THE BOTANICAL REVIEW

VOL. VII OCTOBER, 1941 No. 10

APOMIXIS IN THE ANGIOSPERMS

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INTRODUCTION

Parthenogenesis, apospory and other substitutes for sexual reproduction have been regarded by most American botanists as "freak" phenomena. Their existence in a few species and genera is recognized, but the study of apomixis has too often been considered a side track which has little connection with the main lines of botanical research. Recent work has, however, shown that the study of apomixis by means of the modern method and principles of cytogenetic research will yield results which are both interesting in themselves and of great value in the solution of several major problems confronting botanists today.

The latest review of apomixis in plants, that of Rosenberg (1930), described all the important cases known at that time. The present reviewer aims partly to revise and enlarge Rosenberg's discussion, partly to show the connection between the problems of apomixis and other major problems.

TERMINOLOGY AND DESCRIPTION OF PHENOMENA

Several systems have been proposed for the classification of the phenomena of apomixis. That of Winkler (1908, 1920, 1934) has been most widely accepted, but is incomplete in the light of present knowledge. Stebbins and Jenkins (1939) and Fagerlind (1940*a*) have proposed revisions, of which the latter is the most complete. In the opinion of the present reviewer, Fagerlind's system is satisfactory in every way and should be generally adopted in order to secure uniformity in the description of these phenomena. It is represented in Figure 1 which is adapted from Table I of Fagerlind's paper. Of the several definitions of the term apomixis (Winkler, 1908; Edman, 1931; Darlington, 1937; Fagerlind, 1940*a*), the

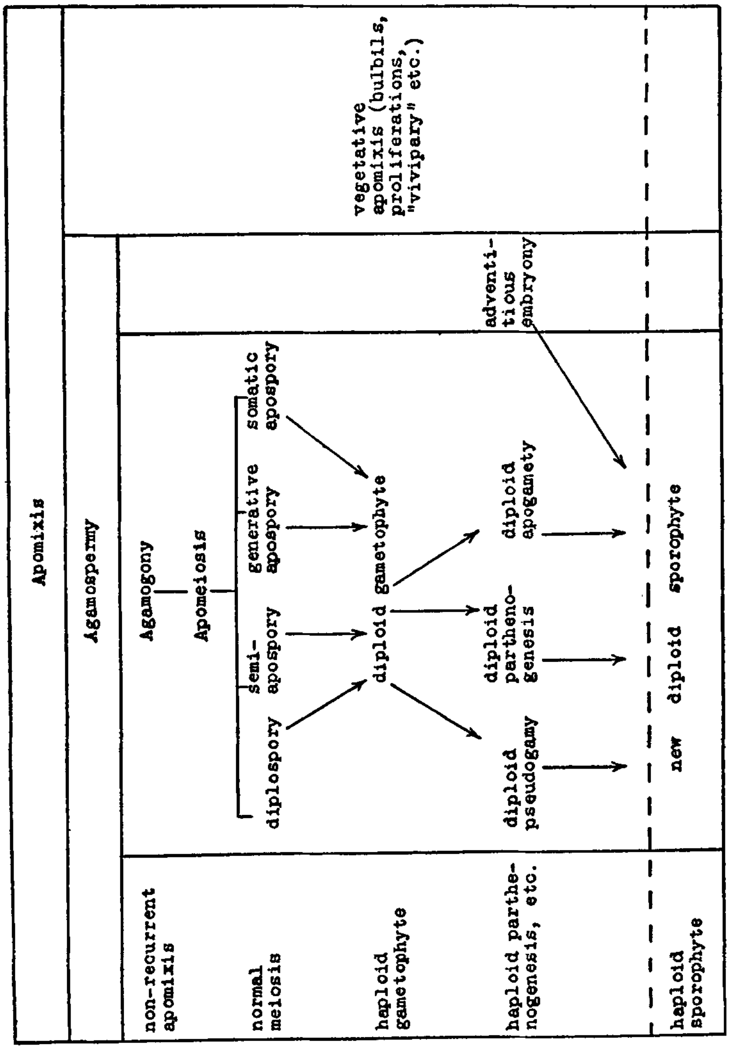

FIG. 1. Chart illustrating the interrelationships of the various apomictic processes.

original one of Winkler seems to the present writer the most satisfactory. It may be translated as follows: "apomixis is the substitution for sexual reproduction of another, asexual reproductive process that does not involve nuclear or cellular fusion (that is, fertilization)." The two main types of apomixis are vegetative apomixis and agamospermy, or apomixis through seed production.

Naturally, not all types of vegetative reproduction can be termed apomixis, but only those that are substitutes for the sexual method. These include mainly the occurrence of vegetative buds, bulblets or proliferations in the place of flowers or inflorescences. Good reviews of the known cases are given by Ernst (1918) and Goebel (1931). Most botanists are familiar with such cases as various *Allium* spp., *Polygonum viviparum, Saxifraga stellaris* var. *comosa, Agave* spp., *Cyperus* spp. and the so-called "viviparous" races of various grasses (*cf.* Turesson, 1926, 1930, 1931; Flovik, 1938). The term vivipary should not be used for this type of proliferation, since it is properly applied to a very different phenomenon, namely, the germination of seeds while still upon the mother plant (Goebel, 1932). So far as the writer is aware, no careful developmental analysis of this type of reproduction has yet been attempted.

Agamospermy is in turn divided into three main categories: adventitious embryony, in which the new sporophyte is a direct proliferation from the ovular tissue of its parent (the term nucellar embryony is misleading, since the new embryo often develops from the inner ovular integument rather than from the nucellus); agamogony, in which alternation of generations occurs (although not in respect to chromosome number); and the non-rècurrent types of apomixis, in which normal meiosis takes place and a haploid egg gives rise to a haploid sporophyte.

Adventitious embryony resembles vegetative reproduction in that the new sporophyte develops directly from the old, and the gametophyte, though usually formed, does not function. Many cases of this phenomenon were recorded in the earlier literature (Schnarf, 1929; Rosenberg, 1930), and more recently that of *Citrus* has been carefully studied (Swingle, 1932; Frost, 1926, 1938*a, b*) while several additional cases have been reported (see Table I). Archibald (1939) recognizes three types of adventitious embryo formation: 1) that dependent on fertilization and endosperm development, as in *Citrus* (Frost, 1926, 1938*a, b*); 2) that dependent on endosperm development but not on fertilization, as in *Coelebogyne* (*Alchornea*) *ilicifolia* (*cf.* Schnarf, 1929); 3) that dependent neither on fertilization nor on endosperm development, as in *Opuntia aurantiaca.* These types parallel the types of apomictic embryo formation from an egg, namely, pseudogamy and parthenogenesis. Webber (1940) has reviewed thoroughly the literature on adventitious embryony.

In *Ochna serrulata* (Chiarugi and Francini, 1930) diplospory and somatic apospory regularly take place, so that the gametophyte is normally diploid. Nevertheless, the egg cells most often fail to develop, and the parthenogenetic embryos, when formed, always degenerate. They are replaced by adventitious embryos formed from the inner integument of the ovule. These embryos begin growth some time after anthesis.

In spite of the fact that it eliminates practically all of the processes associated with sexual reproduction, adventitious embryony retains an important physiological characteristic of the sexual process, and of other types of agamospermy, namely, the ability to produce the distinctive characteristics of the seedling. In *Citrus* (Swingle, 1932; Frost, 1938*a;* Hodgson and Cameron, 1938) plants reproduced vegetatively by means of cuttings have the characteristics of the adult stock, while those grown from apomictically produced seed have all of the morphological features (cotyledons, thorns, *etc.*) as well as the vigor of growth found in seedlings of a normal sexual progeny. This shows that the appearance of juvenile characteristics is not the result of sexual reproduction, but is produced by the physiological environment within the developing ovule and young seed. Although Horn (1940) has suggested that the peculiar reduced nature of the embryo of *Garcinia mangostana* is due to its adventitious origin, Sprecher (1919) describes this type of embryo in several other species of the family Guttiferae, so that it appears to be characteristic of both sexual and apomictic members of the family.

