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Embryological study on diploid and triploid populations of *Iberis saxatilis* subsp. *saxatilis (Brassicaceae*) in the Bulgarian flora

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Abstract. *Iberis saxatilis* subsp. *saxatilis* occurs in the Bulgarian flora in few localities in the eastern and southwestern mountainous parts of the country. A comparative embryological study of three populations with different ploidy levels has been carried out. The mode of reproduction, peculiarities of male and female gametophytes, and embryo- and endospermogenesis are established. The embryological processes are reported in close connection with the ploidy levels. The diploid population is strongly amphimictic, while the two triploid populations are amphiapomictic, and diplospory as well as sporadical apospory are considered. Some ideas on the evolution of embryological processes and the structures of *I. saxatilis* subsp. *saxatilis* are suggested.

Key words: apomixis, apospory, diplospory, embryology, *Iberis*, male and female gametophyte

Introduction

Iberis L. contains about 30 species. The highest species diversity is known for the Iberian Peninsula, where eight endemic taxa of *Iberis* occur. Twenty species are distributed in Europe, eight out of which in the areas of South and Southeast Europe (Da Silva & Do Amaral Franco 1993).

Four basic numbers $x = 7, 8, 9, 11$ are known in the species with European area of distribution (Ene 1968, 1973; cf. Jalas & al. 1996). Polyploidy is not of common occurrence in *Iberis*. Diploid, tetraploid and hexaploid karyotypes have been found in species with $x = 11$: *I. saxatilis* L. subsp. *saxatilis* ($2n = 22$) (Gustavsson 1978; Moreno 1985), *I. saxatilis* subsp. *cinerea* (Poiret) Font Quer ($2n = 22, 44$) (Moreno 1985), *I. sempervirens* L. ($2n = 66, 70$) (cf. Jalas & al. 1996), as well as $2n = 22$ (Ančev 1978), and *I. semperflorens* L. ($2n = 22, 44$) (cf. Jalas & al. 1996).

Iberis saxatilis subsp. *saxatilis* is distributed in South Europe, from the Iberian Peninsula eastwards to the Balkan Peninsula, Romania (Dobroudzha) and Crimea (Da Silva & Do Amaral Franco 1993). In Bulgaria the species occurs in the Eastern Balkan Range, in the transitional zone between the oak-hornbeam and beech forest belt, at altitudes from 900 m up to 1100 m, as well as in the North Pirin and Slavyanka mountains, in the coniferous vegetation belt from 1900 m up to 2300 m a.s.l. (Ančev 2001)

From all 30 species of genus *Iberis* probably only two, *I. amara* L. and *I. umbellata L.*, are embryologically studied but the data are fragmentary and scanty (Belyayeva & Rodionova 1983).

The present paper gives the results of a comparative embryological investigation of three Bulgarian populations of *I. saxatilis* subsp. *saxatilis*: one diploid population with $2n = 22$ and two triploid ones with $2n = 33$ (Ančev & Goranova 1997; Anchev & Goranova 2002).

Material and methods

The material used for the embryological study belongs to plants of three populations, collected in the mountain localities of East and Southwest Bulgaria, transplanted and growing in the experimental greenhouse at the Institute of Botany, Sofia (Table 1). Vouchers are deposited in SOM.

Flower buds, open flowers and seeds in various stages of development were collected during May-July 2000–2001 and fixed in FAA mixture (formalin: glacial acetic acid: ethanol in the correlation 5: 5: 90 parts with 70 % ethanol). The material was treated according to classical paraffin methods (Romeis 1948). The serial paraffin sections 6–15 μm thick were stained with Heidenhain' s haematoxylin. The permanent slides were mounted with Canada balsam. Some stages of microsporogenesis were observed on the temporary slides made after squashing fresh young anthers stained with 1 % acetocarmin. The observations were carried out on the permanent slides, with Amplival light microscope. The microphotographs were made with Nf-matic.

Table 1. Chromosome number (2*n*) and origin of the studied populations

Taxon	2*n*	Origin
Iberis saxatilis subsp. *saxatilis*	22	Balkan Range (*Eastern*), Sliven Mt, Sinite Kamuni, in open grassland on calcareous gravely terrains, on slopes and ridges, in meso-xerophylous plant communities, ca. 1050 m, A 9911
	33	Mt Slavyanka, peak Golem Tsarev, high montainous grassland on gravely calcareous terrains, on slopes mostly with southern exposition, ca. 2100 m, A 9549 (Ančev & Goranova 1997)
	33, 32	North Pirin Mts, close to the timberline, near Dolen Kazan circus, 2100 m, A 9799 (Anchev & Goranova 2002)

Results and discussion

Flowering biology and reproduction

The development of flowers is protandrous. During opening of the flower buds the anthers, turned inside and shedding pollen, almost close the corolla throat. In some flowers pollen adheres to the stigma. Subsequently, the filaments elongate and the anthers of the long stamens reach above the stigma level. The anthers of the short stamens are somewhat lower. Flower development and position of the inside- turned anthers characteristic of autogamous Crucifers lead to presumption that at least some seeds result from autogamy.

