Microsporogenesis and chromosome number in *Cytinus Hypocistis* L.

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The present paper is a continuation of the embryological and cytological studies (Guzowska 1964) in *Cytinus Hypocistis* (family *Rafflesiaceae*). This species is an obligate parasite of *Cistus* roots (Chiarugi 1924). Very few and incomplete investigations have been done on its embryology and cytology.

The flowers of *Cytinus Hypocistis* are unisexual (Mobius 1912), but frequently contain degenerate organs of the opposite sex (Heinricher 1917; Harms 1935). Male and female flowers, according to Hayek (1912) are similarly constructed. In the male flower, instead of a pistil with stigma, there is totally similar, homological

Fig. 1. Scheme of the flower structure according to Hayek.

1 — Female flower. 2 — Male flower. *p* — perianth; *br* — bract; *st* — stigma; *n* — nectary; *an* — anther.

organ, a fleshy stamen column, on top of which there is a ring built out of the connective appendages. The anthers are situated on the place exactly corresponding to the stigma papillae of the female flower.

In the literature only data concerning the number of stamens in *Cytinus Hypocistis* have been found by the author. It is interesting that these findings differ in particular references. Baillon (1886) — quoted after Bernard (1903) — mentions their number as four to ten, Thome (1904) — eight, Hayek (1912) — five, Heinricher (1917) — six to ten and even more, Harms (1935) — eight to twenty.

The purpose of the present paper was to investigate the development and structure of the anther, of the pollen grains and the chromosome number of *Cytinus Hypocistis*.

MATERIAL AND METHODS

The material for the researches has been collected by Professor S. Krupko in Kyrenia, Cyprus, and by Dr H. Piotrowska in the South of France, in the vicinity of Montpellier.

The following fixatives have been used: Regaud, F.A.A., Carnoy and Navashin.

The preparations were stained by: Feulgen reaction, iron hematoxylin after Heidenhain, crystal violet, Altman's method, celestine blue „B”, safranine „O”.

For the purpose of defining the chemical nature of mucilaginous substances appearing abundantly in anther lobes, a series of staining reactions have been applied: for pectin mucilage — ruthenium red, for cellulose mucilage-iodine in potassium iodide with an addition of 65% H_2SO_4 , for lignin — a saturated solution of benzidin in icy acetic acid, for polysaccharides — the PAS reaction (Eltman 1960).

The large quantities of mucilaginous substances of pectine and cellulose origin contained in the material, were eliminated from sections by means of several methods (Guzowska 1964).

Several attempts were carried out to identify the food materials in the pollen grains. Fats were identified by Sudan III, black Sudan „B”, and 1% and 2% osmic acid, starch and cellulose by a solution of zinc chloride with iodine and Lugol's liquid, protein — by the biurette, xanthoprotein and Millon's reactions.

The measures of cells given in the text were obtained on ground of an average calculation of 50 measurements.

RESULTS

Development of the anther and pollen grains

The perianth of the male flower of *Cytinus Hypocistis* is single, tubular, and four to six-lobed.

At the base the tube is grown together with a fleshy, central stamen column. In the investigated material, around the column there are 10 very elongated anthers adhering to it along all its length. Each anther is composed of four lobes lying parallelly one beside the other (Fig. 2).

On the transversal section of the stamen column, 10 vascular bundles are disposed in one whorl (Pl. I, Phot. 1). Each bundle, thus supplies one anther (Pl. I, Phot. 2).

The wall of the anther in its youngest development stage has two layers. The mass of sporogenous cells is separated from the epidermis by a primary parietal layer (Pl. I, Phot. 3). In its further development, out of this layer arises only endothecium and a considerable part of the middle layer. Out of the sporogenous tissue, pollen grain mother cells and tapetum differentiate.

During the period of separation of the microspore mother cells (M.M.C's) and their entering into meiosis, there follows an extension of the anther wall. At this time in the anther lobe are occurring complexes of the M.M.C's overlapping one another (Pl. I, Phot. 4). The first distinct differentiation on the circumference of these complexes takes place in preleptotene. The M.M.C's possess large nuclei

with prominent nucleoli and a dense, unvacuolized, strongly stained cytoplasm. The moment when the tapetum separates from the sporogenous tissue is rather easily perceived. External groups of cells acquire another character. The cells which differentiate in the tapetum manifest distinct differences in relation to the rest of the sporogenous tissue. Their cytoplasm stains very poorly, the size of the nuclei and nucleoli is much smaller (Pl. I, Photos. 5, 6).

