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СООБЩЕНИЯ

DEVELOPMENT OF FEMALE AND MALE REPRODUCTIVE STRUCTURES IN *BORODINIA MACROPHYLLA* (BRASSICACEAE)

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For the first time, cytoembryological study of the female and male reproductive structures development in the East Siberian endemic, *Borodinia macrophylla* (Turcz.) O.E. Schulz (order Capparales, family Brassicaceae, tribe Boechereae), is presented. The general plan of the reproductive structures development occurs similarly to the studied species of *Boechera*. The anther contains 4 microsporangia with four layers, namely epidermis, endothecium, middle layer, and tapetum at the beginning of development; as the anther matures, the wall becomes two-layered. The anther tapetum is unevenly 2-layered, microsporocytes develop simultaneously; most pollen grains in mature anthers are bicellular. The ovule is ortho-campylotropous, bitegmic, medionucellate. The embryo sac is 7-celled, 8-nucleate, formed according to the monosporic Polygonum type. The polar nuclei of the central cell in the mature embryo sac do not fuse. Female gametophytes developed in all the ovules studied. In *B. macrophylla*, only a sexual mode of reproduction was observed; no apomictic development was detected.

Keywords: *Borodinia macrophylla*, Boechereae, Brassicaceae, ovule, anther

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The tribe Boechereae of the Brassicaceae family is mainly known for the genus *Boechera* Á. Löve & D. Löve, which has become a model plant system for apomixis studies, as well as for environmental genomics and evolutionary biology (Brukhin et al., 2019; Hay et al., 2023). Plants of the tribe Boechereae have undergone a long and winding evolutionary path before reaching their current taxonomic position. Most species from this tribe grow in North America, from the Atlantic to the Pacific coast. Until now, only two species from this tribe have been reported to grow in Russia: *Boechera falcata* (Turcz.) Al-Shebaz in the Far East (Al-Shehbaz, 2005; Kiefer et al., 2009; Alexander et al., 2013; Hay et al., 2023; Vinogradova et al., 2023), which is an example of the East Asian – North American floristic disjunction, and *Borodinia macrophylla* (Turcz.) O.E. Schulz endemic to the Baikal region and Northeast Asia. Molecular genetic and phylogenetic studies have shown its close relationship with seven species of *Borodinia* N. Busch from the eastern United States (Al-Shehbaz, German, 2010; Alexander et al., 2013; Hay et al., 2023). As confirmed by Mandáková et al. (2020), the tribe Boechereae includes nine genera. Seven of these (*Anelsonia* J.F. Macbr. & Payson, *Cusickiella* Rollins, *Nevada* N.H. Holmgren, *Phenicaulis* Nutt. ex Torr. & A. Gray, *Polyctenium* Greene, *Sandbergia* Greene, and *Yosemitea* P. J. Alexander & Windham) contain only one or two species and are found in the western United States (except for a few localities across the Canadian border). The *Boechera* has been identified as a monophyletic genus, and seven eastern North American species previously assigned to *Boechera* (Al-Shehbaz, 2003; Al-Shebaz and Windham, 2010) have formed a weakly supported clade with *Borodinia macrophylla*, the type species of *Borodinia*. As a result, Alexander et al. (2013) published new combinations for these taxa under the older generic name. Thus, the *Borodinia* genus currently includes eight species (Alexander et al., 2013), seven of them inhabiting eastern North America, and one, *B. macrophylla*, is endemic to Siberia and coastal Northeast Asia (Hay et al., 2023). Based on 1114 low-copy nuclear genes using the Hybpiper pipeline, supermatrix, and species coalescence methods, Hay et al. (2023) performed a molecular phylogenetic analysis of members from the Boechereae tribe and found strong support for monophyly in both Boechereae and *Boechera* as well as other genera of the tribe, represented by two or more genera (*Borodinia* and *Sandbergia*). *Nevada* was found to be a close relative of *Borodinia*, and the Siberian *B. macrophylla* (=*B. baicalensis*, or *B. tilingii*) was found to be the closest relative of the eastern North American *Borodinia* species. Since it is near-threatened (NT) species it is included in the Red Book of the Republic of Buryatia (Anenkhonov, Chimitov, 2023).