I. saxatilis subsp. *saxatilis*, both the diploid and polyploid populations, also reproduce vegetatively, forming a long branched underground rhizome, rooting at the nodes and often developing vegetative and flowering stems.

Embryology

Embryological characteristics of the diploid population. $2n = 2x = 22$ (Table 1).

Anther and development of the male gametophyte

The anthers are tetrasporangiate and develop centrifugally according to the Dicotyledonous-type (Davis 1966), as in most *Brassicaceae* genera, especially *Hesperis*, *Eruca*, *Lepidium*, *Syrenia* (Belyayeva & Rodionova 1983). No reduction of the anther locules has been observed in the studied material. The anther wall consists of epidermis, endothecium, one-two middle layers and tapetum. The cells of the epidermal layer are one-nucleate, large in size, wide, almost rectangular, tangentally lengthened during ontogenesis and rounded up outside. The endothecial cells are smaller in size but wider. They develop fibrous thickenings (Plate I, Fig.1) usually clearly expressed when two-celled pollen has already formed in the anthers. The middle layer consisting of small-sized cells is not ephemeral and remains vital up to the end of homeotypic division of the meiosis in the microspore mother cells (MMCs). In this population two middle layers have been observed in some anthers.

Initially, the tapetum is glandular (Plate I, Fig. 2) consisting of one-nucleate, large, polygonal or rectangular cells. Occasionally, the tapetum cells are morphologically unequal. During anther ontogenesis, after subsequent mitoses they become two-, four-nucleate. Usually, the cells of the inner tapetum (towards the periphery of the anther wall) are different in size, shape and speed of their development as compared to those of the outer integument (towards the cavity of the anther locule). Glandular tapetum transforms into ameboid false periplasmodium (Plate I, Fig. 3) after the formation of two-celled pollen in the anthers, as in some species of the genera *Arabis*, *Bunias* and *Hesperis* (Beljaveva & Rodionova 1983). Soon after its differentiation the ameboid anther tapetum almost completely degenerates (Plate I, Fig. 4). Mature pollen in the open flowers is 3- and 2- celled (Plate I, Figs 3, 4). At this stage from the anther wall layers, only the epidermis and endothecium, often disrupted, are preserved. The sporogenous tissue in the anther locules is multilayered and

usually consists of two-three layers. Each of the polygonal, one-nucleate sporogenous cells further enlarges, rounds up and differentiates into a microspore mother cell (MMC). The meiosis in MMCs runs normally, which is typical for most Angiosperm diploid taxa (Poddubnaya-Arnoldi 1976). Some insignificant deviations, mainly during the heterotypic division of the meiosis in MMCs, are occasionally observed, namely: single lagging chromosomes; chromosomes out of the spindle; 1–2 univalents together with bivalents in diakinesis and mitosis I. Simultaneous microsporogenesis results predominantly in tetrahedral microspore tetrads formation. In some anthers, isobilateral tetrads have been found occasionally.

Pollen in the anthers is usually equal in size. Mature pollen in the open flowers is threecolpate, three-celled, but often in some anthers, at the time of shedding, two-celled pollen has been also observed (Plate I, Figs 3, 4). Besides threecolpate, tetracolpate (Plate I, Fig. 1) and sporadically large-sized pollen grains have been found occasionally in the anthers too. As a result of normal meiosis and microsporogenesis, the pollen of this diploid population is in the highest degree vital and fertile (over 90 % in each anther).

Ovule and development of the female gametophyte

In each locule of the two-locular inferior ovary, a single ovule always develops basally. The ovule is bitegmic, funiculous and its funiculus is very long. The initiation of the two integuments begins almost simultaneously on the ovule primordium as in other *Brassicaceae* (Bouman 1974, 1975; Shamrov 2002). Initially, both the inner and outer integuments are two-cell thick and later on are secondarily thickened by periclinal divisions of their constituent cells. When the ovule has matured, the inner integument is more vigorous: 3-, 4- to 5- layered and the outer is usually 2-, 3- layered. Neither the inner, nor the outer integument are vacuolized and no vascular bundles have been observed in them. The outer integument usually elongates more than the inner one, so that the micropyle is always formed by the two integuments. During onthogenesis, the ovule curves and this is accompanied by assymetrical growth of the integuments towards its dorsal (inner) side. Consequently, the two integuments in that part become considerably longer.

On the basis of the evidence of the entire ovule genesis it must be characterized as ana-amphitropous (Boquet 1959), tenuinucellate and bitegmic. The one-row nucellar epidermis usually completely degenerates after the 4-nucleate stage of ES development.

