# FLOWER ABNORMALITIES

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## INTRODUCTION

Because of its possible importance for future research, it seemed advisable to begin a study of the available information on abnormal flowers. Most references to abnormal structure of plants are in papers dealing primarily with other subjects. Obviously, study of all contributions relating to flowering plants is an impossible task. The primary concern of this review is to collect information about the various external and internal factors which can cause development of sepals, petals, stamens, or pistils, or of their constituent parts, particularly their development in parts of the plant or parts of the flower where they normally do not occur. Although published reports of abnormal flowers are few and widely scattered after 1900, only papers of exceptional interest are discussed if they appeared before that date, when the science of genetics began to develop. Because there are several excellent reviews of the literature on male-sterility of plants, papers dealing exclusively with that subject will be omitted.

Among the unexplored areas in the field of biology, organ differentiation may well be the most challenging. Abnormal flowers could be particularly useful for studying the process of differentiation, for the following reasons. (1) Most Angiosperms produce many flowers. In nearly all instances the flowers of any one plant are genetically identical. Consequently, it is possible to study variability within one genotype as a single plant differentiates sets of reproductive organs (flowers) over and over. (2) Many flower abnormalities are heritable. Thus it is possible to study gene interactions and gene dosage effects when they influence the degree of abnormality expressed by the plant. (3) In many situations cytoplasm has significant effects on the expression of floral abnormalities. In some reciprocal crosses the different cytoplasms produce entirely different phenotypes. (4) The external environment can be very important. For some plants, abnormal differentiation can be promoted or suppressed at will by control of cultural conditions. (5) Given a combination of the four points listed above, i.e., an ever-blooming plant with a genetically controlled flower abnormality subject to modification by cytoplasm and environment, it should be possible to obtain new kinds of data about the processes and conditions which determine whether the apical meristem uses its genetic information for differentiating a leaf or for differentiating a carpel.

## METAMORPHOSIS OF FLORAL ORGANS

All of the organs of the flower are capable, in some plant or other, of developing in the form of any of the other organs present in the normal flower. Goethe's essay on metamorphosis (1790) is the best-known early statement of the theory that all appendices of the leafy shoot-leaves, bracts, sepals, petals, stamens, and pistils-are homologous. The ability of organs to undergo transformation was important in Darwin's development of his theories of natural selection and evolution. Masters quotes Darwin frequently in his "Vegetable Teratology" (1869), still one of the most useful check-lists for species likely to furnish structural surprises. Penzig's "Pflanzen-Teratologie" (1890), although incomplete, gives an exhaustive treatment of the abnormalities reported in the plant families discussed. Even though Worsdell's "The Principles of Plant Teratology" (1916) was published after the rediscovery of Mendel's laws of heredity, it too is entirely Nineteenth Century in outlook; nevertheless, his discussions of the phylogenetic implications of organ metamorphosis argue points still being raised in botanical literature. Table I lists the plants for which floral abnormalities have been reported. Bailey's classification of plants by families in "The Standard Cyclopedia of Horticulture" (1941) was used as the structural basis for the list. In nearly all instances the plants are listed under the names assigned to them by the original authors, even though the names often are known to be obsolete or suspected to be incorrect. Wherever possible, the original paper reporting the abnormality was checked, but in many older papers the literature citations are haphazard, incomplete, or entirely lacking. Author citations are frequently, perhaps usually, lacking from species names in the older papers. Because there is no way to determine what species a man actually studied in 1830, authorities for species have been omitted from the text wherever they could not be stated with confidence. For the same reason, and also because Table I is intended to suggest genera and perhaps families likely to furnish abnormalities, the species are listed in Table I without authors' names. Particular emphasis is given to reports published after 1900 in the following discussions of the various types of metamorphosis of floral organs.

#### PHYLLODY AND BRACTEODY

Phyllody is leaflike development of floral organs. In the most extreme form the organ involved is replaced by a foliage-type leaf. Any floral organ, even the ovule, may become leafy in form or color. Of all organs in the flower, the stamen is least likely to become phylloid. Since many authors do not distinguish between phyllody and bracteody in their reports, the two abnormalities will be considered together.

In photoperiodic plants the induction of flowering "switches" the meristems from vegetative growth to the production of flowering shoots and floral organs. Harder (1948), working with Kalanchoë blossfeldiana, found that with low stimulus for floral initiation the scalelike bracts of the inflorescence are subject to phyllody. However, among the thousands of flowers examined during his experiments, none of the floral parts were ever transformed to leaves. Raghaven (1961) and Raghaven and Jacobs (1961) reported the production of sterile structures resembling the cones of *Selaginella* when buds of *Perilla frutescens* (L.) Britt. grown in culture were maintained under long days. Indoleacetic acid in the medium produced similar effects. In preliminary experiments with *Petasites hybridus* (L.) Gaertn., Warldaw (1963) found that if an early transition apex was bisected it reverted to the vegetative state. Primordia which would have developed into bracts became normal leaves up to 10 cm. in width. Treatment with gibberellin partially or completely prevented reversion to the vegetative state.

Cold-requiring plants are also likely to develop phylloid floral organs under threshold levels of induction, or under treatment conditions which counteract some of the effects of the cold treatment. Thompson (1939) reports that sugar beets become vegetative at high temperatures even after the flower stem has grown to full height and the buds have developed. Chroboczek (1934) showed that when grown at 50-60°F. the garden beet developed seedstalks under a photoperiod of eight hours, but the seedstalks were barren. Detjen (1927) reported annual reversion of floral organs of cabbage to the vegetative state at irregular intervals. Tschermak (1932) found foliose calyces in over-wintered *Primula*. Hillman and Smith (1965) induced flowering in a vegetative clone of hybrid *Nicotiana* by a combination of gibberellic acid, low temperature, and short days. The abnormal petals shown in their illustrations are obviously phylloid. In the "green rose," a frondescent variety of *Rosa indica* Lindl. still commercially available, all of the organs of the flower are replaced by small, simple leaves which do not resemble the ordinary foliage-leaves of the plant.

Heritable phyllody has been reported for few genera. Recessive genes produce the phyllody reported in *Antirrhinum majus* L. by Baur (1924), *Torenia fournieri* Linden by Simon (1924), and *Zea mays* L. by Postlethwait and Nelson (1964).

Phyllody (also bracteody, chloranthy, or virescence) has been reported in the following genera:

Entire flower: Acer, Actaea, Agrostemma, Alyssum, Anagallis, Anchusa, Anemone, Angelica, Anthriscus, Apium, Aquilegia, Arabis, Arenaria, Barbarea, Begonia, Brassica, Brownea, Bunias, Cakile, Calendula, Capsella, Cardamine, Cerastium, Chelidonium, Corchorus, Corydalis, Crotalaria, Daucus, Delphinium, Desmodium, Dianthus, Dielytra, Dionaea, Diplotaxis, Dipsacus, Draba, Drosera, Epilobium, Erica, Erucastrum, Ervum, Erysimum, Eudianthe, Euphorbia, Fragaria, Galanthus, Galega, Geranium, Geum, Gilia, Gronovia, Helleborus, Hesperis, Isatis, Juncus, Lavatera, Lathyrus, Lilium, Lunaria, Lupinus, Lychnis, Lysimachia, Mathiola, Matricaria, Medicago, Melianthus, Melilotus, Myosotis, Myrrhis, Nicotiana, Nigella, Nymphaea, Pelargonium, Peltaria, Petasites, Pisum, Polygala, Potentilla, Poterium, Primula, Prunus, Ranunculus, Raphanus, Reseda, Rhamnus, Rhus, Rosa, Rubus, Rumex, Saxifraga, Scabiosa, Scrophularia, Sedum, Selinum, Sempervivum, Silene, Sisymbrium, Spiraea, Stachys, Stellaria, Thlaspi, Torenia, Torilis, Trifolium, Trillium, Triumfetta, Tropaeolum, Turritis, Verbascum, Vicia, Viola, Vitis.

Bracts: Actaea, Ajuga, Amorpha, Centaurea, Corydalis, Glyceria, Heracleum, Hypericum, Kalanchoë, Lythrum, Norantea, Oenanthe, Parthenium, Perilla, Plantago, Rosa, Taraxacum.

Calyx: Anemone, Athamanta, Brassica, Cakile, Caltha, Campanula, Carduus, Carum, Cattleya, Centranthus, Cheiranthus, Cirsium, Clematis, Colchicum, Convallaria, Convolvulus, Cucumis, Cucurbita, Daucus, Delphinium, Diplotaxis, Epilobium, Eschscholtzia, Fragaria, Fuchsia, Galanthus, Gentiana, Geranium, Geum, Helenium, Heteropteris, Hypericum, Hypochaeris, Kalanchoë, Lagenaria, Laurus, Lycium, Mespilus, Papaver, Peltaria, Petunia, Philadelphus, Potentilla, Primula, Prunus, Pyrus, Ranunculus, Ribes, Rosa, Scorzonera, Senecio, Sisymbrium, Spiraea, Thlaspi, Tragopogon, Trifolium, Tulipa.

Corolla: Actaea, Alyssum, Anagallis, Anemone, Anthriscus, Antirrhinum, Aquilegia, Begonia, Brassica, Calendula, Campanula, Cattleya, Cerastium, Cheiranthus, Cirsium, Daucus, Delphinium, Dictamnus, Diplotaxis, Epilobium, Erysimum, Galanthus, Gentiana, Geranium, Geum, Gilia, Helenium, Heracleum, Hesperis, Lathyrus, Lonicera, Lychnis, Malva, Nicotiana, Oenothera, Peltaria, Petunia, Phyteuma, Polemonium, Potentilla, Primula, Prunus, Ranunculus, Raphanus, Reseda, Rosa, Rubus, Scabiosa, Senecio, Sisymbrium, Spiraea, Stachys, Stellaria, Symphytum, Thlaspi, Trifolium, Triumfetta, Tropaeolum, Turritis, Verbascum.

Stamens: Anagallis, Anemone, Anthriscus, Antirrhinum, Araucaria, Daucus, Delphinium, Dielytra (Dicentra), Dictamnus, Epilobium, Euphorbia, Glyceria, Heracleum, Jatropha, Lonicera, Nymphaea, Petunia, Primula, Rosa, Salix, Trifolium, Tropaeolum.

*Carpels:* Adonis, Anchusa, Aquilegia, Brassica, Cardamine, Carduus, Cerastium, Cheiranthus, Daucus, Delphinium, Dianthus, Diplotaxis, Epilobium, Heracleum, Lathyrus, Lonicera, Lychnis, Medicago, Melilotus, Nymphaea, Paeonia, Primula, Prunus, Ranunculus, Reseda, Rosa, Salix, Saxifraga, Scrophularia, Sisymbrium, Sterculia, Trifolium, Triumfetta, Tulipa.

Ovules: Adonis, Agrostemma, Alliaria, Anagallis, Anemone, Anthriscus, Aquilegia, Brassica, Carum, Cheiranthus, Crepis, Cupressus, Delphinium, Desmodium, Dictamnus, Drosera, Erucastrum, Fragaria, Gaillardia, Gilia, Hesperis, Hyacinthus, Lonicera, Lysimachia, Medicago, Melilotus, Nasturtium, Nigella, Pastinaca, Phyteuma, Primula, Prunus, Raphanus, Reseda, Rosa, Rumex, Scrophularia, Sisymbrium, Stachys, Stellaria, Symphytum, Thlaspi, Trifolium, Triumfetta, Tropaeolum, Turritis.

#### SEPALODY

Sepalody is a relatively uncommon abnormality. Sepalody of entire flowers has been reported only for *Dianthus* and *Erica*. Penzig (1890) reported sepaloid bracts in *Aconitum* and *Anemone*. *Sepaloid* petals have been found in *Anemone*, *Aquilegia*, *Cheiranthus*, *Delphinium*, *Origanum*, *Primula*, *Prunus*, *Pyrus*, *Rosa*, and *Silene*. Sepaloid anthers have been reported only for *Aquilegia*, *Delphinium*, *Nigella*, and *Trollius*; sepaloid carpels for *Anemone*, *Delphinium*, and *Rosa*.

The only two instances of sepaloid petals known to Masters (1869) were the St. Valery apple, and de Candolle's report of a calyx-like corolla in *Primula*  auricula L. Heinricher (1931) found two calyx-like corollas in the flowers of one seedling of Primula kewensis W. Wats. Germination of its seeds was very poor, and none of the seedlings had sepaloid corollas. Appl (1933) found a wild clone of Origanum vulgare L. with the corolla transformed into a second calyx and all of the stigmas carpelloid. The plants could not be selfed, but some of the seedlings of the abnormal plant had a double calyx, and one had a triple calyx. Crosses of the corollaless mutant with garden marjoram always gave 100 per cent plants with corollas. The petals are sepaloid or lacking in the mutant Cheiranthus cheiri L. which will be discussed under carpellody. Worsdell (1916) reports that in "rogue" roses, in which a second flower forms within the first, the carpels of the mother flower become superior, green, and inversely oriented, and serve as the calyx of the second flower. Many of the reports of organ transformation in the Ranunculaceae appear due to the fact that the plants were more flexible than the taxonomists. A flower with fewer petals and more sepals than usual was quite likely to be reported as an instance of sepalody.

### Petalody

Petalody is by far the commonest flower abnormality. The stamens are the organ which most commonly becomes petaloid, but the calyx and the pistils may also be affected. There is one record of petaloid ovules in *Begonia* (Worsdell 1916), and Penzig (1890) describes one case of petaloid leaves of *Rosa centifolia* L. Penzig also lists species of *Anemone, Hydrangea*, and *Prunus* reported to have petaloid bracts.

A petaloid calyx produces the "hose-in-hose," "catacorolla," or "calycanthema" flower, as reported for *Gloxinia*, *Mimulus*, *Nicotiana*, *Primula*, and *Rhododendron*. For *Campanula*, the petaloid calyx is normal in some species. In the Ranunculaceae, as mentioned above, the number of petals and sepals may vary, and this may be reported as either sepalody or petalody. A petaloid calyx in the orchids or *Calceolaria* may produce a second "lip."

Petaloid stamens are so common that they can hardly be considered an abnormality. Any good general seed catalog will list at least a hundred examples of heritable petalody (double flowers), and new double flowers are released by plant breeders each year. Development of petaloids is sometimes affected by environmental conditions, and this is discussed on page 178.

In many flowers with extreme doubling, the carpels as well as the stamens are affected. Rolfe (1890) reports the occurrence of an *Epidendrum* in which all four whorls present were petaloid. Worsdell notes that a petaloid carpel, or part of it, is normal in *Iris*. In this instance the style becomes petaloid and has well-developed median lamellae. The terminal portions of the lamellae form the upper bifid lip of the stigma in this genus.

Petalody has been reported in the following genera:

Calyx: Aceras, Anagallis, Anemone, Aquilegia, Brassica, Calceolaria, Campanula, Carum, Clematis, Crataegus, Crocus, Delphinium, Fuchsia, Galanthus, Gloxinia, Helianthemum, Helleborus, Mimulus, Nicotiana, Nigella, Orchis, Peltaria, Philadelphus, Primula, Ranunculus, Rhododendron, Robinia, Rosa, Rubus, Silene, Syringa, Trollius.

