Observations on 'Chromatin Bodies' and their Relation to the Nucleolus in *Galtonia candicans*, Decsne.

BY

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With Plates XXXIII and XXXIV.

INTRODUCTION.

IN the course of an investigation of the first meiotic division of the pollen mother-cells of *Galtonia candicans*, it was noticed that during the pre-synaptic and synaptic nuclear stages a most constant extrusion of 'chromatin bodies' takes place. This process is so striking in these cells that it seemed advisable to follow it out in detail, especially as somewhat similar phenomena have lately been described by several writers both in animal and plant cells.

METHODS.

Care has been taken to check the work by using various methods both in 'fixing' and in staining. Buds have been fixed on bright warm days between 11 a.m. and 1 p.m. in (1) Strong Flemming, (2) Hermann, (3) Alcohol and Acetic. The material, for the most part, has been run up through the glycerine method, and has been left in paraffin, and that always at a low temperature, for three to three and a half hours. The stains used have been many, including Heidenhain with a counter stain; Flemming's Triple; Breinl (17); Iodine Gentian-Violet and Orange G.; Thionin Blue and Ruthenium Red; Methylene Blue and Eosin. The sections have been cut of various thicknesses, the greater number at $3\ \mu$, but some at $6\ \mu$ and at $9\ \mu$.

PRESYNAPSIS AND SYNAPSIS.

When the nucleus is preparing to go into synapsis there is a gradual concentration of the nuclear contents (Pl. XXXIII, Fig. 1) which eventually mass together at one side of the nucleus. At synapsis the nucleus lies excentrically in the cell (Pl. XXXIII, Figs. 7, 8, 9, &c.), the chromatin mass being always on the side of the narrow strip of cytoplasm. This mass, as

a rule at full synapsis, stains uniformly and resembles a heap of tightly compressed wood chips in which no structure can be seen. Sometimes in a superficial section it is possible to recognize the linin matrix with more deeply staining patches of chromatin embedded in its substance. In such a section favourably stained with Breinl's method the chromatin is coloured purple, the linin blue, and the nucleolus yellow. The spherical nucleolus, more or less hidden by the synaptic knot (Pl. XXXIII, Fig. 4), projects into the clear nuclear cavity. In exceptional cases two nucleoli are present (Pl. XXXIII, Fig. 6). There is no definite nuclear wall, the nucleus being bounded by cytoplasmic fibrils.

The ‘chromatic bodies’ may originate either from the nuclear framework (Pl. XXXIII, Figs. 1, 4, 5, 6), or from the nucleolus (Pl. XXXIII, Figs. 7, 8). It is not uncommon to find both modes of origin proceeding simultaneously in the same nucleus (Pl. XXXIII, Fig. 9).

ORIGIN OF ‘BODIES’ FROM THE SYNAPTIC KNOT.

At synapsis buds are seen to be given off from the knot, often from a part in close proximity to the nucleolus (Pl. XXXIII, Figs. 4, 5, 6). These buds become round, or pear-shaped, and are composed of linin in which chromatin of varying amount and density is carried (Pl. XXXIII, Figs. 5 and 6). They arise from the knot in many different ways. Sometimes large pieces round themselves off, and separate in part from the general mass (Pl. XXXIII, Fig. 4); or finger-like portions protrude (Pl. XXXIII, Fig. 2); or a piece of the linin matrix may escape from the general tangle (Fig. 6), and this gradually takes up a chromatin stain and becomes modified to form a ‘body’; or rounded globules of eu-nucleolar substance (Fig. 3) may escape from the knot, apparently independently of the nucleolus, these by degrees show a ‘chromatic’ staining reaction, and become ‘chromatin bodies’. In whatever way the buds originate, they always remain in connexion with the ‘chromatic’ portion of the parent nucleus (Pl. XXXIII, Fig. 4), and this connexion is retained until the final disintegration of the ‘body’. As each ‘body’ becomes differentiated, it draws out with it as a long thick process, that portion of the knot to which it is attached (Pl. XXXIII, Figs. 6, 10). Gradually the ‘body’ moves away, and the process, in response to the continuous strain exerted on its viscous substance, becomes pulled out into a fine thread (Pl. XXXIII, Fig. 4). Having separated themselves from the synaptic knot, the ‘bodies’ pass through the clear nuclear space (Pl. XXXIII, Fig. 4), and the surrounding cytoplasm (Pl. XXXIII, Fig. 4). They may, and often do, penetrate the cell-wall (Pl. XXXIII, Figs. 5, 6), and enter an adjacent cell (Pl. XXXIII, Figs. 5, 6). There is no evidence to show that the ‘bodies’ secrete a ferment which dissolves the wall. Their passage leaves no trace, the hole