The innermost layer of the inner integument differentiates after the 2-nucleate ES stage into endothelium, with clearly radially elongated cells. Subsequently, the endothelium encloses directly the mature ES. This situation obtains even after fertilization in ES, when the endothelial cells and most other cells of the inner integument begin progressively to degenerate.

A single archesporial cell always forms hypodermally in the ovule (Plate II, Fig. 1). Archesporogenesis runs without formation of parietal cells and the archesporial cell functions as a macrospore mother cell (MMC). The MMC is uninucleate, large in size, with dense cytoplasm and vacuolized, and differs easily from the somatic cells of the ovule. As a result of meiosis in MMC, a linear macrospore tetrad forms. Its chalazal cell differentiates into an embryo sac mother cell (EMC) (Plate II, Fig. 2) and soon after three mitotic divisions, subsequently 2-, 4- (Plate II, Fig. 3) and finally 8-nucleate ES develops, according to the monosporic *Polygonum*-type. Polarization of the nuclei in each of above-mentioned stages, as well as vacuolization and differentiation of elements in the mature ES are typical and show that in diploid populations the *Polygonum*-type of female gametophyte development occurs, which is the basic type not only for *Brassicaceae* representatives but for most Angiosperms too (Davis 1966; Poddubnaya-Arnoldi 1982; Belyayeva & Rodionova 1983). The remaining sister macrospores of the tetrad towards the micropyle degenerate progressively (Plate II, Fig. 2), up to the formation of two-nucleate ES.

The mature *Polygonum*-type ES consists of a 3-celled egg apparatus, two polar nuclei and three antipodal cells (Plate II, Fig. 4). The egg cell is usually pyriform in shape, sometimes almost cylindrical, and a clear vacuolization in it has been often observed (Plate II, Fig. 4). Two synergids with fibrillar apparatus are located in its apical pole (towards the micropyle), but not always clearly expressed. Two polar nuclei moving from the two poles to the central part of the ES cavity soon fuse and the resulting central cell (secondary ES nucleus) before fertilization usually fits into the wide basal end of the egg cell.

The three antipodals are small, uninuclear cells, located deeply in the chalazal part of ES, with T-shaped or occasionally linear arrangement. They usually degenerate before fertilization (Plate II, Fig. 4), but their degeneration sometimes is prolonged even to the earlier embryo- and endospermogenesis.

In the ovule usually after the 2-, 4-nucleate ES stage, a hypostase forms in its chalazal region, as in most *Brassicaceae* taxa (Prasad 1977; Vijayaraghavan & Prabhakar 1981; Shamrov 2002). More precisely, many authors have noticed that this structure is located at the basis of the nucellus and integuments, where they border on the chalaze. A bundle approaches the hypostase and the chalazal part of the ovule becomes more active physiologically, increasing its trophical function.

The legitimate embryo and endosperm in this diploid population develope after double porogamous fertilization. The pollen tube penetrating through the macropyle damages one of the two synergids and its degenerating dark-stained parts remain visible for a long time in the mictopylar pole of the mature ES.

The embryo develops following the Onagrad-type embryogenesis (Johansen 1950). The suspensor of the embryo is long, usually 4-, 5- celled, even when the embryo is still young, with a large clearly vacuolized apical (micropylar) cell (Plate II, Fig. 5).

Initially, the endosperm is nuclear (Plate II, Fig. 5). The first mitotic divisions of the free endosperm nuclei run synchronously. Subsequently, this synchrony is disturbed and then the division of endosperm cells runs asynchronously. The endosperm retains its nuclear state for a long time. The cytokinesis between its free nuclei usually begins on the dorsal side of the curved mature ovule, but the endosperm remains nuclear for a long time, especially in its chalazal part. In fact, towards the heart-shaped stage of embryo development the endosperm from initially nuclear transforms into cellular.

The embryological study of the diploid population A9911 has shown it as strongly amphimictic. No apomictic reproduction, nor adventive embryony have been established. Together with the balanced embryological processes and the established stable structures, this fact correlates with the diploid status of this population.

Embryological characteristics of the triploid populations. $2n = 3x = 33$ (Table 1)

Since the general embryological characteristics were basically the same as in the diploid population A9911, for the two triploid populations A9549 and A9799 only the specific embryological features are shown and discussed.

