GENOMANALYSE IN THE HYBRID OF TRITICUM DICOCCUM SCHRNK. X AEGILOPS VENTRICOSA TAUSCH

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Resumen

Análisis de los genomios en el híbrido de *Triticum dicoccum* × *Aegilops ventricosa.*

El autor realizó el análisis de los genomios del hibrido de *Triticum dicoccum* Schrnk. × *Aegilops ventricosa* Tausch. Las observaciones descriptas indicarían que uno de los genomios de *Ae. ventricosa* es homólogo con un genomio de *Tr. dicoccum*. Además algunos cromosomas de otro genomio de *Ae. ventricosa* se aparean con cromosomas de *Tr. dicoccum*.

Los bivalentes forman anillos, el apareamiento es a menudo telosindético. Algunas geminis son heteromorfas.

El segundo genomio no es pues homólogo, porque su apareamiento es parcial. La distribución de los cromosomas responde al comportamiento de los genomios en la meiosis.

En base a las observaciones es necesario supervisar la relación citosistemática entre *Ae. ventricosa* y *Tr. dicoccum*.

No es discutible que el *Tr. dicoccoides* suministró sus genomios AB en los ensayos clásicos de Mc Fadden y Sears (1946) para la síntesis de *Tr. spelta*. Resultaría de esto que la separación cito-taxonómica de *Tr. dicoccum* de los otros miembros de la serie de Emmer presenta contradicciones bien fundadas.

Es más probable que sea necesario modificar la fórmula de *Ae. ventricosa*. El genomio D no es disputable por tener muchos análisis entre los genomios de la sección *Pachystachys*. Posiblemente tenemos que revisar el genomio M cambiándole por uno de los genomios (A o B) de *Tr. dicoccum*.

Es necesario recalcar que *Ae. ventricosa* difiere en su distribución geográfica de los otros miembros de la sección *Pachystachys*.

Esto apoya también los datos arriba mencionados de que la posición citosistemática de *Ae. ventricosa* necesita modificarse.

The value of the methods used when analysing genomes, was seen principally in the result of the investigations with species of *Triticum* and *Aegilops* leading to a knowledge of the origin of tetra- and hexaploid wheats.

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The coincidence existing between taxonomic and cytological work is illustrated by the fact that the genealogical tree sketched by Schulz in 1913 for the systematics of the genus *Triticum* maintains its value still.

The earlier analysis between the distinct species of *Aegilops* and *Triticum* did not give concomitant results as to the origin of the wheat, although the value of this new orientation showed itself clearly. Sax (1922, 1923), Bleier (1921, 1930), Kihara (1919, 1920).

The subsequent work, conscientiously done by Kihara, Sears, Sax & others, eliminated the greater part of the controversy. To-day we see clearly some of the most important chapters of the origin of wheat, Kihara (1929, 1937), Kihara-Lilienfeld, (1934-35, 1949), Berg (1937), Kostoff 1936 a, b,) Longley-Sando (1930), Love (1938, 1940, 1941, 1943), Matsumura (1939), Nikolaeva (1922), Pathak (1940), Percival (1930), Popowa (1938-39), Sax (1922, 1923, 1924), Scharman (1944), Schiemann (1929, 1932), Tschermak (1929), Sears (1939 a, b, 1944, 1948), Mc. Fadden & Sears. (1946 a, 1946 b,).

In 1940, Kihara published the genomic formulas of 21 *Aegilops* species. Based on this result he constructed a cyto-systematics which is for the greater part the same as Zhukovsky's classification. Later on Kihara & other Japonese authors modified some of the formulas, exchanging the genome of the *Pachystachys* section for the denomination D. (*Pachystachys* = Vertebrata section).

Following this, they separated *Tr. timopheevi* and *Tr. armeniacum* from the other tetraploid wheats, changing the genome D for the new denomination G. Lilienfeld-Kihara (1934-35), Love (1941), Popowa (1938-39).