appears to close in and to become obliterated immediately. Arrived in the neighbouring cell, the 'bodies' remain stationary close to the wall (Pl. XXXIII, Fig. 9), so that the cell-wall is invariably seen to lie across the fine thread close to its junction with the body (Pl. XXXIII, Figs. 9, 10).

Great caution needs to be exercised before one can admit the conviction that the 'bodies' do come to lie in the cell adjacent to that from which they originated. There are two main difficulties which have to be considered. Firstly, the refractive index of the wall may be slightly different at the places where it has been perforated; secondly, the walls run obliquely. Although these two possible sources of error have been fully appreciated, there seems, nevertheless, to be no other explanation than that the 'bodies' do migrate from their parent cell into one of the neighbouring cells. Colouring the walls with a contrast stain to that of the nucleus, such combinations as Ruthenium Red and Heidenhain, Congo Red and Heidenhain, Ruthenium Red and Thionin Blue, Methylene Blue and Eosin, have given striking and unmistakable results all confirming the foregoing conclusion.

There is always a clear space in the cytoplasm round each 'body' (Pl. XXXIII, Figs. 1, 4, 5, 6, 9, 10, and Pl. XXXIV, Figs. 11, 15, 16). This is possibly due to an electrical condition connected with the metabolism proceeding in its substance. Possibly it may be compared to the space, which, during certain stages of nuclear division, surrounds the nucleolus. This possibility is strengthened by the fact that the 'bodies' may be of direct nucleolar origin. 'Bodies' belonging to the same nucleus may pass to any of the adjacent cells (Pl. XXXIII, Fig. 6), and they may lie singly or in groups (Pl. XXXIII, Fig. 9). Thus both in transverse and in longitudinal sections of an anther, nuclei are seen, sending out processes and attachments in opposite directions. The fine connexions vary in length according to the distance which the 'bodies' have had to travel before they enter the neighbour cell. Those that come off the knot on the side abutting on to the cell-wall have a short connexion (Pl. XXXIII, Fig. 9), whilst those that have travelled in the opposite direction, and have passed through the broad area of cytoplasm, have a relatively long connexion (Pl. XXXIII, Fig. 10). At complete synapsis nearly every pollen mother-cell of an anther is seen to possess these bodies, and the threads by which they are joined to the parent nucleus are most conspicuous.

ORIGIN OF 'BODIES' FROM THE PRE-SYNAPTIC FRAMEWORK.

The close synaptic stage is the most active time for the formation of 'chromatic bodies', but they may often be seen to be budded off when the nuclear contents are being massed together prior to synapsis (Pl. XXXIII, Fig. 1). Then they can be recognized in the nuclear framework as rounded or oval aggregations of 'chromatin' (Pl. XXXIII, Fig. 1). These bodies behave like those formed during synapsis.

When the nuclei have completed their synaptic rearrangement, and the 'bodies' have been extruded and are lying in the neighbour cells, more or less abutting against the wall dividing the parent cell from the invaded cell (Pl. XXXIII, Fig. 9), the knot begins to loosen and the cells to separate. It is not uncommon in *Galtonia* to find at this time that the whole synaptic knot breaks up into 'chromatic bodies'. This invariably indicates that the nucleus, instead of passing into the subsequent spireme stage, disintegrates and dies. Often two loculi, or even all four, may have their pollen mother-cells in this aborted condition.

WALLS OF THE POLLEN MOTHER-CELLS.

