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Development of the seed, endosperm and embryo in *Cynomorium songaricum* Rupr. (Cynomoriaceae)

This article finishes a statement of results of research on the embryology and life history of *Cynomorium songaricum* Rupr. Results of research on the development of the seed after fertilization, development of the endosperm and the embryo are described. According to the results of this research, the basic features of the embryology of *C. songaricum* are as follows: an apocarpous gynoecium with the characteristic organization of an ovule-ovarian complex (a single-locular ovary with morphologically unexpressed submarginal placenta and a unique trailing orthohemitropic, apotropic ovule); the ovule is highly differentiated, with a well developed vascular system; a nucellus with a pseudonucellular cap; decomposition of tissues of a nucellus occurs during growth and development of the endosperm; a monosporic embryo sac of a normal type frequently with the additional of the formation of long-lasting antipodals; for embryogenesis it lacks a suspensor, variability of the first stages of the development, the typical organization of an embryo in stages of octants and normal course of processes of differentiation of an embryoderm, a rudiment of a mature embryo is characteristic; cellular endosperm, haustorial structures are absent, the first division in the central cell of the embryo sac is transverse; endosperm cells in the mature seed have characteristically thickened walls.

The attributes listed above, together with data about its method of vegetative reproduction, confirms this opportunity to allocate the genus *Cynomorium* to a separate family Cynomoriaceae. In group Cynomoriaceae-Balanophoraceae embryological data allow one to allocate three original types of the embryological organization: *Cynomorium*-type, *Balanophora*-type and *Helosis*-type. This fact confirms heterogeneity of the initial family Balanophoraceae and allows one to raise the question about establishing subfamily Balanophoroideae at the rank of a separate family, included within it the genera *Balanophora* and *Langsdorffia*.

This present article finishes a statement of results of studying the life history and embryology *Cynomorium songaricum* Rupr. - one of the most interesting representatives of parasitic angiosperms (Terekhin et al., 1975; Terekhin, Nikiticheva, unpublished data). This report illuminates features of development and the structure of the seed of *C. songaricum* from fertilization to before maturation, and the development and structure of the endosperm and embryo. In the whole, we obtained quite full characteristic of development of the generative shoot, male and female sexual reproductive structures, micro- and megasporogenesis, development of the embryo sac, ovule, seed, embryo, and endosperm. Morphogenetically separate structures during the development of the seed are shown in interrelation with others amalgamately by developing structures. The analysis of interdependent development of structures in a seed allows one to pose some questions about the functional (biological) and evolutionary value of morphogenetic correlations and about their opportunity for use in phylogenetic research. However, in connection with an insufficient level of scrutiny with respect to the majority of data for representatives of Balanophoraceae for morphogenetic analysis, interfacing the structures of seed development cannot as yet be effectively used to make decisions on the above mentioned above questions.

Therefore the analysis of regular position *Cynomorium* resulted in the present article while is limited by separate structural attributes and to a certain extent separately considered [unique] ways of development of such structures as the ovule (before fertilization), sporogenic complexes, embryo sac, embryo and endosperm.

Some attempts at interfaced analysis and estimation of morphogenetically interconnected structures have been undertaken in a previous article that discusses different types of ovary development in *Cynomorium songaricum* (Terekhin, et al., 1975).

Some results of studying of the embryological organization and development in Cynomoriaceae and Balanophoraceae

Attributes	*Cynomorium*-type	Balanophoraceae: *Balanophora*-type	Balanophoraceae: *Helosis*-type
Gynoecium	Apocarpous	Eliminated	Lysicarpous
Ovule	Crassinucellar, orthohemitropic, apotropic	Rudimentary, but to an origin anatropous, functionally replaces a gynoecium	More or less rudimentary
Nucellus	With a pseudonucellular cap	It is considerably transformed in connection with additional function	It is reduced to some extent
Integuments	One, massive	No	No
Embryo sac	Normal type of development, it is frequent with the increased number an antipodal	Initially normal type, inverted with the reduced chalazal structures	Data are inconsistent
Antipodals	3-6, it is kept long	Are reduced	More or less reduced
Endosperm	Cellular, haustorial structures are absent, the first division cross-wise	Cellular, at the first division emerged the massive chalazal haustorium	Cellular, the first division cross-wise
Endosperm in a mature seed	Multicellular, with characteristic thickenings of cellular walls	Not multicellular, cellular walls not thickened	Multicellular, cellular walls not thickened
Embryogenesis	Early stages of an embryogenesis are similar to those at autotrophic angiosperms	Early stages of an embryogenesis are original and have no analogies among autotrophic angiosperms	Data are fragmentary
Suspensor	No	No	Possibly, is present in the majority of representatives
Embryo in a mature seed	The proembryo is reduced up to multicellular globular. Roundedly-lenticular forms	It is reduced up to few cells, the form rounded, the structure is rather original	The proembryo, egg-like forms is reduced up to globular
Vegetative duplication (from a phase of sprouts)	By formation of secondary protosomes (specialized root-like bodies of vegetative duplication)	As a rule, by "budding" a sprout of a protosoma	As a rule, by "budding" a shoot (a protosoma)