According to our recent knowledge of the cyto-systematics the formula of the hexaploid wheats is ABD, of the tetraploids AB, except *Tr. timopheevi* and *Tr. armeniacum*.

The members of the section *Pachystachys* are: *Ae. crassa* Boiss. (DJ), its hexaploidform (DJ † ?), *Ae. squarrosa* L. (D) and *Ae. ventricosa* Tausch. (DM). The formula of *Ae. juvenalis* (Thell.), still unknown.

In addition, *Ae. cylindrica* Host. contains also genome D which belong to the section *Monoleptathera*.

The karyo-idiogram of *Ae. ventricosa* contains according to Senjaninova-Korzagina (1932), 7 submedian, 4 subterminal, 2 median with unequal chromatids on a side and one SAT chromosome with a trabant. Its area extends from the coasts of oriental Africa to the coasts of the Mediterranean sea in Europe, whilst *Ae. crassa* and *squarrosa* are Asiatic species.

In spite of their different geographical distribution, they belong to the same section containing the same genome D. During the last ten years, with application of colchicin, they have begun to effect the synthesis of new alloploid species.

The artificial alloploids furnished important proofs for the study of the origin of the wheats.

Since we know the *Galeopsis tetrahit* artificially produced by Müntzing, — we have the first direct proof of the rising of a natural species.

Tschermak & Bleier (1926), Tschermak (1929-930) were the first to obtain artificial alloploids, denominating them *Aegilotriticum*. This thought out work resulted in a series of distinct alloploids between *Aegilops* x *Triticum* and *Triticum* x *Triticum*. The most prominent result of this new orientation of synthetic work was the artificial *Tr. spelta*.

Thomson, Britten, Harding (1943) obtained crossings between *Tr. turgidum* x *Ae. speltoides* as well as Sears obtained *Tr. dicoccoides* x *Ae. speltoides* hexaploid species. But these new hexaploids did not ressemble any known natural species. Nor did the backcrossing with *T. vulgare* give a complete homology with the mentioned species.

Sears (1944) obtained amphidiploids in crossing *Ae. cylindrica* x *Tr. durum* and *Ae. ventricosa* x *Tr. durum*. Crossing them back with *Tr. vulgare* he was able to prove that only *Ae. cylindrica* contained the genome C. *Ae. ventricosa* did not really show a "homology", only a "homoeology".

Oehler (1934) between *Ae. caudata* x *Tr. dicoccum* and Sorokina (1928), between *Ae. longissima* x *Tr. durum, (Ae. ventricosa* x *Tr. dicoccum)* x *Tr. dicoccum* and *Ae. vent.* x *Tr. durum* obtained hexaploids. But it is not possible to deduce the origin of *Tr. spelta* or *vulgare* from this result for the only example resembling *vulgare* is probably the product of spontaneous fecundation of one pollengrain belonging to *Tr. vulgare*.

One of the most interesting artificial species among various alloploids is *Ae. triuncialis* (C^uC) which could have been

synthetised (Sears 1941) from the genomes of two distinct natural species. The genome C comes from *Ae. caudata* and the genome C^U from the *Ae. umbellulata.* (Kihara's classific.)

The synthesis of the *Ae. cylindrica* Host by Mc Fadden-Sears (1944) was equally obtained. Its genome C originates from *Ae. caudata* and its genome D from *Ae. squarrosa.*

According to Kihara & Lilienfeld (1944, 1949), a new alloploid species was produced, much ressembling *Tr. spelta* in its gametas without reduction, from a crossing of *Tr. dicoccoides spontaneum nigrum* x *Ae. squarrosa.* This was confirmed by the classical work of Mc Fadden & Sears (1946), who at nearly the same time began the artificial synthesis from the genome of *Tr. dicoccoides* v. *spontaneovillosum* and *Ae. squarrosa.*

These authors were successful in obtaining an artificial synthesis of *Tr. spelta* and consequently the genome D of *Ae. squarrosa* is identical with the genome D of hexaploid wheats.

