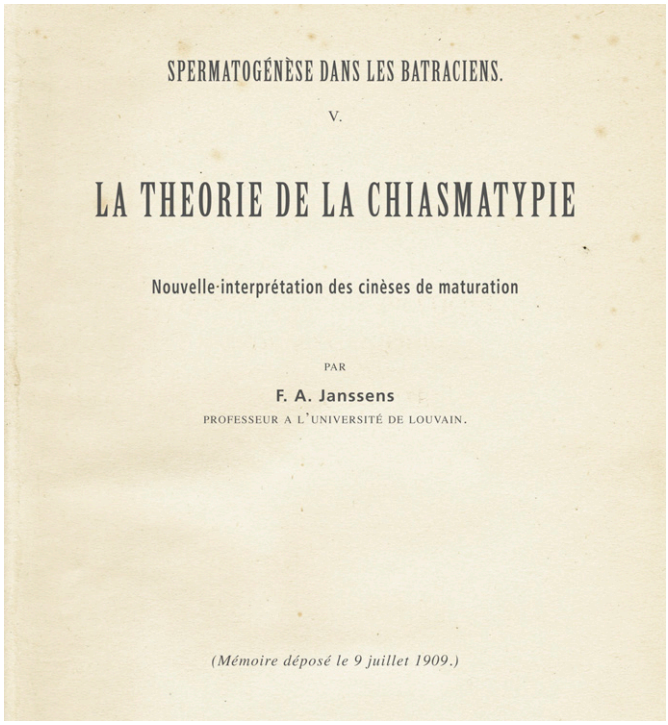
La Theorie de la Chiasmatypie
Nouvelle interprétation des cinèses de maturation

Translated by
Romain Koszul*,†,1 and Denise Zickler‡,1
*Institut Pasteur, Group Spatial Regulation of Genomes, Department of Genomes, †Centre National de la Recherche Scientifique Unité Mixte de Recherche (UMR) 3525, F-75015 Paris, France and Genetics, F-75015 Paris, France, and ‡Institut de Génétique et Microbiologie, UMR 8621, Université Paris-Sud, 91405 Orsay, France

First published in 1909 in *La Cellule*, F. A. Janssens's "The chiasmatype theory. A new interpretation of the maturation divisions" proved controversial and was for several decades resisted by many geneticists and cytologists. In this month's Perspectives, Koszul *et al.* revisit Janssens's findings and the surrounding controversies.

Here, translated for the first time in English, GENETICS republishes the original Janssens's article. The article is presented as closely as possible to the original publication's format and style.[2] GENETICS wishes to thank Romain Koszul and Denise Zickler for their labors in presenting the scientific community with this new translation.



SPERMATOGÉNÈSE DANS LES BATRACIENS.

V.

LA THEORIE DE LA CHIASMATYPIE

Nouvelle interprétation des cinèses de maturation

PAR

F. A. Janssens

PROFESSEUR A L'UNIVERSITÉ DE LOUVAIN.

(Mémoire déposé le 9 juillet 1909.)

doi: 10.1534/genetics.112.139725
[1]Corresponding authors: Institut Pasteur, 25 rue du Dr. Roux, Bat. Monod, 75015 Paris, France. E-mail: romain.koszul@pasteur.fr; and Institut de Génétique et Microbiologie, Université Paris-Sud, Bâtiment 400, 91405 Orsay, France. E-mail: denise.zickler@igmors.u-psud.fr
[2]Translated from the original article, which can be found at http://www.archive.org/stream/lacellule25lier#page/n435/mode/2up.

LA THEORIE DE LA CHIASMATYPIE

Nouvelle interprétation des cinèses de maturation

Following Weismann's theoretical considerations, many authors conceded that hereditary forces are embodied within the germinal plasma as solid particles, which are already present in the sexual elements [eggs and sperms, Translator's Note, (T.N.)] that contribute to the formation of the fertilized egg. These particles must be searched in the chromatic part of the nucleus. Recent studies on the maturation divisions have developed these ideas further, and revealed the remarkable potential of Weismann's theory.

One can say that the strongest argument in favor of this theory is the wonderful agreement between, on the one hand, Mendel's studies made in an era when cytological investigations were not yet born and, on the other hand, the results of cytological studies which were themselves made at a time when the work and the laws of Mendel were still ignored by cytologists.

This concordance has been clearly underlined by Boveri, who concluded that *Mendelian allelomorphic characters are carried by corresponding chromosomes in the nucleus*.

It is known that in many animals and plants the shapes and lengths of chromosomes can vary greatly. Taking advantage of these features, a large number of recent studies have led to the following conclusions:

1° In every somatic cell each chromosome of specific shape and length finds his twin (homolog, T.N.). There are two parallel sets of the different chromosomes, which associate in pairs (with the exception of accessory (sex, T.N.) chromosomes).

2° Twin chromosomes are of different origins. One is provided by the egg and therefore belongs to the female race (lineage), whereas the other is brought by the spermatozoid that fertilized the egg and therefore is of the male race (female and male origin, respectively, T.N.).

3° During one of the early stages of auxocytes (meiocytes, T.N.) maturation, that we named the *amphitene* stage (zygotene, T.N.), twin chromosomes (homologs, T.N.) come into conjunction (synapse, T.N.).

4° During the (ensuing T.N.) cleavage of the *pachytene* filaments these (two T.N.) chromosomes reappear. They are associated with each other in *dyads* and are more or less coiled around one another ["relationally coiled"] [SCHEMA I].

5° The heterotype division (first meiotic division, T.N.) separates these chromosomes, and it is during this separation that qualitative reduction (maternal from paternal T.N.) occurs, as postulated by Weismann and already predicted/foreseen by Mendel in his *law of the segregation of characters in gametes*.

6° Therefore auxocytes II are of pure lineage (haploid, T.N) (Mendel admits that gametes are always of pure lineage), and the following homeotype division (second meiotic division, T.N.) simply multiplies them through a division whose first prophase stages are already visible during the heterotypic segregation (anaphase I, T.N.). This second division follows the first one so quickly that its initial steps overlap with the preceding division. Homeotype is a division that exhibits a longitudinal cleavage of chromosomes as observed in any (non-meiotic, T.N.) division. Therefore it is equational (separation of chromatids, T.N.) (Roux).

These last four propositions have been *mainly* defended by the school of Louvain and by Mr. and Mrs. Schreiner.

However, other authors argue that it is the second of the two maturation divisions that is reductional and that the first division, on the contrary, is equational. And a few authors, among whom we cite mainly Bonnevie and Veydovsky, still consider that both maturation divisions are equational.

* * *

Although very elegant and simple, this theory has never fully satisfied us, at least in regard to the nature of the two maturation divisions and this is why we undertook a more careful study of the two divisions - hetero- and homeotypic. In this short note we present both our concerns regarding the current theory and discuss the main results of our own research. We will occasionally strongly emphasize the different points we address (the original text "à l'occasion" could mean "occasionally" or could refer to an extended publication in opposition with this short note, T.N.)

During the session of May 5th 1908, the scientific board of the Royal Academy of Belgium accepted the deposit of a sealed document that we had sent on April 10th of the same year. This document contains the conclusions we draw from and documented with the material collected during two years of intensive studies and observations of our best preparations of *Batracoseps attenüatus* (California slender salamander) and other triton species. We have kept this study unreported for a reasonable amount of time and we now submit it to the public with the hope that it will help to shed some light on this delicate question.