The term agamogony was suggested by Fagerlind to cover all those types of apomixis in which the daughter sporophyte develops from a diploid gametophyte, so that a morphological alternation of generations is present. As was first pointed out by Winkler (1934) and has been emphasized by Stebbins and Jenkins (1939) and Fagerlind (1940*a*), any agamogonic cycle must involve two distinct processes not found in the sexual cycle: first, a substitute for meiosis, and second, a substitute for fertilization. As is evident from Table I, there are several substitutes known for each process, and the two series are not interdependent. Thus an apomict, if parthenogenetic, must also be either aposporous, diplosporous or semiaposporous, but may be any one of these three. Similarly, an aposporous apomict, if fertile, must in addition be either parthenogenetic, pseudogamous or apogametous, but may be any one of the three. Failure to recognize this simple fact has led to great confusion in terminology in many discussions of apomixis.

The various substitutes for meiosis in apomicts which give a diploid gametophyte are collectively termed apomeiosis. Although many transitions between them exist, the four types recognized by Fagerlind are distinct enough to merit classification. Apospory is the development of a gametophyte by means of a series of purely mitotic divisions. In somatic apospory the embryo-sac initial is a purely somatic cell, usually of the chalazal region, but sometimes of the nucellus. This process has long been known in ferns (Steil, 1939) and in *Hieracium,* subgenus *Pilosella* (Rosenberg, 1930). The more recently reported cases of somatic apospory are in *Ochna serrulata* (Chiarugi and Francini, 1930), *Sorbus* spp. (Liljefors, 1934), *Malus hupehensis* (Dermen, 1936), *Leontodon hispidus* (Bergman, 1935*b*), *Crepis occidentalis, acuminata, etc.* (Stebbins and Jenkins, 1939; Stebbins and Babcock, 1939), *Hypericum perforatum* (Noack, 1939), and *Poa pratensis* (Akerberg, 1939; Tinney, 1940). In generative apospory the archesporial cell develops directly into the embryo-sac mother cell, so that its first division is a purely somatic one corresponding both in appearance and in the age of the ovule when it occurs, to the first division of the macrospore in the related sexual species (Stebbins, 1932*b;* Fagerlind, 1940*a*). The processes of meiosis and megaspore formation are therefore completely omitted. This is called by Rosenberg (1930) the *Antennaria* method of parthenogenesis. Conditions intermediate between somatic and generative apospory are found in species in which the distinction between archesporial and nucellar cells is not well defined, for example *Oxyria digyna* (Edman, 1929) and *Athraphaxis frutescens* (Edman, 1931).

Diplospory is the form of apomeiosis in which dyads are formed, and the semiheterotypic division (Rosenberg, 1927) takes place.

It is quite comparable to the formation of dyads of diploid microspores which sometimes takes place in the anthers of many hybrids and other plants with abnormal meiosis, and corresponds to the *Taraxacum* scheme of parthenogenesis (Rosenberg, 1930). Semiapospory is an intermediate condition characterized by the presence of a pseudohomoeotypic division (Gustafsson, 1934*b*, 1935*a*), in which the chromosomes are strongly contracted as in meiosis, but are not at all paired. As Gustafsson (1935*a*) and Fagerlind (1940*a*) have both pointed out, there are various intermediate conditions between these four types of apomeiosis. In some species, such as *Wikstroemia indica* var. *viridiflora* (Fagerlind, 1940*b*), different types of apomeiosis are found in different ovules of the same plant.

In any cycle of recurrent apomixis, apomeiosis must be followed by one of three abnormal types of sporophyte development, namely, parthenogenesis, pseudogamy or apogamety. In some cases, such as *Artemisia nitida* (Chiarugi, 1926) and certain forms of *Oxyria digyna* (Edman, 1929), *Coreopsis bicolor* (Gelin, 1934) and *Leontodon hispidus* (Bergman, 1935*b*), none of these processes occurs, so that apomeiosis leads to non-functional embryo-sacs and sterile ovules. This shows that the two critical processes of the agamogonic cycle are not necessarily linked to each other. To distinguish them from the parallel processes which occur occasionally in normal haploid gametophytes (see below), these methods of sporophyte development from a diploid gametophyte are called unreduced parthenogenesis, pseudogamy, or apogamety.

Unreduced parthenogenesis, in which embryo development from the diploid egg is autonomous, is the most common method of sporophyte development in agamogonic plants. Although the course of embryo development is very similar to that of a sexual embryo, the time when the egg cell starts to divide varies in different genera. In many cases, such as *Hieracium, Erigeron, Ochna* (Chiarugi and Francini, 1930) and *Crepis* (Stebbins and Jenkins, 1939), the embryo has already begun to grow when the flowers first open, while in others, such as *Antennaria* (Stebbins, 1932*b*), it begins later, and in *Malus hupehensis* (Dermen, 1936) it is very much delayed. Endosperm development may precede or follow that of the embryo; both conditions have been described in the same species of *Chondrilla* (Poddubnaja-Arnoldi, 1933).

Unreduced pseudogamy as a regular stage in an apomictic cycle is best known in *Potentilla* (Müntzing, 1928; Popoff, 1935; Gentscheff, 1938; Gentscheff and Gustafsson, 1940*b*), *Rubus* (Gustafsson, 1930; Crane, 1940) and *Poa* (Akerberg, 1936; 1939; Tinney, 1940; Engelbert, 1940). In all three of these genera the origin of the embryo sac is aposporic (*cf.* Gentscheff and Gustafsson, 1940*b*). These latter two authors have found that embryo development in *Potentilla* apomicts may begin autonomously, but that the endosperm develops only after fertilization. The "stimulus" provided by the pollen tube in this and probably other cases of pseudogamy is, therefore, the fertilization of the endosperm nucleus by one of the male nuclei. The same situation apparently exists in *Poa pratensis* (Tinney, 1940).

In a number of cases of facultative pseudogamy, the proportion of hybrid to apomictic offspring varies with the chromosome number of the pollen parent. Darrow and Waldo (1933) found that several tetraploid *Rubus* apomicts ($2n = 28$) yielded few or no sexual offspring when selfed or crossed with other apomicts having the same chromosome number, but one of them, crossed with a diploid strain ($2n = 14$), gave a majority of sexual hybrid offspring. Parallel results were obtained by Crane (1940), using the octoploid *Rubus vitifolius* ($2n = 56$) as the ovulate, a diploid ($2n = 14$) and a tetraploid ($2n = 28$) form of *R. idaeus* as the pollen parent. Pollen from the diploid produced only pentaploid hybrids ($2n = 35$), but that from the tetraploid produced both hybrids and purely matroclinous octoploid offspring. On the other hand, pollen from the hexaploid *R. loganobaccus* ($2n = 42$) produced only hybrids with $2n = 49$. Petrov (1939) found that unreduced eggs of a triploid form of *R. idaeus* ($2n = 21$) produce hexaploid ($2n = 42$) hybrids when crossed with *R. loganobaccus,* but that pollen from diploid *R. idaeus* produces exclusively triploid pseudogamous progeny. The results of Noack (1939) in *Hypericum* agree, in general, with those of Darrow and Waldo in *Rubus*. *H. perforatum,* a tetraploid ($2n = 32$), forms only unreduced eggs by somatic apospory. Under self pollination these give rise almost exclusively to pseudogamous offspring, but when pollen from diploid ($2n = 16$) species of *Hypericum* is used, pentaploid hybrids ($2n = 40$) are often produced. The ability of a facultatively pseudogamous plant to produce apomictic or sexual offspring depends, therefore, both on the proportion of ovules in which viable reduced eggs are formed and on the relationship between the chromosome number of the endosperm, egg and male gametes. For this latter relationship, however, no simple rule can be formulated which fits all the cases cited above. Apparently, other unknown factors are involved.