Kihara & Matsumura (1940-41) showed by backcrossing, that genome C of *Ae. caudata* is perfectly interchangeable with the genome C of *Ae. cylindrica.* This constitutes a confirming proof of the existence of complete homology.

According to a personal communication, Kihara & Matsumoto and Kondo have synthetised a plant quite similar to *Aeg. ventricosa* from the crossing of *Ae. squarrosa* with *Ae. uniaristata.*

Therefore, among the thirteen known alloploids, all derived from the crossing of *Aegilops* x *Aegilops,* three seems to lead to the synthesis of natural species.

The cyto-systematical position of Tr. dicoccum Schrnk. and Ae. ventricosa Tausch

The already known genome-analytical data concerning *Tr. dicoccum* and *Ae. ventricosa* can be found in the following sketches. (see Tab. 1 and 2.)

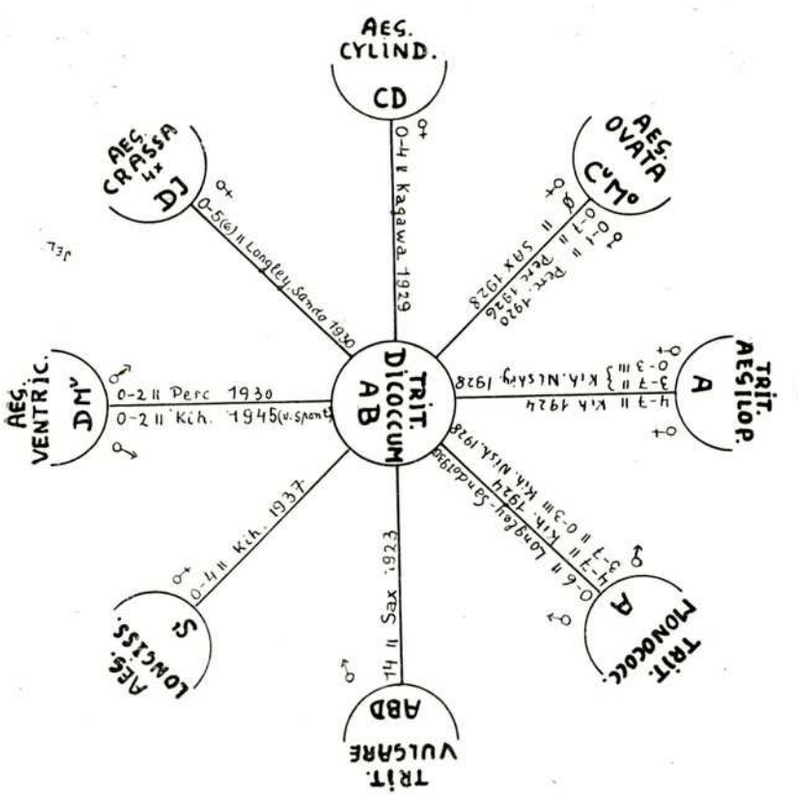
Table Nr. 1. — shows us that *Tr. dicoccum* has just like the other members of the series of Emmer homologous genome with *Tr. aegilopoides, monococcum* and *vulgare.*

As we see from table Nr. 2., *Ae. ventricosa* contains one genome (D) homologous with all the members of the section of

Pachystachys (Ae. squarrosa, Ae. crassa). Ae. ventricosa has besides one homologous genome (D) with *Ae. cylindrica* and one with *Ae. ovata* (M).

Other crossings with other species have shown us in meiosis some bivalents variable in their numbers, very often in telosyndetic and in ringform.

