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Apomixis in *Sorbus sudetica* (Embryological studies in *Sorbus* 1)

Apomixie u jeřábu krkonošského, *Sorbus sudetica* (Embryologické studie rodu *Sorbus* 1)

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JANKUN A.¹) et KOVANDA M.²) (1986): Apomixis in *Sorbus sudetica.* (Embryological studies in *Sorbus* 1). Preslia, Praha, 58 : 7—19.

Sorbus sudetica (TAUSCH) FRITSCH, a hybridogenous species derived from *S. aria* × *S. chamaemespilus*, is shown to be a facultatively apomictic tetraploid ($2n = 68$). The majority of ovules degenerate at an early stage of development. Out of 564 ovules examined, 401 showed signs of degeneration. In well developed ovules functional ESs are apomeiotic, only sporadically meiotic ESs are formed. The embryological observations are, in the main, in agreement with the results obtained for other *Sorbus* apomicts by previous authors, Phenomena not hitherto observed include autonomous haploid parthenogenesis, autonomous development of the endosperm and the presence of polyembryony proper (with apogamy stimulated by the entrance of a sperm). The origin of the species and significance of its breeding system are briefly discussed. There are also observations on karyology, taxonomy, and geographical distribution.

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INTRODUCTION

Since it was described 150 years ago (TAUSCH 1834), the most notable endemic of the Krkonoše (Karkonosze) flora, *Sorbus sudetica* (TAUSCH) FRITSCH has never ceased to challenge the botanists (though fortunately, not the visitors to the mountains, because all its habitats lie remote from the tourist paths) and references to its presence may be found in every flora, floristic list, report of an excursion or article on the mountains, both old and modern. A body of knowledge has accumulated which one of us (M.K.) attempted to collate in a taxonomic review published in 1965. At that time, nothing was known of the breeding system operative in *S. sudetica* but apomixis was suspected. This tentative conjecture can now be substantiated by embryological evidence.

MATERIAL AND METHODS

The material used for examination was collected in a natural habitat in the Krkonoše Mts., Czechoslovakia, in 1981—1983. In addition, the offspring of a wild growing shrub, cultivated in the Experimental Acclimatization Garden of the Botanical Institute of the Czechoslovak Academy of Sciences at Černolice since 1964, were also used (for a list of localities, see Tab. 1). All collections and fixations were made by M.K. Various developmental stages (from flower buds to opened flowers) were gathered, fixed in Carnoy and kept in a refrigerator until examined. The

Tab. 1. — Chromosome numbers in *Sorbus sudetica*

Locality	n	2n
Krkonoše Mts.: Labský důl valley, steep slope (E.-facing) in the upper part of the Navorská jáma cirque, 1250 m	34	68
Krkonoše Mts.: Čertova zahrádka gorge, steep slope (E.-facing) in the upper part, 1100 m (offspring grown in the Experimental Acclimatization Garden of the ČSAV at Černolice)	34	68

indumentum of the flower buds was removed, to allow the fixative to penetrate into the tissues. The material was then embedded in paraffin and microtome sections (10 μm thick) were made by A. J. Heidenhain's haematoxyline was used as a stain with good results. A part of the metaphase plates was examined jointly but the bulk of the material was studied by A. J. and the interpretation of embryological phenomena is entirely his own responsibility. M. K. is responsible for the morphological, taxonomic, karyological and chorological part of the study and for the final version of the manuscript. The Discussion is a condensed and refined record of our many debates (or, sometimes, altercations) and is, on certain points, an amalgamation of contrasting opinions.

RESULTS

Karyology

S. sudetica has previously been shown to be tetraploid, 2n = 68, with the counts based on root-tip mitoses (Kovanda 1983). This chromosome number was confirmed on meiotic divisions (n = 34) as well as on mitoses in ovules (2n = 68; Fig. 5). Liljefors (1934) reported 2n = 68 for cultivated material of unknown origin.

Embryology

Gynoecium and degeneration of ovules

The gynoecium in *S. sudetica* is syncarpic, consisting of two, or rarely three carpels coalesced up to the base of the styles. The ovary is semi-inferior (Kovanda 1961a). As in other species of *Sorbus*, in each loculus of the ovary there are two ovules of which often only one develops into seed. The ovule is anatropous, bitegminous and crassinucellate. The archesporium is multicellular and cuts off the parietal cells. A nucellar cap develops on the top of the nucellus.

In some ovules deviations from the typical development, such as the absence of correlation in the growth of various parts of the ovule (stoppage of the growth of the nucellus while integuments continue to develop, different rates of growth of the integuments) could be observed.