Borodinia macrophylla plants are tap-rooted, small, up to 20 cm tall, with rosettes of leaves forming turfs. The stems bear small, no more than six leaves; basal leaves form rosettes. The inflorescence is a few-flowered raceme containing small flowers with pale yellow petals, 6–8 mm in diameter. The siliques are narrow (3–4 mm), up to 5 cm long (Fig. 1) (Anenkhonov, Chimitov, 2023). *B. macrophylla* is endemic to North Asia. Found in Buryatia, Irkutsk region, Transbaikal region and Khabarovsk region. *B. macrophylla* grows in highlands, in gravelly and lichen tundras, on scree and rocks (Chimitov, Imetkhenova, 2019).

The *Borodinia* species so far mentioned in literature are sexual diploids (Li et al., 2017; Hay et al., 2023). However, embryological studies of *Borodinia* species were not found in scientific publications, in addition, there is hardly any information about the Siberian species *B. macrophylla*.

Previously, we studied the development of female reproductive structures in the Far Eastern endemic *Boechera falcata* (Vinogradova et al., 2023); in this paper we analyze the formation of female and male reproductive structures in another endemic belonging to the tribe Boechereae – *Borodinia macrophylla*, growing in the Baikal and Transbaikal region, as well as in the Sea of Okhotsk region, information about the reproductive characteristics of which was absent so far.

MATERIAL AND METHODS

Inflorescences of *Borodinia macrophylla* (Fig. 1) were collected in the summer 2021 on Bayan-Khongor Mount (remnants in the upper part of the forest slope) in the vicinity of Bayangol village, Khorinsky district, Republic of Buryatia (Chimitov, Imetkhenova, 2019).

Buds, flowers and ovaries at different stages of their development were fixed in FAA (formalin: glacial acetic acid: 70% ethyl alcohol in a ratio of 7: 7: 100) for 7 days, then the material was washed with 70%

Fig. 1. *Borodinia macrophylla* in Buryatia. *1* – flowering plant, *2* – plant with siliques.

Рис. 1. *Borodinia macrophylla* в Бурятии. *1* – цветущее растение, *2* – растение с плодами.

ethyl alcohol and used for preparing permanent slides following by their analysis under light microscopy (LM).

Processing of the material and preparing the slides followed common cytoembryological technique (Pausheva, 1980). Sections of 8–10 μm thick were made using a Microm HM 325 microtome (Carl Zeiss, Germany). The sections were stained with hematoxylin according to Ehrlich and with Alcian blue. The slides were analyzed under an Axio Imager Z1 microscope (Carl Zeiss, Germany) of the Core Facilities Center at the Komarov Botanical Institute RAS; photographs were taken with an Axiocam MRc5 digital camera and processed with Zen Blue Editor software (Carl Zeiss, Germany).

RESULTS

Analysis of the reproductive structures development in *Borodinia macrophylla* was performed at cytomorphological level. Male and female reproductive structures in this species develop in the same way as in the studied *Boechera* and other Brassicaceae species. *Borodinia macrophylla*, studied here for the first time, showed a sexual mode of reproduction.

Development of male reproductive structures in Borodinia macrophylla

The analysis of the male reproductive structures development showed normal formation of all six anthers in the flower. The anther of *B. macrophylla* is tetrasporangiate; numerous microsporocytes are formed in each microsporangium. Microsporogenesis occurs according to the simultaneous type, with both meiotic divisions following one after the other without cytokinesis, which results in a cell with 4 nuclei (Fig. 2, *1*), between which cell walls are then formed, to produce a tetrad of microspores. No abnormalities in meiosis were observed. The tetrads break up into individual microspores (Fig. 2, *2*). At these stages, the anther wall is 4-layered, consisting of epidermis, endothecium, middle layer and tapetum (Fig. 2, *3*). It should be noted that, in contrast to *Boechera falcata* with the tapetal cells dividing without cytokinesis and becoming binuclear (unpublished), in *Borodinia macrophylla* the tapetum is secretory, consists of uninuclear cells and becomes unevenly 2-layered as a result from the division of some of its cells (Fig. 2, *3*). Subsequently, lysis of the middle layer and destruction of the tapetum occurs; in microspores, mitotic division and cytokinesis lead to the formation of vegetative and generative cells (Fig. 2, *4*). As the pollen grain matures, the cytoplasm of the vegetative cell becomes dense, devoid of vacuoles (Fig. 2, *5*). At this time, the tapetum is completely lysed, and the endothecium cells, on the contrary, enlarge and acquire fibrous thickenings on their walls (Fig. 2, *6*). The majority of pollen grains observed in mature anthers were bicellular, however, in some cases divisions of the generative cell were observed (Fig. 2, *5*). It is possible that pollen grains become 3-celled, but at later stages of anther development, by the time of its opening. This assumption requires further study.