Apogamety (this term, coined by Renner, has been adopted by Fagerlind in preference to the more familiar apogamy, because of the indiscriminate use of the latter term in the older literature) is the development of an embryo from a nucleus of the gametophyte other than the egg. It occurs occasionally in few angiosperms, but no authentic case is known in this group of apogamety as a regular method of embryo formation. The cases of *Ochna serrulata* (Chiarugi and Francini, 1930) and *Athraphaxis frutescens* (Edman, 1931) are well established. The remarkable situation inferred by Jeffrey and Haertl (1939*a*, *b*) for *Trillium* needs further confirmation.

Reduced parthenogenesis, pseudogamy or apogamety results from the stimulation to development of the haploid egg cell of a gametophyte which has developed from a normal megaspore, the product of typical meiosis. Since these reduced apomictic processes usually produce sterile haploids, and are not repeated from generation to generation, they are termed non-recurrent apomixis. Darlington (1937) gives a complete list of the haploids then known in angiosperms, with the methods by which they were produced. A few (*Datura, Zea, Triticum*) were produced by means of cold or heat treatment, but the majority were obtained by the stimulation of pollen, either of a very different species, of its own pollen in a self-incompatible form, or of pollen treated with x-rays. Since in all of these latter cases the development of the egg was presumably stimulated by the action of some type of pollen incapable of fertilizing it, they should be considered cases of pseudogamy rather than parthenogenesis in the strict sense of the word. Redinger (1938) has produced completely homozygous diploids and tetraploids in *Petunia* by the application of pollen of *Salpiglossis*. As Redinger has demonstrated cytologically, these are cases of reduced pseudogamy with subsequent doubling of the chromosome number. The development of this method holds great possibilities for the plant breeder. If pseudogamous diploid progeny can be induced in large numbers in complex hybrids, true breeding homozygotes may be produced immediately, thus eliminating the long process of "fixing" the valuable new combinations obtained from interracial or intervarietal hybridization.

Reduced pseudogamy often takes place at the same time as fertilization, so that a seed with two embryos results, giving rise to twin seedlings, one of which is haploid, the other diploid. Webber (1940) has already made a thorough review of this subject.

EVIDENCE FROM APOMIXIS AS TO THE NATURE OF MEIOSIS

The study of meiotic abnormalities found in apomicts is one of the most promising methods for an attack on the problem of the mechanism of meiosis in general, as has been pointed out by Gustafsson (1935*a*, 1938*a*, *b*, 1939*b*). In this connection the first fact to be emphasized is that the abnormalities of meiosis in the anthers of apomicts are not correlated with those found in their ovules (Gustafsson, 1938*a*). Darlington (1932) has attempted to show some points of parallelism between the male and female meiosis of apomicts, but his evidence is based on a few selected cases. His chief point is that apomicts with gametophyte formation by means of somatic apospory, and with pseudogamy or adventitious embryony, have, in general, fairly regular meoisis in the pollen mother cells, while diplospory or generative apospory in the ovules is usually accompanied by breakdown of meiosis in the anthers. In all groups, however, of which a large number of apomicts has been studied cytologically, there are now known to exist some apomicts with fairly normal and others with very abnormal or no microspore meiosis, regardless of whether the apomixis in these groups is facultative or obligate, or of the type of abnormalities which characterize the apomictic cycle. In *Hieracium* subg. *Pilosella,* which has facultatively somatic apospory followed by parthenogenesis, *H. aurantiacum* has fairly normal meiosis and pollen formation, while *H. excellens* has abnormal meiosis and no pollen (Rosenberg, 1917). In the American species of *Crepis,* with the same methods of reproduction, *C. occidentalis* (no, 2169) and *C. intermedia* have fairly normal meiosis, while in *C. acuminata* (no. 2163) the pollen mother cells degenerate before meiosis begins (Stebbins and Jenkins, 1939). In *Potentilla,* with facultative or obligate somatic apospory (probably) and pseudogamy, *P. argentea* has regular, *P. collina* and *P. hirta* irregular microspore meioses (Müntzing, 1928, 1931; Popoff, 1935). In *Taraxacum, Hieracium* subg. *Archieracium* and

Antennaria, all with diplospory or generative apospory followed by parthenogenesis, we have *T. Norstedtii, T. fulvum* and *T. melanthoides, H. umbellatum* and *A. fallax* with nearly normal P. M. C. meiosis, whereas several *Taraxaca, Hieracia* and *Antennaria canadensis* have very abnormal P. M. C. meiosis (*cf.* Gustafsson, 1938*a*). Furthermore, in the facultatively apomictic groups there is no evidence of correlation between the percentage of apomictic development and the amount of abnormality in the P. M. C.'s This is particularly clear in *Crepis* (Stebbins and Jenkins, 1939) in which the authors made a direct attempt to obtain such evidence. The meiotic abnormalities in the male and female cells must therefore be considered as separate phenomena.

Convincing evidence of this lack of correlation is presented by Gustafsson (1938*a*) who lists several species of *Taraxacum* and *Antennaria* in which the course of meiosis in the ovules is much more abnormal than in the anthers of the same plant. Since there is no doubt that the physiological disturbances which produce these abnormalities are quite different in the two sets of organs, the genetic factors controlling them are probably different. This point must be remembered in all future studies of apomixis; in the past, too much emphasis has been given by many workers to the meiotic abnormalities found in the pollen mother cells of apomicts.

As Gustafsson (1935*a,* 1938*a, b;* Gentscheff and Gustafsson, 1940*a*) has shown, the meiotic abnormalities in both the anthers and ovules of certain apomicts include a series of stages progressing from normal meiosis toward a typical somatic mitosis. In both cases the abnormalities are only in part due to the lack of homology between chromosomes. Rather, they are due to physiological alterations in the tissues concerned, the nature of which is not yet understood, but which should, when attacked from the experimental point of view, give us valuable clues as to what causes the differences between normal meiosis and a normal somatic mitosis.

Before the evidence now available can be applied to the current theories of meiosis, one point should be made clear. The P. M. C.'s and E. M. C.'s of certain apomicts, in particular *Hieracium* subg. *Archieracium,* differ not only in the degree of "mitotisation" (*i.e.,* conversion of meiosis into mitosis), but also in the way in which this mitotisation has occurred. In both sexes there are found, usually in different species or races, but sometimes in different flowers of the plant, two types of division intermediate between meiosis and mitosis. These are the semi-heterotypic division (Rosenberg, 1927, 1930) and the pseudo-homeotypic division (Gustafsson, 1934*b*, 1935*a*). In the former, the chromosomes resemble in degree of contraction those of the first (heterotypic) division of meiosis, and, as in that division, do not pass normally to the poles, so that a restitution nucleus is formed. In the pseudo-homeotypic division the chromosomes are contracted as in meiosis, and are unpaired, but form a typical equatorial plate, split, and the daughter chromosomes pass normally to the poles, so that the division is in its effect an equational one, like an ordinary somatic mitosis. There are numerous transitions between these different types. Although Stebbins (1932*b*) considered that the first embryo-sac division in the generative apospory of *Antennaria* is a typical somatic mitosis, Gustafsson (1935*a*, 1939*b*) believes that it never is. This is because, even when the chromosomes at metaphase and anaphase are in shape and behavior typical of somatic mitosis, the nucleus at prophase and the premitotic resting stage is abnormally large and there is great "hydration" of the chromosomes. The writer has reexamined his slides in the light of Gustafsson's observations, but has not been able to verify them. In the sexual species of *Antennaria,* the mitotic prophase nucleus in the first division of the haploid megaspore is also very large; the prophase nucleus in the first embryo-sac division in the apomicts is 4–6 times larger, with 6 times as many chromosomes present. Furthermore, the "hydration" (weak staining, apparently small and diffuse granules) of the chromosomes in the resting nucleus is most evident in younger archesporial nuclei of the apomicts, and becomes progressively less as the onset of prophase approaches. Hence the writer reaffirms his opinion that the first division of the archesporial nucleus in typical generative apospory is a normal somatic mitosis. That this is true in the microsporocytes of some *Hieracium* apomicts is quite certain (Gustafsson, 1935*a*).