Besides the results of studying the embryology of *Cynomorium* and some members of Balanophoraceae, as presented in the summary table (in the text), we also consider as one approach to research the role of morphogenetic correlations in evolutionary transformations.

The opinion on fruitfulness of a comparative study of morphogenetic correlations for the purpose of a phylogenetic analysis is based on representation, that changes of such correlations occur during evolution to greater work, than separate, though and enough complex structures. Such changes, obviously, are connected with variation in a large number of ectogenetic factors (the large number of interacting factors defining a way of life), rather than changes in separate embryological structures. From this it follows that studying morphogenetical correlations of embryological structural complexes can appear more significant for discovering phylogenetic interrelationships, moreso than research on separate structural complexes (for example, embryo sac, endosperm, etc.).

In connection with the stated series of works devoted to studying the embryology and life history of *Cynomorium songaricum*, we consider as some kind of preparation for the direction of research planned above.

Materials and Methods

The material has been collected in semidesertic zone of Issyk-kul lake (Kirghiz SIR), where *Cynomorium songaricum* parasitizes *Nitraria sibirica* Pall. and *Peganum harmala* L.

The structural material was fixed in FAA (100 parts 70% ethanol: 7 parts of formalin: 7 parts of acetic acid) and it was also dehydrated for inclusion in paraffin by usual cytological techniques. Preparations were stained with Shiff reagent with a coloring alcyan dark blue, and also gentian-violet on Newton with differentiation in JKJ and "Orange G"in clove oil. Sections of mature seeds were stained with Sudan.

Results of the Research

Development of the endosperm. In *Cynomorium songaricum* we observed the normal process of double fertilization. The pollen tube enters into the embryo sac through one of the synergids, thus destroying it. Both synergids are ephemeral structures. The secondary nucleus of the central cell before fertilization comes nearer to the egg-cell apparatus where it merges with the second sperm nucleus, forming the triploid endosperm nucleus (fig. 1). The latter moves to the middle part of the central cell which increases considerably in size during preparation for division.

In cases observed by us, the first division of the endosperm was cross-wise [transverse] (fig. 2, the table, 2, see insert). In the two formed daughter cells the nucelli divide synchronously, and a new cellular septum develops at an angle to the septum of the first division (fig. 3, 4). The further divisions occur in different directions and not synchronously (fig. 5-8). Finally a multicellular endosperm of almost spherical form (fig. 8, 12) is formed.

During mitotic activity, endosperm cells have thin-walled cellular walls and vacuolised cytoplasm with a significant quantity of reserve materials (fig. 7-10).