In all anthers, the pollen grains were well formed and even in size, although occasionally small empty pollen grains were found (Fig. 2, *4–6*), which probably died at the early stages of development. These observations suggest high pollen grain fertility in this species.

Development of female reproductive structures in Borodinia macrophylla

Compared to previously studied *Boechera* species, with 45 to 60 ovules being formed in the ovary (Vinogradova et al., 2023), the ovaries of *Borodinia macrophylla* contain only 18–25 ovules.

A single megasporocyte differentiates in the subepidermal layer of the nucellus with the the onset of the integuments initiation (Fig. 3, *1*). In some cases, a parietal cell is formed above the megasporocyte (Fig. 3, *2*). Meiosis and the subsequent two cycles of cytokinesis lead to the formation of tetrads or triads of megaspores (Fig. 3, *3*), and occur in all ovules of the ovary relatively synchronously, in contrast to the *Boechera* species, where tetrads, dyads, and megasporocytes may be observed at the same time (Vinogradova et al., 2023). The stage of the tetrad of megaspores is long, at this time the ovule actively increases in size and bends into a hemitropous position, the outer integument grows quickly and extends beyond the nucellus, the inner one reaches the apex of the nucellus; in the nucellus active divisions occur in its basal part (Fig. 3, *3*). As the ovule develops, the micropylar megaspores in the tetrad degenerate, and the chalazal megaspore increases in size, becomes functional (Fig. 3, *4*) and divides to form a 2-nuclear embryo sac (Fig. 3, *5, 6*). During further development, the growth of the ovule continues, its nucellus in the basal part increases, the inner integ-

