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CYTOEMBRYOLOGICAL STUDIES ON EASTERN GALEGA (*GALEGA ORIENTALIS* LAM.) – A NEW PAPILIONACEOUS PLANT

ABSTRACT

Embryogenesis, microsporogenesis and pollen development in eastern galega (*Galega orientalis* Lam.) have been analysed. Generally, the embryogenesis in eastern galega is similar to that of goat's rue (*Galega officinalis* L.). It is typical for eastern galega to form linear proembryos to the phase of 8 or 9 cells. The proper embryo develops from apical cells of the proembryo, while the remaining cells form the suspensor. The embryo of eastern galega typically forms a long, massive suspensor consisting of several irregular rows of cells on the side of the proper embryo and one large cell on the side of the micropyle. Suspensors were preserved in developing seeds possessing embryos with elongated cotyledons and a massive hypocotyl. In the initial phase of embryogenesis the endosperm is of a nuclear type. The transformation of the nuclear into cellular type of endosperm begins at the heartlike embryo phase and proceeds from the micropylar to chalazal end. Observations on the embryogenesis in eastern galega revealed the presence of degenerating ovules. Causes of degeneration were not analysed.

Meiotic division in PMCs leads to the formation of microspore tetrads via simultaneous cytokinesis. Mature pollen grains are two–celled with well–formed sporoderm and three germ pores through which pollen tube can emerge.

Key words: embryogenesis, microsporogenesis, pollen development, eastern galega, fodder galega, eastern goat's rue, *Galega orientalis* Lam.

INTRODUCTION

The genus *Galega* (*Papilionaceae=Fabaceae*) comprises six species, including two most common ones: *Galega officinalis* L. (goat's rue, French lilac) and *Galega orientalis* Lam. (eastern galega, fodder galega, eastern goat's rue). *Galega officinalis* L. has been known as an ornamental and medicinal plant for a long time (Broda and Mowszowicz 1979, Ożarowski and Jaroniewski 1987). However, as its green matter contains guanidino–alkaloids galegine and 4–hydroxygalegine as well as pyrroloquinazoline vasicine (peganine), *Galega officinalis* L. cannot be used as animal fodder (Gresham and

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Booth 1991, Ożarowski and Jaroniewski 1987). On the other hand, although *Galega orientalis* Lam. has various antinutrients in its vegetative parts, they are present in very small quantities (Benn *et al.* 1996, Laakso *et al.* 1990, Saloniemi *et al.* 1993). Raig (1994) suggested that the plant should be named fodder galega as it can be used for fodder making. *Galega orientalis* Lam. originates from the Caucasus area (Metlitskaya 1994 after Rollov 1908). It is found wild growing in the mountainous areas of Armenia, Georgia, Dagestan and Azerbaijan (Komarov 1945). The species has many favourable properties. Plants are perennial, winter hardy and are capable to vegetative propagation, therefore it is possible to establish long lasting plantations. Overground parts of plants, rich in protein, can be used to produce green fodder, hay, silage, haysilage or high protein dried fodder. Perennation of plants, high mass of residues after harvest, high yielding and considerable soil fertilisation potential make eastern galega a suitable plant for recultivation of devastated soils (Ignaczak and Wojciechowska 1992, Nõmmsalu *et al.* 1996, Raig 1994, Varis 1986). The first commercial cultivar of eastern galega called "Gale" was registered in Estonia in 1987. Work on the introduction of eastern galega in Poland has been carried out for several years, but due to lack of natural sites for this species the studies have concentrated solely on Estonian and Finnish forms (Ignaczak and Wojciechowska 1992, Packa *et al.* 1999, Wojciechowska and Ignaczak 1992 a, b).

In 1996 there were undertaken studies on the biology of flowering and fruiting of the Finnish form of the eastern galega grown in the province of Warmia and Mazury at the Department of Plant Breeding and Seed Production – University of Warmia and Mazury in Olsztyn. The aim of this study was to examine the course of embryogenesis, microsporogenesis and pollen development of eastern galega (*Galega orientalis* Lam.).

