

On the Synapsis in Amphibia.

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[PLATES 20—23.]

In 1903 and 1904 one of us, in conjunction with Professor Farmer, described the maiotic process in a variety of animals and plants.* From the observations then accumulated it was in the first place shown that what we termed the maiotic process appears to be the same throughout the animal and vegetable kingdoms. In the second it was pointed out that the general scheme we were able to formulate was in accord with the particular description of the metamorphosis given by Korschelt† for *Ophryotrocha* as long ago as 1895, as well as with the account of the same change in some amphibia given by Montgomery‡ in the same year as ourselves.

According to this conception of the maturation process, the reduction in the number of chromosomes to one half is brought about by a pairing of somatic chromosomes which takes place in the prophase of the first maiotic (heterotype) divisions. In this way we have in some mammals, for example, 16 pairs of chromosomes in the place of 32 single elements.

These chromatic *gemini*, as we propose to call them, go on to the spindle in the same way as ordinary premaiiotic or somatic chromosomes. But during the division each of the respective *gemini* separate into the two component parts; so that in the cases of mammals above referred to there are 16 premaiiotic chromosomes distributed to each daughter cell.

According to this view it would appear that during the first maiotic division no longitudinal fission of the chromosomes composing the *gemini* comes into play, and the longitudinal split which is visible in the spirem figure only effects that incomplete fission of the daughter elements first observed by Flemming in the diasters of the first maiotic division in amphibia (see fig. 22).

In this way the longitudinal split of the thread which takes place in the spirem stage only becomes completed and effective during the second

* Cf. Farmer and Moore, 'Roy. Soc. Proc.,' May, 1903; Farmer and Moore, 'Quart. Journ. Micros. Sci.,' vol. 48; Farmer and Shove, 'Quart. Journ. Micros. Sci.,' vol. 48; Moore and Robinson, 'Quart. Journ. Micros. Sci.,' vol. 48.

† Korschelt, 'Zeitschr. für Wiss. Zool.,' vol. 9.

‡ Montgomery, 'Biol. Bull.,' vol. 4, 1903.

maiotic (homotype) division. Consequently these two divisions with their respective prophases form a stage in the cell cycle of plants and animals which differs entirely from the divisional sequence before and after it.

The present communication deals with the prophase of the first maiotic division in Triton, and with the subsequent division up to the appearance of the diaster. As we have worked out the stages in this animal in great detail, we propose to give the results of our observations without discussion in the text, but to indicate by means of footnotes those points in which the fresh observations differ from the existing accounts of the maturation process in general, and of the same phenomena among amphibia in particular.

It may however be pointed out that the results of this investigation have been entirely to confirm the general interpretation of the maiotic metamorphosis already published by Professor Farmer and one of ourselves.*

At the same time it should be noted from the beginning that this view of the maiotic process entails a complete revision of the older conceptions of the nature of the first maiotic (heterotype) division among the higher vertebrata, such as those embodied in the able works of Flemming, Meves, and many others.

During the early summer (June) in England the testes in Triton are found to present all the phases in the cell cycle, from premaiiotic cells dividing in their characteristic manner, to the spermatids that have been produced by the second maiotic (homotype) division (see fig. 1, Plate 20).

From this figure it will be seen that in the section of the testes which the drawing represents the spermatogenesis is proceeding from the top towards the bottom of the Plate. Immediately below the peritoneal attachments groups of cells are seen, some with their nuclei at rest, others dividing; while in the region marked (*c*) nuclei are seen as we pass downwards, which are at first indistinguishable from those in (*b*), but which gradually alter in the appearance until we reach the lower part of (*c*).

The division figures encountered in region (*b*) are all of the ordinary premaiiotic type, and the appearance which comes over the resting nuclei in (*c*) as we pass downwards is the appearance produced by the advent of the synaptic metamorphosis in Triton when seen under a low power. Still lower than the region (*c*) the two maiotic divisions (heterotype and homotype) are encountered together.

The above will serve to orientate the original and relative positions of the cells which have been taken as individual illustrations of the successive phases of the synaptic change. But before leaving the small scale figure, it may be noted that upon examination the resting nuclei in region (*b*) differ

* Farmer and Moore, *loc. cit.*

from those in the (c) area in that they obviously contain more of the apparently nucleola bodies scattered within the membrane.

When resting cells of the region (b) are examined under a high power, it is seen that nucleolus-like bodies visible under a lower power resolve themselves into the short chromatic rods represented in figs. 2 and 3.

These bodies are seen to lie more or less parallel to one another within the cells, so that the appearance of the nuclei varies from that given in fig. 2, where the chromatic rods are seen from one side, to that represented in fig. 3, where the same rods are looked at from one end.

The definite nature of these bodies is sufficiently obvious from the figures, but their significance only became apparent upon ascertaining that their number is always about 24; that is to say, it was found, after counting in about 50 individual cells, that the number 24 was obtained for the great majority, while in the few cases in which it was above or below this figure such divergence was limited to one or two, and in nearly all these exceptions it was possible to attribute the divergence to some optical difficulty. The bodies lay over one another in the line of vision, or were hidden and confused by the nuclear membrane and the like.

The premaiiotic resting cells in the testes of Triton are found then to contain in their nuclei chromatic structures which at first might be, and generally have been, regarded as "chromatin nucleoli" (Flemming); but they correspond in numbers to the chromosomes of the premaiiotic prophase and division figures, for in this animal the number of the premaiiotic chromosomes is 24. These bodies correspond in fact exactly to what in 1904 we have already described as the Anlagen of the premaiiotic chromosomes in the corresponding cells in the testes of *Periplaneta*,* and there can be no doubt that they represent also the structures subsequently alluded to as prochromosomes by Overton,† Miyake,‡ and Strasburger§ in the same stage in certain mono- and dicotyledonous plants.

In Triton these structures are not restricted to the premaiiotic cells of the testis, but are equally apparent and have the same relationships in other tissues of the animal's body.

In some respects the bodies in question are more definite and stainable in the resting premaiiotic cells of Triton than they are in the corresponding elements of *Periplaneta*, and in both cases their subsequent history during the

* Farmer and Moore, 'Quart. Journ. Microsc. Sci.,' vol. 48, *loc. cit.*, Plate 38 and text.

† Overton, J. B., 'Über Reduktionsteilung in dem Pollenmutterzellen einiger Dikotylen.'

‡ Miyake, K., 'Über Reduktionsteilung in dem Pollenmutterzellen einiger Monokotylen.'

§ Strasburger, E., "Typische und Allotypische Kernteilung," 'Jahrb. für Wiss. Botanik,' vol. 42.

premaiotic divisions is perfectly simple. In Triton each Anlagen (or prochromosome) becomes gradually enlarged and thickened into the long premaiotic chromosomes of the spirem figure, while in *Periplaneta* they gradually assume the form of dense short rods characteristic of the premaiotic division figures of that arthropod.

In both cases the chief interest of these bodies lies in the fact that they obviously represent the chromosomes of division during rest; and we may say without reserve that their presence at all stages of rest between the successive premaiotic divisions seems to conclusively prove the permanence of the chromosomes from one cell generation to another.

Examination of the resting maiotic nuclei given in figs. 1 and 2 shows that, so far as can be seen, the Anlagen consist of irregular rods composed chiefly of chromatin, and either suspended in a fine linin meshwork within the nucleus or attached to the nuclear membrane, where the chromatin is seen to be spread out, and to give to the membrane itself the peculiar thickened appearance characteristic of the stage. No other structures with the exception of irregular nucleoli are visible within the resting premaiotic nuclei.

Before the maiotic metamorphosis sets in the Anlagen are seen to be single and discrete, figs. 2, 3; but as we pass to an examination of the cells in the later phases in the region *c*, where the synaptic change is gradually proceeding towards the formation of the coarse spirem, we find that the Anlagen are no longer single, in fact, the diminution in the number of what, under a low power would be taken for nucleoli is seen to be produced by a pairing of the bodies while the nuclei themselves still remain at rest.