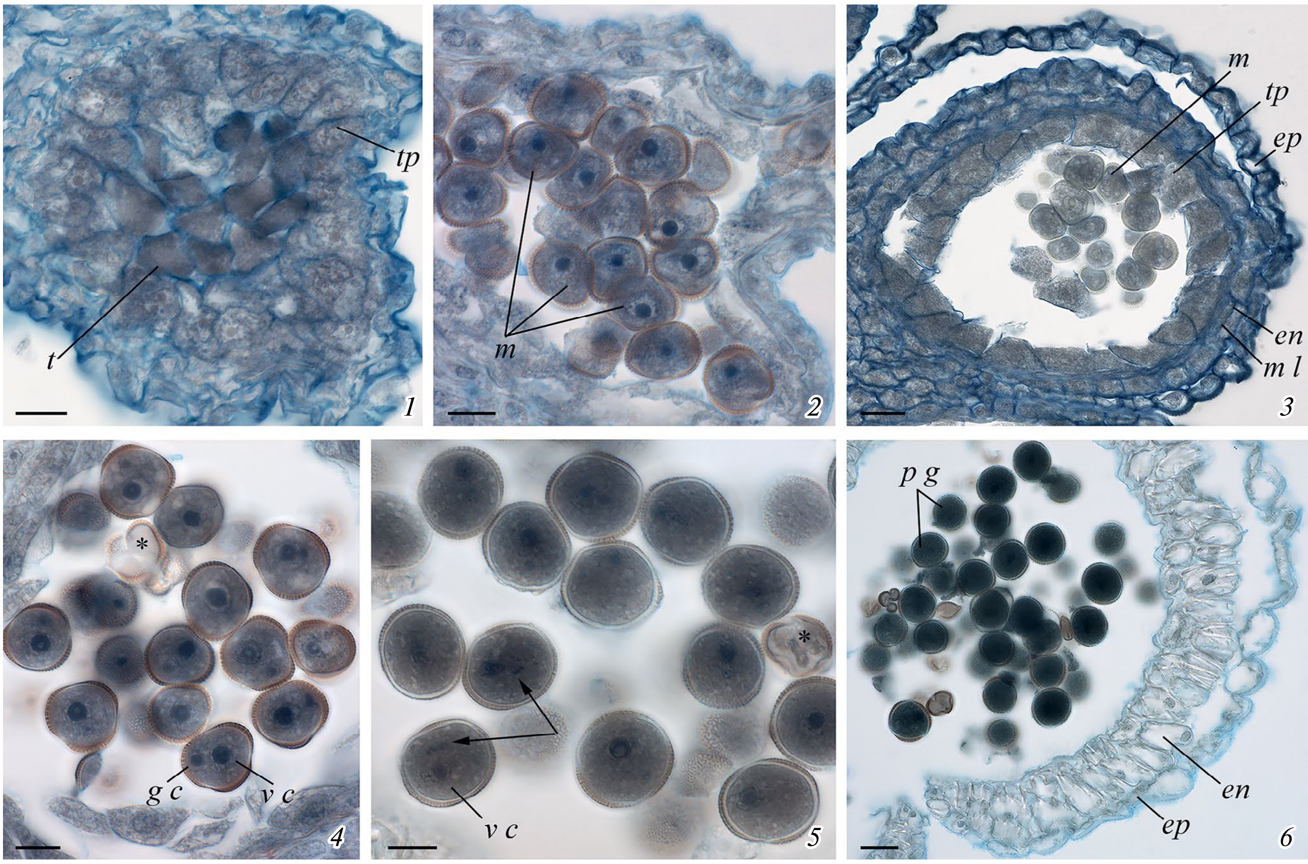

Fig. 2. Anther structure and male gametophyte development in *Borodinia macrophylla*: *1* – anther locule at the stage of meiosis in microsporocytes (4 nuclei are visible in one cell before the formation of cell walls); *2* – microspores; *3* – structure of the anther wall at the microspore stage; *4* – bicellular pollen grains; *5* – mature pollen grains, in some of them the division of the generative cell is visible (indicated by arrows); *6* – the structure of the wall of a mature anther.

* – sterile pollen grain; *ep* – epidermis; *en* – endothecium; *g c* – generative cell, *m* – microspore; *m l* – middle layer; *p g* – pollen grain; *t* – tetrad of nuclei in microsporocyte, *tp* – tapetum; *v c* – vegetative cell.

Scale bars, μm: 10 (*1–2*, *4–5*), 20 (*3*, *6*).

Рис. 2. Строение пыльника и развитие мужского гаметофита у *Borodinia macrophylla*: *1* – гнездо пыльника на стадии мейоза в микроспороцитах (видны 4 ядра в одной клетке до заложения клеточных стенок); *2* – микроспоры; *3* – строение стенки пыльника на стадии микроспор; *4* – 2-клеточные пыльцевые зерна; *5* – зрелые пыльцевые зерна, в некоторых видно деление генеративной клетки (указано стрелкой); *6* – строение стенки зрелого пыльника.

* – стерильное пыльцевое зерно; *ep* – эпидерма; *en* – эндотеций; *g c* – генеративная клетка; *m* – микроспора; *m l* – средний слой; *p g* – пыльцевое зерно, *t* – тетрада ядер в микроспороците; *tp* – тапетум, *v c* – вегетативная клетка.

Шкала, мкм: 10 (*1–2*, *4–5*), 20 (*3*, *6*).

ument completely overgrows the nucellus and takes part in the formation of the micropyle (Fig. 3, *6*). The hypostase differentiates at the base of the inner integument near to the procambial cells of the vascular bundle (Fig. 3, *3*, *8*). The embryo sac undergoes 2 more mitotic divisions, forming first a 4-nuclear gametophyte (Fig. 3, *7*), and then an 8-nuclear gametophyte. The last mitosis is accompanied by cell formation resulting in a 7-celled, 8-nucleate embryo sac. Thus, the female gametophyte in *Borodinia macrophylla* develops according to the monosporic Polygonum type. The formed ovule is ortho-campylotropous, bitegmic, medionucellate (Fig. 3, *8*). The embryo sac is small in volume and at the micropylar pole contains the egg apparatus, which includes two synergids and an egg; in the chalazal pole – three antipodes; polar nuclei in the central egg cell close together, but not fused (Fig. 3, *9*, *10*).

The development of female gametophytes was observed in all ovules of the studied ovaries. The embryo sac developed normally, no apomictic development was found.