The tapetum, thus, most frequently originates from the sporogenous tissue. One can, however, find dispositions of cells which show that in certain places a small

Fig. 2. Stamen column with 10 anthers adhering to it.

group of cells can sometimes have a parietal origin, while in the same lobe the tapetum has, in principle, a sporogenous origin.

The development of the middle layer in different places of the anther wall may have a various course. Usually two middle layers arise and they may be of two origin: 1) a parietal one, 2) the external one of the two layers has a parietal origin and the internal one has a common origin with the tapetum — hence a sporogenous one (Pl. I, Photos 4, 5, 6,). The separation of the middle layer from the cells which are transformed into the tapetum, can also be observed in preleptotene.

During the formation of the anther wall, the transformation of the sporogenous cells into the M.M.C's is completed. Since the stage of the I meiotic prophase the tapetum is already well developed. Most frequently tapetum cells contained 1 or 2 nuclei (Pl. II, Phot. 7), seldom 4. The tapetum, in principle, has 1 layer, but sometimes, particularly in the internal side of the anther lobes, it is disposed, in two and even three layers and links with the sporogenous tissue. The „linking” of M.M.C. complexes with tapetum cells is a characteristic feature (Pl. II, Phot. 8).

In the period of a long lasting prophase of the I meiotic division tapetum develops rapidly. The cells of this tissue get strongly enlarged, particularly in the radial direction. There appear in the cytoplasm minute vacuoles, the chondriome is rich, but still not differentiated.

At this stage begins a gradual digestion of the middle layer through the tapetum. Its first symptom is the vanishing and weak staining of the cytoplasm. Particular cells elongate and become flattened.

Among the observed stages of the I meiotic prophase, the most numerous are the leptotene, pachytene and diakinesis stages. In spite of a far advanced synchronism, it is sometimes observed in the same lobe in its top part nuclei in synizesis and in its lower part well disposed chromosomes in preleptotene. In the metaphase of the

Fig. 3. 1-nucleate pollen grain.

Fig. 4. 2-nucleate pollen grain.

j. gen. — generative nucleus; *j. weg.* — vegetative nucleus

I meiotic division, 16 small, spherical bivalents of different dimensions are found. In the anaphase a non-synchronized movement of the chromosomes toward the opposite poles sometimes occurs.

The cell wall is formed after the telophase of the I meiotic division. It is often observed that in the same lobe the M.M.C's occur in different stages of division from metaphase I to telophase II. In metaphase II, sometimes a retarded movement of 1 or 2 chromosomes to the poles was observed.

The appearance of tetrads in *Cytinus Hypocistis* runs according to the successive type similar to the one in *Rafflesia patma* and *Brugmansia zipelli* (Ernst, Schmidt 1913).

Out of several possibilities of the disposition of microspores in tetrads it is the isobilateral type that prevails, though one can often find tetrads disposed according to the „deccusate” type (Pl. II, Phot. 9). The diameter of the microspores amounts to about 11 μ . They have small vacuoles and are rich in minute chondriosomes. In the formation stage of the tetrads, the tapetum cells attain their maximum development (Pl. II, Phot. 10). Their particular cell components become maximally differentiated. The first symptoms of the onset of degeneration in the tapetum cells are observed in the stage of uni-nucleate pollen grains (Pl. II, Phot. 11). Their cytoplasm is dense and contracted with lumpish formations strongly staining with hematoxylin after Regaud's fixative. They make the impression of plastids. Simultaneously the two middle layers present a picture of strongly flattened, vanishing remnants, while the endothecium begins to develop very vigorously.

The uni-nucleate pollen grains have small vacuoles (Fig. 3). No appearance of one large central vacuole has been observed. It is probable that in *Cytinus Hypocistis*, as well as in *Juncus*, *Luzula*, *Hawortia* (Steffen 1963) the shifting of the nucleus

Plate I

Phot. 1. Stamen column — transverse section. $\times 30$.

Phot. 2. Stamen column. Each anther is supplied by 1 vascular bundle. $\times 50$.

Phot. 3. Anther lobe. The sporogenous tissue is separated from the epidermis by a primary parietal layer. $\times 300$.

