

CYTOLOGICAL STUDIES OF STERILITY AND POOR FERTILITY IN THE YELLOW MELILOT (*MELILOTUS OFFICINALIS* L.)¹

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Summary. The studies were focussed on the female sterility and poor fertility in the yellow melilot with typical flowers and in plants with flowers shaped like a small ball. In female sterile plants the processes of meiosis and microsporogenesis proceeded without large disturbances. In this connection it is suggested that the cause of female sterility are irregularities in the process of megasporogenesis and megagametogenesis.

A poorly fertile plant, during the chromosome reduction and divisions in the pollen mother cells, was found to have some deviations (lagging chromosomes, division into chromatids in anaphase I). However, in view of a relatively small percentage of cells with disturbances, they cannot be a cause of poor fertility. The atypical course of microsporogenesis and the entire 4-nuclear microsporocyte transformation into a microspore and then into bi- and multinuclear pollen grains should be considered the basic cause of that phenomenon. Binuclear pollen grains are tetraploid and multinuclear pollen grains contain di- and haploid nuclei. There are also mononuclear pollen grains. After fertilization of a haploid female gamete with a polyploid male one there arise polyploid nonorthogonal zygotes, which presumably die causing a low fertility of the studied plant.

When accumulating material for collection and studies from the territory of Poland, seeds of the yellow melilot were also gathered. This year, during flowering and fruiting, attention has been paid to several plants, which flowered, but did not set pods or had only few pods. There were totally seven sterile and poorly fertile plants. An attempt has been made to elucidate that phenomenon.

MATERIAL AND METHODS

There arose a suggestion that the cause of poor fertility and sterility of the studied plants of yellow melilot may be deviations in the process of conjugation and then, in division of chromosomes, as well as during microsporogenesis and

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Table 1. Variation of the pollen grain diameter in fertile, female sterile and poorly fertile plants of yellow melilot

Plants	No. of analysed PMC	Diameter of pollen grain (in micrones)												Total No. of pollen grains	Average diameter (in micrones)	
		21.14	24.30	27.53	30.64	33.75	36.89	40.03	43.17	46.31	49.45	52.95	55.73			58.87
Fertile	<i>n</i>	10	24	240	36										300	27.72
	%		8.0	80.0	12.0											
Sterile 1	<i>n</i>	1	12	85	96	7									200	29.08
	%		6.0	42.5	48.0	3.5										
Sterile	<i>n</i>	1	18	77	55										150	28.35
	%		12.0	51.3	36.6											
Sterile, ball-shaped flowers	<i>n</i>	4	45	183	122										350	24.96
	%		12.8	52.2	35.0											
Poorly fertile	<i>n</i>	1				3	46	96	123	53	49	25	5		400	46.76
	%					0.8	11.5	24.0	30.8	13.2	12.2	6.2	1.2			

pollen maturation. With that in view, small flower buds were fixed in Carnoy's solution and then, from the pollen mother cells squeezed out of the anthers squashed preparations were made and stained with propionocarmine.

RESULTS

The plants under study differed by the structure of their flowers. Three of them had typical flowers, four had their petals closed in the calyx, the petal apices and the pistil style stick out of the calyx. The lower and middle parts of the calyx grew bigger and the flowers looked like small balls (Phots 1, 2).

Table 2. Viability of pollen grains in fertile, female sterile and poorly fertile plants of yellow melilot

Plants	No. of analysed plants	Pollen grains with plasma (viable) %
Fertile	10	95.2 - 97.8
Sterile with typical flowers	2	93.7 - 96.4
Sterile with flowers in the ball shape	4	75.2 - 97.4
Poorly fertile with large pollen grains	1	76.8

Pollen from plants with typical flowers differed in size and shape. In two sterile plants it was similar to that of fertile plants (Phots 3, 4; Tables 1, 2), whereas in poorly fertile plants the pollen grains were markedly larger in diameter, different in shape, and the percentage of grains with plasma was smaller than that in fertile plants (Tables 1, 2; Phots 4, 5). The pollen grains looked as if after the second division of nuclei, the microsporocyte did not divide and the sporoderma was formed only on the external, adjacent to the callose, part of the protoplast, which in some places was somewhat deeper towards the center of microsporocyte. Thus, the pollen grains looked as if arisen from the entire microsporocyte (Phots 6, 7 and 8). Externally they are similar to those typical of *Calante veitchii*, a species of the orchidaceous (Poddubnaja-Arnoldi 1976).

Pollen from sterile plants with flowers in the form of a small ball did not differ much in shape, diameter and viability from pollen grains of fertile plants (Table 1).

Table 3. The number of pods and seeds in the cluster of fertile and poorly fertile plants of yellow melilot

Plants	analysed clusters	Number of							
		pods in cluster			seeds in cluster			including two-seeded pods	
		min.	max.	average	min.	max.	average	min.	max.
Fertile	10	45	60	57.0	44	70	68.0	7	15
Poorly fertile	48	1	27	8.6	1	24	7.7	0	2

Sterile plants were flowering from the middle of June till the first ground frosts in September. They did not set pods either after self-pollination or after cross-pollination. A plant with large pollen grains set few pods (Table 3, Phot. 9).

MEIOSIS

At pachytene, homologous chromosomes of sterile plants with typical flowers were paired in bivalents. One of the plants, at diakinesis, was found to have a single nucleolus and 8 bivalents, 5 of which were ring-shaped and 3 were rod-shaped (Phot. 10). Another one during diakinesis was found to have 8_{II} in each pollen mother cell and instead of a single nucleolus — from 5 to 8 spherical bodies different in diameter, stainable with carmine like the nucleolus (Photos 11, 12). During the first metaphase the analysed cells had 8_I each (Phot. 13), except only one, which had 7_{II}2_I (Table 4). The first and second divisions proceeded without disturbances (Phot. 14; Table 5) and microsporocytes transformed into tetrads of microspores (Phot. 15, 16; Table 6).

Table 4. Diakinesis and metaphase I in female sterile and poorly fertile plants of yellow melilot

Plants	Chromosomes linked at								
	diakinesis			metaphase I					
	No. of analysed PMC	8 _{II}	7 _{II} 2 _I	No. of analysed PMC	8 _I	7 _{II} 2 _I	6 _{II} 4 _I	5 _{II} 6 _I	6 _{II} 1 _{IV}
Sterile 1	62	62	—	30	30	—	—	—	—
Sterile 2	17	17	—	116	115	1	—	—	—
Sterile with ball-shaped flowers	12	12	—	119	106	9	1	2	1
Poorly fertile	109	106	3	149	128	20	1	—	—

At pachytene in plants with flowers in the shape of a ball (Photos 1, 2), the analysed cells were sporadically found to have conjugations of four chromosomes as well as nonconjugated fragments in bivalents (Phot. 17). Also at the transition stage, between diakinesis and the arrangement of conjugated chromosomes into a metaphase plate, there were sometimes 7 configurations: 6_{II}1_{IV} (Phot. 18), whereas other analysed cells were sometimes found to have: 7_{II}2_I (Phot. 19 and 20), 6_{II}4_I, 5_{II}6_I. Cells with a larger or smaller than 8 number of chromosome configurations during the first metaphase were few, mostly having 8_{II} each (Phot. 21; Table 4). The first and second divisions proceeded without noticeable deviations (Table 5) and pollen mother cells transformed into typical tetrads of microspores (Table 6).