During seed maturation the endosperm cells obtain the correct many-sided form. Their cellular walls are thickened due to the formation of a secondary wall in the form of a powerful layer of amorphous substances (it is probable, basically hemicellulose, covered by a thinner layer of the pectinaceous substances stained dark blue by alcyan).
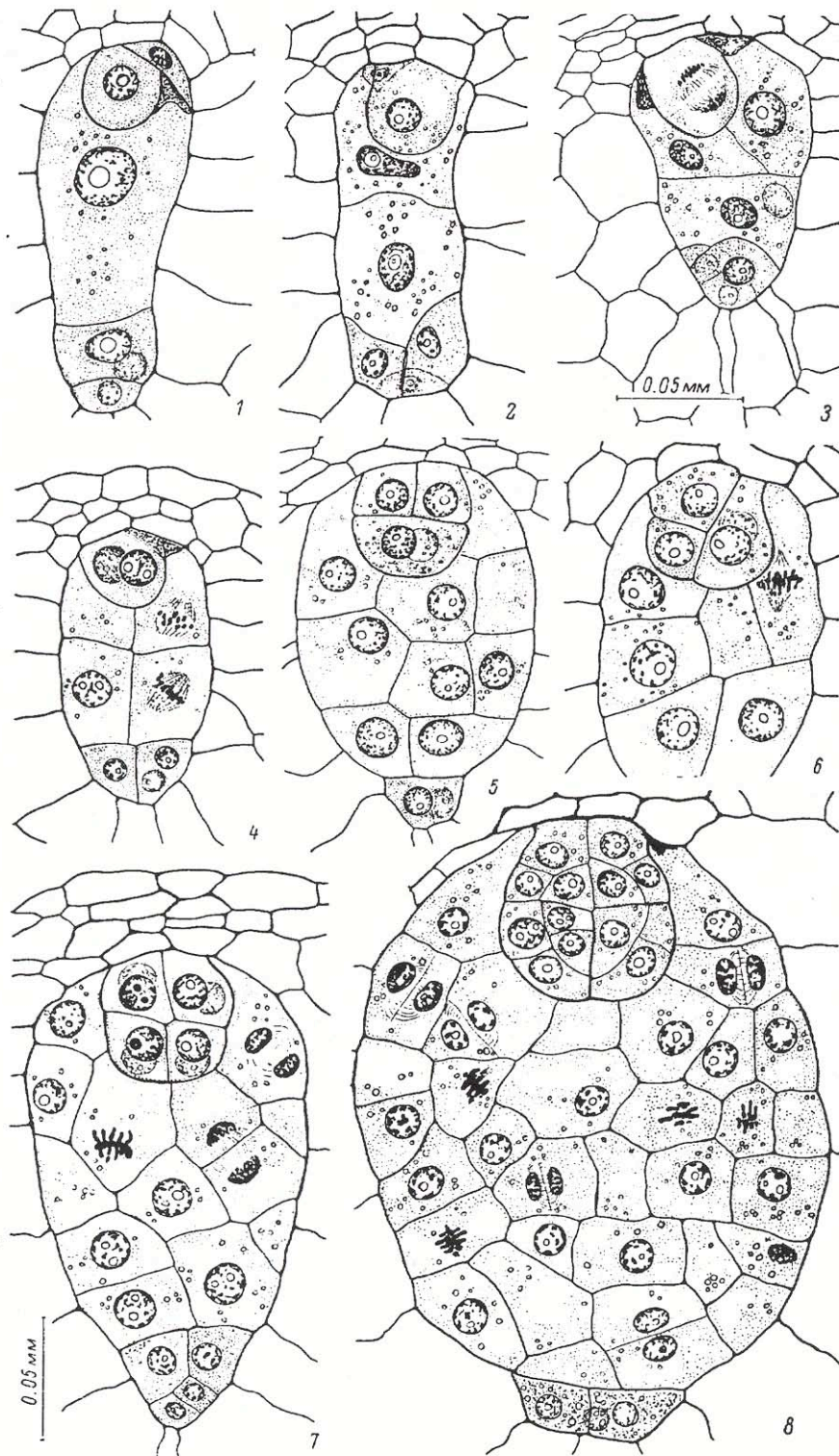
Fig. 1-11. Development of the embryo and endosperm in *Cynomorium songaricum* Rupr. 1 - a embryo sac after fertilization; 2 – first division of the endosperm; 3-8 - development of the endosperm and the initial stages of embryogenesis.
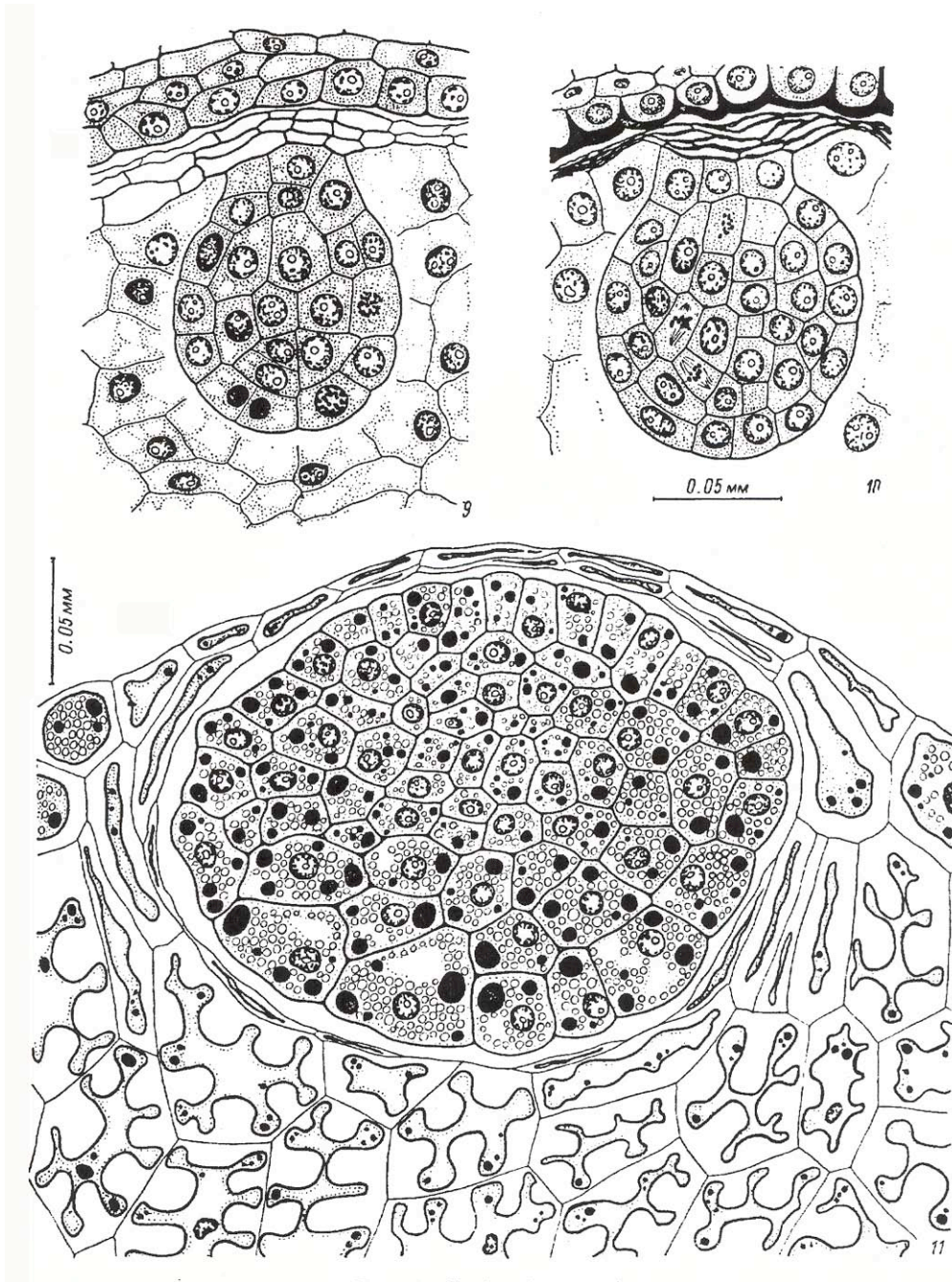
Fig. 1-11 (continued). 9-10 - average stages of development of the embryo; 11 – embryo and endosperm in a mature seed.

