Preslia, Praha, 60 : 193—213, 1988

Apomixis at the diploid level in *Sorbus eximia* (Embryological studies in *Sorbus* 3)

Apomixie na diploidní úrovni u jeřábu krasového, *Sorbus eximia* (Embryologické studie rodu *Sorbus* 3)

Andrzej Jankun and Miloslav Kovanda

Jankun A.[1]) et Kovanda M.[2]) (1988): Apomixis at the diploid level in *Sorbus eximia*. (Embryological studies in *Sorbus* 3). — Preslia, Praha, 60 : 193—213.

Keywords: *Sorbus*, apomixis, apospory, diplospory, parthenogenesis, pseudogamy, hybrid speciation, taxonomy, morphology.

Sorbus eximia Kovanda, a hybridogenous species of *S. aria* × *S. torminalis* parentage, is shown to be an apomict with two cytotypes, diploid (2n = 34) and tetraploid (2n = 68). Special attention was paid to the embryology of the diploid cytotype where apospory and diplospory were found to be present. The disturbed meiosis in macrosporogenesis leads to the origin of macrospores with unbalanced chromosome numbers. Exceptionally ESs with a reduced chromosome number may be formed. The origin of apomixis at the diploid level is considered. Analysis of morphological characters is provided. The species is shown to be a neoendemic of the Bohemian Karst, Czechoslovakia, where it has been recorded in 10 localities. The total number of individuals is about 90. Notes on ecology and ecobiology are given. Both parent species are diploid with 2n = 34.

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INTRODUCTION

Our previous studies of the breeding systems of hybridogenous *Sorbus* species (Jankun et Kovanda 1986, 1987, 1988) have indicated that they are in the main similar to those operating in Scandinavian hybrids investigated by Liljefors (1953, 1955). Apomixis and polyploidy, previously suspected, were found to be present. At the same time, some phenomena not previously known to occur in other species of *Sorbus* were noted, raising new problems and making further detailed research necessary. Examples include autonomous haploid parthenogenesis in *S. sudetica* (Tausch) Fritsch (Jankun et Kovanda 1986) and adventive (nucellar) embryony as well as chromosome summation in *S. bohemica* Kovanda (Jankun et Kovanda 1987). It seemed worthwhile therefore to make an embryological study of a diploid of hybrid origin, because almost all the *Sorbus* hybrids studied hitherto proved to be polyploid (triploid or tetraploid; see Liljefors 1953, 1955, Jankun et Kovanda 1986, 1987, 1988). Thus the main topic of the present paper is the breeding system of *S. eximia* Kovanda, involving *S. aria* (L.) Crantz (subg. *Aria*) and *S. torminalis* (L.) Crantz (subg. *Torminaria*) as the parent species.

Vol. 60 No. 2 (p. 97—192) editum 11. 4. 1988

Tab. 1. — Chromosome numbers in *Sorbus eximia* and the parent species, *S. aria* and *S. torminalis*

Species	Locality	2n	n
S. eximia KOVANDA	Bohemian Karst, summit area of Doutnáč hill, limestone, 433 m	68	34
	Bohemian Karst, Ve skalách karst plain, near Koda, limestone, 360 m	34	17
S. aria (L.) CRANTZ	Bohemian Karst, summit area of U kříže hill, near Svatý Jan pod Skalou, limestone, 380 m		17
S. torminalis (L.) CRANTZ	České středohoří Mts., summit area of Lovoš hill, near Lovosice, basalt, 570 m	34	

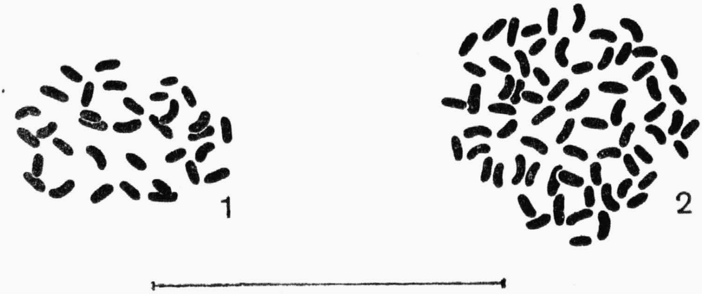
MATERIAL AND METHODS

The material for the present investigations was collected in two localities in the Bohemian Karst, Czechoslovakia, in 1982 and 1984—1986 (Tab. 1). The methods of embryological and karyological examination have been described in the first paper of this series (JANKUN et KOVANDA 1986). The responsibilities for the various parts of the study remain the same.

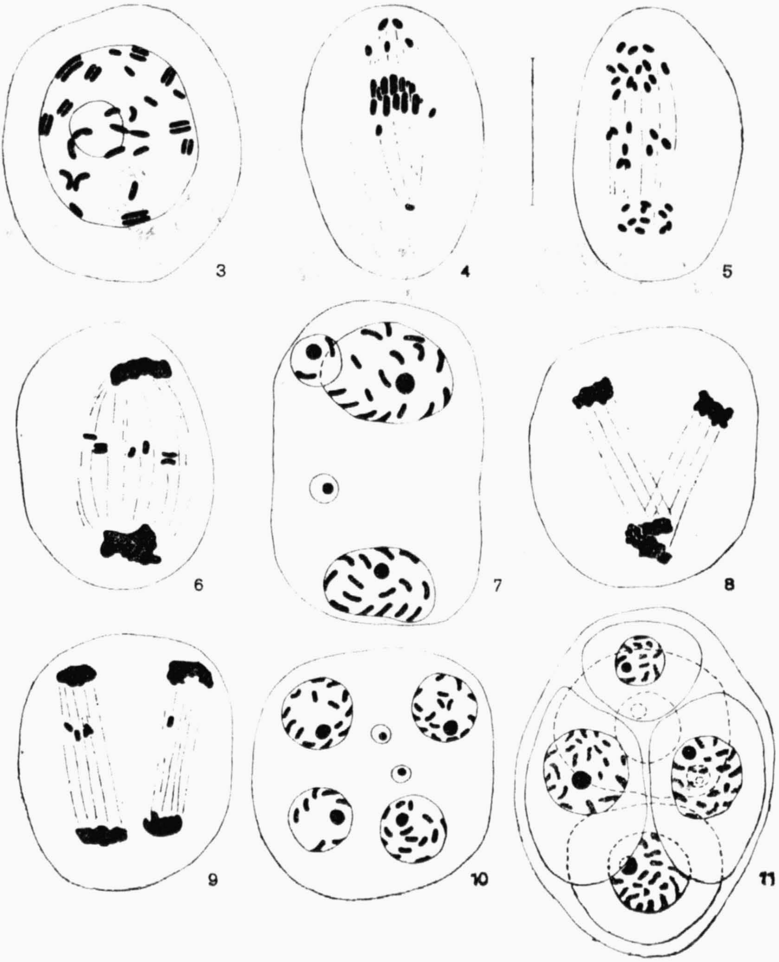
RESULTS

Karyology

S. *eximia* has previously been described as a tetraploid, with 2n = 68 (KOVANDA 1984). An examination of additional material revealed that diploids, 2n = 34, are also present (Tab. 1, Figs. 1, 2). The counts were made on squashes of young anthers and on mitotic metaphases from hypanthium or root-tips of young pot-grown plants. Further study is required to determine the morphological characters, ecological preferences and geographical distribution of the two cytotypes. Diploids seem to have leaves more obtusely and more shallowly lobate than tetraploids but at present this is a mere guesswork. Both the parent species, *S. aria* and *S. torminalis*, are diploid with 2n = 34.



Figs. 1—2. — *S. eximia* — metaphase plates. 1, diploid cytotype, 2n = **34 (from nucellus)**. 2, tetraploid cytotype, 2n = 68 (from hypanthium). Bar = 10 μm.



Figs. 3–11. – *S. eximia* – microsporogenesis in the diploid cytotype. 3, diakinesis ($10_{\mathrm{I}} + 12_{\mathrm{II}}$). 4, meta-anaphase I. 5, anaphase I. 6–7, telophase I. 8–10, telophase II. 11, polyad of microspores. Bar = 10 μm.

Embryology

Microsporogenesis

In flower buds of *S. eximia*, the whole course of meiosis could be observed, from early stages of the meiotic prophase to the tetrads of microspores. Disturbances characteristic of hybrid taxa occur in the microsporogenesis of the diploid cytotype (Fig. 3–11). The course of early meiotic prophase was regular. Only bivalents and univalents ($12_{\mathrm{II}} + 10_{\mathrm{I}}$) were seen in the diakinesis (Fig. 3). In metaphase I, the congression¹) of chromosome associations in the metaphase plate was not always regular, univalents occurring quite often outside the equatorial plane of the spindle. In anaphase I, univalents

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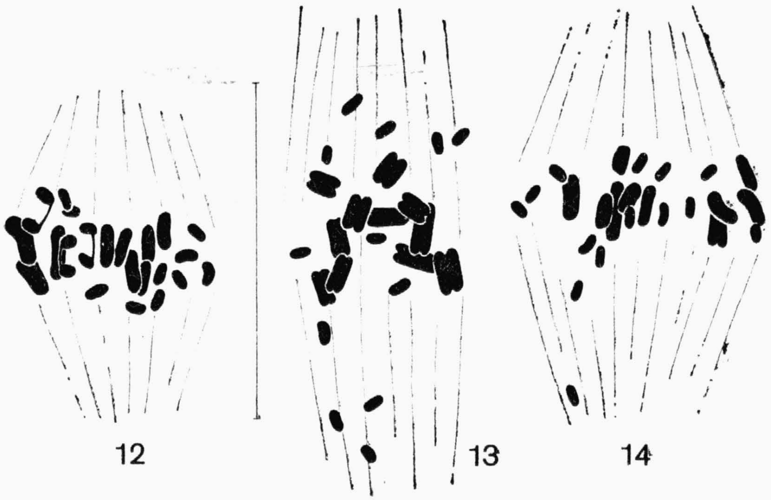
¹) See Darlington 1937.