At pachytene a poorly fertile plant was rarely found to have a quadrivalent or a short, nonconjugated fragment of a bivalent (Phot. 22).

During diakinesis, the pollen mother cells had 8_{II} each: 5 ring-shaped and 3 rather rod-shaped chromosomes (Phot. 23); three of the analysed cells were found to have 9 chromosome configurations each — 7_{II}2_I (Table 4). The division plate of

Table 5. The course of anaphase I, metaphase II and anaphase II in female sterile and poorly fertile plants of yellow melilot

Plants	Division stage	Number of PMC		Kind of irregularities
		total	with irregularities	
Sterile 1	anaphase I	17	--	
	metaphase II	31	--	
	anaphase II	43	--	
Sterile 2	anaphase I	37	--	
	metaphase II	24	--	
	anaphase II	25	--	
Sterile with ball-shaped flowers	anaphase I	36	--	
	metaphase II	43	--	
	anaphase II	90	--	
Poorly fertile	anaphase I	153	26	unequal division, univalents dividing into chromatids
		13	13	divided chromosomes at one pole
	metaphase II	100	5	chromosomes in 3 groups -- at poles 2-8, the remaining ones are in the plane of the first division
	anaphase II	105	4	chromosome bridge and laggards

the first metaphase was mostly found to have 8_{II} each (Phot. 24), and sometimes only cells with $7_{II}2_1$, as well as a single cell with $6_{II}1_{VI}$ (Table 4).

During anaphase I, in most of the cells 8 chromosomes moved towards one of the opposite poles of the division spindle (Phot. 25; Table 5). There were, however: cells, in which one of the bivalents divided with a delay (Phot. 26); cells with part of the chromosomes at the poles (Phot. 27); cells in which lagging chromosomes in the number of 7 divided into chromatids (Phot. 28); finally, cells, in which the chromosomes remained in the cytoplasm after the first division, divided into chromatids (Phot. 29). In 13 out of the analysed cells, after the division of bivalents, all the chromosomes migrated towards one of the poles (Table 5). Such cells at telophase and the formed telophase nucleus had only one nucleolus.

The second metaphase and anaphase proceeded without disturbances in the majority of the analysed cells (Phot. 30 and 31). At the stage of telophase II a chromatid bridge (Phot. 32) and lagging 1-2 chromosomes (Table 5) were encountered only sporadically. In the microsporocyte after the second division 4 nuclei were

Table 6. Microsporogenesis in female sterile and poorly fertile plants of yellow melilot

Plants	Tetrads	Tetrad + 1 micronucleus	Diads	Triads
Sterile 1	457	0	0	0
Sterile 2	400	0	0	0
Sterile with ball-shaped flowers	155	0	0	0
Poorly fertile	678	7	9	6

formed (Phot. 33), and in few — additionally a micronucleus (Phot. 34). Sporadically diads and triads were formed (Table 6).

In sterile plants with typical flowers and flowers with petals closed in the calyx, the 4-nuclear cenocyte transformed into microspore tetrads (Phots 15, 16). Regarding a poorly fertile plant it is difficult to speak about a typical process of microsporogenesis. In the 4-nuclear cenocyte (Phot. 33), in places, where normally intine and exine are formed, dividing the cenocyte into four microspores, there appears a small depression (Phots 35, 36), the nuclei migrate towards the central part of the cenocyte and out of a 4-nuclear cell, without division, there occur large, different in shape "pollen grains" (Phots 5, 6, 7, 8).

Table 7. The number of vegetative and generative nuclei in the pollen grain of a poorly fertile plant of yellow melilot

No. of pollen grains	Pollen grains with the nuclei				
	1 vegetative 1 generative	2 vegetative 2 generative	1 vegetative 2 generative	1 vegetative 3 generative	1 nucleus
156	125	29	2	1	1

The process of differentiation of large, 4-nuclear microspores — each of the initial nuclei divide independently of the remaining ones, but simultaneously, into a vegetative and generative nuclei. After division, the vegetative nuclei link with each other and the generative nuclei do the same. A formed pollen grain may contain:

two large tetraploid nuclei — vegetative and generative (Table 8); when after the division of the initial nuclei the formed nuclei linked in 2 — a matured pollen grain was 4-nuclear—with 2 generative and 2 vegetative nuclei containing a diploid chromosome number; if four vegetative nuclei fused into a single vegetative fusion nucleus and the generative nuclei fused in 2 — they gave rise to a pollen grain with a tetraploid vegetative nucleus and two diploid generative nuclei;

grains with 4 nuclei — vegetative tetraploid and three generative — one diploid and two haploid;

mononuclear grains probably resulting from fusion of four initial nuclei of the cenocyte (Table 7).

Averagely, there were 84.9% less pods and 88.9% less seeds in the cluster of a poorly fertile plant than in that of fertile plants (Table 3). There were also less two-seeded pods. Throughout the vegetation season a large part of clusters did not set pods (Phot. 9).

Table 8. Pollen mother cells with undivided nucleus in a poorly fertile plant of yellow melilot

Division phase	Number of PMC		
	total	with undivided nucleus	
		number	%
Pachytene	97	6	6.2
Tetrads	397	23	5.8

Seeds from a poorly fertile plant with large pollen grains were normally developed and did not differ from those of fertile plants. Sown out after scarification, the seeds did not germinate even after 2 weeks, whereas seeds from fertile plants germinated after 2 days. It may be suggested that the cause of the seed incapability to germination in the studied plant is a nonorthogonal polyploidy of zygotes arisen after fertilization (triploid and pentaploid ones).

Among the analysed pollen mother cells some had an undivided nucleus during all the stages of chromosome division (Table 8). The nucleus of such cells differ in structure from that of a typical cell (Phot. 37) and from those in a four-nuclear cenocyte (Phots 38, 36). It was shrunken and its structure was not sharp. Sometimes desintegration of the nucleus and cells followed the first division (Phot. 40), such cells differed from the typical diads.

DISCUSSION

Many authors give the chromosome number $2n=16$ for the yellow melilot (Bolkhovskikh et al. 1969), whereas Lesins (1952) gives $2n=32$ chromosomes for the obtained tetraploid. In plants of that species studied by us, sterile and poorly fertile with typical flowers and with ball-shaped flowers, the number n chromosomes after reduction amounts to 8. Therefore, the studied plants were diploid.

Only few pollen mother cells during chromosome conjugation were found to have a single quadrivalent and a short, not conjugated bivalent fragment. In the majority of the analysed cells the chromosome conjugation proceeded regularly. Encountered in diakinesis and metaphase I single univalents were formed through premature disjunction of chiasmata. The first and second divisions in sterile plants with typical and ball-shaped flowers were without deviations. After the second division the microsporocytes transformed into regular tetrads of microspores.