In a mature seed, superficial endosperm cell layers have at regular intervals thickened walls, a viable nucellus and a dense cytoplasm rich with lipids and fiber. In the internal cells of the endosperm the amorphous layer of cellular walls has another structure: at some sites ledges of this layer come deeply inside the cell whereas at other sites this layer, on the contrary, is thin enough. Primary walls in this case keep the initial position.

The uneven development of of secondary cellular wall thickenings grow from peripheral cells to the central part of the endosperm; in cells of this part are observed long, interweaving grows (fig. 11, the table 4, see insert), representing a typical picture of a labyrinth of walls.

Formation of a labyrinth of walls in the internal endosperm cells is accompanied by reduction in the quantity of cytoplasm and reserved substances, and also deformation and disorganization of the nucellus (fig. 11, the table, 4). Thickened walls from polysaccarides, making up the great bulk of endosperm in a mature seed, are possibly the most convenient form for this plant for the preservation of nutrients during embryo maturation and their mastering during its germination.

Thus, endosperm of *C. songaricum* is characterized by a cellular type of development. The tissue of the endosperm is simple in structure, consisting of homogeneous cells and is deprived of any specialized formations of a haustorial type.

Prominent feature of cells of the mature endosperm of *C. songaricum* are thick-walled secondary walls from polysaccarides (representing the basic reserve substance of the endosperm) and ruminate processes on the internal surface of these walls.

Antipodals. The embryo sac of *C. songaricum* forms from 3 to 5 antipodals. They represent large cytoplasmically dense cells of a glandular type (table, 1, 2, see insert). Antipodal cells are kept in an active condition during the long period of seed development (fig. 1-8), up to that time when an expanding endosperm supersedes the rests of a nucellus in the chalazal area of the ovule.