In the initial stages of the development of the ovule, when the integuments do not yet enclose entirely the nucellus, and the archesporium cells only begin to differentiate, degeneration of the nucellus was observed in the majority of ovules. At first, groups of degenerated cells occur at the base of the nucellus, below the differentiated cells of the archesporium. Sometimes these groups

Tab. 2. — A summary of the ovules examined

Stage	Number of ovules
Viable ovules	
Primordia of ovules	32
Archesporium	8
Degenerated archesporium or its cells	18
Remnants of a dyad	1
Viable tetrad of macrospores	1
Degenerated tetrads	6
Initial cells of apomeiotic ES	38
1-nucleate meiotic ES	2
1-nucleate apomeiotic ES	14
2-nucleate ES	7
4-nucleate ES	3
6-nucleate ES	1
8-nucleate ES	11
Egg cell + nuclear endosperm	5
Embryo + polar nuclei	3
Embryo + nuclear endosperm	13
Degenerating ovules	
Young stages (integuments have not yet reached the top of the nucellus)	219
Older ovules	176
Ovules with 8-nucleate ES	5
Ovule with 16-nucleate ES	1
Total	564

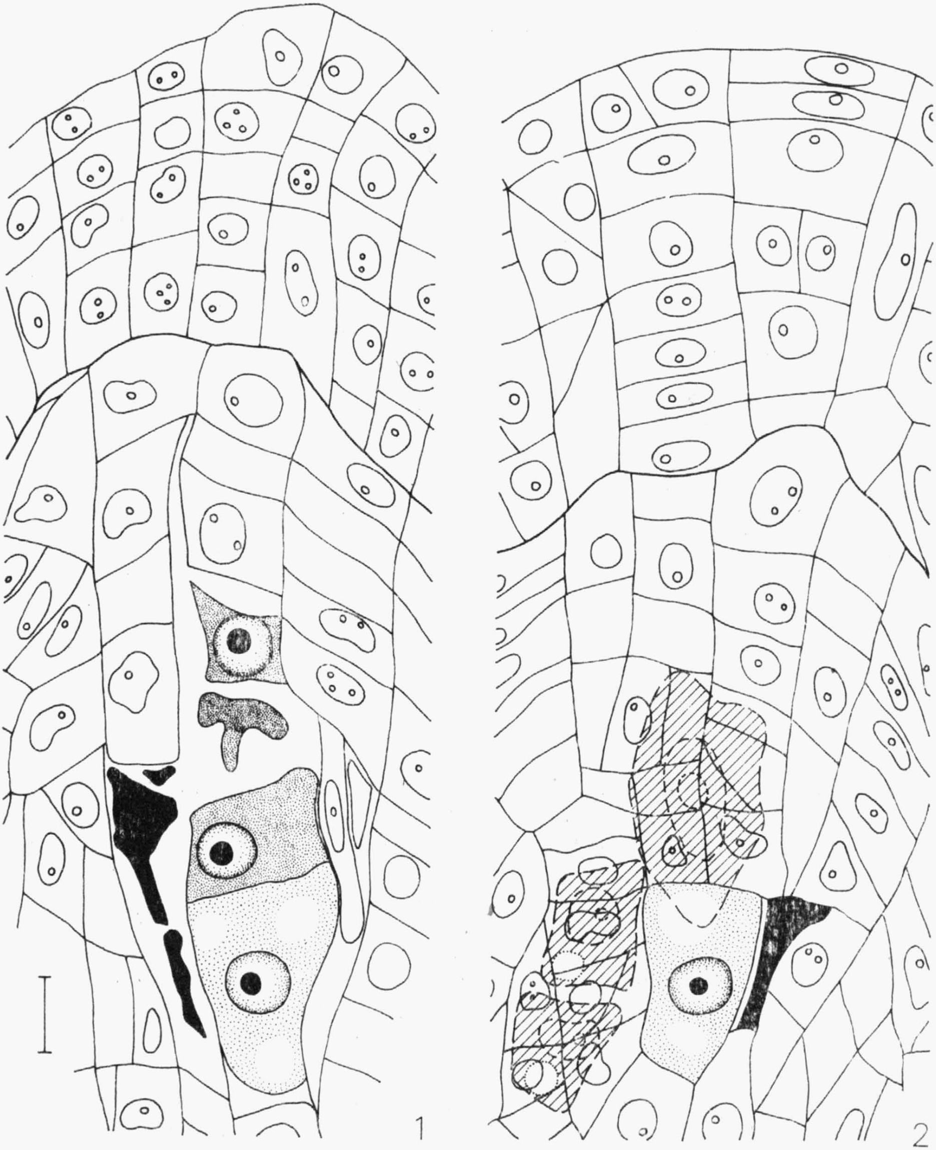
are located laterally, sometimes centrally. A frequent situation is a completely degenerated nucellus surrounded by two integuments of living cells. In further stages the cells of the integuments degenerate as well and so do, in the end, the cells of the funicle.

The degeneration processes often concerned all ovules of a given flower. The degeneration of the other ovules begins later when already 4- or 8-nucleate ESs are present. Only a few ovules reach the stage in which the embryos and viable endosperm are differentiated in their ESs. Out of 564 ovules investigated, 401 showed signs of degeneration (Tab. 2).

