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Cytological differentiation of the embryo sac in *Boraginaceae*

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Abstract

In *Lycopsis arvensis, Cerinthe minor, Lithospermum arvense* and *Echium vulgare* the endosperm is divided into two parts: central and lateral. In *Lithospermum* and *Echium,* high polyploid single endosperm haustoria are formed and take part in nourishment of the embryo. In *Lycopsis* and *Cerinthe,* the lateral cells are lower ploid, while the polyploid synergids supply the embryo with nourishment.

This paper compares the results of my embryological investigations of *Boraginaceae* with the description given by Svensson (1925). Processes which are active in the karyological differentiation of the embryo sac are also discussed. The embryo sacs in *Boraginaceae* show high diversity with respect to their origin and differentiation of their elements. The main variability may be seen during the development of the endosperm. Svensson (l. c.) had distinguished five types of endosperm development: nuclear (*Borago*-type), cellular (*Myosotis*-type) and intermediate forms: *Lappula*-, *Lycopsis*- and *Echium*-type. The present author investigated this process in species belonging to *Lycopsis*- and *Echium*-types. According to Svensson (l. c.), both these types are characterised by development of two parts of endosperm: a large central part (endosperm proper), which is always nuclear and a smaller lateral part, which in *Lycopsis*-type is four-celled and in *Echium*-type consists of two 8-nucleate cells. The present author investigated *Lycopsis arvensis* (Małecka, unpublished), *Cerinthe minor* (Małecka, 1979) and *Lithospermum arvense* (Małecka, 1977) (*Lycopsis*-type) and *Echium vulgare* (Małecka, 1975) (*Echium*-type) (Table 1).

Endosperm development in *Lycopsis arvensis* and *Cerinthe minor* coincides generally with the pattern given by Svensson (l. c.). Slight differences appear in the chronology of cytokinesis. In *Lycopsis*, it occurs after the second mitotic division, whereas in *Cerinthe* the first mitosis of the primary endosperm nucleus is followed by cytokinesis, separating

the central and lateral part of the endosperm. In later stages, the nuclei of the lateral endosperm increase endomitotically their polyploid level up to 6n in *Lycopsis arvensis* and up to 12n in *Cerinthe minor*.

Endosperm development in *Lithospermum arvense* is quite different from the *Lycopsis*-type. The first mitosis of the primary endosperm nucleus gives rise to two-free nuclei. The second mitosis occurs first in the nucleus situated deeper in the ES. The resulting two nuclei surrounded by a dense cytoplasm and by a cell wall form a separate binucleate cell within the central cell (Fig. 1). Afterwards, this cell is pushed towards the wall of the ES and is transformed into a coenocytic haustorium (Fig. 2).

The common feature of *Lithospermum* and *Echium* is the formation of a coenocytic haustorium, however in the latter species it originates in a different way. Cytokinesis follows the first mitosis of the primary endosperm nucleus. The smaller lateral cell divides once, giving rise to two cells: the "higher" and the "lower" lateral cells. Both cells undergo three mitoses without cytokinesis and reach an 8-nucleate stage. At the stage of the proembryo, the nuclei of both lateral cells enlarge endomitotically and attain the level of 24n. At the stage of the globular embryo, the "higher" lateral cell degenerates, whereas the "lower" cell enlarges and transforms itself into a coenocytic haustorium (Fig. 5). Haustoria in *Lithospermum* and *Echium* assume the shape of a funnel which invades the integumental tissues. In both species the haustoria nuclei increase their polyploid level. In *Lithospermum* they attain 24n, at first, by means of inhibited prophases, later by endomitosis (Figs 3, 4).

In *Echium*, however, the main manner of polyploidisation is by five of six endomitotic cycles (Fig. 6). The nuclei attain 48n or 96n. In later stages, the nuclei of the haustorium partially resume their mitotic activity, which manifests itself in inhibited prophases (Fig. 7). It must be emphasized that the case of two different processes leading to polyploidisation in the same nuclei is very rare.