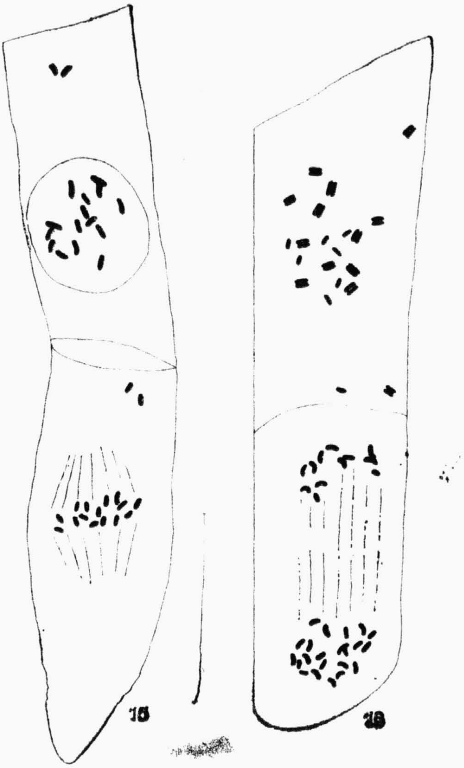


Figs. 12—14. — *S. eximia* — macrosporogenesis (metaphase I) in the diploid cytotype. 12, $10_{I} + 12_{II}$. 13, $12_{I} + 11_{II}$. 14, $14_{I} + 10_{II}$. Bar = 10 μm.

had already reached the poles of the spindle while bivalents persisted in the equatorial plane (Fig. 4). Sometimes a part of the chromosomes continued in the equatorial plane while the others had reached the opposite poles (Fig. 5). In addition to these disturbances, in the majority of interphase cells only two daughter nuclei occurred. In the telophase it was possible to discern chromosomes remaining in the cytoplasm (Fig. 6) and micronuclei (Fig. 7). In metaphase II, the axes of spindles were positioned vertically or parallel to each other (Fig. 9); the oblique position (Fig. 8) may result in a fusion of telophase groups. Lagging chromosomes (Fig. 9), sometimes producing micronuclei (Fig. 10), could be seen among these groups. The majority of tetrads had a typical structure. The micronuclei cut off the cytoplasm, producing microcytes, or continued in the cytoplasm of the microspore (Fig. 11). Besides normal pollen grains with a reduced number of chromosomes and microcytes, giant pollen grains with an unreduced chromosome number were present. The stainability of pollen as shown by the acetocarmine test was c. 63 %.

Gynoecium and the development of ovules

The gynoecium of *S. eximia* is syncarpic, consisting of two or rarely three carpels coalesced up to 1/3—1/2 of the length of the styles (Fig. 26). The ovary is semi-inferior, each loculus containing two ovules of which, as a rule, only one develops into seed. In the early stages of the development, subepidermal cells in the apical part of the ovule increase in size (primary archesporium cells) and cut off the parietal cells. As in other species of *Sorbus*, the archesporium is multicellular and it is very difficult to define any distinct boundary between the secondary archesporium cells and the outer cells. When mature, the ovule is anatropous, bitegumInous and crassinucellate. In many ovules it is possible to observe degeneration of the primary or secondary archesporium cells.



Figs. 15—16. — *S. eximia* — macrosporogenesis (second meiotic division) in the diploid cytotype. 15, micropylar cell of a dyad: prophase nucleus containing 15 chromosomes, 2 chromosomes remaining in the cytoplasm as a result of disturbances in the first meiotic division. Chalazal cell: metaphase with 15 chromosomes, 2 chromosomes remaining in the cytoplasm as a result of disturbances in the first meiotic division. 16, micropylar cell of a dyad: metaphase with 21 units (13 chromosomes with 2 chromatids from the division of bivalents and 8 from univalents whose sister chromatids divided in the first meiotic division). Chalazal cell: irregular division of chromosomes in anaphase: 12 + 22. Apparent conjugation in metaphase I: $8_{\mathrm{I}} + 13_{\mathrm{II}}$. Bar = 10 μm.

Macrosporogenesis

The entire course of macrosporogenesis was studied only in the diploid cytotype (Tab. 2). The stages of meiotic prophase were regular.

A pre-meiotic stage (synapsis) was observed, as a rule, in one cell of the ovule but ovules with two or three cells in synapsis were also noted. Meiosis may take place in two adjacent cells.

In a number of cases, we observed meiosis in the mother cells of embryo sacs. In metaphase I, congression of chromosomes is quite regular (Fig. 12). In addition to bivalents, there are also univalents present. The conjugation of chromosomes varies over a wide range; there were for instance 13 bivalents + 8 univalents, 12 bivalents + 10 univalents (Fig. 12), 11 bivalents + 12 univalents (Fig. 13), 10 bivalents + 14 univalents (Fig. 14). Univalents seem to proceed towards the pole. Some lagging chromosomes may remain in the cytoplasm of the dyad cells (Fig. 15). Daughter nuclei of the dyad have a reduced and sometimes also diminished number of chromosomes (15 instead of 17; Fig. 15). As a rule, the second meiotic divisions are not synchronic in the two cells of the dyad. The micropylar cell of the dyad is smaller and is retarded in relation to the chalazal cell (Fig. 15).

Some of the plates seen are difficult to interpret. For instance, the chromosome numbers occurring in the cell of a dyad (Fig. 16) may be understood only by assuming that univalents divide in anaphase I; such a phenomenon has been observed by LILJEFORS (1955) in the microsporogenesis of a number of species of *Sorbus*. In the dyad discussed, 21 metaphase chromosomes are present in the micropylar cell, while 34 anaphase chromosomes are seen in the chalazal cell. It seems likely that in metaphase I there were 13 bivalents + 8 univalents present. In anaphase I, following the division of univalents and bivalents the daughter nuclei possessed 21 chromosomes (13 + 8) instead of 17. In anaphase II, only chromosomes arising from bivalents divide, resulting in 13 + 13 chromosomes and 8 chromosomes from the univalents. In the case analysed, the division of chromosomes in anaphase II was irregular; at one pole there were 12 chromosomes while at the other there were 22.

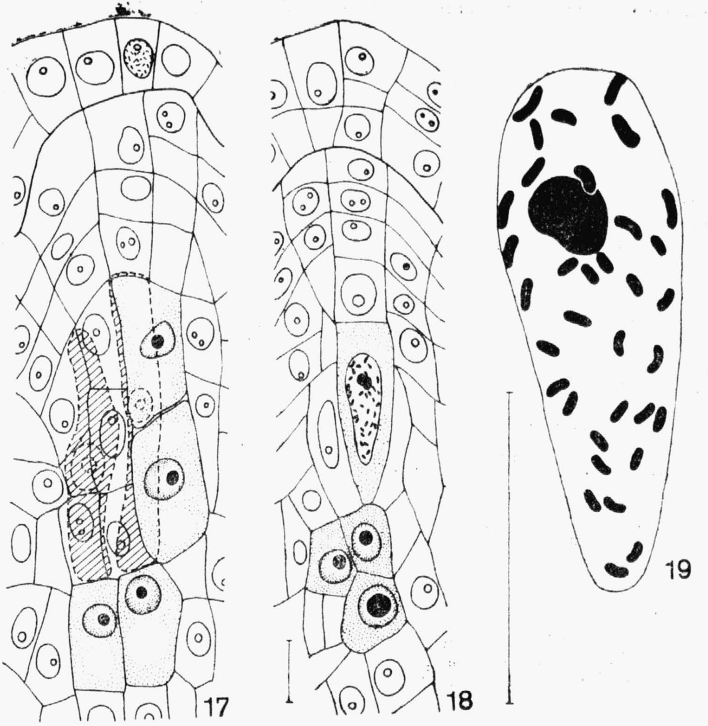
A dyad was also observed containing two nuclei in the micropylar cell and three nuclei of different size in the chalazal cell. These disturbances result in the origin of an unviable dyad with an unbalanced chromosome number. Only dyads with chromosome numbers approaching the haploid number may be expected to continue their development. Following the second meiotic division a tetrad of macrospores originates, usually arranged linearly. In two cases the vertical arrangement of the spindles suggested that tetrad of the T type originate. Only in three instances in the diploid cytotype and in two instances in the tetraploid cytotype was the development of a 1-nucleate ES from the chalazal macrospore seen (Fig. 20).