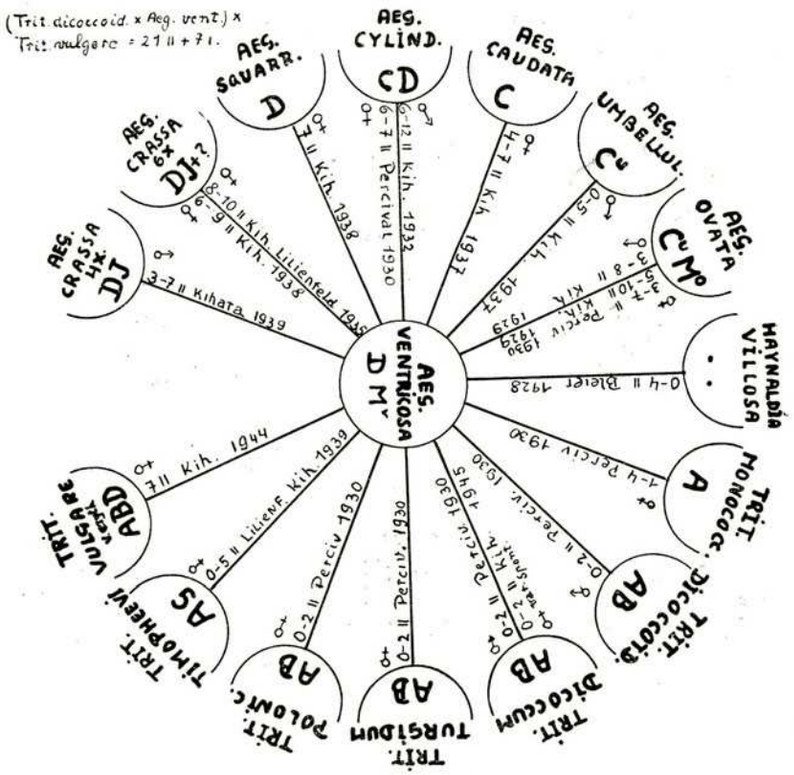
Table Nr. 1



Percival has analysed *Ae. ventricosa* and *Tr. dicoccum* and did not find any homologous genomes.

Kihara and Lilienfeld (1934-35) found that *Ae. ventricosa* has no homologous genomes with *Tr. timopheevi.* Sears (1944) reported amphidiploids between *(Ae. ventricosa* x *Tr. durum)* x *Tr. vulgare.*

Table Nr. 2.



OBSERVATIONS ON THE CROSSING OF TR. DICOCCUM SCHRNK. X AE. VENTRICOSA TAUSCH.

The above mentioned species were crossed by the author in 1948 in the "Instituto Fitotécnico de Santa Catalina" (see figs. 1 and 2.). The hybrid was vigorous but steril (fig. 3.) The rachis was not fragil. The spikes are morphologically intermediates (fig. 4.) The stems are semi-rastrerous. The pollen-material is sufficiently homogeneous and the number of abortive grains relatively low.

Studying the meiosis in three different thecas we could

determine the chromosomic configuration in 36 pollen mother cells. Carnoy 3:1 without chloroform was used for fixing and iron aceto-carmin for staining.

The data for the configurations: uni- bi- and trivalents etc. are summarized in the following table:

Table Nº 3

	7_{II}	8_{II}	9_{II}	10_{II}	11_{II}	12_{II}	13_{II}	
Scattered in the cytoplasm	+ 2I	+ 1II–II	+ 2II		+ 2I		+ 2I	
	– 7II + 14I	8II + 12I	9II + 10I	10II + 8I	11II + 6I	12II + 4I	13II + 2I	
	1III + 7II + 1II	7II + 1II	1III – 7II + 7I	1III – 10II + 5I	1III – 11II + 1I	2III – 12II – ??	13II –	
	– 7II + 12I	– –	9II + 10I *	–	– –	–	– –	
	3 1 1	5 1 –	5 1 1	4 2	3 1	3 1 –	3 1 –	36
	5	6	7	6	4	4	4	Nr. total of PMCs.

* 9 II + 10 I; various scattered in the cytoplasm.

The unions between the gemini are often loose and several are telosyndetic (end to end). Sometimes we find in the plasma uni- and bivalents without any orientation, and besides those, lagging chromosomes. The phases of the meiosis are not synchronized in the theca.

Fig. Nr. 5. General view of the PMCs of a theca principally in meta and anaphase.