It is necessary here to sketch the history of the walls of the pollen mother-cells, which come into such close relationship with the 'chromatic bodies'. During the stages leading to synapsis, the cells are polyhedral in shape, and form a closely fitting and compact mass (Pl. XXXIII, Fig. 9). The cell-walls are thin and evidently are composed both of pectose and of cellulose, as they stain brightly with Methylene Blue and with Ruthenium Red (pectic stains), and even more brilliantly with Congo Red (cellulose stain). They consist of a clear middle lamella, which stains homogeneously, and in which occasionally granules, apparently cytoplasmic, may be found; this layer is bounded on either side by fine membranes. The cytoplasm of the cells extends to the walls. When the cells are preparing to separate the middle lamella swells considerably but unevenly (Pl. XXXIV, Fig. 11): in some places it may be considerably thickened, whilst in others it remains thin; at the same time it loses its staining capacity and appears as a colourless space.

Some chemical change is apparently proceeding in the interior of the wall, that is to say in the colourless layer, which causes the swelling, and forces the delicate membranes severally to round off and limit the cytoplasm of the cell with which they are in contact. In *Funkia Sieboldiana* a thin membrane, a specialized part of the middle lamella, has been seen in the clear space of the wall, but in *Galtonia* this is not visible. Protoplasmic connexions across the walls are most obvious (Pl. XXXIV, Fig. 14). Thus each pollen mother-cell is enclosed in its own wall (Pl. XXXIV, Fig. 17). The cytoplasm gradually contracts, so that by the time that the nucleus contains definite chromosomes there is a wide space between the circular enveloping wall and the enclosed, somewhat irregularly outlined cytoplasm (Pl. XXXIV, Fig. 18). The wall has by this time resumed its staining reaction, and appears as a thin membrane, often with many adhesions and granules on its surface. The wall persists, with slight modifications in its structure, throughout the first and second meiotic divisions, and is only finally broken down when the pollen grains are set free in the cavity of the pollen-sac.

FURTHER HISTORY OF 'CHROMATIC BODIES'.

As the pollen mother-cells begin to separate from one another, the fine threads, connecting the 'bodies' with the parent nucleus, may be seen traversing the clear space in the wall. As events proceed and the walls swell, forcing the cells apart, the connexions are still to be seen (Pl. XXXIV, Fig. 11). It is usual at this stage, when the nuclei are coming out of synapsis, to find the 'chromatic bodies' lying at the extreme edge of the cytoplasm, united by long connecting threads to the mother-nucleus (Pl. XXXIV, Figs. 15, 16).

Whereas at synapsis nearly every nucleus has attached 'chromatic bodies', at the later nuclear stages only a small percentage of nuclei possess them. This fact indicates that the 'bodies' are gradually disintegrating.

As the synaptic knot loosens and grows out into beaded or thready loops, so likewise the 'bodies' become granular (Pl. XXXIV, Fig. 16). Often the connexions are in direct continuity with the loops of the spireme, and it is just possible that they are transferring some of their substance back into the parent-nucleus. The connexions are broken when the spireme has become more or less unravelled, and the loops are distributed throughout the nuclear cavity. The 'bodies' generally remain in the cytoplasm of the invaded cell, but sometimes they appear to be dragged across the space to the nucleus from which they originally came, as very occasionally a 'chromatic body' or a piece of one is seen adhering to the exterior of the nucleus. In any case the 'bodies' now disintegrate. Often portions revert to the eu-nucleolate condition, fragments of eu-nucleolar staining substance being found attached to the disorganizing 'chromatin' fragments. When the nucleus has returned to the centre of its surrounding cytoplasm, there is a sudden disappearance of the 'body' remains. The destruction must be extremely rapid, as in most cases at the 'open spireme' the cytoplasm appears homogeneous, but under favourable fixing and staining conditions the 'chromatic bodies' can still be recognized as brightly staining granules scattered in the cytoplasm (Pl. XXXIV, Fig. 17). This rapid fragmentation has its parallel in the sudden disappearance of the nucleolus when ejected from the equatorial plate in the somatic division.

ORIGIN OF 'BODIES' FROM THE NUCLEOLUS.

It is also common to find 'bodies' originating as buds from the nucleolus, but they are not given off in such numbers as from the nuclear framework.