Stamens: Abutilon, Achimenes, Adonis, Aesculus, Allamanda, Althaea, Alyssum, Anagallis, Anemone, Anthyllis, Antirrhinum, Aquilegia, Arabis, Arbutus, Asphodelus, Atragene, Azalea, Barbarea, Begonia, Berberis, Bignonia, Brassica, Calceolaria, Calepina, Calluna, Caltha, Camellia, Campanula, Cardamine, Carum, Catasetum, Cattleya, Cereus, Cheiranthus, Chelidonium, Citrus, Clarkia, Clematis, Clerodendron, Clitoria, Colchicum, Commelina, Convallaria, Convolvulus, Cornus, Coronilla, Corvdalis, Crataegus, Crocus, Cyclamen, Cypripedium, Cytisus, Datura, Daucus, Delphinium, Deutzia, Dianthus, Digitalis, Epilobium, Erica Fragaria, Fritillaria, Fuchsia, Galanthus, Gardenia, Genista, Gentiana, Geranium, Geum, Gladiolus, Gloxinia, Godetia, Gossypium, Gratiola, Helleborus, Helianthemum, Hemerocallis, Hesperis, Hibiscus, Hippeastrum, Hyacinthus, Hydrocharis, Iberis, Impatiens, Ipomoea, Iris, Ixora, Jasminum, Kerria, Knautia, Lathyrus, Laurus, Leucojum, Lilium, Linaria, Lonicera, Lotus, Lychnis, Malva, Mathiola, Medicago, Melandrium, Melianthus, Miltonia, Mimulus, Mirabilis, Myrtus, Narcissus, Nelumbium, Nerium, Nesaea, Nicotiana, Nigella, Nymphaea, Orchis, Orobanche, Oxalis, Paeonia, Papaver, Pelargonium, Petunia, Philadelphus, Photinia, Prunus, Punica, Ranunculus, Rhododendron, Ribes, Robinia, Rosa, Rubus, Ruta, Sagina, Sagittaria, Sambucus, Sanguinaria, Saxifraga, Scabiosa, Scilla, Serissa, Silene, Solanum, Sparmannia, Spartianthus, Spiraea, Sternbergia, Streptocarpus, Syringa, Tabernae-montana, Thalictrum, Thea, Tofieldia, Torenia, Tradescantia, Trifolium, Trollius, Tropaeolum, Tulipa, Ulex, Veronica, Viburnum, Vinca, Viola.

Carpels: Althaea, Anemone, Arabis, Camellia, Dianthus, Fragaria, Hibiscus, Impatiens, Iris, Lonicera, Melandrium, Miltonia, Narcissus, Nigella, Papaver, Potentilla, Primula, Prunus, Ranunculus, Robinia, Trichosporum, Viola.

### STAMINODY

Staminody is less common than one might expect, in view of the fact that many authors consider all of the floral organs within the calyx to be phylogenetically derived from sporophylls. Staminody of the sepals is extremely rare. A report by Gris (1858) of such staminody in *Philadelphus* was the only case known to Masters. Worsdell (1916) reported only a few additional examples: (1) *Crocus*, laterally lobed sepals, which Worsdell regards as imperfect reversions to the stamens from which they originally sprang, (2) *Trifolium*, one or two semi-petaloid sepals bore anthers, and (3) *Tulipa*, sepals had lateral lobes, and one bore an anther.

Penzig (1890) describes Licopoli's (1867) illustrations of inflorescences of *Melianthus major* L., in which the lower flowers were entirely normal, the upper ones progressively reduced until at the tip of the inflorescence there were only rosettes of bracts partially or entirely transformed to anthers. Penzig also cites a report by Guillard of *Sinapis (Brassica) arvensis* L. with petals completely lacking, stamens partly fused with sepals, and the carpels free from each other and open.

In contrast to the hundreds of genera with petaloid stamens, staminoid petals have been found in only a few genera:

Amelanchier, Aquilegia, Asphodelus, Avena, Berberis, Capsella, Cardamine, Crocus, Daucus, Digitalis, Fuchsia, Geum, Gloxinia, Heracleum, Melilotus, Monarda, Myosurus, Narcissus, Odontoglossum, Ophrys, Orchis, Papaver, Phaseolus, Prunus, Saxifraga, Solanum.

Worsdell reports (1916) that in *Alpinia* the petaloid labellum resulting from the union of two anterior stamens of the inner whorl resolved into its original constituents and the stamens became fertile.

Staminoid pistils are also quite unusual. They have been reported in:

Allium, Armoracia, Begonia, Bunias, Campanula, Chamaerops, Cochlearia, Colletia, Euphorbia, Gentiana, Geum, Hyacinthus, Impatiens, Linaria, Mathiola, Ophrys, Paeonia, Prunus, Ruta, Saxifraga, Scilla, Sempervivum, Tofieldia, Tulipa.

In a few instances normal stamens have replaced ovules inside of the ovary. Masters (1869) pictures and describes at length normal-appearing flowers of *Baeckia* which he dissected, and which had normal stamens growing from the inside walls of the carpels, many of the stamens shedding pollen. Worsdell (1916) cites Agardh's report of a double hyacinth with an open ovary, in which anthers were borne on the same placenta as ovules. Buchenau (1903) described abnormal flowers of *Melandrium*; a calyx and a central placenta were lacking, and a circle of stamens formed inside the ovary at the base. Worsdell's Fig. 136 is a photograph of a tulip with a 9-merous pistil. The ovary is split open on one side, and two carpels are transformed into stamens. Worsdell's Plate 49 shows a carpel of *Begonia* bearing an anther. Martz (1928) reports that tulips sometimes bear carpels in which the rows of ovules are replaced by pollen sacs.

### CARPELLODY

Carpellody is one of the more frequent floral abnormalities. Not only may any of the floral organs become carpelloid, but Marx and Mishanek (1964) report the formation of rudimentary carpels on the foliage leaves of photoperiodic peas maintained in the vegetative condition for six months or longer. The only other report of carpelloid leaves seems to be Kirschleger's (1866) description of transformation of the leaflet of *Astragalus cicer* into a carpel, with ovules on the suture.

Lutz (1897) described flowers of *Crocus* in which stamens, perianth-leaves, and even the bracts, bore stigmas. Worsdell (1916) states, "It is not rare for the sepals of tulip and crocus to become partially carpelloid, bearing ovules on their margins; in these cases all transitions have been found between carpels and sepals." Masters (1869) also reports pistillody of the perianth to be frequent in the tulip. Penzig (1890) mentions carpelloid sepals of *Pyrus*. Duchartre (1860) described alternating whorls of sepals and carpels of *Delphinium*, with numerous transitions between the two. Gottschalk (1961) produced a recessive gene mutation by irradiating pea seeds; petals were reduced or absent, and extra carpels formed from anther and calyx tissue.

Besides the carpellody of the perianth already described for *Crocus* and *Tulipa*, petals of the following genera develop some or all of the structure normal for carpels. Flowers of a highly abnormal plant of *Gossypium hirsutum* L. have all of the stamens, and frequently some of the petals, replaced by beaked carpels (Meyer, unpublished). Graf (1919) described the floral anatomy of a *Linaria* collected by Geisenheyner (1919); carpels replaced the stamens, and sometimes replaced the nectaries. C. Schimper (1829) reported carpellody of the corolla for *Paeonia moutan* Sims., *Rhinanthus*, and *Stachys*. Dahlgren (1932) cites Correns' report of the *polycarpa* strain of *Silene*. Not only stamens, but also petals, are transformed to carpels. Only a bundle of stigmas protrudes from the calyx.

Carpellody of the androecium occurs in many genera. It ranges in degree from stigma-like extensions on the connectives of otherwise normal anthers to development of carpels with typical stigma and style, bearing ovules capable of development into normal, viable seeds. In Baur's (1924) Globosa strain of Antirrhinum majus, the plants form a branched shoot instead of a single flower, each shoot ending in a number of irregularly formed flowers. The flowers usually contain a many-carpelled ovary surrounded by a thick sheath of calyx-like leaves. Among hundreds of these plants, an occasional fertile anther may develop. Tepfer (1953) discovered teratological flowers and fruits of Aquilegia formosa Fisch., in which there were numerous open, pedicellate carpels and also abnormal stamens of similar general structure, but with "submarginal" pollen sacs instead of ovules. Bateson and Sutton (1919) were apparently the first to report the occurrence of masses of exposed ovules at the base of the petals of Begonia flowers in the terminal position normally occupied by male flowers. Worsdell (1916) reports that petaloid stamens of Caltha occasionally bear marginal ovules. Usteri (1907) states that when stamens of Carica papaya L. are converted into carpels, the normal ovary aborts. *Cheiranthus cheiri* has probably furnished more reports of carpelloid stamens than any other species. Allman (1851) first reported transformation of the anthers to a ring of carpels. He discusses the anatomy and homology of the floral organs, as illustrated by the abnormal flowers. Later reports (Masters 1869, Chittenden 1914, Worsdell 1916, Sirks 1924, Nelson 1928-1929) discuss the development of viable seeds in the supernumerary carpels, and also the recessive inheritance of the abnormality. Worsdell cites Smith's (1908) report of a coconut palm, in the Buitenzorg Botanic Garden, which "bore, instead of the few ordinary fruits at the base of the spadix, great numbers of small, crowded, narrow (quite banana-like) fruits, which created wonderment until it was found that the phenomenon was due to the transformation of many or all of the male flowers into female." Masters (1869) discusses replacement of stamens by carpels: "One of the most curious cases of this kind recorded is one mentioned by Mr. Berkeley, wherein a large white seeded gourd presented a majority of flowers in which the pollen was replaced by ovules . . ." Martz (1928) described hybrids of Digitalis species, in which the androecium, normally of four stamens, was reduced and partially fused with the corolla. Anatropous ovules were scattered around the filament, along the line of anther dehiscence, and at the base of the anther next to the ovary. Meyer and Buffet (1962) found external ovules on carpel-like tissue at the tip of the androecium of Gossypium interspecific hybrids. Rehder (1911) discovered Hypericum flowers with three to ten pistillodes per flower, between the pistil and stamens, and bearing numerous exposed ovules on each margin. Pistillodes with fertile anthers were rare. Worsdell (1916) reports that Larix and Pinus stamens are sometimes seen to bear ovules. Graf (1919) and Geisenheyner (1919), in companion papers, report and describe a collection of Linaria with carpels, outside of the normal two-celled ovary, replacing stamens and sometimes nectaries. Martz (1928) states that in some varieties of cultivated Narcissus the same anther simultaneously bears pollen and ovules. Pistilloid stamens of Nicotiana, sometimes bearing ovules, have been reported by Costerus (1907), White (1914), Avery (1929), Goodspeed (1930), and Goodspeed and Avery

(1934). In Nicotiana some types of pistillody are very uniform in expression, others exceedingly variable. Both genes and cytoplasm affect development of the stamens in Nicotiana hybrids. Von Mohl (1837) discussed pistillody of the stamens of Papaver as evidence for the foliar origin of stamens. Transformation of the inner stamens to fertile carpels or stamino-carpels is common in the genus (See Table I). For Primula, Masters (1869) reports carpellodic stamens varying from petaloid to those bearing ovules and stigmas. The petaloid carpels had ovules not only on their margins, but also on their upper surfaces. (Other reports are listed in Table I.) Tukey (1922) and Smith (1927) describe two different Prunus hybrids in which stamens were replaced by pistils. Masters (1867) describes an example in Rosa in which stamens exhibited almost every conceivable gradation between their ordinary form and that of the carpels, whereas some of the ovules contained pollen in more or less abundance. Bremer (1928) found carpellodic stamens, some bearing ovules, on seedlings of a Saccharum usually propagated vegetatively. Apparently the first published report of pistillody of the stamens in any plant was by Du Petit-Thouars (1807), for Sempervivum. The transitional stages between stamen and carpel have been described many times since then (see Table I). Worsdell (1916) cites a report by Miss D. G. Scott (1906) of potato stamens with normal anthers, and with ovules on the filament and in an internal cavity of the filament. Leighty and Sando (1924), Calder (1930), and Porter, Lahr, and Atkins (1965) report carpellody of wheat stamens. Worsdell cites Roeper's description of a tulip in which the inner whorl of stamens was transformed to three carpels which alternated with the three outer stamens, the normal whorl of carpels being suppressed. Carpellody of the stamens is common in Zea mays. Table I lists some of the many reports of genetic and environmental effects on "tassel-seed."

Penzig (1890) notes K. Schimper's illustration of virescent carpels in *Desmodium canadense* (L.) DC., with ovules transformed to little carpels.

Carpelloid stamens have been reported in: Amaryllis, Antirrhinum, Aquilegia, Asphodelus, Bambusa, Barbarea, Begonia, Bocconia, Caltha, Campanula, Carica, Cheiranthus, Citrus, Cochlearia, Cocos, Crocus, Cucumis, Cucurbita, Delphinium, Dianthus, Digitalis, Dionaea, Epilobium, Erica, Euphorbia, Fuchsia, Gentiana, Glochidon, Gossypium, Helleborus, Hypericum, Ipomoea, Larix, Lilium, Linaria, Magnolia, Myrtus, Narcissus, Nicotiana, Papaver, Pinus, Pisum, Platanthera, Polemonium, Primula, Prunus, Pyrus, Ranunculus, Ribes, Rosa, Rumex, Saccharum, Salix, Saxifraga, Scabiosa, Sedum, Sempervivum, Solanum, Spiraea, Stachys, Thalictrum, Triticum, Tropaeolum, Tulipa, Zea.

#### CHANGE OF SEX

# DIOECIOUS PLANTS

Dioecious plants frequently produce either hermaphrodite flowers or flowers of the opposite sex. It is now generally accepted that all flowers are potential hermaphrodites. Even such genera as *Melandrium* and *Spinacia*, with distinct sex-chromosomes, are subject to modification of developing primordia through the effects of environment, modifier genes, or chemicals. These are discussed further in subsequent sections. Modification of sex has been reported for the following dioecious or diclinous plants:

Acer, Aesculus, Aucuba, Begonia, Breynia, Bryonia, Callitriche, Cannabis, Carex, Cleistanthus, Cluytia, Conceveiba, Crozophora, Cucumis, Cucurbita, Empetrum, Fagus, Gunnera, Hermesia, Humulus, Juniperus, Leitneria, Lychnis, Melandrium, Mercurialis, Mozinna, Myrica, Myristica, Phyllanthus, Pistacia, Populus, Restio, Ricinus, Rumex, Salix, Schismatophora, Sedum, Spinacia, Stauntonia, Suregada, Taxus, Urtica, Zea.

#### MONOECIOUS PLANTS

Monoecious plants occasionally are subject to suppression of development of either anthers or carpels. In most such instances the male organs are nonfunctional or lacking. This could well be due to the fact that female-sterility would be more of a disadvantage than male-sterility in natural selection. Entirely male or entirely female flowers or plants have been reported in the following usually bisexual genera:

Arisaema, Callitriche, Cleome, Fragaria, Hippurus, Honckenya, Hymenanthera, Juglans, Lathyrus, Leptospermum, Morus, Origanum, Ranunculus, Sedum, Spiraea, Streptocarpus, Thymus, Trinia.

## DEVELOPMENT OF POLLEN IN OVULES

This abnormality has been reported in three genera. Goebel (1908) found pollen grains inside the nucellus of *Begonia*. Salter (1863) is cited by Masters as reporting the formation of pollen within the ovules of two species of *Passiflora*. Masters himself (1867) found pollen in greater or lesser abundance in some of the ovules of a form of *Rosa arvensis* Huds. in which the stamens showed every possible transition between stamen and carpel.