The structure of the antipodals, the long period of their ability to live coterminous with the period of growth of the endosperm and decomposition of the nucellus, testifes to their active metabolic function as intermediary between these two tissues.

Embryo development. After the sperm merges with the egg cell nucleus, the zygote gets the tension condition. Its nucleus settles down in the center of the cell, abundant cytoplasm is formed, and in regularly distributed intervals a vacuole is observed. Before division the zygote represents a large spherical cell with poorly expressed polarity and a large area of attachment to tissues of the nucellus (fig. 1-3). The first division of the zygote, as a rule, is transverse (fig. 3, table, 2, see insert). The planes of divisions in apical and basal cells of the 2-celled proembryo settle down perpendicularly to a plane of division of the zygote and to each other. As a result of these divisions the 4-celled proembryo with the cells located transverse (fig. 5) is formed. A subsequent "wave" of mitoses leads to the formation of a spherical proembryo with a typical two-storied structure, with four cells in each "floor" (a stage of octants) (fig. 7, table, 3, see insert).

In some cases formation of a typical structure of octants is reached in embryogenesis in another way. The zygote divides along an axis (fig. 4), connecting a place of its attachment to a nucellus and the apical part, however already following (perpendicularly located to the first and to each other) divisions in daughter cells lead to the characteristic formation of a 4-celled proembryo (fig. 6). As a result of the subsequent "wave" of mitoses in cells of the proembryo, the usual structure of a octants stage is also formed.

The variation in orientation of divisions of the zygote and 2-cellular proembryo in *C. songaricum* can explain that for this investigated genus embryogenesis proceeds without formation of a suspensor (fig. 1-8, the table, 2, 3, see an insert) and, hence, removes the necessity for a strict determination of the orientation and sequence of the first two divisions. Observations by Hofmeister (1859) about presence a suspensor on the embryo of *C. coccineum* have not proved to be true in our research. Data by Weddel (1861) and Juel (1903), no less than our materials, have led us to the conclusion that, not only in embryogenesis of *C. songaricum*, but also in the embryogenesis of the genus *Cynomorium* as a whole, suspensors are not formed.

At the following stage of development of the embryo there is a separation of embryoderm histogenes [initials?] as a result periclinal cell divisions of octants (Fig. 8). In the further cells of an embryoderm share anticlinal, and internal cells globular a proembryo share both in longitudinal, and in

cross-section directions, forming a multicellular tissue in which, however, there is no further differentiation on histogenes [initials?] of periblema and pleroma (fig. 9, 10).

At all stages of development the embryo has a spherical or oval form and is attached to a nucellus by a surface of initially one, and then two and four cells (fig. 1-10). These basal cells also carry out the function of suspensors.

After the termination of mitoses, during preparation of an embryo for transition to a resting condition, its cell, being approximated, lose the meristem-like faceted form. In the basal area of the embryo it remains small, in the apical part it considerably increases in size. A consequence of this is the appreciable histologic differentiation of an embryo into two poles. The embryo in a mature seed (fig. 11) attains the characteristic flattened-oval form, the embryoderm is not sharply separated from the basic tissue. Cells of a mature embryo contain abundant reserve substances - lipids and rounded particles of fiber. The level and character of differentiation of an embryo in the mature seed of *C. songaricum* correspond to those in others taxa of highly specialized parasitic angiosperms (for example, Orobanchaceae - Terekhin, 1973).

The analysis of the structure of the embryo in mature seeds of *C. songaricum* [observations of Weddel (1861) on early stages of germination in *C. coccineum* and our observations above on the development of the shoots in *C. songaricum* (Terekhin, Nikiticheva, unpublished data)] allow us to come to the conclusion that, for the embryo of genus *Cynomorium*, unipolar development during germination due to concentration of morphogenetical potentialities in their basal area are characteristic.

Thus, embryogenesis in *C. songaricum* is characterized by the following laws: 1) absence of differentiation of a suspensor; 2) variability in orientation and sequence of the first two divisions; 3) typical for the majority of angiosperms and of autotrophic plants, a stage of octants and typical initial differentiation of embryoderms; 4) arrest of development at the stage of a multicellular globular proembryo: 5) unipolar development during germination.