§ I.

Theoretical arguments against the current hypothesis

1° The tetraspore (the four products of the two meiotic divisions, TN) is found within the entire animal and plant kingdoms, starting most likely with the most evolved red algae. This formation is therefore of capital importance. If *four* and not only *two* spores are formed, it is likely because each of them must hold something unique. However, all modern cytological studies have concluded that two, and only two types of spores are formed. Therefore, there is something within the facts that has remained enigmatic until now.

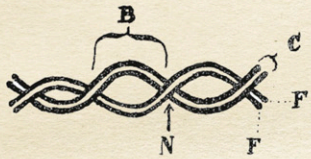


SCHÉMA I.

We will in this note call *dyads* a couple of chromosomes at the strepsinema stage just before their attachment to the spindle. SCHEMA I *dyad*. C, *chromosomes*. We call filaments F the two sister-chromosomes (chromatids T.N.) issued from a longitudinal cleavage of chromosome F. The site N where the two chromosomes of a dyad cross is called *chiasma* or *knot*; B is the *loop* or *inter-node* formed by the two chromosomes between two knots; finally, a *segment* is the part of *one* chromosome included between two *knots* or *chiasmata*.

2° The reason for the occurrence of a classical division at the end of the maturation processes is not at all understood, and the egg seems as suitable for fertilization after the polocyte expulsion (first polar body, T.N.) than as after the second polar globule expulsion. Therefore the *homeotype* or second maturation division appears as superfluous and complicated and, until now, a completely inexplicable feature.

3° The "hetero-homeotype" theory also fails to explain the long duration of the *pachytene* stage. It is not better explained if one considers, despite many observations suggesting the opposite, that pachytene does not involve the fusion of the two parallel chromosomes. As a matter of fact, this is not at all understood.

4° The significance of the coiling stage, called strepsitene (diplotene/diakinesis, T.N.), which is so characteristic and general, is also not understood. If its unique objective would be to separate two chromosomes, it would be a miniscule result relative to the weeks, sometimes months, of effort required to get to this stage. The current theory takes notice of these observations but does not interpret them. At most, the coiled aspect of chromosomes at this stage provides an argument against Flemming's old hypothesis saying that it is the result of a simple longitudinal cleavage of pachytene coils.

However, the association of the two chromosomes in loosely coiled loops remains enigmatic.

5° Finally, although the hetero-homeotype theory certainly provides an interesting explanation for the (first, T.N.) law of Mendel, it cannot explain it completely. Indeed, cases have been reported where the number of clearly distinguishable allelomorphic characters exceeds (by a lot) the number of distinct pairs of chromosomes.

Therefore, here again, the theory in vogue does not provide a complete explanation.

* * *

Since all these arguments rely only upon controversies raised by theories, they are not very valuable. They would hardly even be worth mentioning if all of these theories had been drawn from a single set of observation. This is not the case for the findings presented in this paper, which gives the criticisms developed above much greater significance.

§ II.

The theory lacks consistency with the facts

1° *"Heterotypic"* figures are prominently characterized by the *longitudinal cleavage* of chromosomes during *anaphases*.

a. First, we must point out that longitudinal cleavage does not occur at that stage of the division (therefore at anaphase, T.N.). This phenomenon usually occurs either before onset of division, or at the equator at metaphase.

b. If each chromosome was cleaved while being pulled to the poles, *the cleavage should disappear due to the traction* to which the chromosome is subjected during this ascending movement. Such traction would tend to bring

together and join the two elements of the chromosome rather than separate them. Instead, we observe the opposite.

For example, in the "E"-like chromosomal shapes (see example in SCHEMA V, T.N.) the longitudinal cleavage, if it exists, *should be seen without difficulty within the two free branches* (arms, T.N.) *of the chromosome*. However, it is exactly in this part of the figure that, most often the cleavage is not observed. If two threads do appear, it is usually in the long, clearly stretched vertical jamb (to which the free branches are linked, T.N.). Therefore it is unlikely that there is any longitudinal cleavage of the chromosome.

c. At late anaphases, it is frequent that most chromosomes, except one or two, are already at the poles, each in a double V configuration (with four arms emanating from each kinetochore, T.N.). In this case, as seen FIG. 37 and 38, some double V's often show three branches at the poles, *still linked to the equatorial plane by the fourth branch*. It is unlikely that one of the two elements resulting from a longitudinal cleavage should remain united longer than the other element. They should separate simultaneously.

2° It is unlikely that association of (homologs T.N., SCHEMA I) chromosomes in dyads results from a simple *coiling* of two *anatomically* independent elements around one another.

a. The two chromosomes of a dyad remain too tightly associated as they are pulled to opposite poles. Coiling by itself, especially because it is often loose cannot explain such association. Another explanation must be found.

b. At anaphase, if a simple coiling would hold the chromosomes together, the uncoiled parts of the dyads should be in the continuity with the coiled parts. This is hardly ever the case. Especially during late anaphases, there should be few if any connections between chromosomes and their (intertwined, T.N.) extremities should at most cross each other at a very obtuse angle such that they are almost parallel SCHEMA II, 1. The opposite occurs. Especially at the end of anaphases, the two free ends are oriented perpendicularly to the ascending filaments. In addition, these two free segments are not positioned one above the other SCHEMA II, 2, but lie exactly in line with one another SCHEMA II, 3.

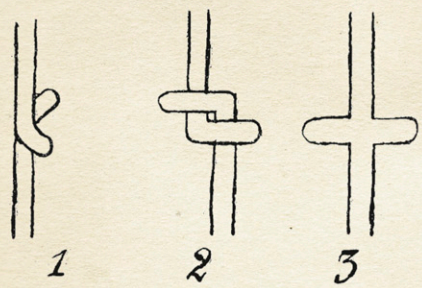


SCHÉMA II.

§ III.

Numerous evidences directly contradict the "hetero-homeotypic" theory

1° If the Vs seen at anaphase of the "heterotypic" division were really undergoing a longitudinal cleavage of their arms during the "heterotype" anaphase movement, the resulting sister filaments (chromatids, T.N.) would remain parallel, especially as long as they keep connections with the remaining coiled elements of the dyad from which they originated. But such parallelism is rarely observed; on the contrary those (sister, T.N.) filaments are frequently widely separated (FIG. **19**, **20**, **21** and **22**). This observation is irreconcilable with the theory that equational cleavage occurs in the V-shaped chromosomes during the course of heterotypic anaphases.

2° Very often, the links between the chromosomal part already *in anaphase* (moving towards a pole, T.N.) and the part still at the equatorial plane do not conform to the former theory.

a. For example, ring chromosome figures almost always present two thickenings, like two bezels, at the free extremities of the dyads. Each of these bezels exhibits two knobs (like a bezel housing a gem/stone, T.N.) that correspond to the extremities of the two chromosomes initially coiled. To satisfy the requirement of the heterotype theory, the chromosome branch that comes into contact with the thickening should end *entirely* within one of the knobs, for instance the right one, and the arm from the opposite side should end *entirely* within the other knob, for instance the left one. This is *never* the case. The branches of the V coming from either pole always send an extension within each of these two knobs. These knobs are themselves most often already divided into two parts. Therefore, each thickening represents a small tetrad of four spherules, each of which is connected to the ring. In the center one sees an empty space SCHEMA III.

SCHÉMA III.