MATERIAL AND METHODS

Plants of *Galega orientalis* Lam. were grown in the field of the Experimental Station at Bałcyny (Packa *et al.* 1999). Plant material for the study on embryogenesis consisted of ovaries from overblown flowers and green pods of different sizes. Ovaries, new pods or seeds from older pods were fixed in FAA (formalin 40%, acetic acid 100%, ethanol 70%, at 5:5:90 ratio). The fixed material was dehydrated and stored in 70% ethanol until the analysis were started. Slides for the observation of embryogenesis were prepared according to the traditional paraffin method. Ovules were stained with iron hematoxylin and fast green (Gerlach 1972, Wędzony 1996).

The course of microsporogenesis and pollen development was analysed from the pollen mother cells stage (PMCs) to two–celled pollen

grains in the material fixed in Carnoy's solution and stained with acetocarmine or acetoorceine.

Analysis of the slides was conducted under a light microscope Jenamed 2. Microphotographs were taken with a photographic camera MF–AKS 24x36 on a black and white film Orwopan 25. Enlargements were given in individual photographs.

RESULTS

Structure of ovules

The ovary of eastern galega contains from 5 to 12 ovules. Ovaries with 8 ovules were most frequent in the pistils of open flowers (Fig. 1, quoted after Packa *et al.* 1999). Ovules are bitegmic, campylotropous, bent to the upper part of the ovary towards the style of the pistil. The micropylar end is situated near the chalazal end, on either side of the funicle.

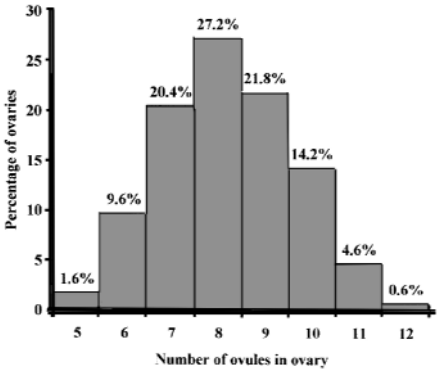
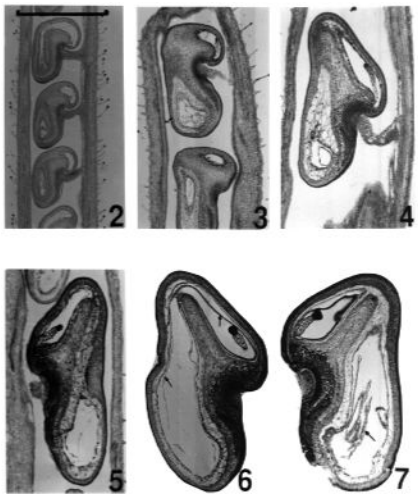


Fig. 1 Frequency of ovules in the ovary of eastern galega (*Galega orientalis* Lam.)

Development of embryo and nuclear endosperm

The development of embryo and nuclear endosperm is presented in Figs. 2 – 20. In order to compare the size of an ovules – Figs. 2 – 7 were enlarged to the same scale.

The fertilisation, first division of the zygote and subsequent division of daughter cells in the ovules of eastern galega were not analysed. However, based on the pattern of cells in proembryos composed of several cells it is possible to suggest that the first divisions are transversal, leading to the formation of proembryos built of 8 to 9 cells arranged in a linear pattern (Figs. 8–10). Apical cell of the linear proembryo, together with one or two adjacent cells, are usually small and contain dense cytoplasm which is easily stained. The cells found over the apical cells, on the micropyle side, are usually larger and vacuolised to a different degree. Linear proembryos composed of several cells were observed in the ovules shown in Fig. 2.