Nucellus. Before fertilization the nucellus is already presented as quite generated tissue, 3-4-layered in the terminal and lateral areas and more massive in the chalazal part (Terekhin, etc., 1975). After fertilization, cells of the nucellus expand considerably and attain a parenchymous character (fig. 1-4, table, 1; see insert). They have a large vacuole and a very significant quantity of cytoplasm. Growth of cells of the nucellus occurs non-uniformly. While cells of the terminal area of the nucellus (area of a pseudonucellular cap) almost do not change, cells of the central part of a nucellus increase in several times.

During development of an endosperm in a nucellus, there are simultaneously two processes: increase in cell sizes, and thereof also the total amount in the nucellus, and a gradual absorption of its cells by an expanding endosperm. Parenchymous cells of the basal area of the nucellus, and also the cells of a pseudonucellular cap which are gradually squeezed by a developing embryo (fig. 10) are long maintained. By the time of a mature seed the nucellus is almost completely consumed by the endosperm. Its remains can be found in the form of a thin film between the endosperm and the integument.

Thus, prominent features of the nucellus of *C. songaricum* are the absence of destructive processes during the development of an embryo sac and the first stages of endosperm development. Decomposition of a nucellus is shifted by the time of a mature seed and connected not with development of an embryo sac, as in the majority of angiosperms, but with late stages of development of the endosperm (fig. 12).

Integument. During fertilization the unique integument of *C. songaricum* consists of 6-8-cell layers with poorly expressed tissue differentiation (Table 1, see insert). During seed development certain structural changes are observed in cells of the integument.

After fertilization, during the first divisions of the proembryo, further specialization of cellular layers in the tissues of the integument occur. Integumental tapetum consists of fine rectangular cells with dense cytoplasm, identified by their high nucleoplasm attitude. Cells of the layer adjoining the integumental tapetum are close to it in size, but more vacuolized. 2-3 layers following them are presented by large vacuolized cells containing abundant starch grains. Lastly, cells of the integumental epidermis are also strongly vacuolized, have a tabular form and also contain starch. During this period of development the cells of the integumental tapetum have thin walls.

The increase in seed size is accompanied by stretching of integumental cells, mainly in length; increase in cell width is insignificant.

During seed maturation the cell walls of the integument are thickened. In cells of the integumental tapetum the most thickened appear in the walls adjoining the endosperm, and also in the radial walls (fig. 10). In these cells living protoplasm is retained. Cells adjoining the integumental tapetum layers are compressed a little. Rounded large cells of the basic integumental parenchyma are filled with reserve substances. In all cells of the integument there are at this time substances stained orange in color (possibly from the anthocyanin group).

For cells of the integumental epidermis a thickened cutinized external wall forms and atop it a peculiar cutin layer.

It is rather interesting that in a mature seed all layers of the integument are maintained. They form the seed wall rich with reserve nutrients and represent a firm covering of the seed (fig. 12).

A prominent feature of seed wall development in *C. songaricum* is the absence of destruction of integumentary tissues during seed maturation. Unlike the majority of angiosperms in which an integumental tapetum develops after destruction of a nucellus, for *C. songaricum* it is formed in the presence of massive nucellar tissue.
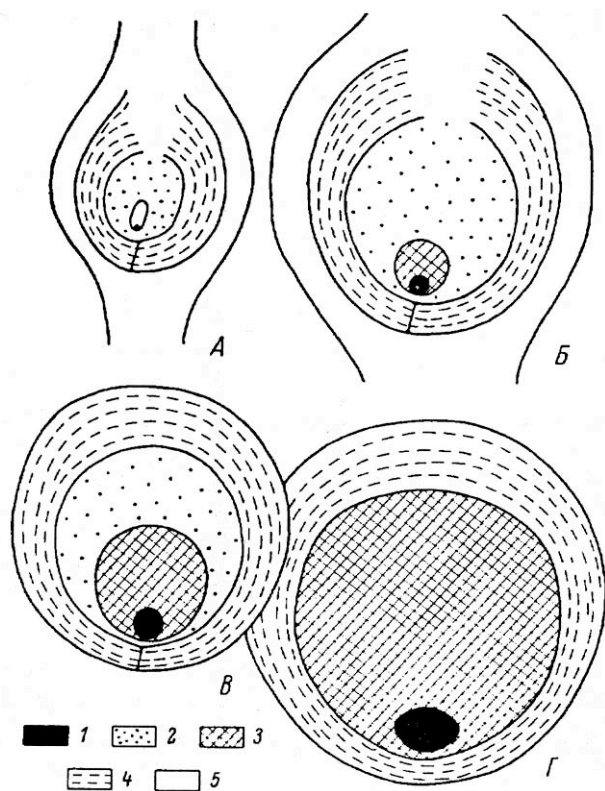

Fig. 12. Changes in the structure of the seed in *Cynomorium songaricum* Rupr. during development after fertilization.