When newly formed at the close of the telophase of the last archesporial division, the nucleolus takes up a chromatin stain. As the nucleus passes on into the early meiotic prophase, the nucleolus gradually takes a cytoplasmic stain and becomes a typical true or 'eu'-nucleolus (20). It is especially colourless in *Galtonia* as compared to other plants. Chromidia

are always associated with a plasmosome of this nature. The nucleolus is approximately spherical, but its outline, though definite, may be undulating.

From the early prophases onwards the nucleolus may show what appear to be vacuoles (Pl. XXXIII, Figs. 3, 5). These may be scattered in the nucleolus, or they may form a small group towards the centre. Although these nucleolar buds may be found at the early prophases, it is at complete synapsis that the nucleolus becomes the most active. Then it may be studded with buds, some in the act of breaking off (Pl. XXXIII, Fig. 9), whilst others may be free in the nuclear cavity (Pl. XXXIII, Fig. 7), and others again may have already travelled into the surrounding cytoplasm (Pl. XXXIII, Fig. 7). Wherever they are, they instantly begin to assume the character of 'chromatic bodies'. Sometimes the buds, while still attached to the nucleolus, initiate this activity, and may be seen to have a tiny cap of 'chromatin' on their outer surfaces (Pl. XXXIII, Fig. 8), just as Page May and Walker (11) have described in the nucleolar buds of nerve cells of certain mammals.

With appropriate staining a marked differentiation can be obtained between the small globule of nucleolar material and the angular block of 'chromatin' to which it is attached. Stained with combinations of basic and acid dyes, the nucleolus and the newly differentiated buds take up the acid stain; but as the buds get into the cytoplasm they absorb the basic dye in an ever increasing degree. In time the nucleolar fragments are absorbed, and there remains no trace of the portions of eu-nucleolus adhering to the 'chromatic bodies'. Whether the 'bodies' so formed secondarily connect themselves with the parent-nucleus, and whether they pass through the cell-walls, it is impossible to say. Isolated, unconnected 'bodies' may be often seen in the cytoplasm, but whether the connexions are so cut as to render them invisible, or whether they never existed, could not be determined.

The nucleolus persists throughout the later nuclear stages, and is always in close connexion with the spireme, and later with the chromosomes, especially with one of the small pairs. As the chromosomes are forming, it begins once more to show vacuoles, and the nucleolus finally falls to pieces in a shower of globules (Pl. XXXIV, Fig. 19), much like the buds that were given off in the prophases and at synapsis; but they are less definite at this stage of the mitosis. Some pass into the cytoplasm where they disappear, while others apparently become absorbed in the nucleus. This final destruction of the nucleolus has been recorded and figured by Miyake in *Galtonia* (9). Sometimes when the chromosomes are being differentiated, the nucleolus breaks up into several rounded nucleoli, each small nucleolus adhering to one of the paired chromosome segments (Pl. XXXIV, Fig. 18).

MEGASPORE MOTHER-CELL.

No definite formation of 'bodies' has been seen in the synaptic stages of the megaspore mother-cell. The knot resembles that of the pollen mother-nuclei; it is a dense mass thinning out towards the periphery where shreds of linin escape (Pl. XXXIV, Figs. 12, 13). Fragments of linin may become detached; these round themselves off and lie in the nuclear cavity (Pl. XXXIV, Fig. 13). Occasionally similar bodies may be found in the adjacent cell (Pl. XXXIV, Fig. 13), but no connexion with the parent-nucleus is retained. As a rule these portions remain colourless, but they may also become chromatic. They are not always present, and even when found they are indefinite and insignificant as compared with the 'chromatic bodies' of the pollen mother-cells.

The nucleolus may be of the nature of a plasmosome (Pl. XXXIV, Fig. 13), and take an acid stain, but more often it is densely chromatic in staining reaction (Pl. XXXIV, Fig. 12). Wilson (20) states that 'plasmosomes sometimes seem to have no envelope, but in many cases (e.g. in leucocytes) are surrounded by a thin layer that stains like chromatin'. This would explain the differently staining nucleoli found in the megaspore mother-cells; moreover, a pale nucleolus has been seen emerging from one that stains more deeply. Nevertheless, in most cases the chromatin in the 'chromatic nucleolus' is more than a 'thin layer', as in a section through such a nucleolus both portions stain with equal density. The deeply staining nucleolus is generally vacuolated (Pl. XXXIV, Fig. 12). It may be close to, and partly enveloped by, the synaptic knot, or it may lie apart. In the latter case it is united to the 'chromatin' mass by a narrow strip of linin (Pl. XXXIV, Fig. 12), recalling the 'chromatic body' with its thread-like connexion.