Development of embryo sac

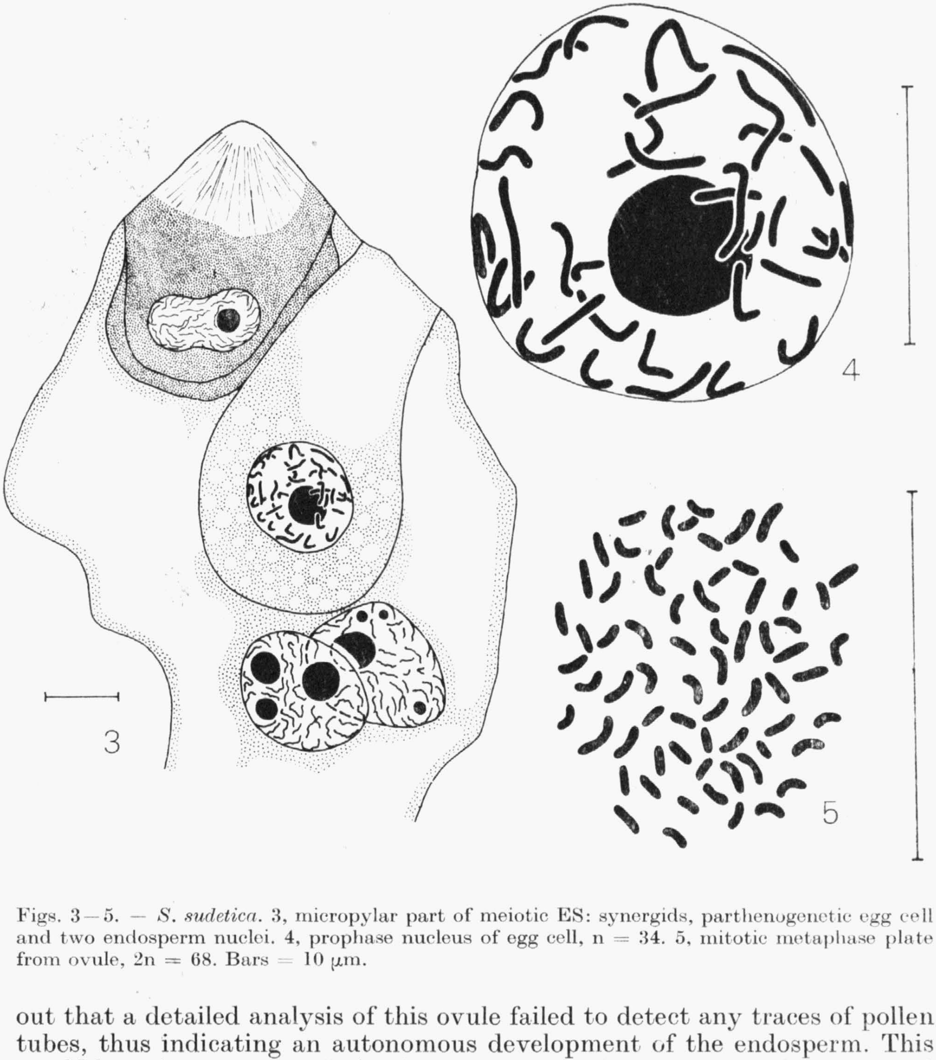
Relatively few ovules continued to develop. In total, 163 ovules could be examined (see Tab. 2). In some ovules secondary archesporium cells in prophase I (leptotene, zygotene) were observed. They were separated from the epidermis of the nucellus by two or three rows of parietal cells. In the central part of such ovules, remnants of groups of degenerated archesporium cells could be seen. In other ovules remnants of dyads and tetrads were observed but the nucellus cells surrounding them did not show any tendency to develop into initial cells of an apomictic embryo sac (ES). It should be added that in some ovules it was difficult to define a sharp boundary between the archesporium cells and surrounding vegetative nucellar cells.

In two ovules the 1-nucleate ESs developed from the chalazal macrospore (Fig. 1). Meiotic ESs reached maturity in some ovules and embryos were



Figs. 1–2. — *S. sudetica*. 1, meiotic ES and remnants of degenerating macrospores. 2, three apomeiotic uninucleate ESs and one initial cell of apomeiotic ES. Bar = 10 μm.

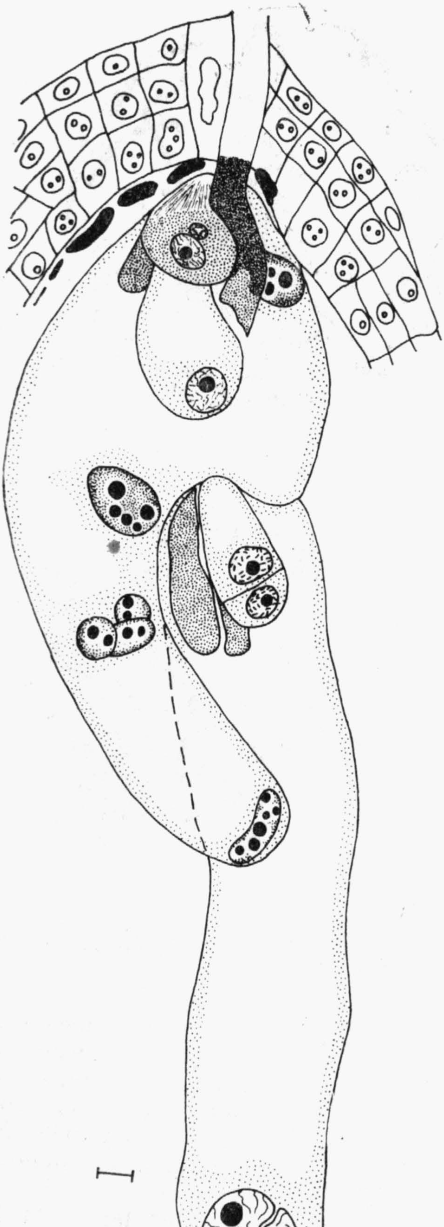
formed. In one meiotic ES the egg cell contained (in prophase) a nucleus with a reduced chromosome number, n = 34 (Fig. 4); two nuclei of the endosperm were positioned near the egg apparatus (Fig. 3). It would appear therefore that exceptionally a parthenogenetic development of the egg cell with a reduced number of chromosomes may take place. It should be pointed