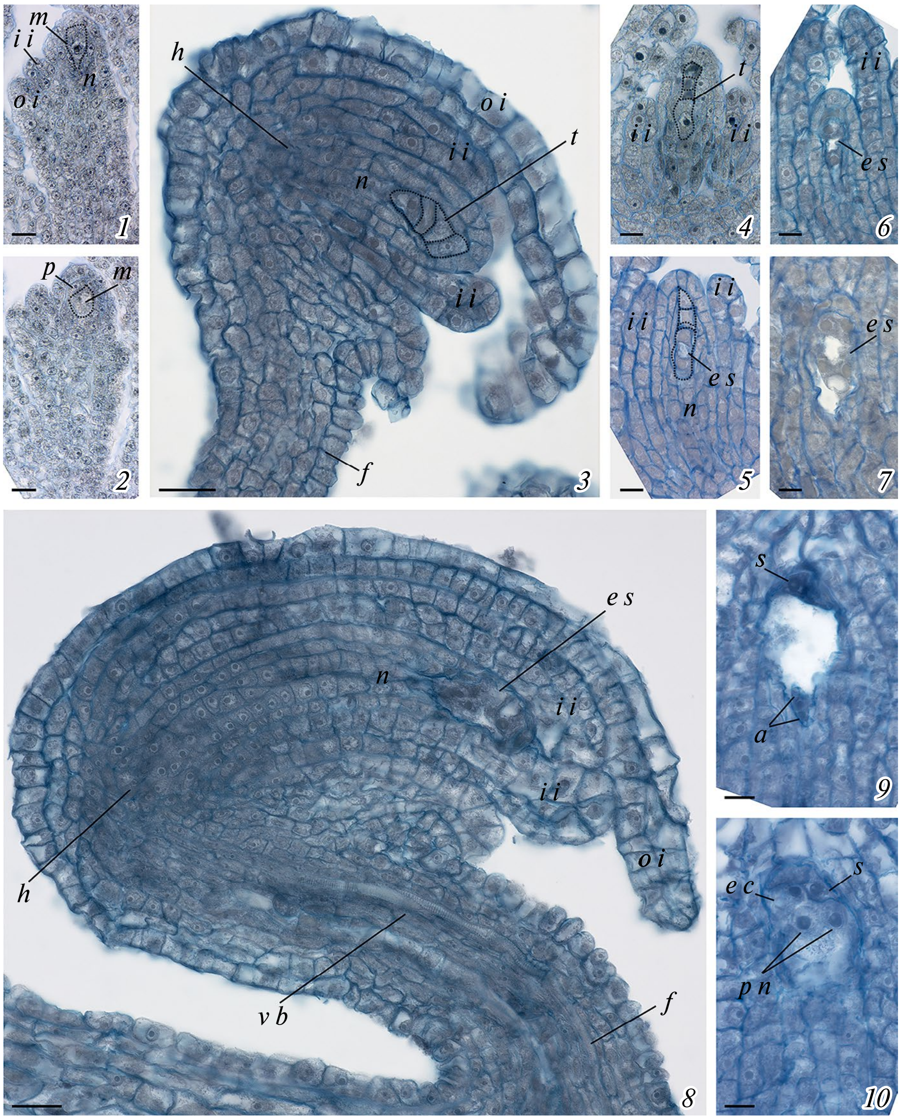

Fig. 3. Development of the ovule and female gametophyte in *Borodinia macrophylla*: *1–3* – structure of the ovule at the stages of: megasporocyte developing without a parietal cell (*1*) and with a parietal cell (*2*), tetrad of megaspores (*3*); *4* – tetrad of megaspores with differentiation of the chalazal megaspore and degeneration of three micropylar megaspores; *5* – division of the functional megaspore with the formation of a 2-nuclear coenocyte, micropylar megaspores are preserved; *6* – 2-nucleate embryo sac; *7* – 4-nucleate embryo sac; *8* – structure of the formed ovule; *9*, *10* – successive sections of the mature embryo sac: antipodals on the chalazal pole and one synergid on micropylar one (*9*), egg apparatus consisting of the egg cell and the second synergid at the micropylar pole, two polar nuclei of the central cell (*10*) are located nearby.

a – antipodals; *e c* – egg cell; *e s* – embryo sac; *f* – funiculus; *h* – hypostase; *i i* – inner integument; *m* – megasporocyte; *n* – nucellus; *o i* – outer integument; *p* – parietal cell; *p n* – polar nuclei; *s* – synergid; *v b* – vascular bundle.

Scale bars, μm: 10 (*1*, *2*, *4–7*, *9*, *10*), 20 (*3*, *8*).