Photos. 4, 5, 6. Anther lobe at the moment when the tapetum separates from the sporogenous tissue. Phot. 4. $\times 180$, phot. 5. $\times 500$, phot. 6. $\times 850$. t.c. — tapetum cell.

Plate II

Phot. 7. 1- and 2-nucleate tapetum cells. $\times 550$.

Phot. 8. „Linking” of M.M.C's with tapetum cells. $\times 450$.

Phot. 9. Tetrads. $\times 1100$.

Phot. 10. Maximal development of the tapetum cells. $\times 400$.

Phot. 11. Stage of 1- nucleate pollen grains. The tapetum degenerates. $\times 400$.

Phot. 12. Endothecium. $\times 800$.

Phot. 13. Germinating pollen grain. $\times 800$.

towards the wall also occurs without the participation of a large vacuole. The sporoderm is composed of a very thin intine and exine whose external part — the sexine, has a delicate carving and the nexine is rather thick and optically empty. Erdtman (1952) classifies the pollen grains of *Cytinus Hypocistis* among the subisopolar ones. The apertures are not distinct. They are covered by a thin membrane. The most frequently met grains are bilateral with two apertures.

In the maturing period of the pollen grains, a progressive degenerative process of the tapetum layer takes place. Originally, in the area of the cell wall there occurs a disintegration of the cytoplasm and nucleus. At last, whole cells contract and

Figs. 5, 6. Germinating pollen grains.

j. gen. — generative nucleus; j. weg. — vegetative nucleus

disintegrate. Their strongly staining residues sometimes fuse. In the tapetum cells a vanishing of their walls is never observed and periplasmodium is not formed. Thus, the tapetum of *Cytinus Hypocistis* belongs to the secretory type. Directly after the complete degeneration of the tapetum in situ (in stage of 2 — nucleate pollen grains), the most vigorous development of the endothecium follows with its distinctly fibrous thickenings. (Pl. II, Photo 12). In the stage of mature pollen grains the endothecium becomes bent and the anther lobes open bursting lengthwise.

The mature pollen grains are small (Fig. 4) and, according to Erdtman's classification (1952), ought to be reckoned among „sporae minutae”. Their size amounts to $14,5 \mu \times 20,5 \mu$. The generative cell has a lenticular shape. Its nucleus which is very intensively stained by Heidenhain's iron hematoxylin is surrounded by a distinct, separate cytoplasm distinguished from the cytoplasm of the vegetative cell. The

nucleus of the vegetative cell rapidly degenerates. Feulgen's reaction allows to distinguish in the nucleus of the generative cell nucleoli which are in the middle, as well as numerous, more strongly staining chromocentres concentrated near the nucleus membrane. The nucleus of the vegetative cell gives a weak Feulgen's reaction what is a proof of a smaller DNA content (La Cour 1949) as compared to the nucleus of the generative cell. In *Cytinus Hypocistis* the mature pollen grains are bicellular.

It seems interesting that pollen grains germination can begin in the closed pollen lobes, inside the mucilage filling these lobes (Pl. II, Photo 13).

Germination is associated with the formation inside the pollen grain of a central vacuole which pushes the cytoplasm out to the tube, as was similarly observed by Wóycicki (1926) in *Haemanthus Katharinae*. Most frequent both the generative and vegetative nuclei enter together into the pollen tube (Fig. 5), and the adaptation of the vegetative nucleus shape to the size of the aperture in the pollen tube has been observed. Usually, however, the generative nucleus enters first into the pollen tube and is then followed by a degenerating, amorphous vegetative nucleus (Fig. 6). Often, after the generative nucleus has entered the pollen tube, one does not perceive around it its own cytoplasmic sheath any more.

As a result of numerous experiments with the purpose of finding food materials in the pollen grains, it was ascertained that no starch appear in mature pollen grains. Neither there were any fats, but they could have been rinsed off by the fixative.

Chromosome number

Chromosome number in *Cytinus Hypocistis*, just as in many other representatives of the *Rafflesiaceae* (Darlington, Janaki 1945, Darlington, Wylie 1955), has not been established until now. Darlington's Atlas of chromosomes

Fig. 7. Metaphases of the I meiotic division.

Fig. 8. Somatic metaphase.

(1955) gives their number as $2n = 40$ for *Mitrastemon yamamotoi* and *Mitrastemon kawa-sasakii*. Ernst and Schmidt (1913) give the haploid number for *Rafflesia patma* as 12 chromosomes (4 long ones, 4 middle — sized and 4 short ones) and Olah (1959) also $n = 12$ for *Rafflesia Arnoldi*.