The appearance which such cells present is represented in figs. 1, 4, and 5. Fig. 4 shows a cell in this condition in the same relative position as that represented in fig. 2. The associations produced in this way (which we propose to call *gemi**ni*) are again represented in fig. 5, where the *gemi**ni* are seen end on, as were the single Anlagen in fig. 3.

We have then in the testis of Triton premaiotic cells which, like the premaiotic or somatic cells of rest of the animal's body, possess structures that represent during rest the individual chromosomes of the successive division figures, and these bodies during the first phase of the synaptic metamorphosis that is perceptible, conjugate or pair so as to form 12 *gemi**ni* in the place of the 24 single Anlagen (prochromosomes).

When the *gemi**ni* have been produced it is seen, as in fig. 4, that they are related in a conspicuous manner by shreds and strings of linin to chromatin patches on the membrane of the nucleus; and there are indications that before the *gemi**ni* are formed the linin of each single chromosome extends out to the limits of the nucleus.

At all events, when the gemini have been produced each chromatic rod rapidly extends outwards along linin threads in the manner represented by fig. 6. In this we soon get an appearance which would be quite easy to misinterpret as a fission in a spirem were not the earlier stages of the process present in the surrounding tissue.

A somewhat later stage is represented in fig. 7, where it is seen that the original components of the gemini are rapidly elongating out into loops or polarised chromatic bands. Cells possessing the characteristics represented in figs. 6 and 7, constitute, in fact, the only representative in Triton of the strong synaptic contraction figure so conspicuous in many other forms of animals and plants. At a later stage the gemini, although still clearly visible, have so far elongated and moved from their original positions as to give the appearance represented in fig. 9.

This movement, which corresponds to the unwinding of the synaptic loops in mammals and other forms, is seen to have reached a further stage in fig. 8. Here the condition of the early coarse spirem stage is clearly foreshadowed, and by stages such as those represented in figs. 10 and 11 the characteristic polarised loops of the late spirem figure become gradually formed.

It appears then that the polarised loops are produced by the growth and elongation of the original gemini, and that consequently each loop represents two premitotic chromosomes, which may be associated together at one, or both, of their ends. In general, in Triton and elsewhere the chromosomes forming the loops remain connected together only by the ends which originally lay towards the nuclear interior, the outer pair of ends abutting upon some portion of the nuclear membrane, and always in the late stages of the spirem figure becoming widely detached from each other.

Stages in the formation of the individual loops and the mode of attachment of the chromosomes together at the round ends of the loops can be seen in figs. 9, 10, 11, and 12.

From the original formation of the gemini until the production of the spirem loops, figs. 10 and 11, the chromatin in each lateral component or chromosome is seen to be in the form of irregular granules, and remains scattered along a linin framework; but at subsequent stages (figs. 12, 13, and 14) these chromatin particles become arranged, or split as it were, into two longitudinal rows, and the loops from this time onwards present the characteristic split appearance represented in figs. 13, 14, 15, and 16. In stages such as that given in fig. 14 every loop is completely divided throughout its entire length, and the longitudinal halves of the thread may divaricate from each other as far as is to be seen in portions of the loops

represented in fig. 15. At this stage, and after, the loops are very long indeed, stretching in some cases completely round the whole nucleus, and it is, we think, without doubt chiefly owing to this circumstance that their history has been in general misinterpreted.*

A comparison of figs. 14, 15, and 16 will show that the split after becoming, as in fig. 15, very conspicuous, gradually closes up again, fig. 16, whilst in figs. 17 and 18 the closing process is still further completed. Even in fig. 18, however, the split is in places still visible, and at fig. 19, when the loops have been finally resolved into the adult gemini of the first maiotic division figure, the fission is not in all cases completely lost.

In other animals at the same stage, *Periplaneta* for example, the fission, as has been shown in a former work,[†] is often visible throughout the whole spindle figure of the first maiotic mitosis, and in such cases the origin of the fission of the daughter chromosomes is obvious.

In the final stages of the prophase in *Triton* (figs. 18 and 19) the gemini assume the various forms characteristic of the first maiotic division, and during the diaster the rings and loops break apart in the manner represented in figs. 21 and 22.

As soon as the diastral V's have been formed the original longitudinal split becomes here also again clearly visible (fig. 22). It is moreover quite easy to show in *Triton* as in other cases that it is this fission which functions in the final maiotic (homotype) division.

To recapitulate (see diagram):—In *Triton* it is found, when sufficient

* As is well known, Flemming, and after him many others, originally regarded the split of the spirem as opening out in lengths to form the rings and loops presented by the adult so-called heterotype chromosomes, and the longitudinal fissions of the daughter elements in the diaster of this division as a subsequent and independent fission. Dixon ('Roy. Ir. Acad. Proc.,' vol. 3) regarded the split seen in the spirem as due to an approximation similar to that witnessed in the formation of the gemini. Berg ('La Cellule,' vol. 21), Overton, and Miyake (*loc. cit.*) have adopted a similar view, regarding the late split in the spirem as a lingering expression of the conjugation during the formation of the several gemini. At times a similar view has been taken by Strasburger (*loc. cit.*) and others. We regard our present observations, as well as those upon numerous other forms dealt with in our former paper with Professor Farmer, as incompatible with the idea contained in the works of the above authors, namely, that the split in the spirem of the first maiotic division is due to an approximation, and are inclined to think that this view can only have originated through a confusion having been made between the conjugation during the formation of the gemini and the longitudinal fission which, without any doubt whatever, does take place during the spirem stage.

Montgomery ('Biol. Bull.,' vol. 4), in the same year as ourselves (Farmer and Moore, 'Roy. Soc. Proc.,' 1903, *loc. cit.*), regarded the split in the spirem in Amphibian heterotype prophases as not constituting the opening of the loop or ring of the spindle figure, and the fission of the daughter diastral elements as due to the split visible in the spirem.

† Farmer and Moore, 'Quart. Journ. Micros. Sci.,' vol. 48, *loc. cit.*

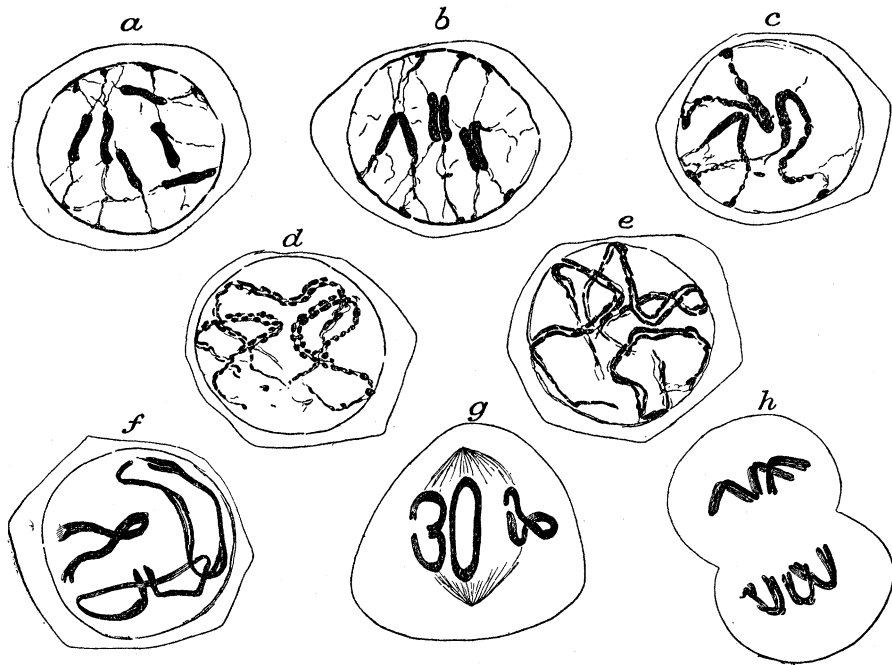


Diagram representing the course of the synaptic metamorphosis. For the sake of clearness only six chromosomes are represented in the premaiiotic resting cell (*a*). At (*b*) the chromosomes are uniting; (*c*) shows the conversion of the gynemini into the young loops. At (*d*) is seen the split in the chromosomes; (*e*) shows a later stage; (*f*) shows the transformation of the loops into the adult gynemini (heterotype chromosomes); (*g*) represents their appearance on the spindle; (*h*) shows the diastral chromosomes, three in each cell, with the longitudinal split begun in the preceding prophase.

optical power and efficient preservation are combined, that: The somatic chromosomes are visible in the resting cells; that during the inception of the synaptic phase these chromosomes pair so as to form double bodies which are the forerunners of the adult gynemini (heterotype chromosomes, allotype chromosomes, bivalent chromosomes, etc.); that by growth and elongation the gynemini constitute the polarised loops of the first maiotic prophase; that these loops become longitudinally split, and later each longitudinally fissid aggregate rolls itself up into one or other of the forms assumed by the adult gynemini; that in these later stages in Triton the longitudinal fission of the chromosomes becomes almost, but not quite closed up, and in the diaster the separated chromosomes again exhibit it; while finally it is seen that this split functions in the second maiotic (homotype) division.