In the part of PMCs of a poorly fertile plant during anaphase I, the chromosomes migrated towards the poles in unsimilar numbers, part of them remained in the equatorial plane of the cell, where they subsequently divided into chromatids. In some cells during that division phase the chromosomes — 16 in number — migrated towards one pole.

Except a single cell with a chromatid bridge, the second division generally proceeded normally. Few tetrads after the second division were found to have an additional micronucleus and some microsporocytes transformed into diads and triads.

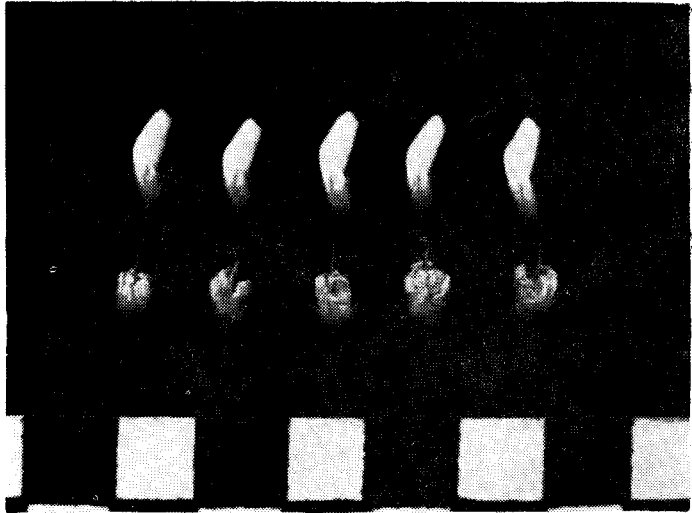
The further process of microsporogenesis and pollen formation in a poorly fertile plant, beginning with the tetrad phase, proceeded in a different way than in sterile plants. The microsporocyte did not divide into microspores. On its surface there occurred small depressions at places, where normally intine is formed, and the entire four-nuclear cenocyte transformed into a large "pollen grain" similar in shape to the pollen laid in some *Orchidaceae*, e.g. *Calanthe veitchii* (Poddubnaya-

-Arnoldi 1976). Fused in a tetrad laid pollen of *Calanthe veitchii* differ from large pollen grains of the melilot. In *Calanthe veitchii* each pollen grain fused in a tetrad is binuclear and is surrounded by its own sporoderm; a large pollen grain of the melilot is surrounded by a single, common sporoderm.

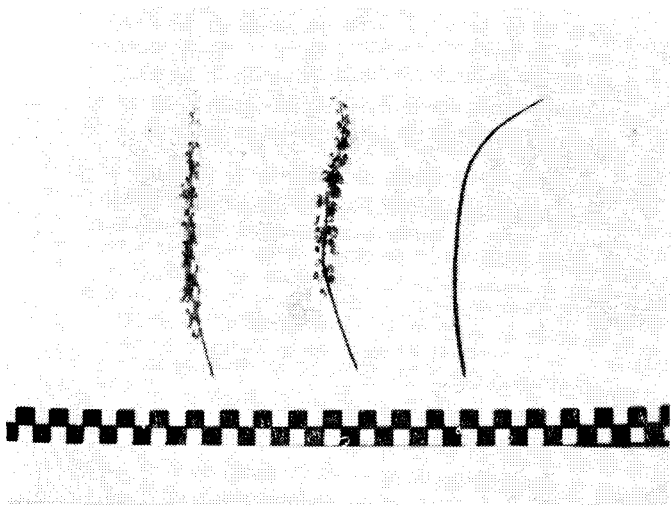
Female sterility of the melilot phenotypically is similar to that described in cotton (Deshi 1966) and tobacco (Hsiung Wan-Mann 1967) and differs from sterility in sugar beet (Jassem 1967, 1971) and yellow lupin (Kazimierski, Kazimierska 1976). Similar in that, that in female sterile plants of cotton, tobacco and melilot the ovaries develop normally. Female sterility, though different from that of sugar beet with flowers without ovary and different from that of yellow lupin, the flowers of which contained ovaries, was absolutely correlated with male sterility.

Sterility of melilot plants with flowers in the shape of small balls seems to be analogous to that found in *Lupinus mutabilis* (Kazimierski, Kazimierska, in preparation). However, even a large similarity of external symptoms in the mentioned species to sterility of yellow melilot provides no bases to consider that in all the cases genetic factors conditioning that trait are the same. The course of meiosis, microsporogenesis and a high vitality of pollen in sterile plants with typical flowers and in plants with flowers in the shape of small balls, give no sufficient grounds to explain the reasons of that phenomenon. In our opinion, these reasons should be detected in the formation and development of female gametophyte.

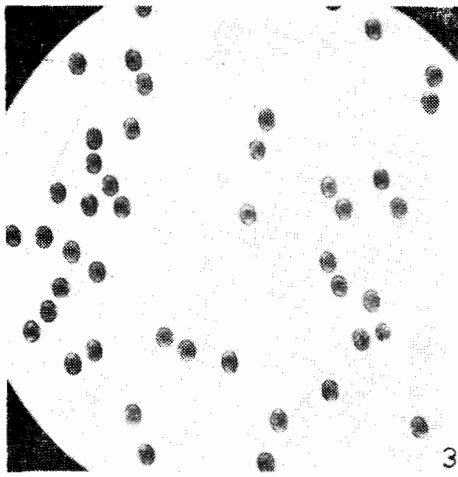
It is difficult to consider that the cause of a low fertility of plants with typical flowers and large pollen grains are deviations in the chromosome division during anaphase I — the remaining of part of the chromosomes in the equatorial plane of a cell, division into chromatids, moving of all the chromosomes towards one of the cell poles — the more so, as anomalies of that kind were found only in 23.5% of the analysed cells. Not dividing PMCs with a shrunken dying nucleus, encountered among typical cells from pachytene to the tetrad stage of microspores, which were about 6%, could not either to have a significant influence on the fertility of plants. According to us, the main cause of a poor fertility of a studied plant may be the transformation of entire tetrads into microspores and then, into large, shapeless pollen grains. Normal mature seeds from a poorly fertile plant did not germinate. The cause of that may be their polyploidy. After division of 4 initial pollen nuclei into a vegetative and generative nuclei and after their subsequent fusion there occurred the following pollen grains: tetraploid — with a single generative and vegetative nuclei; diploid — with two vegetative and generative nuclei as well as with a single vegetative and two generative nuclei; with a mixed ploidy — with a single vegetative nucleus and three generative nuclei with the chromosome number 16, 8 and 8. Assuming, therefore, that the process of megasporogenesis and that of megagametogenesis proceeded normally and that a haploid egg cell was formed, after fertilization there might be formed the zygotes: pentaploid, triploid and diploid. It may be that in the yellow melilot nonorthogonal polyploid seeds (zygotes) as a result of lethal defects are incapable to live and do not germinate because of that.



