Reinvestigation of embryo sac development, fertilization and early embryogeny in *Cytinus Hypocistis* L.

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INTRODUCTION

Cytinus Hypocistis was chosen for this investigation as it was of interest whether the parasitic habit of this species would in any way be reflected in the pattern of its embryological development or in the structure of the embryo sac and the young embryo.

The material was collected by Professor S. Krupko on mountain slopes near Kyrenia, Cyprus, during March and April 1941. The species was presented in abundance growing among maquis type vegetation. Pistils and anthers were fixed on the spot.

In May 1961 Dr H. Piotrowska further collected some whole inflorescences near Montpellier in the South of France.

Cytinus Hypocistis belongs to the Rafflesiaceae (Tribe Cytinae, Engler 1924, 1935), which family is next to the Balanophoraceae in importance among families comprizing tropical parasitic plants (Hutchinson 1959).

The species has already been described by Clusius in 1576 (Wettstein, 1917) under the name of *Hypocistis varia*. In 1753 it was described as *Asarum Hypocistis*. Its present name *Cytinus Hypocistis*, dates from Linneus' "Systema Naturae" volume II, 1767.

In the Mediterranean region the most frequently encountered *Cytinus* species (Wettstein 1917) is one described under the name of *Cytinus Hypocistis* subspecies — *ochraceus* by I. Gussone ("Flora siculae") 1844. It is parasitic on *Cistus monspeliensis* and *Cistus salvifolius*. It has pale yellow flowers and occurs chiefly in Sicily.

Hypocistis lutea and *Cytinus Hypocistis* var. *lutea* (Wettstein 1917) are further synonymus for *Cytinus Hypocistis*.

P. Ascherson 1864 reported the occurrence of *Cytinus Hypocistis* in Sardinia. Arcangeli 1874 and Bicknell reported the presence of *Cytinus Hypocistis* on the Riviera where it was a parasite on the roots of the white flowering *Cistus monspeliensis* and on *Cistus salvifolius* (Wettstein 1917).

R. Wettstein (1917) studied *Cytinus Hypocistis* at the Adriatic coast, where it was parasitic on *Cistus vilosus* L. He observed that the

external appearance of *C. Hypocistis* is dependant on the species of the host *Cistus*.

Cytinus Hypocistis is the only member of the *Rafflesiaceae* which has spread in some areas outside the tropical regions (Africa, Madagascar). Its natural sites are found in Sardinia and Corsica and in other areas of Southern Europe and the Mediterranean region, mainly France (Coste 1937).

Cytinus Hypocistis is an obligate parasite. It lacks chlorophyll and its vegetative organs are much reduced.

G. Nicolas 1912 (Heinricher 1934) was the first to state that *C. Hypocistis* was a parasite on roots of shrubs belonging to the genus *Cistus*, family *Cistaceae* (Chiariugi 1924). The whole plant lives inside the host tissue (Gajewski 1956) and only fleshy flowering shoots protrude above the surface. These shoots are covered with scale-like, lanceolate leaves. The inflorescence is a raceme or a spike and the flowers are coloured ochre to pale yellow.

There is an orange or scarlet — red bractiole below each flower (Thomé 1904). The flowers are unisexual and frequently contain degenerate floral organs of the opposite sex (Heinricher 1917). Flowers are either sessile or carried on short stalks. They contain large quantities of mucilaginous substances, which originate from the ovules. This mucous substance and the bright colouring are probably important in pollination and in seed dispersal. It is not yet known how seeds are dispersed (Wettstein 1935).

METHODS

Five fixatives were used: Regaud, F.A.A., Carnoy, Navashin, and Navashin following A.A. Carnoy and Regaud were found unsuitable.

Sections were cut to a thickness of 8 μ , 10 μ , 15 μ , following Navashin and F.A.A. and to a thickness 5 μ , following Regaud (used by professor Krupko in Cyprus).