Anther and development of the male gametophyte

In the two triploid populations the thickenings of endothecium often have not been distinctly expressed in all its constituent cells. The middle layer is more ephemeral and begins to degenerate earlier, frequently before the homeotypic division of the meiosis in MMCs. The anther tapetum degenerates as cellular, without transforming into ameboid periplasmodium. Various types of deviations have been registered during the meiosis in MMCs, namely: asynchrony of the meiosis in MMCs even in an anther locule; inhibited meiosis or microsporogenesis in the same anther; different number of univalents together with bivalents during diakinesis – metaphase I; different number of lagging chromosomes; chromosome out of the spindle and chromosome bridges have been often observed. In the anthers of triploid populations, as a result from disturbed meiosis and microsporogenesis, along with tetrahedral, T- shaped and linear micropore tetrads, monads, dyads, triads, and sporadically polyads have also formed (Plate III, Fig.1).

A supressed meiosis has been also observed, more often in the anthers of population A9979 and, consequently, mature pollen and inefficient microspore tetrads have been found in one and same anther locule (Plate III, Figs 2, 3). Furthermore, microspore tetrads with micronuclei, pollen grains with two vegetative cells instead of one, have been found too. In the two triploid populations, mainly heteromorphous threecolpate, but also tetracolpate and giant feminized pollen grains are often formed (Plate III, Fig. 4).

In some anthers, a strong degeneration of the sporogenous tissue, tetrads, mature pollen, or even of the whole anthers has been observed and, in fact, these flowers become functionally female. As a result of these disturbances, sterile, darkly stained, degenerated (Plate III, Fig. 4), and inefficient pollen appears in the triploids (often over 30 %, especially in some anthers of population A9799). Mention deserves the fact that a great amount of sterile and feminized pollen is often reported for apomictic Angiosperms (Poddubnaya-Arnoldi 1976; Czapik 1994).

The unbalanced and disturbed meiosis and microsporogenesis registered during our study in the anthers of the two triploid populations are a major embryological characteristic of the polyploid, apomictic and evolutionary younger taxa in which active intraspecies formation is usually in progress.

Ovule and development of the female gametophyte

The nucellus of the ovules (especially the nucelar epidermis) is short-living and usually degenerates towards the two-nucleate ES stage. In most ovules, archesporogenesis generally results in a linear macrospore

tetrad as in the diploid population A9911. Usually from its chalazal macrospore, after three mitoses, 2-, 4 and mature 8-nucleate ES develops, according to the *Polygonum*-type as in A9911.

Degeneration of the macrospore tetrad (Plate IV, Fig.1) has been observed, especially in population A9799, and such ovule stops its further development becoming complitely sterile. In some ovules (more often in A9799), a destroyed first division of the meiosis in the macrospore mother cell (MMC), instead of a tetrad has resulted in the formation of a dyad of macrospores. In these ovules the development of ES runs following diplospory (Asker & Jerling 1992) or aneuspory, according to Battaglia (1963). Crane (2002) gives nine major types of the diplosporic development of ES. Our observations have proven that in the ovules of triploid populations of *I. saxatilis* subsp. *saxatilis* ES follows the *Taraxacum*- type of diplospory, according to Crane (2002: 28). In this type of diplospory the first division of the meiosis is disturbed in the macrospore mother cell of the ovule, resulting usually in a restitution nucleus, while the second meiotic division runs normally and a dyad of diploid macrospores forms.

ES develops from the chalazal macrospore of the dyad that becomes EMC (Plate IV, Fig. 2) and, after three rounds of mitosis, subsequently 2-, 4- (Plate IV, Fig. 3) and 8-nucleate diploid (unreduced) ES form. The organization of elements in the mature 8-nucleate diplosporous ES is identical to that in the mature *Polygonum*-type ES observed in the diploid population A9911, namely: three-celled egg apparatus (Plate IV, Fig. 4); two polar nuclei (after their fusion the central cell of ES forms); three antipodal cells, but clearly ephemeral in the triplod populations. In some ovules of the two triploid populations, unpolarized 6-8 nucleate ES have been observed that are characteristic of apomictic species (Czapik 1994).

In the diplosporous ES, the egg cell develops into an embryo via unreduced parthenogenesis (diplospory with parthenogenesis after Gustafsson 1946), without fertilization (observed particularly in A9799) or pseudogamy. Pseudogamy is traditionally defined as asexual embryo formation that requires pollination. However, Crane (2002: 27) gives a more restricted definition, "Pseudogamy is seed set through fertilization of the central cell, but not egg, in the absence of adventitious embryos".

In the micropylar region of some ES the penetration of the pollen tube, or its darkly stained degenerated traces have been observed (Plate IV, Fig. 4). That suggests at least a stimulating role (pseudogamy) of the pollen in the embryo- and endospermogenesis. In this sense, in some cases of diplospory in the ovules of the triploid populations, pseudogamy occurs and probably the stimulative role of the pollen is necessary for the beginning of endospermogenesis (first division of the central cell) (Plate IV, Fig. 5). Unreduced parthenogenesis with pseudogamy was reported for *Brassicaceae* by Poddubnaya-Arnoldi (1982).