We believe that this same situation occurs in all heterotypic *rings*. Although the relationships in those structures are sometimes hard to see, they nonetheless definitely exist.

b. Some other times, in the most advanced anaphases, the following pattern can be seen. On one side of a chromosome, the two filaments of the branch cleaved in anaphase are closely associated, whereas on the other side they are far apart and touch their counterpart filaments either externally (on either side of the pair, T.N.) SCHEMA IV A or by intermingling with each other as

schematized in SCHEMA IV B. This is an indisputable finding that we observed frequently (FIG. **23** and **35**).

c. We put in the same category patterns like those observed FIG. **31**. In such cases, we observe frequently that at least two of the anaphase filaments going to opposite poles remain somehow parallel to the equatorial plane, FIG. **31**, **32** [**24**, **25**, **29**].

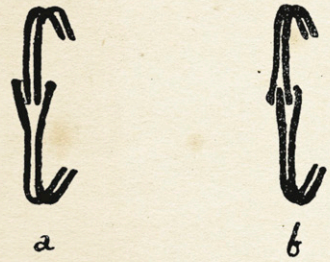


SCHÉMA IV.

d. Such a disposition can be seen for each of the two filaments of segments at anaphase. Relatively complicated figures are then observed, that cannot be reconciled with the "hetero-homeotype" theory (FIG. **17**, **18** and **22**). SCHEMA V illustrates such a case in an E-shaped chromosome. One can notice that the chromosomal segments still at the equator are cleaved longitudinally, and that the resulting filaments within each pair will ultimately segregate towards opposite poles as in a somatic division. Therefore, in such cases, the parallel chromosomal filaments pulled together towards one pole do not come from the cleavage of a V jamb, which was primarily single, but actually originate from two different chromosomal segments.

SCHÉMA V.

Several authors have described similar figures. We cite among them, Mr. and Mrs. Schreiner, 1905, I, FIG. 48, 49, 52, 56, and others. On page 24 of their work, the Norway scientists try to explain this organization. According to them, it would result from a secondary connection. They recognize, however, that their interpretation is very hazardous: "Wir vermogen uns keine klare Meinung daruber zu bilden, durch welche Krafte diese eigentumliche Formveranderung der Chromosomen bewirkt werden." (translated as: "It is difficult for us to provide a clear explanation for the force which acts on the chromosomes to give them such configurations"). The same comment applies, according to them, to similar figures observed in salamander, Fig. 22a (ibidem, II). Figures of this kind have also bothered many other distinguished authors, preventing them from accepting the "hetero-homeotype" theory. Among these should be mentioned Misses K. Foot and E. Strobell 1905, whose splendid photographic reproductions 123, 126, 127 provide us with beautiful examples of such chromosomes. Also, Fig. Ic and Id from Miss. K. Bonnevie 1908, led the author conclude that the *so-called "heterotype" divisions should be related to the ordinary divisions, where chromosomes undergo a longitudinal and equational cleavage*.

As we will see later, we share this point of view, at least for this specific part of the chromosomes.

§ IV.

After all of the above considerations, does the theory of a longitudinal cleavage of each of the chromosomes of a dyad during heterotype metaphase not appear as evident?

However, as far as we know, this theory was never explicitly articulated until now. H. Dixon's interpretation (1899, Fig. 17 and 18) is the closest to what the theory should be. However, this author proposed a different explanation for the reduction and the formation of the dyads. The theory would easily explain the events we just described as well as many others, such as figures from Strassburger and Mottier cited in Grégoire 1905.

1° However, we must point out that all the theoretical arguments we developed previously against the "hetero – homeotype" theory, apply here as well.

2° Some spindle arrangements and chromosomal configurations are irreconcilable with this theory. We will briefly mention:

a. The two upper arms oriented in opposite directions of the chromosomes with ***f*** shapes (Schreiner, Fig. 57) cannot result from a longitudinal cleavage;

b. In D-shaped chromosomes, the arms lying on the paunchy (bowed, T.N.) side of the D are often (and this is already visibly at the equator) *far apart from each other*. The longitudinal cleavage theory cannot explain these arm configurations. These are in fact *full* (unsplit, T.N.) *chromosomal segments* that are being pulled by the contracting filaments towards the poles.

§ V.

An intermediate explanation is required

We must admit that *when a dyad enters anaphase* the contracting fibers (spindle fibers T.N.) of the first maturation division move to the poles both *full [unsplit] chromosomal segments* as well as *filaments originating from chromosomes longitudinally cleaved* at the equator. This theory, already emerging from the observations described above, will become more and more evident as more preparations are analyzed and illustrations from various authors revisited. According to us, it is the only one that:

A. accounts for all the figures observed during the *heterotype anaphase*;

B. derives from a rigorous observation of the shape and relationships of chromosomes *within dyads*, and,

C. during the *homeotype division*.

* * *

A. Some features of "heterotype" figures can only be explained with this interpretation. Indeed, we frequently observe chromosomes, which clearly exhibit both characteristics in the same anaphase.

1° Some rings, among those exhibiting the D shape, show on the straight side of the D, ascending filaments (chromatids being pulled to opposite poles, T.N.) that are widely separated and connected at the equator, revealing a clear longitudinal cleavage, whereas on the bowed side of the D, chromosomes remain joined with their ends pointing in opposite directions SCHEMA VI. We believe that most of the E patterns directly originate from these D shapes.

SCHÉMA VI.

Some ***f*** figures of other authors are particularly convincing in this regard (SCHEMA VII, Schreiner 06, I, Fig. 57; Bonnevie 08, II, Fig. Id).

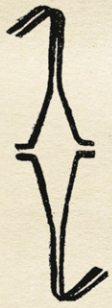


SCHÉMA VII.

The tailed Vs described by Grégoire SCHEMA VIII (Bonnevie 08, I, Fig. 85) appear for us also very illustrative. Here indeed, on the side where chromosomes are free, and where by consequence, if the longitudinal cleavage would be autonomous, the cleavage should be obvious, it is not (Grégoire) or only barely (Bonnevie). In contrast, on the side where chromosomes are still linked together at the equator they are clearly divergent and are contiguous with segments of the dyads that are clearly separated, often similar to geminated/twin buttons.

SCHÉMA VIII

On the side of the *tail, entire chromosomal segments* already cleaved (as any chromosome at the equator during a division) are moved towards the poles, while on the V sides, the jambs are issued from *equatorially cleaved chromosomes* and are pulled to the poles as in a somatic division. Therefore we can say already here, that for each chromosome the division is partially equational and partially reductional.

2° Most ring figures can be interpreted similarly. Dyads generating rings are most often attached to the pulling fibers near the bulge of a strepsitene dyad

SCHÉMA IX.

SCHEMA IX. At this point of the attachment the chromosomal segment is intact (not cleaved, T.N.). However, at late anaphases, the arrangements previously described in §III, 2.a are often observed. It should be noted that these figures are sometimes even more evident and are close to SCHEMA X our FIG. **22**, Schreiner I, 06, Fig. 51, 52, 57 and Foot, Fig. 123, 126. In those cases, a V shaped chromosome is formed at the tip by an intact chromosomal segment, and at each of its free ends, by two filaments resulting from the equatorial cleavage of two chromosomal segments. These are clear observations calling for an obvious interpretation.

SCHÉMA X.

