APOMIXIS IN THE ANGIOSPERMS. II [1]

AXEL NYGREN

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Since G. L. Stebbins' paper, " Apomixis in the Angiosperms ", was published in 1941, the work by Åke Gustafsson, " Apomixis in higher plants " (1946–47), as well as that by Stebbins, " Variation and evolution in plants " (1950), have been printed. In an adjacent field, " Problems of cytology and evolution in the Pteridophyta " by Manton came out in 1950, and " Apogamy, apospory and parthenogenesis in the Pteridophytes " was reviewed by Steil in 1951. Because of these contributions the present writer has considered in the supplement at hand only those papers which are not mentioned by Gustafsson or those which were published after his work appeared. The significant study on *Crepis* by Babcock was very carefully treated by Stebbins in 1950 and has therefore not been taken up in the present review.

The terminology given by Gustafsson in 1946–47 has been used here, even though different authors have proposed other terms (cf. Battaglia, 1947*d*, 1951; Fagerlind, 1947*a*: 245; Rutishauser, 1946–49). Thus apospory is used in the sense of Rosenberg (1907) to mean that a cell outside the EMC gives rise to the ES (= somatic apospory according to some authors), while diplospory (Edman, 1931) is used for those cases in which the EMC forms the ES (= gametic apospory according to some authors).

That the formation of restitution nuclei in the EMC is of great importance for ES formation has been pointed out by several authors working with the genera *Antennaria, Chondrilla, Erigeron, Rudbeckia, Statice* and *Taraxacum*. On the other hand it has been reported that a diploid chromosome number may be produced by endomitosis in the egg cell (*Primula*) or in the embryo (*Trillium*,

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[1] Supplement to article in The Botanical Review 7: 507–542. 1941. EMC = endosperm mother cell; ES = embryo sac; PMC = pollen mother cell.

Tradescantia) of reduced ES's. In *Saccharum* a peculiar combination of parthenogenesis and endopolyploidy has been described, and in *Rudbeckia* the phenomenon " semigamia " gives rise to embryo chimeras. In orchids embryos of different degrees of polyploidy (*n–6n*) occur in the ES. On the other hand, double reduction of the chromosome number has been found in a hybrid derivative of *Poa alpina* × *pratensis,* while in *Hieracium* a tetraploid produced by chromosome doubling frequently has given diploid offspring, a phenomenon which has been reported also in *Sorghum.* Different division types in diverse panicles of the same plant or in different parts of the same raceme are known in *Calamagrostis* and *Arabis.* The inheritance of diplospory and apospory in *Potentilla* has been discussed as well as inheritance of apospory in *Parthenium.* In both genera it has been found that two doses for apomixis outweigh one for sexuality. The importance of pseudogamy is shown in *Ranunculus auricumus* in the most careful and comprehensive study made up to now of the chromosome number in the endosperm of apomictic plants. Finally, our knowledge of the type and species formation in apomictic plant genera has been considerably increased during recent years by comprehensive studies in the genera *Calamagrostis, Crepis, Poa, Potentilla* and *Rubus.* New smear methods have been worked out for the study of endosperm cells (Rutishauser and Hundziker, 1950) and embryo sacs (Heitz, 1951).

AMARYLLIDACEAE

ZEPHYRANTHES. *Zephyranthes texana* belongs to the classical materials in the study of apomixis. In 1913 Pace demonstrated that the central nucleus of the ES in this species requires fertilization. The species is diplosporous, parthenogenetic and pseudogamous. In 1951 Brown reinvestigated *Z. texana* and proved the EMC to be divided by a mitotic division. At the same time he confirmed that the central nucleus or the two polar nuclei sticking together need fertilization in order to form an endosperm. *Z. texana* has $2n = 24$, and the endosperm cells hold 60 chromosomes $(24 + 24 + 12)$. The species is self-fertile, in contrast to *Zephyranthes atamasco, caudata* and *carinata* which are all self-sterile. In plant genera including pseudogamous apomictic species it is a very common phenomenon that the sexual species are self-sterile (cf. Gustafsson, 1946–47).

COOPERIA.   Quite recently Coe reported *C. pedunculata* to be diplosporous, parthenogenetic and pseudogamous (1953). Semigamy in it has also been established.

ANACARDIACEAE

MANGIFERA.   It has been known for a long time that adventitious embryos occur in *Mangifera* and that therefore polyembryony is common in the genus (cf. Gustafsson, 1946–47: 307). According to Leroy (1947), the agamospermy in the genus is genetically controlled and probably due to the effect of one or more recessive genes.   Leroy supposes that East India is the primary centre of origin of *Mangifera indica* and reports that this area contains " monoembryonic " forms carrying dominant genes.   On the other hand, Cochin China, the Philippines and the Sunda Isles constitute a secondary centre of origin which holds forms with recessive genes and polyembryony.

CANNABACEAE

HUMULUS.   In the Report for 1944 by the Society for encouraging the cultivation of malting barley and hops in France, a parthenogenetic development of certain strains of *Humulus lupulus* are supposed to cause the variation in seed setting.

COMMELINACEAE

TRADESCANTIA, see LILIACEAE: TRILLIUM.

COMPOSITAE

ANTENNARIA.   In 1932 Stebbins showed that a number of tetraploid West American species of *Antennaria* ($2n = 28$) are sexual (1932*a*), while some hexaploid to dodecaploid species are diplosporous (1932*b*).   Bergman verified Stebbins' observations (1935*c*) and made a list of the species investigated up to 1935 (p. 222).   In 1937 he added the octoploid *A. magellanica* to the number of diplosporous species in the genus.   Bøcher found that a relative to *A. alpina,* namely *A. glabrata,* from Greenland is nonaploid with $2n = 63$ (1950), and at the same time *A. Porsildii* from Scandinavia, which is closely related to *glabrata,* was proven to be diplosporous and to have the same chromosome number as the Greenlandic species (Nygren, 1950*b*: 484).   In 1951 Bergman published some interesting observations on Scandinavian *Antennaria carpatica.*   He found that *A. carpatica* forms ES's in a normal sexual

way at the same time that it is able to form diplosporous and apos-
porous sacs. Production of restitution nuclei in the species is so
common that Bergman believes there must be a special factor
favouring this formation (p. 504). This factor does not affect
microsporogenesis, however. Aposporous sacs are rare in *A.
carpatica,* but Bergman has found some 20 cases, which means that
the observation does not depend upon mere chance. A very pecul-
iar circumstance is, however, that the species, in spite of the fact
that it forms ES's in three ways, is hardly able to produce any
seeds. In Bergman's study only one single embryo was found in
the mature ES's investigated; therefore the species is presumed to
propagate in nature mainly by runners. The term " rhizoclone "
is proposed for a population formed in this vegetative way. It is
obvious that more of the numerous North American forms of
Antennaria as well as *A. carpatica* from the Alps ought to be in-
vestigated to increase our knowledge of the genus.

ARNICA. In 1924 Afzelius found *Arnica montana* to be a sexual
species with a chromosome number somewhere between $2n = 36$
and $2n = 40$, while Sakai ten years later stated that *Arnica unal-
aschkensis* has $2n = \pm 40$. In 1936 Afzelius proved diplospory to
occur in the three species *Arnica alpina, A. Chamissonis* and *A.
diversifolia.* The specimens of *A. alpina* investigated originated
from northernmost Sweden, and Afzelius counted 60 chromosomes
somatically in this material, while Flovik in 1940 gave the number
$2n = 56$ for the same species from Spitzbergen. In *Arnica* the
basic number no doubt is 5, since Battaglia has found the West-
American *A. longifolia* to be diploid with $2n = 10$ (1952*d*: 5). On
the other hand, the writer has confirmed Flovik's determination of
$2n = 56$ for *A. alpina* (Nygren, unpubl.), a number also given by
Sørensen and Westergaard for material from Greenland (Löve and
Löve, 1948, p. 101). The writer has raised two consecutive gen-
erations of *Arnica alpina* from seeds of the same population in
northenmost Sweden, from which Afzelius' material originated. In
both generations all plants were of the maternal type. Ten plants
of each generation were counted, all having the number $2n = 56$.
This means that the only apomictic species in the genus, which has
been chromosome-counted, does not fit into the 5-series of the
sexual species. No doubt an investigation of the numerous North
American species of *Arnica* is badly needed.

CHONDRILLA. In her classical study of the genus *Chondrilla,* Poddubnaja-Arnoldi (1933) reported one diploid species with the chromosome number $2n = 10$ and eight triploid and tetraploid species. The diploid, *C. ambigua,* was sexual; the triploids and tetraploids were apomicts. Battaglia has verified Poddubnaja-Arnoldi's statement that *Chondrilla juncea* reproduces apomictically (1949). He found that the 15 chromosomes were unpaired during meiosis in the EMC. They do not go to the poles of the cell but form a restitution nucleus which later is divided by a mitotic division. This division gives a dyad, the chalazal cell of which forms the complete ES, while the cell close to the micropyle degenerates. Thus *Chondrilla* follows the *Taraxacum* scheme of ES formation. Bergman has investigated two clones of *Chondrilla juncea* (1950), one cultivated in Stockholm, the other at Uppsala. Bergman found a considerable difference in the formation of pollen in the two clones. The Uppsala clone was fairly regular and as a rule showed 6 II and 3 I at M I, while the clone from Stockholm in some loculi was partially asynaptic with one or two bivalents, in other loculi totally asynaptic with no bivalent formation at all. In both clones restitution nuclei were formed during microsporogenesis, but, while this in the Uppsala plant occurred only in 1% of the cases, the Stockholm plant as a rule formed restitution nuclei which were divided by a mitotic division and gave rise to dyads with unreduced chromosome number. Meiosis in the EMC was as a rule asynaptic in both clones. A restitution nucleus is formed, which divides mitotically and gives rise to a dyad, the chalazal cell of which forms the ES. According to Bergman the two clones from Stockholm and Uppsala are genetically different, i.e., the dissimilarities in formation of pollen can not be caused by external conditions only. In 1952 Bergman increased our knowledge of the genus *Chondrilla* by finding a new diploid sexual species, *Chondrilla chondrilloides* (1952b). In another paper (1952c) he shows that apomictic *C. juncea* has three morphologically similar genoms, which makes it probable that the species is an autopolyploid.

CHRYSANTHEMUM. Apomixis has not been found in *Chrysanthemum.* In 1952 Bergman, however, reported some interesting data from an investigation of diploid ($2n = 18$), triploid and tetraploid *C. carinatum.* The tetraploids were obtained after colchicine treatment of diploid seeds; the triploids occurred in the offspring

of the tetraploids. All chromosome races have more or less regular meiosis on the male side, while the female side shows irregularities. Complete asynapsis was found in 19% of the EMC's of the diploid, in 41.9% of the EMC's of the triploid with two extra chromosomes ($2n = 26$), and in 20.0% of the EMC's of a triploid with five extra chromosomes ($2n = 29$). A tetraploid plant showed 20.3% asyndesis, while a pentasomic one with $2n = 37$ had 70% asyndetic EMC's. In spite of the high percentage of asyndetic cells, no restitution nuclei were detected; degeneration begins after the anaphase stage in the asynaptic cells. Bergman considers the asynapsis in *C. carinatum* genetically caused and points out that this is the first case known among amphimictic plants with total asyndesis on the female side and full syndesis on the male side.

ERIGERON. In the genus *Erigeron* sexual species have the chromosome numbers $2n = 18$, 36 and 54, while two apomictic species, *E. annuus* and *E. ramosus,* are triploids with $2n = 27$. A third apomictic species, *E. mucronatus,* has not been too well investigated. In 1947 Fagerlind studied this species, however, and found that *E. mucronatus* forms unreduced ES's in a frequency of about 70%, while *E. annuus* has 100% unreduced ES's. In both species restitution nuclei can be formed during any of the meiotic stages from the heterotypic prophase to the heterotypic anaphase. The nuclei divide and give rise to dyads which develop directly into unreduced ES's. Formation of these restitution nuclei is more common in *E. annuus* than in *E. mucronatus.* Fagerlind has tried to find Gustafsson's pseudohomotypic division in *Erigeron,* but believes that this division does not play any role in the species, if it occurs at all. According to one of Fagerlind's drawings (fig. 1 h, l.c.: 225), the type of division in question does occur in *E. mucronatus,* however. The complete ES is formed according to the diplosporous *Taraxacum*-scheme. Fagerlind does not give the chromosome number of the *mucronatus* plant investigated by him, but he mentions (p. 224) that up to 34 univalents occur in meiosis. Battaglia, on the other hand, who studied the same species in 1950, reports the number $2n = 32$ for his material. Battaglia finds that 80% of the meioses in the EMC's give rise to restitution nuclei, while the remaining 20% give haploid nuclei. Normally dyads with diploid nuclei are formed. The ES is completed according to the diplosporous *Ixeris*-scheme. On the male side irregularities

occur with the formation of univalents, trivalents and tetravalents. The end products of meiosis are generally normal tetrads, however.

HIERACIUM. In 1948 M. and M. A. Christoff published an interesting paper on *Hieracium hoppeanum*. The species normally has the chromosome number $2n = 45$, but a plant with $2n = 90$ was produced by colchicine treatment already in 1939. In the offspring of this doubled plant, seedlings were obtained in 1940 with 45 chromosomes somatically, while in 1941 the same mother plant produced offspring with $2n = 45$ as well as with $2n = 90$. The same results were attained in the years 1942, 1945 and 1946. Thus there could scarcely have been any mistake in the experimental work. An embryological investigation revealed that both chromosome races are aposporous and non-pseudogamous. In both races even the macrospore mother cell degenerated at an early stage. The Christoffs made the observation that " some cells of the integument commenced an unusual development. They increased in size, . . . and their nuclei acquired an outward appearance identical with that of early meiotic prophase " (p. 40). The authors are of the opinion that aposporous cells with reduced chromosome number originate from " somatic cells which have passed through meiosis " (p. 40). In *Potentilla collina* A. and G. Müntzing in 1943 observed frequent formation of seedlings with $2n = 42$ in the offspring of a mother plant with $2n = 84$. In aposporous *Poa pratensis* Kiellander (1942) and Åkerberg and Bingefors (1953) have reported some similar cases, i.e., plants with high chromosome numbers gave rise to offspring plants with half the haploid number of the mother plant. We still do not know by which embryologic method these offspring plants with low chromosome numbers are formed, however, and therefore the observations made by the Christoffs have general interest. In *Rudbeckia* Battaglia (1947a) has described a phenomenon called " semigamia ", which might be of importance in this connection.

In 1951 Heitz showed that it is possible to make smear preparations of ES's in *Hieracium*. By this method he was able to prove apomixis in the species *H. alpicola, glaciale, praecox, piliferum* and *tomentosum* from Valais canton in Switzerland as well as in the Hispanic species *H. bombycinum*.