Two important facts are known which give a clue to the nature and causes of these physiological disturbances of meiosis. In the first place, they are usually, perhaps always, different in the ovules and anthers of the same species (Gustafsson, 1938*a*). Restitution nuclei and the semi-heterotypic division, although often found in the P. M. C. of *Hieracium* and *Antennaria,* have never been found in the E. M. C. in these genera. Secondly, the abnormalities are always associated with a difference in the timing of the divisions with respect to the condition of the surrounding tissue, as well as in the relative growth and division rates of the tissues involved (Gentscheff and Gustafsson, 1940*a*). In *Hieracium* the somatic and semi-heterotypic types of division in the anthers take place when the sporocytes are relatively small and the tapetal cells have just begun their growth and division cycle; that is, at an early stage in anther and tapetal development compared to the time of normal meiosis. The "premeiotic" resting stage, as well as the prophase itself, are much curtailed, and the sporocytes fail to grow to normal size. The pseudo-homeotypic division in the microsporocytes of *H. amplexicaule* enters prophase at a developmental stage similar to that of normal meiosis, but the growth of both sporocytes and tapetal cells between early prophase and metaphase is considerably less in cells which undergo the pseudo-homeotypic division than in other sporocytes of the same apomict which form bivalents. Either the duration of prophase is abnormally short, or the growth rate of both sporocytes and tapetum during this stage is abnormally slow. A third type of abnormal division, found only in the microsporocytes of *H. robustum,* similar to the "double reproduction" of chromosomes well known in *Spinacia* and other genera, is associated with an abnormally great growth of the sporocytes, and a slow growth of the tapetum. In every case meiosis with bivalent formation can take place only when prophase is initiated at the same time, is of the same duration, and growth of both sporocytes and tapetum is the same as in the normal meiosis of the sexual species.

In the ovules of all apomicts with failure of meiosis, the megasporocyte divisions take place later than in their normal sexual relatives, and the greater the delay of the divisions, the more they resemble somatic mitosis (Gustafsson, 1935*a,* 1938*a, b,* 1939*b;* Gentscheff and Gustafsson, 1940*a*). The divisions, when they occur, are carried through very rapidly, and, as in the microsporocytes, the prophase is much shorter than in normal meiosis. The delay, a prolonged resting stage, is usually associated with considerable growth and hydration or vacuolisation of either the cytoplasm or the nucleus, or both. Gustafsson has, therefore, advanced the hypothesis that the delay in onset of meiosis has produced a conflict between the meiotic tendency and certain forces of vacuolisation which normally act on the developing megaspore. These forces are said to inhibit meiosis. Fagerlind (1940*b*) has criticized this hypothesis, mainly on the grounds that with our present lack of knowledge of the physiology of meiosis, the concept of vacuolisation forces has little meaning. In addition to this criticism, there can be cited some observations which indicate that the observed vacuolisation and hydration are incidental phenomena, rather than any direct indication of the cause of the failure of meiosis. Stebbins and Jenkins (1939) pointed out that whereas in generative apospory the hydration or vacuolisation affects first the nucleus, then the cytoplasm, in somatic apospory the reverse is the case, and the invading nucleus looks normal until it has already replaced the megasporocyte. If vacuolisation forces were the primary causal factors in both somatic and generative apospory, they should act similarly in the two cases.

The abnormal meiotic processes in apomicts provide direct evidence on the two principal hypotheses about the relation between mitosis and meiosis, namely, the precocity theory of Darlington (1932, 1937) and the retardation theory of Sax and Sax (1935). Darlington maintains that the chromosomes attract each other in pairs when single, but not when double; that normally the chromosome is single in the resting stage and divides before the onset of the mitotic prophase. The onset of meiotic prophase, however, is said to be precocious, so that the chromosomes have not yet divided and, being single, are able to pair. Sax and Sax, on the other hand, maintain that meiosis is occasioned by a retardation and prolongation of the prophase, permitting the chromosomes to uncoil more completely than they ever do in the meiotic prophase, so that linear point-by-point pairing is possible. Beasley (1938) has added the important observation that, while the onset of both mitotic and meiotic prophase is accompanied by a conspicuous growth and water intake of the nucleus, this process is much greater in the prolonged prophase of meiosis than in mitosis.

As was pointed out by Bergman (1935*a, b*), Darlington's hypothesis is well supported by behavior of the megaspore mother cells of many apomicts, which begin their first division abnormally late, and carry out either a semiheterotypic, a pseudohomeotypic, or a mitotic division. The situation in the anthers of *Hieracium*, however, is in direct contradiction to the precocity hypothesis, since there an abnormally early onset of prophase leads to the same mitosis-like abnormalities. In fact, no hypothesis which lays primary stress on the time of onset of the division can be reconciled with the situation in both the anthers and the ovules of apomicts.

On the other hand, the emphasis placed by Sax and Sax upon the condition of the entire nucleus during prophase is well supported by the evidence from apomicts. In every instance in which meiosis is replaced by some type of division in which pairing is omitted, whether the onset of the division is precocious or delayed, both the long duration of prophase and the sudden rapid growth of the nucleus are absent. In the anthers, both nuclei and cells usually remain abnormally small (Gentscheff and Gustafsson, 1940*a*). In the ovule the megaspore mother nuclei remain in the interphase condition at the time when meiosis would normally take place, and grow gradually. When they are ready to enter prophase, the normal time for meiosis is long past, and the initial nuclear size permits no such rapid growth as accompanies early meiotic prophase in sexual plants. This is clearly shown by observation of megaspore mother nuclei in *Antennaria* (Stebbins, 1932*b*) in which the ovules of neighboring florets may, on the one hand, go through an abnormal but in many ways characteristic type of meiosis, and, on the other, a prolonged resting stage followed by somatic mitosis and generative apospory. The nuclei which are in pachytene, prepared for meiosis, are many times larger than those in the resting stage and destined to undergo generative apospory.

To be sure, the phenomenon of meiosis cannot be really understood until the cause is discovered of the prophasic nuclear growth and chromosome uncoiling. Nevertheless, the suggestion of Oehlkers (1937), that meiosis and chromosome pairing are governed by the entire physiology of the plant, is a step in this direction which is well supported by the evidence from apomicts. In particular may be cited the relation between the behavior of the tapetal cells and the sporocytes in apomicts with abnormal meiosis.

Gentscheff (1937; Gentscheff and Gustafsson, 1940*a*) found that the abnormal divisions of the P. M. C.'s of some *Hieracium* apomicts were associated with an abnormally weak growth of the tapetal cells. Stebbins and Jenkins (1939) found that in an apomict of *Crepis acuminata* in which the P. M. C.'s always degenerate in early meiotic prophase, this degeneration is always preceded by the abnormal appearance and the degeneration of the tapetal cells.

Gustafsson (1939*b*) has, on the basis of these observations, advanced the hypothesis that the failure of meiosis is due to inhibiting substances released by the degenerating cells. An equally plausible alternative is that certain substances necessary for meiosis are normally transmitted to the P. M. C.'s by the tapetum, so that any influence, external or internal, which disturbs the normal function of these latter cells also inhibits meiosis. Two recent experiments make more likely the latter hypothesis. Zürn (1939) found that in flower stalks of *Oenothera* that were cut and placed in water, meiosis took place very quickly and chromosome pairing was reduced, while the abnormalities of both the tapetum and the tetrad nuclei resemble closely those found in *Hieracium* apomicts. On the other hand, stalks of the same plants placed in glucose solution were quite normal as to both meiosis and tapetal development. Gregory (1940) concluded from culture experiments with excised anthers and inflorescences that certain accessory substances necessary for meiosis are supplied by the vegetative organs of the plant. On this basis, the genetic complexes producing the abnormal meiosis of apomicts could act either through inhibiting the formation of these substances or through affecting the ability of the tapetal cells to absorb them and transmit them to the P. M. C.'s. At any rate, the problem of the relation between mitosis and meiosis is now open to experimental attack through the medium both of environmentally and of genetically controlled abnormalities.