* * *

B. We must emphasize that despite how obvious this interpretation appears, it has never been proposed by any author. Indeed, it appears so irreconcilable with our ideas about the heterotypic prophase that it is tempting to reject it a *priori*.

But we were able to find among our samples and in figures from the literature indications that convinced us that dyads had often not been sufficiently scrutinized and that they are still holding some secrets. We even believe that we have discovered some of the secrets. Are we being presumptuous? Time will tell.

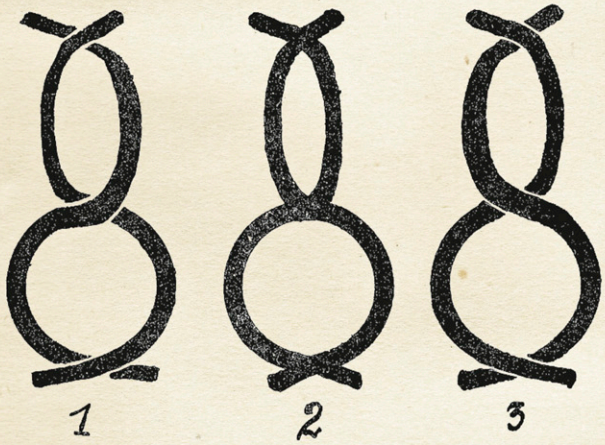
But first, a comment about the structure of somatic chromosomes: are these chromosomes really indivisible units? We do not know with certitude, but for a long time some evidences have made us doubt. In 1901, we pointed out the existence of split chromosomes during metakinesis (Plate II, Fig. 70). Similar observations have since been made elsewhere, but no one ever characterized the origin or the significance of these events. In addition, in many cases, some chromosome sections appear more resistant to perturbations acting during the resting period between two divisions (ibid.). It is therefore unlikely that the structure and properties of chromosomes are uniform along their lengths. Chromosomes exhibit positions of lower resistance; they are probably divided into units or segments.

1° Concerning *dyads in rings*, it is generally accepted that the chromosomes that constitute these rings are subjected to a secondary *connection* at their *two extremities*. We think that it is necessary to *extend* this observation

to most of the locations where the two chromosomes of a dyad come into contact. This is so systematic that it is extremely difficult to say which of the two chromosomes involved in a strepsinematic chiasma is located above or under the other. Anyhow *at these sites the chromosomes more or less co-penetrate one another*.

2° It even happens that sometimes no technical solution can help resolving this structure, not even with the help of an immersion binocular microscope, which otherwise renders great services. The four chromosome ends that come together converge towards the same point. Moreover, at these positions, a clear space is often observed, very similar to those we had described in somatic chromosomes (FIG. **4**, **6** and **12**). It thus becomes extremely difficult to predict the original organization of the chiasma, especially because the converging chromosomal segments that meet there are usually not bent in the same plane. The disposition is generally the following: the segments from one loop are disposed in a plane perpendicular to that formed by the adjacent loop. This disposition can result in either a left- or a right-handed winding. By the end of dyad development it usually becomes very difficult to distinguish one disposition from the other.

The stereoscopic SCHEMA XI gives an idea of the appearance of such dyads when observed through a binocular microscope.



SCHEMA XI: (superimpose FIG. 1 on FIG. 2 and 2 on 3) (a tentative to depict the stereoscopic image as seen by the author T.N.)

3° These two observations prove that the two chromosomes in a chiasma are at least partly inter-penetrated. They are sufficient to explain the secondary fusions that we have often observed between the filaments of these chromosomes when the cleavage becomes evident, *i.e.* during the late heterotype prophases. At the chiasma level, especially when the fixation treatment was particularly good and the staining not too intense (1), one can often see one of the two filaments passing from one loop to the other without a chiasma, whereas the two others intersect (SCHEMA XII; FIG. **1**, **2**, **8**, **9**, **10**, **11**, **13**, **14** and **15**).

We think that in this case the filaments that cross are those that are further apart, i.e. which occupy those parts of the chromosomes that do not co-penetrate. The filaments that remain unconnected by a chiasma, on the contrary, are those that have undergone a secondary connection at the sites where the chromosomes have inter-penetrated and fused. The series of stereoscopic SCHEMAS XIII, XIV AND XV reveal the gradual inter-penetration of two chromosomes at the level of a chiasma, with fusion of the two filaments that touch each other first. These illustrations exempt us, at least we hope, from long and tedious descriptions.

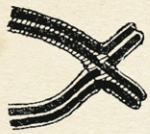


SCHÉMA XII.

Several authors have observed figures similar to ours, and have reported them without interpretations. Most notably note Fig. 119 of Misses K. Foot and E. Strobell, and Fig. 11 of Mc Clung, both reproduced in PLATE II.

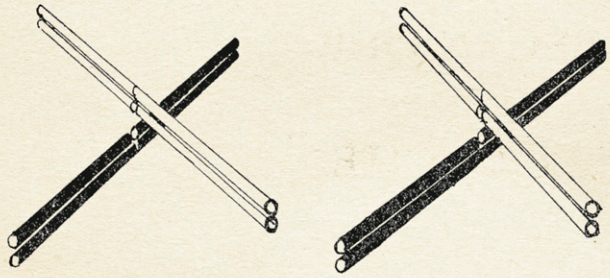


SCHÉMA XIII.

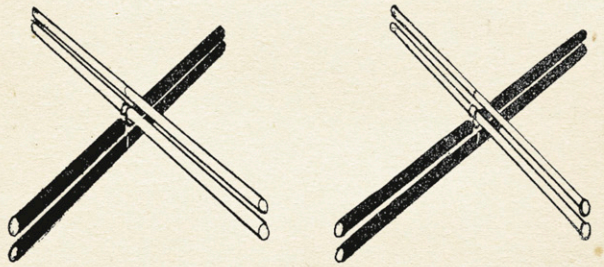


SCHÉMA XIV.

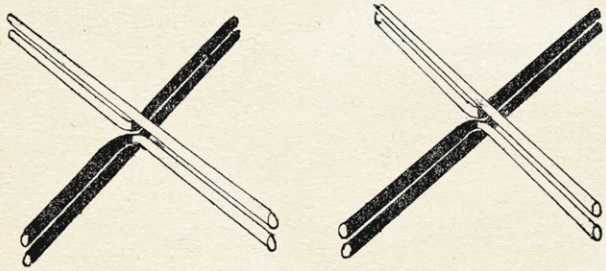
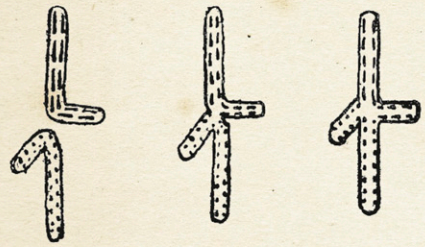


SCHÉMA XV.

4° When chromosomes of a dyad do not intersect, analogous facts can be observed. We believe, *without having had the opportunity to confirm it* yet that X shapes with equal or unequal arms and with a brighter cross in the middle must be interpreted analogously. According to us, these crosses must result from two squares fused by their edges. This idea is likely present in de Sinéty's work (Fig. 106a and our PLATE II). However, it is especially the photography 116 of Misses K. Foot and E. Strobell (that we tried to

reproduce without losing too much of its natural character) that corroborates our idea.