When the nucleolus is of a plasmosome nature, it may protrude from the synaptic mass as in the nuclei of the pollen mother-cells (Pl. XXXIV, Fig. 13). It is vacuolated and often throws off tiny buds. These buds remain colourless, and are inconspicuous. Occasionally the plasmosome is hour-glass shaped, and becomes nipped into two at the constriction. This mode of duplication of the nucleolus is often seen in the early prophases of the somatic divisions of the root, only in these cases the nucleoli take a basic stain. Rosen (12) has figured these two lobed nucleoli in the root of *Vicia Faba* var. *megalosperma*, but he concludes that they are in the act of fusing, and not of separating.

GENERAL COMPARISONS.

There exists a considerable literature dealing with the elimination and casting out of substance from the nucleus. This elimination has been observed both in animals and in plants, and both in vegetative and reproductive cells.

Balbani (1) in 1864 noticed the vacuolated nucleoli in the ova of *Geophilus longicornis* which he believed functioned as excretory organs. Since then many writers have confirmed Balbani's views.

Tangl (16) has described vacuolated nucleoli in the pollen mother-cells of *Hemerocallis fulva*. These bud off small colourless nucleoli, which pass out into the cytoplasm where they are reabsorbed.

Scharff (13) found 'a small nucleolus being constricted off from a large one' in the intra-ovarian ovum of *Conger vulgaris*. In the ovum of *Gadus virens* he figured 'spots' in the cytoplasm, which he thought might possibly be 'escaping nucleoli which have travelled through the nuclear membrane into the surrounding protoplasm'. In *Trigla gurnardus* protuberances appear on the nucleus, and into these fragments of nucleolus are drawn. The protuberances separate from the nucleus and appear as vesicles. They travel towards the surface of the egg. The vesicles with their nucleolar contents are the yolk-spherules.

Miss Nicholls (10) in *Sarracenia* has figured granules in connexion with the nucleolus, and mentions that the nucleolus, after synapsis, is vacuolated.

Cardiff (3), in *Acer platanoides*, found that a small papilla often projects at the point of contact of the linin thread with the nucleolus. 'In some preparations this nucleolar papilla looked like one of the vacuoles escaping.'

Wilson (21), in the spore mother-cells of *Mnium hornum*, has described the presence of a small deeply staining rounded body in the nucleus, in addition to the nucleolus. 'A careful examination leads to the conclusion that this body arises from the nucleolus by a process of budding.'

In 1891 Brauer (2), in the course of his work on *Hydra*, found that the large nucleolus budded off small portions which tended to group themselves round the large one.

Recently Walker and Embleton (18) have investigated *Hydra fusca*, and have shown that nucleolar budding takes place in the resting cells both of the ectoderm and endoderm. The buds pass out of the nucleus, and eventually disintegrate in the cytoplasm. They may remain joined to the nucleus by a membranous process for a considerable period.

Page May and Walker (11) have found in the nerve cells of some mammals that an excrescence is formed on the nucleolus. This separates and grows until nucleolus and excrescence are indistinguishable. Then one of these two nucleoli passes out of the nucleus into the cytoplasm and wanders to the periphery of the cell. It may pass bodily through the surface membrane, and be set free among the surrounding cells. In other cases the nucleolus lies on the inside of the surface membrane of the nerve cell, and 'here the substance of the nucleolus seems to pass piecemeal through several small openings, and to be absorbed into the cytoplasm of the neighbouring cell'.

Walker and Tozer (19) have made further investigations into the nucleolar budding in the vegetative cells of animals and plants. The buds pass out of the nucleus into the cytoplasm. While in the nucleus they take a basic stain, but arrived in the cytoplasm their staining reaction gradually alters, until they take the acid stain more deeply than the surrounding cytoplasm. In the formation of the chromatic bodies from the nucleolar buds in *Galtonia* the staining reaction is reversed.