PARTHENIUM. The extensive literature of this genus has been reviewed up to 1946 by Gustafsson (l.c.: 132–136). All data of

general interest for the understanding of the apomictic processes in *Parthenium* are also discussed in Gustafsson's work. In 1949 Rollins stated that sexual forms of *P. argentatum* have the chromosome number $2n = 36$, while facultative apomicts have $2n = 54$ or $2n = 72$. In Mexican populations *P. argentatum* shows introgressive hybridization with *P. incanum* ($2n = 72$). Individuals belonging to such populations are sexual in spite of the fact that they have the chromosome number $2n = 72$. Pure *P. argentatum* is most common in the centre of the area investigated (N. Mexico–S. Texas), while introgressive forms occur in the outer parts (Central Mexico and SW Texas). Sexual forms as a rule occur in the central area, where the introgressivity is less established. There is a positive correlation between the degree of apomixis and the degree of introgressivity. Rollins also pronounces the opinion that *P. argentatum* had its origin in the Durango area in Mexico. Gerstel and Mishanec (1950) have made some observations similar to those of Rollins in *Parthenium argentatum*. Moreover they report that in crossings two doses for apomixis dominate over one dose for sexuality, while, on the other hand, one dose for sexuality is dominant over one dose for apomixis. Diploid apomicts produce a much less proportion of parthenogenetic offspring than do triploids which have two genoms from an apomictic diploid plus one genome from a sexual parent. A polyhaploid has been especially well investigated. The plant was diploid and facultatively apomictic. The cross between the polyhaploid and sexual diploid *P. argentatum* gave four classes of plants in the offspring: maternals, diploid F_1 plants, triploids, and plants with high chromosome numbers. The reciprocal cross, on the other hand, gave rise to diploid F_1 plants only. The triploids from the first cross were facultative apomicts, while tetraploids obtained after doubling of the diploid type were sexual. In 1953 Gerstel, Hammond and Kidd were of the opinion that apomixis in guayule is controlled by at least four recessive genes. Gerstel and Riner have shown that there is a very strong mechanism of incompatibility in guayule, *P. argentatum* (1950), and Gerstel in another paper (1950*b*) points out that in the offspring of two diploid guayule plants there occur four incompatibility classes. Gerstel presumes the presence of a multiple allelic series and names the different alles R_1, R_2, R_3 and R_4. He proves dominancy to be at hand in the style but not in the pollen

for the allele R_2 over the other alleles, and for R_1 and R_3 over R_4. Gerstel is of the opinion that this dominancy would explain the reciprocal differences which have been obtained in certain crosses in *P. argentatum* (p. 504). While Tysdal (1950) has found that interspecific hybrids in *P. argentatum* are promising for rubber production, Johnson (1950) has made a comparison between strains obtained from a mass collection of seeds from five plants at Durango in Mexico (G. accession 4265) and the most cultivated strain in California, nr 593. The two strains 4265 I and 4265 II were better than 593 regarding the amount of rubber and resin produced. All three strains compared were apomictic. Gerstel has also made a study of the resistance to *Verticillium* wilt in races of *P. argentatum* with the chromosome numbers $2n = 36$, $2n = 54$ and $2n = 72$ (1950*a*). In two independent experiment series two diploid strains gave the average figures of 15.9 and 23.8% resistance, respectively, while five triploids in the first series gave the mean 4.58%, and three other triploids that of 6.53% in the second series. The corresponding tetraploids were six in number in the first series with an average value of 2.28%, and four in the second series which gave the mean of 2.53%. The differences in the three chromosome races are obvious and therefore of great general interest. Catcheside has made two studies (1947 and 1950) of the occurrence of B-chromosomes in *P. argentatum*. He found that up to five B-chromosomes appear in certain individuals (1950). These chromosomes are heterochromatic and lose their color before M I; later they uncoil and appear long and slender in late A I (1947). They do not distribute themselves normally in A I but have a tendency to go to one of the poles in this stage of meiosis (1950). The B-chromosomes are also later than the other chromosomes and are therefore often lagging in A I.

RUDBECKIA. In three publications of recent years, (1946, 1947, 1952) Battaglia studied the reproduction of different species of the genus *Rudbeckia,* one of which in 1946 was also investigated by Fagerlind. According to Battaglia the seven apomictic species in the genus are all tetraploid ($2n = 76$) and diplosporous. Their ES's develop according to the *Ixeris*-scheme. In *R. laciniata* sometimes accessory restitution nuclei appear during meiosis (1946*b*: 440). As a rule one restitution nucleus with unreduced chromosome number is formed, but sometimes two restitution nu-

clei of different sizes may be produced during the first or even during the second division. A special phenomenon, which Battaglia calls " semigamia ", is of particular interest. A sperm nucleus enters the egg cell but does not fuse with the egg nucleus; on the contrary it divides one or more times. This sometimes is followed by the formation of chimaeras having cells with the somatic chromosome number and half the somatic chromosome number in the same embryo. The phenomenon is very well illustrated in the paper of 1947a, figs. 1–15.

TARAXACUM. Fagerlind (1947) and Battaglia (1948) very carefully have studied the development of the macrospore mother cell in *Taraxacum*. Fagerlind does not mention which microspecies he investigated, while Battaglia has examined *T. " vulgare "* and *I. mongolicum*, both with the chromosome number $2n = 24$, and *T. megalorrhizon* with $2n = 32$. Both authors have followed the development of the EMC from its youngest stages, and both have come to the same conclusions: unpaired chromosomes appear in early stages, and later on a restitution nucleus is formed, which divides with a mitotic division and forms a dyad, the chalazal cell of which develops into an ES. According to Battaglia the restitution nucleus divides with a division which corresponds to the pseudohomotypic division of Gustafsson (1935). Thus Battaglia regards this division as incorrectly interpreted by Gustafsson. Fagerlind is of the opinion that it has not yet been proved that the pseudohomotypic division occurs in *Taraxacum;* if it occurs at all, it must be very rare (p. 377). Battaglia has also studied microsporogenesis, and he finds that restitution nuclei or cells with two to four nuclei are regularly formed. Cooper and Brink have examined the development of endosperm and embryo in *T. officinale* (1949). They find that neither the egg cell nor the central nucleus needs to be fertilized. Both the egg cell and the central nucleus therefore often develop independently of each other, and seeds containing a unicellular embryo and a multicellular endosperm are found just as often as are those having a multicellular embryo and two polar nuclei. The egg cell has an " extensive prestorage of food materials ", and therefore development of the embryo proceeds normally, even in seeds with a very limited number of endosperm cells. Tschermak-Woess (1949) has found diploid as well as triploid species of the *vulgare* group to occur in Wien and Viedsn-

Österreich. This makes it necessary to investigate the *vulgare* populations of middle and southern Europe more carefully.

CRUCIFERAE

ARABIS. Bøcher has investigated the amphi-apomictic complex of *Arabis Holboellii* (1947, 1951) which has its main distribution areas in western North America and in western Greenland (cf. map in 1951: 50). Diploids with $2n = 14$ and triploids with $2n = 21$ of the var. *typica* have been studied from Greenland as well as diploids of var. *retrofracta* from Alaska. Some diploids are sexual, while others are apomictic as are all triploids studied. The apomictic forms have a male meiosis which is disturbed in the same way as is that in *Calamagrostis* (Nygren, 1946) and *Euhieracium* (cf. Gustafsson, 1946–47). The flowers at the top of the raceme develop good pollen, while those below show asyndesis followed by formation of dyads and, more commonly, of monads. Flowers at the middle of the raceme display transitional development. Some of Bøcher's data are condensed in Table I (cf. l.c.: 55) and make it very probable that the development of meiosis in *Arabis Hoelboellii* is influenced by hormones, the action of which seems to be obvious but the composition of which we do not know.

The EMC develops diplosporously. No fertilization of the central nucleus occurs, however, and thus the endosperm is tetraploid in diploid apomicts and hexaploid in all triploid forms. Probably the pollen causes some kind of stimulation of importance to the development of the endosperm, for it germinates on the style and emasculation is followed by sterility.

GRAMINEAE

BOUTELOUA. In 1942 Fultz reported chromosome numbers in *Bouteloua curtipendula* to vary from $2n = 85$ to $2n = 101$. In 1948 Harlan claimed that apomixis occurs in the species and that the first metaphase in the PMC's is irregular. In 1949 he found the pairing of chromosomes in the PMC's to be weak at the same time as he observed the first division of the EMC to be irregular. Division of the EMC as a rule gives rise to two cells: one cell with a more or less unreduced chromosome number, the other with very few chromosomes (l.c.: 498). The second division is normal; an ES is formed by the chalazal cell. Parthenogenesis is probable but

has not been proven. Snyder and Harlan in 1935 reported the chromosome numbers $2n = 20, 40, 60, 42$ and 84 in *B. gracilis,* the polyploids having wider distribution in western Texas and New Mexico than the diploids.

TABLE I

DEVELOPMENT OF MICRO- AND MACROSPORES IN DIFFERENT PARTS OF THE RACEME IN TRIPLOID *Arabis Holboellii*

Development as a consequence of physiological differences in the longitudinal direction of the raceme	Male side (mainly based on observations)		Female side (mainly hypothetical)		Position in the raceme
Delayed	Syndesis; 2 divisions	Tetrads with reduced number	?	?	At the top
Normal	Asyndesis; 2(1–0) divisions	Tetrads (dyads–monads)	Syndesis–asyndesis	Tetrad or dyad (restitution nucleus)	
Premature	Asyndesis; 1(–0) division	Dyads (monads)	Syndesis–asyndesis	Restitution nucleus; dyads; degeneration of upper dyad cell	
Greatly premature	Asyndesis; (1–)0 division	Dyads (monads)	(Syndesis) Asyndesis	The same or pseudo-homotypic div.; developm. of both dyad cells	Below

CALAMAGROSTIS. The present writer has been working with *Calamagrostis* many years. In 1946 experimental, cytological and embryological data were given for most of the European species, and it was proven that amphimictic as well as apomictic species occur in the genus. The apomictic species are diplosporous and develop embryos parthenogenetically. The central nucleus in the ES divides and develops an endosperm without fertilization or stimulation by pollen growing on the stigma. The apomictic species gen-

erally do not produce pollen at all; as a rule the PMC's fuse, form-
ing more or less big plasmodia which fill the loculi. The anthers
do not dehisce in some species; very often they are yellow and I-
shaped in florets just opened, while in pollen-producing species
they are purple and X-shaped. Two of the European apomictic
species are very polymorphous and at the same time highly poly-
ploid. Thus *C. purpurea* has chromosome numbers running from
$2n = 56$ to $2n = 91$, while *C. lapponica* shows a variation in numbers
between $2n = 42$ and $2n = 112$. By way of contrast is may be men-

TABLE II

OCCURRENCE OF MEIOTIC AND MITOTIC DIVISION TYPES IN ONE CLONE
OF *C. purpurea* IN 1943 AND 1944 (NYGREN, 1946: 182)

Fix. date	Fix. nr.	PMC's with		EMC's with		Number of				
		Meiosis	Mitosis	Meiosis	Mitosis	Florets	Florets with pollen	EMC's	PMC's	
		%	%	%	%		%			
8, 9/6–43	135, 163	100.0	0	100.0	0	506	100.0	27	6.666	
22/6–44	269, 270	30.8	69.2	45.5	54.5	344	46.0	66	2.672	
22/6–44	244	8.2	91.8	71.4	28.6	134	1.5	7	122	
22/6–44	271, 272	7.1	92.9	33.3	66.7	67	18.0	12	1.191	
22/6–44	273, 274	0	100.0	27.5	72.5	402	0.5	80	5.042	
							1.562	209	16.052	

tioned that a third apomictic species, *C. chalybaea,* has always been
found to be hexaploid with $2n = 42$. *C. purpurea* has arisen from
the amphimictic *C. canescens* $(2n = 28)$ and its hybrid derivatives
with other amphimictic species, while *C. lapponica* shows relation-
ship to the amphimictic tetraploid *C. neglecta* as well as to the
North American *C. inexpansa* $(2n = 28$–over 100). In *C. pur-
purea,* as in *C. lapponica,* there are facultatively apomictic strains
which are able to produce reduced sexual ES's and diplosporous
unreduced sacs in the same panicle. This has been reported for
17.6% of the 174 *purpurea* strains studied as well as for three of
the 28 examined *lapponica* plants (1946). While most *lapponica*
strains develop pollen in their anthers, only one single *purpurea*
clone from nature had this ability. *C. chalybaea* does not form
pollen; in the non-diplosporous EMC's semiheterotypic divisions

occur. Restitution nuclei on the female side have been observed only in *purpurea*. It was shown early in the investigations on *C. purpurea* that a certain time relationship exists in the development of different division types. This is evident from Table II which gives the data for a facultatively apomicitc clone, Gäll. 1-41, the only pollen-producing one of the 174 clones studied. This clone in 1943

TABLE III

Offspring of Bagged *Calamagrostis purpurea* with Pollen
(Nygren, 1949: 287)

Mother clone	Chromosome number of mother clone $2n$	Number of I_a^1 plant	Chromosome number of I_a^2 plant $2n$	Chromosome numbers of the I_a^2 plants. Each row represents the offspring of one bagged panicle
J 3-41	56	1-2	56	$2n = 70, 80, 84$
D 2-41	56	1-3	56	$2n = 56$
		1-4	56	$2n = 56, 56, 56$
		2-2	56	$2n = 56, 56, 56$
		2-3	56	$2n = 56, 58, 70$
			56	$2n = 56, 56$
			56	$2n = 68, 69, 70, 70$
		2-4	56	$2n = 56, 56, 56$
		3-2	56	$2n = 63, 64, 68, 68$
S 2-38 A	56	1-1	56	$2n = 63, 64, 68, 68$
G 1-41 A	56	1-4	56	$2n = 65$
J 2-41 B	56	1-1	56	$2n = 69, 70, 70$
		2-4	56	$2n = 67, 70$
			56	$2n = 70, 71, 71$
		3-1	56	$2n = 56, 56, 56, 56$
		3-4	56	$2n = 56, 56, 56, 56, 56$
R 1-41 B	56	3-1	56	$2n = 67$
A	56	1-1	56	$2n = 66, 66, 67$
		4-1	56	$2n = 66, 70$

The heading " Mother clone " has reference to plants from nature, while I_a^1 denotes descendants of the mother clone raised after bagging. Next generation of these I_a^1 plants, raised after bagging, is designated I_a^2, and so on.

showed meiosis with semi-heterotypic divisions in all PMS's as well as EMC's studied, while in 1944 it gave meiotic or mitotic divisions in different florets on the male as well as on the female side. It could be proven that the panicles with meiotic divisions were the first developed that year, while those having mitotic divisions developed later. In 1947 only mitotic divisions were found in all panicles studied of this clone.