SCHEMA XVI illustrates what happens, according to us, in similar cases. This is likely also true for the crosses with unequal arms found in *Tomopteris* spermatocytes, according to Mr. and Mrs. Schreiner (Plate II, Fig. 43, 44, etc.), which will very likely generate ***f*** chromosomes at "heterotype" anaphases.



SCHEMA XVI is related to FIG.116 of K. Foot and E. Strobell.

In conclusion, the process is similar to the case of strepsitene chromosomes. There is inter-penetration of two chromosomes and secondary fusion of the filaments at this position.

5° In the example described above in 2), we believe that both filaments can undergo a secondary fusion and as a consequence destroy (resolve, T.N.) the chiasma. In such case a full chromosome will be split into two segments that will fuse to the segments from its partner and consequently generate *new combinations of [whole] chromosomal segments*. For example, if a chromosome containing segments A and B, is associated in a dyad with a chromosome containing segments a and b, after breakage and secondary fusions, the dyad will be composed of chromosomes A*b* and a*B*. This proposition is fully supported by observations of complete splitting at chiasmata. Such splits are usually visible only in highly stretched dyads and for one or the other of the chiasmata located in the middle of the dyad. Sometimes, when the modified loops are clearly in the same plane, the disposition corresponds to the drawings of SCHEMAS XVII AND XVIII, depending whether the dyad is straight or has maintained a curved conformation, respectively.

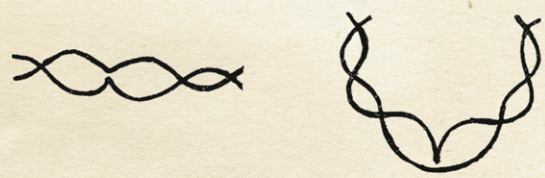


SCHÉMA XVII et XVIII.

But very often the two loops that have undergone these breakages followed by secondary fusions form a right angle in respect to each other, generating very complicated figures whose structure can only be resolved with the help of a binocular microscope (stereoscopic SCHEMAS XIX AND XX).

The event described here is not very common according to our observations; indeed, at the location of the split there are often small bits, delicate to analyze, but which could well be the two filaments in a chiasma disposition, which would bring us back to point 4.

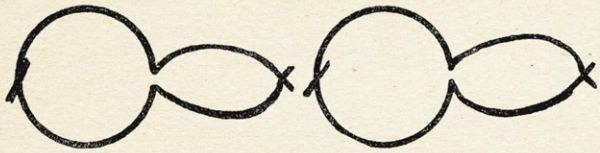


Schéma XIX.

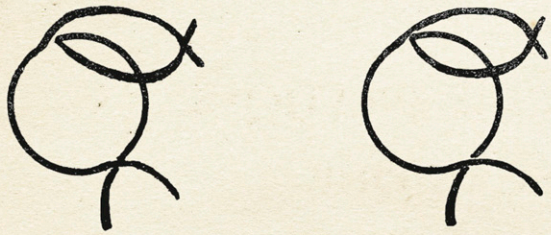


Schéma XX.

Addressing this issue will only be possible through, and will always necessitate ideal fixations on very favorable samples.

* * *

C. As shown in this brief statement, interactions between chromosomes in dyads are far from being as simple as believed until now. When chromosomes are in contact with each other at chiasmata sites, which according to us, is the rule, we do not think that they remain independent. Their filaments are involved in contacts that can modify their organization from one segment to the next. This will generate new segmental combinations, which will be different for the two filaments of a same chromosome (see B.3 and B.4 above), or which can affect the entire chromosomal segment (B.5).

Before considering the consequences of these observations on the understanding of "heterotypic" anaphases, and particularly the shape of "homeotypic" chromosomes during the prophase of the second maturation division, we wish to make a *comment*.

According to our new comprehension, the first maturation division, which we will temporarily keep calling "heterotype", is an ordinary division in regards to chromosomal longitudinal cleavage. This cleavage is achieved for all chromosomes when they are attached to the spindle as in an ordinary somatic mitotic division.

Concerning the spindle positioning itself, we think that the "heterotype division" differs considerably from a somatic mitotic division. The active fibers (microtubules, T.N.) of the amphiaster do not usually attach to each of the two filaments (chromatids, T.N.) constituting a chromosome as during a somatic mitosis, but to the whole chromosome.

In this case, the attachment usually occurs in the middle of a loop.

However, the attachment site can also be positioned as during an ordinary division and then occurs preferentially where a knot/chiasma is formed.

Now we should analyze what can happen for a dyad exhibiting a loop, a knot, and on one side of the loop two free chromosomal ends. For one of the chromosomes, we will call A the segment encompassed within the loop, and B the free end, whereas a and b will represent the corresponding parts of the other chromosome, respectively SCHEMA XXI. First we will assume, according to our proposal in B.3, that the chiasma involves only one of the two chromosomal filaments. This will lead to SCHEMA XXII.

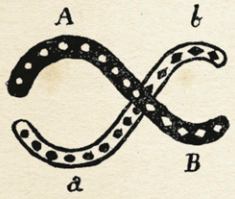


SCHÉMA XXI.

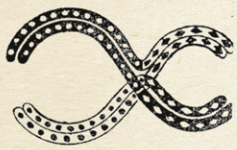


SCHÉMA XXII.

During anaphase, dispositions similar to those in FIG. **17**, **18**, **24**, **30**, **31**, etc. will emerge. They can be interpreted using a schematic representation similar to the one in Mr. and Mrs. Schreiner, 1905-1, but whose significance is now, according to us, entirely different SCHEMA XXIII.

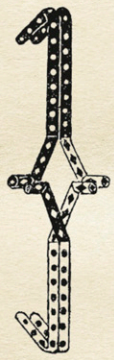
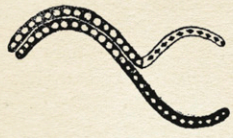


SCHÉMA XXIII.

Spermatocytes II nuclei will contain chromosomes showing a segment made of clearly parallel filaments, but with diverging ends (SCHEMA XXIV and FIG. **41a** and **b**, **40**, **47**, **48**, **50**, **51** and **52**). The upper panel of the schema shows that the *complete* A segment contains halves of the b and B segments; in the lower panel, the *complete* a segment contains halves of the B and b segments. Therefore, the first division is reductional for segments A and a, and equational for segments B and b.



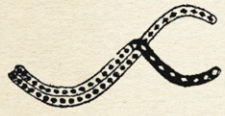


SCHÉMA XXIV.

We notice that the second division, or "homeotype", will also be partly reductional for B and b, and partly equational for A and a. The four resulting spermatids will carry, for this particular chromosome, 1° AB, 2° Ab, 3° ab and 4° aB. Therefore the four gametes within a tetrad will be different.

Now let us assume that, at the site of a single knot or at several knots (an uncommon event that can however happen), the chiasma is kept for neither of

the two filaments, as described in B.5. In such a case, entire chromosomal segments will fuse together, with one chromosome in the dyad now made of Ab and the other of aB SCHEMA XXV. In this case, the first division will be reductional and the second equational and the four spermatids within a tetrad will carry 1° Ab, 2° Ab, 3° aB and 4° aB. Consequently, the reduction will not be as powerful.

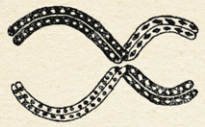


SCHÉMA XXV.

In that second case, the attachment to the spindle at the first maturation division occurs preferentially at a knot and therefore divides chromosomes along their length. We then obtain pictures similar to FIG. **20**, whose interpretation is very close to SCHEMA XXVI.