DESCRIPTION OF PLATES.

[Figs. 2—22 are drawn with a 3-mm. long-tube Zeiss apochromatic 1.40 aperture, and a 27 ocular.]

PLATE 20.

- FIG. 1.—Section of testis of *Triton* (June) as seen under a low power lens. At the upper margin is the attachment between the testis and the body wall and the membrane which surrounds the tubules. The foot-cells are not shown. Near the upper margin to the right are two "male ova"; towards the left are tubules with cells in the premaiotic (somatic) stage dividing at (*b*). The region marked (*b*) contains the zone of transformation wherein the synaptic gemini are constituted. Late synaptic (heterotype) prophase is seen at (*c*), and the first and second maiotic divisions lower down.
- FIG. 2.—Cell from the upper premaiotic region, the nucleus showing bodies representing the 24 chromosomes while in a condition of complete rest.
- FIG. 3.—Cell from the same region as fig. 2, viewed from a direction at right angles to the foregoing; the bodies representing chromosomes seen end on.
- FIG. 4.—Cell in the first phase of the synapsis, showing the bodies representing the resting premaiotic chromosomes uniting in pairs to form the gemini.

PLATE 21.

- FIG. 5.—Cell from the same region as fig. 4, viewed from a direction at right angles showing the gemini end on.
- FIG. 6.—Cell advancing in the synapsis, the gemini elongating.
- FIG. 7.—Synapsis further advanced, the gemini elongating into loops.
- FIG. 8.—Synapsis still further advanced, the gemini moving from their original central position.
- FIG. 9.—The gemini becoming converted into loops.
- FIG. 10.—The gemini becoming polarised into the loops of the coarse spirem figure.

PLATE 22.

- FIG. 11.—Cell showing the coarse spirem, the threads not split.
- FIG. 12.—Same as fig. 11, but showing the first traces of the longitudinal split.
- FIGS. 13, 14.—Longitudinal split more apparent.
- FIG. 15.—The split seen at its maximum.
- FIG. 16.—The split seen closing up at places.

PLATE 23.

- FIGS. 17, 18.—Cells showing the ends of the loops with portions of the split closed up, others open.
- FIGS. 19, 20, 21.—Stages in the first maiotic division.
- FIG. 22.—The diaster of the first maiotic division, showing the split in the diastral chromosomes.
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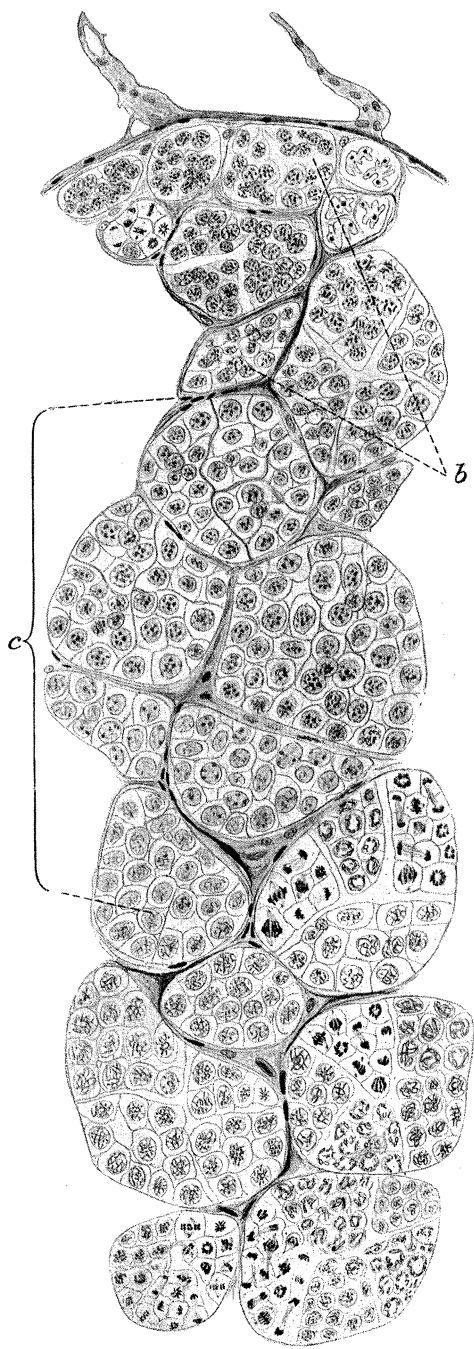


FIG. 1.

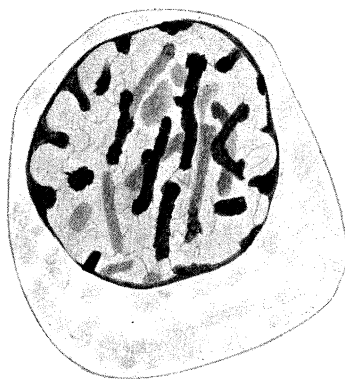


FIG. 2.

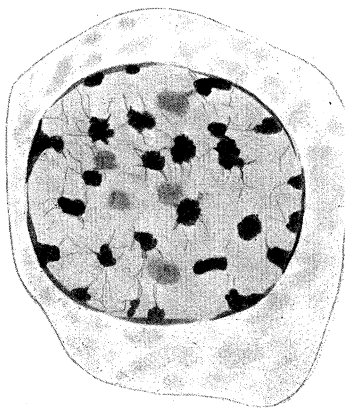


FIG. 3.

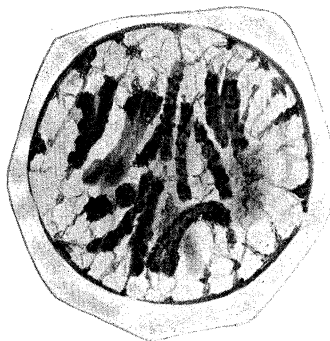


FIG. 4.

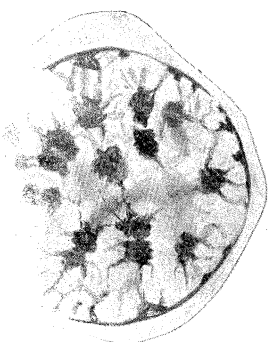


FIG. 5.

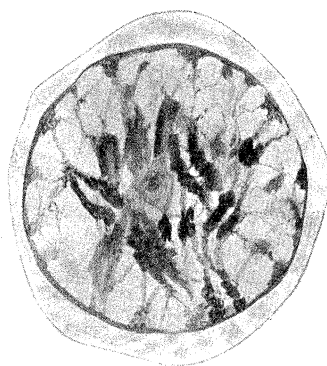


FIG. 6.

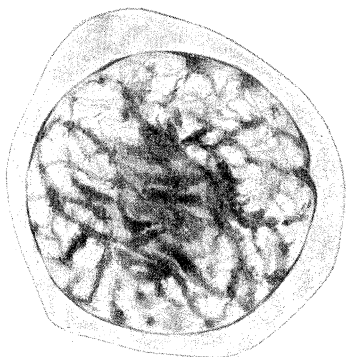


FIG. 7.