The six staining methods used were: 1) iron hematoxylin after Heidenhain followed by Fast green in clove oil; 2) crystal violet and orange G in clove oil; 3) the Feulgen stain followed by an alcoholic solution of light green; 4) Schiff's reagent following oxidation in periodic acid; 5) ruthenium red; 6) iodine in potassium iodide with an addition of H_2SO_4 .

The plant material was found to contain large amounts of mucilaginous substances originating from cellulose and pectin of the mature ovules. Repeated attempts were made to remove these substances from sections, eg. 1) hot water, 2) 1% $KMnO_4$, 3) H_2O_2 in sunlight, 4) 50% alcohol + H_2O_2 , equal parts by volume, 5) absolute alcohol, ether, chloroform, carbon tetrachloride in equal proportions, 6) Stockwell's method.

None of these methods were completely satisfactory. The ovules had

Plate II

Fig. 10. First division of the zygote. Metaphase. Polar nuclei fusing. Mag. $\times 1035$

Fig. 11. Triploid endosperm nucleus in metaphase. Zygote. Antipodal cells. Mag. $\times 785$

Fig. 12. Zygote divided into an apical cell and a basal cell, Primary endosperm nucleus. Burst pollen-grain tube. Mag. $\times 670$

Fig. 13. Three cells of the proembryo. Six endosperm nuclei in anaphase (the sixth endosperm nucleus is covered by the central proembryo cell). Mag. $\times 1035$

Fig. 14. Proembryo, four cells. Four endosperm nuclei. Mag. $\times 670$

Fig. 15. Embryo. Eight cells, five layers, massive end. tissue, squashed degenerating cells of the nucellus and inner int., massive seed coat tissue. Mag. $\times 670$

Fig. 16. Embryo. Ten cells, six layers. Mag. $\times 735$

Fig. 17. Embryo. Seed coat showing thickened cross walls and simple pits. Mag. $\times 465$

Plate I

- Fig. 1. The ovule, early developmental stage. The nucellus has not differentiated. Mag. $\times 900$
 Fig. 2. The archesporial cell, inner integument beginning to be recognizable. Mag. $\times 900$
 Fig. 3. Megaspore mother cell. Leptotene. Mag. $\times 1035$
 Fig. 4. Megaspore tetrad. Chalazal cell. Mag. $\times 1035$
 Fig. 5. 2-nucleate embryo sac, three tetrad cells degenerating. Mag. $\times 1035$
 Fig. 6. 4-nucleate embryo sac. Mag. $\times 1035$
 Fig. 7. Embryo sac in the seven nuclei stage. Mag. $\times 1035$
 Fig. 8. Embryo sac. Early fertilization. Mag. $\times 1035$
 Fig. 9. Double fertilization, beginning of syngamy. Mag. $\times 1400$

Abbreviations: *s* — synergid; *E* — egg cell; *En* — egg cell nucleus; *sp* — sperm nucleus; *pn* — pollar nuclei; *in int* — inner integument; *outer int* — outer integument; *end* — endosperm; *end c* — endosperm cell; *end n* — endosperm nucleus; *ant* — antipodal cells; *m* — micropyle; *ca* — apical cell; *cb* — basal cell

decomposed into the mucilaginous material and shrivelled. They stained badly and differentiation was very difficult. They were poorly fixed as the ovary wall had proved too thick for the fixative to penetrate. It was found that it was only possible to obtain a clear picture of the ovule tissues in the rare cases when the fixative penetrated due to damage in the ovary wall.

Drawings were done with the aid of a Zeiss drawing apparatus.

RESULTS

The pistil in *Cytinus Hypocistis* is relatively large. The style ends in a rounded stigma and the ovary has a diameter of 1,3 cm. The ovary is inferior, 1-chambered and has 8 branched, tree-like, parietal placentae. The ends of the branches of each placenta bear numerous ovules. These are orthotropous and tenuinucellate.