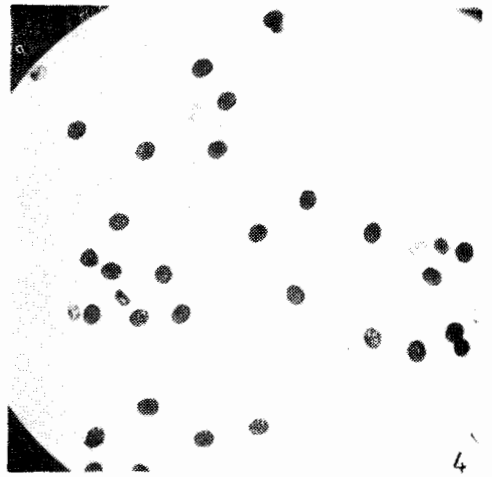
Phot. 1. Flowers: upper row — typical, lower row — corola almost completely closed in the calyx, the pistil style is protruding beyond the corola



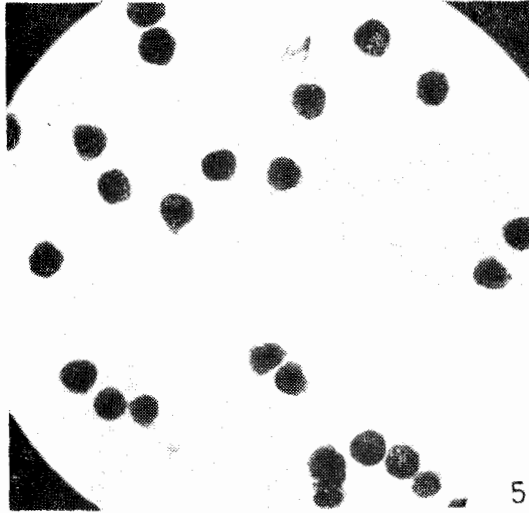
Phot. 2. Inflorescences: on the left side — with typical flowers, in the centre — with the corola closed in the calyx, on the right — petiole without pods



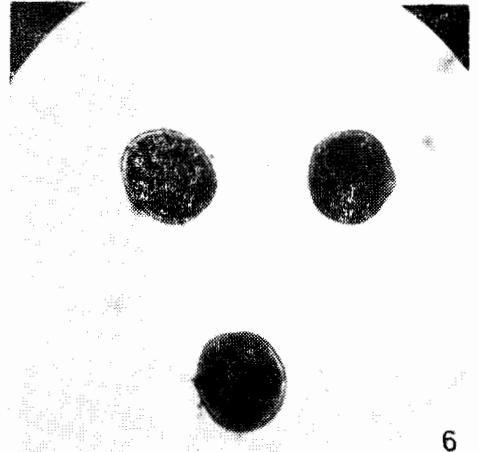
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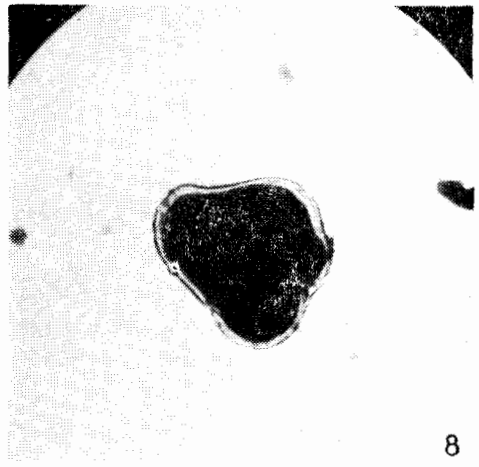
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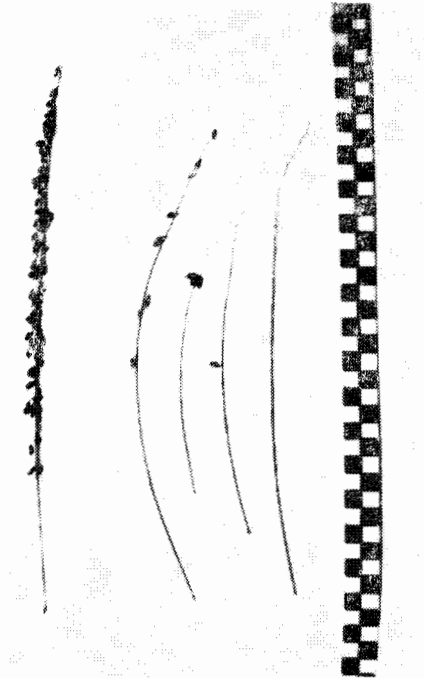


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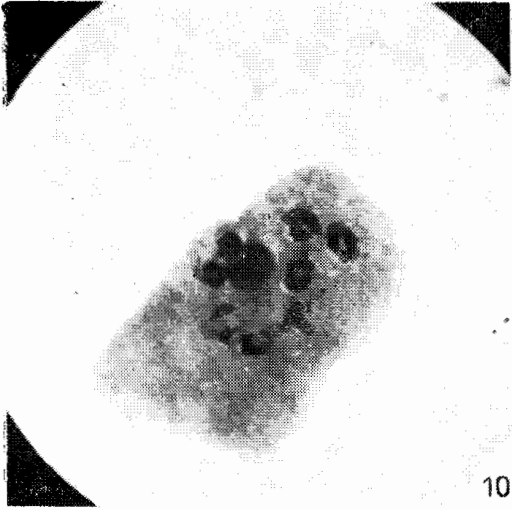


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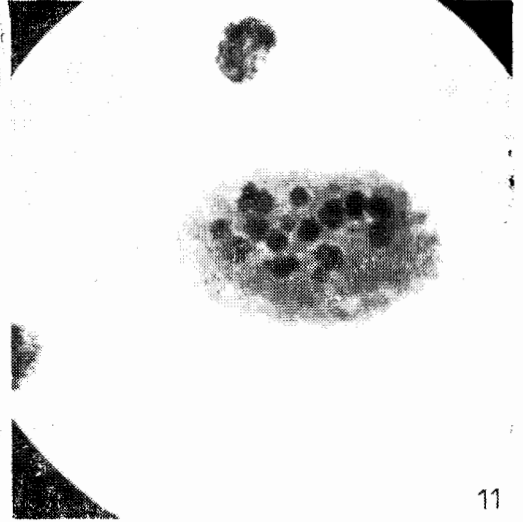
Phots 3 - 8. Pollen. 3 - from a female sterile plant; 4 - from a fertile plant; 5 - from a poorly fertile plant (Phots 3 - 5 - 100 \times); 6 - from a fertile plant; 7 - 8 - from a poorly fertile plant (Phots 6 - 8 - 440 \times)