Furthermore, mention deserves the fact that flower development and the position of anthers turned inside at shedding time, which is characteristic of most autogamous *Brassicaceae*, suggest that at least in some ovules the seeds develop as a result of autogamy, i.e. not only the egg cell but the central cell also develops autonomously.

In the triploid population from the North Pirin Mts, somatic apospory has been found occasionally too. In these cases, a somatic cell deeply located in the chalaze begins to develop in an aposporous ES (Plate IV, Fig. 6), usually outside the cavity of the legitimate ES. However, subsequently no embryo formation via this somatic aposporous ES has been observed. On these grounds, somatic apospory in A9549 shall be regarded only as a tendency and must be characterized as "non-functional" (Czapik 1996).

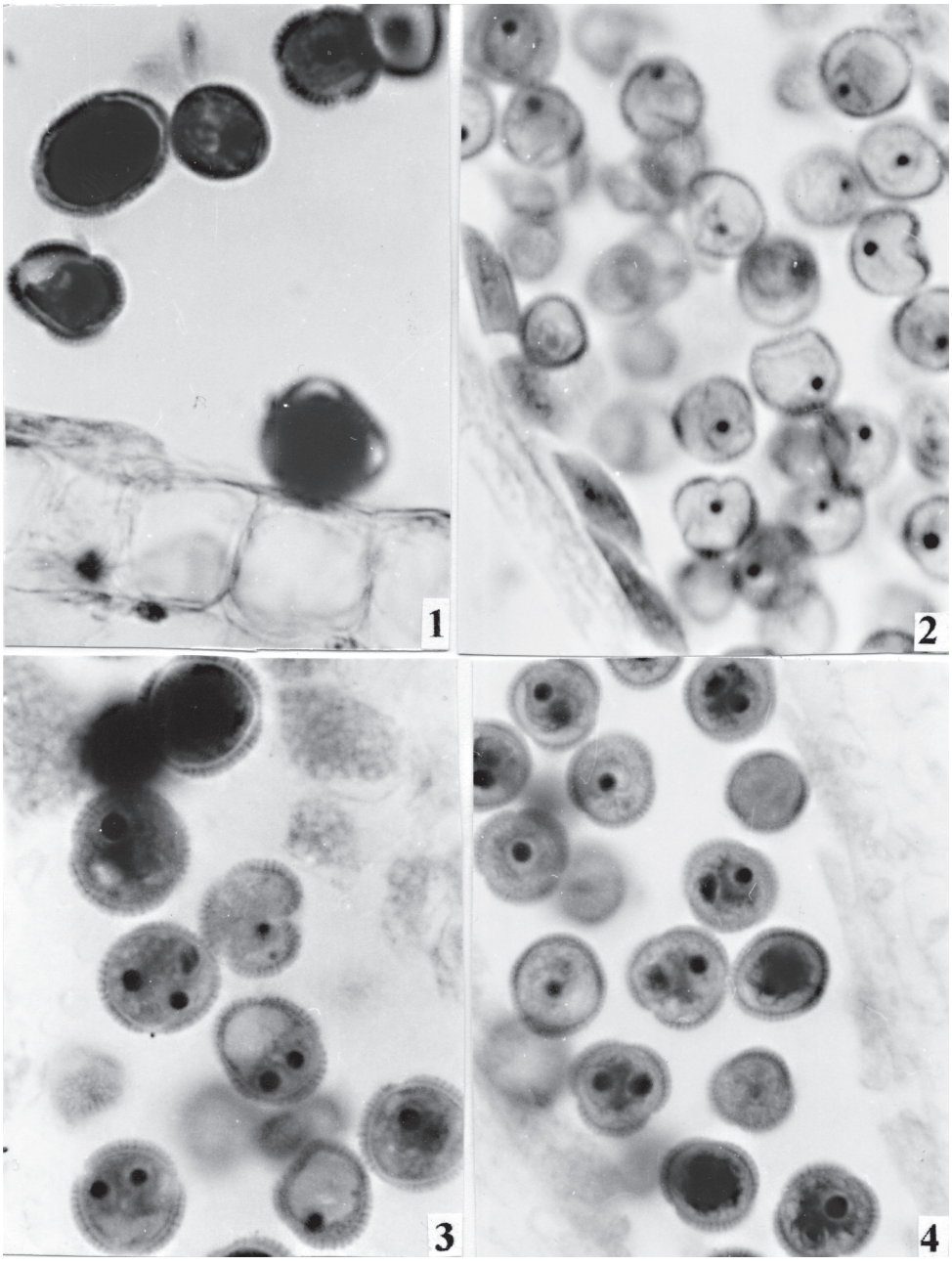
The triploid populations of *I. saxatilis* subsp. *saxatilis*, as compared to the diploid one, are characterized with unbalanced embryological processes and a higher plasticity of the male and female gametophyte.