An ovule in which the nucellus has not yet differentiated is shown in Fig. 1. The archesporial cell forms directly beneath the epidermis. It is larger than the surrounding nucellus cells. Its cytoplasm is denser and its nucleus and nucleolus are larger than those of its neighbours (Fig. 2). No indication was ever found of the division of the archesporial cell into a parietal cell and a megaspore mother cell proper.

The tissues of the first integument are recognized at about this time as bulges on either side of the nucellus (Fig. 2). This is the inner integument and it grows and develops further at the time when the megaspore mother cell undergoes meiotic division. It forms the micropyle, which is wide open at first i.e. at the 2- and 4-nucleate embryo sac stages. From the 8-nucleate embryo sac stage onwards the micropyle is shut. The outer integument begins to be visible at the megaspore mother cell stage as two out-growths on either side of the nucellus (longitudinal section), but its development is inhibited and it never grows any further (Figs. 3, 4, 5). Meiotic divisions in the megaspore mother cell were observed. Leptotene and diakinesis were the most frequent stages (Fig. 3).

Tetrads arise in the usual manner, the arrangement of the cells is linear (Fig. 4). The lowest, chalazal cell is the functional megaspore cell as is the case in *Rafflesia patma* (Ernst, Schmidt 1913). The other three cells degenerate. Their remains are long visible, even at the 4-nucleate embryo-sac stage (Fig. 6).

The chalazal megaspore undergoes the usual three somatic divisions giving rise to the 8-nucleate embryo sac, *Polygonum* Type. Numerous 2-nucleate embryo sacs were found (Fig. 5). They are filled with dense cytoplasm. The nucleoli are very big. The nuclei push away from each other, moving to the opposite poles of the embryo sac. The two nuclei are usually separated by a large vacuole. The 4-nucleate embryo sac is two to four times bigger than the 2-nucleate one. At the 4-nucleate embryo

sac stage the inner integument is massive, consisting of three layers (Fig. 6).

The shape of the embryo sac is narrow and elongate at the 2- and 4-nucleate embryo sac stage but becomes oval and often wider at the micropylar end at the stage of mature, eight nucleate, seven celled, embryo sac (Fig. 7). There were no 8-nucleate embryo sacs found at the free — nuclei stage. The egg apparatus consists of the usual egg cell and two synergids. The synergids however, are not placed one on each side of the egg cell. One of the synergids lies above the egg cell and the other one to one side of it (Fig. 7). The large vacuole lies in the lower portion of the egg cell instead of the upper part of the egg cell which is the most frequent position. The antipodal cells persist for a long time. They were still to be observed during the division of the primary endosperm nucleus (Fig. 11).

The polar nuclei are usually placed next to the embryo sac side-wall and commonly fuse before fertilization (Figs. 7 and 9). A large number of 7-nucleate embryo sacs were found. Fusion of the polar nuclei sometimes occurs much later eg. when the zygote has began dividing (Fig. 10). The normal double fertilization does take place. It is probably premitotic (Fig. 9). Triple fusion was observed in one case (Fig. 8).

One primary endosperm nucleus was found in the metaphase stage of division (Fig. 11). The chromosomes were well spread out. The endosperm nucleus begins to divide at about the same time as division begins in the proembryo. It is common for the zygote to begin dividing a little sooner and in such case the endosperm nucleus seems to be going through some sort of a resting stage (Fig. 12). There are no more than 4—6 free nuclei in the endosperm at the time when the proembryo has 3—4 cells. Endosperm development seems to be retarded in comparison to embryo development (Figs. 13, 14). The first divisions of the endosperm nucleus are not accompanied by wall formation (Figs. 13, 14). These first divisions are synchronized although sometimes irregular eg. a stage with six free endosperm nuclei, all in anaphase (Fig. 13) was found. Apparently an irregularity in the course of division led to the formation of 6 endosperm nuclei instead of the expected 8. Cross walls around the free endosperm nuclei form early. By the time the zygote consists of 8 to 10 cells the endosperm surrounds it forming a one or two layered tissue, with very large cells (Figs. 15, 16, 17). These cells squash the cells of the nucellus, which is a long lasting tissue. The large nucellus cells still surround the embryo sac when the proembryo is at the 3 and 4 cell stage (Fig. 13 and 14).