APOMIXIS AND THE ALTERNATION OF GENERATIONS

As has been already stated by several students of the subject (Bower, 1935), our knowledge about apomixis has a definite bearing on the theories of the alternation of generations. In cases of stabilized recurrent apomixis, involving either apospory or apomeiosis, there is a regular alternation of morphological gametophyte and sporophyte generations without any change in the chromosome number. Furthermore, we now know many cases of haploid sporophytes and of diploid or polyploid gametophytes (*cf.* Wettstein, 1928), and in no case does the lowered or raised chromosome number make the sporophyte resemble in any way the gametophyte, or the gametophyte the sporophyte. In other words, the evidence from apomixis has demonstrated conclusively that the haploid-diploid chromosome cycle and the morphological alternation of generations are not necessarily interdependent. Either one can take place without the other.

This concept is strengthened by the remarkable mutant form found by Andersson-Kottö (1932, 1936; Andersson-Kottö and Gairdner, 1936) in *Scolopendrium vulgare,* in which a single recessive gene produces a gametophyte-like aposporous plant. This worker has concluded that the morphological sporophyte and gametophyte are primarily physiologically controlled growth phases, which are normally integrated into the life cycle as a whole, and are usually associated with, but not caused by, the changes in the chromosome number.

Andersson-Kottö did not apply her findings to the theories of the alternation of generations, as recently discussed by morphologists (Bower, 1935; Eames, 1936), but this application may nevertheless be appropriately made here. Bower (1935) has rightly, in the opinion of the reviewer, pointed out that the terms "antithetic" and "homologous," as applied to the opposing theories for the nature of the alternation of generations, have in themselves caused much difficulty because they are not explicit, and has suggested that the terms "interpolation theory" and "transformation theory" be substituted. The use of these terms reduces the controversy to the definite historical question of how the alternating cycle originated, a question to which the answer lies outside the realm of cytogenetics. It is evident, however, from the facts stated above, that neither theory can rely for its support on cytological, genetical or physiological evidence. That in heterozygous "peculiar" plants of *Scolopendrium* the jump from sporophyte to spermatozoid can be taken with the gametophytic stage omitted shows that the interpolation of a gametophytic or a sporophytic stage into the life cycle by means of a genetic change or changes, is not inconceivable, while the presence in many apomicts of a morphological alternation of generations without alteration of the chromosome number shows that this could have been the original condition. Furthermore, the recent work on *Rubus* and *Hypericum* (Petrov, 1939; Noack, 1939) has shown that the egg of an aposporous diploid gametophyte can be fertilized and give rise to vigorous hybrid offspring. This shows that under certain conditions a gametophyte, both typical morphologically and normal in its physiological capabilities, can arise as a state in the vegetative somatic growth cycle of a sporophyte-like plant.

HYPOTHESES AS TO THE CAUSE OF APOMIXIS

To explain the appearance of apomixis in plants, four different agencies have been invoked. These are hybridization, polyploidy, genetic factors and necrohormones. The hybridization hypothesis of Ernst (1918) is now widely known, and is fully discussed elsewhere (Rosenberg, 1930; Darlington, 1932, 1937; Sharp, 1934; Gustafsson, 1935*a*). It is based on two assumptions: first, that all apomicts are of hybrid origin; and second, that the meiotic disturbances found in apomicts are occasioned by hybridity, and that these disturbances are responsible for the formation of diploid gametophytes and egg cells, or for the degeneration of haploid gametophytes. The first assumption holds nearly as well now as when first postulated. The great majority of apomictic forms among the higher plants are probably allopolyploids, or back-cross derivatives from allopolyploids, and therefore ultimately of hybrid origin (Stebbins, 1932*b;* Gustafsson, 1933; Babcock and Stebbins, 1938; Stebbins and Babcock, 1939). In *Crepis, Antennaria* and probably other genera (Babcock and Stebbins, 1938), many of the polyploid apomicts are morphologically very similar to certain diploid sexual species, so that the apomicts are, from the systematic point of view, intraspecific polyploids. Although this evidence points toward an autopolyploid origin for them, cytological studies of some of these same apomicts indicate an allopolyploid origin (Stebbins and Jenkins, 1939). In some cases, however, such as *Hieracium umbellatum* f. *apomictica* (Bergman, 1935*a*) and certain *Rubus* apomicts (Thomas, 1940), both the cytological and the taxonomic evidence suggests an autopolyploid or non-hybrid origin. Such apomicts may have been derived from sexual diploid forms by the direct doubling of the chromosome set.

The second assumption has become much more difficult to hold in the light of new discoveries about apomicts. As mentioned above, the meiotic abnormalities are often very different in the ovules from those found in the anthers. In a large number of apomicts of hybrid origin, the abnormalities which lead to the formation of diploid gametophytes are definitely greater than would be expected on the assumption that they are caused solely by lack of homology between the parental chromosomes (Gustafsson, 1935*a*), while in other cases these abnormalities are due wholly or in part to autopolyploidy (Thomas, 1940). They could not, therefore, be the result of hybridity alone. The view now held by most students of the subject (Rosenberg, 1930; Bergman, 1935*b;* Gustafsson, 1935*a;* Stebbins and Jenkins, 1939; Fagerlind, 1940*b*) is that hybridity is an accompanying phenomenon but not a causal agent of apomixis. The hybrid origin of most apomicts is not difficult to explain on other grounds. In hybrid derivatives, many of which are sterile as to their sexual reproduction, parthenogenesis is of high survival value, and so would be favored by natural selection (Darlington, 1937; Thomas, 1940). This is particularly important when we realize that many of these forms show hybrid vigor, or favorable new combinations of the characteristics of their parental species, which enable them to invade habitats not previously occupied by any of their relatives (*cf.* Babcock and Stebbins, 1938).

The close correlation between apomixis and polyploidy has been noted by all students of this subject. Darlington (1932, 1937) has listed four apomicts purportedly diploid, but his list must be modified since three of the species listed by him, *Chondrilla juncea* (Poddubnaja-Arnoldi, 1933), *Zephyranthes texana* (*cf.* Sato, 1938) and *Allium odorum* (Modilewski, 1930), are all now known to be polyploids. A revised list of apomictic or partially apomictic diploids includes the following species: *Alnus rugosa* (Woodworth, 1930), *Potentilla argentea formae* (Müntzing, 1928, 1931) and *P. arguta* (Popoff, 1935), various species of *Citrus, Poncirus* and *Fortunella* (Frost, 1925, 1926, 1938*b*) and *Eugenia* spp. (Pijl, 1934). The multitude of other apomicts now known are polyploids with anywhere from 3 to 15 times the basic haploid number for the genus; the last number in *Potentilla* (Clausen, Keck and Hiesey, 1940). The significance of this correlation is not yet understood. Polyploidy itself can not be the cause of apomixis, since the sexual polyploid plants greatly outnumber the apomicts. Furthermore, as Gustafsson (1935*a*) has pointed out, sexual polyploids exist in a number of genera, such as *Rubus, Rosa* and *Antennaria,* in which apomictic polyploids are also known. In *Rubus,* apomixis is prevalent in the European species of the subgenus *Eubatus,* but their close relatives in America, although mostly polyploid, are only rarely apomictic (Gustafsson, 1930; Crane and Thomas, 1939). In *Taraxacum* both autopolyploids (Kostoff and Tiber, 1939) and interspecific hybrids (Koroleva, 1939; Poddubnaja-Arnoldi, 1939) have been produced artificially from diploid sexual species of which the natural polyploid relatives are all apomictic. None of these artificial creations showed any signs of apomixis. This is strong evidence that neither interspecific hybridization nor polyploidy alone is responsible for apomixis in this genus.[1]

The first evidence that apomixis may be at least in part governed by genetic factors was obtained by the experiments of Ostenfeld (1910) on *Hieracium*. That from the *Rubus* hybrids of Lidforss (1914), as interpreted by Gustafsson (1930) is, however, more definite. In *Rubus* there is evidently a single recessive factor which determines the presence or absence of pseudogamous development. On the other hand, Müntzing (1940) found that in a cross between a sexual and an apomictic biotype of *Poa alpina*, not only was the entire F_1 population apparently sexual, but, in addition, out of 31 F_2 plants tested, none was completely apomictic. Müntzing concludes, therefore, that the mechanism of inheritance of apomixis in *Poa* must be more complex than a single recessive gene. The presence in this genus of many biotypes showing all degrees of development of apomixis supports this conclusion.