# EMBRYO-SAC-LIKE POLLEN GRAINS

Giant pollen grains with the appearance and nuclear arrangement of embryosacs have been reported in anthers of *Hyacinthus* by Nemec (1898), Naithani (1937), Stow (1930, 1933), and de Mol (1933). Geitler (1941) found similar embryo-sac-like giant pollen grains in *Ornithogalum*. He states that the other authors' drawings and descriptions agree with his findings, so they are probably correct. Nakamura (1936) found giant pollen grains in anthers of *Impatiens* exposed to high temperatures.

# AGENTS CAUSING ABNORMAL DIFFERENTIATION

#### **UNUSUAL CLIMATIC CONDITIONS**

Unusual climatic conditions frequently cause or modify abnormal flower development. Other factors of the external environment, such as available nutrients or soil moisture, can also affect differentiation. The first authors to attribute abnormal differentiation to the effects of unusual environmental conditions observed a suddenly higher incidence of "a teratological phenomenon" following some particularly noticeable weather. A few of the more recent papers on plant differentiation report experiments with plants in growth chambers, or with precise measurements of field environments correlated with plant development. In some of the experiments the chemical basis of the environmental response has been investigated also. No sharp boundary can be drawn between the environmental agent, the chemical or physical process it affects, and development of the plant organ which is suppressed or stimulated. Nevertheless, for discussion purposes it is desirable to examine each major influence separately, before briefly considering the complex interactions which finally produce a more or less abnormal flower.

The effects of environment on production of stamens and pistils are particularly noticeable in dioecious plants, or in monoecious plants with unisexual flowers distributed in some definite pattern. Atkinson (1898) controlled the sex of inflorescences of *Arisaema* by varying the nutritional level of the plant. Camp (1932) stated that *Arisaema triphyllum* (L.) Torr. is not a true dioecious plant, and that the sexual states are relatively unstable. He found that plants producing staminate flowers arose from corms light in weight and high in catalase activity whereas those producing carpellate flowers came from heavier corms with a lower catalase activity. Transitional or monoecious plants had intermediate corm weight and catalase activity.

Cannabis sativa L., the hemp plant, has been the basis for many experiments in sex reversal. Gasparrini (1862) was probably the first to report monoecious plants in this unusually dioecious species. Another genus in the same family, Humulus, was frequently used in parallel experiments by the same authors. Tournois (1911) reported transformation of stamens into carpels on the first flowers of early-planted hops. Seed planted at the usual time produced only normal flowers, and the early-planted hops also produced normal flowers during the normal flowering season. Tournois attributed the observed phenomenon to early sowing and to atmospheric conditions the plants were subject to at the beginning of their development. Schaffner (1921, 1923, 1925, 1931) found the relative length of daylight to induce sex reversal of hemp in a high degree. He also found that for any given daylength, percentage of reversal was greater in soil with abundant nitrogen than in a poor substratum low in nitrogen. In an experiment with greenhouse plants grown under natural short day in winter, percentage of male plants producing female organs rose gradually with decreasing daily illumination from zero to 100, and then fell again to zero with increasing daily illumination. Hemp was particularly troublesome during the first stages of developing a genetic theory of sex determination for dioecious plants. In nearly every instance the ratio of male:female plants was 1:1, and yet sex reversal occurred under some conditions. Black (1945) found fertilizer to have little effect on sex ratios of hemp. Talley (1934) and Borthwick and Scully (1954) pointed out that the tendency to produce male or female plants was undoubtedly determined genetically, but that the actual determination of sex for any one flower depended to some extent on environmental conditions. Borthwick and Scully noted that time of flowering and incidence of intersexual flowers on monoecious plants was modified to varying degrees by the interaction of other environmental factors with photoperiod. Köhler (1958) stated that sex expression of hemp seemed correlated with leaf size, since the flowers formed in regions with primarily large leaves were male, and those in regions with primarily small leaves were female.

Corn (Zea mays) frequently produces spikes with some or all of the flowers showing sex reversal. Schaffner (1927) found that 75 per cent of the corn plants grown in a winter greenhouse produced carpellate tassels, but the same variety showed no such reversal when grown under summer field conditions. Richey and Sprague (1932) produced partially or completely pistillate tassels on corn plants grown in the greenhouse during the winter in an environment of short days, low light intensity, normal growing temperatures, and abundant water. Increasing either temperature or light decreased the number of silks in the tassels. A difference of  $10^{\circ}$  F. in temperature was about as effective as four and one-half hours of illumination.

As early as 1869, Masters was concerned with the role of environmental factors in differentiation. "Knight and other vegetable physiologists have been of the opinion that a high temperature favours the production of stamens, while a lower degree of heat is considered more favorable to the production of pistils ... Mr. Darwin cites from various sources the following details relating to strawberries which it may be useful to insert in this place, as throwing some light on the production of unisexual flowers. 'Several English varieties, which in this country are free of any such tendency, when cultivated in rich soils under the climate of North America commonly produce plants with separate sexes. Thus a whole acre of Keen's seedlings in the United States has been observed to be almost sterile in the absence of male flowers ....'" Masters continues his discussion, "Stratiotes aloides has been said to produce its carpels with greater abundance towards the northern limits of its distribution, and its stamens, on the other hand, are stated to be more frequently developed in more southern districts ... Honckenya peploides affords another illustration of the sexual arrangements in the flower being altered as it would seem by climatal conditions. Thus, in the United States, according to Professor Asa Gray, the flowers are frequently hermaphrodite, while in this country they are usually sub-dioecious ... Treviranus says that the flowers of Hippurus and Callitriche are apt to be hermaphrodite in summer, but female at a later period."

Perhaps the first experimental study of environmental effects on differentiation was performed by Shattuck in 1910. He prevented the formation of megaspores in Marsilia, a fern, by means of a spray of cold water. Many observations and experiments since that time have concerned a wide range of plant species, organs affected, and climatic factors involved. Meade (1913) reported supernumerary carpels at the center of cotton bolls from widely separated locations (Maryland, California, Texas). He attributed the formation of supernumerary carpels to unusually low night temperatures. Tukey (1922) was uncertain whether the pistillody he described in a hybrid plum was a varietal characteristic or the result of a frost which occurred at the time of blossoming. Simon (1924) found that maximum development of flower abnormalities occurred in mutant Torenia plants grown under the hot, dry conditions of the cactus-house, and nearly normal plants were produced under warm, moist, shady conditions. Transferring either group of plants to the other environment reversed the expression of the abnormality. Detjen (1927) reported that reversion of carpels and other organs of cabbage to a vegetative stage occurred annually at irregular intervals. Appl (1929) found formation of perfect flowers of marjoram to be suppressed to some extent early in the season or under conditions of poor nutrition. As noted earlier, the formation of giant pollen grains depends on abnormally high temperatures during differentiation (see p. 174). Goodspeed (1930) reports considerable variation in pistilloid *Nicotiana tabacum* L.: "At the start of the flowering season practically no viable pollen is produced in flowers of this type, whereas towards its close the anthers uniformly exhibit less structural abnormality and contain a considerable proportion of viable pollen."

Tschermak (1932), in studies of Primula, found that even for one individual, calycanthemy and doubling were at a different level in summer than in winter flowers. Foliose calyx, accompanied by vestigial sex organs, occurred in some of his overwintered Primula stocks. Later flowers of the same plants were entirely normal, so apparently this was an example, not of heritable abnormality, but of one produced by cold. Chroboczek (1934) states that favorable conditions of light and temperature are essential to the development of a fertile inflorescence of beets, as well as to the initiation of the flower primordia. The results of Harder's experiments, involving phyllody in Kalanchoë, are discussed on page 167. Kihara (1951) found that environment had important effects on fertility in Triticum, material grown at Kyoto being considerably more fertile than that sown on the same date in Sapporo. The lower fertility was due to two kinds of defects in reproductive organs-pollen abortion and pistillody of stamens. Pistillody was more frequent in late maturing plants. Daylength ceems to play an important role in producing pistillody; in Sapporo, where the summer days are longer than at Kyoto, pistillody was always very conspicuous, and the fertility of the Aegilops backcrosses to T. vulgare Vill. was very low. Lang (1952) reported that low light intensity may block development of anthers of Lycopersicon or Bryophyllum.

Galun (1956) found that cold treatment would reduce the number of nodes before the first female flower was produced by some, but not by other, cucumber varieties. Shifriss, George, and Quinones (1954) found the varying sex expression of different cucumber strains to be controlled by weak or strong male-determining genes which acted by speeding or slowing the normal transition from male to female flowers as the plant aged. Thomas (1956) delayed production of female flowers in Cucurbita pepo L. and in Ambrosia by growing plants at high temperatures and under long photoperiods. In natural summer conditions monoecious plants of *Mercurialis ambigua* L. fil. produce one female flower and a cluster of male flowers in each leaf axil, but long days significantly delayed production of female flowers, as did increasing the temperature from 15.5° to 24°C. Male flowers were produced at the lowest flowering node of female plants grown in continuous light for 45 days at a day temperature of 21-26° C. and a night temperature of 15.5-21° C. and then transferred to eight-hour photoperiods at the same temperature. Thomas states, "These results are particularly interesting as they indicate the possibility that growth of female as well as monoecious plants through a male phase before they produce female flowers is a general phenomenon. Female plants normally reach the female phase before flowers develop and usually produce no male flowers, but by artificially delaying the attainment of femaleness, male flowers are produced."

Zabka (1961) found that, although Amaranthus caudatus L. will initiate flower primordia on long days, normal development of the inflorescence requires short photoperiods. Noack (1962) reported that in two successive years there was a distinct positive correlation between hours of daily sunshine and the number of perfect flowers replacing male Begonia flowers. Semeniuk (1964) carried out growth-chamber experiments with rose seedlings. The maximum number of petals was formed at 62° F., whereas at 82° and 92° F. the number of petals was reduced to five, the basic number in the wild rose species. Also, stamens were fewer and pistils and filaments relatively longer at lower temperatures. His results probably account for the observation published by Violle (1911). A partial translation follows: "During the holidays, I had the opportunity of observing an occurrence which appears noteworthy to me. This was produced by a magnificent rose plant of Gloire de Dijon planted in the open ground at Fixin, about ten years ago, remarkable in development and vigor: all by itself it forms an arbor above a large door and for months at a time produces an abundant and constantly renewed flowering of superb roses. However it did not undergo the torrid heat of last summer without suffering, and during the month of August flowers were less beautiful and less numerous than usual. Then, suddenly, about September 12, it produced on all of its branches a complete flowering of absolutely single roses, which were succeeded 8 days later on the same branches by a full crop of the beautiful roses usual for it, and which were still being produced by the plant when I left a few days ago."

Wijewantha and Stebbins (1964) found the expression of the *agropyroides* gene, affecting the number and type of appendages differentiated in the barley spike, to be greater under field conditions than in the greenhouse. Meyer (1965) found a negative correlation between minimum daily temperature 17-18 days before anthesis and the number of external ovules produced by cotton plants with the EO gene; there was also a significant positive correlation between relative humidity 23 days before anthesis, and the number of anthers per flower produced by Upland cotton and its hybrids with the EO gene.

# HERITABLE ABNORMALITIES

Heritable abnormalities are responsible for the majority of the reports of abnormal differentiation during the past 50 years. Strictly speaking, virtually any mutant gene interferes in some way with normal differentiation. The oldfashioned reports of singular occurrences of teratological phenomena have been replaced by studies of the mode of action of mutant genes. A non-heritable abnormality is unlikely to be reported in modern journals, unless it can be either reproduced by physiological manipulation or propagated vegetatively.

Recessive genes are responsible for anomalous flowers in many genera. Baur (1924) discusses the inheritance of 40 different factors in *Antirrhinum*, most of them recessive mutants, six of them producing highly abnormal flowers. The many reports of pistilloid stamens in *Cheiranthus cheiri* all agree that the property seems due to a single recessive gene. Either the same gene must mutate rather often, or the anther primordia of *Cheiranthus* must respond similarly to many different mutant genes. Corn, tobacco, and *Primula* have several different flower abnormalities attributed to single genes. Other recessive abnormalities are known in *Hordeum*, *Latbyrus*, *Papaver*, and *Pisum*. Chromosome abnormalities seem to be associated with the carpellody of *Saccharum*.

A disproportionately high number of aberrations occurs in interspecific hybrids. In some instances the two sets of chromosomes may not cooperate as well as chromosomes from within one species; in others the genes of one species are unable to function effectively in another cytoplasm. Bateson and Sutton (1919) had considerable difficulty explaining the results they got from crosses between normally monoecious Begonia species. When they crossed pollen of a single-flowered B. davisii on a double B. lloydii all plants were at least partially double-flowered. The reciprocal cross and the self of *B. davisii* were single. The double flowers were in the terminal position ordinarily occupied by male flowers in the Begonia inflorescence, but in this example the double flowers bore masses of exposed ovules at the bases of the petals. In Begonia lloydii the terminal double flowers are male, and they readily produce pollen if the plants are grown under stress conditions. Bateson and Sutton (1919) state: "The view that plants e. g. Graf Zeppelin, in which the terminal flowers are female, instead of male as normally, may be homozygous females is rather attractive, but we see no means of testing it; nor if such an idea could be entertained, would it at all account for the fact that in a full double which must certainly be accepted as a recessive, homozygous in doubleness, the normal female flowers standing in the lateral positions are single . . . Since B. davisii is a genuine wild species and bears exclusively single flowers, the conclusion to which our observations have led us, namely that its male side is genetically all double, seems not a little remarkable." Noack, working with Begonia hybrids (1962a), and observing essentially the same sort of flowers as did Bateson and Sutton, found that the results could be quite simply explained by assuming a combination of segregating nuclear and plasmatic factors and pollen-tube competition.

Heilbronn and Basarman (1942) found sex determination of *Bryonia* hybrids to be complex. *B. alba* cytoplasm prevents formation of fertile germ cells in the hybrid, but *B. dioica* cytoplasm does not. Sex determination within the species is controlled by different genes. They conclude that phylogenetic development of a mixed-sex species into a separate-sexed one with genotypic sex determination can occur in different ways, through mutation in different chromosomes; the finally-fixed method of sex determination can vary, even in closely related forms, i.e., unifactorial, bifactorial (or plurifactorial?).

Rainio (1927) is of the opinion that interspecific hybridization may be a factor involved in all of the monoecious plants of *Populus* and *Salix*. Since most such reports concern single trees found growing spontaneously in various parts of the world, and since the genera are wind-pollinated, that seems a reasonable assumption. Peto (1938), Seitz (1952), and Schlenker (1953) all state that perfect flowers occur regularly in experimental hybrids of *Populus*. Arnal's (1952) report of an androgynous *Salix* concerns *S. sepulcralis* Simonkai, believed to be a hybrid between *S. alba* L. and *S. babylonica* L.

Other floral abnormalities reported for interspecific hybrids include external ovules in Gossypium (Meyer and Buffet 1962), petaloid and pistilloid

Nicotiana (White 1914, Burk 1960), corollaless Origanum (Appl 1933), phyllody and calycanthemy in Primula (Heinricher 1931, Ernst 1931), pistillody and staminody in Prunus (Tukey 1922, Smith 1927), deformed and indehiscent flowers in Solanum (Grun, Aubertin, and Radlow 1962), pistillody in Streptocarpus (Oehlkers 1940), and pistillody in Triticum (Kahara 1951).