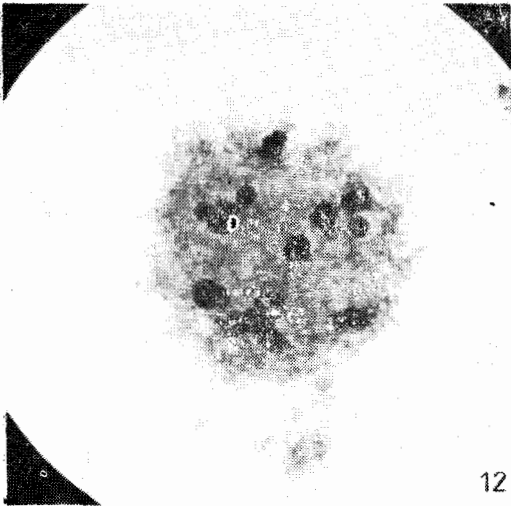
Phot. 9. Fructifications: first from the left — from a fertile plant, the remaining ones — from a poorly fertile plant



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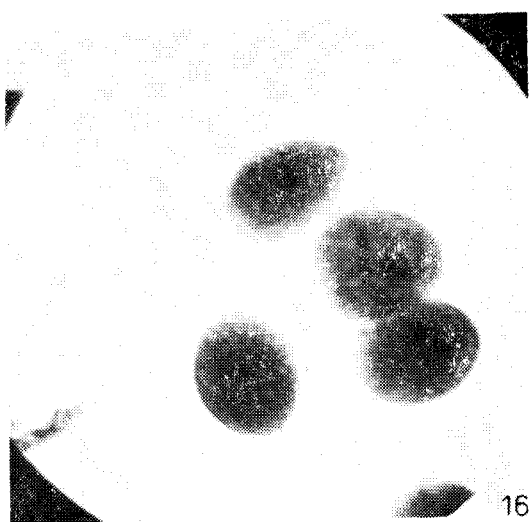
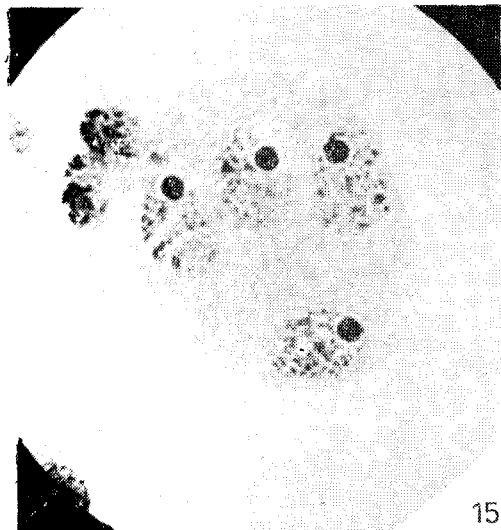
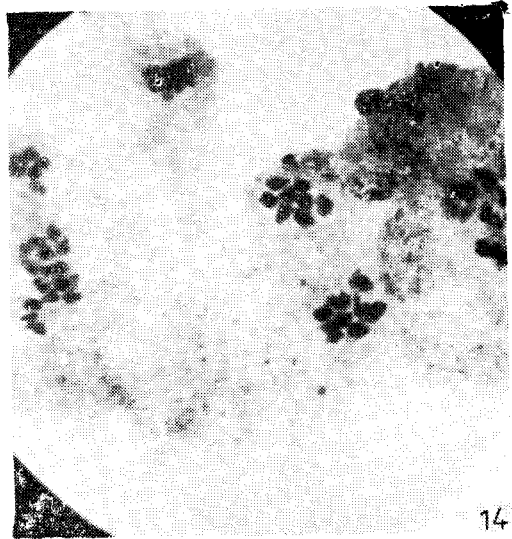


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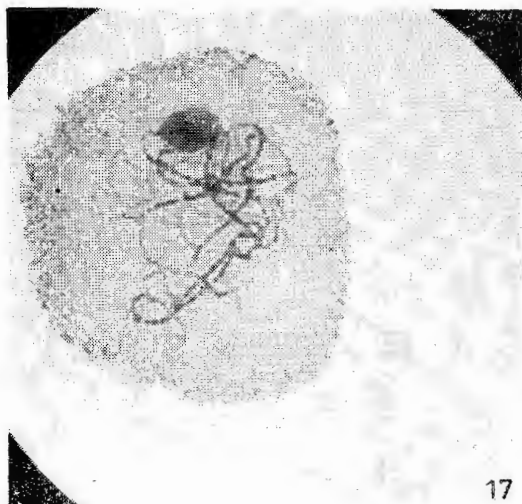


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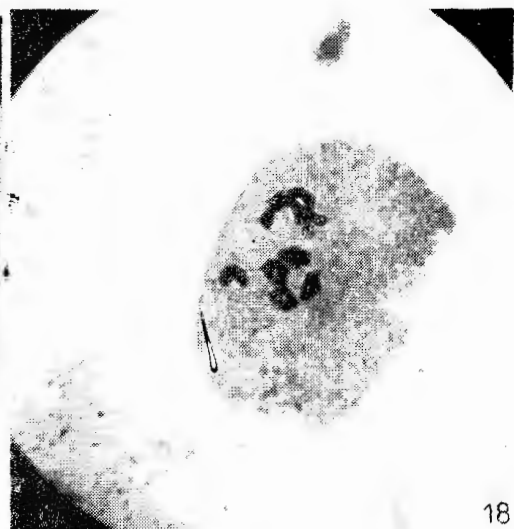
Phots 10 - 12. Diakinesis in female sterile plants. 10 — a single nucleus and 8_{II}; 10 - 12 — numerous spherical bodies stainable with carmine and 8_{II}



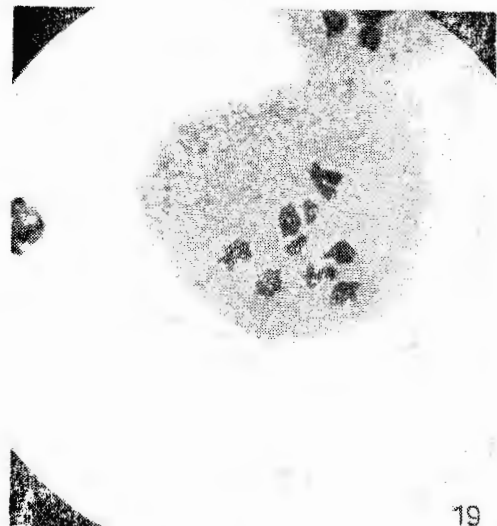
Phots 13 - 16. Female sterile plants. 13 — metaphase I, 8_{II} ; 14 — anaphase I with 8 chromosomes at each pole; 15 — a four-nuclear cenocyte; 16 — tetrad of microspores