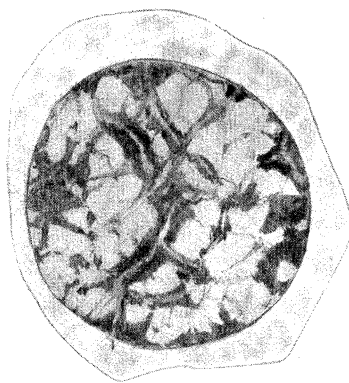


FIG. 8.

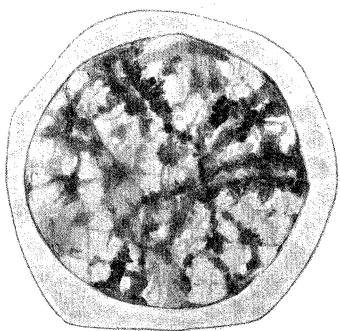


FIG. 9.

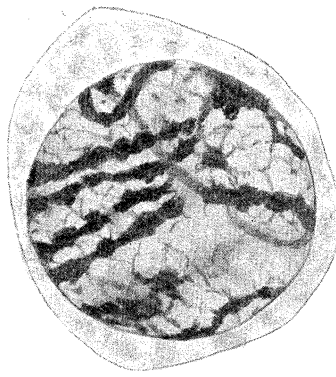


FIG. 10.

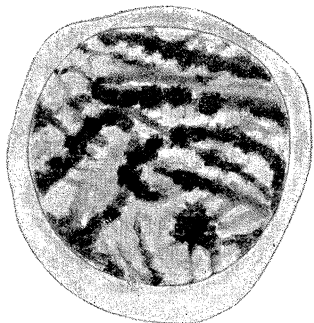


FIG. 11.

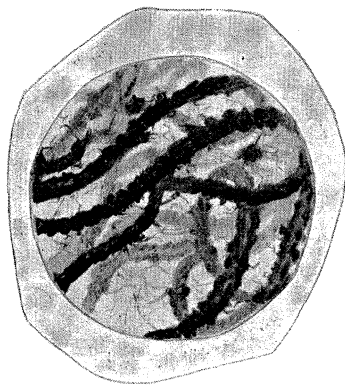


FIG. 12.



FIG. 13.

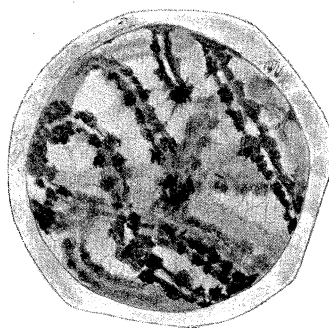


FIG. 14.

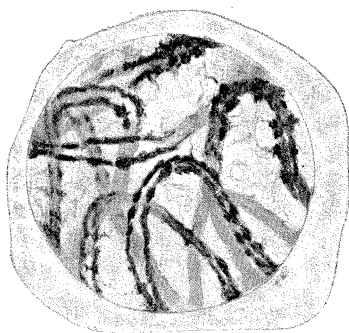


FIG. 15.

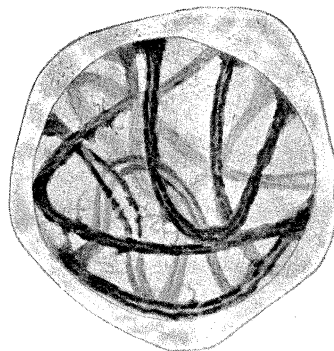


FIG. 16.

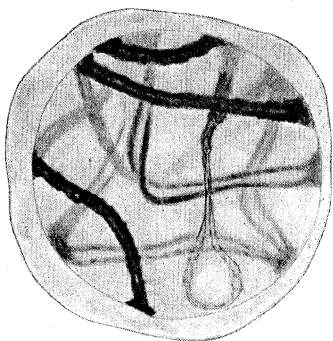


FIG. 17.

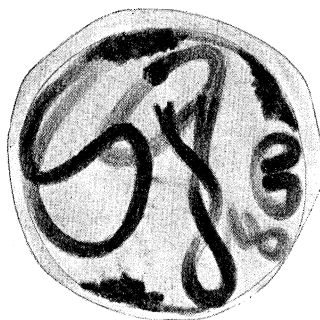


FIG. 18.



FIG. 19.

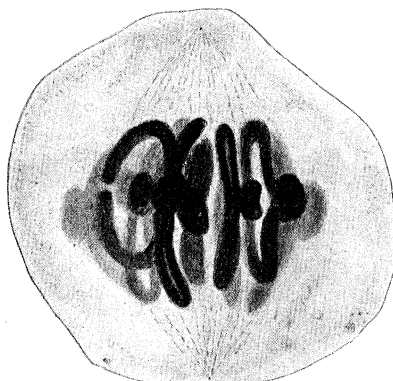


FIG. 20.

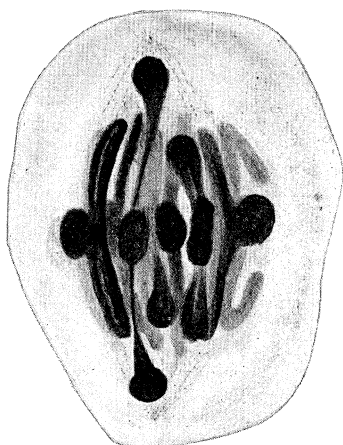


FIG. 21.

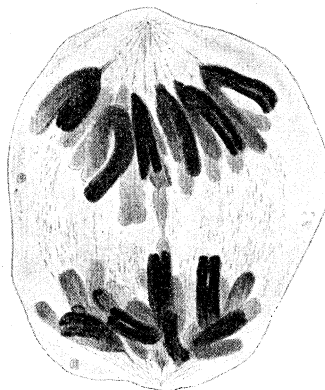


FIG. 22.

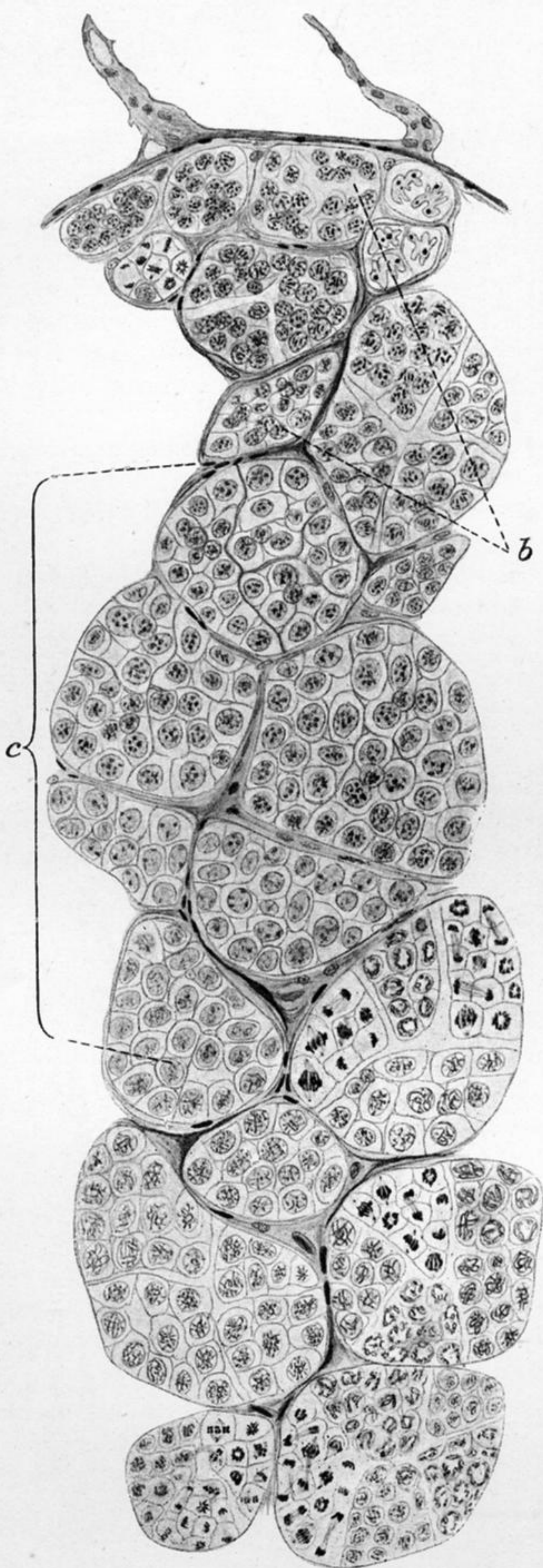


FIG. 1.