Figs. 2 – 7 Longitudinal cross–sections of ovules with nuclear type endosperm.
The scale bar = 1 mm

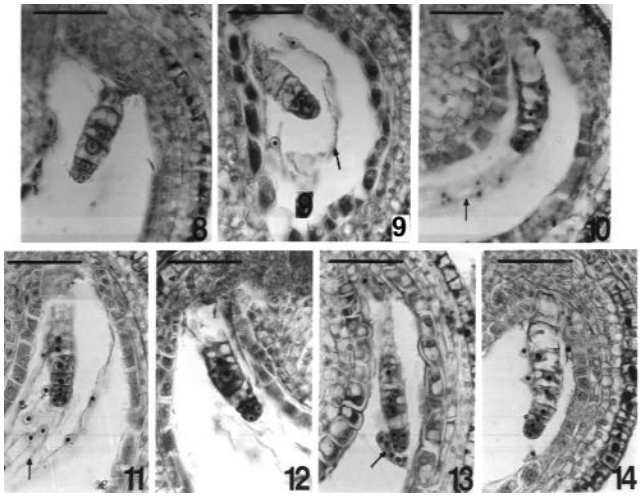
2 – Longitudinal cross–sections of ovules with linear proembryos built of several cells

3, 4 – Longitudinal cross–sections of ovules with the subglobular embryo

5 – Longitudinal cross–sections of an ovule with the globular embryo

6 – Longitudinal cross–sections of an ovule with the globular embryo. Partial layer of nuclear endosperm (arrows) surrounding the central vacuole

7 – Longitudinal cross–sections of an ovule with the embryo slightly flattened at the apex. The arrow indicates the nuclear endosperm



Figs. 8, 9, 10 Longitudinal cross–section of ovules containing linear proembryos built of 6 to 9 cells and the nuclear endosperm

Figs. 11, 12 Proembryos after longitudinal division of the apical cell

Figs. 13, 14 Embryos proper built of four cells, with cells of the suspensor seen above them.
The scale bar = 50 μm. The arrows indicate the nuclear endosperm

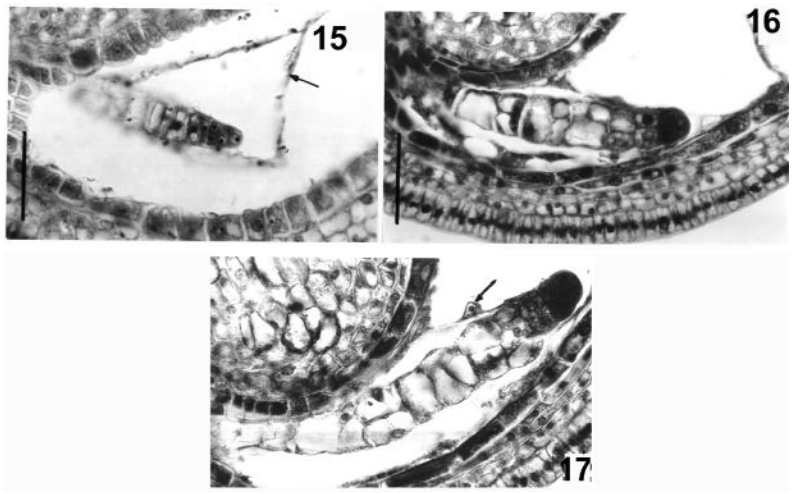
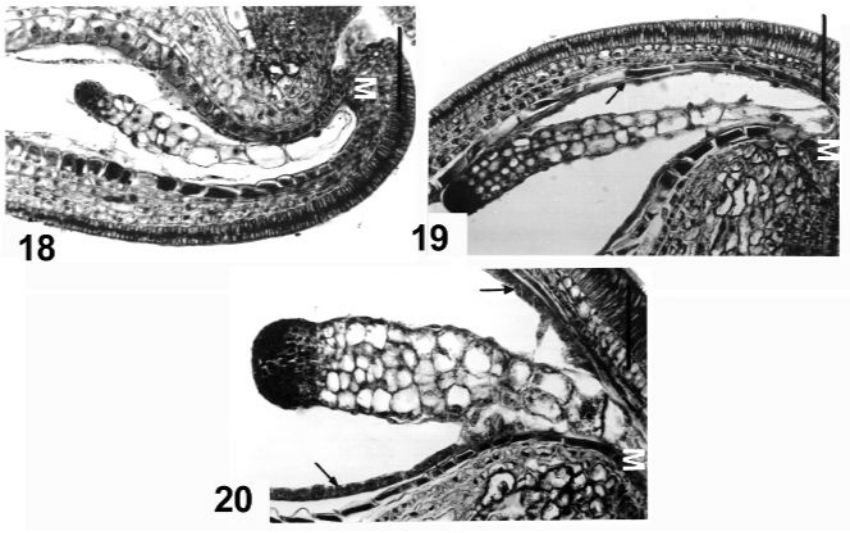