Figs. 3—5. — *S. sudetica*. 3, micropylar part of meiotic ES: synergids, parthenogenetic egg cell and two endosperm nuclei. 4, prophase nucleus of egg cell, n = 34. 5, mitotic metaphase plate from ovule, 2n = 68. Bars = 10 μm.

out that a detailed analysis of this ovule failed to detect any traces of pollen tubes, thus indicating an autonomous development of the endosperm. This would be quite unique in *Sorbus* because all apomictic species so far examined embryologically proved pseudogamous, i. e. the fertilisation of the secondary nucleus is necessary for the endosperm to develop (Liljefors 1953). Should the development in the meiotic ES continue to form a parthenogenetic embryo, a polyhaploid might arise.

In the majority of cases, besides the central group of degenerated cells, initial cells of an apomeiotic ES developed. These cells possessed a dense, dark stained cytoplasm and large nuclei as well as nucleoli (if compared with other cells of the nucellus). In two initial cells of apomeiotic ES the somatic chromosome number 2n = c. 68 was counted. The initial cells of the apomictic ES developed at the level of degenerated remnants (Fig. 2), below them or above them, in relation to the micropyle. The initial cells of apomeiotic ESs



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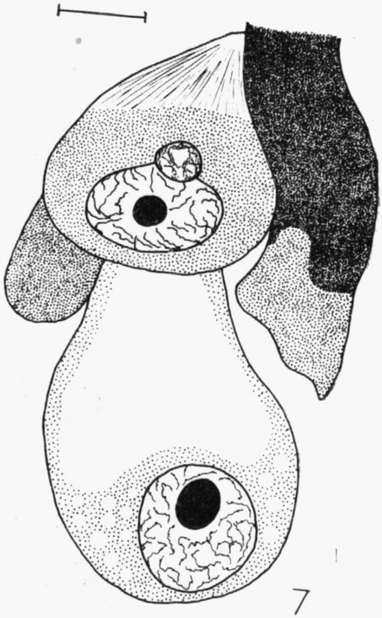

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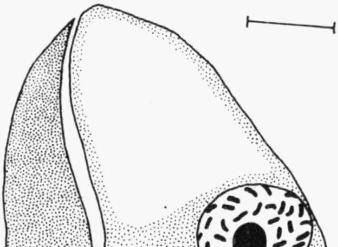

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may also be positioned linearly. These cells undergo vacuolation and turn into 1-nucleate ESs. In older apomeiotic ESs the nucleus is found in the centre while the vacuoles are at the poles. In 2-nucleate ESs the cell nuclei are found at the opposite poles and the central part is occupied by a large vacuole. The structure of 4-nucleate ESs is similar. In typical mature ESs the egg apparatus consisting of the egg cell and two synergids is found at the micropylar pole; the central cell contains two polar nuclei and three antipodals are at the chalazal pole. The synergids have a characteristic fibrillar apparatus on the micropylar side. The antipodals in *S. sudetica* are short-lived. In one case an atypical structure of an 8-nucleate ES was seen: the egg apparatus consisted of an egg cell and one synergid, in the central cell there were three polar nuclei and at the chalazal pole three antipodals. Another aberration was a multiple, undifferentiated 16-nucleate ES which probably arose by fusion of two ESs.

In addition to the ovules in which only one ES developed we also observed cases of parallel development of two and four ESs. As a rule they differred in the stage of their development — e. g. at the micropylar pole a typical 2-nucleate ES developed and below it (in immediate contact) there was an ES containing the egg cell and several nuclei of the endosperm. In another case where also two ESs developed in parallel, one of them contained the egg cell, degenerating synergids and six nuclei of the endosperm. In the micropylar part of this ES a pollen tube was seen next to the egg apparatus and a sperm near the nucleus of one of the synergids (Figs. 6, 7). This would suggest that in apomeiotic ESs of *S. sudetica*, pseudogamy is present. Next to this ES another ES developed holding a 2-celled embryo and two partly fused polar nuclei (Figs. 6, 7). The third type is an ovule containing four ESs. Two of them are 2-nucleate, the third is 6-nucleate and the fourth 8-nucleate. The presence of a 6-nucleate ES indicates that in certain cases the divisions of the nuclei in a developing ES are not synchronised.

Embryo and endosperm

Observations of the course of embryo and endosperm development are rather incomplete and further study is needed.

In *S. sudetica* two ways of the development of the endosperm seem to occur: autonomous (in some meiotic ESs) and pseudogamous (in apomeiotic ESs). The karyology of the endosperm is complicated because, besides typical ESs with two polar nuclei, aberrant ESs with e. g. three polar nuclei may also occur. A tendency towards the polyploidisation of the endosperm nuclei was also noted. In some ovules striking size differences between the nuclei of the endosperm were observed (Fig. 6).

It is important to note that in *S. sudetica* there is no definite correlation between the development of the egg cell and that of the endosperm. Sometimes the former precedes the latter but at other times the contrary is the case.