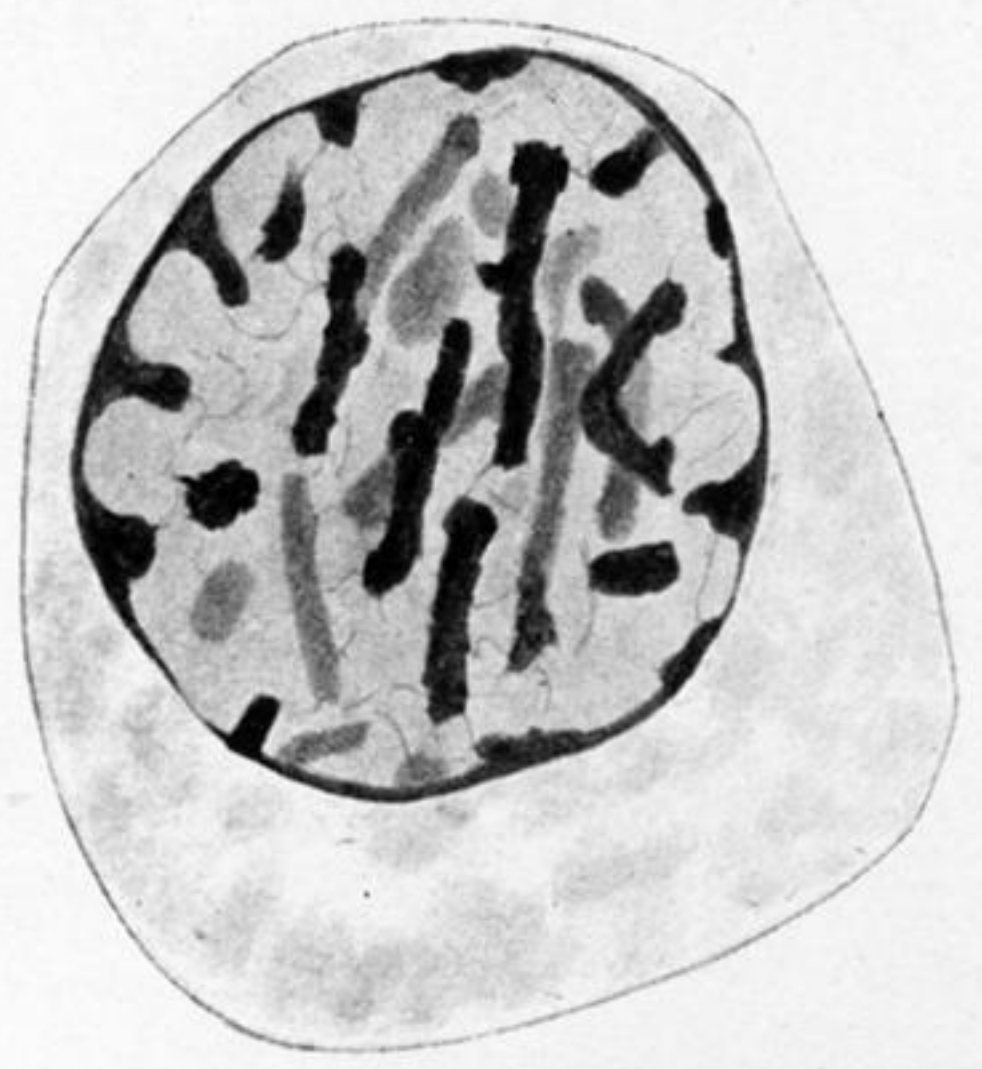


FIG. 2.

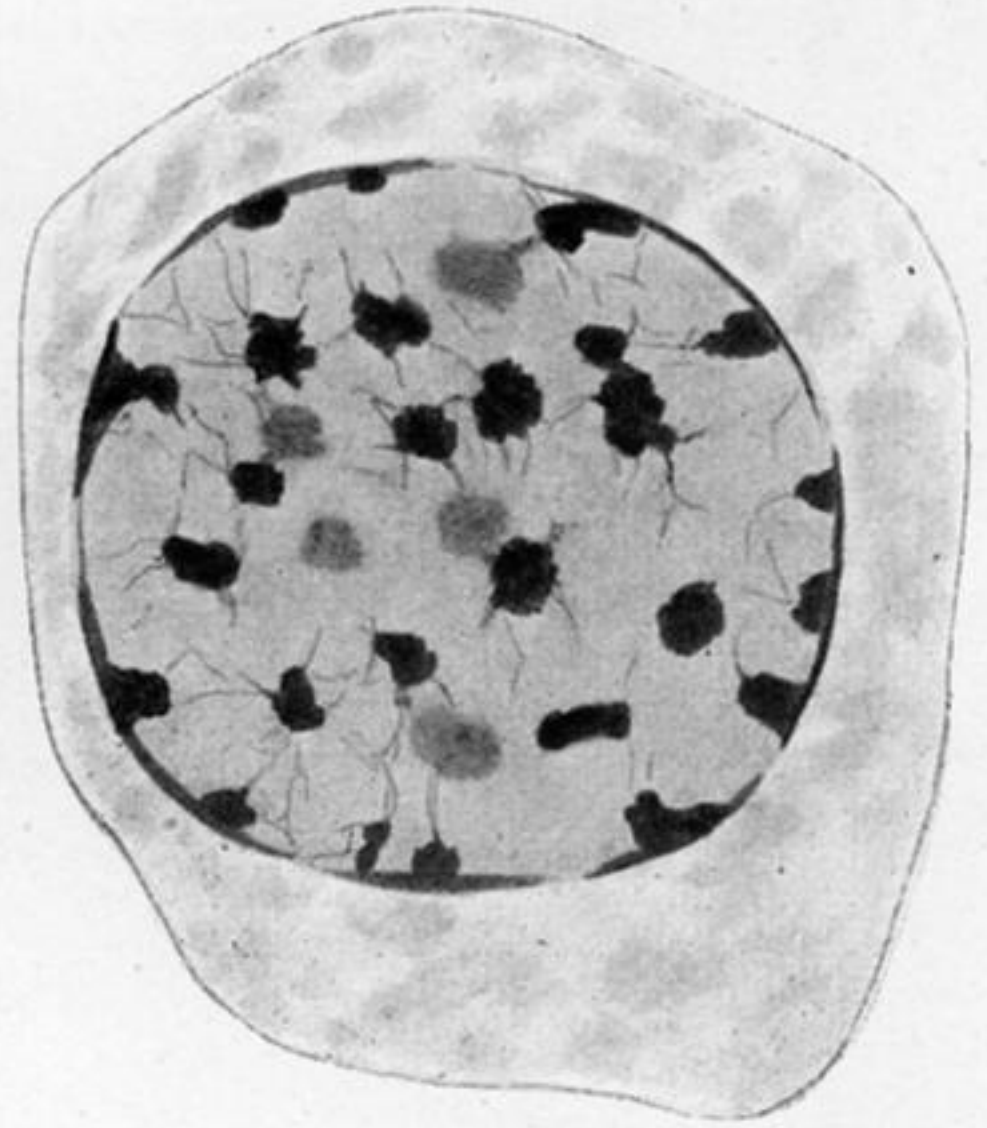


FIG. 3.