Development of apomeiotic embryo-sacs

In the majority of ovules examined, the somatic cells surrounding the archesporium cells increase in size, their cytoplasm becomes more stainable and they turn into mother cells of apomeiotic ESs (Fig. 18).

In the diploid cytotype, the presence of diplospory (with nuclei of the archesporium cells entering mitotic prophase; Figs. 18, 19) was noted sporadically. Apospory is certainly the prevailing type of the development of ESs in the diploid *S. eximia*.

In certain ovules, one or several apomeiotic ESs may develop (Fig. 17). They may differ in the stage of their development: for instance, four 1-nucleate ESs + two 2-nucleate ESs, 8-nucleate ES + 2-nucleate ES + 1-nucleate ES (Tab. 2). The initial cells of apomeiotic ESs increase in size, undergo vacuolation and become 1-nucleate ESs (Fig. 17). The vacuoles are found either in the chalazal or micropylar part or at both poles of the cell. The following mitotic divisions give rise to 2-nucleate ESs, then to 4-nucleate and finally to 8-nucleate ESs. The 2-nucleate and 4-nucleate ESs showed regular polarisation, while in several 8-nucleate ESs irregular polarisation was noted: two nuclei at the micropylar pole and six at the chalazal pole, with all the nuclei found in the chalazal part of the ES. In yet another case, the nuclei were found in the marginal part of the ES. A typical mature 8-nucleate ES possesses the egg apparatus at the micropylar pole (egg cell + two synergids with fibrillar apparatus), two polar nuclei in the central cell



Figs. 17—19. — *S. eximia* — origin of ESs in the diploid cytotype. 17, four 1-nucleate apomeiotic ESs and two degenerating cells of secondary archesporium (hatched). 18, diplospory: mitotic prophase in a cell of secondary archesporium. Note the three initial cells of apomeiotic ESs below the archesporium cell. 19, prophase nucleus of archesporium cell, 2n = 34. Bars = 10 μm.

and three short-lived antipodals in the chalazal part. In the material analysed both ESs with reversed polarisation and monopolar ESs (with egg apparatus and antipodals at the chalazal pole) occurred.

The present embryological studies have also shown that in the tetraploid cytotype of *S. eximia* the aposporous type of development of ESs is prevalent (Tab. 3). The 1-nucleate meiotic ESs were seen only in two instances. Apomeiotic ESs develop as a rule from the cells below or at the side of the group of archesporium cells. In one case a 4-nucleate apomeiotic ES was observed developing above the tetrad of macrospores (Fig. 21), with an additional 2-nucleate apomeiotic ES at the level of the tetrad. The disturbances in polarisation and structure of ESs characteristic of apomictic taxa were also present. The 16-nucleate ES seen in Fig. 22 apparently originated by a fusion of two 8-nucleate ESs. Two antipodals were formed at the micropylar pole, an egg apparatus at the chalazal pole, another egg apparatus is found in the central part of the ES and two groups of polar nuclei (3 + 5) are found in the central cell. Yet another ES with reversed polarisation (Fig. 23) has three antipodals at the micropylar pole and one synergid + two egg cells after fertilisation at the chalazal pole; in the central cell there are two nuclei

Tab. 2. — **Summary of the ovules examined** (diploid cytotype, 2n = 34)

Stage	Number of ovules
Viable ovules	
Primordia of ovules	41
Early stages of development (prior to differentiation of archesporium)	54
Primary archesporium	14
Secondary archesporium	118
Secondary archesporium + initial cells of apomeiotic ESs	25
Synapsis	11
Synapsis + initial cells of apomeiotic ESs	7
Synapsis + two 1-nucleate apomeiotic ESs + initial cells of apomeiotic ESs	2
Synapsis + two apomeiotic ESs	2
Leptotene	4
Leptotene + two apomeiotic ESs	1
Zygotene	2
Zygotene + initial cells of apomeiotic ESs	1
Pachytene	1
Diakinesis	1
Diakinesis + initial cells of apomeiotic ESs	1
Metaphase I	7
Ana-telophase I	1
Telophase I	1
Dyad	1
Dyad + initial cells of apomeiotic ESs	1
Dyad + two 1-nucleate apomeiotic ESs	1
Second meiotic division	4
Remnants of a dyad	2
Tetrad	3
Tetrad + initial cells of apomeiotic ESs	3
Tetrad + 2-nucleate apomeiotic ES + 4-nucleate ES	1
1-nucleate ES developing from the chalazal macrospore	3
1-nucleate diplosporous ES	6
Remnants of a tetrad	2
Remnants of degenerate archesporium	27
Remnants of archesporium + initial cells of apomeiotic ESs	7
Remnants of archesporium + 1-nucleate apomeiotic ES	3
Remnants of archesporium + two 1-nucleate apomeiotic ESs	1
Two 1-nucleate apomeiotic ESs	7
Four 1-nucleate apomeiotic ESs	1
2-nucleate ES	11
2-nucleate ES (metaphase, 2n = 34)	1
Two 2-nucleate ESs	4
Two 2-nucleate ESs + one 1-nucleate ES + initial cells of apomeiotic ESs	1
4-nucleate ES	14
Two 4-nucleate ESs (metaphase, 2n = 34)	1
4-nucleate ES + two 2-nucleate ESs	1
8-nucleate ES (with regular polarisation — nuclear stage)	3
8-nucleate ES (with irregular polarisation — nuclear stage)	2
8-nucleate mature ES (with regular polarisation)	117
8-nucleate mature ES (with reversed polarisation)	2
8-nucleate mature ES (with egg apparatus and antipodals at the chalazal pole)	1
8-nucleate ES + two 1-nucleate ESs	1
8-nucleate ES + 2-nucleate ES + 1-nucleate ES	1
8-nucleate ES + 4-nucleate ES	3
Two 8-nucleate ESs	11

Tab. 2 (contd.)

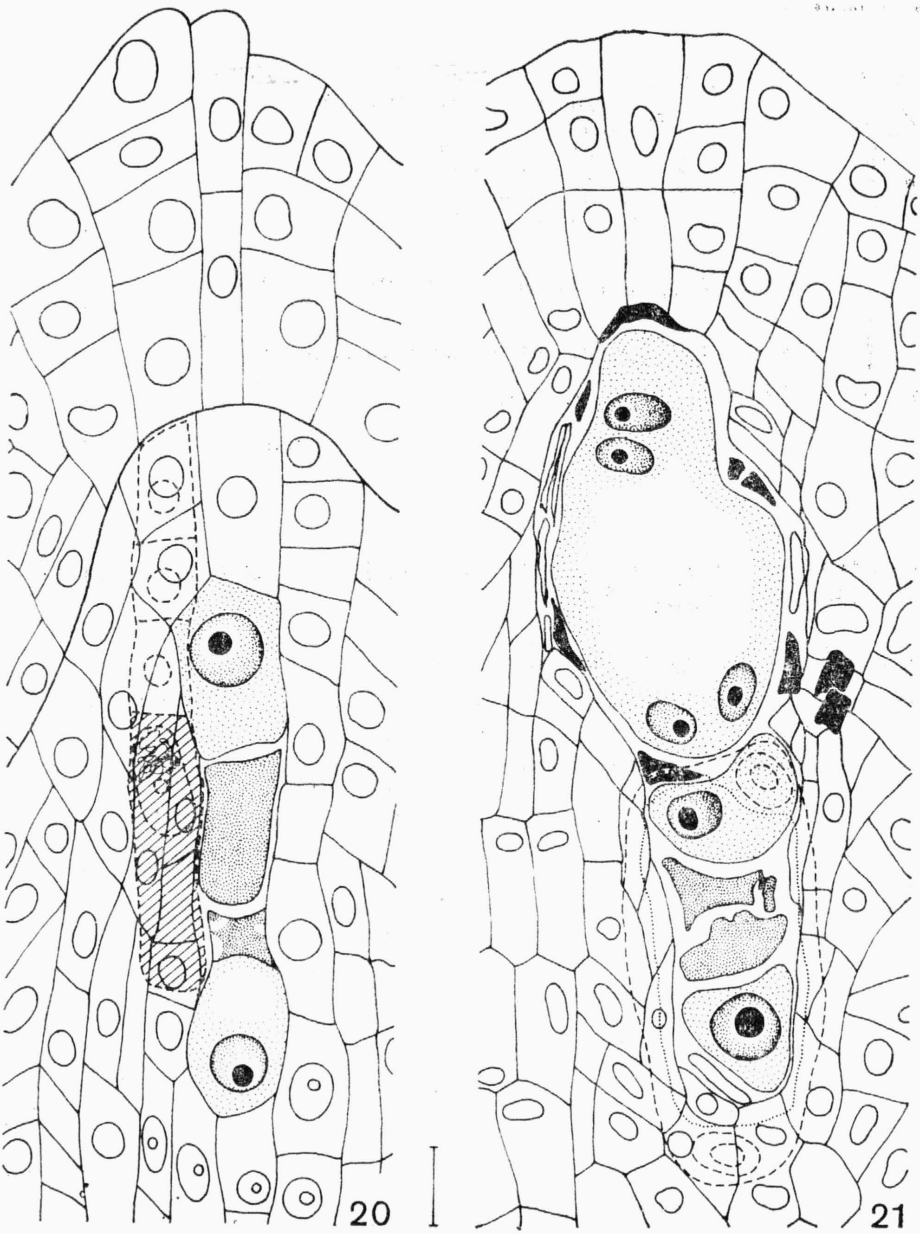
Egg cell (mitotic prophase) + two polar nuclei	1
Remnants of degenerate egg apparatus + nuclear endosperm	4
Multicellular embryo + nuclear endosperm	15
Two multicellular embryos + nuclear endosperm	1
Three multicellular embryos + nuclear endosperm	1
Multicellular embryo + cellular endosperm	14
Multicellular embryo + degenerating endosperm	2
Degenerated ovules	
Young ovules (integuments have not yet reached the top of the nucellus)	8
Older ovules	4
8-nucleate ES	67
Collapsed walls of ES (probably representing the degeneration of an 8-nucleate ES)	88
Multicellular embryo + nuclear endosperm	4
Total	769

each of which has been fertilised. This accumulation of anomalies is suggestive of the aposporous origin of the ESs.