Apospory without apomixis is conditioned by recessive genetic factors in *Scolopendrium* (Andersson-Kottö, 1932) and *Leontodon hispidus* (Bergman, 1935*b*). The aposporous *Leontodon* plant gave normal progeny after open pollination, but upon selfing segregated not only for apospory but for asynapsis as well, suggesting a genetic connection of some kind between the factors producing these two types of abnormality. The presence of recessive genes producing asynapsis and other meiotic abnormalities is now, well known (*cf.* Sharp, 1934; Darlington, 1937). Since, as has been shown above, the presence of apomixis is correlated with and partly conditioned by abnormalities of meiosis produced by causes other than non-homology of the chromosomes, there is good reason to believe that the underlying tendencies toward apomixis are produced by genetic mechanisms similar in their effect on the plant to these known genes. That such genetic mechanisms may be widespread and not infrequent in the higher plants is suggested by the presence of occasional apospory in a number of normally sexual plants in addition to those already mentioned (*cf.* Bergman, 1935*b*). *Oxyria digyna* (Edman, 1929), *Antennaria dioica* (Haberlandt, 1923*b*), *Coreopsis bicolor* (Gelin, 1934) and *Picris hieracioides* (Bergman,

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[1] The writer has not been able to see the paper of Christoff (1940) which apparently deals with this same subject.

1935*b*) are all examples of this. It is particularly significant, as Bergman has pointed out, that the majority of these examples are in the Compositae, a family which contains an exceptionally large number of apomictic genera.

The hypothesis now held by most students of apomixis, therefore, is that the original tendencies toward this process are genetically controlled, either by single recessive genes or more likely by constellations of complementary factors. Hybridization is probably important in bringing together complementary factors (*cf.* Rosenberg, 1930), and undoubtedly plays a large rôle through the production of vigorous sterile or partly sterile types in which apomixis has a very high selective value. Polyploidy is usually necessary for the full expression of these genes, and probably acts as a modifying agent by changing the physiological condition of the cells. This hypothesis is highly plausible and can be attacked experimentally from several different angles.

Haberlandt (1923*a, b*) developed the theory that the stimulus for apomixis is supplied by necrohormones produced by degenerating cells in the vicinity of those that develop. Gustafsson (1935*a*) and Stebbins and Jenkins (1939) have shown, however, that diploid gametophytes may start development by either diplospory or apospory before any of the somatic cells of the ovule has started to degenerate, indicating that the necrohormone theory cannot account for the apomeiotic development of the gametophyte. Gustafsson (1935*a*, 1938*a*) suggested that Haberlandt's hypothesis may have a limited application to the pseudogamous development of the diploid egg cell, but later evidence (Gentscheff and Gustafsson, 1940*b*) casts considerable doubt on even this suggestion.

APOMIXIS IN RELATION TO SPECIES DIFFERENTIATION AND PLANT DISTRIBUTION; THE AGAMIC COMPLEX

The development of apomixis in a group of plant species has the following two important effects on its evolution. First, by means of this process a species complex gives rise to innumerable microspecies, or "clonal species" (Darlington, 1932, 1937) which are genetically constant and are separated from their nearest relatives by the most minute differences. Second, through the perpetuation by apomixis of sexually sterile hybrid derivatives, the genetic and morphological barriers between the original species from which the apomicts arose are obliterated, so that in any predominantly apomictic group distinct species comparable to those found in sexually reproducing organisms cease to exist (Dobzhansky, 1937; Babcock and Stebbins, 1938). These two facts have long been recognized as the underlying causes of the taxonomic difficulty of such genera as *Hieracium, Taraxacum, Antennaria,* and some sections of *Rubus.*

As a result of their studies on the largely apomictic American species of *Crepis,* Babcock and Stebbins (1938) concluded that the best way to analyze a species complex in which polyploidy and apomixis are prevalent is on the basis of its diploid sexual members. They found that among the apomictic forms an enormous number of "micro-species" could be recognized, all forming a more or less continuous series of intergrading forms, but that not a single one of these possessed any new morphological characteristics. Every feature of the apomicts could be explained either as a result of the recombination of characteristics found in two or more of the seven sexual diploids, or as the direct result of an increase in the chromosome number. Furthermore, the seven diploids are very distinct from each other. The difficulties which botanists have had in distinguishing between these species are due entirely to the presence of auto- and allopolyploid apomicts. Such a species complex was called an *agamic complex* (Babcock and Stebbins, 1938). Agamic complexes are probably numerous and widespread throughout the angiosperms. The following is a list of genera in which the presence of an agamic complex is definitely established (listed in capital letters) or may be inferred (listed in italics). There are, of course, species groups in all of these genera in which apomixis does not occur. For the method of apomixis, the following abbreviations are used: V = vegetative apomixis; AE = adventive embryony; SA = somatic apospory; GA = generative apospory; D = diplospory or semiapospory; P = parthenogenesis; Ps = pseudogamy. In some genera more than one method occurs. The reference list aims to be complete only for the more recent publications; the older references are purposely omitted when they are well reviewed by Ernst (1918), Schnarf (1929) and Rosenberg (1930).

Several other genera are listed by Schnarf which may contain regularly apomictic species, but the evidence in these is either disproved or needs further confirmation. Among these are *Notho-*

TABLE I

Agamic Complexes in Angiosperms

Family	Genus	Method	References
Gramineae	FESTUCA	V	Turesson, 1926, 1930, 1931; Flovik, 1938
	POA	V; SA, GA + Ps	Müntzing, 1933, 1940; Akerberg, 1936, 1939; Kiellander, 1935, 1937; Flovik, 1938; Brown, 1939; Tinney, 1940; Tinney and Aamodt, 1940; Engelbert, 1940
	Deschampsia	V	Flovik, 1938
	Calamagrostis	GA + P	Stenar, 1935
Liliaceae	*Allium*	V; AE + P	Haberlandt, 1923*a*, *b;* Modilewski, 1930; Cappeletti, 1931; Weber, 1929; Levan, 1940
	Funkia (*Hosta*)	AE	Schnarf, 1929; Rosenberg, 1930
	Zephyranthes	GA + Ps	Pace, 1913; Sato, 1938
Burmanniaceae	*Thismia*	GA + P	Ernst, 1918; Schnarf, 1929; Rosenberg, 1930
Orchidaceae	*Nigritella*	AE	Afzelius, 1928, 1932
	Zygopetalum	AE	Suessenguth, 1923
Saururaceae	*Houttuynia*	D, GA + P	Okabe, 1930
Betulaceae	*Alnus*	AE	Woodworth, 1930
Urticaceae	*Elatostema*	GA + P	Ernst, 1918; Schnarf, 1929; Rosenberg, 1930
Balanophoraceae	*Balanophora*	GA + P	Ernst, 1918; Schnarf, 1929; Rosenberg, 1930; Zweifel, 1939
Polygonaceae	*Athraphaxis*	AE; SA + P	Edman, 1931
Ranunculaceae	*Ranunculus*	?	Marsden-Jones and Turrill, 1935; Metcalfe, 1939
Rosaceae	*Pyrus,* subg. *Malus*	SA + P	Dermen, 1936
	Pyrus, subg. *Sorbus*	SA + P	Liljefors, 1934
	POTENTILLA	SA + Ps	Müntzing, 1928, 1931; Popoff, 1935; Gentscheff, 1938; Gentscheff and Gustafsson, 1940*b;* Clausen, Keck and Hiesey, 1940

TABLE I (*Continued*)