Offspring raised from seeds obtained after bagging 40 different clones with $2n = 56$ were examined in 1948 and 1949, and it was revealed that 31 plants belonging to eight of these clones developed pollen, in spite of the fact that neither their parents nor other descendants of the same clones had this ability. In all, 673 descendants of the 40 clones were checked. All these 673 plants had the same chromosome number, $2n = 56$, and had the same morphology as the descendants not having pollen in the clones studied (1948). All pollen-developing offspring plants were bagged at the same time as crossings were made with these plants as mothers. The result of the baggings and of the crossings as well are presented in Tables III and IV. In Table III the clone D 2-41 : 2-3 is of particular interest because here maternal offspring has been developed from only one panicle, while from two other panicles descendants with higher numbers have been formed as well. Similar observations of different offspring being raised from diverse panicles in the same clone were made already in 1946 in the pollen-producing *purpurea* clone, Gäll. 1-41. Table IV shows the same scheme to occur when crossings are worked out with amphimictic species. Thus one panicle of D 2-41 : 1-4 has given rise only to maternal offspring at the same time that another one formed maternals as well as hybrids. Summing up, we find that in *C. purpurea* different panicles of the same pollen-producing plant may give rise to offspring with the same or deviating chromosome numbers compared to the mother clone. These results fit very well with those obtained in *Poa* by Clausen and co-workers, even though these scientists did not analyze the chromosome numbers of offspring from each panicle of the mother.

Embryological studies of the *purpurea* offspring with higher chromosome numbers than $2n = 56$ and of the hybrids formed show that diplosporous and sexual ES's are developed in the same individual (1951). Thus maternals as well as deviating offspring will be formed even in the next generation. In 1951 it was shown that nine offspring out of eleven of the second bagged generation (= right column of Table III) deviated morphologically from the first bagged generation as well as from the original mother clone. In most cases such deviating offspring would continue the formation of new types in the following generations. The hybrids of Table IV, just as the earlier produced ones (1946), also continue

TABLE IV

RESULTS OF CROSSES BETWEEN *C. purpurea* AND DIFFERENT
AMPHIMICTIC SPECIES (NYGREN, 1949: 290)

Mother clone	Chromosome number of mother clone 2n	Number of I.¹ plant	Chromosome number of I.¹ plant 2n	Father species	Chromosome number of father species 2n	Chromosome numbers of descendants. Each row represents the offspring of one crossed panicle
J 3-41	56	2-1	56	C.ep.	56	2n = ± 58
J 5-38	56	1-4	56	C.can.	28	2n = 56, 56, 56, 56, 56, 56, 56
D 2-41	56	1-4	56	C.a.	28	2n = 56 (12 plants)
			56	C.a.	28	2n = 56 (10 plants), 70, 70
S 2-38 A	56	1-1	56	C.can.	28	2n = 54, 56, 57, 60, 62, 62, 63
G 1-41 A	56	2-1	56	C.a.	28	2n = 66, 66
		2-3	56	C.can.	28	2n = 64
J 2-41 B	56	1-1	56	C.can.	28	2n = 70, 72
			56	C.can.	28	2n = 77
R 1-41 A	56	1-4	56	C.ep.	56	2n = 56
			56	C.can.	28	2n = 49, 70, 70, 70
			56	C.can.	28	2n = 67, 70, 70, 70, 70, 70
			56	C.can.	28	2n = 67, 67, 67, 70 (10 plants) 72

The heading " Mother clone " has reference to plants from nature, while I.¹ denotes descendants of the mother clone raised after bagging. The crosses were effected on these I.¹ plants. In the column headed " Father species ", C.a. = C. arundinacea, C.can. = C. canescens, C.ep. = C. epigeios.

the type formation in the same manner in later generations. This has been clear from studies of a great number of F_3 generations raised from deviators as well as from maternals in the F_2 of the original hybrids. The data from these studies are not published as yet, but it may be mentioned that the formation of new types follows the same scheme as that found in the Stanford *Poa* experiments. The complete *C. purpurea* biotype formation scheme is given in Table V.

It might be added that genes for apomixis probably occur in populations of the amphimictic species in the distribution area of *purpurea* (1948b, 1951). These genes are spread by introgressive hybridization between *purpurea* and different sexual species. When forms having such genes are brought together, they intermingle and give rise to new apomicts.

During recent years diplospory has been reported also in *Cala-magrostis canadensis, langsdorffii* and *purpurascens* (Nygren, 1954).

DESCHAMPSIA. The present writer has studied polymorphous *Deschampsia caespitosa* and its viviparous relative *D. alpina* (Nygren, 1949). *D alpina* is an autopolyploid of *D. caespitosa* and has chromosome numbers running from $2n = 26$ to $2n = 52$, while *D. caespitosa* in all studied biotypes has $2n = 26$. Diploid *alpina* is non-viviparous, and, according to Flovik (1938), triploid *alpina* ($2n = 39$) from Spitzbergen had such weakly developed bulbils that they could hardly be detected without using a magnifying glass. Tetraploids or aneuploids with numbers between $2n = 39$ and $2n = 52$ are facultative–obligately viviparous. Thus the degree of vivipary increases with the chromosome number. A biotype of

TABLE V

BIOTYPE FORMATION IN *Calamagrostis purpurea* (NYGREN, 1951: 531)
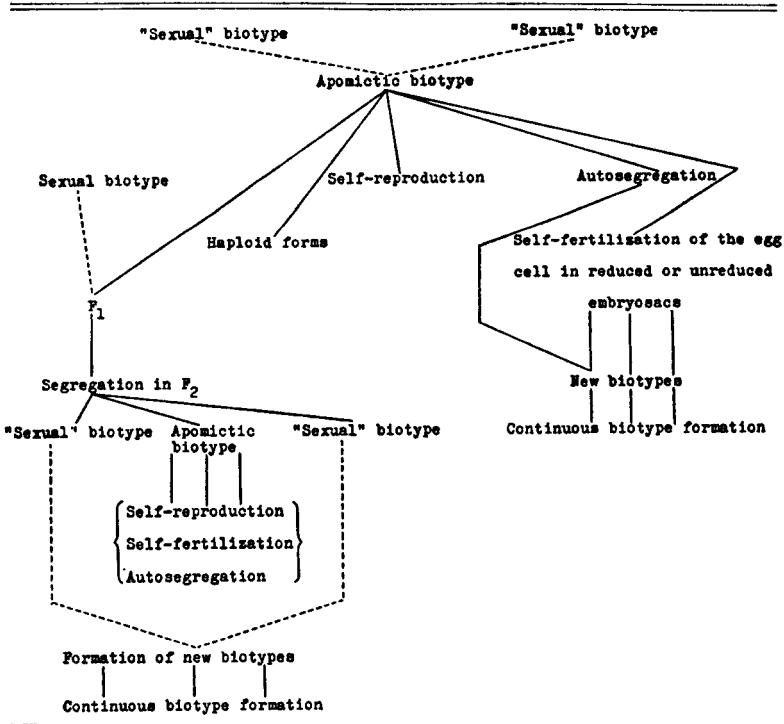
D. caespitosa (2n = 26) developed viviparous propagules after short-day treatment. The offspring raised from these propagules were non-viviparous (Nygren, unpublished), which means that vivipary in *Deschampsia* is caused by a recessive gene system. In 1950 Lai-Yung Li reported vivipary in *Eleusine coracana* and *Setaria viridis*. This report needs confirmation.

PANICUM. Warmke thinks that apomixis may occur in *Panicum maximum* (1951), a possibility suggested by the intravarietal uniformity in this species and by the absence of hybrids in the offspring produced by open pollination. In 1954 he proved facultative apomixis as apospory combined with pseudogamy to exist in this species, however.

PASPALUM. Smith has found (1948) that apospory followed by diploid parthenogenesis occurs in the common cultivated form of *Paspalum dilatatum*. It is uncertain that the species is also pseudogamous because in some emasculated florets seeds have been developed. Multiple ES's are at hand, and the number of twins and triplets varies between one and six per cent. Smith is of the opinion that the common form is of hybrid origin. Burton (1948) suggests that apomixis occurs in common Bahia grass, *Paspalum notatum*, but the data given are not convincing enough to prove this assumption. An embryological investigation of the species is necessary.

POA (Diplosporous species). *Poa alpina* reproduces in three ways: sexually, apomictically by diplosporous ES development, and by viviparous propagules. Development and type formation in sexual and diplosporous *P. alpina* are well known through the investigations by Müntzing and Håkansson (cf. Gustafsson, 1946–47). In the years 1946–49 Müntzing studied a peculiar sexual strain containing, as a rule, 14 chromosomes in the root tips but with additional chromosomes at meiosis. The strain was obtained from Innsbruck, but probably had its origin in southern Russia. By a very ingenious method the accessories are eliminated in the somatic tissues, while they still are present in the germ line (1948). Håkansson (1948) has investigated the embryology of this peculiar strain without finding any elimination of the accessories during development of the embryo except in the " primary roots of some mature embryos ". He suggests that the accessories are probably

absent only from the adventitious roots (l.c.: 247). Skalinska (1952) examined 111 clones of viviparous *Poa alpina* in the Tatra district of Poland and reports the occurrence of seven chromosomic types in this area. (l.c.: 255). The chromosome numbers are given in Table VI. Of particular interest is the viviparous diploid type. Skalinska also suggests that the clones with $2n = 22$ are secondary diploids and those with $2n = 33$ secondary triploids. The other chromosome numbers can easily be explained as derivatives from crosses between the two basic systems. Skalinska also gives some ecological data which show that some clones are restricted to areas with limestone, while others grow on acid soils. This year (1954) Müntzing published an extensive study of his

TABLE VI

ALTITUDINAL DISTRIBUTION OF CHROMOSOMIC TYPES OF *P. alpina* L.
VAR. *vivipara* L. (SKALINSKA, 1952: 273)

Vertical areas	Chromosomic types (2n):							Total numbers of biotypes
	14	22	26	28	33	34	35	
Lower mountain layer		2	2					4
Foothills		2	1	1				4
Higher mountain layer	1	15	6	6	1	1		30
Layer of subalpine forests		7	9	4	7	2		29
Layer of *Pinus montana*		6	8	5	10		1	30
Alpine layer		1	4		6	2	1	14
Total	1	33	30	16	24	5	2	111

experiments with *Poa alpina* during the past 14 years. In this paper data are given for viviparous clones as well.

The present author has studied 13 viviparous clones of *Poa alpina* from Scandinavia (Nygren, 1950). The chromosome numbers in these clones run from $2n = 36$ to $2n = 57$. Pollen meiosis was examined in two clones with $2n = 37$ and $2n = 46$, respectively, and found to be fairly regular. Mainly bivalents were formed; the highest average number of univalents was 2.05 per PMC. Very few trivalents and quadrivalents were in both clones. In the clone with $2n = 37$ the percentage of morphologically good pollen was 67.4. Viviparous *alpina* is thus able to produce pollen, which means that the genes for vivipary can be spread to non-viviparous populations. We do not know the genetical background of vivipary in *Poa* because no experimental data have been reported as yet,

but we do know that the degree of vivipary can be modified experimentally within certain limits in viviparous clones. We also know that vivipary sometimes can be induced in non-viviparous clones by changing the external conditions compared to those occurring in the growing area of the plant in question. These facts make it possible that several recessive genes are involved in this gene system, but at the same time they by no means exclude vivipary in *Poa* as caused by one single recessive gene. In Scandinavia *Poa alpina vivipara* forms hybrids with *Poa laxa* subsp. *flexuosa* as well as with *Poa pratensis,* which latter combination also occurs in the Arctic. The first mentioned hybrid is called *Poa jemtlandica,* the second *Poa herjedalica,* by Swedish authors. These hybrids have been studied by the present writer (Nygren, 1950). *P. jemtlandica* has a restricted distribution in central Scandinavia and Scotland (cf. Nannfeldt, 1937), whereas *herjedalica* is spread all over the Scandinavian mountain range. *P. jemtlandica* is morphologically uniform and has the chromosome number $2n = 37$ in its Scandinavian area of distribution, while *herjedalica* is morphologically polymorphous with numbers running from $2n = 47$ to $2n = 80$. *Jemtlandica* probably originated only once (Nannfeldt, 1937), while it is obvious that *herjedalica* is of polyphyletic origin. *Jemtlandica* as well as *herjedalica* occur only as viviparous forms in nature. At least *herjedalica* generally produces good pollen, just as *Poa alpina vivipara,* and therefore it can act as pollen parent in crosses with different *Poa* species and spread the genes for vivipary. Embryological investigations have revealed that only sexual or aposporous ES's appear in the nucellus of *herjedalica.* Thus the diplosporous system of *alpina* is not rebuilt in this hybrid, an observation which also fits with the experimental data by Åkerberg and Bingefors (1953) for the cross between *Poa pratensis* and non-viviparous *alpina.* These authors have studied F_1–F_4 of the combination mentioned, and found only sexual and aposporous ES's in the nucellus. The high chromosome numbers obtained in later generations (Table VII) depend upon the facts that preferably unreduced egg cells are functioning and that therefore the chromosome numbers increase for every generation. The experimental results of Åkerberg's and Bingefors' study agree very well with the situation found in the field with respect to viviparous hybrids.

TABLE VII

CHROMOSOME VARIATION IN THE THIRD GENERATION OF *Poa pratensis* × *alpina*. DATA FROM ÅKERBERG AND BINGEFORS, 1953

Hybrid combination and chromosome number		Chromosome number of parents (2n)		Number of F₃ families studied	Chromosome variation in F₃	Number of F₃ plants studied
		P. prat.	P. alpina			
B 1.Ä 62/7	$2n = 45$	50	37	2	(16), 60–112	50
B 2.Ä 62/9	$2n = 69$	50	37	6	50–112	34
C 1.Ä 733:						
pl. 1, 2, 4	$2n = 70, 66, 70$	90	50	3	75–119	13
C 2.Ä 734:1	$2n = 66$	90	50	3	50–72	6
D 1.Ä 629:7	$2n = 95$	80	..	4	98–114	13
D 2.Ä 269:8	$2n = 102$	80	..	5	100–106	10
Sum				24	50–122	126

The plant with $2n = 16$ in B 1.Ä 62/7 is of particular interest because of its morphological similarities with the sexual *Poa trivialis*. It has been formed by double reduction from a F_2 plant with $2n = 75$, just as a subhaploid plant with $2n = 18$ was obtained by Kiellander in 1942 from a mother plant with $2n = 72$.