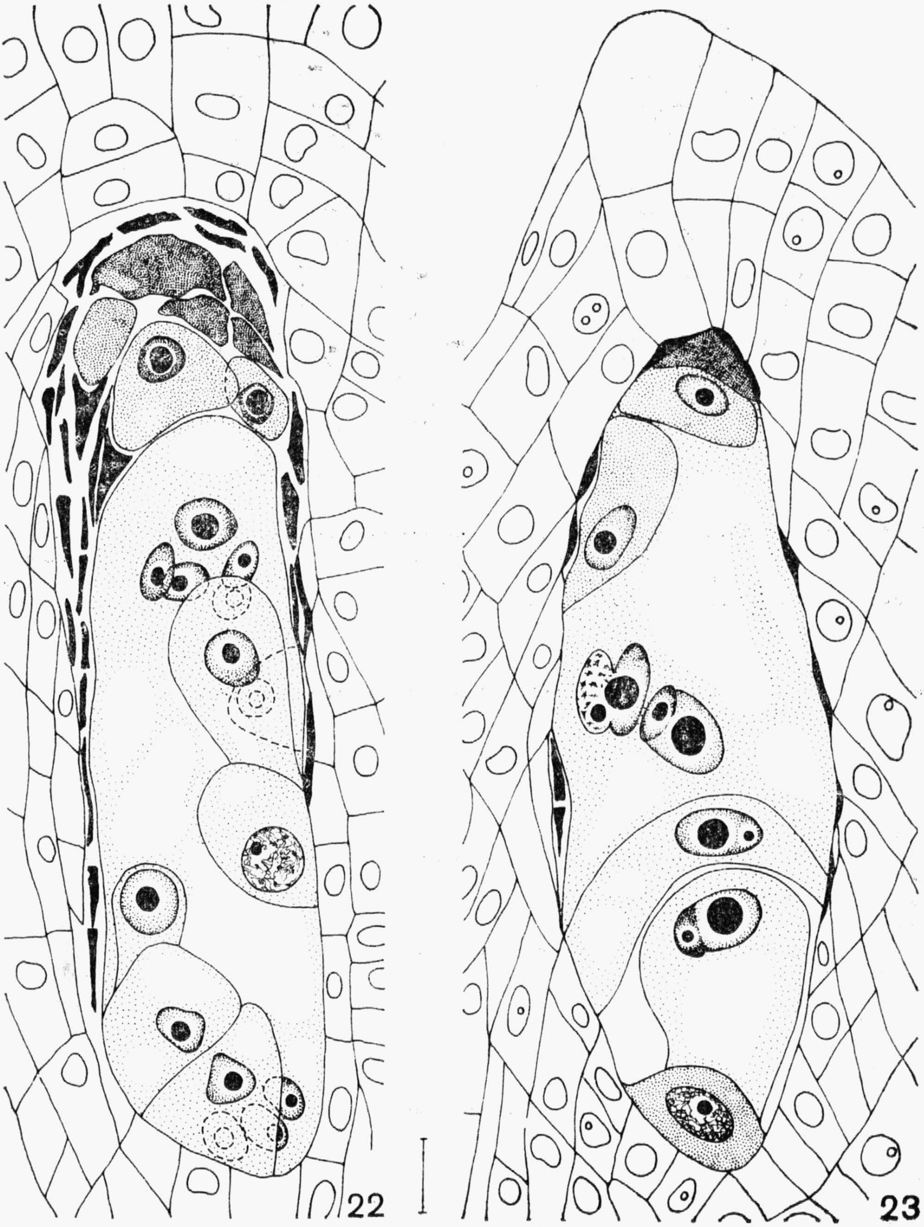
Development of the embryo and endosperm

The egg cell of apomeiotic ESs develops parthenogenetically but the fertilisation of the secondary nucleus is necessary for the development of the endosperm — a case of pseudogamy. The presence of pseudogamy has been experimentally proven in both the cytotypes of *S. eximia*: emasculated and isolated flowers failed to produce any fruits (see below). Another proof in the diploid cytotype is the chromosome number of the endosperm, 5n = c. 85 (Fig. 24). In one ovule of the diploid cytotype the chromosome number 6n = c. 102 (Fig. 25) was counted, probably a result of fertilisation by two sperms (34 + 34 + 17 + 17) or by a sperm with unreduced chromosome number.

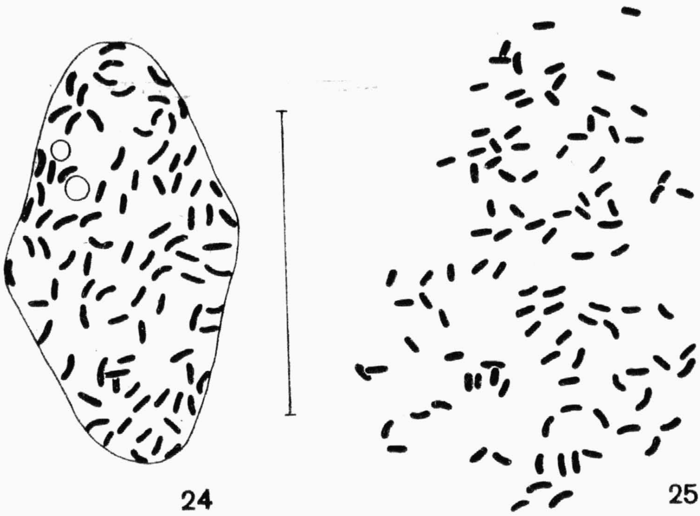
The occurrence in *S. eximia* of different numbers of polar nuclei and their separate fertilisation (unfused; Fig. 23) suggests that there may be different initial chromosome numbers in the endosperm. It should be noted that beginnig from the stage of nuclear endosperm, disturbances leading to the polyploidisation of nuclei occurred. In the cellular endosperm there were cells with single nuclei at different ploidy levels as well as multinucleate cells. The embryo develops at the micropylar pole. There is however no definite correlation between the development of the embryo and that of the endosperm. In one case we observed a prophase in the egg cell and two polar nuclei, elsewhere remnants of degenerating egg apparatus were found together with nuclear endosperm. Two cases of polyembryony proper were noted in the diploid cytotype. Besides embryos that originated from the egg cell, nucellar embryos also developed.



Figs. 20–21. — *S. eximia* — origin of ESs in the tetraploid cytotype: 20, tetrad of macrospores: a 1-nucleate ES developed from the chalazal macrospore. The broken line delimits the archesporium cell at synapsis and three parietal cells. 21, tetrad of macrospores (with outer cells living, inner degenerate). The apomoiotic ES at the level of the tetrad of macrospores delimited by the broken line. Bar = 10 μm.



Figs. 22—23. — *S. eximia* — irregularly polarised and organised ESs. 22, 16-nucleate ES. Micropylar pole — two antipodals, central part — egg apparatus, chalazal pole — another egg apparatus, central cell — two groups of polar nuclei (5 + 3). 23, 8-nucleate ES. Micropylar pole — 3 antipodals, central part — two fertilised polar nuclei, chalazal pole — one synergid and two fertilised egg cells. Bar = 10 μm.



Figs. 24—25. — *S. eximia* — (pseudogamy) — chromosome numbers of endosperm in the diploid cytotype. 24, prophase with 5n = c. 85 (two polar nuclei with the somatic chromosome number and a sperm with a reduced number: 34 + 34 + 17 = 85). 25, metaphase with 6n = c. 102 (probably two polar nuclei and two sperms: 34 + 34 + 17 + 17). Bar = 10 µm.