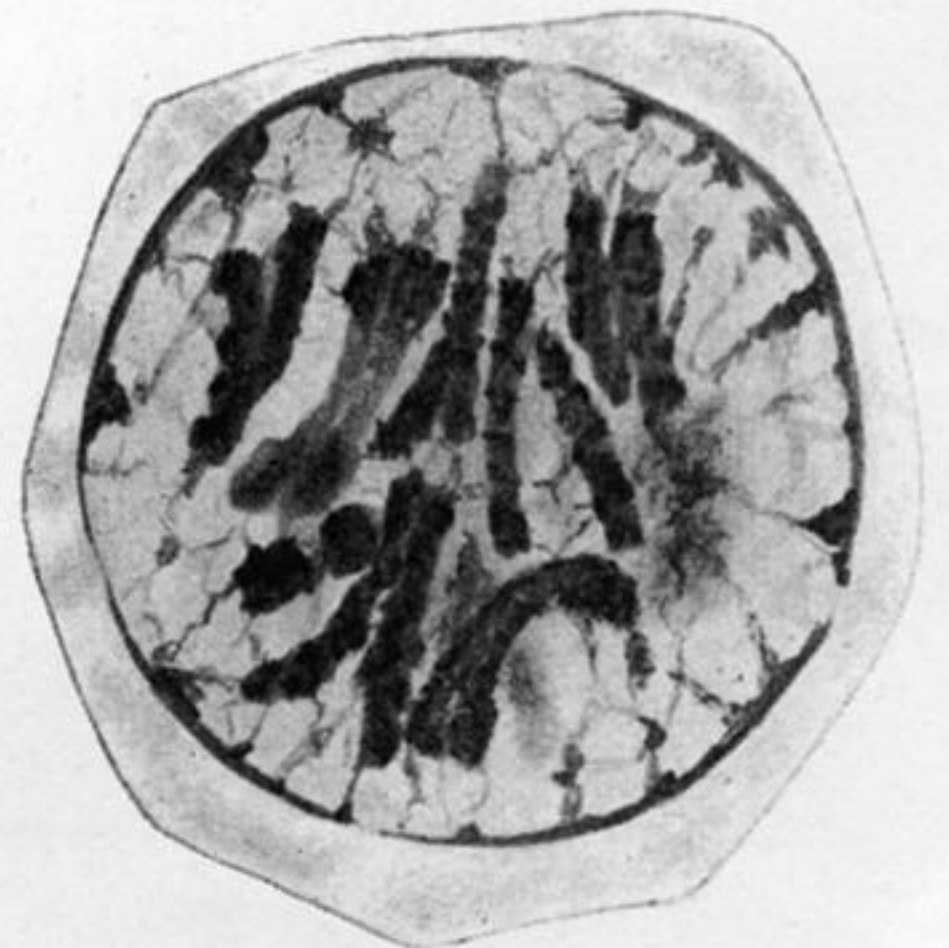


FIG. 4.

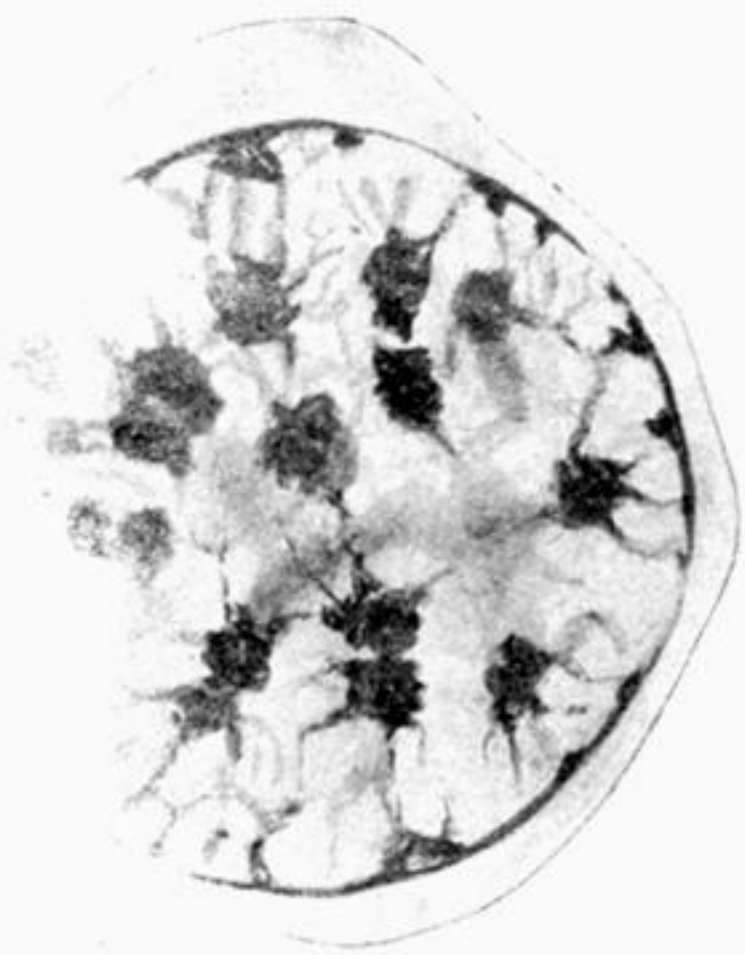


FIG. 5.



FIG. 6.

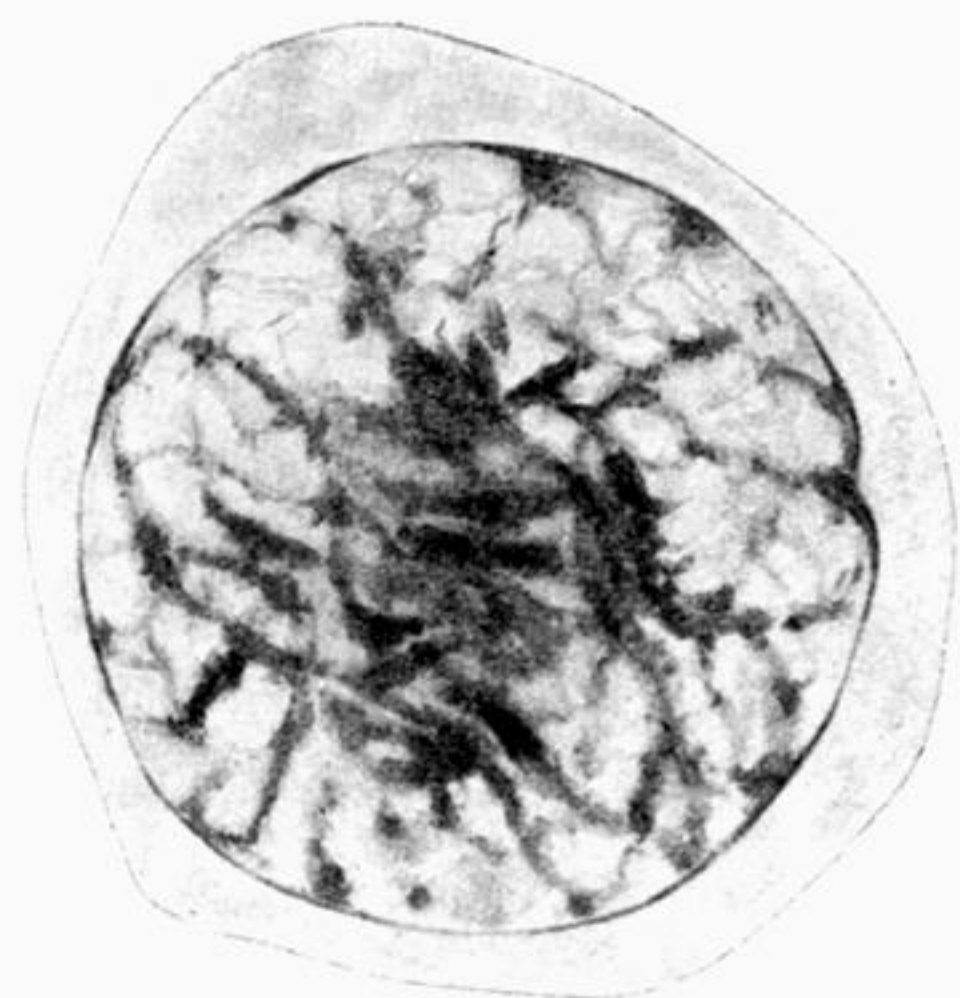


FIG. 7.



FIG. 8.