Besides ovules with a typically developed embryo, polyembryony was observed in two ovules (a plant from Černolice). In such cases, near the

Fig. 6—8. — *S. sudetica*. 6, two ESs: one ES with egg apparatus, pollen tube and nuclear endosperm, the other with 2-celled embryo and partly fused polar nuclei. 7, egg apparatus and pollen tube — sperm near the nucleus of the synergid. 8, 2-celled embryo and remnants of synergids. Bars = 10 μm.

embryo (with a suspensor) developing from the egg cell another embryo (without a suspensor) was present; the latter arose probably from the synergid (apogamy stimulated by the entrance of a sperm). The structure of the two kinds of embryo was quite different.

Pollen grains

Considerable differences were found in the size of the pollen grains observed in the anthers before anthesis: from 14 to 20 μm (in diameter) in abortive and from 20 to 28 μm in viable. Some pollen grains were poorly developed and sometimes failed to be released from the tetrads. In some loculi giant pollen grains (from 36 to 46 μm) could be seen. The percentage of abortive (from 2 to 51 %) and giant (from 0 to 80 %) pollen grains may vary even from one anther to another within a flower.

Taxonomy

The genus *Sorbus*, as circumscribed at present (i. e. excluding *Micromeles*), may be conveniently divided into five natural groups, each including one Linnean species (KOVANDA 1961a, CHALLICE et KOVANDA 1978): *Torminaria* [*S. torminalis* (L.) CRANTZ], *Chamaemespilus* [*S. chamaemespilus* (L.) CRANTZ], *Aria* [*S. aria* (L.) CRANTZ], *Cormus* (*S. domestica* L.) and *Sorbus* s. str. (*S. aucuparia* L.). While *Aria* and *Sorbus* s. str. contain many species each, the remaining three groups are monotypic. The various species of *Sorbus* are readily classified within this system. The exceptions are the numerous taxa of hybrid origin which combine the characters of *Aria* × *Torminaria*, *Aria* × *Chamaemespilus* and *Aria* × *Sorbus* s. str. No other hybrid combinations are so far known but an experimental test of incompatibility has never been attempted (KOVANDA 1961b).

A thorough morphological analysis demonstrated that *S. sudetica* combines the characters of *S. aria* and *S. chamaemespilus*. Its intermediate position is especially apparent in the structure of the flower and fruit, suggesting that the species may be hybridogenous. This contention is not at all new. Possibly the first to propose a hybrid origin for *S. sudetica* was FOCKE (1881), followed by BECK (1892), KOEHNE (1893), HEDLUND (1901) and others. It was not until 1965, however, that an attempt was made, based on circumstantial evidence, to reconstruct its genesis. At the same time, the hypothesis was propounded that the species is apomictic (KOVANDA 1965). Unfortunately, these considerations were published in a nature conservancy periodical and have never become commonly known to the botanical public. Parts of the story were later reiterated in publications by others authors, both scientific and popular, but the source of information was misquoted or not at all given.

TAUSCH (1834) described this species as *Pyrus sudetica* because in his time the majority of *Sorbus* species (except those with pinnate leaves) were merged with *Pyrus*. The correct name in *Sorbus* is thought to be *Sorbus sudetica* (TAUSCH) FRITSCH 1896 (see e. g. WARBURG et KÁRPÁTI 1968) but it seems likely that the transfer to *Sorbus* was made much earlier than Fritsch.[1])

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[1]) A new name, *Sorbus corcontica* HOLUB, was recently proposed (see HOLUB 1984: 13).

Geographical distribution

Evidence was presented that *S. sudetica* is an endemic of the Krkonoše (Karkonosze) Mts. where it occurs in several localities (Kovanda 1965). It is a plant of tall grass communities (alliances *Calamagrostion villosae* and *Calamagrostion arundinaceae*) in an altitudinal zone from 1050 to 1350 m above sea level. Jeník (1960) should be consulted for details of distribution and ecology. His estimate of the total number of individuals was 70 to 80; a recent survey by the staff of the Krkonoše National Park Management has however succeeded in finding further specimens so that the present population is about 135 individuals (Štursová, personal communication). Interestingly, all the localities of *S. sudetica* are found in the Czech part of the mountains. A solitary report from near the Wielki Staw (Grosser Teich) in the Polish Karkonosze Mts. (Göppert 1864) has never been confirmed.

In addition to these 135 spontaneous individuals a number of seedlings have recently been planted by the Management in suitable habitats to strengthen the population and to ensure its survival in an environment suffering heavily by pollution from an industrial area in S. W. Poland and an adjacent part of the German Democratic Republic. The material for the present study was collected from spontaneous shrubs.

Reports of *S. sudetica* from other European mountains refer to related taxa of the *S. aria* × *S. chamaemespilus* parentage which are all quite distinct in their morphology. They include: *S. margittaiana* (Jáv.) Kárp. (Malá Fatra, Czechoslovakia), *S. pseudaria* (Spach) Hedl. (department Côte-d'Or, France), *S. ambigua* (Decaisne) Hedl. (Alps, Schwarzwald, Jura, Carpathians), *S. arioides* Rouy et Camus (Alpes de Savoie, Jura) and *S. erubescens* Kerner (Alps).