Some monotypic genera also apparently have cytoplasmic differences which can affect gene action to produce abnormal flowers or flowering. At least one of the pistillate varieties of *Ricinus* requires both "pistillate" cytoplasm and the proper dominant genetic factor to produce entirely pistillate plants (Parkey 1957). Although Stein (1965) is dubious about possible cytoplasmic influences in the expression of "everted ovule" gene in *Ricinus*, some of the mutant genes affecting fertility are expressed differently in cytoplasm from different sources within the genus. The extreme variability of Simon's (1924) mutant *Torenia*, together with its virtually complete disappearance in the  $F_2$  and later generations from some test-crosses with normal plants, suggests that cytoplasmic abnormalities may be involved in this case also.

## PARASITISM

Parasitism was one of the first causes of abnormal differentiation to be widely recognized. Goethe (1790) mentions its effects on flower development, but specifically excludes description and discussion of such abnormalities from his essay on metamorphosis. Peyritsch (1881) observed many cases of aphiscaused phyllody in crucifers. He also produced phyllody artificially in Cerastium glomeratum Thuill. by infestation with Psylla cerastii. Worsdell (1916) lists many reports of petalody as a result of infestation by parasites: stamens of Knautia arvensis (L.) T. Coulter changed to violet petals as a result of attack by Peronospora violacea; double flowers of Saponaria officinalis L. caused by the smut fungus Ustilago saponariae; petaloid stamens of Primula officinalis Hill caused by presence of the fungus Demalium in the roots; doubleflowered plants of Saponaria officinalis L. infected in their rhizomes with Fusarium, while single-flowered plants were free of it; petalody in Scabiosa columbaria due to galls of Heterodera radicicola-normal plants transplanted to the same location became double. Molliard (1904) describes a phylloid gynoecium of Trifolium repens L. due to presence in the stem of an insect larva, probably Hylastinus obscurus; in Melilotus arvensis all plants with phylloid flowers had larvae of Apion melilotii in the neck and branches of the stem. The same author also found abnormal flowers resulting from insect infestation in Senecio jacobaea L. and Cardamine pratensis L. Allan and Zotov (1930) found that the rust Aecidium otagense produced female flowers in male inflorescences of Clematis. Erlenmeyer and Geiger Huber (1935) report a smut fungus which causes development of anthers in female flowers of Melandrium album Garcke; spores of the fungus are then formed within the anthers instead of the normal pollen of the plant. Loehwing (1938) notes the development of stamens in pistillate flowers of Lychnis dioica L. infested with Ustilago, and the hermaphroditism of staminate willow trees, induced by Eriophid mites. Heslop-Harrison (1959) discusses the formation of female flowers in the normally male terminal inflorescence of Zea mays as a result of infection by Ustilago zeae.

# CHEMICAL TREATMENT

Chemical treatment has been used in many ways to modify plant development, including that of the inflorescence. The auxins were the first group of chemicals to be used for intensive studies. Later studies involved many single compounds, of known and of unknown structure, and other groups of substances, such as gibberellins and cytokinins. Important information has resulted from experiments to determine effects of growth substances when they are applied to growing plants at particular stages of differentiation.

Löve and Löve (1940) performed one of the earliest experiments on the chemical modification of sex in plants. They applied animal sex hormones to young growing points of *Melandrium rubrum*. Treatment of normal female plants with testosterone increased development of the rudimentary staminates normally present in the flowers. Gynohermaphrodite plants treated with oestrin became purely female with no staminates. Normal male plants have no rudimentary gynoecium, but in a few instances a very small hairlike formation is to be found in the flower. By treating normal male plants with oestron such hair develops, grows, and sometimes forms a little gynoecium with two stigmas. An andro-hermaphrodite treated with oestron produces a large gynoecium with no staminates. In most situations oestron on female plants and testosteron on male plants exercised a poisonous effect and often killed the sprouts.

Wittwer and Hillyer (1954) reported that a single application of maleic hydrazide to cucurbits resulted in a high percentage of plants with only pistillate flowers. Repeated applications produced many male-sterile plants. Pistillate flowers on such plants were normal and fertile.

Laibach and Kribben (1950) found that 3-indoleacetic acid (IAA) could cause development of female flowers on nodes of cucumber plants which normally have only male flowers. Heslop-Harrison (1956) used a-naphthaleneacetic acid (NAA) to cause formation of female flowers in genetically male plants of hemp. Galun (1956) reduced the number of nodes preceding the first pistillate cucumber flower by applying NAA after cold treatment. Brantley and Warren (1958), working with NAA on muskmelon, increased the number of staminate and perfect flowers and the ratio of perfect to staminate flowers. J. and Y. Heslop-Harrison (1958) treated Silene pendula L. with NAA; all of the plants grown in long days were male-sterile to some extent. A feature of the auxin-induced male-sterile flowers was precocious development of the gynoecium. Flowers of this type were mostly female-fertile and gave a normal crop of seed when pollinated artificially. Raghaven (1961) added IAA to the culture medium for photoinduced apical buds of Perilla. Flowering was inhibited in two ways — by delay in appearance of the first signs of flowering at the apex, and by a gradual transition from flower-like structures at lower concentrations of IAA to sterile cones in higher doses. Orr and Postlethwait (1964) prevented complete expression of the fascicled ear gene of maize by the addition of either IAA or NAA.

Peterson and Anhder (1960) induced formation of staminate flowers on gynoecious cucumber plants by gibberellin (GA) treatment. Similar results with cucumbers have been reported by Wittwer and Bukovac (1962b), and Shifriss and George (1964). Shifriss and George report varietal differences in the sensitivity of female plants to sex reversion by gibberellin treatment. Shifriss (1961) found that gibberellin treatment of castorbeans produced a response diametrically opposite to that for cucumbers—a marked increase in female tendency. Wardlaw (1963) used gibberellin to partially or entirely prevent reversion of injured floral apices of *Petasites* to the vegetative state. Hillman and Smith (1965) used a combination of GA, low temperature, and short days to induce flowering in a clone of tobacco which had previously been entirely vegetative.

Carbon monoxide induces auxin-like symptoms in plants. No pure-sexed female plants of *Mercurialis ambigua* exist. J. and Y. Heslop-Harrison (1957) increased the proportion of female flowers by treatment with carbon monoxide.

Wijewantha and Stebbins (1964) found that the effect of barley of the *agropyroides* gene could be partly neutralized by the addition of arginine or one of its precursors, glutamic acid. Tyrosine and adenine sulphate also caused significant changes toward normality in expression of the *agropyroides* character.

Roark, Pfrimmer, and Merkl (1964) studied effects on flower initiation of various chemicals sprayed on cotton. First fruiting branches developed at a higher node of the main axis on plants sprayed with methyl parathion than on control plants sprayed only with solvent + emulsifier. Plants sprayed with phosphorodithoate I also developed first fruiting branches from a higher node of the main axis than on control plants.

Since 1961 experiments have been carried out on the combined or contrasted effects of various groups of chemicals, and of modifications of photo- or thermal- induction by various groups of chemicals. Mitchell and Wittwer (1962) increased pistillate flower formation in monoecious cucumber plants by adding allyl trimethylammonium bromide to the aerated culture solutions used as the root medium. By contrast, gibberellin induced staminate flower formation on gynoecious cucumber plants. The two chemicals also have diametrically opposite effects in tendril formation and vegetative extension.

Wittwer and Bukovac (1962a) comment on the marked species specificity of compounds which affect flowering and fruit setting in higher plants. The N-arylphthalmic acids effect flower formation only in the tomato and possibly the strawberry; 2,3,5-triiodobenzoic acid in the bean, tomato, and only one or two other species; hydrazine derivatives only in the pineapple; 2,4-D only in pineapple and sweet potato; maleic hydrazide only on celery; furfuryl alcohol only on Rudbeckia speciosa Wenderoth; and 2-chloroethyl-trimethylammonium chloride (CCC) only on tomato and Azalea. The gibberellins appear to be the only group of chemicals which exercise predictable and consistent control of flowering over large segments of the plant kingdom. Phenocopies of five recessive genetic characters in the tomato may be induced by treatment with N-m-tolylphthalmic acid. These include determinate growth, fasciation of the flowers, branching of the flower cluster, leafy flower clusters, and blindness. Auxins and CCC shortened the time to anthesis for tomato seedlings; maleic hydrazide, phosphon D, and gibberellin either delayed first anthesis or increased the number of nodes subtending the first inflorescence. An even greater delay occurred with kinetin. Gibberellin delays flowering of peas; kinetin has the

reverse effect. The promotive effects of kinetin on flowering of peas appeared light-dependent.

Nitsch (1962) states that applied growth regulators can modify the development of the flower parts as do environmental factors. Auxins can inhibit development of male flowers and stimulate that of female ones. Gibberellins, on the other hand, increase the male/female ratio not only by delaying the formation of the first pistillate flower, but by actually causing the development of male flowers on genetically 100 per cent female cucumber lines. A substance with the biological properties of a gibberellin has been isolated from photo-induced *Rudbeckia* plants, and can induce flowering of other rudbeckias maintained under non-inductive short days. An endogenous growth substance different from the indolic auxins and the nine first gibberellins has been isolated from cold-requiring plants (chrysanthemum, biennial hollyhock). Although this substance causes flowering of rudbeckias under short days, it did not produce any flowers on unvernalized hollyhocks, but it did cause their bolting.

Tepfer *et al.* (1963) extended the developmental limits of *Aquilegia* buds at nearly all stages by adding indoleacetic acid, gibberellic acid, and kinetin to the basic culture medium.

## DISCUSSION AND CONCLUSIONS

Surprisingly little experimental work has been done on controlled variation of plant form. Many plant species deviate frequently from their normal pattern of flower development. Some physical and chemical treatments are known to affect flower organ formation. Several authors have pointed out that the phenotype of a plant results from interaction of its genes and cytoplasm with each other and with its internal (physiological) and external environment. An experimental approach would seem to be a good starting point for trying to determine what basic mechanism actually causes differentiation.

In 1790 Goethe attributed the serial production of cotyledons, leaves, bracts, calyx, corolla, stamens, and carpels to refinement of the sap as the crude liquid moved from the ground upward and became more ethereal. In 1965 we have other ideas than Goethe did about the process of differentiation, but not many more actual data. The information which is available is fragmentary, contradictory, and scanty. There is so little of it that there are not even opposing theories about the basic mechanisms of flower differentiation.

Few theoretical concepts have been so generally and so quickly accepted as the idea that plant meristems function as reaction systems, with "switch mechanisms" to turn on and turn off the gene-controlled processes involved in producing the various appendages. Wardlaw's (1957) original statement of the theory included the idea that a particular gene only becomes active when the physiological situation has become appropriate to its activity, and that the changes induced by it in the reaction system (or in the protoplasmic substratum) prepare the way for the action of certain other genes. Wardlaw concludes, "Experimental tests of the theory will consist essentially in interfering with the floral reaction system at critical stages in a known manner, followed by observation of such morphological modifications as may be induced. The main impediment to crucial experiments lies in the fact that so very little is known of the factors that are at work in the reaction system."

Zeevaart (1962) assumes that the reaction of an organism to its environment must be completely determined by its genotype. The sequential turning on and off of genes during differentiation he calls programming. His experiments with *Pharbitis* suggest that the photo-periodic stimulus activates the floral genes directly. From the suppression of flowering by specific chemical metabolic inhibitors, reversal of the inhibition by precursors of DNA, and the different effects obtained by varying the time of application of the various chemicals, he concludes that the floral genes can be activated during the multiplication of DNA.

Brink (1964) discusses the process of activation and repression of genes in multicellular organisms. He states that (1) activation of a gene is dependent upon the sequential operation of two sets of factors, one at the chromosomal level, the other at the individual gene level. (2) Two processes are involved at the chromosome level, uncoiling of the chromosome, and dissociation of DNA from the histone sheath which prevents its action. (3) Gene action is repressed in a coiled chromosome segment, and formation of its RNA copy requires absence of the histone sheath. (4) General nuclear processes, not the genes activated, control chromosome uncoiling and histone dissociation. (5) Heterochromatin may act as a non-specific repressor substance by blocking uncoiling. (6) Definitive activation of a gene follows uncoiling of a chromosome segment and dissociation of the histone. It occurs in response to some sort of signal from the cell, specifically related to the locus in question. "The basic requirement to be fulfilled is a mechanism that recognizes the uniqueness of each gene." Brink concludes that the known examples of genetic repression in multicellular organisms provide inadequate evidence for the individual regulation of gene action in accordance with the requirement for orderly development. The mechanism that effects the latter process must be co-specific with the genes themselves.

Wijewantha and Stebbins (1964) treated barley carrying the *agropyroides* character with arginine or its precursors, and produced a significant change of expression toward normality. Apparently the altered biochemical information produced by this gene affects arginine metabolism at all stages in the life cycle of the plant. The visible effect of the gene is probably not due to a time limited initial action of the gene, but to effects of unbalanced arginine metabolism on critical stages of cellular differentiation. They suggest that the connection between the primary effect of the gene on arginine metabolism and its final effect on differentiation is via an abnormal or deficient synthesis of histone proteins.

There is considerable evidence that phytochrome may sometimes trigger the switch mechanism which changes differentiation of the apical meristem from leaf production to flower production (Borthwick 1962, Nitsch 1963). Other evidence suggests that sometimes the auxin level may be of critical importance in the differentiation of the various organs (Heslop-Harrison 1957). In still other examples a competition between two antagonistic substances of different origin and chemistry seems to determine which of two alternative structures will occur (Wittwer and Tolbert 1960, Tolbert 1961).

Every new development in plant physiology or genetics has probably been seriously considered in at least one theory which attempts to correlate the obvious external differences in plant organs with an internal variance during differentiation. Because they are so close together in time and space, and yet so obviously distinct, the male and female organs of flowers have frequently been subjected to comparative analyses or experiments.

Laurent (1906) associated differences in sex of plants with osmotic pressure. He found rootstocks of female hop plants to be heavier than those of male plants in the same plots, female poplars several days earlier than males, lush growth in general associated with female flowers.

After sex chromosomes were discovered in animals, there was an intensive (occasionally successful) search for such chromosomes in dioecious plants. The early workers on genes and chromosomes associated with sex determination in plants frequently had serious doubts that sex of dioecious plants was genetically determined, because environmental factors could alter the usual ratio of 1:1. Emerson (1924) was one of the earliest to point out that the fact that a property is influenced by environmental factors does not mean that a gene makes no contribution to its development. He states that what is inherited is merely the possibility-indeed the necessity-of reacting in a particular way to a particular external and internal environment. In typically hermaphroditic forms where both male and female tendencies are exhibited in the same individual, factors for maleness or femaleness are thought of as being in so delicate a balance that influences analogous to those responsible for the differentiation of vegetative characters effect a more or less regular differentiation of sex organs. Sharp (1925) came to essentially the same conclusions. He considered determination of the heritable characters exhibited by an organism to involve reaction of the genic mechanism with other factors in and through the cytoplasm during the course of the ontogeny.

Allen (1932) also distinguished between sex inheritance and sex determination. He noted that in dioecious bryophytes only one set of sex possibilities is represented in each haploid chromosome complement. Richey and Sprague (1932) point out that although genes which produce a given end product under a wide range of environments are used by most geneticists, the geneticist recognizes clearly that other types of genes exist, and regularly uses a more or less controlled environment in working with such genes. Naithani (1937) endorses the theory advanced by Emerson and Sharp. Sex reversal occurs in the anthers of 'Yellow Hammer' hyacinths, but not in other varieties similarly treated. He attributes this to the genetical balance, which is such in other varieties that the environmental condition which disturbs the balance in 'Yellow Hammer' is not effective. Erlanson and Hermann (1927) reported the production of perfect flowers by Populus tremuloides Michx., a normally dioecious species. "Since the perfect flowered Populus is heterogametic with an XY-sex pair such as found in the normal male, this seems to be another case in which some factor upsets the internal balance which geneticists claim determines the external manifestations of sex."