Fig. Nr. 6. Another theca with different meiotic phases. In-both of the figures irregularities can be observed. Some of the univalents are splitting.

Fig. Nr. 7. Two PMC in early metaphase. A bi- and univalent separated in the cytoplasma.

Fig. Nr. 8. First meta- anaphase in side view. The loose unions can be well observed.

Figs. Nr. 9, 10. Sketches of the two above mentioned microphotos. Observe the bivalents in ring-form. In the cell on the left a trivalent configuration is seen. The bi- and trivalents are marked by arrows.
Fig. Nr. 11. Metaphase with 19 configurations.
Fig. Nr. 12. Metaphase with 15 configurations. A bi- and an univalent separated in the cytoplasma.
Fig. Nr. 13. Second anaphase.
Fig. Nr. 14. Second telophase with unevenly distributed chromosomes.
Fig. Nr. 15. An ana- telophase with lagging chromosomes.
Fig. Nr. 16. Second telophase. Fragments and lagging chromosomes in the state of elimination.
Fig. Nr. 17. A theca with pollen grains, transversal section.

The localisation of the pollen grains and the tetrades are quite regular, but in the pollen grains micronuclei are often formed. In spite of the irregular distribution of the chromatic material, the volume and shape of the pollen did not show the expected irregularity, even though the hybrid is steril.

Discussion

The above described observations show that one of the genomes of *Ae. ventricosa* seems to be homologous with a genome of *Tr. dicoccum*.

Further that some of the chromosomes of second genome of *Ae. ventricosa* pair with the chromosomes of the second genome of *Tr. dicoccum*.

The bivalents often form rings, but their pairing is often telosyndetic. Some of the geminis are heteromorph.

The second genome is not homologous, because its pairing is only partial. The distribution of the chromosomes responds to the behaviour of the genomes in the meiosis.

On the basis of these observations it is necessary to check the cyto-systematic relation between *Ae. ventricosa* and *Tr. dicoccum*.

It is not to be doubted that *Tr. dicoccoides* AB genomes are represented in the classic experiments of Kihara, Mc Fadden and Sears (1946) by the synthesis of *Tr. spelta*. *Tr. dicoccoides* can be accepted as a wild "variety" of *Tr. dicoccum*. Considering these facts we see, that the cytotaxonomic separation of

Tr. dicoccum from the other members of Emmer's series leads to well founded contradictions.

It is more likely, that the formula of *Ae. ventricosa* must be altered. The existence of the D genome cannot be doubted as many analyses made within the section *Pachystachys* prove. It is probable, that we shall have to revise the genome M, changing it with one of the two genomes (A or B) of *Tr. dicoccum*.

It is important to stress that *Ae. ventricosa* differs in its geographical distribution from the other members of the section *Pachystachys*. This supports the above mentioned data, that the cytosystematic position of *Ae. ventricosa* has to be altered.

For the sake of performing hybrids in other climatic conditions we sent our seed-material to Prof. Kihara, Japan, aiming to prove our results, whether the relative high frequence of the chromosmal associations, found in Argentina, could not be influenced by external modification-factors.

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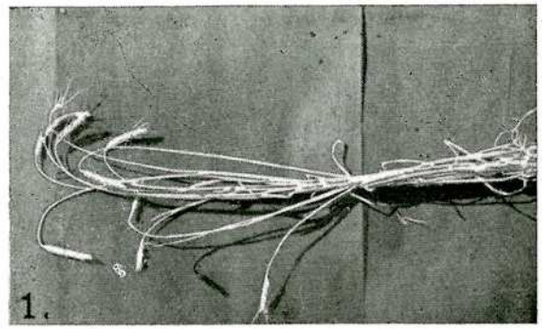