DISCUSSION

The genus *Sorbus* poses many intricate problems, taxonomic, karyological and embryological. A frequent phenomenon is interspecific hybridisation combined with polyploidy and apomixis. *S. sudetica* is now unanimously regarded as a species of hybrid origin, involving *S. aria* and *S. chamaemespilus* as the parent species. Previous karyological studies have demonstrated that it is tetraploid, with 2n = 68 (Liljefors 1934 for material of unknown provenance, Kovanda 1983 for material of known wild origin). These reports have been confirmed in the course of the present study. Chromosome numbers are also available for the putative parent species. In *S. aria*, only diploids (2n = 34) are known to occur (Moffett 1931, Sax 1931, Liljefors 1934, Poucques 1951, Liljefors 1953, 1955, Baksay 1956, Jankun in Skalińska et al. 1976, Kovanda 1984 unpublished). By contrast, three ploidy levels are present in *S. chamaemespilus*. Liljefors (1934) reported 2n = 68 for material of unknown origin, later (Liljefors 1953) n = 17 for plants from the Swiss, German and Austrian Alps and 2n = 51 for plants from Austria. An examination of plants from the Polish Tatra Mts. revealed the presence of diploids, 2n = 34 and tetraploids, 2n = 68 (Jankun in Pogan, Czapik, Jankun et al. 1985).

S. sudetica seems to have originated by means of spontaneous doubling of the chromosome number in a hybrid of *S. chamaemespilus* and *S. aria* (diploid cytotypes). At the present time, the resultant allopolyploid is geographically isolated from its parent species: both *S. aria* and *S. chamaemespilus* are absent from the Krkonoše Mts. but there are good reasons to suppose that they occurred there in the past (KOVANDA 1965). In regions where *S. aria* and *S. chamaemespilus* occur together (Alps, Carpathians), primary F_1 hybrids are not uncommon (PAWŁOWSKI 1956, KÁRPÁTI 1960). They are readily distinguished from *S. sudetica* by the thin, often floccose indumentum of the underside of the leaves (in *S. sudetica*, the leaves are always densely tomentose beneath).

The structure and development of the ovule in *Sorbus* has been described by PÉCHOUTRE (1902), the development of the ES by LILJEFORS (1934, 1953). LILJEFORS (1953) found that the diploid taxa examined reproduce sexually whereas triploids and tetraploids are apomictic (with pseudogamy present).

As mentioned above, *S. sudetica* has not yet been subjected to embryological investigation. *S. aria* and the diploid *S. chamaemespilus* are sexual and produce only gametophytes with a reduced number of chromosomes, while triploid and tetraploid cytotypes of *S. chamaemespilus* produce apomictic ESs with a somatic chromosome number (LILJEFORS 1934, 1953). Based on his embryological studies, LILJEFORS (1953) suggested that in the triploid cytotype of *S. chamaemespilus* facultative apomixis might be involved; besides ESs with a somatic chromosome number, he observed advanced stages of meiosis in embryo sac mother cells (EMC). In the tetraploid *S. salicifolia* (MYRIN) HEDL. and *S. obtusifolia* (DC.) HEDL, (both belonging to *S. aria* agg.), apomictic ESs may arise both by apospory and diplospory (LILJEFORS 1953). LILJEFORS (l. c.) observed the degeneration of EMC in a number of polyploid *Sorbus* species, including *S. arranensis* HEDL. s. l. (2n = 51), *S. Teodori* LILJEFORS (2n = 51), *S. hybrida* L. (2n = 68), *S. Meinichii* (LINDEB.) HEDL. (2n = 68), *S. subsimilis* HEDL. (2n = 68), *S. Mougeotii* SOY. et GODR. (2n = 68), *S. salicifolia* (MYRIN) HEDL. (2n = 68), *S. obtusifolia* (DC.) HEDL. (2n = 68) and *S. intermedia* (EHRH.) PERS. (2n = 68). The majority of them are of hybrid origin. The EMC usually degenerated at an early stage, whereupon one or more of the cells in the lateral rows became initials of the functioning apomictic ESs — a case of apospory (somatic apospory). Both meiotic (reduced) and apomeiotic (unreduced) ESs occurred in Liljefors' material. In *S. hybrida* L. diplospory (generative apospory) was found to be combined with apospory (somatic apospory).

The present observations confirm, in the main, the results obtained by Liljefors. The deviations from a typical development, such as the absence of correlation in the growth of the various parts of the ovule (stoppage of the growth of the nucellus while integuments continue to develop, different rates of growth of the integuments) and the extraordinarily large number of degenerating ovules (beginning from the early stages of development) seem to indicate that the breeding system of *S. sudetica* is not fully balanced — a consequence of its hybrid origin. In addition to apomictic ESs, development of ESs from the chalazal macrospore (with a reduced number of chromosomes) was occasionally observed. The presence of facultative apomixis has previously been reported for one of the parent species, *S. chamaemespilus* (triploid cytotype) (LILJEFORS 1953).

New information discovered in the course of the present study are the supposedly autonomous development of the embryo from the egg cell with a reduced number of chromosomes (haploid parthenogenesis), combined with autonomous development of the endosperm (probably with a diploid chromosome number) and polyembryony proper (where besides the embryo developing from the egg cell another embryo is present, arisen from the synergid — a case of apogamy stimulated by the entrance of a sperm).

