromatin lumps connected by linin threads. It seems to me also that one may just as well interpret the cytoplasm of Overton's Fig. 12, Pl. II, as consisting of bivalent 'heterogeneous' spirems as to apply such a designation to the nuclear structures just mentioned.

The foregoing results of observations upon the prophases of the heterotypic mitosis in the megaspore mother-cell of *Lilium* may, therefore, be briefly summarized as follows:—

1. Previous to synapsis a single nuclear thread is developed, which, in many cases, can be demonstrated clearly as a definite spirem with somewhat regular and uniform chromatin granules.

2. There is no union side by side of two distinct chromatin spirems prior to or during synapsis. Synapsis is regarded as a normal process, but the greater compactness of the balled-up mass may be due partly to the reagents.

3. The hollow spirem following synapsis is double, due to a longitudinal fission, which, as a rule, becomes completely obscured before the cross segmentation.

4. The segments arranging themselves in pairs to form the bivalent chromosomes were placed end to end in the spirem.

5. The separation of the members of each bivalent in the first mitosis is, therefore, a cross segmentation. The heterotypic mitosis is thus reductional, and, if one chromosome differs from another potentially or otherwise, it is also qualitative.

6. In the pre-synaptic phase, that the chromatin may appear as larger lumps instead of smaller and more uniform granules, has been suggested as being due in part to the fixing fluids, the finer more uniform granules being nearer normal. The wide divergence of the halves of the chromatin thread appearing occasionally in the stage of the hollow spirem may also be due in part to the reagents.

February 15, 1909.

PUBLICATIONS REFERRED TO.

- BROWN, WILLIAM H. ('08): The nature of the embryo-sac of *Peperomia*. Bot. Gaz., xlv, 445-60, 1908.
- GATES, REGINALD R. ('08): A study of reduction in *Oenothera rubrinervis*. Bot. Gaz., xlv, 1-34, 1908.
- LEWIS, ISAAC M. ('08): The behaviour of the chromosomes in *Pinus* and *Thuja*. Ann. of Bot., xxii, 529-56, 1908.
- MOTTIER, D. M. ('07): The development of the heterotype chromosomes in pollen mother-cells. Ann. of Bot., xxi, 309-47, 1907.

OVERTON, JAMES B. ('05): Ueber Reduktionsteilung in den Pollenmutterzellen einiger Dikotylen. Jahrb. f. wiss. Bot., xlii, 121-53, 1905.

— ('09): On the organization of the nuclei in the pollen mother-cells of certain plants, with especial reference to the permanence of the chromosomes. Ann. of Bot., xxiii, 19-60, 1909.

EXPLANATION OF PLATE XXIII.

Illustrating Professor Mottier's paper on the prophase of the heterotypic mitosis.

All figures were drawn from sections with the aid of the Abbé camera lucida, and with Zeiss apochromatic immersion 2 mm., apert. I. 40, and compensating ocular 12, excepting those showing outlines of ovules, 1 *a*, 2 *a*, &c., which were drawn with low powers. Magnification of figures of nuclei about $\times 1800$.

Figs. 1 *a*, 2 *a*, &c., represent outline drawings of the ovules in which the nuclei, Figs. 1, 2, &c., respectively occur.

Fig. 1. The nucleus of a megaspore mother-cell at an early stage in the period of growth prior to synapsis. In Fig. 1 *a*, a small piece of the ovule was cut away along the line *x—x* before fixing.

Fig. 2. About the same stage in mitosis as Fig. 1. The chromatin is in form of irregular lumps of varying size. One large and two or more smaller nucleoli are present. In this case the wall of the ovary was not cut away to allow the fixing fluid direct access to the ovule. A layer of tissue six or seven cells in thickness must have been traversed before the fluid reached the ovule. The lumpy condition of the chromatin is supposed to be due in a measure to the action of the reagents.

Fig. 3. A later stage than Fig. 1. The nuclear structure consists of a delicate network holding the small chromatin granules uniformly distributed. A large and two small nucleoli are present. Fig. 3 *a* shows the part of the ovule cut away before fixing.

Fig. 4. A nuclear thread or spirem has been formed which is undergoing synaptic contraction.

Fig. 5. Synapsis has progressed further. The spirem is a single thread, and the chromomeres are somewhat larger than in the preceding figure.

Fig. 6. The stage of the dense synaptic ball.

Fig. 7. The spirem loosening up after synapsis. The longitudinal fission, if present, is not visible.

Fig. 8. The spirem is becoming distributed in the nuclear cavity. Only here and there can any evidence of a longitudinal fission be seen (at the right near a cut end of the thread).

Fig. 9. The stage of the hollow spirem; the section includes a part of the spirem only. The longitudinal fission is quite distinct, the segments diverging somewhat in places.

Fig. 10. The same stage in mitosis as Fig. 9. The spirem is more slender, and the longitudinal segments separate for longer stretches. It is probable that the slender nature of the spirem and the greater divergence of the halves are due partly to the reagents. Fig. 10 *a* (*x—x*) shows the part of the ovule cut away before fixing.

Fig. 11. A later stage, at the time of the second contraction and of the looping and approximation of different parts of the spirem to form the bivalents prior to complete cross segmentation. The longitudinal halves of the spirem, which frequently show a tendency to diverge more or less at an earlier stage, have unmistakably and beyond all question united, so that there is now a single and rather thick and smooth cord. At this stage, both here and in the pollen mother-cell, indications of the longitudinal split may occasionally be made out. Fig. 11 *a* will indicate the structure of the ovule at this stage of mitosis.

Mottier and Black del.

7a.

7.

8.

9.

10.

9a.

10a.

6a.

11a.

11.

Mottier, David M . 1909. "On the prophases of the heterotypic mitosis in the embryo-sac mother-cell of *Lilium*." *Annals of botany* 23, 343–352.

<https://doi.org/10.1093/oxfordjournals.aob.a089224>.

View This Item Online: <https://www.biodiversitylibrary.org/item/236540>

DOI: <https://doi.org/10.1093/oxfordjournals.aob.a089224>

Permalink: <https://www.biodiversitylibrary.org/partpdf/318959>

Holding Institution

Smithsonian Libraries

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: Not in copyright. The BHL knows of no copyright restrictions on this item.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.