Tab. 3. — Summary of the ovules examined (tetraploid cytotype, 2n = 68)

Stage	Number of ovules
Remnants of degenerate archesporium	11
Secondary archesporium + initial cells of apomeiotic ESs	14
Synapsis	8
Tetrad	2
Tetrad + 4-nucleate ES	1
1-nucleate ES developing from the chalazal macrospore	2
1-nucleate apomeiotic ES	20
Three 1-nucleate apomeiotic ESs	1
2-nucleate ES	2
Two 2-nucleate ESs	2
4-nucleate ES + 1-nucleate ES	3
4-nucleate ES + 2-nucleate ES	1
8-nucleate ES (with regular polarisation — nuclear stage)	1
8-nucleate ES (with irregular polarisation: 6 + 2 nuclei)	1
8-nucleate ES (with irregular polarisation — nuclear stage) + 2-nucleate ES	1
8-nucleate mature ES (with regular polarisation)	25
8-nucleate mature ES (with reversed polarisation)	1
8-nucleate mature ES with three polar nuclei	1
Two 8-nucleate ESs	2
Degenerating 8-nucleate ESs	6
16-nucleate ES (with reversed polarisation)	1
ES growing into micropylar canal	2
Nucellus overgrowing micropylar canal	1
Total	109

Taxonomy

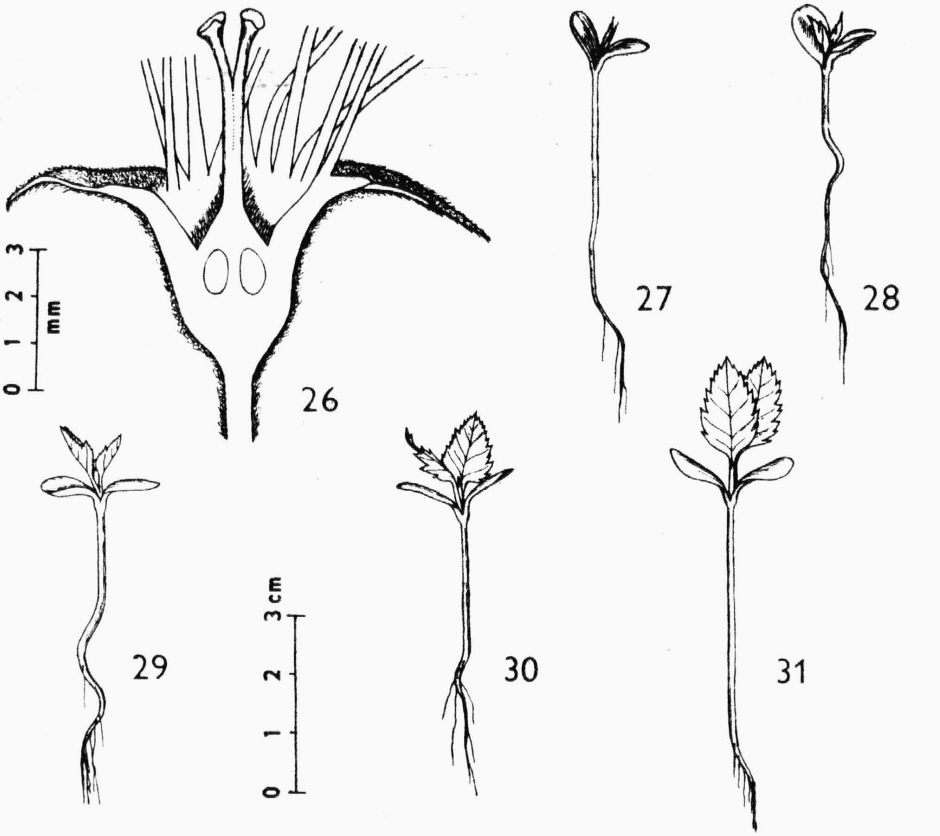
The first collections of the material now referred to *S. eximia* were made by Günther Beck von Mannagetta, then Professor at the German University in Prague, in the vicinity of Srbsko and Hostim in 1918 and 1920. Beck identified some of the gatherings as a hybrid *S. aria* × *S. torminalis* on the labels but never published the records. Neither did Professor Jaromír Klika who collected the plant at Koda in 1942—1946 and also recognised its hybrid nature. Occasional collections by other authors remained unnamed. One of us (M. K.) studied this taxon in the field in 1963—1968 and 1978—1983 and, based on these studies and preliminary results of embryological investigation, described it as a hybridogenous species (Kovanda 1984). Field studies were continued in 1984—1986. A full description is given below:

Sorbus eximia Kovanda Preslia 56 : 170, 1984

Trees or shrubs 3—10 (—15) m tall. Buds acute, almost completely glabrous. Leaf blade broadly ovate to broadly elliptic, pinnatilobate (with acute, serrate lobes), doubly serrate in the upper part, remotely serrate in the lower part, (8.0—) 9.5—11.5 (—12.5) cm long and (5.5—) 6.5—9.0 (—10.5) cm wide, tomentose beneath, glabrescent on the upper side, with (7—) 8—10 pairs of veins; petiole (1.8—) 2.3—2.9 (—3.3) cm long. Inflorescence a rather lax corymbothyrsus with tomentose, glabrescent branches. Hypanthium turbinate, tomentose; calyx-teeth triangular, acute, 2.4—3.2 mm long, patent, persistent; petals broadly ovate to broadly elliptic, with a short claw, 6.4—9.0 mm long, villous at the base on the adaxial side, yellowish-white; stamens 20; anthers yellow; ovary semi-inferior; styles 2, rarely 3 (exceptionally 4), villose at the base, coalesced to 1/3—1/2; stigmas flat. Fruits broadly ellipsoid to globose, (11—) 12—13 (—14) mm long and (9—) 10—11 (—12) mm in diameter, orange, glabrous, shiny, lenticellate; endocarp cartilaginous. Seeds chestnut brown, 4.3—5.1 mm long (Plates XII—XIV, Figs. 26—31).

In these characters, *S. eximia* fits into the group of hybridogenous intermediates linking *S. aria* (L.) Crantz s.l. and *S. torminalis* (L.) Crantz. A number of such taxa have been described from Southern England (Warburg 1957), the German Democratic Republic and the Federal Republic of Germany (Düll 1961), Hungary (Kárpati 1960) and Slovakia (Kovanda 1961, Kárpati 1966); for a review, see also Warburg et Kárpáti (1968). In the Czech Lands, the only other representative of this group so far known is *S. bohemica* Kovanda, derived from hybridisation between *S. danubialis* (Jáv.) Kárpáti and *S. torminalis* (L.) Crantz (see Kovanda 1961b, Jankun et Kovanda 1987). From *S. bohemica*, *S. eximia* is readily distinguished by its larger, mostly ovate leaves, longer petioles, patent calyx-teeth, larger petals, fruits densely lenticellate and thinner endocarp.

It will be seen from Tab. 4 that in its morphology, *S. eximia* combines characters of two distinct species, each representing a different subgenus. In its general appearance, *S. eximia* approaches members of subg. *Aria* rather than *S. torminalis* but differs in the partly fused styles, a character present, in Europe and S. W. Asia, only in *S. torminalis* and its hybrids. The orange colour of the fruits and their lack of indumentum, the flat stigma and the structure of the endocarp are also characters not found in subg. *Aria*.



Figs. 26–31. — *S. eximia.* 26, longitudinal section of flower. 27–31, early stages of ontogenic development. (Orig. J. Soják.)

The fluctuation in the degree of fusion of the styles (even within one individual) is paralleled in *S. bohemica*, a hybrid of the *S. danubialis* × *S. torminalis* parentage (Jankun et Kovanda 1987), and in *S. austriaca* (G. Beck) Hedl., derived from *S. aria* × *S. aucuparia* (Kovanda 1961a), even though, strictly speaking, in the latter species it is the ovaries that coalesce, not the styles.

The stellate lenticels found copiously on the bark of older trunks (Plate XIII, 4) are a distinctive feature of *S. eximia*.

Because the parent species, *S. aria* (L.) Crantz and *S. torminalis* (L.) Crantz are frequent in the distribution area of *S. eximia* (the former species has the centre of its distribution in the ČSR in that area) and often occur in neighbouring habitats, great care was taken to see if there were any traces of introgressive hybridisation or F_1 hybrids in nature. None were found, suggesting perhaps that between the parent species there is a strong barrier which did however once collapse to give rise to the present *S. eximia*.