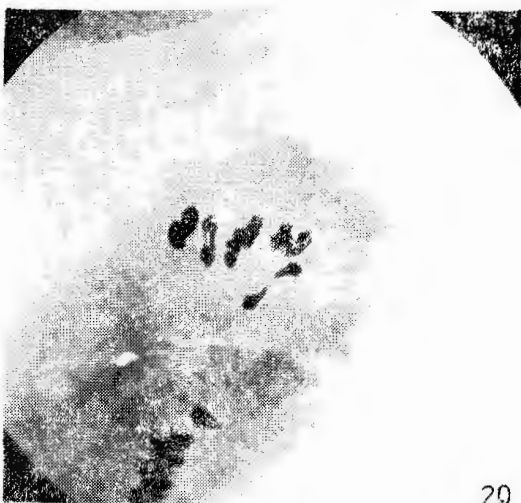
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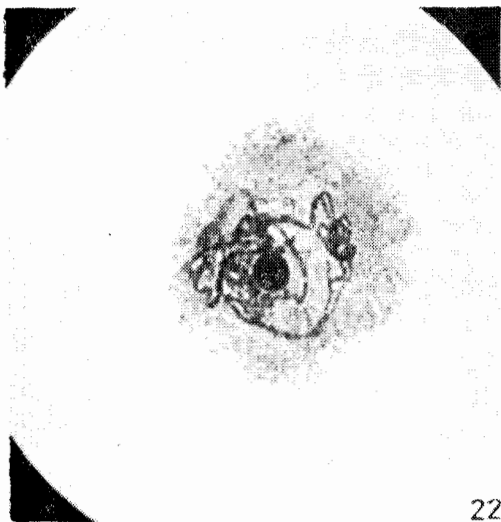


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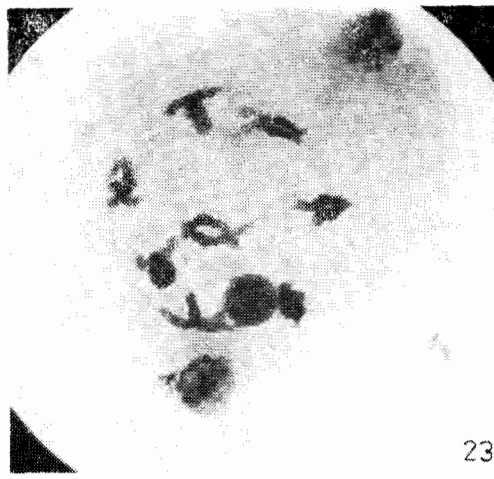


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Phots 17 - 21. Chromosome pairing and division in plants with ball-shaped flowers. 17 - pachytene, a visible tetraivalent; 18 - early metaphase - $6_{II}1_{IV}$; 19 - early metaphase - $7_{II}2_{I}$; 20 - metaphase I - $7_{II}2_{I}$ (univalents from precocious division); 21 - metaphase I with 8_{II}