Chamberlain (4), in the body cells of *Dioon edule*, has described 'black granules' in the cytoplasm. He believes that they have come from the nucleus and have passed through the nuclear wall without becoming soluble. The black granules increase in size by imbibing liquid, until the granule becomes a thin pellicle enclosing a liquid. 'As the pellicle stretches, granules pass through it into the watery interior, and the colour with iron alum hematoxylin gradually changes from black to gray.'¹

There is a suggestive similarity between the above-mentioned cases of the extrusion of nuclear material in the higher animals and plants and the 'chromidia' of the lowly forms. A vast literature has accumulated round the subject of chromidia. Richard Hertwig (7 and 8) was one of the first to insist on the importance of the chromidia and introduced the terms 'chromidia' and 'chromidial net'. The chromidia are believed to be always extruded from the nucleus, and are composed partly of nucleolar, and partly of chromatic substances. They may be scattered in the cytoplasm or arranged in a net-like system. Often, as in *Arcella vulgaris*, each chromidial aggregation forms a new nucleus. Comes (5) has shown in *Gregarines* that the chromidial apparatus varies according to the amount of nutrition absorbed by the animal. In the summer, when well nourished, the chromidia are most abundant, whilst in the winter, when food is scarce, there are very few to be found.

Hartmann and Prowazek (6) have recently confirmed Schaudinn's (14) work on the Trypanosome, *Haemoproteus noctuae*. Before the animal encysts the large nucleus sheds out a portion of its karyosome and this becomes the second nucleus. Both nuclei send off two small nuclear buds which degenerate. The two large nuclei then retreat to the centre of the cell and fuse.

In 1899 Siedlecki (15) observed an elimination of nuclear substance in the *Sporozoa*, and this has since been corroborated by several writers. At the formation of the macrogametes the karyosome divides into small portions. These go to the periphery of the cell and become surrounded by chromatin. The edge of the *Coccidium* cell is seen to be studded with

¹ 'Nuclear gemmation' and 'fragmentation' have been found to take place in the fungus *Synchytrium*. The karyosome of the parent-nucleus buds or fragments, and each portion becomes a new nucleus. Griggs, R. F.: Some Aspects of Amitosis in *Synchytrium*. Bot. Gaz., xlvii, Feb., 1909, pp. 127-38.

these aggregates, and round each there is a clear space in the cytoplasm, as is always to be seen round the 'chromatic bodies' of *Galtonia*. Each aggregate forms a nucleus. Almost identically the same events take place in the formation of the microgametes. During the maturation of the female element the macrogamete extrudes part of its substance which lies as a mass at the side of the nucleus. Siedlecki regards this action as 'une épuration nucléaire'.

It is difficult to resist the conclusion that, in phenomena such as those so strikingly exemplified in *Galtonia*, we are confronted with processes leading to a definite elimination of nuclear substance, and further that the analogy which exists between these higher organisms and the *Protozoa*, in this respect, may turn out to possess a far-reaching significance. Beyond this it would at present be perhaps unsafe to go; but it is plain that the comparison is worth further investigation.

SUMMARY.

1. 'Chromatic bodies' are found to be present in abundance in the pollen mother-cells of *Galtonia candicans* at the pre-synaptic and synaptic nuclear stages.

In the megaspore mother-cell only a few inconspicuous chromatic bodies have been seen.

2. 'Chromatic bodies' may originate as portions of the nuclear framework, or of the synaptic knot, or as nucleolar buds.

3. They are composed of linin, in which chromatin is embedded, or of nucleolar material.

4. Those 'bodies' that come from the 'chromatic' portion of the nucleus retain their connexion with the nucleus, by means of a fine thread, until their final disintegration.

5. The 'bodies' pass from the nucleolar space into the surrounding cytoplasm, penetrate the cell-wall, and enter the neighbour cell.

6. On the separation of the pollen mother-cells, the 'bodies' remain at the extreme edge of the invaded cell. Their connecting threads pass through the space between the cells.