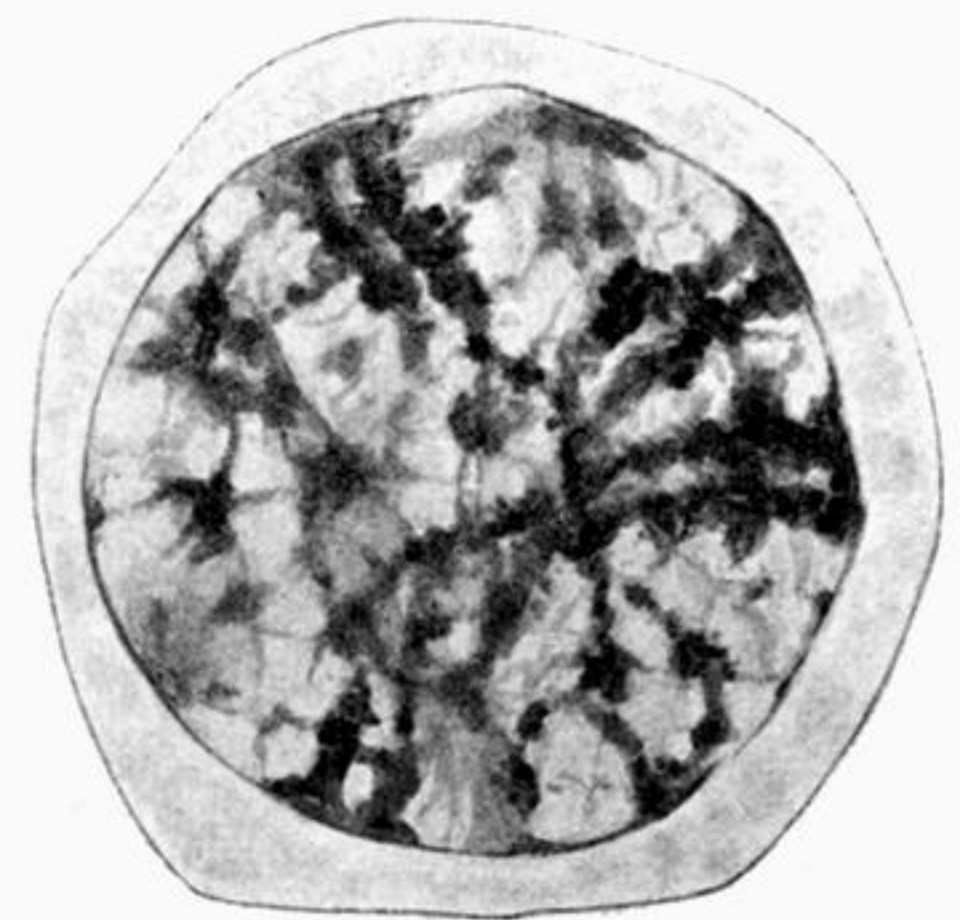


FIG. 9.



FIG. 10.



FIG. 11.



FIG. 12.



FIG. 13.



FIG. 14.

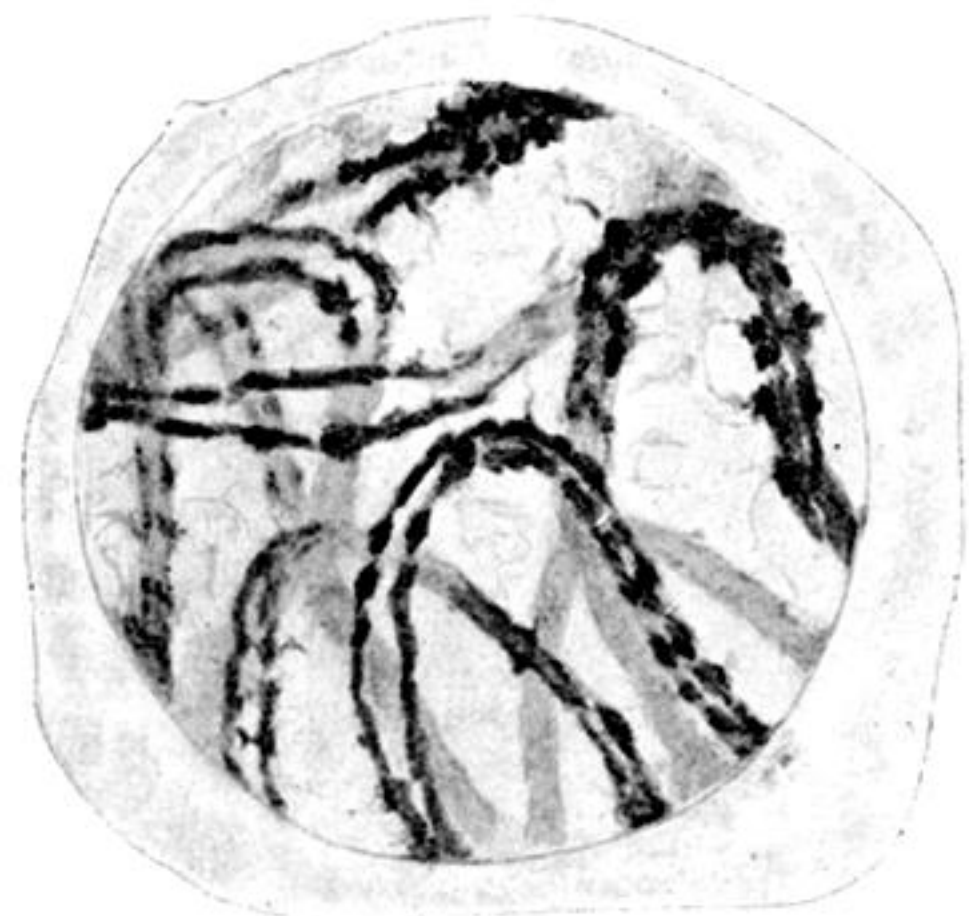


FIG. 15.



FIG. 16.

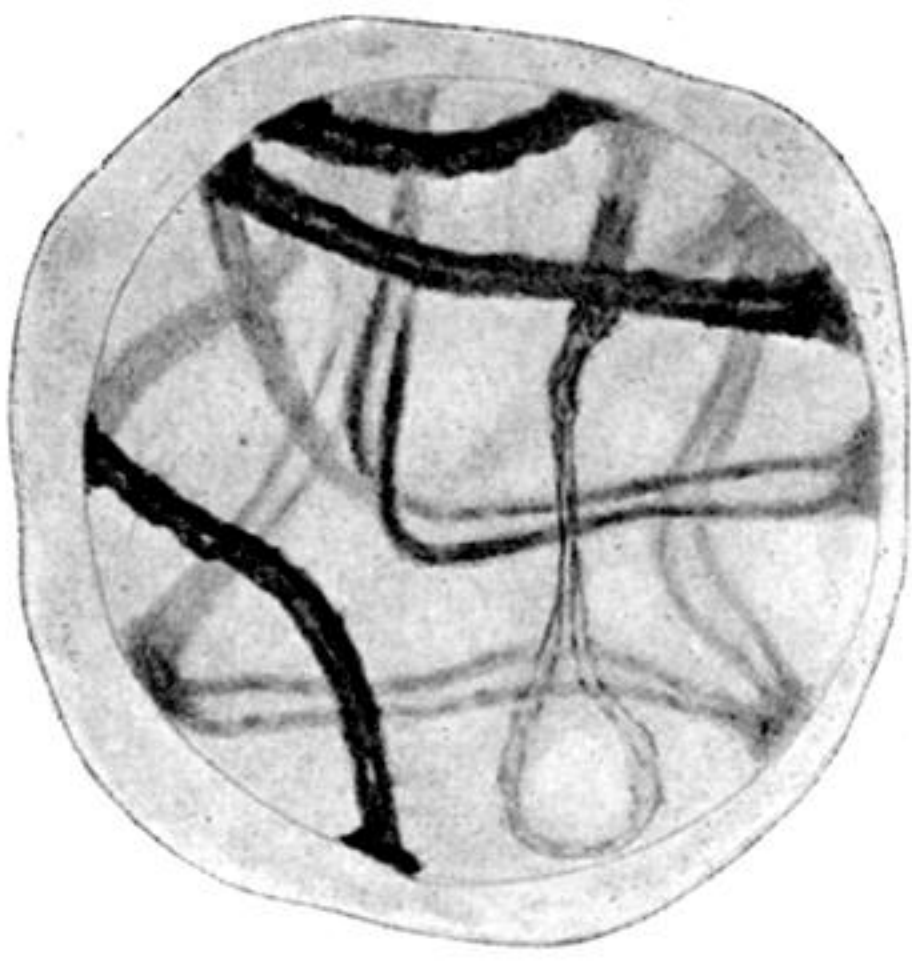


FIG. 17.