The first division in the zygote leads to the formation of two cells, the basal cell (*cb*) and the apical cell (*ca*) (Figs. 10, 12, 18A, B). The basal cell divides transversely before the division of the apical cell (Figs. 13, 18C). When the basal cell has divided to form two daughter cells (*ci* and

m) the apical cell also divides giving rise to two cells (*l* and *l'*) (Figs. 13a, 18D, E). The result of these divisions is the lineary arranged tetrad. In the next divisions cell *l* divides transversely and this is followed by a vertical division in cell *l'* (Figs. 18F, G, 14). The vertical divisions in cells *ci* and *m*, which then occur give rise to the eight celled proembryo (Figs. 15, 18H). An embryo consisting of ten cells and six tiers (diagram) is the final result, following one more vertical division in group *l'* (basal cell) and one more transverse division in cell *l'* (Figs. 16, 18I). The four cells at the micropylar end probably later give rise to the suspensor. The six larger chalazal cells will form the embryo proper. It has been concluded that the last of the described developmental stages is the final one. No evidence of further stages could be found in the material on hand. This is borne

Fig. 18. Scheme of embryo development based on figures 10 to 17.

out by some of the literature, eg. in *Rafflesia patma* and *Brugmansia zippeli* (Johansen 1950, Ernst and Schmidt 1913) proembryos in the oldest developmental stage consist of five layers of cells, of these the two upper layers have four cells each and the two lower layers have two cells each. In *Mitrastemon Yamamotoi* (Watanabe 1933) the mature proembryos have only four cells.

In *Cytinus Hypocistis* the embryo in the mature seed is not differentiated and therefore the different cell complexes of the eldest proembryos examined cannot be assigned a function with certainty. It is therefore impossible to assign it to appropriate embryological classification unit.

The outer layer of cells of the inner integument forms the seed-coat. It consists of large cells with thick, lignified walls which have numerous simple pits (Fig. 17). The tissue at either pole of the seed consists of very small, loose cells, randomly arranged. Many of these cells degenerate. At this time the endosperm is well developed while the nucellus and the inner layer of cells of the inner integument are completely squashed (Fig. 17) (Netolitzky 1926).

The seeds of *Cytinus Hypocistis* are small and very numerous. They are immersed in the mucilaginous contents of the ovary. The fruit is a berry.

DISCUSSION

Cytinus Hypocistis is discussed in the very old literature (Adamovic 1926, Engler 1896, Heinricher 1917, 1934, Kerner von Marilaun 1891, Wettstein 1917). The authors are concerned with the geographical distribution and the morphology of inflorescences, flowers and fruits of this genus.

There is only one paper dealing with the embryology of this plant i.e. Ch. Bernard (1903) "Sur l'embryogenie de quelques plantes parasites". Bernard quotes from a number of other authors concerning flower, ovule and seed anatomy but these data seem unreliable [Planchon 1844, R. Brown 1842, Le Mout et Decaisne 1868, Baillon 1886 (*Historie des Plantes. Aristolochiacees*), Solms-Laubach 1874, 1901 (*Pflanzenreich*), Hofmeister 1859].

Ch. Bernard states that there are 7—11 placenta in the one chambered ovary. There were always eight, conspicuously branched, parietal placenta in the material collected by prof. S. Krupko on Cyprus and in the material from the South of France. The branching increases gradually in the course of ovule development until eventually there are eight tree-like systems. Some authors consider the ultimate end of each branch to be a funiculus but the opinions on this subject are divided. The ovules are small, tenuinucellate.