Examples of autonomous haploid parthenogenesis in the family *Rosaceae* include *Potentilla canescens* Bess. and *P. praecox* F. W. Schultz (Rutishauser 1943). Autonomous development of the embryo and diploid endosperm was reported for *Malus sikkimiensis* (Wenzig) Koehne and *M. hupehensis* (Pam.) Rehd., while in *M. Sargentii* Rehd. pseudogamy occurs (Schmidt 1964). The haploid parthenogenesis referred to above is very important because it may give rise to karyological differentiation — a reduction of the number of chromosomes in the progeny. An example is a hypotetraploid individual (obtained artificially) of *Ranunculus cassubicus* L. (Izmaiłow 1970) and a polyhaploid of *Hieracium aurantiacum* L. (2n = 18) which appeared among maternal sister plants in the cross of a tetraploid with a pentaploid, with the latter as the pollen parent (Skalińska 1971). Aposporous dihaploids have recently been discovered in *Ranunculus argoviensis* W. Koch (Nogler 1984). Another interesting example of reduction in the chromosome number in relation to the mother plant is the hexaploid hybrid *Potentilla* × *mixta* Nolte (*P. anglica* × *P. reptans*) in the progeny of which (obtained from open pollination) 5*x* to 9*x* plants (2n = 35, 42, 56, 63) as well as a single individual with c. 93—97 chromosomes appeared (Czapik 1970).

The autonomous development of the endosperm observed in *S. sudetica* is contradicted by the fact that isolated flowers failed to produce any fruits. This would seem to indicate that, unlike the apomicts examined by Liljefors (1953), pseudogamy in *S. sudetica* is only facultative.

Apogamy in the *Rosaceae* has previously been reported for *Alchemilla sericata* Reichenb. (Murbeck 1902), *Alchemilla hoppeana* (Reichenb.) Dalla Torre and *Fragaria vesca* L. (Lebégue 1952). Izmaiłow (1986) observed embryos developing from vacuolated synergids in *Alchemilla incisa* Buser. The present results provide new examples of this process.

The giant pollen grains occurring in *S. sudetica* support the contention that the species is of hybrid origin. A recent study of the hybrid *Fragaria virginiana* Duchesne × *F. chiloensis* (L.) Duchesne (Staudt 1984) revealed a double restitution resulting in the formation of giant pollen grains. They have also been observed in other interspecific hybrids within the genus *Fragaria*.

It follows from the present observations that the embryology of *Sorbus* is extremely intricate and many problems remain. Studies of other hybridogenous taxa are now in progress.

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SOUHRN

Jeřáb krkonošský [*Sorbus sudetica* (TAUSCH) FRITSCH], hybridogenní druh vzniklý spontánním křížením muku [*S. aria* (L.) CRANTZ] a mišpulky [*S. chamaemespilus* (L.) CRANTZ], je fakultativně apomiktický tetraploid (2n = 68). Většina vajíček odumírá již v časných stadiích vývinu (z 564 studovaných vajíček jich 401 vykazovalo příznaky degenerace). Ve vyvinutých vajíčkách jsou funkční zárodečné vaky apomeiotické, řidčeji meiotické. Zárodečný vak je 1-, 2-, 4-, 6- nebo 8jaderný, u degenerujících vajíček i 16jaderný. Získané výsledky jsou v souladu s pozorováními, která byla provedena u jiných hybridogenních jeřábů. Nově byla zjištěna autonomní haploidní parthenogenese, polyembryonie a autonomní vývin endospermu. Stručně se pojednává o evolučním významu pozorovaných jevů. Jsou připojeny poznámky ke karyologii, taxonomii a zeměpisnému rozšíření.

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E. Mayr:

Die Entwicklung der biologischen Gedankenwelt

Vielfalt, Evolution und Vererbung

Překlad z angličtiny K. de Sousa Ferreira, odborná úprava a úvod H. Autrum. — Springer-Verlag Berlin — Heidelberg — New York — Tokyo 1984, 21 + 766 str., 3 tab., váz. 88,— DM. (Kniha je v knihovně ČSBS.)

Snad žádnou odbornou knihu jsem nečetl s takovým zájmem jako Mayrův Vývoj biologického myšlení. Univerzitní profesor biologie, specialista v zoologické taxonomii, dnes již klasický autor monografií o evoluci, všestranně vzdělaný filozof a výborný učitel nás s rutinou dobrého spisovatele ve své knize vede dějinami vědeckého myšlení od Aristotela k renesančním přírodovědcům a k Linnéovi, od Linnéa k Lamarckovi a Darwinovi a konečně od Darwina k rozkvětu mendelovské genetiky a moderní taxonomie. V eseisticky podaných kapitolách vidíme uzrávat evoluční názory, jak krystalizovaly v hlavách přírodovědeckých myslitelů. Autor nám ukazuje i další cestu mikrotaxonomie jako vědy o druhu na rozdíl od makrotaxonomie čili vědecké klasifikace. Kapitola o evoluci tvoří základní sloup celé knihy. Tak všeobecně pojatý vývoj evolučního myšlení od nejstarších dob lidské vzdělanosti, a zvláště pak od 14. století, nenajdeme u žádného jiného autora.