A - a structure of an ovule after fertilization; B, C, D - structure of the seed at different stages of development; 1 - embryo, 2 - nucellus, 3 - endosperm, 4 - integument, 5 - ovary wall.

Fruit. The wall of the ovary is rather not multi-layered; during fertilization it consists of poorly differentiated parenchymous cells containing starch and other reserve substances. During fruit maturation in the ovary wall there is no appreciable processes of morphological specialization of tissues. The pericarp, at all stages of fruit maturation, consists of a homogeneous parenchymous tissue (epidermis is morphologically unexpressed). In its cells a quantity of reserve substances are kept. It is interesting that at the moment of detaching of a fruit from a parent plant the part of its "leg" and the style base are also detached; they also consist of the parenchymous unspecialized cells filled by reserve substances.

The pericarp of *C. songaricum* collapses soon enough after detaching of the fruits from a parent plant. Unopened fruits of this genus can be defined, probably, like sunflower-seeds.

Discussion

The results stated in the descriptive part of the present work, and also in a previous article devoted to the embryology of *C. songaricum* (Terekhin, etc., 1975), allows one to draw the conclusion that a high degree of originality exists in the organization and development of embryological structures of *Cynomorium*. The basic features of embryology *Cynomorium songaricum* are summarized as follows:

1) an apocarpous gynoecium with the characteristic organization of an ovule-ovarian structural complex; a single-chambered ovary with a morphologically unexpressed submarginal placenta and unique trailing orthohemitropic, apotropic (by position in the ovary) ovule;

2) the nucellus is surrounded by a strong integument; in an ovule the vascular system is well developed; a characteristic attribute is the formation of a pseudonucellular cap and the absence of processes of decomposition of a tissue of a nucellus down to the last stages of the maturing of a seed;

3) the embryo sac develops via the *Polygonum*-type with frequent formation of additional antipodals and rather long functioning of the antipodal apparatus;

4) the embryogenesis is characterized by the absence of differentiation of a suspensor, variability in the first divisions, typical for angiosperms stage of octants, and features of differentiation of an embryoderm, a rudiment of a mature embryo;

5) a cellular endosperm, with its first division of initial cells transverse; haustorial structures are absent; cells of an endosperm in a mature seed are characterized by original thickenings of secondary cellular walls.

The originality of *Cynomorium* embryology is consistenet with that which is natural for parasitic plants – changes in the structures of the embryo (the reduction of its bodies and tissues) are kept highly differentiated structures of an ovule. These last circumstances sharply segregate *Cynomorium* from other representatives of Balanophoraceae and Sanlalales as a whole.

Thus, comparison of results of our research on the embryology of *Cynomorium songaricum* (Terekhin, etc., 1975) and the present message).

By studying the obtaineddata on the embryology of Balanophoraceae (Hofmeister, 1859; Fagerlind, 1945a, in; Terekhin, Jakovlev, 1937, etc.), one is allowed to come to a conclusion about essential distinctions in the organization and development of embryological structures of *Cynomorium* and representatives of Balanophoraceae.

By studying the embryology *Cynomorium* and Balanophoraceae a comparison is given in the table in the text.

In 1967 while studying the embryology within the limits of the family Balanophoraceae, E.S.Terekhin and M.S.Jakovlev have allocated the two types of embryological organization: *Balanophora*-type and *Helosis*-type. Now it is obviously not possible to speak about two, and about three types of the embryological organization in group Balanophoraceae-Cynomoriaceae. Comparison of the data resulted in the table, which shows that the *Cynomorium*-type of organization in all essential

embryological attributes differs sharply from the *Balanophora*-type and considerably from the *Helosis*-type. The most essential distinctions concern the organization and developments of an ovary, an ovule and an embryo. At the same time some general features are found in such attributes in which similarity undoubtedly is caused by the way of life (ectoparasitic). From here follows that basic attention should be given to studying the taxonomic position of *Cynomorium* and its relations in a comparative study of the structures least subject to convergent changes under the influence of a similar way of life, namely - to the organization of an ovule-ovarial complex and features early and during mid stages of embryogenesis.

Following this principle, we posit the following basic conclusions.