7. As the nucleus comes out of synapsis, the threads break up and the 'bodies' begin to disintegrate.

8. At the 'open spireme' nuclear stage they can be recognized only as refractive granules.

9. The 'chromatic bodies' which originate as buds from the nucleolus at first take an acid stain, but as they pass into the cytoplasm they become increasingly 'chromatic'. It is not known whether 'bodies' so formed become secondarily attached to the nucleus.

10. The nucleolus in the synaptic nucleus of the megaspore mother-

cell may take an acid or a basic stain. Insignificant 'bodies' may be found in the nuclear cavity. These are derived either from nucleolar buds or from shreds of the synaptic mass. When deeply staining the nucleolus may lie independently of the knot to which it is attached by a linin strand.

In conclusion I wish to express my gratitude to Professor J. Bretland Farmer for the constant help, advice, and criticism that he has given to me throughout the course of this work.

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BIBLIOGRAPHY.

1. BALBIANI, M.: Sur la constitution du germe dans l'œuf animal avant la fécondation. Comptes Rendus de l'Acad. de Sci., lviii, 1864, pp. 584-8.
2. BRAUER, A.: Über die Entwicklung von *Hydra*. Zeit. f. wiss. Zool., lii, 1891, pp. 169-216.
3. CARDIFF, IRA D.: A Study of Synapsis and Reduction. Bull. of the Torrey Bot. Club, xxxiii, May 1906, pp. 271-306.
4. CHAMBERLAIN, C. J.: Spermatogenesis in *Dioon edule*. Bot. Gaz., xlvii, March 1909, pp. 215-36.
5. COMES, SALVATORE: Untersuchungen über den Chromidialapparat der Gregarinen. Arch. f. Protistenk. Jena, x, 2.-3. Heft, 1907, pp. 416-40.
6. HARTMANN, M., und PROWAZEK, S.: Blepharoplast, Caryosom und Centrosom. Arch. f. Protistenk. Jena, x, 2.-3. Heft, 1907, pp. 306-35.
7. HERTWIG, R.: Über Kerateilung, Richtungskörperbildung und Befruchtung von *Actinosphaerium eichhorni*. Abh. bayr. Akad. Wiss. München, xix, 1899, pp. 633-734.
8. ——— Die Protozoen und die Zelltheorie. Arch. f. Protistenk. Jena, i, 1902, pp. 1-40.
9. MIYAKE, K.: Über Reduktionsteilung in den Pollenmutterzellen einiger Monokotylen. Prings. Jahrb. wiss. Bot., xlii, 1905, pp. 83-120.
10. NICHOLLS, M. L.: The Development of the Pollen of *Sarracenia*. Bot. Gaz., xlv, No. 1, Jan. 1908, pp. 331-7.
11. PAGE MAY, W., and WALKER, C. E.: Note on the Multiplication and Migration of Nucleoli in Nerve Cells of Mammals. Quart. Journ. Exper. Physiol., i, No. 2, April 1908, pp. 203-9.
12. ROSEN, F.: Beiträge zur Kenntniss der Pflanzenzellen. Cohn's Beitr. z. Biol. d. Pflanzen, Breslau, vii, Band 70, 2. Heft, 1895, pp. 225-312.
13. SCHARFF, R.: On the Intra-Ovarian Egg of Some Osseous Fishes. Quart. Journ. Micr. Sc. (New Series), xxviii, 1888, pp. 53-74.
14. SCHAUDINN, F.: Generations- u. Wirtswechsel bei *Trypanosoma* u. *Spirochete*. Arb. Kais. Gesundheitsamt, Berlin, xx, 1904, pp. 387-439.
15. SIEDLECKI, M.: Étude cytologique et cycle évolutif de *Adelea ovata*, Schneider. Ann. de l'Inst. Pasteur, xiii, Tome 3, 1899, pp. 169-92.
16. TANGL, E.: Die Kern- und Zelltheilungen bei der Bildung des Pollens von *Hemerocallis fulva*, L. Denkschr. der kais. Akad. d. Wiss. Wien, xlv, 1882, pp. 65-85.
17. WALKER, C. E.: The Essentials of Cytology. London, 1907.
18. ———, and EMBLETON, A. L.: Observations on the Nucleoli in the Cells of *Hydra Fusca*. Quart. Journ. Exper. Physiol., i, No. 3, Aug. 1908, pp. 287-90.
19. ———, and TOZER, F. M.: Observations on the History and Possible Function of the Nucleoli in the Vegetative Cells of Various Animals and Plants. Quart. Journ. Exper. Physiol., ii, No. 2, March 1909, pp. 187-200.
20. WILSON, E. C.: The Cell in Development and Inheritance. New York, 1906.
21. WILSON, M.: On Spore Formation and Nuclear Division in *Mnium hornum*. Ann. of Bot., xxiii, No. 89, Jan. 1909, pp. 215-36.