Рис. 3. Развитие семязачатка и женского гаметофита у *Borodinia macrophylla*. *1–3* – строение семязачатка на стадиях: мегаспороцита, развивающегося без париетальной клетки (*1*) и с париетальной клеткой (*2*), тетрады мегаспор (*3*), *4* – тетрада мегаспор с дифференциацией халазальной мегаспоры и дегенерацией трех микропилярных мегаспор; *5* – деление функциональной мегаспоры с образование 2-ядерного ценоцита, микропилярные мегаспоры сохраняются; *6* – 2-ядерный зародышевый мешок; *7* – 4-ядерный зародышевый мешок; *8* – строение сформированного семязачатка; *9, 10* – последовательные срезы сформированного зародышевого мешка: антиподы на халазальном полюсе и одна синергида на микропилярном (*9*), яйцевой аппарат из яйцеклетки и второй синергиды на микропилярном полюсе, вблизи располагаются два полярных ядра центральной клетки (*10*).

a – антиподы; *e c* – яйцеклетка; *e s* – зародышевый мешок; *f* – фуникулус; *h* – гипостаза; *i i* – внутренний интегумент; *m* – мегаспороцит; *n* – нуцеллус; *o i* – наружный интегумент; *p* – париетальная клетка; *p n* – полярные ядра; *s* – синергида; *v b* – проводящий пучок.

Шкала, мкм: 10 (*1, 2*, *4–7*, *9*, *10*), 20 (*3*, *8*).

DISCUSSION

The first cyto-morphological study of the development of anthers and ovules of the Baikal species *Borodinia macrophylla* has shown that the development plan of its reproductive structures is similar to the recently studied *Boechera* species (Vinogradova et al., 2023) and other studied species of the Brassicaceae family (Iljina, 1962; Rodionova, 1966a, b, 1979; Shamrov, 2002a, 2007; Kuzmina, Shevchenko, 2008).

The anther is tetrasporangiate; at the microspore tetrad stage, the anther wall is 4-layered, consisting of epidermis, endothecium, middle layer and tapetum; the wall of the mature anther is 2-layered, consisting of epidermis and endothecium with fibrous thickenings. Microsporogenesis follows the simultaneous type. In general, the process of anther development and pollen formation in *Borodinia macrophylla* is similar to that in *Boechera* species and other studied species of Brassicaceae (Kuzmina, 2007; Kuzmina, Shevchenko, 2008). However, a number of peculiar features were also observed. In particular, in contrast to embryologically studied species of the genus *Boechera*, in which at the stage of tetrad microspores the tapetum is usually single-layered, sometimes consisting of binucleate cells, the tapetum in *Borodinia macrophylla* at this stage contains uninuclear cells and in places becomes unevenly 2-layered as a result of division some of its cells. In addition, the majority of pollen grains observed in mature anthers of *B. macrophylla* were bicellular, that is not typical for other Brassicaceae species. Possibly, pollen becomes 3-celled at later stages or during its germination; this requires further verification. In any case, the presence of bicellular pollen at late stages of anther development distinguishes *B. macrophylla* from other species of the Brassicaceae.

The formed ovule is ortho-campylotropous, bitegmic, medionucellate (according to Shamrov, 2008, 2017), as in the recently studied *Boechera* species: *B. falcata*, *B. stricta* (Graham) Al-Shehbaz and M4B accession (Vinogradova et al., 2023).

As reported previously, the presence of a parietal cell, occurring with varying frequency during the early stages of ovule development in some plants from the Boechereae tribe, may indicate a tendency towards a crassinucellate ovule type in this tribe (Mandáková et al., 2020; 2021). In *Borodinia macrophylla* we occasionaly observed fomation of the parietal cell.

The studies have shown that the ovule begins to develop quite early, when integuments are visible as primordia yet. The first meiotic division occurs very quickly, followed by the second meiotic division, unlike *Boechera* species, meiosis in all ovules occurs synchronously, the structure of the ovule undergoes significant changes from the stage of the megasporocyte differentiation to the formation of the tetrad of megaspores. At the same time, the cells of the nucellus increase in size and both integuments enclose it at the tetrad stage, while the outer integument is much longer than the nucellus and partly goes around the latter. The tetrad is linear, with the chalazal megaspore being functional, growing in size and undergoing through three mitoses subsequently forming the embryo sac. The other three megaspores do not develop further and degenerate.