FAMILY	GENUS	METHOD	REFERENCES
	RUBUS	SA + Ps	Focke, 1910–14; Lidforss, 1914; Gustafsson, 1930, 1939*a;* Darrow and Waldo, 1933; Vaaramo, 1939; Petrov, 1939; Crane and Thomas, 1939; Thomas, 1940
	Alchemilla	AE, SA + Ps	Rosenberg, 1930; Gustafsson, 1935*a*, 1939*b;* Gentscheff and Gustafsson, 1940*b*
	Rosa, sect. *canina*	AE?	Täckholm, 1922; Schnarf, 1929; Gustafsson, 1931*a, b*
Rutaceae	CITRUS	AE	Frost, 1925, 1926, 1938*a, b;* Swingle, 1932; H. J. Webber, 1931, 1932; J. M. Webber, 1940
Euphorbiaceae	*Coelebogyne* (*Alchornea*)	AE	Schnarf, 1929; Rosenberg, 1930
	Euphorbia	AE	Schnarf, 1929
Buxaceae	*Sarcococca*	AE	Schnarf, 1929; Wiger, 1930
Anacardiaceae	*Mangifera*	AE	H. J. Webber, 1931; Juliano and Cuevas, 1932; Juliano, 1934, 1937
Ochnaceae	*Ochna*	AE	Chiarugi and Francini, 1930
Guttiferae	*Garcinia*	AE	Sprecher, 1919; Horn, 1940
Hypericaceae	*Hypericum*	SA + Ps	Noack, 1939
Cactaceae	*Opuntia*	AE	Schnarf, 1929; Archibald, 1939
Myrtaceae	*Eugenia*	AE	Schnarf, 1929; Pijl, 1934; Johnson, 1936
Thymeleaceae	WIKSTROEMIA	D, GA + P	Fagerlind, 1940*b*
Gentianaceae	*Cotylanthera*	D + P	Oehler, 1927 (?*cf.* Gustafsson, 1935*a*)
Compositae	*Eupatorium*	GA + P	Holmgren, 1919
	ERIGERON	D, GA + P	Holmgren, 1919; McDonald, 1927; Schnarf, 1929; Rosenberg, 1930; Oka, 1935

TABLE I (*Continued*)

Family	Genus	Method	References
	ANTENNARIA	GA + P	Rosenberg, 1930; Stebbins, 1932*a*, *b*, 1935; Bergman, 1935*c*, 1937
	Arnica	GA + P	Afzelius, 1936
	CHONDRILLA	D + P	Poddubnaja-Arnoldi, 1933
	TARAXACUM	D + P	Schnarf, 1929; Rosenberg, 1930; Gustafsson, 1932, 1935*a*, *b*, 1937; Poddubnaja-Arnoldi and Dianova, 1934. 1937; Turrill, 1938*a*, *b*; Koroleva, 1939; Erlandsson, 1939
	CREPIS (American spp.)	SA + P	Hollingshead and Babcock, 1930; Babcock and Stebbins, 1938; Stebbins and Jenkins, 1939; Stebbins and Babcock, 1939
	Youngia, sect. *Crepidopsis*		Hollingshead and Babcock, 1930; Babcock and Cameron, 1934; Babcock and Stebbins, 1937
	Ixeris	GA + P	Okabe, 1932
	HIERACIUM	SA, GA + P	Ostenfeld, 1910, 1921; Rosenberg, 1917, 1927, 1930; A. H. Gustafson, 1933; Christoff and Popoff, 1933; A. Gustafsson, 1934*a*, 1935*a*, *b*; Gentscheff, 1937; Gentscheff and Gustafsson, 1940*a*

scordum, Spiranthes, Ficus, Helosis (*cf.* Fagerlind, 1928), *Calycanthus, Thalictrum* (*cf.* Kuhn, 1928) and *Erophila.*

The systematic structure of an agamic complex can be understood only when its diploid sexual members are all known, and the limits of their variability have been determined. These may be looked upon as the pillars of the complex, while the apomicts represent its vast, intricate superstructure. Only in the relatively small and geographically restricted complex of *Crepis* has this type of analysis been carried out, although in *Rubus, Antennaria* and *Taraxacum* considerable progress has been made in this direction.

The primary causes of the polymorphism of agamic complexes are, therefore, hybridization, polyploidy and apomixis. Their origin may be pictured in the following manner. In the first place is a group of diploid species, each one well defined systematically, quite distinct from all the others and forming more or less sterile hybrids with them. The species then intercross, and either by somatic or gametic doubling, allopolyploids are produced. An alternative is the initial formation of autopolyploids and subsequent hybridization; either order of events leads to the same eventual result. Then, through the action of complexes of complementary genes brought together by hybridization, by the selection of successive mutations, or by some similar process, apomixis develops. There has been some discussion as to whether the onset of apomixis in such complexes is gradual or sudden. The gradual evolution of this process seems most likely in those complexes in which somatic apospory is present, such as *Hieracium* subg. *Pilosella, Potentilla, Crepis* and *Poa.* These complexes contain many facultative apomicts which regularly produce some sexual offspring. In *Crepis* there is evidence that the obligate apomicts have arisen from the facultative ones (Babcock and Stebbins, 1938).

In those with diplospory or generative apospory obligate apomicts are much more frequent, or are the only types known, as in *Hieracium* subg. *Archieracium* and *Taraxacum* (Gustafsson, 1935*a*). Gustafsson (1935*a*) follows Ernst (1918) in the belief that apomixis has arisen all at once in these groups. His chief argument in favor of this is that "an entirely new type of division had to be introduced in the peculiar kind of parthenogenesis occurring in *Antennaria* and *Hieracium.*" In the opinion of the reviewer this argument is not very strong in the light of Gustafsson's own observations. The "mitotised" divisions which produce the diploid gametophytes in the ovules of these apomicts are merely extreme forms of a series grading toward normal meiosis. Furthermore, the nature of the division is dependent partly upon both the external and the internal environment. Hence, although no such form has yet been found, the existence of a facultative apomict in which some ovules produce diploid gametophytes by means of diplospory, and others haploid ones by means of meiosis, can be postulated without difficulty. Gustafsson's second argument, that in these groups there occur only apomicts derived directly from sexual forms, and with triploid or tetraploid chromosome numbers, does not hold for *Antennaria* or for recent observations on *Taraxacum* (Erlandsson, 1939). Babcock and Stebbins (1938) have suggested that in most or all agamic complexes facultative apomicts precede obligate ones in the development of the complex. The presence of exclusively obligate apomicts in a complex or a section of one may indicate that the group is relatively old, and considerably removed from its sexual ancestors. In the parthenogenetic *Antennarias,* staminate plants, which could arise most easily by occasional sexual reproduction, are usually most frequent within or near the ranges of the sexual ancestors of these apomicts, suggesting that facultative apomicts exist only or chiefly in these regions. The question of the gradual or sudden onset of apomixis is one of the many which must be answered by future observation and experimentation.

The importance of this question lies in its bearing on the origin of polymorphism in agamic complexes. In complexes with initial facultative apomixis, occasional back- and out-crossing, with subsequent segregation, best explain this polymorphy, and this explanation fits very well the pattern of variation found in *Crepis* (Babcock and Stebbins, 1938). If, however, obligate apomixis sets in immediately after chromosome doubling, either in a species or an F_1 hybrid, the secondary back-cross and triple or quadruple hybrid types which appear to be characteristic of agamic complexes can not be formed. Polymorphism could arise, however, in three different ways. First, there might exist fertile sexual allopolyploids, of which various biotypes could from time to time become apomictic. Such sexual forms are now known to exist in *Poa* (Müntzing, 1940) and *Antennaria* (Gustafsson, unpubl.). Second, there might be occasional loss or non-disjunction of chromosomes in one of the critical divisions of the apomictic cycle, leading to variant aneuploids. This process may have been very important in *Poa alpina* and *Poa pratensis,* in which many aneuploid clones exist (Müntzing, 1933, 1940). Third, the process of "apogamic mutation," found by Ostenfeld (1921) in an obligate apomict of the subgenus *Archieracium,* may take place. Darlington (1932, 1937) has sought to explain these "mutations" as the result of pairing and chiasma formation in dissimilar chromosomes, with subsequent formation of restitution nuclei and the segregation in the following division of the new crossover chromosomes. This explanation has been accepted by Bergman (1935*a*, *b*). Gustafsson, however, although he examined "tens of thousands of ovules" (1935*a*) of *Hieracium* at the correct stage, found only 19 prophases with the chromosomes differentiated, and says "there is no evidence of any chromosome pairing at prophase." This reviewer has examined thousands of ovules of *Antennaria* without finding restitution nuclei (Stebbins, 1932*b*). In this genus the division of the archesporial cell is essentially mitotic, or there is an abnormal meiosis which always leads to tetrad formation (Bergman, 1935*c*). There is, therefore, no evidence that the processes postulated by Darlington take place in the formation of the apomictic female gametophyte of these genera.