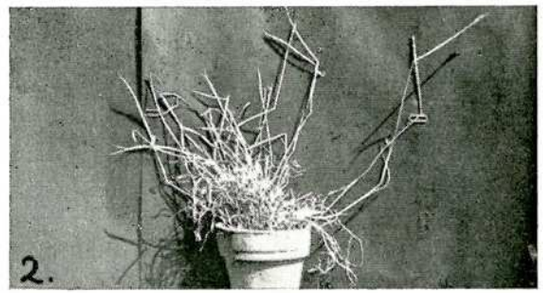

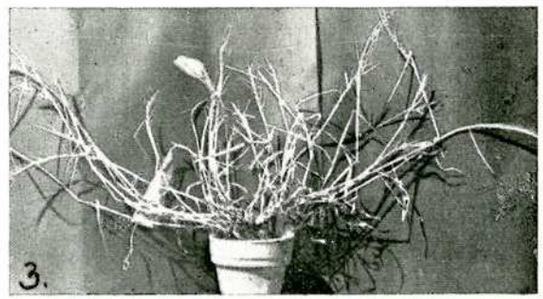

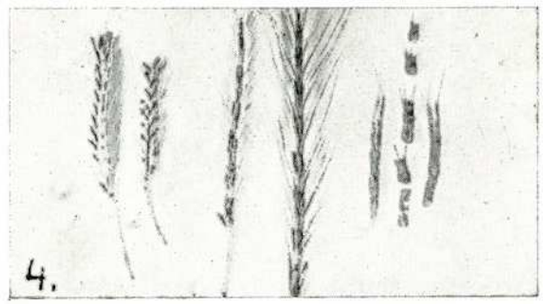

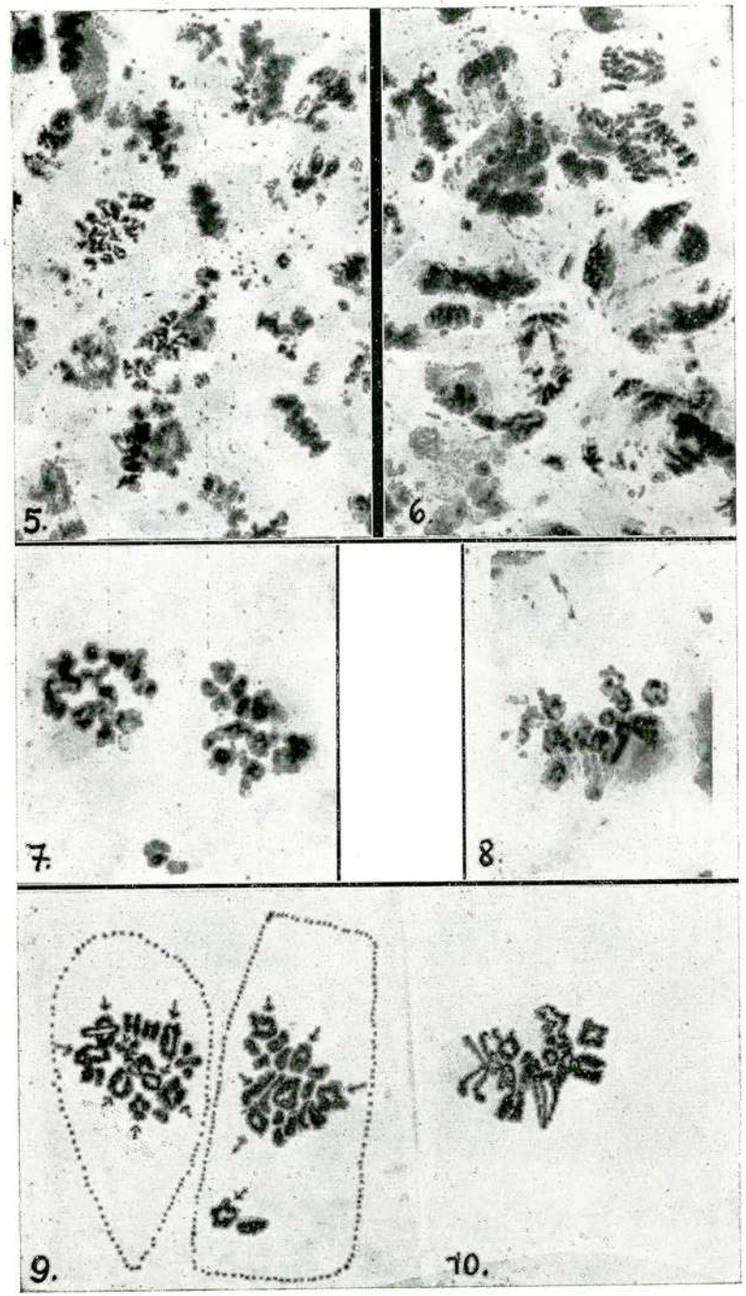