Until 1952 diplospory was known only in *Poa alpina, glauca, nemoralis* and *palustris*. That year Grun added the West American *Poa nevrosa* to the diplosporous Poae. He studied the chromosome number of *nevrosa* from California (Sierra Nevada) and western Washington, and found plants with $2n = 63, 76, 80$ and 81–90, as well as a sexual strain with $2n = 28$ near the mouth of Columbia River. The endosperm in diplosporous *nevrosa* with about 60 chromosomes somatically contains about 120 chromosomes, which means that no fertilization of the central nucleus is needed for the formation of seeds. Apomictic *nevrosa* does not produce pollen, and therefore Grun suggests that the varying chromosome numbers in West American *nevrosa* as well as the morphological differences between populations in its area of distribution may depend upon intercrossing with plants of the *Poa Canbyi–epilis* group, which species often grow intermingled with *Poa nevrosa*.

POA (Aposporous species). During the last decade a very extensive experimental study of the genus *Poa* has been pursued by Clausen and co-workers (1946–52) of the Carnegie Institution of

TABLE VIII

Chromosome Numbers of *Poa* Hybrids (Grun and Triplett, 1953: 121)

Parents		Somatic chromosome numbers		
		Parents		F₁ hybrids
Female	Male	Female	Male	F1 hybrids
ampla Albion	× *pratensis* Mather	64	68	63, 70, 92, 93, 94, 96, 98, 100, 104
Kahlotus	× *pratensis* Athabasca	64	70	77, 79, ca. 83, 84
Heise	× *pratensis* Newport	70	81	73, 75, ca. 79
Condon	× *pratensis* unknown	63	:	ca. 98
Enterprise	× *pratensis* unknown	63	:	96
Albion	× *pratensis* Lapland	63	74	63, 68, 70, 72, 73
Albion	× *pratensis* Athabasca	64	70	75, 103
scabrella Watsonville	× *pratensis* Athabasca	82	70	71, ca. 119
Las Posas	× *pratensis* Lapland	82–84	74	76, 79, ca. 110
Las Posas	× *pratensis* Mather	82–84	68	64, 67, 68, 70, 71, 74, 75
Las Posas	× *pratensis* Athabasca	84	70	69, 70, 71, 72, 73, ca. 74
Las Posas	× *ampla* Kahlotus	82–84	63–4	75–76
Las Posas	× *compressa* Chorsum	84	50	65, 105, ca. 115
Las Posas	× *compressa* Crescent Mills	84	42	63–65, 101
ampla Albion	× *compressa* Chorsum	64	50	ca. 50, ca. 62, 87
compressa Chorsum	× *ampla* Albion	50	64	56, 59
ampla Spokane	× *compressa* Crescent Mills	63	42	ca. 81, 84
Albion	× *arida* North Platte	:	63	ca. 50, 59, 61
arida North Platte	× *ampla* Albion	63	:	ca. 97, 98
scabrella Las Posas	× *arida* North Platte	84	63	67
arida North Platte	× *scabrella* Las Posas	63	84	ca. 105
Canbyi Blue Mts.	× *pratensis* Athabasca	84	70	77
gracillima Slate Creek	× *scabrella* Yager Creek	84	84	86
Falen Leaf L.	× *pratensis* Athabasca	86	70	ca. 72, ca. 74, 76
scabrella Lucerne	× *arachnifera* Stillwater	ca. 63	58	57

Washington at Stanford, Calif. Hybrids have been produced between a number of indigenous North American *Poa* species and other species occurring also outside North America. Most of the parental plants used were chromosome-determined by Hartung in 1946; a list of some of the combinations made and the chromosome numbers obtained in the F_1 is given in Table VIII.

In addition to the hybrids listed in Table VIII, Clausen and co-workers in 1952 reported a number of new combinations with *Poa ampla, arida* and *scabrella* as well as some successful crossing

TABLE IX

CHROMOSOME NUMBERS OF OFFSPRING OF *Poa irrigata* FROM ICELAND
(LÖVE, 1952: 22–23)

Chromosome number of mother plants 2n	Chromosome numbers of offspring								Total
	80	90	100	110	120	130	140	150	
84 (three strains)	125	1		1	14				141
87	42	2	3	1	7	6			61
91		38				1			39
98		42	2				2		46
101		3	39						42
107			34						34
119				35	3				38
126					42				42
129					33	5			38
131					1	36			37
133						38			38
136						34			34
139						30	4		34
140 (two strains)							73		73
143							32		32
147							39		39
Total	167	86	78	37	100	150	150		768

experiments with the dioecious *Poa arachnifera* and the sexual Australian species *P. caespitosa.* It is of particular interest that successful crossings have been made between *arachnifera* and diplosporous *nevrosa.* The present author has studied the embryology of *Poa ampla, arida* and *scabrella,* and has found that they are all aposporous (Nygren, 1951 and unpublished), as is *compressa* (cf. Gustafsson, 1946–47). From Table VIII it is clear that hybrids in most combinations have arisen by fertilization of either an unreduced or a reduced female gamete. This is very striking in the first *ampla-pratensis* combination Albion-Mather, but also occurs in some of the crosses with *scabrella.*

In 1952 Löve gave a survey of chromosome numbers in Ice-
landic *Poa irrigata* and its offspring. *Irrigata* is a close relative of
Poa pratensis. On the whole the chromosome numbers of these
progenies agree very well with those obtained in the interspecific
crosses at Stanford (Table IX).

Grun and Triplett have listed some important characters in *Poa
ampla*, *P. pratensis* and their hybrids produced by fertilization of
an unreduced or a reduced *ampla* egg cell. Table X shows the
morphological differences in the parents and the two kinds of hy-
brids.

Table V shows clearly that the morphology in the two types of
hybrids formed is quite different, but also proves that transgres-

TABLE X

MORPHOLOGY OF FOUR *Poa ampla × pratensis* HYBRIDS AS RELATED TO THE
TYPE OF EGG FERTILIZED (GRUN AND TRIPLETT, 1953: 121)

Species or hybrid	2n	Glaucous-ness grade (1-9)	Leaf stiffness grade (1-9)	Leaf width mm.	Leaf form
P₁ *Poa ampla* Albion	64	9	7	5	Flat
P₂ *Poa pratensis* Mather	68	1	2	3	Folded
F₁					
4535-4 from reduced egg	63	2	2	3	Folded
4535-52 from reduced egg	70	2	2	3	Folded
4535-6 from unreduced egg	96	9	8	5	Flat
4535-6 from unreduced egg	ca. 96	9	8	4	Flat

sions may occur, which is of particular interest in species with
agamospermous reproduction.

Clausen and co-workers worked out a special system of testing
later generations from the interspecific *Poa* hybrids obtained by
crossings. Thus uniform families are classified as apomicts and
segregating ones as sexuals. Many families are intermediate be-
tween the two groups, however, which means that some descend-
ants deviate morphologically from the parental F_1 or F_2 plant,
while others obviously are maternals. In such cases the degree of
apomixis can be expressed in per cent. Offspring plants deviating
from the mother are classified as aberrants. Apomictic offspring
have been obtained from maternal as well as from aberrant mother
plants, which is clear from Table XI.

TABLE XI

NUMBER OF PROGENIES OF INTERSPECIFIC HYBRIDS OF *Poa*.
(CLAUSEN ET AL., 1949: 101)

Hybrid combinations	F₂ progenies		F₃ progenies				Totals
			From aberrants in apomictic F₂'s		From sexual F₂'s		
	Apomictic	Sexual	Apomictic	Sexual	Apomictic	Sexual	
ampla × *pratensis*	20	15	7	2	6	7	57
× *compressa*	1	5	..	..	4	4	14
× *arida*	1	1	..	..	..	..	2
Canbyi × *pratensis*	..	1	..	..	..	3	4
scabrella × *pratensis*	14	25	..	2	20	23	84
× *compressa*	..	1	..	..	..	..	1
× *arida*	2	1	..	..	..	..	3
× *ampla*	2	2	..	..	..	..	4
× *gracillima*	3	3	..	..	..	..	6
Totals	43	54	7	4	30	37	175
	97		11		67		

The complexity in the segregation of apomixis in *Poa* in reality is much greater than is shown by Table XI; in fact, practically every aposporous plant in the genus is able to produce aberrants in its offspring. Most aberrants are weaker than the maternal descendants and may have difficulty in nature competing with other plants. Some aberrants are more vigorous than the mother plants, however, and therefore it is quite obvious that evolution in some apomictic *Poa* species gains by introgressive hybridization (cf. Anderson, 1947-51). In apomictic species this picking up of genes from other species must be of particular importance because many of the derivatives from such interspecific crosses will reproduce more or less apomictically in later generations at the same time that their capacity to produce aberrant offspring to a certain extent gives them a flexibility that is almost as great as that of a sexual species. On the other hand, the successful combinations are able to reproduce themselves agamospermically, which is of particular importance in local races in their struggle for life. From the work at the Carnegie Institution we have learnt that the studied aposporous *Poa* species are able to cross with other sexual or apomictic species. Hybrids may be formed by fusion of reduced as well as

unreduced gametes, and these hybrids will give rise to F_2's which segregate apomictic as well as sexual offspring. This segregation of sexual and apomictic strains will later on continue for every generation. In *Poa pratensis* synthetic products have been produced which are " almost indistinguishable from natural *pratensis,* but nevertheless may inherit certain physiological or reactional characteristics from the other species " (l.c., 1951: 110). Clausen et al. continue: " If such hybrid strains had been discovered in the wild and their pedigrees had been unknown, no morphological characters would have been available to identify them as hybrids ".

Hansson, Garber and Myers in 1952 showed that some combinations of four strains of *Poa pratensis* gave better yield than each of the strains cultivated separately, a result that is of great practical importance. That future breeding work in *Poa pratensis* will gain from the Carnegie results is quite obvious (Nygren, 1953).

The experimental data obtained at Stanford conform extremely well to the situation in nature as it has been studied in *Poa arctica* and *pratensis alpigena* in northern Scandinavia by the present writer (Nygren, 1950). In the very polymorphous northern European *P. arctica* five subspecies have been described by Nannfeldt (1940). These subspecies occur together with a multitude of forms which can not be separated from the main population. There are also transgressional forms between *arctica* and *pratensis alpigena,* and the two species upon the whole form one vast population in Scandinavia, split into a great number of local races, the characteristics of which are not distinct enough to permit the describing of microspecies to such an extent as has been made in the genus *Taraxacum.* Both *Poa arctica* and *pratensis alpigena* are pseudogamous; castration causes seed sterility (Engelbert, 1940, 1941). Since pollination followed by fertilization of the central nucleus is necessary for successful development of seeds, it can easily be understood that even the egg cell may now and then be fertilized at the same time as the central nucleus, and that therefore hybrids are formed in natural populations between *arctica* and *pratensis* as well as between these species and other *Poa* species in the area.

SACCHARUM. In the genus *Saccharum* eight as well as ten are basic chromosome numbers. *Saccharum spontaneum* belongs to the eight-series; *S. officinarum* to the ten-series as do the related species *S. ciliare* $(2n = 40)$, *S. Narenga* $(2n = 30)$ and *Imperata*

arundinacea ($2n = 20$) (Bremer, 1924; Moriya, 1950). *S. officinarum* has $2n = 80$, while in *S. spontaneum* the numbers vary between $2n = 48$ and $2n = 112$ (Moriya, l.c.). Bremer (1934) has studied 13 clones of *officinarum* from Burma, Celebes, Ceylon, Hawaii and the West Indies, and found all to have $2n = 80$.

Already in 1922 Bremer found a hybrid between *S. officinarum* and *spontaneum* with $2n = 136$, and suggested this hybrid to have been formed by the fusion of a reduced gamete with 56 chromosomes from *spontaneum* and an unreduced one with 80 chromosomes from *officinarum*. Hybrids from the Philippines could be proven to have $2n = 120$ ($2 \times 40 + 40$) at the same time as the chromosome number of the Indian strain Coimbatore 205 from Madras was $2n = 112$ ($2 \times 40 + 32$) (Bremer, 1934, 1946). In most combinations in which *officinarum* occurred as mother, unreduced gametes had functioned, and Bremer also could prove that these unreduced gametes came from *officinarum* (1946). Strains of hybrid origin were also studied by Bremer; as an example, the clone 2875 POJ with $2n = 110$ may be mentioned, which, by crossings with a " glagah " strain (= *S. spontaneum*, $2n = 112$) in the offspring, gave numerous hybrids with $2n = 166$ (i.e. $110 + 56$). By contrast a cross was reported between the Indian var. *Saretha* —not belonging to *officinarum*—and *spontaneum* which gave hybrids, in the formation of which only reduced gametes had functioned. The parents had $2n = 92$ and $2n = 64$, respectively, and the hybrids $2n = 76$–78. Embryological studies in *officinarum* have been made by a number of research workers who have reported partially diverse results. Naryanaswami finds (1940) that the species forms a macrospore tetrad, the two lowest macrospores of which fuse and form a " diploid " cell that gives rise to the ES. The egg cell in this sac is able to divide autonomously; it may also be fertilized, however, to form a triploid embryo. Raghavan (1951: 204) confirms the observations made by Naryanaswami, but adds that this development occurs in *spontaneus* as well, even though it is more common in *S. officinarum*. Bremer has observed (1946) that all chromosomes of the chalazal macrospore divide endomitotically, thus doubling the chromosome number of the cell which gives rise to the ES. Subramaniam finally (1946) worked with a pollen-sterile strain, Co.421 ($2n = 118$), which gave two kinds of offspring, descendants with $2n = 118$ and $2n = 86$. An

embryological investigation revealed that the meiosis in the EMC was irregular in that two groups of chromosomes of different sizes were formed in the cell. Thus the 59 bivalents were often arranged in two groups with 43 and 16 bivalents, respectively. The egg cell in the completed ES has a chromosome number lower than 2n, but it divides very early, and, because there is no cell wall formed after this division, the chromosome number is automatically doubled.

In spite of the fact that *Saccharum* has many economically very important forms, our knowledge of its embryology and type formation is still deficient and more studies as well as experiments must be worked out in the genus.

SORGHUM. Garber (1950) has given a cytotaxonomic survey of *Sorghum*, from which it is clear that the variation in chromosome number in the genus runs from 2n = 10 to 2n =60. This very careful study does not give any embryological data, however. On the other hand, Duara and Stebbins in 1952 reported that a hybrid had been produced between an autotetraploid strain of *Sorghus vulgare* var. *sudanense* (2n = 40), made by Dr. Randolph at Cornell, and the tetraploid *S. halepense* with this latter species as mother. The offspring of this hybrid was cultivated for five generations at Berkeley. One F_5 plant (cult. 801) produced only diploid offspring at the same time that another F_5 offspring gave tetraploid descendants. As a control progenies were raised from the F_3–F_6 generations. No diploids were obtained, however. The F_5 plant which gave diploid offspring no doubt produced the descendants by haploid parthenogenesis.