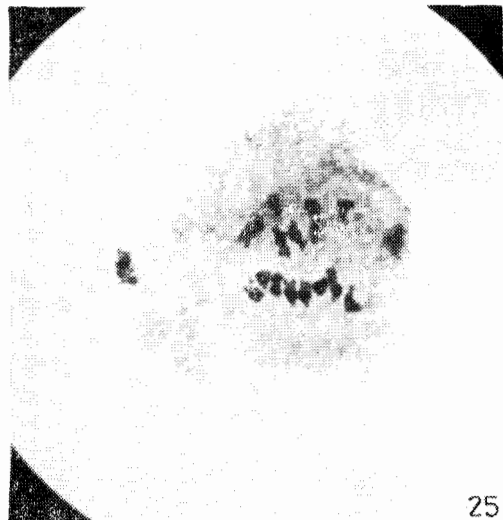
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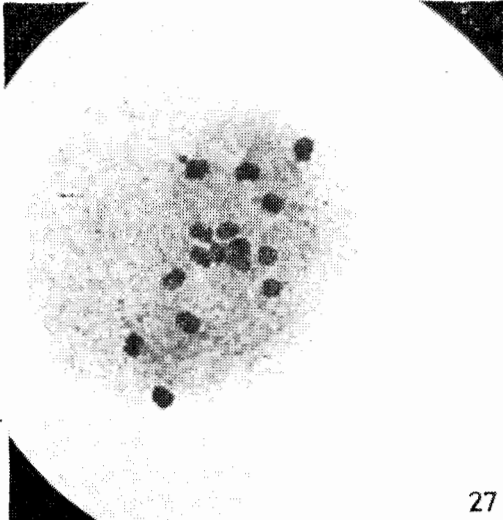
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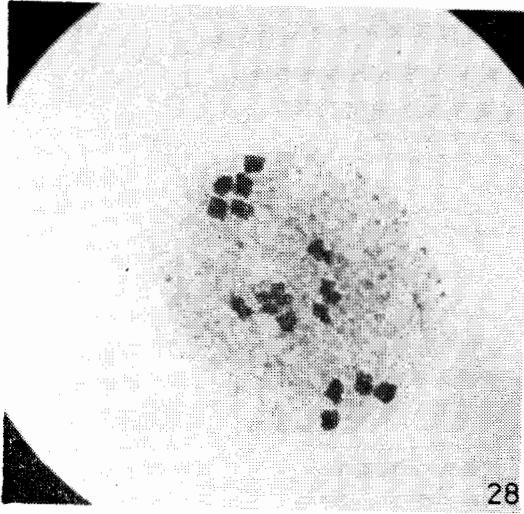
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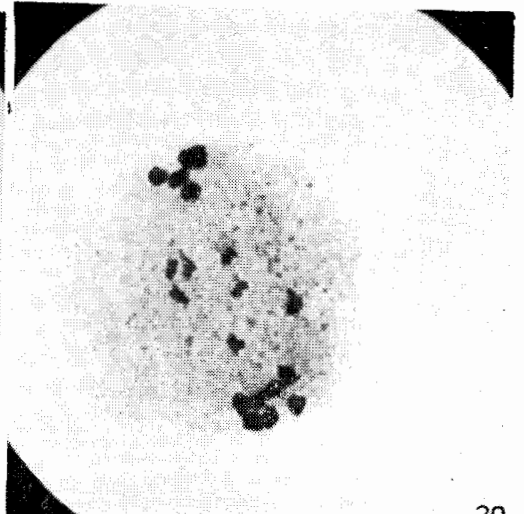
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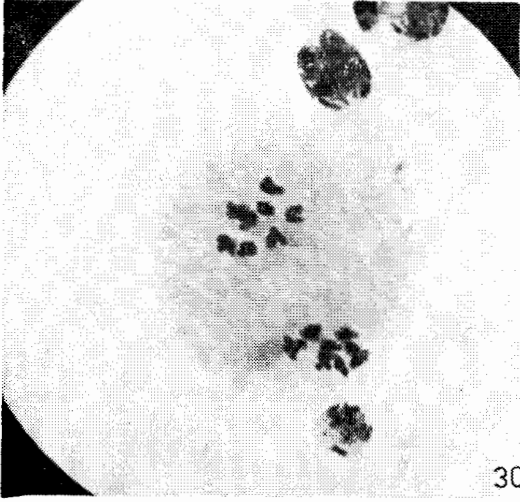
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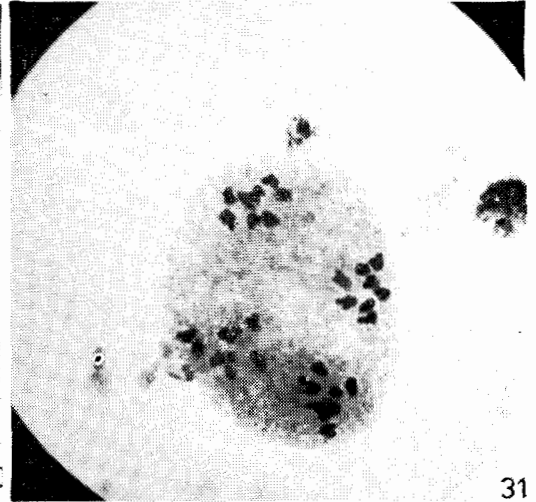
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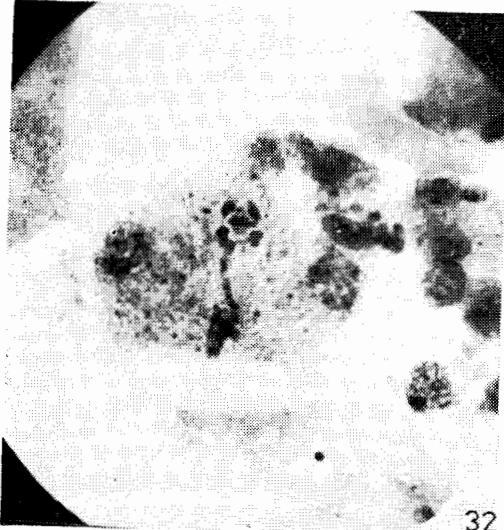
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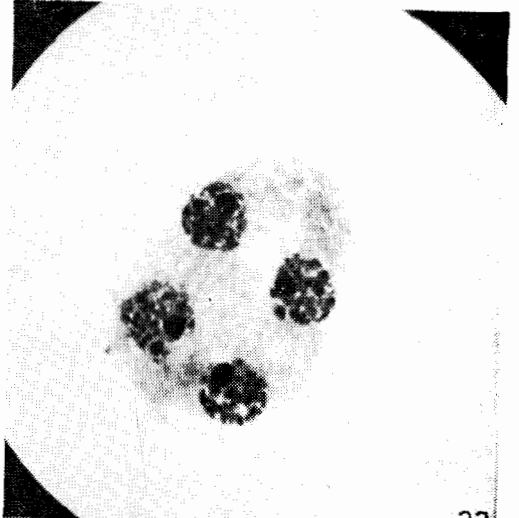
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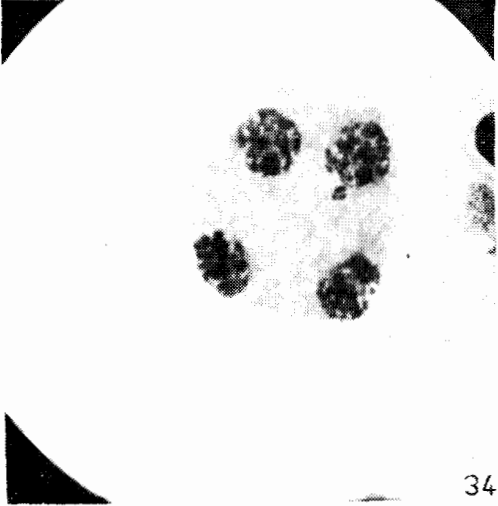
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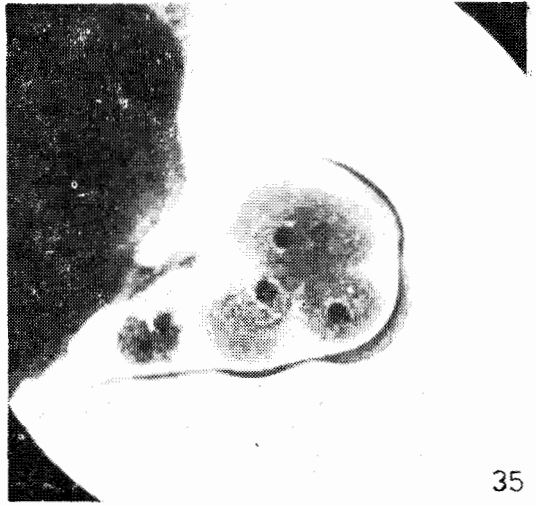
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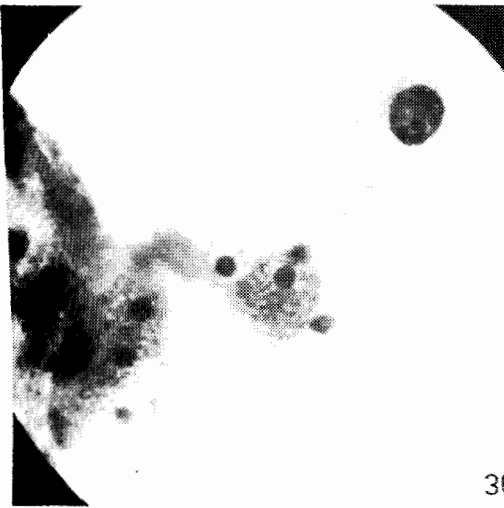
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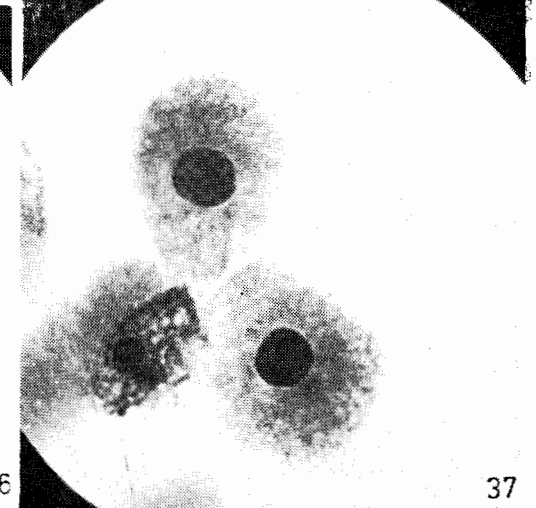
34