Kapitoly o náznacích evoluce před Darwinem nám odkrývají mnoho nových pohledů do myšlení biologů oné doby, kdy ještě většina filozofů byla deisty, ale mnozí již nechtěli dovolit pánu bohu nějaké zásahy do světa, jím jednou již stvořeného. Zásluha Lamarckova o dynamické pojetí organického vývoje, proti statickému pojetí Cuvierovu a Buffonovu, nebyla vždy v dějinách biologie (a není dodnes) spravedlivě hodnocena. Proto obsáhlá kapitola, věnovaná poměru mezi teorií Lamarckovou a Darwinovou, tvoří jakýsi úvod k vlastnímu oddílu o darwinismu. Svědčí o šíři Mayrova studia, udivuje množstvím prostudované literatury a i mistrovskou schopností vyjádřit a zhodnotit všechny různé názory a rozpory v biologii 19. století. Rozbor Darwinových teorií (Mayr jich rozeznává pět) byl sotva kdy tak zasvěceně a s tak fundovanou odborností podán.

Pro českého čtenáře bude snad překvapením obsáhlá kapitola o významu sovětského biologa Sergěje Četverikova, který se významně zasloužil o studium mutací a který jako prvý začal se studiem volně žijících populací *Drosophila melanogaster* z okolí Moskvy. Zde, spolu se svými žáky, Timofeef-Ressovským a Dubininem a s leningradským biologem Dobzhanským začínal studium genetiky na octomilce. Když byl později odstraněn ze svého ústavu, přešlo celé toto studium i s Dobzhanským do Severní Ameriky, kde dosáhlo té úrovně, s jakou se dnes americká věda chlubí.

Autor dále rozebírá, jak se v druhé polovině 19. století začíná evoluční myšlení uplatňovat v biologické systematice a jak se ze studia přirozených populací druhů vyvinulo studium klimatických a edafoklimatických plemen, což vedlo k Turessonovým ekotypům.

V tomto krátkém referátu není možno uvést mnoho dalších pohledů a nových zamyšlení nad různými aspekty organické evoluce, jak se objevovaly v pracích autorů posledního sta let. Je podivuhodné, jak zoolog Mayr má hluboký a široký rozhled i po taxonomii botanické a jak z moderních, botanických monografií byl schopen vyčíst obecné evoluční i taxonomické zákonitosti.

Pojetím druhu a problémem speciace se E. Mayr zabývá již půl století a zastává nekompromisní stanovisko o reálném základu druhu jako izolovaného souboru populací. V celé této složité problematice žádá především jasné formulování otázky, aby mohla být dána jednoznačná odpověď, a na příkladu vysvětlení vzniku druhu dokazuje, že nestačí objasnit původ variability nebo evolučních změn uvnitř populací, ale považuje za nutné objasnit původ izolace mezi populacemi. Vznik druhu neleží, podle Mayra, tolik ve vzniku nových typů, ale daleko více na účinných zařízeních, která brání přílivu cizích genů v genpoolu.

Zajímavou kapitolou je stať o syntéze dvou evolučních směrů v biologii; jednoho, vycházejícího z experimentální genetiky a druhého, háјeného biology, kteří pracují v terénu a omezují se převážně na pozorování („Naturbeobachter"). Zastánci obou směrů, píše E. Mayr mluví různou řečí, kladou si odlišné otázky a zastávají diametrálně odlišné názory. Mayr souhlasí s J Huxleyem o nutnosti syntézy obou (nebo dalších) směrů v biologii a tuto syntézu vidí v uznání pomalého vývoje malými genetickými změnami, izolovanými přírodním výběrem, chápaným v koncepci populací, ovlivňovaných ekologickými faktory stanoviště. Vyřešit tyto komplikované vztahy syntézou kladných stránek různých teorií je schopen jen biolog, kterého Mayr nazývá „architektem syntetické teorie biologické evoluce", mezi které řadí — kromě sebe sama — jen Dobzhanského, Huxleye, Simpsona, Rensche a Stebbinse. Řadě dalších biologů přiznává jen významnou pomocnou úlohu v této syntéze.

Pro současné taxonomy je snad nejdůležitější kapitola o vývoji evolučního myšlení v období, které navazuje na práce těchto architektů. Jsou to statě o molekulární genetice, o přírodním výběru v současném pojetí, o podstatě dědičnosti vlastností organismu a o variabilitě a její dědičnosti. Závěrečné kapitoly o rozkvětu mendelismu, o génové teorii, o chemických základech dědičnosti jsou syntézou současných názorů a trendů v moderní taxnomii a genetice.

Autorův epilog má titul „Na cestě k vědě vědy" a autor se v ní zamýšlí nad sociologií vědy, nad dějinami vědy, nad filozofií a psychologií vědy a končí přesvědčením, že skutečná, vše objímající věda o vědě se může vyvinout jen když zevšeobecnění, odvozená z exaktních věd se budou považovat za stejně hodnostná jako objevené zákonitosti biologických a sociálních věd, a když všechna tato tři odvětví se navzájem propojí. E. Mayr tvrdí, že pro tuto integraci je již dost materiálu připraveno.

Poznámky, slovníček termínů a zvláště obsáhlý seznam citované literatury (37 stran) tvoří cenný soupis pramenů k studiu moderní, obecné i speciální taxonomie. Kromě několika ruských (sovětských) autorů, uvádí z východní Evropy jen Mendla, Studničku, Rádla, Kříženeckého a Vít. Orla.

Kniha E. Mayra by se měla stát biblí taxonomů, genetiků a biologů vůbec, aby jejich práce se neutopily ve formalismu, v popisu nebo laboratorní rutině, ale aby každou prací moderního biologa pronikala především evoluční idea.

J. Dostál