ZEA. In 1952 Chase demonstrated that haploid parthenogenesis occurred in some maize crosses to a certain per cent. Six crosses were worked out from four monoploid-derived autodiploids as well as several double crosses combining the singles. The original strain, Stiff Stalk Synthetic dent corn, yielded haploids at a rate of 1.3 pro mille. Of these haploids 9.4 per cent set seed. The single crosses gave 4.3 pro mille haploids, 33 per cent of which set seed. The double cross group, on the other hand, gave rise to 2.9 pro mille haploids, 30.5% of which were self-fertile. Chase is of the opinion that monoploids will be of importance in maize breeding because of the possibility of raising autodiploid homozygous strains from them.

JUGLANDACEAE

JUGLANS. Zarubin (1949) suggests parthenogenetic development of fruit in proterogynous individuals of walnut. Proterandrous biotypes are self-sterile.

LILIACEAE

ALLIUM. Håkansson (1951) has studied a strain of *Allium nutans* with $2n = 40$–42. In the progeny of this strain descendants with $2n = 60$ and $2n = 80$, respectively, were obtained together with offspring plants having $2n = 40$. The observation was made that in this particular strain the EMC very often had a higher chromosome number than the surrounding somatic tissue. Tetraploid EMC's were more common than diploid ones, and even octoploid EMC's sometimes occurred. Håkansson is of the opinion that these cells increased their chromosome number by endomitosis. In some cases also hexaploid EMC's were found, which might have originated by disturbances in the premeiotic divisions (cf. Manton, 1950). Most egg cells divided autonomously very early and formed multicellular embryos. On the contrary, even two-weeks-old ES's were stated to contain undivided egg cells. After castration an endosperm was only exceptionally formed, but it was proven that even seeds without endosperm were able to germinate. Håkansson finds it possible that adventitious embryos occur in *A. nutans*; they seem to be very rare, however. In old ES's antipodial embryos were observed in some cases, which means that now and then both ends of the ES produce an egg apparatus (l.c.: 162, fig. 4e). Two strains of the species *Allium odorum* were also studied by Håkansson, both having $2n = 32$. In one of these strains up to 50% of the egg cells were formed by the antipodals. In a low frequency also embryos formed from the synergids as well as adventitious embryos were observed in the material studied by Håkansson.

DIANELLA. Apomixis has been proved in *D. tasmanica* (Curtis, 1952). Different chromosome races occur in the species, and $2n = 76$, 80 and 84 have been determined in Tasmanian races, while the race with apomixis is diploid with $2n = 16$ and has been found so far only on the Australian continent. *D. coerulea* ($2n = 16$, 32 and 48) is suspected to have apomictic forms.

NOTHOSCORDUM. Several authors (Strassburger, 1878, 1879; Stenar, 1932; Levan and Emsweller, 1938) have reported adventitious embryony in *Nothoscordum fragans*. Håkansson reinvestigated this species (1953) and found that it forms haploid ES's, the egg cell and polar nuclei of which are regularly fertilized. Adventitious embryos are formed at an early stage of development of the ES; the mature ES's have as a rule only one or two embryos, however, because most adventitious embryos are interrupted in their development. Neither the egg cell nor the polar nuclei divide in emasculated flowers. D'Amato (1949a) has found $2n = 19$ in 38 plants of a population at the Pisa Botanic Garden. Fertilization was proved necessary for the development of adventitious embryos and fruit set.

TRILLIUM. Jeffrey (1948) reports that most *Trillium* and *Tradescantia* species are parthenogenetic. Meiosis in the EMC of these species is normal, but diploid embryos originate by the influence of hormones from pollen on the style. The pollen tubes later degenerate. The diploidy of the embryo is caused by " double division of the chromosomes in the metaphase " (= endoploidy).

MUSACEAE

MUSA. Dodds and Simmonds (1948) have studied a stabilized diploid " type 20 " which they suggest originated by parthenogenesis from the hybrid *Musa Balbisiana* × *M. acuminata*. They do not explain this possible origin, however.

ORCHIDACEAE

In 1947 Hagerup proved haploid parthenogenesis to occur in a low percentage of the ES's in *Listera ovata, Platanthera chlorantha, Orchis strictifolia, Cephalanthera longifolia* and *Cephalanthera damasonium*. In some of these orchids even polyploid embryos were formed; in *Orchis maculata* the embryos had chromosome numbers varying between n and $6n$ (Hagerup, 1944). In *Epipactis* aneuploid chromosome numbers occur in the embryos, which cause new basic numbers in the genus. In *Epipactis* the basic numbers $n = 12, 16, 18, 19$ and 20 have been found up to now (Hagerup, 1947; Young, 1953). According to the present author orchids are able to produce embryos without fertilization more easily than most other plants because no endosperm is formed in

this family, which makes double fertilization unnecessary. Because of this, biotypes having an inherent capacity to produce embryos autonomously are able to form seeds without the obstacle that the need for fertilization of the central nucleus generally means in sexual and pseudogamous species.

PLUMBAGINACEAE

LIMONIUM. In 1954 Baker claimed that by repeated emasculation, apomixis could be induced in a number of species in this genus. It has been definitely established as occurring in *L. binervosum* and *L. lychnidifolium*.

STATICE. In 1940 D'Amato suggested that apomixis takes place in *Statice oleaefolia* var. *confusa,* but not until 1949 were data given. The variety in question has the chromosome number $2n = 27$, but in spite of the triploid number it shows unusually regular meiosis during pollen formation; only single univalents are formed in the first metaphase. The EMC generally develops diplosporously; sometimes it goes through a regular meiosis, however. Formation of restitution nuclei has been recorded in 80% of the ES's investigated, while in the remaining 20% of the ES's meiosis runs normal and gives rise to reduced sacs of the *Adoxa type.* Further development of the cells with restitution nuclei follows the same general scheme as in *Ixeris dentata.* D'Amato finds that the development of the EMC and ES in *Statice* shows similarities with the " *Erigeron* II type " of Battaglia (1946) as well as with *Erigeron Karwinskianus* var. *mucronatus* studied by Fagerlind (1947).

POLYGONACEAE

ACETOSA. In 1942 Löve reported facultative agospermy in the *Acetosa arifolia, pratensis* and *thyrsiflora.* The highest frequency was in *arifolia* from Iceland and northern Sweden (2.3% in 53% of all plants studied), while *thyrsiflora* had the lowest frequency (0.3% in 21% of the investigated plants). In 1949 Löve related a more obvious case in *arifolia* from the neighbourhood of Reykjavik in Iceland. One plant was found to have complete seed setting on three bagged branches as well as on the branches outside the bag. The karyotype of this particular plant $(2n = 14)$ was 10 i + 2 i* + 2 X. All offspring plants raised from seeds of the bagged

branches had $2n = 14$ and belonged to the same karyotype as the mother plant. No embryological investigations have been made as yet, however.

PRIMULACEAE

PRIMULA. In four lengthy papers published in the years 1949–51 Ernst has discovered the origin of so called " maternal hybrids " in the genus *Primula*. By this term Ernst refers to maternal off-spring produced by certain species of *Primula* after interspecific pollination. The progeny plants are reported to have the same morphology and somatic chromosome number as the mother species (1949: 95). Maternal hybrids are supposed to be formed by " automixis " (1951: 285), which term refers to a pseudogamous development of the egg cell combined with autonomous doubling of the chromosome number by endomitosis (1949–51). Ernst suggests that this organization would be a kind of protection against too strong heterosis. Twenty-one maternal hybrids have been reported between *Primula Wilsoni* and *P. Cockburnia;* while *P. japonica,* crossed with *P. Cockburnia, chungensis* and *pulverulenta,* has produced 48 (1950, 1951*a*). In his second paper of 1951 Ernst discussed all the material obtained and pointed out that maternal hybrids have been obtained only in some specific combinations. He also reported that the descendants have the same appearance and chromosome number as the mother plants, and that the fertility, vitality and non-segregation of their offspring exactly match those of the mother. The number of " hybrids " formed is very low, however, only a few per thousand in each combination. Ernst takes up the " faux hybrides " in *Fragaria* (1951*b*: 277) and finds that in this genus together with, or instead of, real species hybrids, maternal or maternal and paternal descendants are formed. The cytology of these progeny plants in *Fragaria* has not been satisfactorily studied, however. The results obtained in Ernst's comprehensive work during 20 years studies in *Primula* should be taken into consideration, but students of this phenomenon must be careful not to confuse maternal hybrids with pseudofertility (cf. Fagerlind, 1937; Clausen, Keck and Hiesey, 1945; Nygren, 1946).

RANUNCULACEAE

RANUNCULUS. After apomixis had been demonstrated in *Ranunculus auricomus* by Rozanova (1932) and W. Koch (1933),

Häflinger in 1943 gave the first cytological data of the phenomenon in this genus. Häflinger investigated one diploid $(2n = 16)$, ten tetraploid $(2n = 32)$, one pentaploid $(2n = 40)$ and one hexaploid $(2n = 48)$ species native to Switzerland (l.c.: 347). By his experimental studies of the group he became convinced that all species investigated by him were pseudogamous. On the other hand, he determined the chromosome number of one single endosperm cell in tetraploid *R. auricomus* and found that this cell had 64 chromosomes. This means that the cell in question was octoploid, not decaploid as it ought to have been if the central nucleus had been fertilized by a sperm nucleus with 16 chromosomes. In all

TABLE XII

CHROMOSOME NUMBER IN ENDOSPERM OF SEXUAL PLANTS
IN THE *Ranunculus auricomus* GROUP

| Seedplant | $2n$ | Pollenplant | $2n$ | Chromosome number of endosperm | | | | Sum |
				24	32	40	40	
R. cassubici-		*R. cassubici-*						
folius 2/3	16	*folius* 2/3	16	4				4
"	16	*R. puberulus*	32		2			2
"	16	*R. argoviensis*	32		1			1
R. cassubici-		*R. cassubici-*						
folius 11	16	*folius* 11	16	7				7
"	16	*R. puberulus*	32		5			5
"	16	*R. argoviensis*	32		2			2

other pseudogamous genera studied, fertilization of the central nucleus is necessary if any seeds are to develop at all, and therefore it is important to be sure of the situation in *R. auricomus*. In 1950 Rutishauser and Hunziker found an excellent method of preparing smear preparations of endosperm cells. Using this technique, Rutishauser (unpublished data) has made a series of determinations of chromosome number in the endosperm of different microspecies of the *auricomus* complex. All microspecies in this investigation are tetraploids with $2n = 32$, except *R. cassibicifolius* which is a diploid with $2n = 16$. Rutishauser's data are condensed in the Tables XII–XV.

It is clear from Table XII that the two diploid *R. cassubicifolius*

races studied behave just as normal sexual species, forming triploid endosperm after selfing and tetraploid endosperm after being crossed to tetraploid pollen parents.

It is obvious from the data in Table XII that the great majority of the counted endosperm cells have precisely those chromosome numbers which would be expected in pseudogamous species. The central nucleus of an unreduced ES of *R. auricomus* with $2n = 32$ will have 64 chromosomes before fertilization, 96 after fertilization with an unreduced male gamete, and 80 after fertilization with a reduced gamete. Not less than 148 of the 163 cells in Table XIII

TABLE XIII

CHROMOSOME NUMBER OF THE ENDOSPERM IN DIFFERENT APOMICTIC
auricomus MICROSPECIES AFTER SELF-POLLINATION. ALL MICRO-
SPECIES LISTED ARE TETRAPLOID $(2n = 32)$

Species	2n	Chromosome number of endosperm							Sum
		32	48	64	80	96	112	128	
R. argoviensis	32		2	1	9	5			17
R. auricomus s. str.	32					6			6
R. cassubicifolius	32				4	11			15
R. cassubicus	32				3	5			8
R. distentus	32		3	1	2	11		1	18
R. fragifer	32					7			7
R. gracillimus	32				2	6			8
R. grossidens	32		2		10	3		1	16
R. laeteviridis	32				2	1	1		4
R. pseudocassubicus	32			1	2	4			7
R. puberulus	32	2			3	52			57
		2	7	3	37	111	1	2	163

$(= 90.8\%)$ belong to this group. The remaining 15 cases can be interpreted in the following way:

  a) In 2 cases the endosperm has been developed in reduced ES's without fertilization.
  b) In 7 cases the endosperm has been developed in reduced ES's with fertilization of reduced gametes.
  c) In 3 cases the endosperm has been developed in reduced ES's with fertilization of unreduced gametes.
  d) In 1 case the endosperm has been developed in an unreduced ES after fertilization by one reduced and one unreduced gamete.

e) In 2 cases the endosperm has been developed in unreduced ES's after fertilization by two unreduced gametes.

The two numbers 112 and 128 can be interpreted in several ways. The number 128 is obtained if an endosperm cell with 64 chromosomes is doubled just as well as if a male gamete with the double somatic number fertilizes the central nucleus in an unreduced ES. It is interesting that Rutishauser in three cases has obtained the number 64, i.e., the same as was counted by Häflinger. In the opinion of the present author, interpretation *c* above is the most probable, even in Häflinger's case. In two ES's out of 163, Rutis-

TABLE XIV

CHROMOSOME NUMBER OF THE ENDOSPERM IN DIFFERENT *auricomus*
MICROSPECIES AFTER CROSS-POLLINATION. ALL MICROSPECIES
LISTED ARE TETRAPLOID (2n = 32)

Seedplant	2n	Pollenplant	2n	Chromosome number of endosperm							Sum
				32	48	64	80	96	112	128	
R. argoviensis	32	cassubicifolius[1]	32				2				2
R. cassubicus	32	argoviensis	32				1	5			6
"	32	puberulus	32					4		1	5
R. distentus	32	argoviensis	32				1				1
"	32	puberulus	32				1				1
R. fragifer	32	argoviensis	32					1			1
"	32	puberulus	32					18			18
R. laeteviridis	32	argoviensis	32					3			3
"	32	puberulus	32					13			13
R. puberulus	32	argoviensis	32					6			6
"	32	cassubicifolius[1]	32				1	9			10
"	32	grossidens	32				1	8			9
							7	67		1	75

hauser counted 32 chromosomes, however, which means that the central nucleus was not fertilized. Such cases are known also in other genera (*Poa arctica*, Nygren, 1950), but they seem to be very rare. It is rather remarkable that in Table XIV only one ES is reported having a chromosome number other than as expected, while after self-fertilization close to ten per cent showed deviating numbers.

The chromosome number to be expected here in an unreduced ES is 72, which has been found in only one case, while the number 80, which indicates fertilization of an unreduced ES by an un-

reduced male gamete, is the most common. A reduced tetraploid ES has been fertilized by a reduced male gamete in two and by an unreduced gamete in one reported case.

Rutishauser's investigation of the chromosome numbers in the endosperm of *Ranunculus auricomus* no doubt is the most comprehensive and careful investigation which has been made in a pseudogamous genus. The results obtained show very clearly that the central nucleus in *auricomus* generally is fertilized, but that in two cases out of 269 (= 0.74%) endosperm cells developed without fertilization.