Conclusion

The embryological studies of a diploid and two triploid populations of *Iberis saxatilis* subsp. *saxatilis* in the Bulgarian flora have been carried out. Differences were observed between the diploid population from the Eastern Balkan Range, which is strongly amphimictic (sexual) and the triploid ones from Mt Slavyanka and the North Pirin Mts, which are amphiapomictic with sexual type of reproduction combined with apomixis (diplospory and somatic apospory). Their pollen morphology and fertility/sterility pollen ratios undoubtedly correlate with their diploid and respectively polyploid (triploid) levels.

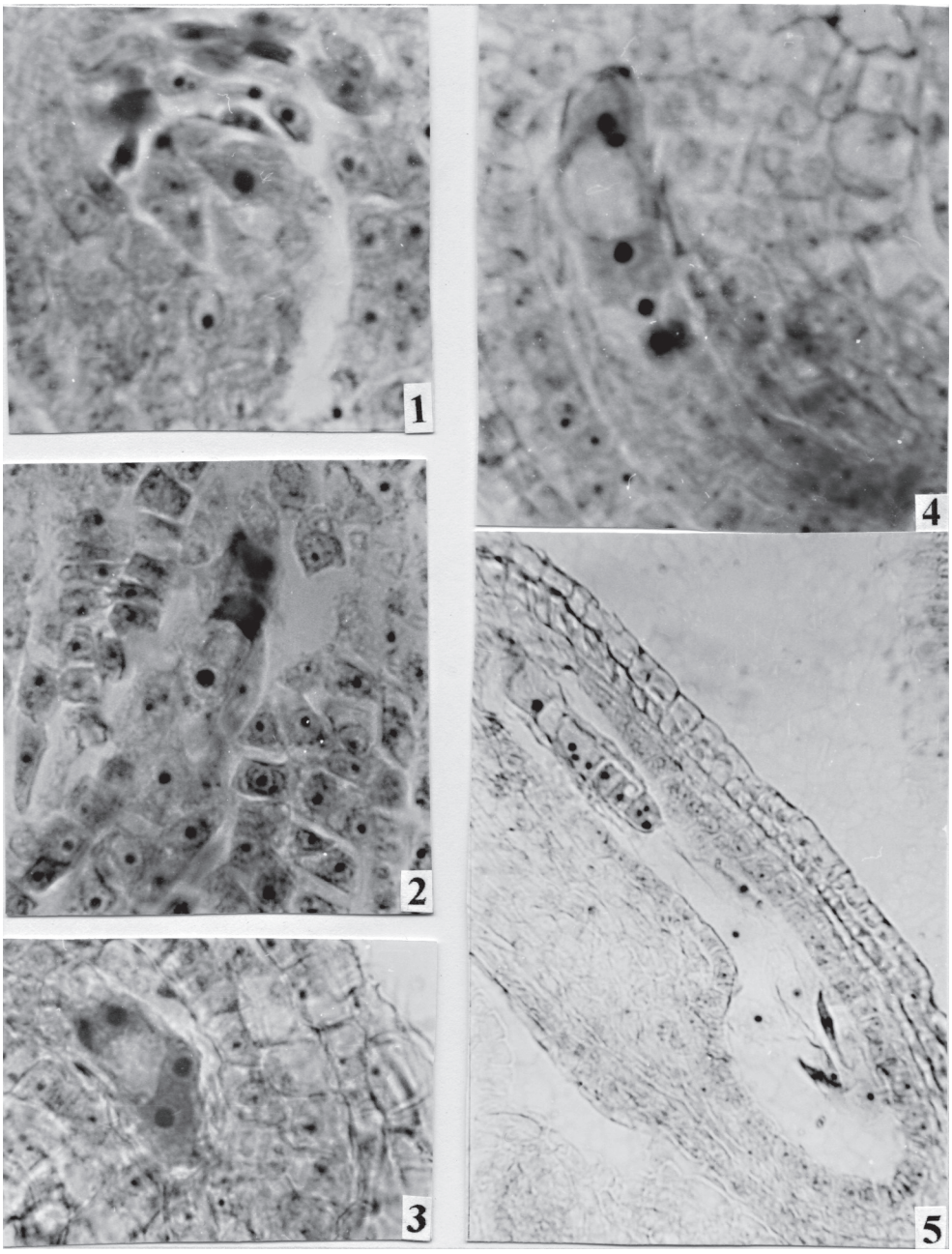
In our opinion, the triploid amphiapomictic populations distributed in the high mountains of the Rhodopi mountain massif, Mt Slavyanka and the North Pirin Mts, are products of the local processes of genetic differentiation, stimulated by the continuous climatic changes in the Quaternary and the subsequent successive cycles in the vegetation in these mountains.