The development of the endosperm in all the species precedes considerably the first mitosis in the zygote. In the species in which the high polyploid haustoria are formed, the first mitotic division of the zygote starts at the stage of well developed proper and lateral endosperm. It may be supposed that the embryo requires a strong flow of nutrients for its development.

In *Lycopsis arvensis* and *Cerinthe minor*, the first mitosis in the zygote starts earlier when the endosperm proper is only few-nucleate and the lateral endosperm is not quite differentiated. Here too, the zygote needs a strong flow of nutrients, but they are attained in another way. Namely, the synergids are active in the nourishment of the zygote. In *Cerinthe minor* in the synergid nuclei of 8-nucleate ES the euchromatin

Table 1

Developmental stages of the endosperm

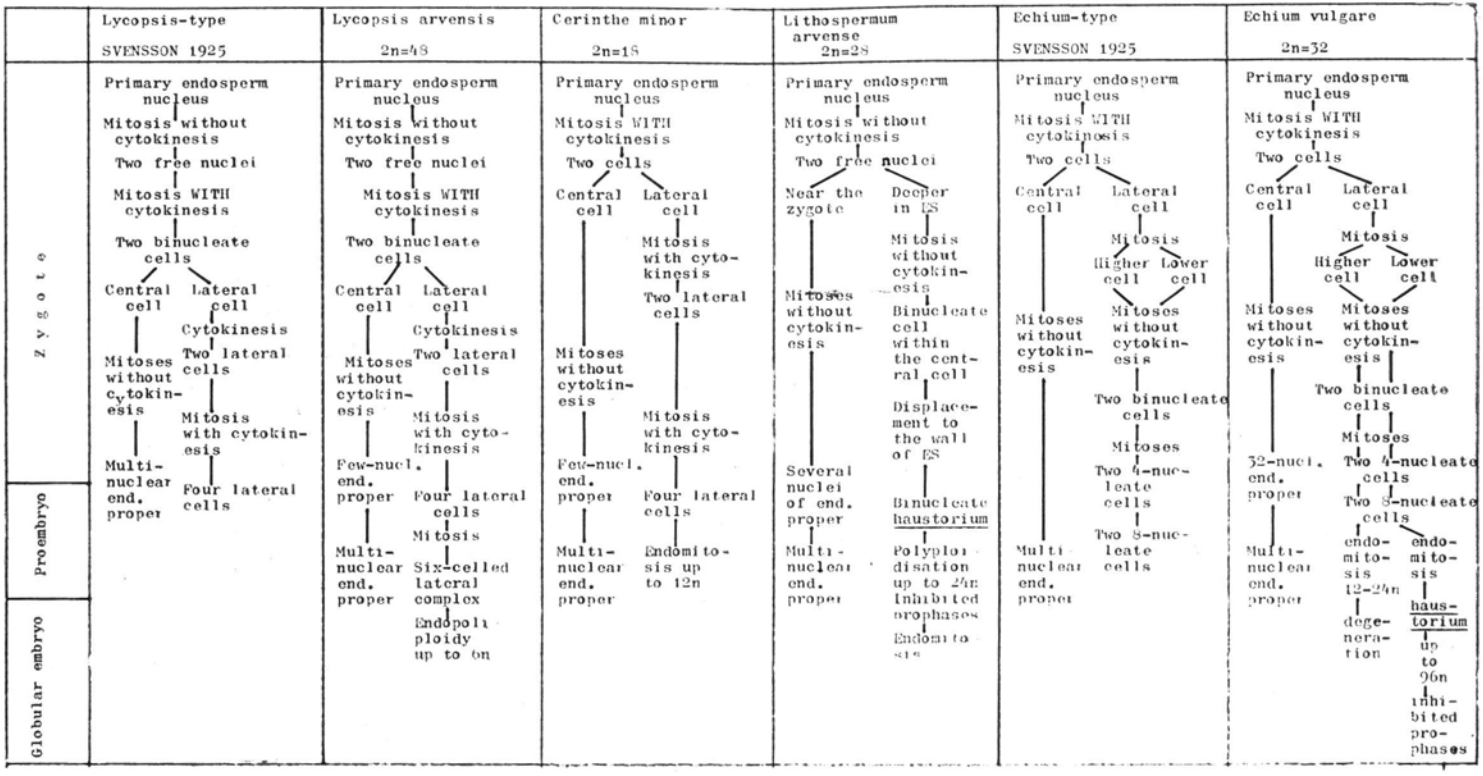
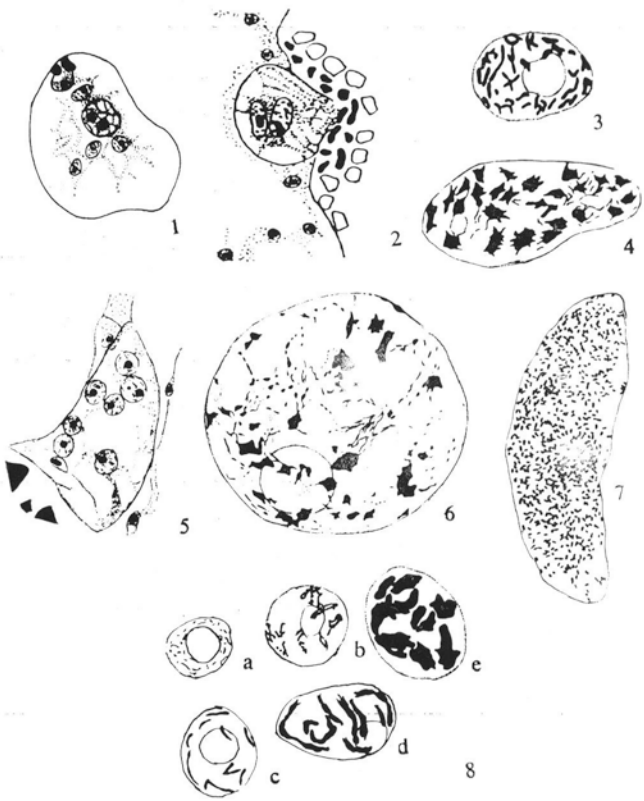