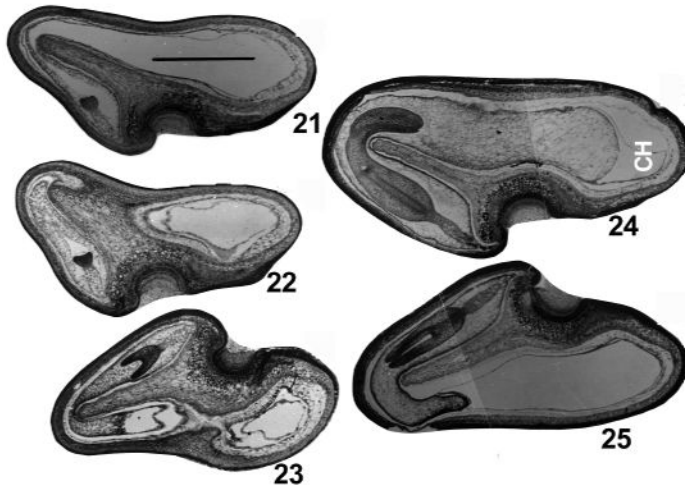
Fig. 15 The embryo propercomposed of five cellswith vacuolised cells of the suspensor seen above. The scale bar – 50 μm. The arrow indicates the nuclear endosperm

Figs. 16, 17 Successively developing proper embryosand suspensors. Some suspensor cells ar–ranged in two rows. The scale bar = 50 μm. The arrow indicates the nuclear endosperm



Figs. 18, 19 The subglobular stage embryo with the suspensor consisting of several rows of cells on the side of the embryo proper; on the side of the micropyle (M) suspensor cells arranged in one row. The scale bar = 100 μm. The arrow indicates the nucler endosperm

Fig. 20 The globular embryo with the whole suspensor visible. On the side of the proper embryothe suspensor is composed of several irregular rows of cells. On the side of the micropyle (M) one row cell wisibke. The nuclear endosperm in the form of a thin partial band surrounding the central vacuole (arrows). The scale bare = 100 μm



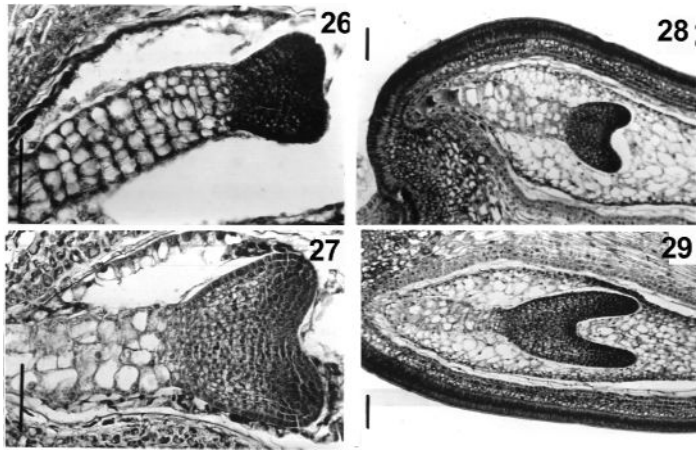
Figs. 21 – 25 Longitudinal cross–sections of ovules (new seeds) with the cellular and nuclear endosperm. The scale bar = 1 mm