S. eximia has previously been shown to contain flavone O-glycosides (luteolin 7-O-rhamnosylglucoside, luteolin 7-O-diglucoside, luteolin 4′-O-gluco-

Tab. 4. — The distinguishing characters of *S. eximia*, *S. aria* and *S. torminalis*

	S. eximia	*S. aria*	*S. torminalis*
Underside of leaves	Tomentose	Tomentose	Glabrous or sparsely hairy
Number of veins (pairs)	(7—) 8—10	(7—) 9—11 (—13)	(5—) 6—7 (—8)
Length of petiole (mm)	(18—) 23—29 (—33)	(7—) 9—18 (—20)	(18—) 20—38 (—54)
Inflorescence	Lax, branches tomentose	Dense, branches tomentose	Lax, branches Glabretcent
Calyx-teeth	Patent, 2.4—3.2 mm long, persistent	Deflexed, (3.5—) 4.0—4.8 (—5.0) mm long, persistent	Patent, 2.0—2.5 mm long, deciduous
Petals	6.4—9.0 mm long, shortly unguiculate	6.2—8.0 mm long, shortly unguiculate	4—5 mm long, exunguiculate
Ovary	Semi-inferior	Semi-inferior	Inferior
Styles	2 (—3), coalesced to 1/3—1/2, woolly at base	2—3, free, wooly at base	2, coalesced to 1/3—1/2 glabrous
Stigma	Flat	Convex	Flat
Indumentum of fruit	Absent	Present	Absent
Colour of fruit	Orange, shiny	Red, shiny	Brown, not shiny
Mesocarp	Heterogenous	Heterogenous	Homogenous
Endocarp	Cartilaginous	Cartilaginous	Stony

side), characteristic, in Europe, of *S. torminalis* and *S. chamaemespilus* as well as their hybrids. Vitexin (apigenin 8-C-glucoside) was found to be absent, indicating that *S. eximia* may have resulted from back-crossing of the F_1 hybrid (*S. aria* × *S. torminalis*) with *S. aria* during which the genes for flavone C-glycosylation have become segregated from the genes for flavone O-glycosylation. Other taxa of the *Aria* × *Torminaria* parentage, including *S. bakonyensis* (Jáv.) Kárpáti, *S. semiincisa* Borbás, *S. bohemica* Kovanda and *S. slovenica* Kovanda, are supposed to have originated in the same way (see Chalice et Kovanda 1978, 1986). In *S. bohemica*, this hypothesis has been corroborated by embryological evidence (Jankun et Kovanda 1987).

Geographical distribution

S. eximia is confined to the warm (average annual temperature, 9 °C) area of Devonian limestones between Prague and Beroun, which since the 1950s has been known as the Bohemian Karst (Český kras). It has to date been confirmed from 10 localities (Fig. 32, 33), none separate by a gap of more than 4 km. At the time of publication of the name *S. eximia* (Kovanda 1984), only four localities were known. The fifth, the karst plain Ve skalách near Koda, was discovered in 1984 (see Challice et see Kovanda 1986) and the sixth, Svatý Jan pod Skalou, in 1985. Four more stations were found in 1986. The following complete list of localities is arranged from west to east and from north to south:

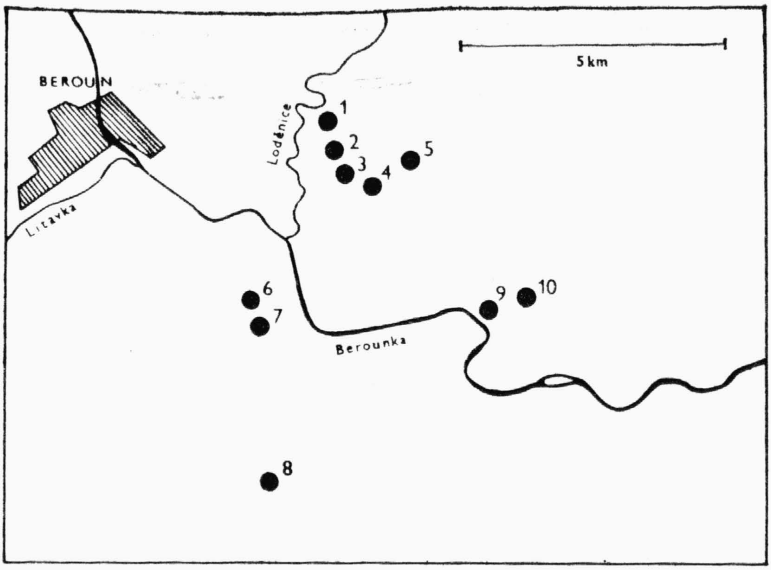


Fig. 32. — Distribution of *S. eximia* in the Bohemian Karst. 1, U kříže hill. 2, Vysoká stráň hill. 3, between Hostim and Bubovice. 4, Doutnáč hill. 5, Paní hora hill. 6, Koda forest. 7, Ve skalách karst plain. 8, Mramor hill. 9, Plešivec hill. 10, Haknová hill.

1. Summit area of U kříže hill, 396 m, near Svatý Jan pod Skalou
2. Summit area of Vysoká stráň hill, 435 m, near Hostim
3. On road from Hostim to Bubovice, 1 km from Bubovice, 350 m
4. Summit area of Doutnáč hill, 433 m, near Srbsko
5. Summit area of Paní hora hill, near Bubovice, 380 m
6. Koda forest, N. slope (N. of point 390 m), 360—380 m
7. Ve skalách karst plain, near Koda, 360—380 m
8. Mramor hill, near Liteň, N. margin of the plateau, 450 m
9. Summit area of Plešivec hill, 362 m, near Karlštejn
10. Summit area of Haknová hill, 402 m, near Karlštejn

It will be seen that the altitudinal range is small, from c. 350 m (near Bubovice) to c. 450 m (Mramor hill). Both *S. aria* and *S. torminalis* are frequent in the area and even extend to the adjacent cooler regions (districts of Křivoklátsko, Podbrdsko and Střední Povltaví) but *S. eximia* does not.

Because *S. eximia* clearly prefers summits of hills for its habitats, a survey of them was made in 1985—1986 in an attempt to detect more stations. The following list of hills is of those where the species has not been recorded:

Kolo hill, 407 m, near Loděnice
Herinky hill, 440 m, near Lištice
Nameless hill (point 390 m) N.W. of Hostim
Boubová hill, 430 m, near Hostim
Velká hora hill, 422 m, near Srbsko
Chlum hill, 348 m, near Srbsko
Javorka hill, 384 m, near Karlštejn
Kněží hora hill, 357 m, near Karlštejn
Výška hill, 425 m, near Mořina
Koukolová hora hill, 471 m, near Popovice
Damil hill, 396 m, near Tetín
Zlatý kůň hill, 475 m, near Koněprusy

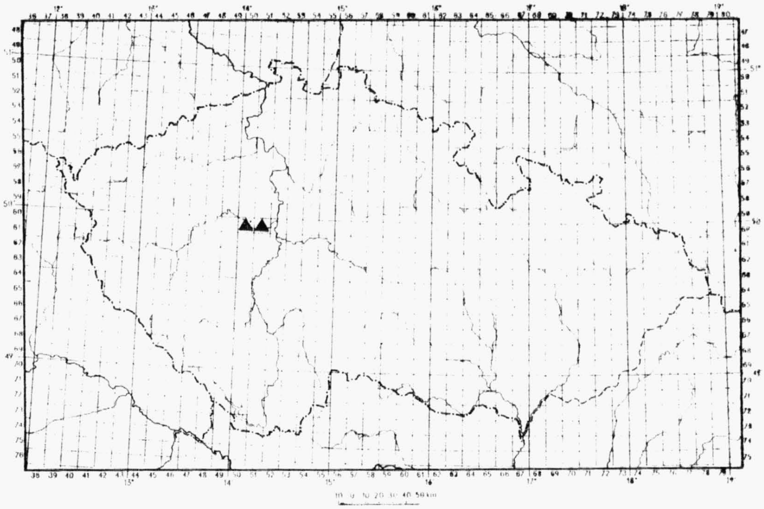


Fig. 33. — Distribution of *S. eximia* in the ČSR.

Tobolský vrch hill, 467 m, near Tobolka
Kobyla hill, disused quarry, 430—470 m
Vysoká skála hill, 472 m, near Všeradice
Bacín hill, 499 m, near Vinařice[2])
Šamor hill, 481 m, near Vinařice

However careful, this survey only indicates where *S. eximia* has not been found, not where it does not occur. If the search is continued, it will certainly bring to light new records.

Ecology and phytocenology

Whereas *S. aria* and *S. torminalis* occupy, to a certain extent, separate ecological niches, *S. eximia* manages to merge the requirements of both the parent species, thus acquiring considerable ecological plasticity. It is found growing in a number of plant communities, ranging from *Quercus pubescens*-scrub, subxerophilous oak woodlands (alliance *Quercion pubescenti-petraeae*) and xerothermous herb communities on shallow skeletal soils (alliance *Festucion valesiacae*) to the species-rich mesophilous oak-hornbeam and oak-lime woodlands (alliance *Carpinion*, order *Fagetalia sylvaticae*).

Aspect seems to be of little importance. The largest population (Ve skalách near Koda) is on the southern slope but the next two largest both face north and on the Doutnáč hill the specimens are found scattered on all sides of the hill except the forest steppe on the S. E.

Ecobiology

S. eximia flowers in the latter half of May and its fruits ripen in late September. Fruits are produced in quantity every year. Second flowering, frequent in *S. bohemica*, has not yet been observed in this species.

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2) The highest elevation in the Český kras Protected Landscape Area.

The number of seeds per loculus varies as it does in *S. bohemica*, the most frequent type of fruit being one with a bilocular endocarp, one loculus containing one seed, the other empty, followed by a bilocular endocarp with one seed in each loculus.

The viability of seed was found to be good, varying from 48 to 59 %. For the seeds to germinate, stratification or sowing in pots embedded in soil over winter is required. The seedlings have two cotyledons that are broadly elliptic to suborbicular, obtuse, cuneate at base, entire, 6—8 mm long and 5—7 mm wide. In the first year of life, one to three leaves are produced. (Figs. 27—31, Plate XIV, 6). In nature, seedlings are of frequent occurrence in the Ve skalách topodeme but rather rare elsewhere. It is obviously the closed woodland in these habitats that hinders the establishment and survival of the seedlings.