The megaspore mother cell is directly beneath the epidermis. It has a large nucleus and a large vacuole (Figs. 2 and 3). Hofmeister was of the opinion that the above cell is the mother cell of the embryo sac. Bernard states that a linear tetrad is formed and that it is the top, or the micropylar cell in this tetrad which develops to form the embryo sac. (pg. 176, lines 4—6: "C'est la cellule superieure de cette serie axile qui deviendra sac embryonnaire, tandis que les 3 inferieures subiront un rapide ecrasement" Pl. VI, Fig. 4).

This is contrary to the sequence found in the material used in this work. It is the lowest cell of the tetrad, the chalazal megaspore, which gives rise to the embryo sac (Fig. 4). The same sequence occurs in *Rafflesia patma* (Ernst, Schmidt 1913). According to Bernard the 3 remaining cells degenerate quickly. In our material the remains of these cells could still be found at the 4-nucelar embryo sac stage and even later (Fig. 6).

There is further difference of opinion concerning the number and position of the integuments. The present investigation has shown that the inner integument in *Cytinus Hypocistis* develops fully while the outer integument stops growing at an early stage and may be recognized as two outgrowths, one on either side of the embryo sac (Figs. 3, 4, 5, 6, 8, 12, 15). The work of Netolitzky (1926) and Maheshwari (1950) confirms this. Brown (1842) considers the underdeveloped

second integument to be an arillus. Planchon (1844) is of the opinion that the arillus fuses with the integuments proper while Baillon (1866) writes: "the ovules have two integuments and the top of their funiculus grows out to form an arillus — like structure". There was no structure in the present material which could be regarded as an arillus.

According to Ch. Bernard the polar nuclei fuse early. This was not always found to be the case in the present material. Fusion sometimes took place at the time when division began in the zygote (Fig. 10).

Perhaps the most important finding, based on the present material, which contradicts Bernard's work, concerns the formation of cell walls around the antipodal nuclei. Bernard states that the antipodal nuclei soon degenerate and proper cells are never formed (pg. 178, lines 1 — 2: "... trois noyaux antipodaux, non superposés et qui ne forment jamais de cellules antipodiales"). This is known to be a characteristic of many parasitic plants. In the present investigation the antipodals were normal cells (Figs. 7, 8, 11) and they did not degenerate early (Fig. 11). According to Bernard fertilization does not take place in *Cytinus Hypocistis* (pg. 178, lines 30 — 32, "Nous n'avons jamais pu apercevoir la fécondation chez *Cytinus* et nous avons quelque raison de croire quelle n'a pas lieu"). He reports that he never found any traces of pollen grain tubes although embryo sac development proceeded as if fertilization had occurred.

In the material used in the present investigation double fertilization undoubtedly did take place. Most of the normal mature embryo sacs showed traces of pollen grain tubes (Figs. 8, 9, 11, 12). Sometimes a passage, formed due to the entrance of the pollen grain tube, was also visible (Fig. 8).

The pollen grain tube enters the embryo sac at the spot where the micropyle should be. In mature ovules the micropyle is often completely shut due to considerable dimensions of the cells of the inner integument at this stage (Fig. 9). The pollen grain tube pushes its way in between these cells, growing across the nucellus (porogamy) and it destroys one of the synergids before it pours its contents into the embryo sac. One of the sperm nuclei fuses with the egg cell nucleus and the other one fuses with either the polar nuclei (triple fusion, Fig. 8) or with the secondary nucleus (Fig. 9). A sure proof of the occurrence of double fertilization in *Cytinus Hypocistis* is the finding of a metaphase plate of a primary endosperm nucleus $\pm$ triploid (Fig. 11).

The present findings disagree with those of Bernard also in relation to endosperm development. Bernard reports that in *Cytinus Hypocistis* the endosperm is cellular. Schürhoff (1926) states that in all members of the *Rafflesiaceae* endosperm formation is preceded by a free nuclei stage. His findings agree with those of Solms — Laubach

(1892) for *Rafflesia Rochusensis* and with those of Endriss for *Pilostyles nigrae*.