21 – Longitudinal cross–section of an ovule with a heartlike embryo. The cellularendosperm in the micropylar part

22, 23, 24 – Successive stages of the embryo differentiation

24 – The cellular endosperm fills nearly half of the central vacuole

25 – The differentiated embryo with the cotyledons bent over the parenchymal apex. The cellular endosperm fills the major part of central vacuole. In the chalazal part (CH) the endosperm is still nuclear



Figs. 26, 27 Embryos at the heartlike stage. Starting from the early heartlike stage the nuclear endosperm begins to transform itself into the cellular endosperm. The scale bar = 100 μm

Figs. 28, 29 Successive stages of the embryo differentiation. Successively elongating cotyledons and hypocotyl. The cellular endosperm visible around the embryo. The scale bar = 100 μm

Fig. 30 The differentiated embryo with the whole suspensor (S) visible. A massive hypocotyl (H) and two cotyledons (C) visible in embryo. On the side of the micropyle (M) one large suspen–sor cell. The scale bar = 100 μm

Fig. 31 Longitudinal cross–section of the ovary with ovules containing embryos at the subglobular stage. Four out of seven ovules have degenerated. The scal ba = 1 mm

Longitudinal or diagonal division of the proembryo apical cell into two daughter cells initiates the formation of the proper embryo(Figs. 11, 12). However, there are exceptions. Longitudinal or diagonal division of the proembryo apical cell may be preceded by longitudinal divisions in the cells situated above the apical cell. By transversal and longitudinal divi–sions the head of the proembryo grows larger, producing in effect the proper embryoconsisting of several small cells with thick cytoplasm (Figs. 13–15). The cells located on the micropyle part grow larger, continue vacuolisation and form a suspensor. Initially, the cells of the suspensor are arranged in a linear pattern, one above another. They are distinctly different from the cells of the proper embryo, as they are larger and more vacuolised.

The proper embryo and its suspensor successively grow larger (Figs. 16, 17). The subglobular stage is formed, consisting of small cells with thick cytoplasm (Figs. 18, 19). By longitudinal and diagonal cells divisions the suspensor increases in width (Figs. 16, 17), forming several rows of cells on the side of proper embryo. The suspensor of subglobular embryos is composed of three or four rows of cells in the part adjacent to the proper embryo (Figs. 18, 19). The further away from the embryo we look, the fewer rows of the suspensor cells we can observe, and on the side of the micropyle there is only one row of large, highly vacuolised cells (Figs. 18, 19). The subglobular stage was observed in the ovules presented in Figs. 3 and 4.

Subsequently, the globular embryo of the axial symmetry is formed. Globular embryos have massive suspensors, composed of four or five rows of cells in the part near the proper embryo. Closer to the micropyle we look, the larger suspensor cells we observe (Fig. 20).

The endosperm in eastern galega is initially of the nuclear type. The primary endosperm nucleus and its derivatives undergo mitotic divisions, but caryokinesis is not accompanied by cytokinesis. In effect, one multinuclear cell is formed with nuclei lying in a thin layer of cytoplasm (Figs. 9. 10, 11, 13, 15). When the embryo reaches the globular stage, the endosperm in form of a thin layer of cytoplasm with numerous nuclei is usually found lying on peripheries of the embryo sac (Figs. 6, 20). Thicker layers of the nuclear endosperm gather at the micropylar and chalazal ends. At the chalazal end huge nuclei was observed with a clear chromatin net. The multinuclear endosperm was also noticed in ovules with embryos slightly flattened at the apex (Fig. 7). This was the last stage of embryo development at which the nuclear endosperm was ob–served.