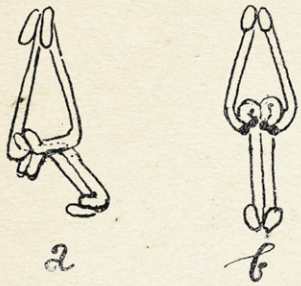


SCHÉMA XXVI,
is related to our FIG. 20.

* * *

Our theory provides a natural and obvious explanation for many of the chromosomal arrangements observed during homeotype prophases that were not explained by the "hetero-homeotype" theory.

This is the case, for example, for the prophase of FIG. **39** (as well as **44**, **46** and **49**). It represents a "homeotype" dyad likely issued from a "heterotype" dyad similar to the one of FIG. **7**, where the chiasmata would have been suppressed. It is therefore an illustration of the event described in B.5, according to SCHEMA XXV AND XXVII, N°1.

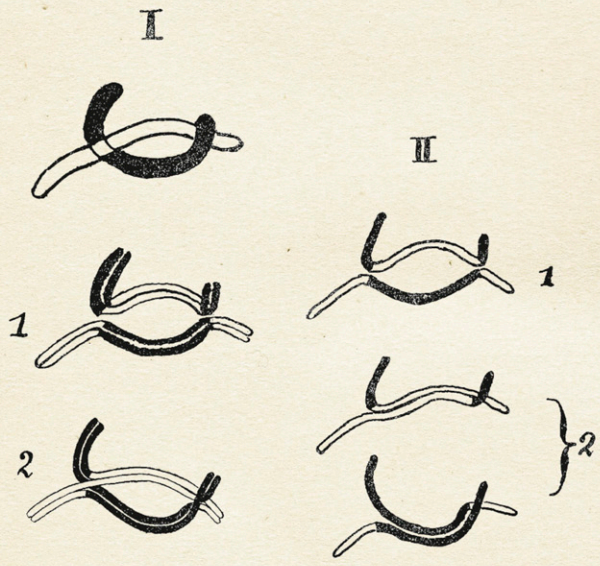


SCHÉMA XXVII.
I, heterotypic prophases; II, homeotypic prophases.

However, in FIG.7, both in its middle and at the extremity, one of the filamentous chiasma is resolved whereas the other is not. This indicates that any of the combinations (2° or 1°) is possible and that the dyad of FIG. **7** can provide

homeotype chromosomes with very different shapes and significance, but with a central part made of an entire chromosomal segment and with the extremities made of filaments coming from different segments according to SCHEMA XXII, XXIV AND XXVII, 2°. This last schema explains both "heterotype" prophase (FIG.**7** and many others), and "homeotype" prophases (FIG. **40**, **50**, **51** and **52** as well as **41a** and **b**).

§ VI.

This solution satisfies all observations and theoretical requirement.

We think that our theory can explain clearly all configurations, even the most complicated ones, observed during the spematogenesis of batrachians. It is even strengthened by the fact that it accounts for all the details that were irreconcilable with all of the other theories. We propose to name it:

The chiasmatype theory

1° This theory especially provides a clear explanation for the figures seen during anaphases of the first maturation division, which are so embarrassing for the "heterotype theory" (FIG. **17**, **18**, **19**, **20**, **21**, **22**, etc.)

2° Only this theory can explain and account for the *otherwise completely inexplicable interweavings* observed between the filaments which segregate to one of the poles during the heterotype anaphases, whereas the filaments pulled towards the other pole remain completely parallel, FIG. **17**, **18**, **19** (**31**) and, more particularly, the clear and beautiful FIG. **33**.

3° The "heterotype" division now appears as an ordinary division as far as longitudinal cleavage of chromosomes is concerned.

4° The theory explains the most "extraordinary" figures observed during the "homeotype" prophases and anaphases.

5° It provides a very simple interpretation of the strepsinema stage, which otherwise remains an enigma.

6° It outlines the meaning of chromosome conjugation (synapsis, T.N.), which, likely already during the pachytene stage, brings pieces of chromosome segments into connection in preparation for strepsinema.

7° It explains the 'raison d'être' of *two* maturation divisions, both of them being potentially reductional.

8° The theory allows us to understand the existence of the tetraspore.

9° It opens the way to a broader cytological application of Mendel's theory.

(1) Samples were fixed in the Carnoy solution and stained gently according to Heydenhain

BIBLIOGRAPHY

DE SINETY, R., 1901 Research on biology and anatomy of Phasma (Recherches sur la biologie et l'anatomie des Phasmes). La Cellule, **19** (1).

GREGOIRE, V., 1899 Spore-mother cell cinesis/division in *Liliaceae* (Les cinèses polliniques dans les Liliacées). La Cellule, **16** (2).

GREGOIRE, V., 1905 Results on maturation cinesis in the two kingdoms (first volume) [Les résultats acquis sur les cinèses de maturation dans les deux règnes (premier mémoire)]. La Cellule, **22** (2).

JANSSENS, F.A., 1901 Spermatogenesis in Triton species (La Spermatogenèse chez les Tritons). La Cellule, **19** (1).

JANSSENS, F.A., and R. DUMEZ, 1903 Maturation cinesis in *Batracoceps* attenuatus et *Pletodon cinereus* (Cinèses de maturation du *Batracoceps* attenuatus et *Pletodon* cinereus). La Cellule, **20** (2).

JANSSENS, F.A., and G.A. ERLINGTON, 1904 Maturation division in *Aplysia punctata* egg (Divisions de maturation dans l'oeuf de l'*Aplysia punctata*). La Cellule, **21** (2).

MC CLUNG, C.E., 1903 The Spermatocyte divisions of the *Locustidae*. The Kansas University Science Bulletin, 1, sept 1902.

MOTTIER, D.M., 1903 The Behavior of the Chromosomes in the spore mother cells of Higher plants (etc). Bot. Gaz. **35**.

KOWALSKI, J., 1904 Reconstitution of the nucleus and chromosome formation during somatic cinesis/division of Salamander larvae (Reconstitution du noyau et formation des chromosomes dans les cinèses somatiques de la larve de salamandre). La Cellule, **21** (2).

STRASBURGER, E., 1900 About reduction division, spindle formation, Centrosome and cilia/flagella morphogenesis in the plant kingdom (Ueber Reductionsteilung, Spindelbildung, Centrosomen und Cilienbildner im Pflanzenreich). Iena.

VEJDOVSKY, F., 1907 New studies on maturation and fertilization (Neue Untersuchungen über die Reifung und Befruchtung). Königl. Böhm. Ges. D. Wiss., in Prag.

SCHREINER, K.E., and A. SCHREINER, 1905 New studies on chromatin maturation in germinal cells, vol. I (Neue Studien über die Chromatinreifung der Geschlechtszellen I). A. de Biol. **22**.

FOOT, K., and E. STROBELL, 1905 Prophases and metaphase of the first Maturation Spindle of *Allolobophora foetida*. The Amer. Journ. of Anat. 4.

BONNEVIE, K., 1907 "Heterotypical" mitosis in *Nereis limbata*; Biol. Bull. **13**.

BONNEVIE, K., 1908 Chromosomal studies II (Chromosomenstudien II). Arch. F. Zellforschnung, **2**.

DIXON, H., 1899 On the first Mitosis of the Spore-Mother cells of *Lilium*. Royan Irish Academy, Dec 11.