Camp (1929) found a distinctly higher catalase activity in male than in

female plants of dioecious species, with floral structures generally showing a greater difference than vegetative parts. Talley (1934) found that male hemp plants had values for reducing sugars two to three times as high for male as for female hemp plants. Staminate plants also had a relatively lower nitrogen content than female plants. Joyet-Lavergne (1935) attributed sexual differences to physico-chemical differences in metabolism.

Goldschmidt (1938) considered Oehlkers' *Streptocarpus* hybrids to be subject to sex determination in the same way as his *Lymantria* intersexes. The various degrees of intersexuality were due to balances between genic and cytoplasmic sex determiners of differing strengths, distributed at meiosis and at fertilization.

Loehwing (1938) believed flowering to be induced by hormones. He considered the sex processes to be as different from one another metabolically as are the vegetative from the fruiting phase of plants as a whole. He discussed the Manoilov technique for measuring differences in oxidation potential, and noted that female tissues are generally more reducing in character.

Arnal (1952, 1954) found evidence for a sexual gradient in willows. In his theory of sex determination there are three fundamental types of gradient: simple, double (female-male-female), and multinodal (a gradient at each bud). When the gradient is weak, the switch from one sex to the other is subject to external control; when it is strong, external factors have little effect. Arnal considers the usual hermaphrodite flower of the Angiosperms as only a special example of high-level sexual gradient always oriented in the same direction. When the level of the gradient is diminished, stamino-carpels may appear.

Heslop-Harrison (1957) presents a theory based on initiation of flowering through the agency of an auxin-controlled, self-duplicating nucleoprotein. "The course of floral morphogenesis, once initiated, is established by genetic factors at the reacting apex, and the activity of these is to some extent regulated by auxin levels there. The growth of stamen and pistil primordia is governed by auxin in the characteristic manner, the response following an optimum curve. The concentration promoting maximal stamen growth is lower than that promoting maximal pistil growth, so that auxin level at the differentiating apex determines the sex balance of the flowers produced. In some plants this level is susceptible to local control in the apex by such influences as temperature, and through the auxin economy of the whole plant, by such factors as nutrition and photoperiodism. Through these agencies the sex balance of the flowers may be modified." Beuzenberg's (1961) observations of sex differentiation and cytotaxonomy in some New Zealand Violaceae are in accordance with Heslop-Harrison's theory. In some of the dioecious species of Melicytus and Hymenanthera the developmental pattern of the flower reflects a gradient pattern. Anthers are well developed and sporogenous cells sharply defined before ovular development is even apparent. Late and almost mature flowers in some male plants show much more extensive female development. The bisexual potentiality in a genotypically male plant can be realized, during growth, through a gradual increase in available auxin, especially if the sex balance is near equilibrium.

It is probably more than coincidence that the early authorities on "vegetable teratology" were closely associated with botanical gardens, and that fewer abnormalities seem to appear in modern botanical collections. Collections of newly discovered species from throughout the world were grown in the temperate zone gardens of northern Europe. Several factors which would favor development and discovery of floral abnormalities were much more common then than now. First, although skilled labor was available for giving exotic plants individual care and attention which are rarely possible today, close control of daylength and temperature was not attempted. Plants which had evolved under very different climatic conditions were maintained in a relatively lush state; species which required particular conditions of daylength or temperature for initiating flowers were under inductive conditions only by chance, and frequently only for a short time. The abnormal flowers which sometimes occur under threshold conditions of induction would consequently appear fairly often. Also, collections of new species were likely to originate from a few seeds or bulbs; any seed obtained from these plants would be used to maintain the collection, and to send stocks to other botanical gardens. Consequently, species which were normally outcrossed in their original habitat were subject to a rather close inbreeding, and recessive genes became homozygous. Then too, collections of species from different habitats and different continents were frequently grown side by side, with the result that interspecific hybridization could occur either intentionally or by chance. Another favorable factor was the new theory of natural selection, and the resulting theoretical importance to scientists of deviations from the normal structure, particularly heritable deviations.

Further studies of abnormal flowers would seem most likely to be of value in two very widely separated fields: first, the series of processes by which a particular gene is "turned on," a particular cytoplasmic structure is instructed to carry out a chemical process, the upper and lower limits of the reaction rate are determined, the resulting substance moves to other parts of the cell and perhaps other parts of the plant, and finally a structure recognizable as a petal or a carpel is produced; second, the means by which the heritable components of the genes and cytoplasm adjust to either the short-term fluctuations of climate to which an individual plant must adapt in order to survive, or to the long-continued climatic changes which have occurred several times during the evolution of the species we know.

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### THE BOTANICAL REVIEW

# TABLE I

# SPERMATOPHYTES FOR WHICH FLORAL ABNORMALITIES HAVE BEEN REPORTED

# Key to classes of abnormalities:

ABNOR	MALITY	ORGAN INVOLVED	TYPE OF CHANGE
Ι.	Phyllody	A. Entire flower	J. To male flowers only.
п.	Bracteody	B. Leaves	к. To female flowers only.
III.	Sepalody	c. Bracts	L. To male and female
IV.	Petalody	D. Sepals	flowers on same plant.
V.	Staminody	E. Petals	м. To male and female flowers
VI.	Carpellody	F. Stamens	in same inflorescence.
VII.	Change from	G. Carpels	N. To some or all hermaph-
	monoecism	н. Ovules	rodite flowers.
VIII.	Change from		o. Complete sex reversal.
	dioecism or dicliny		P. Unspecified flower
	-		deformities.

# FAMILY

Genus and Species	Abnormality	Author	Year
RANUNCULACEAE			
Aconitum lycococtinum	III-C	Penzig	1890
Actaea spicata	I-E	Masters	1869
"	I-A, I-C	Penzig	1890
Adonis amurensis	I-G	Worsdell	1916
autumnalis	I-G, IV-F	Masters	1869
Anemone spp.	IV-F, IV-G	Masters	1869
"	III-G	Worsdell	1916
alpina	III-C, IV-F	Penzig	1890
baldensis	III-C	Penzig	1890
coronaria	I-D, I-F	Masters	1869
"	I-A, I-D, III-C, IV-F, IV-G	Penzig	1890
dichotom <b>a</b>	I-D	Penzig	1890
fulgens	IV-F	Penzig	1890
hortensis	I-D	Masters	1869
**	I-A, III-C, IV-F, IV-G	Penzig	1890
nemorosa	I-D, I-F	Masters	1869
**	I-A	Penzig	1890
**	IV-E	Velenovsky	1909
		(in Worsdell)	1916
patens	III-C	Penzig	1890
pratensis	I-D, IV-F	Penzig	1890
pulsatilla	I-D	Masters	1869
ranunculoides	I-E	Worsdell	191
"	I-D, IV-F	Penzig	189
rivularis	I-A	Penzig	189
sylvatica	I-F	Penzig	189
sylvestris	I-D	Masters	186
"	IV-F, IV-G	Penzig	189
vernalis	IV-C	Penzig	189
vulgaris	I-D, I-H, III-C, III-F	Penzig	189
Aquilegia spp.	I-H, III-E, IV-D, IV-F, V-E	Worsdell	191
atraia	I-A	Penzig	189

MILY Converged Species	Abnormality	Author	Ye
Genus and Species	Abnormality		10
canadensis	IV-F	Penzig	18
coerulea	III-E, III-F	Penzig	18
formosa	I-G, V-H	Tepfer	19
skinneri	I-H	Masters	18
vulgaris	I-A, E, G, H; IV-F	Masters	18
"	I-A, III-E, III-F, IV-F	Penzig	19
Atragene spp.	IV-F	Penzig	1
Caltha palustris	I-D, IV-F	Masters	15
"	IV-F, VI-F	Worsdell	1
Clematis spp.	IV-F	Masters	1
"	IV-F	Penzig	18
flammula	IV-F	Penzig	18
foetida	VIII-O	Allan & Zotov	1
florida	IV-F	Penzig	1
fortunei	I-D	Worsdell	1
integrifolia	IV-C	Penzig	1
patens	IV-F	Penzig	1
viticella	I-D	Worsdell	1
Delphinium spp.	IV-F	Masters	1
<i>n</i>	IV-D, IV-F	Worsdell	19
ajacis	1-D, E, G, H	Masters	1
"	III-G, VI-D	Worsdell	19
"	I-H, IV-A, IV-F, VI-F	Penzig	18
amoenum	I-G	Masters	18
consolida	I-A, II-A	Penzig	1
crassicaule	I-E, F, G, H	Masters	1
dictyocarpum	I-H	Masters	18
elatum	I-F, G, H	Masters	18
"	I-A, VI-F	Penzig	18
montanum	I-A	Penzig	1
orientale	II-A, III-E, III-F	Penzig	18
staphisagria	I-E	Penzig	18
Helleborus sp.	VI-F	Martz	19
foetidus	I-A, VI-F	Penzig	18
niger	IV-F	Penzig	19
olympicus	IV-D	Masters	1
Hepatica sp.	IV-F	Masters	18
Myosurus sp.	V-E	Worsdell	19
Nigella sp.	IV-D	Worsdell	1
damascena	I-H, IV-F, IV-G	Masters	18
"	I-A	Penzig	18
Paeonia moutan	VI-E	Schimper	18
officinalis	I-G, IV-F, V-G	Masters	18
Ranunculus spp.	IV-F, IV-G	Masters	1
<i>"</i>	IV-F	Penzig	1
abortivus	III-E	Penzig	18
acris	I-D	Masters	18
"	I-D, IV-F	Penzig	18
"	VII-K	Whyte	19
	IV-A	Penzig	18
asiaticus			

TABLE I, Continued

# THE BOTANICAL REVIEW

FAMILY			
Genus and Species	Abnormality	Author	Year
auricomus	I-A, IV-D, V-G, VI-F	Penzig	1890
**	IV-D	Masters	1869
bulbosus	IV-F, VII-J	Penzig	1890
californicus	I-A	Penzig	1890
nemorosus	IV-D	Penzig	1890
philonotis	I-E, IV-F, IV-G	Penzig	1890
repens	I-E, I-G	Masters	1869
"	I-A	Penzig	1890
tuberosus	I-A	Penzig	1890
Thalictrum sp.	IV-F	Masters	1869
anemonoides	I-A, IV-F	Penzig	1890
minus	VI-F	Masters	1869
Trollius sp.	IV-F	Masters	1869
18	ÍV-D	Worsdell	1916
MAGNOLIACEAE			
Magnolia fuscata	VI-F	Masters	1869
BERBERIDACEAE			
Berberis sp.	IV-F	Masters	1869
canadensis	V-E	Penzig	1890
Podophyllum sp.	IV-F	Masters	1869
17	VI-F	Penzig	1890
<b>LARDIZABALACEAE</b>			
Stauntonia latifolia	VIII-L	Masters	1869
NYMPHAEACEAE			
Nelumbium spp.	IV-F	Masters	1869
Nymphaea spp.	IV-F	Masters	1869
dentata	I-F, I-G	Masters	1869
lotus	I-A	Masters	1869
PAPAVERACEAE			
Bocconia (Macleya)			
cordata	VI-F	Gris	1858
"	VI-F	Masters	1869
Chelidonium sp.	IV-F	Masters	1869
"	IV-F	Molliard	1905
majus	I-A	Masters	1869
"	I-A	Penzig	1890
Eschscholtzia crocea	I-D	Masters	1869
Papaver spp.	VI-F	von Mohl	1837
"	IV-F, IV-G	Masters	1869
"	VI-F	Penzig	1890
"	VI-D, VI-E	Vuillemin	1910
**	VI-F	Martz	192
bracteatum	VI-F	Masters	1869
malvaeflorum	V-E	Worsdell	191
nudicaule	VI-F	Masters	1869
**	VI-F	Worsdell	1916

TABLE I, Continued

FAMILY			
Genus and Species	Abnormality	Author	Year
orientale	I-D, IV-F	Masters	1869
**	I-D, VI-F	Penzig	1890
**	IV-F	Chittenden	1914
"	VI-F	Worsdell	1916
rhoeas	I-A, IV-F, VI-F	Penzig	1890
**	VI-F	Molliard	1905
"	VI-F	Worsdell	1916
somniferum	VI-F	Masters	1869
**	VI-A	Penzig	1890
"	IV-F	Chittenden	1914
"	IV-F	Kajanus	1918
Sanguinaria sp.	IV-F	Masters	1869
UMARIACEAE			
Corydalis aurea	I-A	Masters	1869
solida	I-C	Masters	1869
"	I-C, I-D, IV-F	Penzig	1890
Dielytra (Dicentra) sp.	I-A	Penzig	1890
"	I-F	Worsdell	1916
Fumaria officinalis	I-A	Penzig	1890
CRUCIFERAE			
Alliaria officinalis	I-H	Masters	1865
**	I-H	Penzig	1890
Alyssum incanum	I-E	Masters	1865
,,	I-A, IV-F	Penzig	189(
Arabis alpina	I-A, VI-F	Penzig	1890
" -	IV-F, IV-G	Worsdell	1916
Armoracia rusticana	V-G	Masters	1869
Barbarea sp.	IV-F	Masters	1869
stricta	I-A	Penzig	1890
11	I-A	Worsdell	1916
vulgaris	VI-F	Masters	1869
**	I-A, IV-A, IV-F, VI-F	Penzig	1890
Brassica (Sinapis) spp.	IV-F	Masters	1869
alba	I-A	Penzig	1890
arvensis	I-A, E, G, H	Masters	1869
79	I-A, I-H, IV-F, V-D	Penzig	1890
**	I-F	Molliard	1896
napus	I-H	Masters	1869
**	I-A, I-H	Penzig	1890
nigra	I-A	Penzig	1890
oleracea	J-A, D, E, G, H	Masters	1869
**	IV-D	Penzig	1890
Rapa	I-A	Penzig	1890
Bunias sp.	I-A	Masters	1869
**	I-A, V-G	Penzig	1890
orientalis	I-A	Penzig	1890
Cakile maritima	I-D	Fournier	186
"	I-A	Penzig	1890
Calepina corvini	IV-F	Penzig	1890