Plate I



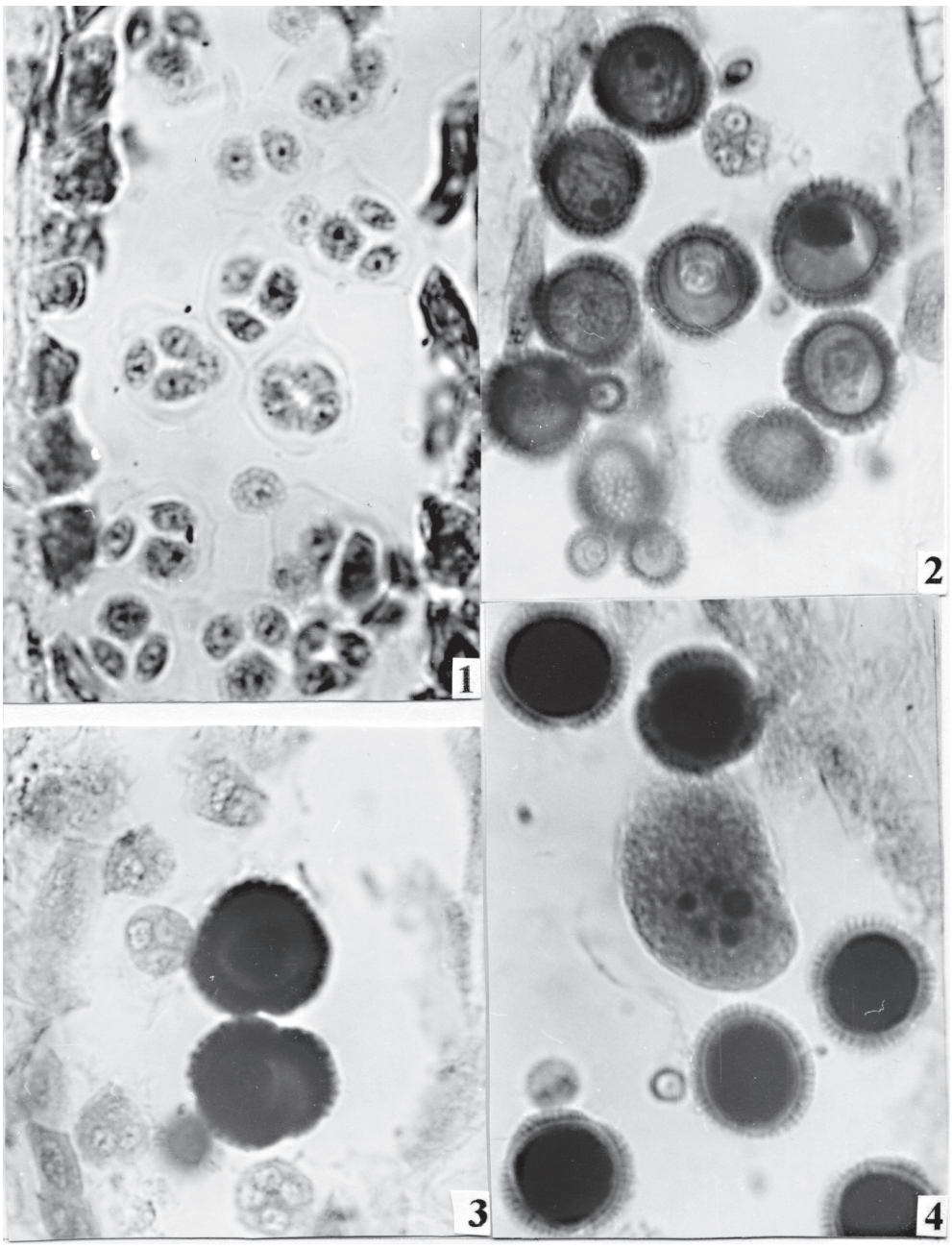
Figs 1-4. Male gametophyte development in a diploid population of *I. saxatilis* subsp. *saxatilis*.
1, fibrous endothecium, three- and tetracolpate mature pollen (× 160); **2,** secretory tapetum and one-nucleate pollen (× 100); **3,** ameboid tapetum, three- and two-celled mature pollen (× 160); **4,** mature pollen in an anther without tapetum layer (× 160).