In *Citrus* (Frost, 1926) there are cases of undoubted apomictic mutation which can not be explained on Darlington's hypothesis, since the apomictic embryos are in this genus adventitious. The most frequent mutants found were albino or variegated seedlings, but some mutations from navel and seedless to non-navel and seedy fruits were also found. These were interpreted as due first to the highly heterozygous condition of the clones, which would make possible the manifestation of many recessive genes simply by the mutation of their dominant alleles; and second, to the possible chimaeric condition of the tissue from which the mutant embryos arose, which would make possible the occurrence of a genetic change at almost any stage in the development of this tissue. The latter hypothesis is strongly supported by the occasional appearance of tetraploid adventitious embryos. Frost has concluded (1938*a*) that "nucellar embryony, by favouring the evolution of excessive heterozygosis, has been a dominant agency in establishing the remarkable generative and somatic variation of *Citrus*." This conclusion may be of wide application to agamic complexes in general.

The systematic treatment of the agamic complex is one of the most difficult problems confronting the taxonomist. The method which has been widely adopted by Scandinavian botanists, who have done most of the work on these complexes, has been to describe each apomict as a distinct species. This practice has been defended by Du Rietz (1930) and more recently by Marklund (1938) and Darlington (1940) on the following grounds. First, different sexual species, even within the same genus, may differ widely from each other in the amount of intraspecific variation that they contain, so that there is nothing inconsistent in the recognition of absolutely constant species separated from each other by minute differences, provided there is no intergradation. Second, if the apomicts are not regarded as distinct species, there are no larger entities which can be clearly separated from each other. The definition of species as entities separated from each other by a series of morphological characteristics which show no intergradation or overlapping is impossible in agamic complexes unless the individual apomicts are considered as species. The explanation for this fact is, of course, the hybrid origin of a majority of the apomicts.

Although these arguments themselves have not been refuted, the practice of recognizing individual apomicts as species of the same taxonomic rank as the species of sexual groups has been attacked by Müntzing, Tedin and Turesson (1931), Fernald (1933), Turrill (1938*a, b*) and Babcock and Stebbins (1938). The first objection which has been raised is that the recognition of apomicts as species has produced such a bewildering swarm of "species" that none but the specialist can have the remotest conception of their interrelationships. There is good reason to believe that even the *Taraxacum* and *Hieracium* specialists, or at least a considerable number of them, have focused their attention so long on minute differences that they can not fully understand their genera as wholes; "they can not see the forest for the trees." Secondly, in complexes containing sexual and apomictic forms which parallel each other in their morphological variation, the two standards of species delimitation become absurdly incongruous. In *Crepis acuminata,* for instance (Babcock and Stebbins, 1938), and in *Poa alpina* (Müntzing, 1940) there is a series of autopolyploid apomicts of which the morphological variation is entirely within the range of the sexual form. The recognition of these apomicts as species would create a series of species which would be morphologically indistinguishable from another series of completely interfertile biotypes. A similar situation was found by Gustafsson (1937) in a sexual population of *Taraxacum,* and very probably exists in other species containing autopolyploid apomicts, such as *Hieracium umbellatum.*

Babcock and Stebbins (1938) have proposed another method of treating these complexes, in which the different sexual forms are the basis of species delimitation. This reduces the number of species enormously, and makes the complexes more nearly comparable systematically to the related sexual groups. The apomicts may be described if they are important for any reason, particularly in connection with problems of plant geography (see below), but are not given taxonomic recognition, so that they will not clutter up the indices and floras. One drawback to this method is that an intimate knowledge of the entire complex is necessary before the method can be applied to any part of it. The sexual forms may be very restricted in distribution, and may occur in such remote regions that they are not available for study, but until they are all known, the complex can not be understood. If, as is quite possible, some of the sexual ancestors are extinct, the complex becomes particularly difficult to analyze, and the method may have to be modified.

Agamic complexes, although they most certainly are anomalous or "freakish" from the systematic point of view, nevertheless deserve careful study, since they can provide us with much valuable information on plant distribution, both present and past (Gustafsson, 1935*b*; Turrill, 1938*a, b*; Babcock and Stebbins, 1938). In the first place, a large part of their phylogenetic history can be placed on a sound factual rather than a speculative basis. There is no doubt that the apomicts have been derived from the sexual members of the complex; hence the geographic regions or climatic provinces occupied by the sexual species are those from which the complex originated, while those inhabited by apomicts only have been occupied relatively recently. Thus northeastern California has been established as the main center of origin of the *Crepis* complex, while its members in the Rocky Mountains are all derived. The centers of origin of some other agamic complexes is also suggested by what we know of the distribution of their sexual members. The central Appalachian mountain region is the center for *Antennaria* in temperate eastern America, and contains five sexual species (Stebbins, 1935), while additional centers for this large agamic complex are in the central Rocky Mountains, the Sierra Nevada and Alaska. Most of the *Taraxacum* species known to be sexual center about southeastern Europe and southwestern Asia (*cf.* Gustafsson, 1932), which is undoubtedly the center of origin for the genus, but the occurrence of three sexual species in the Thian-Shan mountains of west central Asia (Poddubnaja-Arnoldi and Dianova, 1934) suggests that this may be an important secondary center, and perhaps one in which many of the widespread groups of Arctic apomicts originated.

Furthermore, apomicts are excellent material for experiments on the effect of the environment on the genotype (Curtis, 1940) and on natural selection (Sukatschev, 1932). Also, because of their narrow range of tolerance and their morphological uniformity, they serve as excellent indicators of plant communities and as key species for the tracing of plant migrations (Gustafsson, 1935*b;* Babcock and Stebbins, 1938; Stebbins and Babcock, 1939). Also, on the basis of their populations of apomicts, the relative ages of different floras can be estimated. Those which are young should have a large proportion of apomicts, while the older floristic regions should contain the sexual members of several different agamic complexes. In this connection it is interesting to note that the distributional centers of the American *Crepis* complex in northeastern California and of the eastern American *Antennaria* in the Appalachians are both areas considered by plant geographers to have an ancient flora (Babcock and Stebbins, 1938; Fernald, 1931). On the other hand, 5 of the 12 genera listed by Fernald as "heteromorphic tangles" found in the youthful areas of the eastern United States are known to include agamic complexes, while the flora of the recently glaciated Scandinavian region has also a very large proportion of apomicts. The application of the distribution of apomicts to several specific problems in the plant geography of the western United States has been made by Babcock and Stebbins (1938) while Gustafsson (1935*b*, 1939*a*) has made similar use of the apomicts of *Taraxacum* and *Rubus* in Scandinavia.

From the evolutionary point of view, the agamic complex is a "closed system" which will never give rise to anything except new combinations of a given series of characteristics. Apomicts are splendid "opportunists"; due to the remarkable polymorphism of the complexes and often the hybrid vigor of the apomicts, they are frequently aggressive weeds, like the dandelions and hawkweeds. They are, however, adapted to taking great advantage of conditions prevailing when they come into existence, rather than to adjusting themselves to changing conditions over a long period of time. When separated from their sexual ancestors, apomicts will in time become relic species and die out (Babcock and Stebbins, 1938). Apomixis, therefore, is not a major factor in evolution, however important it is in increasing the polymorphism and the geographic distribution of the genera in which it is found.

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