Both in the Cyprus material and in the material from Southern France the first divisions of the endosperm nucleus were never accompanied by wall formation. There is a distinct free nuclei stage (Figs. 13, 14). Walls are formed much later giving rise to an endosperm tissue characterized by very large cells. One or two layers of this tissue surround and closely adhere to the developing embryo.

Johansen 1950 after Ernst and Schmidt 1913 states that the basal cell of the proembryo in *Rafflesia patma* and *Brugmansia zippeli* divides vertically while the apical cell divides transversally. The present findings show that both these cells divide transversally (Figs. 13, 14) forming a proembryo composed of four linearly arranged cells. Embryos of almost mature seeds of *Cytinus Hypocistis* were found to be composed of ten cells in this investigation (Figs. 16, 17). In *Rafflesia patma* the number of cells is also much reduced. In *Mitrastemon Yamamotoi*, a parasite on the roots of *Quercus cuspidata* (Watanabe 1933) and the only representative of *Rafflesiaceae* in Japan, embryos of mature seeds consist of only 4 cells.

There is no evidence of any kind of haustoria formation in *Cytinus Hypocistis* in endosperm as well as in embryo, and their development are normal. *Striga lutea*, *Scrophulariaceae*, a facultative parasite on the roots of the *Graminae* (maize) in South Africa, also shows no embryological evidence of its parasitic mode of life (Michell 1915).

Bernard studied four obligate parasites: *Lathrea squamaria*, *Orobanche* sp., *Phelipaea coerulea* and *Cytinus Hypocistis*. He found distinct endosperm haustoria in *Lathrea squamaria* and normal or nearly normal endosperm in *Cytinus Hypocistis*. He considers the types represented by *Phelipaea coerulea* and *Orobanche* sp. to be transitional between the *Lathrea squamaria* abnormalities and the normal *Cytinus Hypocistis* which has no parasitic characters at all in the development of its embryo sac, embryo and endosperm.

SUMMARY

Embryological investigations in *Cytinus Hypocistis* led to the following conclusions:

1. The ovary is inferior, 1-chambered and contains eight branched (tree-like) parietal placentae.
2. Mature ovules disintegrate and the ovary is filled with mucilaginous substances originating from the celluloses and pectins of the ovules.
3. The ovules are tenuinucellate. The inner integument is fully developed. The development of the outer integument is inhibited at an early stage.
4. The embryo sac belongs to the *Polygonum* type. Three antipodals persist quite a long time.

5. Double fertilization does take place. It is probably premitotic.
6. The endosperm is nuclear. Divisions in the endosperm occur simultaneously with those in the proembryo or begin sometimes after the proembryo has begun dividing.
7. The first divisions in the zygote are transverse. The tetrad cells have a linear arrangement. The embryo in the mature seed consists of 10 cells arranged in 6 tiers.

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Ponowne badania nad rozwojem woreczka zalążkowego, zapłodnienia i wczesnej embryogenii u Cytinus Hypocistis L.

Streszczenie

1. Zalążnia u *Cytinus Hypocistis* jest dolna, 1-komorowa z ośmioma drzewkowato rozgałęzionymi łożyskami parietalnymi.
2. W zalążni znajdują się olbrzymie ilości śluzów błonnikowych i pektynowych powstałych z ześluzowaciałych zalążków.
3. Zalążek jest cienkoosrodkowy z jednym normalnie rozwiniętym integumentem wewnętrznym. Integument zewnętrzny jest zupełnie zatrzymany w rozwoju.
4. Woreczek zalążkowy jest typu *Polygonum*. Trzy komórki antypod zachowują się stosunkowo długo.
5. Zachodzi podwójne zapłodnienie prawdopodobnie premitotyczne.
6. Bielmo jest typu nuklearnego, jego podziały zachodzą równolegle z podziałami prazarodka lub niekiedy są opóźnione w stosunku do rozwoju prazarodka.
7. Pierwsze podziały zygoty są poprzeczne. Tetrada jest linearna. Zarodek w dojrzałym nasieniu jest 6-piętrowy, 10-komórkowy.