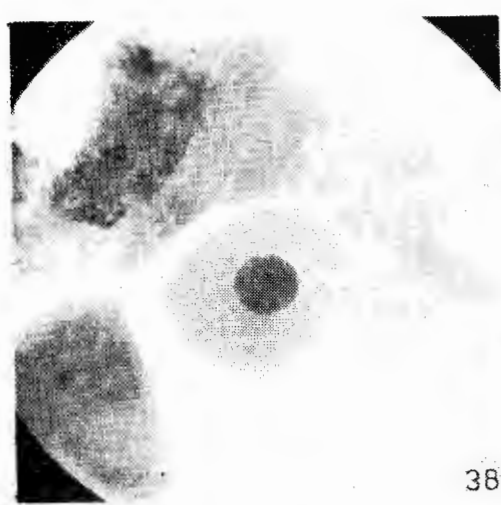
35



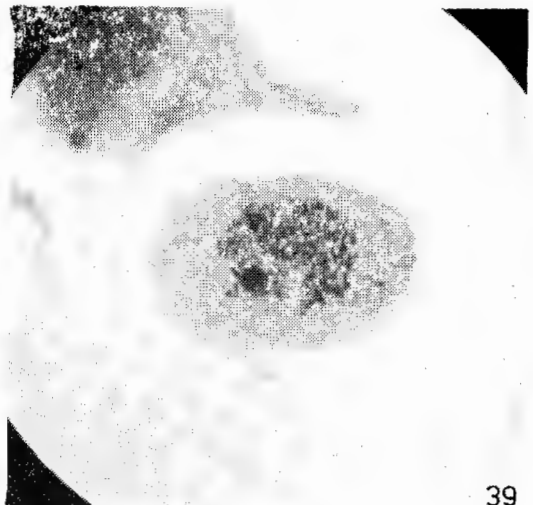
36



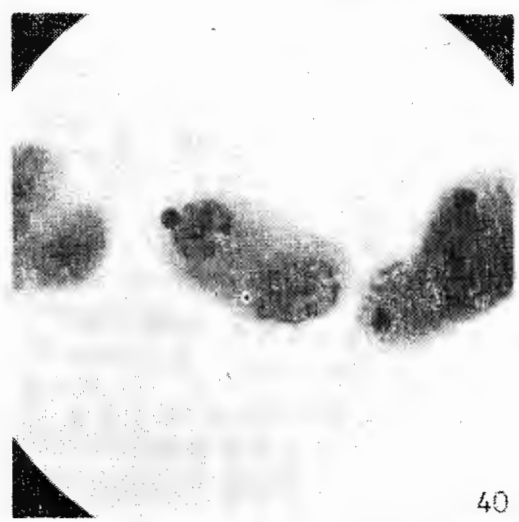
37



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40

Phots 22 - 40. Chromosome pairing and division in a poorly fertile plant. 22 - pachytene - a quadrivalent and unpaired sections; 23 - diakinesis 8_{II} and a single nucleus; 24 - metaphase I 8_{II} ; 25 and 26 - anaphase I with 8 chromosomes moving to each pole; 27 - 29 - anaphase I, part of the chromosomes remain in the equatorial plane, then divide into chromatids; 30 - metaphase II with 8 chromosomes in each plate; 31 - anaphase II with four 8-chromosome-groups; 32 - telophase II-chromatid bridge; 33 - 36 - four-nuclear cenocytes: 33 - typical; 34 - with a micronucleus; 35 and 36 - nuclei moving towards to cenocyte center; 37 - 39 - undivided pollen mother cells with untypical nucleus; 37 - during pachytene in the anther; 38 and 39 - four-nuclear cenocytes in the anther; 40 - a binuclear cell with degenerating nuclei from the anther with 4-nuclear cenocytes

CONCLUSIONS

1. Female sterility in the studied plants of yellow melilot — with typical flowers and with flowers in the shape of a small ball — probably results from irregularities in megasporogenesis and megagametogenesis. The processes of meiosis and microsporogenesis in such plants proceed without large disturbances.

2. Though in a poorly fertile plant some deviations (lagging chromosomes and their division into chromatids at anaphase I) were encountered during chromosome reduction and both divisions, in our opinion, they are not the only cause of its poor fertility.

3. We consider that the main cause of poor fertility is atypical course of microsporogenesis — transformation of the entire four-nuclear cenocytes into microspores and then, into bi- and multinuclear pollen grains. Binuclear pollen grains are tetraploid, among four-nuclear grains are ones with 2 diploid generative nuclei as well as with a single diploid nucleus and two haploid nuclei.

4. Presumably after fertilization of haploid female gamete with polyploid male one in yellow melilot there occur sublethal and lethal zygotes, which mostly die in the process of ontogenesis.

5. The lack of vitality of matured seeds from a poorly fertile plant is probably also a result of their nonorthogonal ploidy.

6. Atypical course of microsporogenesis may be a cause of the formation of pollen grains with a larger than haploid chromosome number, and therefore, in consequence, it may cause the formation of new cytotypes.

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BADANIA CYTOLOGICZNE NIEPŁODNOŚCI I SŁABEJ PŁODNOŚCI NOSTRZYKU ŻÓLTEGO (*MELILOTUS OFFICINALIS* L.)

Streszczenie

Zbadano przyczyny żeńskiej niepłodności i słabej płodności u nostrzyku żółtego o kwiatach typowych i w kształcie niewielkiej kulki. U roślin żeńsko niepłodnych procesy mejozy i mikrosporogenezy przebiegały bez większych zakłóceń. W związku z tym przypuszcza się, że przyczyną niepłodności żeńskiej są zaburzenia w procesie megasporogenezy i megagametogenezy.

U rośliny słabo płodnej, podczas redukcji chromosomów i ich podziałów w komórkach macierzystych pyłku, spotykano pewne odchylenia (opóźnione chromosomy, podział na chromatydy w pierwszej anafazie). Jednakże, z uwagi na stosunkowo niewysoki procent komórek z zaburzeniami, nie mogą one być przyczyną słabej płodności. Za przyczynę zasadniczą należy uważać nietypowy przebieg mikrosporogenezy i przekształcanie się całego czterojądrowego mikrosporocyta w mikrospore a następnie w dwu- i wielojądrowe ziarna pyłku. Ziarna dwujądrowe są tetraploidalne, w wielojądrowych natomiast znajdują się jądra di- i haploidalne. Są także ziarna 1-0-jądrowe. Po zapłodnieniu haploidalnej gamety żeńskiej poliploidalną gametą męską powstają poliploidalne nieortogonalne zygoty, które przypuszczalnie w większości giną. Stąd niska płodność badanej rośliny.

ЦИТОЛОГИЧЕСКИЕ ИССЛЕДОВАНИЯ СТЕРИЛЬНОСТИ И СЛАБОЙ ПЛОДНОСТИ ЛЕКАРСТВЕННОГО ДОННИКА (*MELILOTUS OFFICINALIS* L.)

Резюме

Исследованы причины женской стерильности и слабой плодородности у лекарственного донника с типичными цветами и с цветами в форме небольшого шарика. У женско-стерильных растений процессы мейозы и микроsporогенеза протекали без больших нарушений. В связи с этим можно предположить, что причиной женской стерильности являются нарушения в процессе мегаспорогенезы и мегagamетогенезы.

У слабо плодородного растения во время редукции хромосом и их делений в материнских клетках пыльцы были определённые отклонения (запаздывающие хромосомы, деление на хроматиды в первой анафазе). Однако, в связи с относительно небольшим процентом клеток с нарушениями не могут они быть причиной слабой плодородности. За основную причину следует считать нетипичный процесс микроsporогенезы и преобразование целого 4-ядерного микроsporочита в микроspору, а затем и дву- и многоядерные зёрна пыльцы. Двухядерные зёрна являются тетраплоидными, а в многоядерных зёрнах находятся дву- и гаплоидные ядра. Имеются также одноядерные зёрна. После оплодотворения гаплоидной женской гаметы полиплоидной мужской образуются полиплоидные неортогональные зиготы, которые по всей вероятности в большинстве своём погибают. Отсюда низкая плодородность исследуемого растения.