In order to asses the extent of apomixis and the possible presence of pseudogamy, isolation and emasculation experiments were performed in 1986. Isolated flowers were found to produce no seed. In 150 flowers (of two individuals: 100 + 50) isolated in the Ve skalách locality, no fruit set at all was observed. Of 20 emasculated (and isolated) flowers (from other two individuals: 10 + 10), two did set fruit but their development was soon arrested and they contained no vestiges of seeds.

At present, some 90 specimens of different age (not counting seedlings) are on record. The one thought to be the oldest (Plate XII, 1, 2) was subjected to tree ring analysis and its age was found to be c. 85 years.

DISCUSSION

Perhaps the most important (and most surprising) result of our study in *S. eximia* is the occurrence of two cytodemes, diploid and tetraploid, combined with apomixis. In the plant kingdom, apomixis is known to be largely confined to polyploids and is rare in diploids. In the genus *Sorbus*, all the apomictic hybrids so far examined proved polyploid (triploid or tetraploid; Liljefors 1953, 1955, Jankun et Kovanda 1986, 1987, 1988). The only diploid apomicts on record in the *Malaceae* are apparently certain species of *Malus* (Konstantinov 1958, Krylova 1981). Examples in the *Rosaceae* s. str. include *Potentilla argentea* agg. (Müntzing 1928, 1958, Asker 1971, 1976) and *P. aurea* (Shimotomai 1935); a strong apomeiotic tendency is known to occur in the diploid *Waldsteinia geoides* (Czapik 1985). In other plant families, diploid apomixis has been reported for *Hieracium umbellatum* (Gustafsson 1946), *Arabis Holboellii* (Böcher 1951), the dihaploid *Ranunculus auricomus* obtained experimentally by Nogler (1984), as well as for the aposporous dihaploids of *Ranunculus argoviensis* (Nogler 1984). Nogler (l. c.) considers that in *Ranunculus auricomus* the capacity for apomixis cannot be transmitted by haploid gametes but only by diploid (reduced or unreduced) or polyploid ones. The experimental diploid *Ranunculus auricomus* originated as a dihaploid; its apospory is due to a dominant gene (Nogler 1986). Stebbins (1971) suggests that in some groups, such as the genus *Citrus* and some species of *Potentilla*, apomixis has developed in diploid species or hybrids. According to Rutishauser (1967) and Asker (1971), apomixis at the diploid level is determined by independent systems of recessive genes, which control the elementary apomictic processes: apospory, diplospory and parthenogenesis. The genes have a quantitative effect.

In *Sorbus*, the genetical mechanism of apomixis is still poorly understood. Apomixis at the diploid level in *S. eximia* might have originated in two ways:

(1) By achieving the capability of apomictic reproduction as an escape from sterility by the selection of primary hybrids which inherited the tendency towards the aposporous development of ESs from the parent species. This contention is supported by the fact that in one of the parent species, the diploid *S. aria* (L.) CRANTZ which reproduces sexually, a tendency towards aposporous development of the ES was noted (JANKUN et KOVANDA, unpublished). It is of some interest that KURSANOV et PANFILKINA (1974, 1976) crossed the diploid *S. aucuparia* L. var. *moravica* with different members of the *Malaceae* (*Sorbus aucuparia* L. var. *rossica*, *S. sambucifolia* ROEMER, *Aronia melanocarpa* HEYNHOLD, *Pyrus communis* L. and *Cydonia japonica* PERS.) and obtained a considerable number of seedlings of maternal type. Based on these results, they suggest that apomixis may be present.

(2) By way of parthenogenetical development of an egg cell with a reduced number of chromosomes (as a dihaploid), because in *S. eximia* both diploid and tetraploid cytodemes are known to occur. The tendency towards parthenogenetical development of a reduced egg cell has been observed in the tetraploid *S. sudetica* (TAUSCH) FRITSCH (JANKUN et KOVANDA 1986). NOGLER (1984), studying *Ranunculus auricomus*, concludes that diploid apomicts can originate only as dihaploids but not as hybrids. Our findings would seem to indicate that in *Sorbus* other ways of origin of dihaploid apomicts are possible as well. It should be pointed out that some of the apomictic dihaploids of *Ranunculus auricomus* are no doubt vigorous enough to survive in natural selection (NOGLER 1984). If *S. eximia* originated as a dihaploid, it is one more fine example of vigour and full success in natural habitats.

The origin and development of ESs in the diploid taxa of *Sorbus* has so far been studied only in primary (i. e. non-hybridogenous) species, including *S. aria* (L.) CRANTZ, *S. torminalis* (L.) CRANTZ, *S. chamaemespilus* (L.) CRANTZ and *S. aucuparia* L. (LILJEFORS 1953). All these species proved sexual, with regular meiosis. LILJEFORS (1955) also studied meiosis in PMCs of *S. quercifolia* HEDL. (of the *S. aria* × *S. aucuparia* parentage) with $2n = 34$. In metaphase I (PMCs) of this hybrid he found 16 bivalents and 2 univalents. Meiosis was on the whole normal. Univalents occurred in about 10 % of the PMCs. The univalents split up as a rule in the first division. The daughter univalents were enclosed in the interkinesis nuclei. The pollen was fairly regular; unreduced pollen grains did occur occasionally (LILJEFORS 1955).

If meiosis in *S. eximia* is compared with that of *S. quercifolia*, it is evident that the first is much more disturbed. We observed 12 bivalents and 10 univalents. Lagging chromosomes may remain in the cytoplasm; the division of chromosomes in anaphase II is also disturbed. It may be inferred therefore that the genomes of *S. aria* and *S. aucuparia* are more similar than are those of *S. aria* and *S. torminalis*. This is in agreement with morphological (KOVANDA 1961a) and phytochemical (CHALLICE et KOVANDA 1978) evidence.

Many of our considerations are based on the presupposition that the parent species, *S. aria* and *S. torminalis*, are sexual. Their biology is a strong argument in favour of this hypothesis and, in fact, their sexual status has been proven by LILJEFORS (1953, 1955). It should be borne in mind, however, that he worked with a very limited amount of material of each species from Scandinavia and his findings and conclusions do not necessarily apply to

Central European plants. As indicated above, in *S. aria* there is a tendency to apomixis and further studies are required to establish its actual extent and evolutionary implications. The possibility cannot be excluded that the same tendency operates in *S. torminalis* as well. Investigations into the mode of reproduction of these species are now in progress.

ACKNOWLEDGEMENTS

We are grateful to Prof. Dr hab. E. Pogan, Head of the Department of Plant Cytology and Embryology, Jagiellonian University, Kraków, for her never failing interest in our work and to Prof. Dr hab. R. Czapik for stimulating discussions of some difficult problems. Our sincere thanks go to Prof. Dr Z. Černohorský, DrSc., Department of Botany, Charles University, Prague, who read the whole manuscript, making valuable suggestions. The research and collection of plant material in the Český kras Protected Landscape Area was made possible by the kind permission of the Ministry of Culture of the ČSR. Thanks are also due to Ing. J. Kynel for making the tree ring analysis. The embryological part of the present study was partially supported by a grant from the Polish Academy of Sciences under C.P.B.P.04.04.

SOUHRN

Sorbus eximia KOVANDA, hybridogenní druh vzniklý spontánním křížením muku, *S. aria* (L.) CRANTZ, a břeku, *S. torminalis* (L.) CRANTZ, je apomiktem se dvěma cytotypy, diploidním (2n = 34) a tetraploidním (2n = 68). Zvláštní pozornost byla věnována embryologii diploida, kde byla zjištěna aposporie a diplosporie. Poruchy v meiosi během makrosporogenese vedou ke vzniku makrospor s neustálenými počty chromosomů. Výjimečně se tvoří zárodečné vaky s redukovaným počtem chromosomů. Apomixie na diploidní úrovni mohla vzniknout dvojím způsobem: (1) jako únik ze sterility, (2) parthenogenetickým vývinem vaječné buňky s redukovaným počtem chromosomů (jako dihaploid). Jsou uvedeny důvody pro předpokládaný hybridní původ *S. eximia* a rozbor morfologických znaků. Druh je neoendemitem Českého krasu, kde je dosud znám z 10 lokalit (U kříže, Vysoká stráň, mezi Hostimí a Bubovicemi, Doutnáč, Paní hora, Kodské polesí, Ve skalách, Mramor, Plešivec a Haknová). Celkový počet jedinců je asi 90. Jsou připojeny poznámky k ekologii, fytocenologii a ekobiologii. Rodičovské druhy jsou diploidní s 2n = 34.

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Received 19 February 1987

See also Plates XII—XIV in the Appendix.

E. Peveling [red.]:

Progress and problems in lichenology in the eighties

Proceedings of an International symposium held at the University of Münster on 16.—21. March 1986

Bibliotheca lichenologica 25. — J. Cramer in der Gebr. Bornträger Verlagsbuchhandlung, Berlin—Stuttgart 1987, (15)+498 str., 370 obr. (6 barev.), 16 tab., cena brož. 150,— DM. (Kniha je v knihovně ČSBS.)