FIG. 18.



FIG. 19.

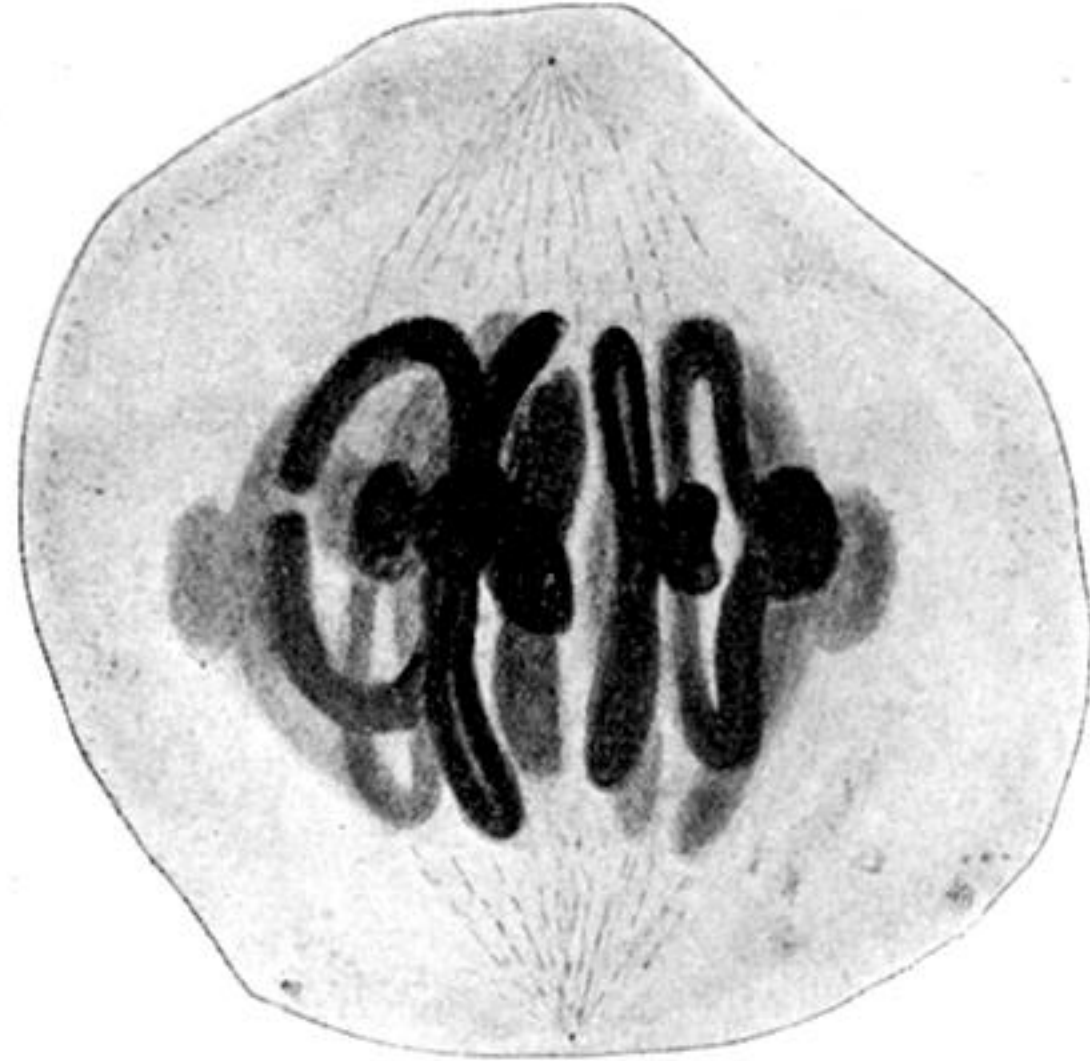


FIG. 20.

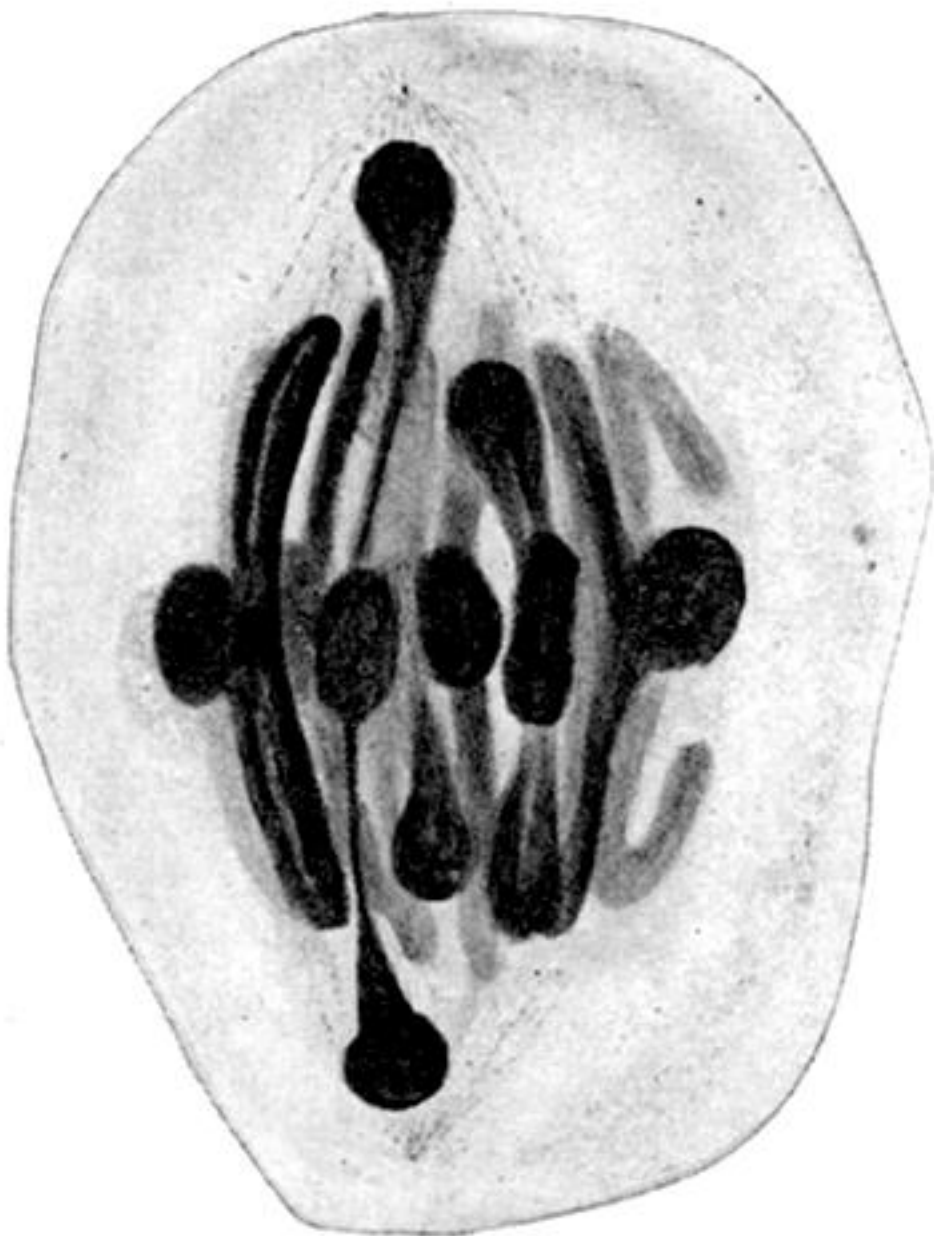


FIG. 21.



FIG. 22.