LEGENDS OF THE SCHEMAS

SCHEMA I: We will in this note call *dyads* a couple of chromosomes at the strepsinema stage just before their attachment to the spindle. SCHEMA I *dyad*. C, *chromosomes*. We call filaments F the two sister-chromosomes (chromatids T.N.) issued from a longitudinal cleavage of chromosome F. The site N where the two chromosomes of a dyad cross is called *chiasma* or *knot*; B is the *loop* or *inter-node* formed by the *two* chromosomes between two knots; finally, a *segment* is the part of *one* chromosome included between two *knots* or *chiasmata*.

SCHEMA XI: (superimpose FIG. 1 on FIG. 2 and 2 on 3) (a tentative to depict the stereoscopic image as seen by the author T.N.)

SCHEMA XVI is related to FIG.116 of K. Foot and E. Strobell.

SCHEMA XXVI is related to our FIG. 20.

SCHEMA XXVII: I, heterotypic prophases; II, homeotypic prophases.

FIGURE LEGENDS

Figures were drawn using an *ABBE's camera lucida*, at the level of the working table; the microscope was equipped with a *WINKEL* fluorite objective with a focal distance of 1.4 mm and with a corrected ocular 5 from *WINKEL* except for FIG. **17** and **18**, which were drawn with an ocular 4, and FIG. **9**, **10**, **11**, **14**, and **22** for which we used *WINKEL's* ocular 6; FIG. **15** and **16** were drawn using the corrected ocular 18 from *ZEISS*.

Triton cristatus.

Fig. **1**, **2**. Dyads right after the nuclear tension stage (prometaphase T.N.) (Janssens, 1901). Chromosomes appear stiffer in the drawing than they are naturally. Chiasmata are often more evident than in the drawings.

Batracoseps attenuatus.

FIG. **3**. Part of a very elongated strepsitene dyad.

FIG. **4**. Slightly later stage. At the right knot, the chiasma is clearly maintained for one of the filaments and not for the other. For the latter, the secondary fusion already occurred at the bottom but not yet at the top, § V. B 3°.

FIG. **5**. Part of a dyad with a knot. Chiasma is resolved for one of the filaments.

FIG. **6**. Dyad at a more advanced stage.

FIG. **7**. Dyad at a slightly earlier stage than in FIG. 6, see p. 404 (of original paper N.T.)

FIG. **8**. Dyad right before spindle attachment. Left, entire chromosomes, right the chiasma is resolved for half of the filaments.

FIG. **9**, **10**, **11**. Dyads at the same stage: in the middle the chiasma is resolved for half of the filaments.

FIG. **12**. Knot in a dyad with interrupted filaments; this will probably lead to the complete elimination of the chiasma.

FIG. **13**. Very nice dyad, case of § V, B 3° seen at each knot, *i.e*. the chiasma is resolved for half of the filaments.

FIG. **14**. This dyad clearly shows the partial resolution of the chiasma at the three knots. These kinds of dyads likely generate anaphases like those seen in FIG. **24**, **25** and **29**.

FIG. **15**. Extremity of a dyad during attachment to the spindle, see p.400 (of original paper T. N.)

FIG. **16**. Dyad partly cut by the razor blade and located at the external border of a fragment fixed with Carnoy's fixative (absolute chloroform, alcohol and acetic acid in equal quantities and sublimated until saturation). The fixation is slightly too harsh on the right side but seems perfect on the left side which is the most internal one. The drawings were made from dyads found more or less at this distance from the cut but a bit deeper.

FIG. **17** to **38**. Anaphases from the first maturation division.

FIG. **17**, **18**. Two dyads in anaphase, illustrating the discussion of pages 397 and 403 (of original paper T. N.). One can see that the chiasma is maintained only on one side of the filaments moving to the pole, see SCHEMA XXIII.

FIG. **19**, **20**. At the equator, the filaments are still intermingled. The strong staining hinders a clear interpretation at this stage.

FIG. **21**. At anaphase, the two left filaments end into spherules indicated here by their contours.

FIG. **22**. See page 398 (of original paper T.N.)

FIG. **23**. Bottom, tailed *V*. At the equator, the ends of the filaments are not associated as predicted by the 'heterotype' theory, but are intermingled, SCHEMA IVb.

FIG. **24**. The equatorial part of the dyad is very complex. The interpretative drawing is truly objective and certain. We have linked by dotted lines the filaments that, we assume, were parallel in a loop already resolved by moving to the pole. The ends of the filaments at the equator are associated as pairs: one vertical on the left, the other horizontal on the right. We think that such anaphase is issued from a dyad similar to the one described in FIG. **14**.

FIG. **25**. On the left of the associated filaments two are distant from each other but remain located at a same level; on the right, complicated but clear intermingling of filaments, which indicates a longitudinal cleavage.

FIG. **26**. The ascending filaments produce two clearly distinguishable knobs.

FIG. **27**. In the short arms of the double Vs in anaphase, the chiasma is maintained at the upper pole, but not at the lower pole; it is the opposite for the long arms.

FIG. **28**. Similar to FIG. **26**.

FIG. **29**. Similar to FIG. **25** for the arms still connected at the equator.

FIG. **30**. Anaphase analogous to FIG. **17** and **18**, but at a later stage.

FIG. **31**. Very well preserved dyad by the preparation, but difficult to draw because the pairs of filaments that are intermingled at the equator are positioned within different levels. Those segments must be issued from a longitudinal cleavage. In the short arms of the chromosomes, a chiasma is present at the lower pole but not at the upper pole.

FIG. **32**. The lower part of this dyad (short arms of the double Vs in anaphase) has been stripped off by the razor blade. For the long arms, two of the filaments reaching opposite poles are still linked at the equator level and parallel.

FIG. **33**. Very clear dyad. At the upper pole, the ascending filaments are parallel; at the lower pole, two chiasmata are visible.

FIG. **34**. The shaded filaments are in a plane located slightly above those only drawn by their outlines.

FIG. **35**. The filaments of the long arms of the double V are intermingled, see SCHEMA IVb.

FIG. **36**. Later anaphase with a similar arrangement and closer to the next figures.

FIG. **37**, **38**. V with three polar arms and one equatorial arm, see p. 393.

FIG. **38**. Note the parallelism of the 2 arms touching each other at the equator.

FIG. **39** to **52**. Prophases from the second maturation division.