Recenzovaná publikace je sborníkem příspěvků z mezinárodního sympozia, jež se konalo na Univerzitě v Münsteru v době od 16. do 21. března 1986. Cílem sympozia bylo shromáždit zástupce různých lichenologických oborů, aby mohli navzájem spolu diskutovat o současném stavu i problémech jednotlivých oborů. Redaktorka sborníku byla rovněž hlavní organizátorkou sympozia. V práci jí pomáhal poradní sbor, v němž byli zastoupeni A. Henssen, O. L. Lange a C. Leuckert. V této souvislosti je vhodné uvést i skutečnost, že se na řízení jednání sympozia podíleli V. Ahmadjian, T. Ahti, P. James, O. L. Lange, J. Poelt a M. Seaward. Už z dosavadního výčtu jmen osob je zřejmé, že na sympoziu nechyběli vedoucí specialisté různého zaměření.

Sborník se člení na tyto části: Předmluva. — Seznam přispěvatelů a účastníků. — Příspěvky. — Věcný rejstřík. — Taxonomický rejstřík.

V předmluvě redaktorka konstatuje, že lichenologie, mnohde zanedbávaná, se v šedesátých a sedmdesátých letech tohoto století bouřlivě vyvíjela. To ostatně vyplynulo už i z jednání lichenologického sympozia v Bristolu r. 1974. Od té doby však došlo k zdokonalení metod užívaných při pěstování lišejníků v umělé kultuře i metod fyziologického a ekologického výzkumu, jakož i preparačních technik pro studium ultrastruktury lišejníků. To všechno přispělo k dalšímu, často mozaikovitému růstu poznání stavby a života těchto komplexních organismů. Nesmíme zapomínat ani na expedice do nejvzdálenějších oblastí Země, které objevily nové taxony a měly možnost studovat lišejníky mnohdy v extrémních vnějších podmínkách. Tento hromadný růst poznatků je následek specializovaných přístupů. Ale vznik úzkých specializací nese s sebou vždy nebezpečí izolace dílčích disciplín. Proto hlavním posláním sympozia bylo zpevnění vazeb mezi všemi oblastmi lichenologie. Redaktorka sborníku to vyjádřila slovy, aby „morfologové, fyziologové, ekologové a taxonomové byli schopni komunikovat a diskutovat o lichenologických problémech v interdisciplinárním prostředí“ (III).

Počet přítomných na sympoziu — 123 účastníků z 15 zemí — svědčí o tom, že pořádání sympozia bylo potřebné. Z uvedeného počtu přítomných bylo 73 přednášejících, a to buď v samostatném (individuálním), nebo kolektivním příspěvku.

Pouze příspěvek redaktorky sborníku je samostatný a pojednává o lichenologii a lichenolozích ve Vestfálsku. Ostatní příspěvky jsou seskupeny do pěti tematických okruhů.

První tematický okruh — Vývojová morfologie a ultrastruktura (str. 15—168) — zahrnuje 16 příspěvků, z nichž jako příklad uvedu pět prací s originálním titulem: H. M. Jahns: New trends in developmental morphology of the thallus. — J. Poelt: On reductions of morphological structures in lichens. — V. Ahmadjian et J. B. Jacobs: Studies on the development of synthetic lichens. — R. Honegger: Questions about pattern formation in the algal layer of lichens with stratified (heteromerous) thalli. — A. Bellemère et M.-A. Letrouit-Galinou: Differentiation of lichen asci including dehiscence and sporogenesis: an ultrastructural survey. — Z tohoto neúplného výčtu je zřejmé, že první tematický okruh se zabývá obecnou a vývojovou morfologií lišejníkových stélek, jakož i problémy izolovaných symbiontů a jejich resyntézy v komplexní lišejník. Poznáváme zde rovněž reprodukční strategie a struktury. Velmi výzamné jsou ultrastrukturní studie.

Druhý tematický okruh se nazývá Biologie a taxonomie rodů a některých skupin (169—293). Jeho náplň dostatečně charakterizuje uvedený název i výběr tří z devíti příspěvků: I. Kärnefelt et J.-E. Mattson: Morphological characteristics and affinities of the genus Cornicularia. — H. Hertel: Progress and problems in taxonomy of Antarctic saxicolous lecideoid lichens. — A. Henssen: Lichenothelia, a genus of microfungi on rocks.

Z třetího tematického okruhu — Ekofyziologie (294—375) — uvedu šest z devíti příspěvků: L. Kappen, M. Bölter et A. Kühn: Photosynthetic activities of lichens in natural habitats in the maritime Antarctic. — T. H. Nash III, L. Kappen, R. Lösch, U. Matthes-Sears et D. W. Larson: Cold resistance of lichens. — C. von Arb: Photosynthesis and chlorophyll content of the lichen Parmelia sulcata Taylor from locations with different levels of air pollution. — V. Wirth: The influence of water relations on lichen SO_2-resistance. — D. W. Larson: The absorption and release of water by lichens. — D. H. Brown: The location of mineral elements in lichens; implications for metabolism. — Tento okruh pokrývá fotosyntézu a vodní provoz lišejníků na různých stanovištích, stejně jako výskyt minerálních prvků v lišejníkových stélkách. Dva příspěvky se aspoň dotýkají problematiky znečištěného ovzduší.

Čtvrtý tematický okruh — Ekologie a rozšíření (377—441) — obsahuje devět příspěvků, z nichž poslouží k bližší charakteristice okruhu čtyři práce: H. Krog: Altitudinal zonation of tropical lichens. — D. J. Galloway: Austral lichen genera: some biogeographical problems. — T. Ahti: Endemism among Cladoniaceae in the Table Mountains of the Guayana Highland, Venezuela. — O. Vitikainen: Distribution patterns of European Peltigera. — Čtvrtý tematický okruh sumarizuje dílčí práce o některých lišejnících/skupinách lišejníků a o jejich rozšíření v určitých oblastech, hlavně na Jižní polokouli a v Evropě.

Pátý tematický okruh — Chemotaxonomie (443—480) — tvoří pět příspěvků zabývajících se identifikací lišejníkových sloučenin a jejich významem v klasifikaci lišejníků. Z těchto příspěvků cituji aspoň dvě práce: H. Kilias: Protein characters as a taxonomic tool in lichen systematics. — M. Geyer et G. B. Feige: Analysis of depsides, depsidones, and other lichen specific aromatics by high performance liquid chromatography.

Sborník je obrazem lichenologie „v pohybu“. Dokumentuje dnešní stav hlavních oborů a přispívá do jisté míry k jejich integraci. Ukazuje problematiku této botanické disciplíny a současně naznačuje cesty, jimiž by se měl výzkum v budoucnu ubírat. Postrádám v něm však fytocenologické příspěvky a větší zřetel k bioindikačnímu významu lišejníků. Během studia sborníku jsem si uvědomoval, že struktury a jevy na ně vázané jsou podstatně složitější, než jak jsme si donedávna myslili. V této souvislosti jsem si opětovně kladl také otázku, proč se chováme u nás k lichenologii macešsky.

Kniha je vytištěna ofsetem na křídovém papíru, vkusně upravena a bohatě ilustrována. Reprodukce černobílých i barevných fotografií jsou vzorné, tiskové chyby vzácností.

Z. Černohorský

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Plate XII. — 1, The oldest specimen (age, c.85 years; DBH, 38 cm) of *Sorbus eximia* on record (right) in a group with *Quercus robur* (middle) and *Carpinus betulus* (left) on the Ve skalách karst plain in early spring. 2, the same group in summer.

A. Jankun and M. Kovanda: Apomixis at the diploid level in *Sorbus eximia* (Embryological studies in *Sorbus* 3)

3

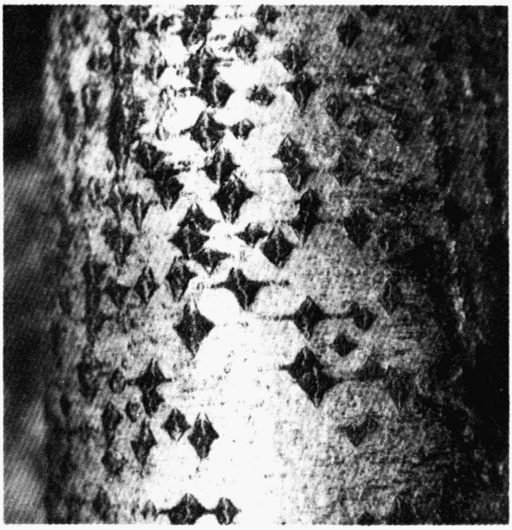

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Plate XIII. — Details of bark of *Sorbus eximia*. 3, at base of stem. 4, at breast height.

A. Jankun and M. Kovanda: Apomixis at the diploid level in *Sorbus eximia* (Embryological studies in *Sorbus* 3).

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Plate XIV. — *Sorbus eximia*. 5, detail of inflorescence. 6, young seedlings (age, 4 months).

A. Jankun and M. Kovanda: Apomixis at the diploid level in *Sorbus eximia* (Embryological studies in *Sorbus* 3)