Development of embryo and cellular endosperm

The development of embryo and cellular endosperm is presented in Figs. 21 – 30. In order to compare the size of developing seeds, Figs. 21 – 25 were enlarged to the same scale.

The globular embryo with cotyledon primordia which begins to appear now, becomes flattened, loses its axial symmetry in favour of the bilateral symmetry and assumes a heartlike shape (Figs. 26, 27). At the early heartlike stage the nuclear endosperm begins to transform into the cellu–lar endosperm. When cotyledon primordia grow larger in the heartlike embryo, cellular type of endosperm is observed around the embryo and suspensor (Figs. 28, 29).

The transformation of the nuclear endosperm into the cellular type be–gins at the micropyle end and gradually proceeds towards the chalazal end, filling the area of the central vacuole (Figs. 21 – 25). During the transformation process between the dividing nuclei and non–sister nuclei phragmoplasts are formed and, subsequently, the cell plate and cell wall are built.

In the ovules, or more precisely in the new seeds with cotyledons bent outside the parenchymal apex, the cellular type of endosperm fills larger part of the central vacuole. Some nuclear type of endosperm is only at the chalazal end (Fig. 25). In a developing seed with a differentiated embryo a suspensor is still preserved , composed of several rows of cells. However, at the micropylar end there is only one large cell (Fig. 30). At this stage of development the embryo possesses a massive hypocotyl with the root apex on the side of the suspensor and two cotyledons with the apex of the shoot placed between them. The coat of the developing seed is composed of elongated cells, adhering one to another and coated externally with some amorphous substance, which covers all the surface of the developing seed.

While observing the development of the eastern galega's embryo some degenerating ovules were noticed, in which the embryo and endosperm were not developped (Fig. 31). Causes of degeneration were not analysed.

Microsporogenesis and pollen development

The pollen mother cells (PMCs), in which meiosis takes place are enclosed in the callose wall. The first meiotic division produces a binucleate cell with a haploid number of chromosomes in each nucleus. The second meiotic division, occurring simultaneously in both nuclei produces a microspore tetrad, still enclosed in the callose wall. The microspore released from the tetrad is covered with its own wall and the nucleus is located in the central part of the cell. At the next stage the nucleus translocates towards the cell wall of microspore and through the mitosis the microspore is divided into two cells: adjacent to the cell wall a small generative cell and a large vegetative cell. The opening anthers contain two–celled pollen grains with a well–developed sporoderm and three pores, through which the pollen tube can emerge. The generative spindle–shaped cell is surrounded by the vegetative cell.

DISCUSSION

The available literature does not include any publication on the embryogenesis of *Galega orientalis* Lam., whereas the embryogenesis in *Galega officinalis* L. was described by Souèges (1949). Souèges claimed that the development of the embryo in goat's rue could be attributed to the Second Period, Series C2, Megarchetype IV. According to Johansen's system it belongs to the type of *Onagrad*. In *Galega officinalis* L. the first division of the zygote is transversal, producing the basal cell (cb) on the micropyle side and the apical cell (ca) directed towards the inside of the embryo sac. The proper embryoof *Galega officinalis* L. and the upper part of the suspensor develop form the apical cell derivatives. Basal cell derivatives constitute the remaining part of the suspensor. In *Galega orientalis* Lam. the first division of the zygote and subsequent divisions of daughter cells are transversal divisions, leading to the formation of linear proembryos composed of 8 or 9 cells. Also in the embryogenesis of lucerne (*Medicago media* Pers.) linear proembryos were observed to the stage of 9 cells (Cebrat 1967). The proper embryoof eastern galega develops from the apical cells of the proembryo, while the suspensor is produced from the cells lying on the side of micropyle end. Suspensor is an ephemeral structure in angiosperms. It usually deteriorates at the termination of the embryogenesis, but prior to this it can be of the different structures and sizes. In *Papilionaceae* suspensors are morphologically diversified (Lersten 1983). Suspensor plays a variety of roles: it gives mechanical support to the new embryo and presses it deep into the endosperm; it absorbs substances synthesised in the endosperm and transports them to the embryo; it synthesises growth regulators, which are then transferred

to the globular and heartlike embryo (Rutishauser 1973, Lersten 1983, Rodkiewicz *et al.* 1996). Globular and heartlike embryos of eastern galega had massive suspensors composed of several irregular rows of cells on the side of the embryo proper. The suspensor was present in developing seeds which contained differentiated embryos.