In 1952 Marsden-Jones and Turrill supposed apomixis to exist in some forms of *Ranunculus acris* and *bulbosus* (l.c.: 30). Ad-

TABLE XV

CHROMOSOME NUMBER OF THE ENDOSPERM IN DIFFERENT *auricomus*
MICROSPECIES AFTER CROSSES BETWEEN TETRAPLOID
($2n = 32$) AND DIPLOID ($2n = 16$) SPECIES

Seedplant	$2n$	Pollenplant	$2n$	Chromosome number of endosperm					Sum
				40	48	64	72	80	
R. argoviensis	32	*R. cassubicifolius*	16		1			17	18
R. puberulus	32	*R. cassubicifolius*	16	2			1	10	13
				2	1		1	27	31

ditional cytological and, above all, embryological data must be collected, however, before the supposition of these authors can be adequately tested.

ROSACEAE

MALUS. Gustafsson (1946–47) states that apospory is reported in triploid *Malus hupehensis* ($2n = 51$). Oldén (1953) has studied two tetraploid trees of *Malus Sieboldii* ($2n = 68$), and he finds that sexual as well as apomictic seed formation takes place in this species. Oldén has crossed *M. Sieboldii* as the pistillate parent with diploid apples, and obtained tetraploid offspring of very uniform appearance. Pollination was necessary for seed formation, but no fertilization took place and therefore the species is pseudogamous.

POTENTILLA. In 1946 Rutishauser published a study of the three species *P. argentea, canescens* and *verna.* The first two are aposporous, while *verna* is diplosporous. Rutishauser supposes that diplospory and probably even apospory in *Potentilla* are controlled by special genetic factors. In 1947 he found *P. canescens* to form three kinds of offspring after crossing: maternals; B_{II}-plants originating from reduced egg cells; and B_{III}-plants from unreduced fertilized egg cells. Real hybrids occur of the B_{II}-type as well as of the B_{III}-type. As a result of data collected from crossing and back-crossing work in *Potentilla,* Rutishauser suggests that diplospory is caused by one recessive gene, g, and apospory by another recessive gene, s. If two parental plants with the constitutions ssGG and SSgg, respectively, are crossed, F_1 hybrid with the formula SsGg will be sexual. By back crossing this F_1 to the SSgg type, four genotypes will appear in the next generation: SSGg, SSgg, SsGg and Ssgg. SSgg and Ssgg will both be diplosporous. A plant with the constitution SSsGgg will be diplosporous because gg dominates over G. In 1949 Rutishauser gave the data from his comprehensive crossing work in five *Potentilla* species. They are: *P. canescens* (one race), *argentea* (one race), *praecox* (one race), *verna* (five races), and *heptaphylla* (one race). *P. heptaphylla* is diploid ($2n = 14$), all other species are hexaploid ($2n = 42$). In the crossings two races of *P. arenaria* were used; 25 with $2n = 35$, 25 with $2n = 42$. The diploid *heptaphylla* is sexual, all other species are apomictic and pseudogamous. The ratio between the number of unreduced and reduced egg cells is called the degree of apomixis (of apospory according to Rutishauser's terminology). This degree is 99.32% in *P. canescens* (p. 280). In crossings with the species *argentea, canescens, praecox* and *verna* this particular *canescens* type gave only one B_{II} hybrid in 147 descendants. Furthermore there was one B_{III} hybrid formed with the chromosome number $2n = 63$. *P. argentea* is 100% aposporous, but in nine combinations with *P. canescens, praecox* and *verna* it gave rise to six B_{III} hybrids out of 344 offspring plants (p. 281). *P. praecox* is an obligate, aposporous species, which in eight combinations has produced only one B_{III} hybrid in 119 descendants. *P. verna* 4 is also totally aposporous, but in 11.8% of the cases studied the egg cell has been fertilized. In 223 progeny plants from 11 combinations there were 25 B_{III} hybrids formed. The *P. verna*

races 2, 10, 15 and 18 are obligately aposporous. *Verna* 18 is the only race that in its progeny has yielded one B_{III} hybrid (p. 284). While *P. heptaphylla* in crossings with other biotypes of its own species as well as in crosses with *arenaria* has produced two B_{II} hybrids only, *P. arenaria* 25 has formed one B_{II} and seven maternals; *arenaria* 29, on the other hand, yielded three maternals only. Rutishauser points out that the *Potentilla* types which have their origin in northern Switzerland as an average include a higher proportion of partially sexual species and races than do types of other areas. Embryological investigations have shown that the races 3, 4, 10 and 18 of *P. verna* are diplosporous, while *P. argentea, canescens, praecox* and *verna* 15 are aposporous. The egg cell in an aposporous ES develops without fertilization but degenerates if the endosperm is not completed. Different races vary considerably in this respect, however; *P. verna* 10 produces embryos in more than 80% of all ES's studied, while *P. verna* 18 in 49 nucelli formed only a single two-celled embryo during two years experiments. The quality of morphologically good pollen varies considerably in some races of *P. verna*. In *verna* 18 the figures in the same season were 0, 2, 5, 6 and 40.5%. Rutishauser is of the opinion, however, that this pollen sterility does not influence seed setting, even after crossing (p. 297). The hybrid *P. canescens* × *argentea* 44/94, 21 with $2n = 63$, is aposporous but has yielded two descendants in a back-cross to *argentea*, which have the chromosome numbers $2n = 48$ and $2n = 49$, respectively. In these cases sexual ES's must have functioned (p. 300). *P. canescens* × *verna* 3 (28/26, 9) is highly sterile but has produced 7.1% seeds after back-crossing to *verna* 3, in spite of this sterility, and 18.4% seeds after back-crossing with *verna* 10 (p. 304). After the back-cross to *verna* 10 nine B_{II} hybrids were formed, which were all sexuals having the chromosome numbers $2n = 39$, $2n = 40$ and $2n = 43$. One B_{III} hybrid was produced with 63 to 65 somatic chromosomes. *Potentilla argentea* has formed one hybrid with *P. canescens*, three with *verna* 10, and two with *verna* 15. All these hybrids have $2n = 63$ except the plant 43/79, 13 (a hybrid with *verna* 10), which has $2n = 64$. The best pollen fertility in Rutishauser's experimental *Potentilla* material, 74.8%, was in the hybrid *P. argentea* × *canescens*, while, on the other hand, there is a variation between 30.7 and 55.6% in the combination *P. argentea* × *verna*. In the

progeny of *P. argentea* × *verna* (combination 42/68, 52), 15 maternals and 15 B_{II} hybrids were raised, while, on the contrary, all back crosses with *argentea* gave maternals only in their offspring. The maternals have the chromosome number $2n = 63$, while the B_{II} hybrids, which were produced in a back-cross to *verna* 10 ($2n = 42$), had $2n = 53$. These numbers indicate that the B_{II}'s mentioned originated by fusion of two gametes with 21 and 30–32 chromosomes, respectively. One plant was morphologically very similar to *argentea*. This particular descendant, 45/111, 24, had the chromosome number $2n = 30$ and obviously was formed by haploid parthenogenesis. The hybrid 42/68, 52 in the combination *argentea* × *verna* is aposporous but has the ability to undergo meiosis and to form tetrads in the EMC. The author mentions that this plant has a tendency towards diplosporous development of EMC's, a circumstance which ought to be investigated very carefully, as this tendency has great general importance (cf. Bergman, 1951). The *argentea* × *verna* hybrid in question gives, however, a lower number of autonomously developed embryos than both parents (p. 322). The hybrid 37/14, 13 between *P. praecox* and *argentea* has the chromosome number $2n = 64$ ($42 + 22$) and has just as good fertility as the parents. By back-crossing this hybrid, only one descendent was produced, a maternal with $2n = 64$. The combination *P. arenaria* 25 × *verna* 10 mainly gave sexual hybrids which, however, showed aposporous tendencies. Hybrids within the form circle of *verna* have given rise to 25 plants with $2n = 63–64$ (*verna* 4 × *verna* 10: 24 descendants; *verna* 4 × *verna* 18: one plant). All progeny plants in the combination *verna* 4 × *verna* 10 were morphologically different, which means that the staminate plant was heterozygous, since the mother plant forms diploid ES's only. All descendants in this combination were diplosporous. The hybrid produced by back-crossing *canescens* × *argentea* to *argentea*, plant 45/119, 16, has $2n = 48$ and thus constitutes a B_{II} hybrid. In spite of this it is aposporous. *P. canescens* × *verna* 3 back-crossed to *verna* 3 gave rise to eight progeny plants (42/64, 1–6, 8, 10, 11), the offspring of which have been investigated after pollination with *P. verna*. The descendants 42/64, 2 ($2n = 39–40$), 5, and 11 ($2n = 40$) have yielded sexual offspring exclusively, mainly B_{II} hybrids, while 42/64, 8 as well as 10 have produced maternal progeny only. The plant 42/64, 6 has

given maternals as well as B_{II} and B_{III} hybrids. The offspring of the sexual plant 42/64, 5 shows a variation in chromosome numbers between $2n = 39$ and $2n = 43$. The plant 42/64, 10 as well as 42/66, 1 (*canescens* × *verna* 3 back-crossed to *verna* 3) are both diplosporous. A second back-cross has also been made, (*canescens* × *verna* × *verna*) × *verna*, 44/91. The yield was 30 progenies, six of which have been studied. Three descendants were sexual, while the other three were partially or obligately diplosporous. The segregation ratio thus is 1:1.

Rutishauser's *Potentilla* studies can be summarized as follows:

a) B_{II} hybrids between aposporous and diplosporous parents will form sexuals with a weak tendency towards apomixis.

b) B_{III} hybrids produced by parents belonging to the same type of apomixis are pseudogamous and show a strong tendency toward apomixis of the same type as the parents.

c) B_{III} hybrids between aposporous and diplosporous parents are aposporous with a weakened degree of apospory.

d) The back-cross generation (*P. canescens* × *verna* 3) × *verna* 10 segregates in the following ratio: three sexuals: two partially diplosporous apomicts: one obligately diplosporous and pseudogamous apomict.

e) One B_{II} hybrid (*canescens* × *argentea* × *argentea* has been found to be aposporous like the parents. Rutishauser supposes that different genetic systems are responsible for the development of apospory and diplospory (1947, and l.c.: 392), and he suggests that the genes for diplospory are transferred to the back-cross hybrid by the pollen. In the first back-cross generation there will be segregation into three sexual hybrids to four partially or obligately apomictic hybrids. In the second back-cross generation the segregation would be: three sexuals to three partially or obligately apomictic hybrids. Some B_{III} hybrids are diplosporous because two recessive genes outweigh one dominant (cf. 1947). In some first back-cross combinations Rutishauser obtained the ration 1:1 which will be the result if a cross between the two genotypes SsGg and SSgg is worked out (p. 398). In spite of the fact that the apomictic and the pseudogamous mechanisms constitute obstacles to variation, the number of forms in the genus *Potentilla* is permanently increased by the origin of new B_{III} hybrids. In the experiments such B_{III} plants with chromosome numbers up to $2n = 84$ have been obtained (p. 415).

f) It has been suggested that the pseudogamous system in *Potentilla* has arisen by several mutation steps. In 1949 Rutishauser investigated the time factor in the development of the embryos. In *P. verna* 4 four days are needed after pollination with *verna* 10, and 18 to develop an embryo. When the central nucleus is fertilized, differentiation into an embryo and a suspensor follows. This differentiation does not take place if the central nucleus is not fertilized. The frequency of B_{III} hybrids in *verna* 4 varies considerably after pollination with other races of the same species. Thus *verna* 4 × *verna* 10 gives 27% B_{III} plants, while *verna* 4 × *verna* 15 produces 1.9% B_{III} hybrids, and *verna* 4 × *verna* 18 only 1.85% B_{III} hybrids. The difference between *verna* 4 × *verna* 10 and *verna* 4 × *verna* 18 is highly significant and gives a χ^2 of 9.375. As a comparison Rutishauser uses the figures obtained in combinations of *argentea* × *verna*, i.e., 1.6%, and of *argentea* × *verna* 15, i.e., 2.2%, which combinations have given about the same values.

RUBUS. The apomictic system in the genus *Rubus* of the old world is well known through the classical studies of Lidforss and the extensive investigations of Gustafsson (1943, 1946–47). The blackberries of the new world were little known, however, until 1947, when Einset found that the chromosome numbers of a great many North American species run from $2n = 14$ to $2n = 63$. In 1951 he gave his experimental data which show the same conditions in North American Rubi as in the European species. Einset has examined the chromosome numbers of 1,620 seedlings from different crosses. His studies are best illustrated by three tables (XVI–XVIII) of the combinations made and the chromosome numbers obtained. The high numbers of haploids in Table XVII are of particular interest. As is also pointed out by Einset (p. 769), these plants obviously have arisen through haploid parthenogenesis.

It is clear from Einset's study that 90.78% of the 1541 descendants reported in Tables XVI–XVIII have the same chromosome numbers as the maternal clones. We also find that *R. flagellaris*, which is the only species investigated with $2n = 63$, has given 100% maternals, while the species with $2n = 28$ show the lowest figure, 86.9% maternals. The other chromosome races have given the following values: species with $2n = 21$, 93%; species with $2n = 35$, 87.5%; species with $2n = 49$, 94.9%. Einset points out that all species investigated are pseudogamous. Waldo and Darrow

TABLE XVI

CHROMOSOME NUMBERS OF SEEDLINGS OF 21-CHROMOSOME PLANTS (l.c.: 769)

21-chromosome seed parent	Cross	Pollen parent and 2n numbers	Chromosome numbers of seedlings							
			14	21	26	28	30	35	42	49
R. canadensis	×	Self		2						
	×	R. bellobatus (28)		7						
	×	Open-pollinated		41		1		14		
R. Rosa	×	R. bellobatus (28)		5		1		3		
	×	Open-pollinated		23						2
R. bellobatus	×	R. bellobatus (28)		19						
	×	R. Wiegandii (36)		16						
	×	Open-pollinated		217	1			7		
Kittatinny (probably R. bellobatus)	×	R. bellobatus (28)		27		1				
	×	R. Cardianus (35)		10						
	×	R. plicatifolius (63)		40					1	
	×	Open-pollinated	1	29			3	1		
R. localis	×	Open-pollinated		55				4		
R. abactus	×	Open-pollinated		53	1			3		
Hanes 1676 (probably one of Arguti)	×	R. bellobatus (28)		33						
	×	Open-pollinated		8						
Totals			1	585	2	3	3	32	1	2=629

(1948) synthesized the Loganberry by crossing " octoploid native western trailing blackberries " and the tetraploid raspberry " La France ". This is in accordance with Gustafsson's opinion (1946–47: 223) that the Loganberry is a hybrid between R. ursinus $(2n = 56)$ and R. idaeus $(2n = 14)$, formed by a reduced ursinus and an unreduced idaeus gamete. Waldo and Darrow also have synthesized the " Mammothberry " by crossing the octoploid Rubus species used in the Loganberry cross with tetraploid Eldorado.