TABLE I, Continued

### THE BOTANICAL REVIEW

MILY Genus and Species	Abnormality	Author	Yea
Genus and Species	Aonormanty		
Capsella bursa-pastoris	V-E	Masters	186
<i>"</i>	I-A, III-E, IV-F, V-E	Penzig	189
"	V-E	Worsdell	191
Cardamine sp.	IV-F	Masters	186
amara	IV-F, IV-G	Penzig	189
matthiola	I-A	Penzig	189
pratensis	I-A, IV-F, IV-G, IV-H, V-E	Penzig	189
Chieranthus cheiri	VI-F	Allman	185
"	I-D, E, H; IV-F, VI-F	Masters	186
"	I-G, IV-F, VI-F	Penzig	189
"	VI-F	Chittenden	191
"	VI-F	Worsdell	191
	VI-F	Sirks	192
"	VI-F	Nelson	1928-
fruiticulosus	IV-A, IV-F	Penzig	189
incanus	I-D	Masters	186
			189
Cochlearia spp.	VI-F, V-G VI-F	Penzig Masters	186
Armoracia Distastania an	I-D	Masters	186
Diplotaxis sp.	I-D I-A		180
erucoides	I-A I-E	Penzig	185
muralis "	I-E I-A	Masters	
	I-A I-A	Penzig	189 183
tenuifolia "	I-A I-A, I-G	Seringe Masters	186
"	I-A, I-G I-A	Penzig	189
Draba spp.	I-A	Penzig	189
Erucastrum canariense	I-A	Masters	186
"	I-A I-A	Penzig	189
pollichii	I-H	Masters	186
Erysimum barbarea	I-E	Masters	186
canescens	I-A	Penzig	189
cheiranthoides	I-E	Masters	186
"	I-A	Penzig	189
officinale	I-E	Masters	186
Hesperis sp.	I-H	Worsdell	191
matronalis	I-A, I-E, IV-F	Masters	186
"	I-A, I-H, IV-F	Penzig	189
Iberis sp.	IV-F	Masters	186
"	IV-F	Penzig	189
Isatis tinctoria	I-A	Penzig	189
Lunaria annua	I-A	Penzig	189
Mathiola sp.	IV-F, V-G	Masters	186
annua	-	Penzig	189
	I-A, IV-F	Penzig	189
incana Nasturtium sp	I-A, IV-A I-H	Masters	186
Nasturtium sp.	I-H I-A	Penzig	189
		<b>2</b> ,	180
Peltaria alliacea	I-D, I-E	Masters	
	I-A, IV-D	Penzig Worsdell	189 191
n . /			191
Raphanus sp. sativus	I-H I-E	Masters	186

TABLE I, Continued

FAMILY			
Genus and Species	Abnormality	Author	Year
Sisymbrium sp.	I-H	Worsdell	1916
spp.	I-A, II-A	Penzig	1890
officinale	I-A, D, H	Masters	1869
tenuifolium	I-E	Masters	1869
Thlaspi arvense	I-D, I-H	Masters	1869
"	I-A	Penzig	1890
bursa-pastoris	I-E	Masters	1869
Turritis sp.	I-H	Masters	1869
glabra	I-E	Masters	1869
"	I-A	Penzig	1890
CAPPARIDACEAE			
Cleome spinosa	VII-K	Murneek	1927
RESEDACEAE			
Reseda spp.	I-A	Penzig	1890
lutea	I-E, I-H	Masters	1869
odorata	I-A	Masters	1869
phyteuma	I-E, I-G	Masters	1869
CISTACEAE			
Helianthemum sp.	IV-D	Masters	1869
amabile	IV-F	Penzig	1890
vulgare	IV-F	Penzig	1890
VIOLACEAE			
Hymenanthera spp.	VIII-N	Beuzenberg	1961
Viola sp.	IV-F, IV-G	Masters	1869
alba	I-A	Penzig	1890
altaria	IV-F	Penzig	1890
grandiflora	I-A	Penzig	1890
odorata	IV-F, I-A	Penzig	1890
tricolor	IV-F	Penzig	1890
POLYGALACEAE			
Polygala vulgaris	II-A	Penzig	1890
CARYOPHYLLACEAE			
Agrostemma githago	I-H	Masters	1869
"	I-A, I-H	Penzig	1890
Arenaria sp.	I-A	Penzig	1890
Cerastium sp.	I-G	Masters	1869
glomeratum	I-A	Masters	1869
triviale	I-A, I-E	Masters	1869
vulgatum	I-E	Masters	1869
<i>n</i>	I-A	Penzig	1890
Dianthus spp.	I-G, IV-F, IV-G	Masters	1869
barbatus	I-A, II-A, IV-F	Penzig	1809
carthusianorum	IV-D	Penzig	1890
caryophyllus	II-A, IV-F, IV-G, IV-H	Penzig	1890
,,	II-A, III-A	Worsdell	1916
	IV-F, VI-F		1910

TABLE I, Continued

FAMILY			
Genus and Species	Abnormality	Author	Year
Eudianthe Coeli Rosa	I-A	Penzig	1890
Lychnis spp.	IV-F	Masters	1869
<i>"</i>	ÎV-F	Penzig	1890
dioica	I-A, I-E, I-G	Masters	1869
"	VIII-O	Shull	1910
sylvestris	I-E	Masters	1869
Melandrium album	VIII-J	Erlenmeyer &	
	-	Geiger-Huber	1935
pratense	IV-F, IV-H	Penzig	1890
rubrum	V-H	Buchenau	1903
"	VIII-N	Löve & Löve	1940
Sagina sp.	IV-F	Masters	1869
Saponaria sp.	IV-F, IV-G	Masters	1869
"	IV-F, IV-G	Penzig	1890
Silene sp.	IV-D	Masters	1869
armeria	VI-E, VI-F	Dahlgren	1932
inflata	I-A, III-E	Penzig	1890
maritima	IV-F	Penzig	1890
pendula	IV-F, IV-H	Penzig	1890
sericea	I-A	Penzig	1890
Spergularia media Stellaria (Alsine)	I-G, I-H	Penzig	1890
media "	I-A, I-E, I-H I-A	Masters Penzig	1869 1890
PORTULACACEAE	¥-7.¥	i chung	1070
Portulaca sp.	IV-F	Masters	1869
HYPERICACEAE			1007
Hypericum nudiflorum	VI-F	Rehder	1011
perforatum	I-C, I-D	Penzig	1911 1890
TERNSTROEMIACEAE			
Camellia sp.	IV-F, IV-G	Masters	1869
Norantea brasiliensis	I-C	Penzig	1890
Thea sp.	IV-F	Masters	1869
MALVACEAE			
Abutilon spp.	IV-F	Penzig	1890
Althaea sp.	IV-F, IV-G	Masters	1869
"	IV-F, IV-G	Penzig	1890
Gossypium hybrids	IV-F	Meyer & Meyer	1961
"	VI-F	Meyer & Buffet	1962
Hibiscus sp.	IV-F, IV-G	Masters	1869
**	IV-F, IV-G	Penzig	1890
Lavatera trimestris	IV-A	Penzig	1890
Malva spp.	IV-F	Masters	1869
<i>"</i>	IV-F	Penzig	1890
silvestris	I-E	Masters	1869
STERCULIACEAE			
Sterculia platanifolia	I-G	Penzig	1890

TABLE I, Continued

FAMILY Genus and Species	Abnormality	Author	Year
TILIACEAE			
Corchorus spp.	I-A	Penzig	1890
Honckenya peploides	VII-L	Masters	1869
Sparmannia africana	IV-F	Penzig	1890
Triumfetta spp.	I-A, I-E, I-H	Masters	1869
MALPIGHIACEAE			
Heteropterys			
chrysophylla	I-D	Penzig	1890
RUTACEAE			
Citrus aurantium	VI-F	Masters	1869
"	IV-F	Penzig	1890
Dictamnus albus	I-F, I-H	Masters	1869
"	I-A	Penzig	1890
"	I-F	Molliard	1896
fraxinella	I-A, I-E, I-H	Masters	1869
Ruta spp.	IV-F, V-G	Penzig	1890
GERANIACEAE			
Geranium sp.	I-D, I-E, IV-F	Masters	1869
columbinum	I-A	Penzig	1890
molle	IV-F	Penzig	1890
Robertianum	I-A	Penzig	1890
sylvaticum	IV-F	Penzig	1890
Pelargonium sp. zonale	IV-F I-A, IV-F	Masters Penzig	1869 1890
TROPAEOLACEAE		8	
Tropaeolum sp.	I-A, E, F, H; IV-F	Masters	1869
<i>"</i>	I-A, IV-F	Penzig	1890
majus	VI-F	Masters	1869
OXALIDACEAE			
Oxalis sp.	IV-F	Masters	1869
spp.	IV-A, IV-F	Penzig	1890
BALSAMINACEAE			
Impatiens sp.	IV-F	Masters	186
"	IV-F, IV-G, V-G	Penzig	189
RHAMNACEAE			
Colletia spinosa	V-G	Penzig	189
Rhamnus fragula	I-A	Masters	186
VITACEAE			
Vitis vinifera	I-A	Masters	186
ACERACEAE			
Acer platanoides	I-A	Penzig	189
saccharinum	VIII-L	Meehan	187
MELIANTHACEAE			
Melianthus major	II-A, IV-F, V-C	Penzig	189

TABLE I, Continued

FAMILY			
Genus and Species	Abnormality	Author	Yea
ANACARDIACEAE	· · · · · · · · · · · · · · · · · · ·		
	VIII N	C 11-	10//
Pistacia lentiscus	VIII-N	Gubler	1862
Rhus copallina	I-A	Penzig	1890
glabra	I-A	Penzig	1890
HIPPOCASTANACEAE			
Aesculus sp.	IV-F	Masters	1869
hippocastanum	VII-K	Penzig	189
LEGUMINOSAE			
Amorpha fruticosa	I-C	Masters	186
Anthyllis cotonilla	IV-F	Masters	186
Astragalus cicer	VI-B	Kirschleger	186
Ĵ.		(in Penzig	1890
Brownea sp.	I-A	Penzig	189
Clitoria sp.	IV-F	Masters	1869
Coronilla sp.	IV-F	Penzig	189
Cytisus sp.	IV-F	Masters	186
Desmodium canadense	I-H	Masters	186
**	I-A, VI-H	Penzig	189
Ervum hirsutum	I-A	Penzig	189
Galega officinalis	I-A	Penzig	189
Genista sp.	IV-F	Masters	186
Lathyrus (Orobus) sp.	IV-F	Masters	186
latifolius	I-G	Masters	186
**	I-A	Penzig	189
odoratus	VII-K	Bateson, Saunders,	
		Punnett	190
Lotus sp.	IV-F	Masters	186
Lupinus sp.	I-A	Masters	186
<i>"</i>	I-A	Penzig	189
Medicago sp.	I-G, IV-F	Masters	186
spp.	I-A	Penzig	189
maculata	I-H	Masters	186
Melilotus sp.	I-G	Masters	186
spp.	I-A	Penzig	189
alba	I-G, V-E	Penzig	189
macrorhiza	I-H	Worsdell	191
Ononis spp.	I-A	Penzig	189
Phaseolus	IV-F	Masters	186
Pisum sp.	IV-F	Masters	186
sativum	VI-D	Laxton	186
77	II-A	Penzig	189
"	VI-D, VI-F	Gottschalk	196
"	VI-B	Marx & Mishanek	196
Robinia pseudoacacia	IV-D, IV-F, IV-G	Penzig	189
Spartianthus sp.	IV-F	Masters	186
Trifolium sp.	I-D, IV-F	Masters	186
spp.	I-A	Penzig	189
elegans	I-A	Penzig	189
hubridum	IG	Masters	186

elegans hybridum "

I-G

I-A

1869 1916

Masters Worsdell

FAMILY			
Genus and Species	Abnormality	Author	Yea
repens	I-A, D, E, F, G, H	Masters	186
- "	II-E, V-D	Worsdell	191
Ulex sp.	IV-F	Masters	186
Vicia biennis	I-A	Penzig	189
ROSACEAE			
Amelanchier			
oblongifolia	V-E	Worsdell	191
Crataegus sp.	IV-F	Masters	186
spp.	IV-D, IV-F	Penzig	189
Cydonia sp.	IV-F	Masters	186
Fragaria sp.	I-D, IV-F, VII-K	Masters	186
<i>"</i>	VII-K	Schaffner	192
spp.	I-A, IV-F	Penzig	189
alpina	I-H	Masters	180
vesca	I-II I-A	Masters	18
Geum rivale			18
	I-A, D, E	Masters	
spp.	I-A, IV-F, V-E, V-G	Penzig	18
Kerria sp.	IV-F	Masters	18
Mespilus germanicus	I-D	Penzig	18
Photinia sp.	IV-F	Masters	18
Potentilla sp.	I-D, IV-F	Masters	18
spp.	I-A, IV-F, IV-G	Penzig	18
argentea	I-A	Masters	18
nepalensis	I-A, I-E	Masters	18
Poterium polygonum	I-A	Masters	18
Prunus spp.	IV-F, V-G	Masters	18
"	I-H, IV-F	Penzig	18
spp. hyb.	V-E, VI-F	Tukey	19
· · · · · · · · · · · · · · · · · · ·	VI-F	Smith	19
amygdalus	I-D, I-E, IV-F, IV-G	Masters	18
"	IV-C, IV-F, IV-G	Penzig	18
avium	I- G	Masters	18
cerasus	I-D, I-E, I-G	Masters	18
"	I-D, I-D, I-O I-A, IV-F	Penzig	18
"	I-G, IV-F	Worsdell	13
persica	I-O, I-E	Masters	19
persica "			-
	I-D, IV-G	Worsdell	19
Pyrus communis	I-D, III-E, IV-F	Penzig	18
malus	I-D, II-E, IV-F, IV-G	Masters	18
"	I-D, III-E, IV-F, VI-D	Penzig	18
	III-E	Worsdell	19
Rosa spp.	I-D, E, F, G; IV-F	Masters	18
**	I-D, III-E, IV-D, IV-F	Penzig	18
"	I-D, I-H, III-G	Worsdell	19
**	IV-F	Semeniuk	19
arvensis	VI-F	Masters	18
centifolia	IV-B	Penzig	18
diversifolia	I-A	Masters	18
indica	I-A	Worsdell	19

TABLE I, Continued

FAMILY Genus and Species	Abnormality	Author	Year
		Masters	10/0
Rubus sp.	I-E		1869
spp.	I-A, II-A, IV-F	Penzig	1890
caesius	I-A, IV-D	Masters	1869
fruticosus	I-A	Masters	1869
	I-D	Worsdell	1916
<i>Spiraea</i> sp.	IV-F	Masters	1869
spp.	I-A, I-D, IV-F, VI-F, VII I-E	Penzig	1890
oblongifolia	1-E	Masters	1869
DROSERACEAE	UT D	Mastan	10/0
Dionaea muscipula "	VI-F	Masters	1869
	I-A	Harshberger	1907
	* **	(in Worsdell)	1916
Drosera intermedia	I-H	Masters	1869
CRASSULACEAE	• •	** 1	
Kalanchoë blossfeldian		Harder	1948
Sedum sp.	VIII-N	Masters	1869
Sempervivum spp.	I-A, V-G, VI-F	Penzig	1890
montanum	VI-F	Masters	1869
tectorum	VI-F	Thouars	180
"	VI-F	von Mohl	183
**	VI-F	Masters	186
"	VI-F	Martz	192
SAXIFRAGACEAE			
Deutzia sp.	IV-F	Masters	186
Hydrangea sp.	IV-C	Penzig	189
Philadelphus sp.	V-D	Gris	185
**	IV-F	Masters	186
"	I-D, IV-D, IV-F	Penzig	189
Ribes sp.	IV-F	Masters	186
"	I-A, IV-F, VI-F	Penzig	189
Saxifraga spp.	I-A, IV-F, V-E, VI-F	Penzig	189
aizoides	I-G, IV-D, V-G	Penzig	189
cotyledon	I-A	Worsdell	191
crassifolia	VI-F	Masters	186
foliosa	I-A	Masters	186
granulata	V-E	Masters	186
HALORAGIDACEAE			
Callitriche sp.	VIII	Penzig	189
Gunnera sp.	VIII-L	Masters	186
Hippuris sp.	VII-K	Masters	186
MYRTACEAE			
Baeckia diosmaefolia	V-H	Masters	186
Leptospermum sp.	VII-L	Penzig	189
Myrtus sp.	IV-F, VI-F	Masters	186
PUNICACEAE			
Punica sp.	IV-F	Masters	18
	IV-F	Penzig	189