Plate II



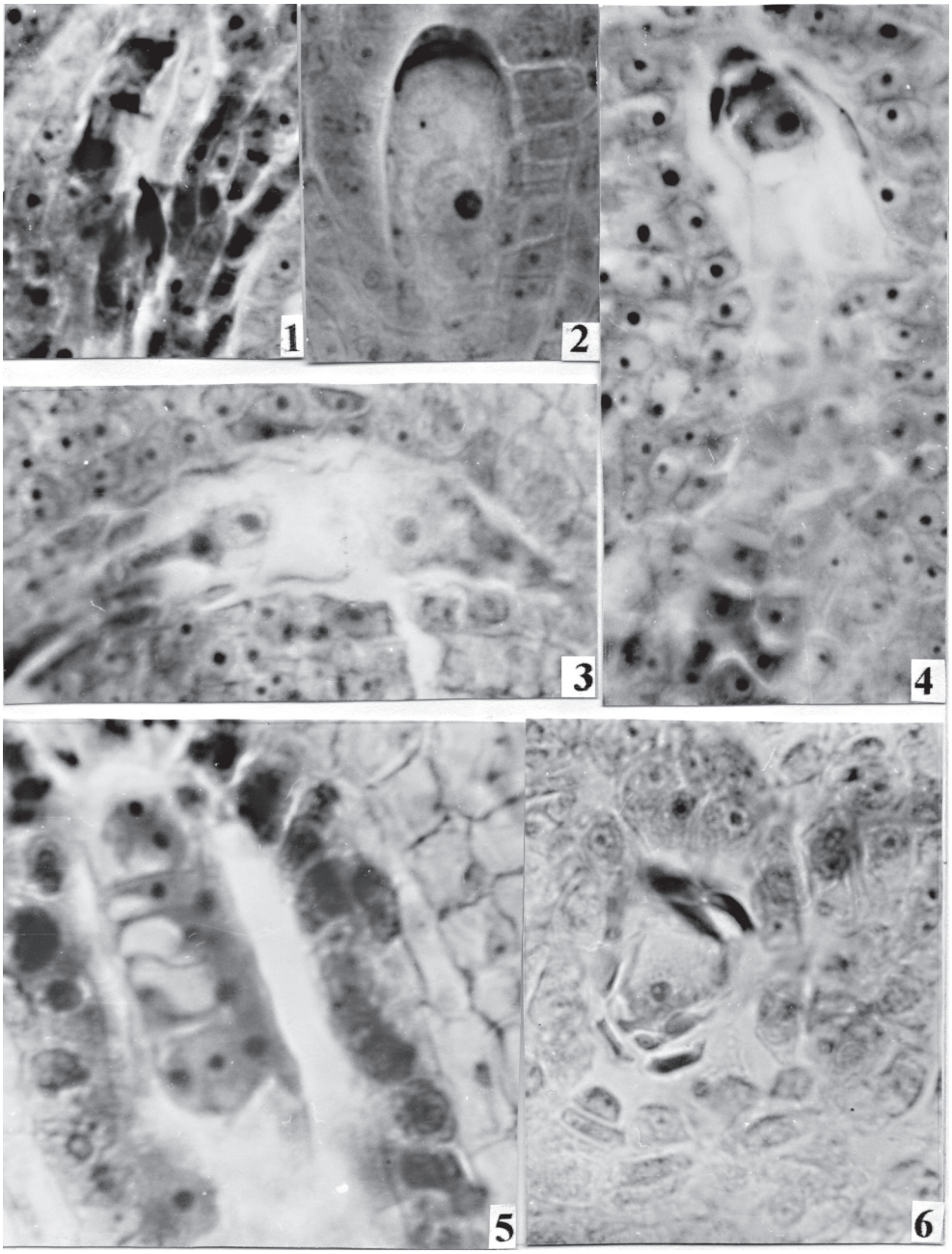
Figs 1-5. Female gametophyte development in a diploid population of *I. saxatilis* subsp. *saxatilis*
1, unicellular archesporium in the ovule (× 160); **2,** ES development from the chalazal macrospore of the tetrad (×63); **3,** four-nucleate ES with endothelium (× 100); **4,** mature ES with degenerating antipodals (× 100); **5,** onagrad-type young embryo and nuclear endosperm (×63).

Plate III



Figs 1-4. Male gametophyte development in triploid populations of *I. saxatilis* subsp. *saxatilis.*
1, microspore monads, dyads, triads, tetrads in an anther of population A9799 (× 160); **2**, mature pollen and inefficient microspore tetrads in a single anther of population A9549 (× 160); **3**, mature pollen and inefficient microspore tetrads in a single anther of population A9979 (× 160); **4**, degenerating and giant feminized pollen in population A9799 (× 160)..

Plate IV



Figs 1-6. Female gametophyte development in triploid populations of *I. saxatilis* subsp. *saxatilis*.
1, degenerated macrospore tetrad in population A9799 (× 100); **2**, diplosporous development of ES from the chalazal macrospore of a dyad in population A9799 (× 400); **3**, four-nucleate ES in population A9549 (× 160); **4**, egg cell, degenerating parts of the synergids and pollen tube traces in population A9799 (× 160); **5**, young parthenogenetical embryo in population A9799 (× 400); **6,** one-nucleate aposporous ES in the chalaze in an ovule of population A9549 (× 160).

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