Christer (1953) studied the embryology of Rubus idaeus $(2n = 14)$ and its hybrid with R. caesius. The ES's of R. idaeus develop sexually, while the hybrid $(2n = 21)$ forms sexual as well as diplosporous ES's. Christer suggests that the tendency to diplospory has been transferred to the hybrid from R. caesius. The gene d for diplospory is only partially recessive to the dominant D for sexuality.

SORBUS. Very recently (1954) Liljefors has published an extensive study of a great number of species and hybrid combinations in this genus.

RUBIACEAE

COFFEA. In 1946 Mendes reported that a tetraploid strain of *Coffea arabica* $(2n = 44)$ had given rise to diploid, hexaploid and octoploid offspring, and in 1947 he communicated that the different so-called *monosperma* forms of *Coffea arabica* are diploids formed by haploid parthenogenesis from normal tetraploid strains. The parthenogenetically produced haploids, " di-haploids " according to Mendes (1949), are highly sterile.

TABLE XVII

CHROMOSOME NUMBERS OF SEEDLINGS OF 28-CHROMOSOME PLANTS (l.c.: 770)

28-chromosome seed parent	Cross	Pollen parent and 2n numbers	14	21	28	29	30	32	33	34	35	40	42	49
R. Huttonii	×	Open-pollinated			40								3	
R. allegheniensis (Lowden)	×	Self		2										
	×	R. flagellaris (63)											2	
R. Rosa (Eldorado)	×	Self		1	1									
	×	R. bellobatus (Erie) (28)		2	70	3								
R. Rosa (Snyder)	×	Self			2									
R. Hanesii	×	Open-pollinated			37									
R. bellobatus	×	Self		4	61								5	
	×	R. Wiegandii (36)		1	5									
	×	R. meracus (49)		3	20						1			3
	×	Open-pollinated		4	29									
R. bellobatus (Erie)	×	Self		1	46						1		5	
	×	Kittatinny (21)		2	48						1		5	
	×	R. Cardianus (35)		1	31		1	3	1	1	1			1
R. bellobatus (Brewer)	×	Self	5	2	2						1			
	×	Open-pollinated	1		1									
R. bellobatus (Mersereau)	×	Self		2	1									
	×	Open-pollinated			2									
R. bellobatus (Kittatinny)	×	Self		1	32		1						2	
	×	R. Cardianus (35)			7							1		
	×	Open-pollinated	14		157								2	
			43	3	592	3	2	3	1	1	4	1	24	4 = 681

RUTACEAE

CITRUS. Adventitious or nucellar embryology has been known in the genus *Citrus* for a long time, and it has been proposed by Frost (1926) that formation of the adventitious embryos is dependent on some stimulus from the pollen or from the fertilized egg cell. According to Gustafsson (1946–47: 36), " it seems very probable that *Citrus* seeds do not often form without pollination, although seedless fruits sometimes do so, even in varieties normally seedy ". The degree of polyembryony in *Citrus hystrix* has been studied by Moreira and Gurgel (1947), and they find that the number of supernumerary embryos varies between zero and 34%

TABLE XVIII

CHROMOSOME NUMBERS OF SEEDLINGS OF 35-, 36-, 49- AND 63-CHROMOSOME PLANTS (l.c.: 771)

Seed parent and 2n numbers	Cross	Pollen parent and 2n number	Chromosome number of seedlings							
			28	30	35	36	42	49	50	63
R. noveboracus (35)	×	Open-pollinated	1	4				1	1	
R. abactus (35)	×	Open-pollinated		17						2
R. Cardianus (35)	×	Self		6						
	×	R. bellobatus (28)		8						
R. Wiegandii (36)	×	Open-pollinated			68	1				
R. geophilus (49)	×	Open-pollinated						50		
R. meracus (49)	×	Open-pollinated						6		3
R. flagellaris (63)	×	Open-pollinated								63
			1	35	68	1		57	1	68 = 231

in this species. On the other hand, 53.1% polyembryony was detected in the hybrid between *C. reticulata* and a species of the East Asiatic genus *Fortunella*. Some seeds in this combination had seven embryos, in one case up to 20. Furusato (1952) has studied the number of embryos in *C. unshu* and observed pronounced individual variation. Between 20 and 30 embryos per seed were normally examined in this species. In *C. daidai* Furusato stated an average number of 16 embryos per seed, one to four of which gave rise to seedlings. By using embryo culture technique much better results have been obtained, however. Crosses between species forming one and species forming many embryos per seed have been made, and an examination of the hybrids formed has made it obvious that the type of pollen does not influence the number of

embryos.   Hofmeier and Oberholzer (1948) made the observation that plants raised from adventitious embryos give better trees than those raised from cuttings.   The cuttings are infected by different kinds of virus which do not occur in the nucellar embryos.

SOLANACEAE

SOLANUM.   Dodds (1950) has reported the formation of two polyhaploids with $2n = 36$ and $2n = 39$, respectively, in *Solanum demissum* $(2n = 72)$ and suggests that they originated by haploid parthenogenesis.

APPENDIX

SPECIES WITH KNOWN OR SUSPECTED APOMIXIS IN 1953

(A = apospory; AE = adventitious embryony; D = diplospory; P = parthenogenesis; V = vivipary)

Family, genus and species	Type of apomixis	2n number	References
Amaryllidaceae			
Agave angustiflora	V	60, 90	Berger, 1915; Vignoli, 1936, 1937a, b; Granick, 1944;
" candelabrum "	V	90	Darlington and Janaki-Ammal, 1945
cantula	V	60, 90	
fourcroydes	V	ca. 140	
Leespinassei	V	60	
lurida	V	90	
Salmiana var.	V	120	
sisalana	V	(138, 141-)150	
vivipara	V	60	
zapupe	V	(110-)120	
Calostoma Cunninghamii	(AE?)	....	Schlimbach, 1924
purpureum	(AE?)	....	
Cooperia pedunculata	D + P	48	Coe, 1953
Fourcroya cubensis	V	....	Ernst, 1918; Darlington and Janaki-Ammal, 1945
gigantea		60	
Zephyranthes texana	D + P	24	Pace, 1913; Darlington and Janaki-Ammal, 1945; Brown, 1951
Anacardiaceae			
Mangifera indica	AE	40, ca. 52	Strasburger, 1878; Webber, 1931; Juliano and Cuevas, 1932; Juliano, 1934, 1937; Darlington and Janaki-Ammal, 1945; Leroy, 1947
Apocynaceae			
Amsonia Tabernaemontani	(AE?)	....	Andersson, 1931
Araceae			
Spathiphyllum Patinii	AE	18	Schürhoff and Jüssen, 1925; Darlington and Janaki-Ammal, 1945

Family, genus and species	Type of apomixis	2n number	References
Balanophoraceae			
Balanophora globosa	D + P	High	Fagerlind, 1945; Darlington and Janaki-Ammal, 1945
japonica	(D + P)	94–112	
Betulaceae			
Alnus rugosa	AE (D + P?)	28	Woodworth, 1930
Burmanniaceae			
Burmannia coelestis	D + P	64–72	Ernst and Bernard, 1912; Schock, 1920
Buxaceae			
Sarcococca Hookeriana	AE	....	Orr, 1923; Wiger, 1930, 1935; Simonet and Miedzyr-zecki, 1932
pruniformis	AE	28	
ruscifolia	AE	56	
humilis	AE(?)	....	
zeylanica	AE(?)	....	
Cactaceae			
Opuntia aurantiaca	AE	....	Braun, 1860; Ganong, 1898; Montemartini, 1899; Hull, 1915; Archibald, 1939
findus indica	AE	....	
leucantha	AE	....	
Rafinesquii	AE	....	
glaucophylla	(AE?)	....	
tortispina	(AE?)	....	
Calycanthaceae			
Calycanthus fertilis	(D + P?)	22	Peter, 1920; Schürhoff, 1923; Darlington and Janaki-Ammal, 1945
floridus	(AE?, D + P?)	22	
occidentalis	(AE?, D + P?)	....	
Campanulaceae			
Adenophora latifolia	....	....	Sukacev, 1940
liliifolia	....	....	
Potaninii	....	....	
utriculata	....	....	
Capparidaceae			
Capparis frondosa	AE	....	Mauritzon, 1934
Isomeris arborea	....	17?	Billings, 1937

Family, genus and species	Type of apomixis	2n number	References
Celastraceae			
Celastrus scandens	AE	46	Andersson, 1931; Bowden, 1940
Evonymus americanus	(AE?)	64	Braun, 1860; Strasburger, 1878; Bally, 1916; Andersson, 1931
europeus	(AE?)	64	
latifolius	AE	....	
Compositae			
Antennaria alpina	D+P	84	Kerner, 1876; Juel, 1900; Fernald, 1899, 1933, 1936; Porsild, 1915; Fries, 1919; Ekman, 1927; Stebbins, 1932, 1935, 1941; Bergman, 1935c, 1951; Bøcher, 1950; Nygren, 1950b
Brainerdii	D+P	42	
canadensis	D+P	83–86	
carpatica	A,D+P?	40–42	
fallax	D+P	84	
glabrata	D(?)+P(?)	63	
groenlandica	...	...	
intermedia	D+P	ca.80	
magellanica	D+P	56	
neodicica	D+P	ca.52	
occidentalis	D+P	75–85	
Parlinii	D+P	84	
petaloidea	D+P	75–80	
Porsildii	D+P	63	
Arnica alpina	D+P	58, (80)	Afzelius, 1936; Flovik, 1940
Chamissonis	D+P	...	
diversifolia	(D+P)	...	
Artemisia nitida	A,D; no P	27	Chiarugi, 1926
Centaurea cyanus	A; no P	24	Bergman, 1935a
Chondrilla acantholepis	D+P	15	Rosenberg, 1912; Poddubnaja-Arnoldi, 1933; Bergman, 1944, 1950, 1952b, c; Battaglia, 1949
brevirostris	D+P	15	
coronifera	(D+P)	15	
graminea	D+P	20	
juncea	D+P	15	
Kouznezowii	(D+P)	15	
lejosperma	(D+P)	15	
ornata	(D+P?)	20	
pauciflora	D+P	15	

Family, genus and species	Type of apomixis	2n number	References
Coreopsis bicolor	A; no P	24	Gelin, 1934
Crepis acuminata	A+P	22–88	Babcock and Stebbins, 1938; Stebbins and Jenkins, 1939; Babcock, 1947, I and II
atribarba	A+P	22–88	
Bakeri	A+P	22–55	
barbigera	A+P	44–88	
intermedia	A+P	33–88	
modocensis	A+P	22–88	
monticola	A+P	22–88	
occidentalis	A+P	22–88	
pleurocarpa	A+P	22–88	
Erigeron annuus	D+P	(26), 27	Holmgren, 1919; Tahara, 1921; Carano 1921; McDonald, 1927; Söderberg, 1929; Okabe, 1932; Gustafsson, 1935; Ikeno, 1935; Oka, 1935; Bergman, 1942, 1944; Fagerlind, 1947a; Battaglia, 1950
Karvinskianus var. mucronatus	D+P	32–34, 36	
ramosus	D+P	27	Holmgren, 1919
Eupatorium glandulosum	D+P	51	
Hieracium Subg. Euhieracium (apomicts)	D+P	18, 27, 36	Ostenfeldt, 1912; Rosenberg, 1907, 1917, 1927, 1930; Schnarf, 1919, 1929; Haberland, 1921; Alton Gustafsson, 1933; Christoff and Popoff, 1933; Christoff, 1940, 1942; Christoff and Christoff, 1948; Bergman, 1935b; Gustafsson, 1935; Gustafsson and Nygren, 1946; Gentcheff and Gustafsson, 1940; Gentcheff, 1937, 1941; Battaglia, 1947c; Heitz, 1951
Subg. Pilosella (apomicts)	A+P	27, 36, 42, 45	
Ixeris dentata	D+P	21	Okabe, 1932; Darlington and Janaki-Ammal, 1945
Leontodon hispidus	A; no P	14	Bergman, 1935a
Parthenium argentatum (apomicts)	A, D+P	(36, 37), 54–72–144	Bergner, 1944, 1946; Esau, 1944, 1946; Gardner, 1946a, b; Powers, 1945; Powers and Gardner, 1945; Powers and Rollins, 1945; Rollins, 1945a, b, 1949; Catcheside, 1947, 1950; Gerstel, 1950a, b; Gerstel and Mishanec, 1950; Gerstel and Riner, 1950; Gerstel, Hammond and Kidd, 1953
incanum	A, D+P	54–90	

Family, genus and species	Type of apomixis	2n number	References
Picris hieracioides	A; no P	10	Bergman, 1935a
Rudbeckia californica	D+P	76	Battaglia, 1945, 1946a, b, 1947a–d, 1952a–c; Fagerlind, 1946
Deamii	D+P	76	
laciniata	D+P	76	
speciosa	D+P	76	
Sullivantii	D+P	76	
triloba	D+P	76	
Taraxacum vulgaria apomicts	D+P	24	Gustafsson, 1932, 1935; Poddubnaja-Arnoldi and Dianova, 1934; Matsuura and Suto, 1935; Poddubnaja-Arnoldi, 1939; Turrill, 1938; Koroleva, 1939; Erlandsson, 1939; Sörensen and Gudjónsson, 1945; Fagerlind, 1947; Battaglia, 1948; Cooper and Brink, 1949; Tschermak-Woess, 1949
oblatua "	D+P	24, 32	
erythrosperma "	D+P	24, 32	
spectabilis "	D+P	32	
maculigera "	D+P	24, 48	
palustria "	D+P	(24), 32	
arctica "	D+P	40	
ceratophora "	D+P	24, 32	
Other apomicts	D+P	24, 32, 40	
Youngia Sect. Crepidopsis	....	....	Stebbins, 1941
Cruciferae			
Arabis Holboellii	D+P	14, 21	Bøcher, 1947, 1951
Euphorbiaceae			
Alchornea (Caelobogyne) ilicifolia	AE	.. ..	Strasburger, 1878
Euphorbia dulcis	AE	12, 28	Carano, 1925, 1926; Perry, 1943
Gentianaceae			
Cotylanthera tenuis	(D+P?)	....	Oehler, 1927; Schnarf, 1929
Gramineae			
Agrostis stolonifera tenuis	V	....	Åberg, 1940
tenuis	V		
Bouteloua curtipendula	(D?+P?)	28–101	Fultz, 1942; Myers, 1947; Harlan, 1948, 1949
gracilis	?	20–84	Snyder and Harlan, 1953
hirsuta	?	21, 37, 42	