TABLE I, Continued

FAMILY			
Genus and Species	Abnormality	Author	Year
LYTHRACEAE			
Lythrum salicaria	I-C	Penzig	1890
Nesaea verticillata	IV-F	Penzig	1890
ONAGRACEAE			
<i>Clarkia</i> sp.	IV-F	Masters	1869
"	IV-F	Penzig	1890
Epilobium spp.	I-A, IV-F	Penzig	1890
hirsutum	I-A, D, E, F, G	Masters	1869
Fuchsia sp.	I-D, IV-F, VI-F	Masters	1869
"	I-D, IV-D, IV-F, VI-F	Penzig	1890
	V-E	Worsdell	1916
<i>Godetia</i> sp.	IV-F	Masters	1869
	IV-F	Penzig	1890
Oenothera striata "	I-E I-A	Masters	1869
	1-A	Penzig	1890
LOASACEAE			
Gronovia scandens	I-A	Penzig	1890
PASSIFLORACEAE			
Passiflora spp.	V-H	Salter	1863
CARICACEAE			
Carica papaya	VIII-N	Masters	1869
"	VII-K	Usteri	1907
		(in Worsdell 1916)	1907
CUCURBITACEAE			
Acanthosicyos sp.	VIII-N	Penzig	1890
Bryonia spp. hyb.		Heilbronn &	1090
	VIII-L. VII-K		
	VIII-L, VII-K		1942
Gucumis sp.	VIII-L, VII-K VI-F	Basarman	194 <b>2</b> 1869
Cucumis sp. spp.			1942 1869 1890
•	VI-F	Basarman Masters	1869
spp. melo sativus	VI-F I-D, VI-F, VII-N J, K, L, N O	Basarman Masters Penzig	1869 1890
spp. melo sativus "	VI-F I-D, VI-F, VII-N J, K, L, N O VII-K	Basarman Masters Penzig Brantley & Warren	1869 1890 1958
spp. melo sativus "	VI-F I-D, VI-F, VII-N J, K, L, N O VII-K O	Basarman Masters Penzig Brantley & Warren Laibach & Kribben	1869 1890 1958 1950
spp. melo sativus ", ",	VI-F I-D, VI-F, VII-N J, K, L, N O VII-K O VII-J, VII-K	Basarman Masters Penzig Brantley & Warren Laibach & Kribben Wittwer & Hillyer Peterson & Anhder Mitchell & Wittwer	1869 1890 1958 1950 1954
spp. melo sativus " "	VI-F I-D, VI-F, VII-N J, K, L, N O VII-K O VII-J, VII-K VIII-J	Basarman Masters Penzig Brantley & Warren Laibach & Kribben Wittwer & Hillyer Peterson & Anhder Mitchell & Wittwer Nitsch	1869 1890 1958 1950 1954 1960 1962
spp. melo sativus " " "	VI-F I-D, VI-F, VII-N J, K, L, N O VII-K O VII-J, VII-K VIII-J VIII-J VIII-J	Basarman Masters Penzig Brantley & Warren Laibach & Kribben Wittwer & Hillyer Peterson & Anhder Mitchell & Wittwer Nitsch Wittwer & Bukovac	1869 1890 1958 1950 1954 1960 1962 1962 1962
spp. melo sativus " " " " "	VI-F I-D, VI-F, VII-N J, K, L, N O VII-K O VII-J, VII-K VIII-J VIII-J O	Basarman Masters Penzig Brantley & Warren Laibach & Kribben Wittwer & Hillyer Peterson & Anhder Mitchell & Wittwer Nitsch Wittwer & Bukovac Shifriss & George	1869 1890 1958 1950 1954 1960 1962 1962 1962 1964
spp. melo sativus " " " " Cucurbita spp.	VI-F I-D, VI-F, VII-N J, K, L, N O VII-K O VII-J, VII-K VIII-J VIII-J O VIII-N, VI-F	Basarman Masters Penzig Brantley & Warren Laibach & Kribben Wittwer & Hillyer Peterson & Anhder Mitchell & Wittwer Nitsch Wittwer & Bukovac Shifriss & George Masters	1869 1890 1958 1950 1954 1960 1962 1962 1962 1964 1869
spp. melo sativus " " " " " Cucurbita spp.	VI-F I-D, VI-F, VII-N J, K, L, N O VII-K O VII-J, VII-K VIII-J VIII-J O VIII-N, VI-F I-D, VI-F, VIII-N	Basarman Masters Penzig Brantley & Warren Laibach & Kribben Wittwer & Hillyer Peterson & Anhder Mitchell & Wittwer Nitsch Wittwer & Bukovac Shifriss & George Masters Penzig	1869 1890 1958 1950 1954 1960 1962 1962 1962 1964 1869 1890
spp. melo sativus " " " Cucurbita spp. " spp.	VI-F I-D, VI-F, VII-N J, K, L, N O VII-K O VII-J, VII-K VIII-J VIII-J O VIII-N, VI-F I-D, VI-F, VIII-N O	Basarman Masters Penzig Brantley & Warren Laibach & Kribben Wittwer & Hillyer Peterson & Anhder Mitchell & Wittwer Nitsch Wittwer & Bukovac Shifriss & George Masters Penzig Thomas	1869 1890 1958 1950 1954 1960 1962 1962 1962 1964 1869 1890 1956
spp. melo sativus " " " " " Cucurbita spp.	VI-F I-D, VI-F, VII-N J, K, L, N O VII-K O VII-J, VII-K VIII-J VIII-J O VIII-N, VI-F I-D, VI-F, VIII-N O VI-F	Basarman Masters Penzig Brantley & Warren Laibach & Kribben Wittwer & Hillyer Peterson & Anhder Mitchell & Wittwer Nitsch Wittwer & Bukovac Shifriss & George Masters Penzig Thomas Masters	1869 1890 1958 1950 1954 1960 1962 1962 1962 1964 1869 1890 1956 1869
spp. melo sativus " " " " Cucurbita spp. " spp. pepo "	VI-F I-D, VI-F, VII-N J, K, L, N O VII-K O VII-J, VII-K VIII-J VIII-J O VIII-N, VI-F I-D, VI-F, VIII-N O VI-F VII-J, VII-K	Basarman Masters Penzig Brantley & Warren Laibach & Kribben Wittwer & Hillyer Peterson & Anhder Mitchell & Wittwer Nitsch Wittwer & Bukovac Shifriss & George Masters Penzig Thomas Masters Nitsch	1869 1890 1958 1950 1954 1960 1962 1962 1962 1964 1869 1890 1956 1869 1956
spp. melo sativus " " " Cucurbita spp. " spp. pepo " Ecballium sp.	VI-F I-D, VI-F, VII-N J, K, L, N O VII-K O VII-J, VII-K VIII-J VIII-J O VIII-N, VI-F I-D, VI-F, VIII-N O VI-F VII-J, VII-K VIII-N	Basarman Masters Penzig Brantley & Warren Laibach & Kribben Wittwer & Hillyer Peterson & Anhder Mitchell & Wittwer Nitsch Wittwer & Bukovac Shifriss & George Masters Penzig Thomas Masters Nitsch Penzig	1869 1890 1958 1950 1954 1960 1962 1962 1962 1869 1890 1956 1869 1956 1869 1962 1890
spp. melo sativus " " " Cucurbita spp. " spp. pepo "	VI-F I-D, VI-F, VII-N J, K, L, N O VII-K O VII-J, VII-K VIII-J VIII-J O VIII-N, VI-F I-D, VI-F, VIII-N O VI-F VII-J, VII-K	Basarman Masters Penzig Brantley & Warren Laibach & Kribben Wittwer & Hillyer Peterson & Anhder Mitchell & Wittwer Nitsch Wittwer & Bukovac Shifriss & George Masters Penzig Thomas Masters Nitsch	1869 1890 1958 1950 1954 1960 1962 1962 1962 1964 1869 1890 1956 1869 1956

FAMILY Genus and Species	Abnormality	Author	Year
BEGONIACEAE	······		
Begonia spp.	IV-F, VIII-M	Penzig	1890
"	V-H	Goebel	1908
"	IV-H, V-G	Worsdell	1916
cathayana	VI-F	Worsdell	1916
"	N	Noack	1962
frigida	VI-F	Masters	1869
<i>lloydii</i> hyb.	VI-E, VI-F	Bateson & Sutton	1919
hyb.	VI-E, VI-F	Noack	1962
pearcei	I-E, IV-F, IV-G	Worsdell	1916
CACTACEAE			
cereus spp.	IV-F	Penzig	1890
UMBELLIFERAE			
Angelica sp. Anthriscus	I-A	Penzig	1890
(Torilis) sp.	I-A, E, F, H	Masters	1869
	I-F	Molliard	1896
Apium sp.	I-A	Penzig	1890
Athamanta cervaria	I-D	Masters	1869
Carum carvi "	I-H, IV-D	Masters Penzig	1869 1890
	I-A, IV-D, <b>IV-F</b> I-G	Worsdell	1916
Daucus sp. carota	I-O I-D, E, F, G; IV-F, V-E	Masters	1869
"	I-A, IV-F, V-E	Penzig	1890
Echinophora sp.	I-A	Penzig	1890
Heracleum sp.	I-F, I-G	Masters	1869
"	I-C, V-E	Penzig	1890
sphondylium	I-E	Masters	1869
Myrrhis (Seseli) sp.	I-A	Masters	1869
Oenanthe sp.	I-C	Penzig	1890
Pastinaca sp.	I-H	Masters	1869
Selinum carufolium	I-A	Masters Penzig	1869 1890
Trinia sp.	VII	Tenzig	1070
CORNACEAE	VIII N	Masters	1869
Aucuba sp.	VIII-N	Penzig	1809
Cornus sp.	IV-F	renzig	1870
CAPRIFOLIACEAE		<b>N</b> <i>A</i> .	10/0
Lonicera sp.	I-H, IV-F, IV-G	Masters	1869
periclymenum	I-E, I-F, I-G	Masters	1869
<i>"</i>	I-E	Worsdell	1916 1869
xylosteum	I-E IV-F	Masters Masters	1869
Sambucus sp. Viburnum sp.	IV-F	Masters	1865
RUBIACEAE			
Gardenia sp.	IV-F	Masters	1869
Ixora sp.	IV-F	Masters	1869
Serissa sp.	IV-F	Masters	1869

FAMILY			
Genus and Species	Abnormality	Author	Year
VALERIANACEAE			
Centranthus	I-D	Masters	1869
macrosiphon			
DIPSACACEAE			
Dipsacus fullonum	I-A	Masters	1869
Knautia arvensis	IV-F	de Bary (in	
		Worsdell)	1884
Scabiosa sp.	IV-F, IV-G	Masters	1869
agrestis	I-E	Masters	1869
Columbaria	I-A, I-E	Masters	1869
"	I-A, I-E	Masters	1869
"	IV-F	Worsdell	1916
COMPOSITAE			
Ambrosia sp.	VIII-J	Thomas	1956
Calendula			
officinalis	I-A, I-E	Masters	1869
Carduus			
heterophyllus	I-D, I-G	Masters	1869
tataricus	I-D, I-G	Masters	1869
Centaurea jacea	I-C	Masters	1869
Cirsium arvense	I-D	Masters	1869
tricephalodes	I-E	Masters	1869
Crepis sp.	I-H	Masters	1869
Gaillardia sp.	I-H	Masters	1869
Helenium autumnale	I-C, I-E	Worsdell	1916
Hypochaeris radicata Matricaria	I-D	Masters	1869
parthenium	I-A	Masters	1869
Parthenium inodorum	I-C	Masters	1869
Petasites hybridus	I-A	Wardlaw	1963
Scorzonera	* 1 *	Waltiaw	1703
octangularis	I-D	Masters	1869
Senecio vulgaris	I-D, I-E	Masters	1869
Taraxacum	1 D, 1 D	iviasters	1007
officinale	I-C	Masters	1869
Tragopogon	- 0	Tradicity.	100,
orientale	I-D	Masters	1869
pratense	I-D	Masters	1869
"	I-C	Worsdell	1916
CAMPANULACEAE		ii oladeli	1710
Campanula sp.	I-D	Masters	1869
glomerata	I-E	Masters	1869
medium	IV-D	Worsdell	1916
persicifolia	IV-D, IV-F, V-G	Masters	1869
"	IV-D, IV-I, V G	Worsdell	1916
pyrimidalis	I-A	Masters	1869
rapunculoides	VI-F	Masters	1869
Phyteuma odorata	I-H	Masters	1869
spicatum	I-E	Masters	1869
Platycodon sp.	IV-F	Masters	1869

FAMILY			
Genus and Species	Abnormality	Author	Year
ERICACEAE			
Arbutus sp.	IV-F	Masters	1869
Azalea sp.	IV-F	Masters	1869
Calluna sp.	IV-F	Masters	1869
Erica sp.	IV-F	Masters	1869
cinerea	III-A	Worsdell	1910
tetralix	VI-F	Masters	1869
	II-A	Worsdell	1910
Rhododendron sp.	IV-F	Masters	1869
indicum	IV-D	Worsdell	1916
PRIMULACEAE			
Anagallis arvensis	I-A, I-F, I-H, IV-D, IV-F	Masters	1869
phoenicea	I-E, I-H	Masters	1869
webbiana	I-A	Masters	1869
Cyclamen sp.	IV-F	Masters	1869
Lysimachia			
ephemerum	I-A, I-H	Masters	1869
Primula sp.	IV-F, IV-G	Masters	1869
"	I-H	Worsdell	1916
acaulis		Tschermak	1932
<i>acautis</i> "	I-D, VI-F IV-F, IV-G	Masters Tschermak	1869 1932
auricula	I-H, III-E	Masters (de	1934
auricuia	1-11, 111-E	Candolle)	1869
calycanthema	IV-D	Masters	1869
elatior	I-D	Masters	1869
"	IV-F, IV-G	Tschermak	1932
kewensis	I-E, IV-F	Heinricher	1931
officinalis	I-D, IV-D	Masters	1869
""	IV-F	Molliard (in	
		Worsdell)	1901
"	IV-F, VI-F	Marsden-Jones &	
		Turrill	1931
**	IV-D, VI-F	Montford	1931
"	VI-F	Dahlgren	1932
"	IV-F, IV-G	Tschermak	1932
praenitens	I-H	Masters	1869
sinensis	I-A, I-E, I-F	Masters	1869
veris	VI-F	Rytz	1921
vulgaris	VI-F	Masters (in	
"	I-D, IV-D	Worsdell) Worsdell	1878 1916
	1-D, 14-D	vy orsuen	1910
OLEACEAE			
Jasminum sp.	IV-F	Masters	1869
Syringa sp.	IV-F	Masters	1869
persica	IV-D	Masters	1869
GENTIANACEAE			
Gentiana sp.	IV-F	Masters	1869
amarella	I-E, VI-F	Masters	1869
campestris	I-D, V-G	Masters	1869