The number of chromosomes in *Cytinus Hypocistis* has been investigated in the I meiotic metaphase in the M.M.C's, in dividing cells of external parts of nucellus

in very young buds, and in sporadic cases, in mitoses appearing in archesporial cells of pollen grains. In one case in a dividing triploid endosperm nucleus 45—48 chromosomes were found. On the base of counting bivalents in 80 plates of the I metaphase (material belonged to 6 male flowers) it was revealed 16 as the haploid chromosome number for *Cytinus Hypocistis* (Fig. 7). They are, on the whole well disposed, and owing to this fact their counting up does not present any difficulties. Particular bivalents are very minute and spherical in outline.

The somatic number of chromosomes found in the external parts of nucellus in very young buds and in the archesporial cells of pollen grains is $2n = 32$ (Fig. 8). The distinction of particular chromosomes in the mitosis was very difficult. They have indistinct outlines, are stuck and badly disposed. Therefore, we did not succeed in making an idiogram for them. They show great differences in their length and morphology. In some chromosomes one could observe a primary constriction. No appearance of satellites was ascertained.

DISCUSSION

In the structure of the stamen of *Cytinus Hypocistis* certain primitive features are noted. Because of that, one can compare its structure with the stamen of more or less primitive families: *Magnoliaceae*, *Nymphaeaceae*, *Annonaceae*, classified (Schnarf 1931) together with the family *Rafflesiaceae* into the order of the *Polycarpiceae*. The representatives of these families, as well as *Cytinus Hypocistis*, have no distinct border between the filament and the anther. Most frequently the filament fuses with the anther. The connective, similarly as in *Magnoliaceae* (Eames 1961) is very massive and passes directly into the filament, thanks to that the filament, the connective and its appendage are not distinctly separated. The appendage of the connective which is so distinct in *Cytinus Hypocistis*, is also a typical feature of the anther of primitive families. If one compare the typical structure of a primitive stamen with that of *Cytinus Hypocistis*, one can suppose that the central column of the stamen arose from the fusion of massive connectives and stamen filaments (Bernard 1903).

Analysing the changes taking place in the external layer of the sporogenous tissue which begin in preleptotene, it was found that part of the cells belonging to one complex becomes determined as the tapetum and part as the M.M.C's. The sporogenous origin of the tapetum in *Cytinus Hypocistis* constitutes a very primitive feature of the *Rafflesiaceae* family and indicates its relationship with less specialized groups of the *Polycarpiceae* order. The tapetum of sporogenous origin appears in the first place in the *Polycarpiceae* and *Helobiae* orders, and was described for the first time by Coulter (1898) in *Ranunculus septentrionalis* and by Swingle (1908) in *Myosurus minimus*. Jalan (1963) has established the parietal origin of the tapetum in *Actea spicata*.

Schnarf (1929, 1931) following Ernst and Schmidt (1913) found that the tapetum cells of *Rafflesia* are uni-nucleate. In the material used for the present study, the author has often met 2 and 4 nuclei in the tapetum cells of *Cytinus Hypo-*

cistis. In *Rafflesia* like in *Cytinus*, the tapetum does not form any periplasmodium. The successive division of the pollen mother cell is common for both these plants.

The sexine in the pollen grain of *Cytinus Hypocistis* has a delicate, not very distinct carving. According to Erdtman (1952) the pollen grains of *Mitrastemon yamamotoi* are similarly constructed, though their size is somewhat larger and amounts to $19,5\mu \times 25\mu$. *Rafflesia patma*, however, has pollen grains of the "psilate" type, without apertures.

One could always observe around the generative cell nucleus, a distinct cytoplasmic sheath. The existence in the pollen grain of the generative cell with its own, separate cytoplasm seems now already quite certain (Krupko 1926; Cooper 1936; Poddubnaja-Arnoldi 1936; Maheshwari 1950; Gerassimova-Navashina 1960, 1961; Steffen 1963), though Venema and Koopmans (1962) deny the existence of a „cell in a cell" in the pollen grain of *Tradescantia virginiana*.

The vegetative nucleus entering the pollen tube showed symptoms of a far advanced degeneration. Poddubnaja-Arnoldi (1936), too, considers the vegetative nucleus as a degenerating structure of the pollen grain, though Bishop and McGowan (1953) suggest that the vegetative nucleus plays some role in generative nuclear mitosis.