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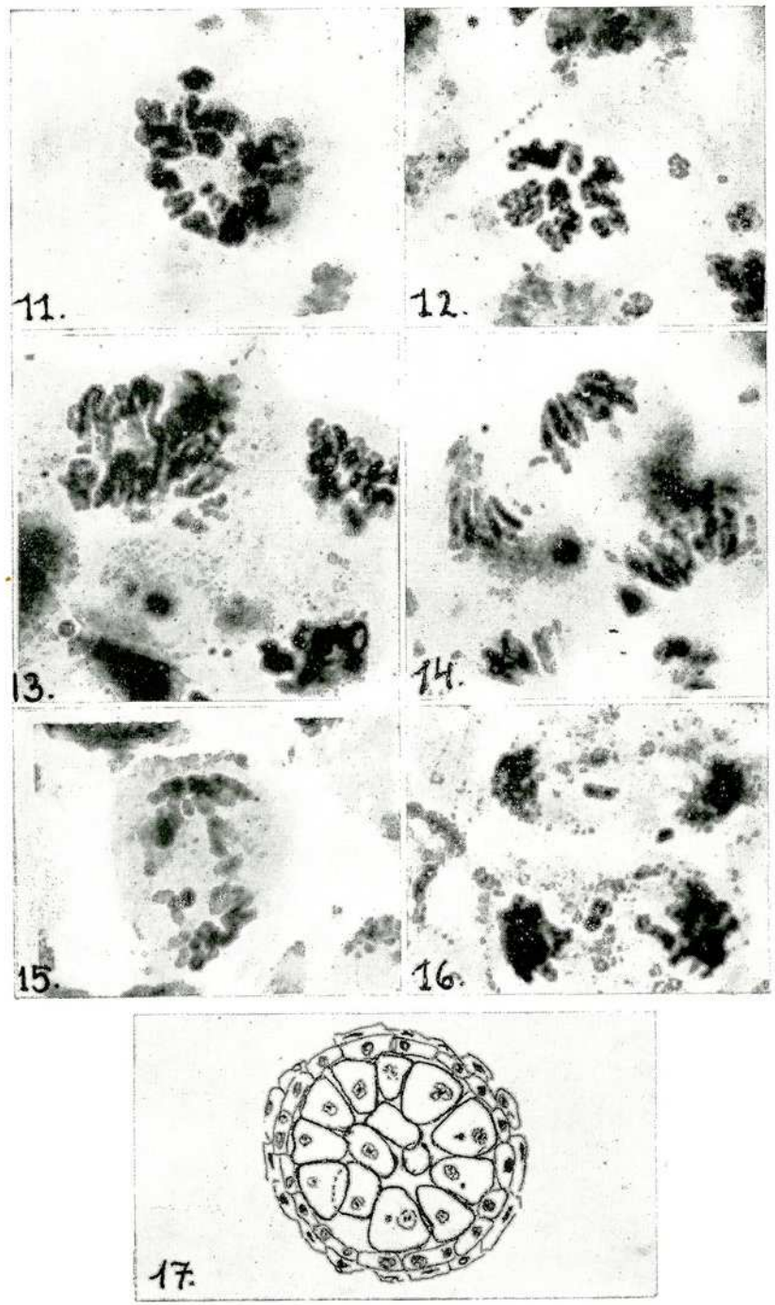
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