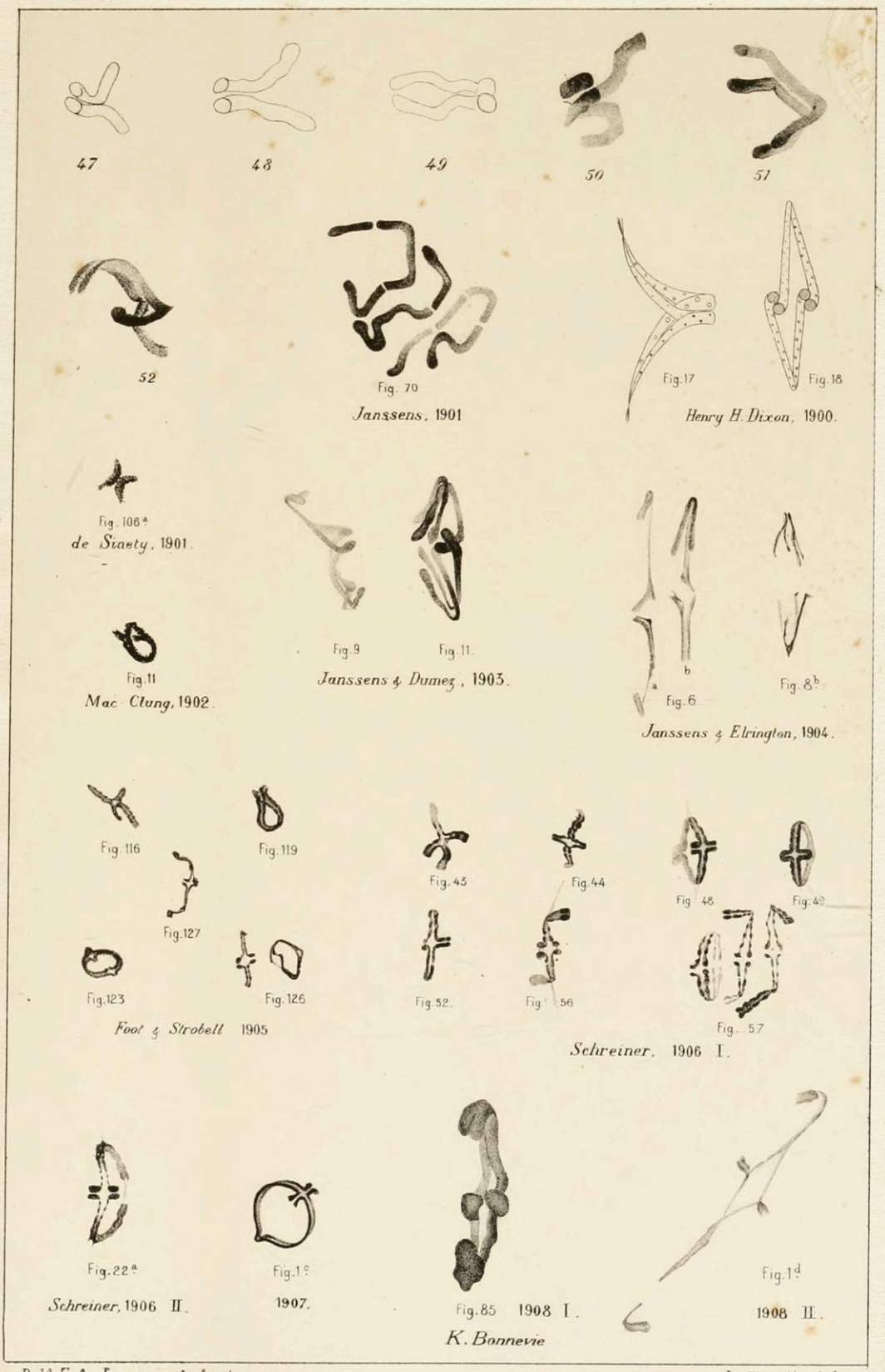
FIG. **39**, **40**. Early prophases.

FIG. **41** to **52**. Dyads during spindle attachment, see p. 402 and following pages (of original paper N.T.)

The figures reproduced from other authors are given with their respective names and year of publication, as well as with the numbers published in the original paper.

Plate I

Plate II



Appendix

Sealed document deposited in 1908 at the Royal Academy of Belgium

F. A. Janssens, Professor at the University de Louvain. April 9th 1908

The interpretation of maturation divisions ("cineses") as it was originally described by Flemming and after long discussions admitted for plants by Strassburger, Guignard and Grégoire, and for animals by most authors and especially M. and Ms. Schreiner and myself, can no longer be retained.

The demonstration of this proposition relies upon a series of observations that I will publish soon and which can be organized as follows.

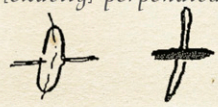
A *The hetero-homeotype theory is scarcely likely to be true.*

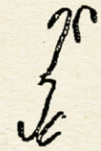
1°) According to this theory, only one of the two maturation divisions is needed for reduction. For the authors cited above it is the first one. The second division has no significance within this theory. The phenomenon could be restricted to the formation of spermatocytes II and everything would be completed. In reality there is an additional division very characteristic whose peculiarities have not been identified so far by experimentalists.

2°) During the heterotypic polar segregation a) the arms of the double V that should result from the longitudinal cleavage of anaphase chromosomes are very often widely separated. This observation is not compatible with the cleavage theory. b) This latter could not have occurred at that time because of the exertion of the contracting fibers (spindle fibers, T.N.), which would tend to join together these elements [to be illustrated with original figures and figures from other authors].

3°) During spindle positioning the rings already formed during the earlier stages are closing up and the two chromosomes are now closer. This kind of synapsis [fig.] has no "raison d'être" within the theory cited above.

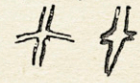
4°) The two intertwined branches, which are not yet under the pulling force of the contracting filaments, are always within a plane [exactly] perpendicular to the plane formed by the ascending filaments and the spindle filaments.





5°) C-shaped chromosomes often show shapes that contradict the theory. It is unlikely that these two branches result from the longitudinal cleavage of a unique chromosome.

B *But there is more. The theory is not possible.*

1°) The relationship between the two elements resulting from the supposedly longitudinal cleavage of anaphase chromosomes is in contradiction with figures like those of  *and also from [other] authors.*

2°) Very often at a chiasma site the two filaments (arms) coming from one side are located internally in comparison with the two other filaments coming from the other side 

3°) Often also like 

C A theory implying the longitudinal cleavage of each chromosome at the equator during heterotype metaphase appears evident. e.g. Dixon.

Such theory is more in agreement with the general laws of the divisions but has against it:

1°) The same improbability that A. 1). Only the homeotype division would be reductional.

2°) Some spindle arrangements cannot be interpreted by this way and make this theory impossible. 

D The only option is to accept an intermediate solution.

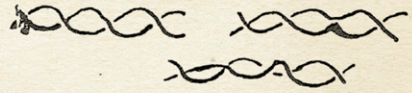
1°) Fig.  likely relevant for all the 6-shapes.

2°) It applies also for most of the rings  splendid fig. In addition the spindle positioning is undoubtedly like in  ; the middle loop is in the plane of the paper, the surrounding loops are in a plane perpendicular to the paper]. At the center the chromosome is undoubtedly intact and if it is cleaved later the two sides are the two longitudinal halves of a same chromosome. In the following loop the cleavage is different  very beautiful figure.

E How can such a "manege" be explained?

1°) Credibility is conferred (to this manege) because it provides a "raison d'être" for the coiling of chromosomes which (otherwise, T.N.) remained inexplicable. It is at the contact sites between coiled chromosomes that, according to my explanation, the secondary fusions take place [fusions between segments of either full chromosomes or of already cleaved chromosomes].

2°) It is undeniable that true fusions take place at these sites [fig. authors]. These fusions are beyond doubt in stereoscopic observations.

3°) During more advanced stages, coils have sometimes very strange shapes that can be easily explained by intimate connections between chromosomal segments.  ; when seen from one side it shows this shape.

4°) The very clear figures  and others [to be published], which explain the change in fusion between two halves of a chromosome. Can very easily be explained through stereoscopic views. This theory explains all the shapes even the most complicated ones.

F Theoretical considerations.

1°) My theory confers a reductional dimension to both, the hetero- and homeotype divisions.

2°) It successfully fulfills all the gaps left by other theories concerning the applications of Mendel's laws.