The most curious moment in the development of the anther in *Cytinus Hypocistis* is a mass germination of the pollen grains inside the closed anther lobes. This phenomenon was not noted until now, except in cleistogamic flowers. Mature pollen grains are immersed in a pectino-cellulose mucilaginous mass and begin to germinate in it. This is surely an uncommon adaptation for pollinating (insects probably transport the germinating pollen grains in mucilage), the manner of which is not yet exactly known for *Cytinus Hypocistis*. Hayek (1912) mentions many interesting details concerning the adaptation of the flower structure for pollination, but has not ascertained which insects visit the flowers of *Cytinus*. Wettstein (1935) mentions that dipterous insects and bumblebees were observed on the flowers of this plant. According to McLean and Ivimey-Cook (1956), the flowers of *Cytinus Hypocistis* which excrete the smell of putrid meat are visited by certain flies nourishing on carrion and they probably mediate in pollination. Prof. S. Krupko (personal informations) suggests the participation of snails in distributing the seeds of this plant.

The negative results of the reaction on starch in the pollen grains of *Cytinus Hypocistis* are in agreement with Guilliermond and Mangelot (1946) statement concerning the *Rafflesiaceae* family.

SUMMARY

The author has described the development and the structure of the anther, of pollen grains and chromosome number of *Cytinus Hypocistis*, a parasite of the *Rafflesiaceae* family, completely lacking chlorophyll. Its vegetative organs are much reduced. The material came from Cyprus and the South of France.

In *Cytinus Hypocistis* there are 10 anthers built out of 4 elongated anther lobes disposed in parallel beside each other. They are adhering in their full length to the central stamen column.

The anther wall is composed of 5 layers: the epidermis, the endothecium, 2 middle layers and a secretory tapetum.

It has been ascertained that the tapetum has a sprogenous origin. This constitutes a very primitive feature of the *Rafflesiaceae* family and points to its relationship with less specialized families of the *Polycarpiceae* order.

Tetrads arise according to a successive type. The arrangement of microspores is isobilateral or „decussate”. The pollen grains are small, bicellular, their size is $15\mu \times 20\mu$.

A curious feature in the development of the anther in *Cytinus Hypocistis* is the germination of the pollen grains immersed in the mass of pectino-cellulose mucilage inside the anther lobes which are closed at that time. This phenomenon is not noted except in cleistogamic flowers.

The number of bivalents in the meiosis amounts to 16, the chromosome number in metaphasal plates of mitosis = 32.

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Mikrosporogeneza i liczba chromosomów u Cytinus Hypocistis L.

Streszczenie

Opisano rozwój i budowę pylnika, ziaren pyłku oraz ustalono liczbę chromosomów dla *Cytinus Hypocistis* — całkowitego bezchlorofilowego pasożyta z rodziny *Rafflesiaceae*. Materiał zebrany został na Cyprze i w południowej Francji.

U *Cytinus Hypocistis* występuje 10 pylników zbudowanych z 4 wydłużonych, ułożonych równolegle obok siebie komór pyłkowych. Są one przyrośnięte na całej swej długości do centralnej kolumny pręcikowej. Sciana pylnika składa się z 5 warstw: epidermy, endothecium, 2 warstw przejściowego pokładu i tapetum typu sekrecyjnego.

Stwierdzono że tapetum ma pochodzenie sporogenne. Stanowi to bardzo prymitywną cechę rodziny *Rafflesiaceae* i wskazuje na jej pokrewieństwo z mniej wyspecjalizowanymi rodzinami rzędu *Polycarpiceae*.

Powstawanie tetrad przebiega według typu sukcesywnego. Układ mikrospor jest isobilateralny lub „decussate”. Ziarna pyłku są małe o wymiarach $15\mu \times 20\mu$, dwukomórkowe.

Ciekawym momentem w rozwoju pylnika u *Cytinus Hypocistis* jest masowe kiełkowanie ziaren pyłku pogrążonych w masie śluzu pektynowo-celulozowego w obrębie zamkniętych komór pyłkowych. Zjawisko to poza kwiatami kleistogamicznymi nie jest notowane.

Liczba bivalentów w mejozie wynosi 16, a liczba chromosomów w płytkach metafazalnych mitozy = 32.