In *Borodinia macrophylla*, unlike some species of *Boechera* (Iljina, 1962; Carman et al., 2019; Vinogradova et al., 2023), the formation of multiple archesporial cells, megasporocytes or several embryo sacs was not observed.

The embryo sac in *Borodinia macrophylla* develops according to the monosporic Polygonum type. The mature embryo sac is small, 7-celled, 8-nucleate, characteristic for most species of the Brassicaceae family, but the polar nuclei in the central cell do not fuse before fertilization, unlike most other representatives of the Boechereae tribe. Perhaps the fusion of polar nuclei occurs later, and the embryo sac contains a secondary polar nucleus, as in the studied *Boechera* species (Vinogradova et al., 2023). The formation of the embryo sac in all tested ovules revealed strict consistency of the developmental stages with the surrounding tissues of the sporophyte. Thus, during megasporogenesis, the ovule becomes hemitropous, it is still small in size, the integuments barely reach the middle of the nucellus; at the stage of meiosis, there is a significant growth of the nucellus and integuments, which completely cover it, especially the long outer integument, at this stage, the ovule bends into an ortho-campylotropous position. At the stage of gametogenesis, when the formation of the embryo sac occurs, accompanied by its cellularization, the formation of the egg cell, synergids, antipodals and central cell, further growth of the ovule occurs due to an enlargement of the embryo sac, growth of the chalazal bundle, and continued growth of integuments. The development of gametophytes was found in all studied ovules, which distinguishes the reproduction of *Borodinia macrophylla* from apomictic species of *Boechera*, in which abortive ovules were often observed (Vinogradova et al., 2023), the fact once again indicating the sexual mode of reproduction of *Borodinia macrophylla*.

Thus, despite a noticeable morphological difference in the sporophytic generations of the *Borodinia* genus and its separation from the *Boechera* genus on the molecular phylogenetic tree of the Boechereae tribe (Alexander et al., 2013; Hay et al., 2023), the development of female and male reproductive structures in *Borodinia macrophylla* are in many ways similar to those in representatives of the *Boechera* genus, although not without some important particular features. This article is the first study to provide a detailed cytoembryological characterization of the reproductive structures in the only species of *Borodinia* growing in Russia; in the future it would be interesting to perform a comparative embryological characterization of this Siberian relative with the seven North American representatives of this genus.

CONCLUSION

The study of the reproductive structures of *Borodinia macrophylla* revealed a number of developmental features of anthers and ovules that distinguish it from the other species of the Boechereae tribe studied so far. Namely, the formation of a sporadically two-layered tapetum occurs at the microspore tetrad stage, the bicellular pollen is present at the late stages of anther development, the meiosis in all *Borodinia macrophylla* ovules occurs synchronously, and the polar nuclei in mature embryo sacs do not fuse. To make sure that these cytoembryological characteristics are species-specific, it is advisable to study other species and populations of *Borodinia* in the future.

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РАЗВИТИЕ ЖЕНСКИХ И МУЖСКИХ РЕПРОДУКТИВНЫХ СТРУКТУР У *BORODINIA MACROPHYLLA* (BRASSICACEAE)

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Впервые представлены результаты цитоэмбриологического исследования формирования женских и мужских репродуктивных структур у восточносибирского эндемика Бородинии крупнолистной – *Borodinia macrophylla* (Turcz.) O.E. Schulz, порядок Капустоцветные (Capparales), семейство Крестоцветные (Brassicaceae), триба Boechereae. Общий план развития репродуктивных структур происходит аналогично исследованным видам из рода *Boechera*. Пыльник 4-гнездный, в начале развития с 4-слойной стенкой, которая по мере созревания пыльника становится 2-слойной; Тапетум пыльника неравномерно 2-слойный. Микроспорогенез симультанного типа, большинство пыльцевых зерен в зрелых пыльниках 2-клеточные. Семязачаток орто-кампилотропный, битегмальный, медионуцеллятный. Зародышевый мешок 7-клеточный, 8-ядерный, формируется согласно моноспорическому Polygonum-типу. Полярные ядра центральной клетки в зрелом зародышевом мешке не сливаются. Развитие женских гаметофитов происходит во всех исследованных семязачатках. У *B. macrophylla* наблюдался половой способ воспроизводства, апомиктичного развития не отмечено.

Ключевые слова: *Borodinia macrophylla*, Boechereae, Brassicaceae, семязачаток, пыльник