1. Distinctions in the organization and development of an ovary, an ovule and an embryo in *Cynomorium* and the studied representatives of Balanophoraceae confirm an opportunity to allocate the genus *Cynomorium* as separate from Balanophoraceae: Cynomoriaceae (Takhtajan, 1966). Their vegetative propagation also testifies to the same basic distinctions.

2. Distinctions in the organization and development of the basic embryological structures in the subfamily are representative. Balanophoroideae (*Balanophora* and *Langsdorffia*), on the one hand, and other studied representatives of Balanophoraceae on the other, allow one to raise the question about the separation of subfamily Balanophoroideae as a family from the former name (Balanophoraceae). Under this name the plants with three different types of embryological organization were historically united.

3. The degree of embryological homogeneity of the representatives united by us in the *Helosis*-type of organization, now does not yield to analysis owing to an insufficient level of scrutiny of the embryology of this group of parasitic plants. Nevertheless already known features of the organization and development of the ovary, placental structures and ovules in this group of plants testify to some extent to known homogeneity of these plants and their significant differences (at the family level) from representatives of subfam. Balanophoroideae.

4. On the basis of the above embryological analysis, Balanophoraceae is now represented as consisting of three families: Cynomoriaceae, Balanophoraceae (*Balanophora* and *Langsdorffia*) and, apparently, Helosiaceae.

5. The obtained data more likely testify to varied phylogenetic origins of representatives of the three types of embryological organization (*Cynomorium*-type, *Helosis*-type and *Balanophora*-type), than to their early evolutionary divergence from an ancestor. Features of similarity in habit, shoot organization and inflorescence, and also in some terminal, embryological structural attributes, undoubtedly are caused by convergent processes under the influence of a similar way of life. Thereof they cannot form the basis for conclusions.

About a close relationship among the plants considered in the above groups. At the same time radical changes in embryological structures of the plants considered in the above groups are under the influence of a long evolution in the direction of the adaptation to a parasitic way of existence; this rather complicates the establishment of relational lines between them. It is necessary to hope that these questions will receive due illumination after the embryology of group of the plants united by us today by the embryological *Helosis*-type will be fully investigated. Inaccessible representatives for research are many exotic genera here concern us, such as *Helosis*, *Scybalium*, *Corynaea*, *Rhopalocnemis*, *Ditepalanthus*, *Exorhopala* (Helosidoideae), *Ombrophytum*, *Lathrophytum*, *Juelia* (Lophophytoideae), *Sarcophyte*, *Chlamydophytum* (Sarcophythoideae), *Hachettea*, *Dactylanthus* (Dactylanthoideae) and *Mystropetalon* (Mystropetaloideae). The low level of scrutiny on the above-listed plants allows one to look with some share of optimism to future progress in our knowledge of related lines of Balanophoraceae-like representatives of parasitic angiosperms.

LITERATURE

Takhtajan A. (1960). Systematics and phylogeny of angiosperms.

E.S.Terekhin (1973). Laws of evolutionary transformations of embryonal and reproductive structures parasitic Angiospermae. D. Sc. thesises

E.S.Terekhin, M.S.Jakovlev (1967). Embryology of Balanophoraceae (to a question about homologies of "flower" *Balanophora*). Bot. Journ., 52, 6.

E.S.Terekhin, I.Nikiticheva. (1975). Development of a microsporangium, pollen grains, ovules and a embryo sac of *Cynomorium songaricum* Rupr. (Cynomoriaceae). Bot. Journ., 60, 2.

Fagerlind F. (1945a.) Bildung und Entwicklung des Erabryosacs bei sexuellen und agamospermischen *Balanophora*. Arten. Svensk. bot. Tidskr., 39, 1.

Fagerlind F. (1945b.) Bau der floralen Organe der Gattung *Langsdorffia*. Svensk. bot. Tidskr., 39.1.

Fagerlind F. (1945c.) Blute und Bluetenstand der Gattung *Balanophora*. Bot. Notiser, 4 : 330-350.

Hofmeister W. (1859.) Neue Beitrage zur Kenntnis der Embryobildung der Phanerogamen, 1.

Juel H. O. (1903.) Zur Entwicklungsgeschichte des Samen von *Cynomorium*. Beich. Bot. Zblt., 13 : 194-202.

Weddel H. (1858 - 1861). Memoire sur le *Cynomorium coccineum*, parasite de l'ordre des Balanophorees. Archives Museum d'histoire naturelle, Paris 10 : 269-308.s

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