Family, genus and species	Type of apomixis	2n number	References
Calamagrostis canadensis	D+P	42-68	Stenar, 1932b; Nygren, 1946, 1948a, b, 1949a, 1951b, 1954
chalybaea	D+P	42	
inexpansa	D+P	84-103	
Langsdorffii	D+P	56	
lapponica	D+P	42-112	
purpurascens	D+P	42-56	
purpurea	D+P	56-91	
Deschampsia alpina	V	(26)-39-52(56)	Flovik, 1938, 1940; Hagerup, 1939; Nannfeldt, 1940;
caespitosa (apomicts)	V	26, (28)	Lawrence, 1945; Nygren, 1949b; Wycherley, 1953
rhenana	V	....	
Eleucine coracana (apomicts)	V	....	Li, 1950
Festuca ovina (apomicts)	V	21, 28, 42, 49	Turesson, 1926, 1930, 1931; Flovik, 1938; Nannfeldt,
rubra (apomicts)	V	42	1940; Löve and Löve, 1942
Panicum maximum	A	....	Warmke, 1951, 1954
Paspalum dilatatum	A+P	....	Smith, 1948; Burton, 1948; Wycherley, 1953
notatum	?	40	
Poa alpina (apomicts)	V, D+P	14-57	Müntzing, 1933, 1940, 1954; Akerberg, 1941; Akerberg and Bingefors, 1953; Löve and Löve, 1942; Håkansson, 1943; Nygren, 1950a; Skalinska, 1952; Wycherley, 1953
ampla	A+P	63	Nygren, 1951a
arachnifera	V	54-56, 63	W. L. Brown, 1939; Hartung, 1946; Clausen et al., 1952
arctica			
subsp. *caespitans*	A+P	56	Nannfeldt, 1940; Nygren, 1950a
subsp. *depauperata*	A+P	75-79	Nannfeldt, 1940; Nygren, 1950a
subsp. *elongata*	A+P	68-76	Nannfeldt, 1940; Nygren, 1950a
subsp. *microglumis*	A+P	68-82	Nannfeldt, 1940; Nygren, 1950a
subsp. *stricta*	V	(38), 39	Nannfeldt, 1940; Nygren, 1950a
var. *vivipara*	V	56	Flovik, 1938
diff. forms	A+P	56-ca. 100	Armstrong, 1937; Flovik, 1938; Engelbert, 1940, 1941; Nygren, 1950a
arida	A+P	63	Nygren (unpublished)
bulbosa	V	28, 42, 56	Armstrong, 1937; Akerberg, 1941; Hartung, 1946
compressa	A+P	35, 42, 49, 50, 56	Armstrong, 1937; Turesson, 1938; Akerberg, 1941; Brittingham, 1941, 1943; M. A. Christoff, 1942; Hartung, 1946; Clausen et al, 1952

Family, genus and species	Type of apomixis	2n number	References
glauca	D+P	42, 47, 50, 56, 60, 65, 70	Kiellander (Löve and Löve, 1942); Müntzing, 1933; Armstrong, 1937; Åkerberg, 1941
herjedalica (=*alpina* × *pratensis*)	V, A+P	47–80	Nannfeldt, 1937; Nygren, 1950a
jemtlandica (=*flexuosa* × *alpina*)	V	37, (39)	Nannfeldt, 1937; Nygren, 1950a
nemoralis	(D+P)	28, 29–38, 42 / 43, ±56	Kiellander (Löve and Löve, 1942); Müntzing, 1933; Armstrong, 1937; Åkerberg, 1941
nevrosa	D+P	(28), 63, 76, 80, 81–90	Grun, 1951, 1952
palustris	D+P	28, 29, 30, 42	Armstrong, 1937; Kiellander (Löve and Löve, 1942); Hartung, 1946
pratensis subsp. *alpigena*	A+P	46–92	Åkerberg, 1941; Hartung, 1946; Clausen et al., 1947–52; Nygren, 1950a
subsp. *alpigena* var. *vivipara*	V, A+P	38, 42, 52 69–81	Flovik, 1938; Westergård and Sörensen (Löve and Löve, 1942); Nygren, 1950a
subsp. *angustifolia*	A+P	50, 64, 65	Åkerberg, 1941
subsp. *eupratensis*	A+P	41–124	Müntzing, 1933, 1940; Rancken, 1934; Armstrong, 1937; Brown, 1939, 1941; Tinney, 1940; Åkerberg, 1941; M. A. Christoff, 1942, 1944; Nielsen, 1945, 1946; Hartung, 1946; Clausen et al., 1947–1952; Nygren, 1951a; Grun, 1951; Grun and Triplett, 1952
subsp. *irrigata*	A+P	84–147	Åkerberg, 1941; Löve, 1952
Setaria viridis	V	....	Li, 1950
Saccharum officinarum	(D?)+P	80	Bremer, 1922, 1924, 1931, 1934, 1946; Naryanaswami, 1940; Subramaniam, 1946; Moriya, 1950; Raghavan, 1951
spontaneum	(D?)+P	48–112	

Family, genus and species	Type of apomixis	2n number	References
Guttiferae			
Garcinia mangostana	AE		Sprecher, 1919; Horn, 1932
Hypericum perforatum	A + P	32, (60)	Noack, 1939; Hoar and Haertl, 1932
Juglandaceae			
Juglans sp.	? ?	....	Zarubin, 1949
Liliaceae			
Allium amplectens	(D + P?)	24	Levan, 1940, 1944
ascalonicum	V	16	Darlington and Janaki-Ammal, 1945
carinatum	V	16, 24	Levan, 1937; Diannelidis, 1944; Geitler, 1944
cepa	V	16	Darlington and Janaki-Ammal, 1945
nutans	AE?	40–42	Håkansson, 1951
odorum	AE	16, 32	Levan (unpubl.); Darlington and Janaki-Ammal, 1945; Håkansson, 1951
oleraceum	V	32	Levan, 1937
prolijerum	V	16	Darlington and Janaki-Ammal, 1945
roseum var. bulbiferum	V	48	Messeri, 1930
saticum	V	16	Darlington and Janaki-Ammal, 1945
schoenoprasum	V	16, 24, 27, 29, 32	Levan, 1935
scorodoprasum	V	16	Darlington and Janaki-Ammal, 1945
vineale	V	32	Darlington and Janaki-Ammal, 1945
viviparum	V	16	Darlington and Janaki-Ammal, 1945
Dianella tasmanica	?	16 (76, 80, 84)	Curtis, 1952
coerulea	?	(16, 32, 48)	
Hosta coerulea	AE	60	Strasburger, 1878; Akemine, 1935; Suto, 1936
Lilium bulbiferum	V	24	Tischler, 1935–1936
Nothoscordum fragans	AE	16, 18, 19, 24	Strasburger, 1878; Stenar, 1932a; Levan and Emsweller, 1938; Darlington and Janaki-Ammal, 1945; D'Amato, 1949; Håkansson, 1953
Smilacina racemosa	AE		MacAllister, 1913
Tulipa Gesneriana	AE	(24, 36)	Bambacioni-Mezzetti, 1932; Beth, 1938
Trillium sp.	P?	....	Jeffrey, 1948

Family, genus and species	Type of apomixis	2n number	References
Malphigiaceae			
Hiptage Madablota	AE	....	SubbaRao, 1940
Musaceae			
Musa Balbisiana × acuminata	P?		Dodds and Simmonds, 1948
Myrtaceae			
Eugenia Hockeri	AE	28, ± 42, ± 54	Pijl, 1934; Johnson, 1936; Tiwary, 1926, 1929
Jambos	AE	22	
malaccensis	AE		
Cumini	(AE?)	....	
Ochnaceae			
Ochna serrulata	AE	35	Chiarugi and Francini, 1930
Onagraceae			
Taraxia ovata	(P?)	....	Johansen, 1931
Orchidaceae			
Bletilla striata var. *gebina*	Haploid P	32	Miduno, 1940
Cephalanthera damasonium	Haploid P	32	Hagerup, 1947
longifolia	Haploid P	40	Hagerup, 1947
Epipactis latifolia	Haploid **P**	....	Hagerup, 1945
Habenaria platyphylla	?	34, 36	Swamy, 1946b
Listera ovata	Haploid P	ca. 64	Hagerup, 1947
Nigritella nigra (spomicts)	AE	40, 80	Afzelius, 1928, 1932
Orchis maculatus	Haploid P	40	Hagerup, 1944
strictifolius	Haploid P	42	Hagerup, 1947
Platanthera chlorantha	Haploid P		Hagerup, 1947
Zeuxine sulcata	AE	....	Swamy, 1946a
Zygopetalum Mackayi	AE (D + P?)	40	Suessenguth, 1923; Darlington and Janaki-Ammal, 1945
Plumbaginaceae			
Statice olaeefolia var. *confusa*	D + P	27	D'Amato, 1940, 1949
Limonium binervosum	?	32	Baker, 1954
lychnidifolium	?	24	
Polygonaceae			
Acetosa arifolia	?	14	Löve, 1942, 1949
pratensis	?	....	
thyrsiflora	?	....	

Family, genus and species	Type of apomixis	2n number	References
Atraphaxis frutescens	A + P	88(?)	Edman, 1931
Polygonum viviparum	V	83–88, ± 100, ± 110	Löve and Löve, 1942
Primulaceae			
Primula japonica × chungensis	"automixis"	....	Ernst, 1949, 1950, 1951a, b
× Cockburnia	See p. 608	....	
× pulverulenta	....	....	
Wilsoni × Cockburnia	....	....	
Ranunculaceae			
Ranunculus acris	?		Marsden-Jones and Turill, 1935, 1952; Häfiger, 1943; Rozanova, 1932; Koch, 1933, 1939; Sörensen, 1938; Marklund, 1939; Darlington and Janaki-Ammal, 1945; Rutishauser, 1954
auricomus coll.	A + P	16, 32, 40, 48	
bulbosus	?	....	Marsden-Jones and Turill, 1945
Rosaceae			
Alchemilla subg. Aphanes			
arvensis	A + P	ca. 48	Böös, 1924; Gentcheff and Gustafsson, 1940b; Gudjónsson, 1941
subg. Eualchemilla			
alpina coll.	(A + P)	100	Murbeck, 1901; Gentcheff and Gustafsson, 1940b
vulgaris coll.	(A + P)		Murbeck, 1901; Böcher, 1938; Gentcheff and Gustafsson, 1940b; Turesson (Löve and Löve, 1942); Ehrenberg, 1945
acutiloba		ca. 100	
glabra		ca. 90, ca. 100	
glomerulans		64(?)	
micans		ca. 93	
pastoralis		101	
subcrenata		ca. 90	
Crataegus, numerous American apomicts	....	Polyploid	Longley, 1924a; Palmer, 1932; Sax, 1931
Malus hypehensis (= theifera)	A + P	51	Sax, 1932; Dermen, 1936
Sieboldii	? + P	68	Oldén, 1953

Family, genus and species	Type of apomixis	2n number	References
Potentilla adscharica	P	42	Forenbacher, 1914; Müntzing, 1928, 1931; A. and G. Müntzing, 1941–1945; Popoff, 1935; Shimotomai, 1935; Gentcheff and Gustafsson, 1940b; Clausen, Keck and Hiesey, 1940; Clausen, 1951; Christoff and Papasova, 1943; Rutishauser, 1943a, b, c, 1945a, b, 1946, 1947, 1948, 1949; Håkansson, 1946
arenaria	P	35, ±42, (±56)	
argentea	A + P	14, 28, 35, 42, 56	
arguta	....	14	
argyrophylla	....	63	
aurea	....	14	
Breweri	P	±72 to ±102	
canescens	....	42	
chrysantha	....	42	
collina	P	35, 42	
Crantzii	P	42, 42 + f	
dealbata	....	35	
Degeni	....	42	
diversifolia	....	42 to ±101	
dissecta	....	42	
Drummondii	....	±64 to ±108	
flabelliformis	....	56 to ±66	
gelida	....	42	
gracilis	....	56 to ±109	
hirta	....	28	
intermedia	....	28	
kurdica	....	56	
Levieri	....	42	
multifida	....	28	
nevadensis	....	28	
praecox	A + P	42	
pulcherrima	....	56 to ±109	
recta	P	28, 42	
verna (including *P. Tabernaemontani*)	A + P, D + P	42, 49, 84	

Family, genus and species	Type of apomixis	2n number	References
Rubus subg. *Eubatus*			
sect. Moriferi			
European apomicts	(A +)P	21–49	Crane and Thomas, 1940; Gustafsson, 1943; Christer,
caesius	....	28	1953
Corylifolii	....	28, 35, 42, 39(?)	
		+ aneuploids	
Moriferi veri		21, 28, 35	
American apomicts	(A? +)P	21–63	Longley, 1924b; Crane and Thomas, 1940; Einset,
Allegenienses	....	21	1947, 1951; Waldo and Darrow, 1948
Arguti	....	21–36	
Canadenses	....	21	
Cuneifolii	....	28	
Flagellares	....	35–63	
Hispidi	....	21, 28	
Idaeobatus	....	21	
Setosi	....	21, 28	
Sorbus aria coll.	....	68	Mofett, 1931; Sax, 1931; Liljefors, 1934, 1954
(*obtusifolia*)	....	68	
(*rupicola*)	....	68	
chamaemespilus	A + P	68	
hybrida (= *fennica*)	A + P	68	
intermedia	....	68	
lancifolia	....	51	
Meinichii	....	68	
minima	....	51	
Mougeoti	....	51	
sudetica	....	51	
Rutaceae			
Citrus			
Numerous species and varieties, as well as related genera	AE	18, 27, 36	Strasburger, 1878; Osawa, 1912; Frost, 1926; Toxopeus, 1936; Traub, 1938; Webber, 1940; Bacchi, 1943; Krug, 1943; Moreira and Gurgel, 1947; Hofmeier and Oberholzer, 1948; Furussato, 1952

Family genus and species	Type of apomixis	2n number	Reference
Ptelea trifoliata	(AE?)	?	Mauritzon, 1935
Triphasia aurantiola	AE	....	Mauritzon, 1935
Xanthoxylum alatum	(AE?)	....	Longo, 1908; Mauritzon, 1935
Bungei	AE	....	
Saururaceae			
Houttuynia cordata	D+P	(52–56), 94–98, 100–104	Shibata and Miyake, 1908; Söderberg, 1927; Okabe, 1930
Saxifragaceae			
Saxifraga cernua	V	50, ca. 66	Skovsted, 1934; Löve and Löve, 1942; Böcher, 1938b; Harmsen, 1939; Flovik, 1940
foliolosa			
Thymeliaeaceae			
Wikstroemia viridifolia	D+P	27	Fagerlind, 1940
Urticaceae			
Elatostoma acuminatum	A+P	50	Fagerlind, 1944; Krause, 1931
eurhynchum	D+P	52	
latifolium	A+P	60	
machaerophyllum	D+P	60	
peltifolium	D+P	60	
penniverve	....	....	
repens	....	High	
rostratum	....	....	
sinuatum	D+P	80	
Procris frutescens	....	....	

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