The course of the embryogenesis in eastern galega is similar to the embryogenesis of goat's rue (Souèges 1949). However, since early embryogenesis of eastern galega were not studied, it is not possible to de–cide which type of embryogenesis is typical of this species. The proper embryoof eastern galega developed from the apical cells of proembryo, likewise the embryo of *Astragalus glycyphyllos* L. of the tribe *Galegeae* (Bijok *et al.* 1972), *Ornithopus* sp. of the tribe *Coronilleae* (Wojciechowska, 1971), *Lotus corniculatus* L. of the tribe *Loteae* (Wojciechowska 1963), all belonging to the family *Papilionaceae* and classified as the *Onagrad* type of embryonal development.

Much the same as in *Medicago media* Pers. (Cebrat 1967), *Astragalus glycyphyllos* L. (Bijok *et al.* 1972), *Lupinus* sp. (Jaranowski 1962) the en–dosperm of eastern galega is nuclear at the beginning of embryogenesis, and begins to transform into the cellular type at the micropylar end.

The hardiness of eastern galega seeds can be attributed to a relatively thick, impregnable layer of palisade cells of the seed coat, covered with amorphous coating substance.

Depressed fertility of ovules, which is one of the factors contributing to seed setting, requires further research.

Mature, two–celled pollen grains of eastern galega are a product of microsporogenesis and gametophytogenesis. The first meiotic division produces a binucleate cell, as the karyokinesis is not accompanied by cytokinesis. The second meiotic division produces microspore tetrad via simultaneous cytokinesis, which is common in the members of the *Papilionaceae* family, i. e. *Astragalus glycyphyllos* L. of the *Galegeae* tribe (Bijok *et al.* 1972), *Trifolium pratense* L., *Melilotus albus* Med., *Trigonella coerulea* (L.) Ser. of the *Trifolieae* tribe (Bijok 1962, Bijok and Góral 1970), *Lupinus luteus* L. of the *Genisteae* tribe (Packa 1995). Mature, two–celled pollen grains of eastern galega are released.

CONCLUSIONS

Embryogenesis

1. The course of embryogenesis in eastern galega (*Galega orientalis* Lam.) resembles that of goat's rue (*Galega officinalis* L).
2. The first division of the zygote and divisions of daughter cells are transversal, leading to the formation of linear proembryo composed of 8 or 9 cells.
3. The proper embryodevelops from the apical cells of the proembryo.
4. The eastern galega embryo typically forms a massive suspensor.
5. At the initial stage of embryogenesis the endosperm is nuclear.

6. The nuclear type of endosperm begins to be transformed into the cellular type at the heartlike embryo stage and the transformation proceeds from the micropylar to chalazal end.

Microsporogenesis and pollen development

1. The first meiotic division in pollen mother cells (PMCs) leads to the formation a binucleate cell, as the karyokinesis is not accompanied by cytokinesis.
2. The second meiotic division produces a microspore tetrad via si–multaneous cytokinesis.
3. The microspore released from the tetrad is surrounded with its own wall, and the nucleus is located centrally.
4. Mitotic division of the microspore, leading to the small generative cell formation, placed by the wall, and a large vegetative cell.
5. Mature pollen grains of eastern galega found in open flowers are two–celled; the spindle–shaped generative cell is in the centre of a pollen grain, surrounded by the vegetative cell.

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