TABLE I, Continued

FAMILY			
Genus and Species	Abnormality	Author	Year
APOCYNACEAE			
Allamanda sp.	IV-F	Masters	1869
Nerium sp.	IV-F	Masters	1869
Tabernaemontana sp.	IV-F	Masters	1869
Vinca sp.	IV-F	Masters	1869
POLEMONIACEAE			
Gilia capitata	I-A	Masters	1869
glomeruliflora	I-E, I-H	Masters	1869
Polemonium coeruleum	I-E, VI-F	Masters	1869
"	IV-F	Chittenden	1914
BORAGINACEAE			
Anchusa ochroleuca	I-A, I-G	Masters	1869
paniculata	I-G	Masters	1869
Myosotis caespitosa	I-A	Masters	1869
Symphytum officinale	I-E, I-G, I-H	Masters	1869
zeyheri	I-H	Masters	1869
CONVOLVULACEAE			
Convolvulus sp.	IV-F	Masters	1869
(Calystegia)			
sepium	I-D	Masters	1869
Ipomoea sp.	IV-F	Masters	1869
ímperialis	VI-F	Correns (in	
		Dahlgren)	1932
SOLANACEAE			
Datura sp.	IV-F	Masters	1869
Lycium europaeum	I-D	Masters	1869
Nicotiana affinis	VI-F	Costerus	1907
alata	VI-F	Avery	1929
<i>langsdorff</i> hyb.	IV-D, IV-D, VI-F	White	1914
rustica	I-A	Masters	1869
rustica hyb.	I-A, I-G	Hillman & Smith	1965
tabacum "	VI-F	Goodspeed	1930
	VI-F	Goodspeed &	
to be seen that	в	Avery	1934
tabacum hyb.		Burk	1960
Petunia spp.	I-F, IV-F	Masters	1869
violacea S-l	I-D, I-E V-E	Masters	1869
Solanum sp.	V-L	Henslow (in Worsdell)	1007
"	VI-F	Worsdell)	1882
"	VI-F V-E	Scott (in Worsdell Worsdell	
spp. hyb.	P	Worsdell Koopmans	1916
spp. nyo. "	r P	Grun & Radlow	1955 1960, 62
SCROPHULARIACEAE			
	IEIVE	Masters	10/0
Antirrhimum majus "	I-E, IV-F	Masters	1869
	I-A, III-E, III-F, I-E, III-A	Baur	1924

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AMILY			
Genus and Species	Abnormality	Author	Yea
Calceolaria sp.	IV-D, IV-F	Masters	186
Digitalis sp.	IV-F	Masters	186
purpurea	V-E	Masters	186
î,	V-E	Saunders (in	
		Worsdell)	191
purpurea 🗙			
lutea	IV-F, VI-F	Martz	192
Gratiola sp.	IV-F	Masters	186
Linaria sp.	IV-F	Masters	186
vulgaris	IV-F	Heufler	184
**	V-G, VI-F	Worsdell	191
"	VI-F	Geisenheyner	191
"	VI-F	Graf	191
Mimulus spp.	IV-D, IV-F	Masters	186
"	IV-D	Worsdell	191
Rhinanthus sp.	VI-E	Schimper (in	
		Worsdell)	182
Scrophularia sp.	I-H	Worsdell	191
aquatica	I-A, I-G	Masters	186
nodosa	I-A	Masters	186
Torenia fournieri	I-A, I-G, IV-F all transitional forms	Simon	192
Verbascum sp.	I-E	Masters	186
pholomoides	I-A	Masters	186
Veronica sp.	IV-F	Masters	186
IGNONIACEAE			
Bignonia sp.	IV-F	Masters	186
GESNERIACEAE			
Achimines sp.	IV-F	Masters	186
Gloxinia sp.			
(Sinningia)	IV-D, IV-F	Masters	186
"	V-E	Worsdell	19
Streptocarpus sp.	IV-F	Worsdell	193
sp. hyb.	VI-F	Oehlkers	194
Trichosporum sp.	IV-G	Masters	186
<b>ERBENACEAE</b>			
Clerodendron sp.	IV-F	Masters	180
ABIATAE			
Ajuga reptans	I-C	Masters	180
Monarda fistulosa	V-E	Masters	180
Origanum majorana	. 2	Madel 5	100
X vulgare	K, L, M	Appl	19:
Origanum vulgare	III-E, VI-F, III-F	Appl	19
"	VII-K	Lewis & Crowe	19
Perilla frutescens	II-A	Raghaven & Jacobs	19
·		rugharen u jacoba	

TABLE I, Continued

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FAMILY		Anthon	Vaaa
Genus and Species	Abnormality	Author	Year
sylvatica "	I-A, I-E, I-G VI-E	Masters Schimper (in	1869
Thymus vulgaris X		Worsdell)	1829
T. ovatus	VIII-K, VIII-N	Appl	1933
PLANTAGINACEAE			
Plantago spp.	I-C	Masters	1869
CHENOPODIACEAE			
Spinacia sp.	VII-N	Masters	1869
NYCTAGINACEAE			
Mirabilis sp.	IV-F	Masters	1869
POLYGONACEAE			
Rumex arifolius	I-A, I-H	Masters	1869
crispa	VI-F	Masters	1869
hastatulus	VII-J, VII-K	Smith	1963
scutatus	I-A, I-H	Masters	1869
MYRISTICACEAE			
Myristica sp.	VIII-L	Masters	1869
LAURACEAE			
Laurus sp.	IV-F	Eichler (in Worsdell	) 1853
"	IV-F	Masters	1869
cerasus	I-D	Masters	1869
MORACEAE			
Cannabis sativa	VIII-N	Gasparrini (in Figdor)	1862
"	VIII-L, VIII-N	Masters	1862
"	O	Molliard	1896
**	VIII-N	Pritchard	1916
"	VIII-N, O	Schaffner	
		1921, 1923, 192	25, 1931
"	VIII-N	McPhee	1925
<i>יי</i>	VIII-N	Talley	1934
"	J, K, N	Tibeau	1936
"	VIII-J	Borthwick & Scully	1954
"	VIII-K VIII-L	Heslop-Harrison	1956
**	VIII-L VIII-J, VIII-K	Köhler Brodomann <i>et al</i>	1958
Humulus japonicus	VIII-J, VIII-K VIII-J	Bredemann <i>et al.</i> Nypels	1961 1897
<i>"</i>	VIII-L	Giard	1898
"	VIII-N	Figdor	1911
lupulus	VIII-L	Masters	1869
- "	VIII-L	Worsdell	1916
Morus sp.	VII-J, VII-K	Masters	1869
alba	VIII to J, K, L	Schaffner	1929

TABLE I, Continued

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FAMILY Genus and Species	Abnormality	Author	Year
JUGLANDACEAE			
Juglans sp.	VII-K	Masters	1869
LEITNERIACEAE			
Leitneria floridana	VIII-L	Masters	1869
MYRICACEAE			
Myrica gale	VIII-L, VIII-N	Davey & Gibson	1917
EUPHORBIACEAE			
Breynia sp.	Ν	Masters	1869
Cleistanthus	Ν	Masters	1869
Cluytia semperflorens Conceveiba	Ν	Masters	1869
macrophylla	Ν	Masters	1869
Crozophora tinctoria	Ν	Masters	1869
Euphorbia sp.	VI-F	Schmitz (in Worsdell)	1871
esula	VI-F	Masters	1869
geniculata	I-F	Masters	1869
palustris	V-G	Masters	1869
segetalis	I-A	Masters	1869
Glochidon sp. Hermesia	VI-F	Masters	1869
castaneifolia	VIII-N	Masters	1869
Jatropha pohliana	I-F	Masters	1869
Mercurialis sp.	VIII-L and N	Masters	1869
ambigua	VIII-L	Yampolsky	1919
"	Ţ	Thomas	1956
**	I & L	Heslop-Harrison	1957
Mozinna peltata	VIII-L	Masters	1869
Phyllanthus sp.	Ν	Masters	1869
Ricinus communis	N, V-G	Masters	1869
"	VII-K	Parkey	1957
"	VIII-L	Clavier	1961
**	VII-K	Shifriss	1961
		Shifriss & George	1964
17	Everted ovule	Stein	1965
Schismatophora			
distichophylla	VIII-L	Masters	1869
Suregada sp.	Ν	Masters	1869
FAGACEAE			
Fagus sylvatica	Ν	Masters	1869
SALICACEAE			
Populus alba hyb.	VIII-L	Peto	1938
tremula hyb.	VIII to L & N	Runquist (in Seitz)	1951
"	VIII to L & N	Seitz	1952
13	VIII to L & N	Schlenker	1953
tremuloides	VIII-N	Erlanson & Hermann	1927

FAMILY			
Genus and Species	Abnormality	Author	Year
Salix sp. hyb.	V-G, VI-F, N	Rainio	1927
"	IV	Heribert-Nilsson	
	V-G	(in Dahlgren) Masters	1932 1869
sp. "	V-G VIII-L	Wigand (in Worsdell)	1916
alba	VIII to L & N	Worsdell	1916
andersoniana	VI-F	Masters	1869
babylonica	I-G, VI-F	Masters	1869
capraea	I-H	Masters	1869
cinerea	VIII-L	Worsdell	1916
fragilis	V-G	Zimmerman (in Worsdell)	1911
EMPETRACEAE			
Empetrum sp.	Ν	Masters	1869
TAXACEAE			
Taxus sp.	Ν	Masters	1869
PINACEAE			
Cupressus sp.	I-H	Worsdell	1916
Juniperus virginiana	VIII-L	Masters	1869
Larix sp.	VI-F	Worsdell	1916
Pinus sp.	VI-F	Worsdell	1916
HYDROCHARITACEAE			
Hydrocharis sp.	IV-F	Masters	1869
ORCHIDACEAE			
Aceras anthropophora	IV-D	Masters (in Worsdell)	1916
Catasetum sp.	IV-F	Masters	1869
Cattleya loddigesii	I-D, I-E	Worsdell	1916
trianae	IV-D	Worsdell	1916
Cypripedium spp.	IV-F	Masters (in Worsdell)	1916
"	IV-F	Penzig (in Worsdell)	1916
calceolus	IV-F	Heinricher (in	
lawrencianum	IV-D	Worsdell) Heinricher (in Worsdell)	1891 1891
Epidendrum		tt orsucht j	10/1
vitellinum	IV-A	Rolfe (in Worsdell)	1890
Miltonia vexillaria	IV-F, IV-G	Worsdell	1916
Odontoglossum	,		-
crispum	III-E	Worsdell	1916
Ophrys sp.	V-E	Masters	1869
insectifera	V-G	Masters	1869

TABLE I, Continued

FAMILY			
Genus and Species	Abnormality	Author	Year
Orchis sp.	IV-F	Masters	1869
mascula	V-E	Masters	1869
morio	IV-D	Penzig (in Worsdell)	1886
Platanthera bifolia	VI-F	Rytz	1921
IRIDACEAE			
Crocus sp.	IV-F	Masters	1869
"	all transitions		
	between carpels and sepals	Worsdell	1916
graecus	VI-C, VI-E, VI-F	Lutz (in Worsdell)	1897
nudiflorus	VI-E	Masters	1869
sativus	VI-C, VI-E, VI-F	Lutz (in Worsdell)	1897
zonatus	V-D, V-E	Worsdell	1916
Gladiolus sp.	IV-F	Masters	1869
Iris, all species	IV-G	Worsdell	1916
sp.	IV-F	Masters	1869
kaempferi	IV-F	Worsdell	1916
sieboldii	IV-F	Worsdell	1916
AMARYLLIDACEAE			
Amaryllis sp.	VI-F	Masters	1869
Galanthus nivalis	IV-F	Masters	1869
<i>"</i>	II-A, IV-D, I-A	Worsdell	1916
Hippeastrum sp.	IV-F	Masters	1869
Leucojum sp.	IV-F	Masters	1869
Narcissus sp.	IV-F	Masters	1869
<i>wareissus</i> sp.	IV-F, IV-G	Worsdell	1916
pseudo-narcissus	VI-F	Molliard	1896
" "	VI-F	Martz	1928
tazetta	IV-F	Celakovsky (in	
		Worsdell)	1916
Polianthes sp.	IV-F	Masters	1869
Sternbergia sp.	IV-F	Masters	1869
ZINGIBERACEAE			
Alpinia sp.	V-E	Worsdell	1916
LILIACEAE			
Allium			
scorodoprasum	V-G	Masters	1869
Asphodelus sp.	IV-F, V-E	Masters	1869
ramosus	VI-F	Masters	1869
Colchicum	·		
autumnale	I-D, IV-F	Masters	1869
Convallaria maialis	I-D, IV-F	Masters	1869
Fritillaria sp.	IV-F	Masters	1869
		Masters	1869
Hamaracallia			
Hemerocallis sp. Hyacinthus sp.	IV-F 1-G, IV-F, V-G	Masters	1869

FAMILY			
Genus and Species	Abnormality	Author	Year
orientalis	IV-F		
"	embryo-sac-like pollen IV-F	Nemec	1898
"	embryo-sac-like pollen IV-F	Stow	1930
"	embryo-sac-like pollen IV-F	de Mol	193
	embryo-sac-like pollen	Naithani	193
Lilium sp.	IV-F	Masters	1869
candidum	I-C	Worsdell	1916
longiflorum	VI-F	Masters	1869
tigrinum	VI-F	Masters	1869
Ornithogalum			
nutans	embryo-sac-like pollen	Geitler	1941
Scilla sp.	IV-F	Masters	1869
nutans	V-G	Worsdell	1916
Tofieldia sp.	IV-F	Masters	1869
calyculata	V-G	Masters	1869
Trillium			
grandiflorum	I-A, O	Hall	1961
Tulipa sp.	VI-F	Clos	1859
<i>"</i> ¯¯¯	I-G, IV-F	Masters	1869
**	VI-F	Molliard	1896
"	VI-D, VI-E, V-G, I-D, V-D	Worsdell	1916
"	V-H	Martz	1928
gesneriana	I-D, VI-E	Masters	1869
COMMELINACEAE			
Commelyna sp.	IV-F	Masters	1869
Tradescantia sp.	IV-F	Masters	1869
JUNCACEAE			
Juncus lamprocarpus	I-A	Masters	1869
"	II-A	Worsdell	1916
uliginosus	I-A	Masters	1869
ΡΛΙΜΑCEAE			
Chamaerops humilis "	V-G V-G	von Mohl Masters	1837 1869
Cocos sp.	О-К	Smith (in Worsdell)	3, 1916
		1907	, 1710
ARACEAE			
Arisaema triphyllum	J-K or M	Atkinson	1898
"	J-K or M	Schaffner	1922
"	J-K or M	Camp	1932
ALISMACEAE			

TABLE I, Conti	inued
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FAMILY Genus and Species	Abnormality	Author	Year
CYPERACEAE			
Carex sp.	VIII-L	Masters	1869
GRAMINEAE			
Avena chinensis	V-E	Masters	1869
Bambusa sp.	VI-F	Masters	1869
Glyceria fluitans	I-D, E, F	Wigand (in	
	······································	Worsdell)	1856
Hordeum sp.	0	Wijewantha &	
*		Stebbins	1964
Saccharum spontaneum	VI-F	Bremer	1928
Triticum sp. hyb.	VI-F	Leighty & Sando	1924
"	VI-F	Kihara	1951
aestivum	VI-F	Porter, Lahr, &	
		Atkins	1965
vulgare	VI-F	Leighty & Sando	1924
"	VI-F	Calder	1930
Zea mays	VI-F, N	Masters	1869
<i>19</i>	0	Blaringhem 19	04, 1905
**	М, О	Worsdell	1916
"	M, VI-F	Weatherwax 1929	a, 19 <b>2</b> 5b
"	М	Schaffner	1927
**	М	Phipps	1928
**	М	Richey & Sprague	1932
**	М	Heslop-Harrison	1959
**	I	Postlethwait &	
		Nelson	1964
"	II, VI-H	Orr & Postlethwait	1964