EXPLANATION OF PLATES XXXIII AND XXXIV.

Illustrating Miss L. Digby's Observations on 'Chromatin Bodies' and their Relation to the Nucleolus in *Galtonia candicans*.

All the figures were drawn with the camera lucida under a 2 mm. Apochr. Hom. Imm. Zeiss, N.A. 1.40, with Comp. Oc. 18. $\times 2250$.

Figs. 1-11. Nuclei of pollen mother-cells.

Figs. 12 and 13. Nuclei of megaspore mother-cells.

Figs. 14-19. Nuclei of pollen mother-cells.

PLATE XXXIII.

Fig. 1. Nucleus in presynaptic stage showing 'chromatic bodies' being given off from the nuclear framework. Three 'bodies' have passed through the wall.

Fig. 2. Nucleus in synapsis. Finger-like portions protruding from the synaptic knot.

Fig. 3. Synaptic knot showing globules of nucleolar material escaping apparently independently of the nucleolus.

Fig. 4. 'Bodies' still in the parent cell, and united to the nucleus by fine threads.

Fig. 5. Two 'bodies' have passed through the wall and have entered the neighbouring cell. Note the 'chromatin' concentration in the substance of the 'bodies'.

Fig. 6. 'Bodies' from the same nucleus have passed into two neighbouring cells. Two nucleoli present in nucleus.

Fig. 7. Shows the origin of the 'bodies' as nucleolar buds. One bud is still attached to the nucleolus, one is in the clear nuclear space, while one has entered the cytoplasm.

Fig. 8. Nucleolar buds beginning to show 'chromatin' aggregations.

Fig. 9. Three cells showing nucleolar budding and 'bodies' arranged against the wall separating the invaded cell from the parent cell.

Fig. 10. Two adjacent cells with their 'bodies'. One nucleus shows long, the other short, connexions.

PLATE XXXIV.

Fig. 11. Shows the uneven swelling of the cell-walls. The connexions joining the 'bodies' to the nucleus traverse the clear space in the wall.

Fig. 12. Nucleus of megaspore mother-cell, in synapsis, with 'chromatin' staining nucleolus which is joined to the knot by a strand of linin. Nucleolus is vacuolated.

Fig. 13. Synaptic knot of megaspore mother-cell with plasmosome showing buds. Insignificant 'bodies' in nuclear cavity, and one in the neighbouring cell.

Fig. 14. Protoplasmic connexions across the walls.

Fig. 15. The nuclear spireme is unravelling. The cells have separated. The 'bodies' lie at the extreme edge of the cytoplasm of the invaded cell, and are still in connexion with the parent nucleus.

Fig. 16. The spireme shows a beaded arrangement. There is a corresponding appearance in the attached 'bodies'.

Fig. 17. Nucleus in the 'open spireme' stage. Nucleus returned to the centre of the cell. The remains of the 'bodies' appear as bright refractive granules. Note the definite cell-wall, and the contraction of the cytoplasm.

Fig. 18. The nucleolus has divided into several small nucleoli. These are attached to the paired chromosome segments.

Fig. 19. The final disintegration of the nucleolus at the formation of the chromosomes.

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Digby, Lettice. 1909. "Observations on 'chromatin bodies' and their relation to the nucleolus in *Galtonia candicans*, Decsne." *Annals of botany* 23, 491–502.
<https://doi.org/10.1093/oxfordjournals.aob.a089232>.

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