PLATE I



Figs 1-4. *Lithospermum arvense*

1 — Binucleate cell within the central cell of ES (100 ×); 2 — Binucleate haustorium (150 ×); 3 — Inhibited prophase in triploid nucleus (800 ×); 4 — Giant nucleus 24n (800 ×)

Figs 5-7. *Echium vulgare*

5 — Coenocytic haustorium (100 ×); 6 — The nucleus of haustorium 48n (1200 ×); 7 — Inhibited prophase in the giant nucleus of haustorium 48n (400 ×).

Fig. 8. *Cerinthe minor*

The developmental stages of the synergids: a — haploid nucleus; b — the nucleus in the dispersion stage; c — diploid nucleus; d — tetraploid nucleus with polytene chromosomes, e — octoploid nucleus (900 ×)

structure is distinctly marked; the thin euchromatic threads are dispersed over the nucleus. After the fusion of polar nuclei, the nuclei of the synergids enlarge endomitotically to the diploid level. The structure of these nuclei also changes; the thin chromatin threads become thicker and 9 elements may be discerned within the nucleus. During penetration of the pollen tube, one synergid is killed, whereas the nucleus of the second one increases to the tetraploid level. The enlargement of the nuclei is accompanied by a change in their structur. In some nuclei the polytene chromosomes occur as bundles consisting of four threads; in other nuclei, however, the chromosomes remain compact and only their terminal parts are lose. Few nuclei were in the disperssion stage (Figs 8 a-d). The rythmical enlargement of the nuclei as well as the occurrence of polytene chromosomes and the dispersion stage point to endomitosis as the manner of polyploidisation of synergids. At the stage of first division of the zygote, the synergid degenerates. In *Lycopsis arvensis*, the chromosomes consisting of two or four threads, as well as the size of the nuclei suggest that the tetraploid level is also attained by the synergids.

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