# TYPES OF
# FLORAL MECHANISM

## A SELECTION OF
## DIAGRAMS AND DESCRIPTIONS OF COMMON FLOWERS

ARRANGED AS AN INTRODUCTION TO THE SYSTEMATIC STUDY OF ANGIOSPERMS

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# INTRODUCTION

THIS portion of a collection of floral studies, originally prepared for Class purposes, and limited to a hundred types as illustrating what may be termed in popular phraseology 'The Hundred Best Flowers', has been arranged for publication in the hope that it may prove useful not only to other teachers and students, but also to all those who are interested in the study of the Natural History and problems of plant-life.

The types have been selected as presenting features of special botanical interest combined with the fact that they may all be readily cultivated in an ordinary garden, and are again well-known or readily obtainable plants. As it has been found impossible to take one flower by itself as an isolated natural phenomenon, short notices of allied forms have been included in order that each type may appear duly orientated with regard to other organisms. The present part contains twelve Early Spring Types which are the more interesting in that they are obtainable when flowers are otherwise scarce.

As this is not intended as a work of reference, notices of the enormous field of literature have been omitted, though names and dates affording a sufficient guide are given for any points which have not been actually checked, or being only observable with difficulty remain open to question.

The arrangement and general scheme is designed to represent the working method applicable to the subject, and all figures are drawn in the size and style and of the character to be expected of good class student work, and finished off in a manner suitable for reproduction by standard processes.

No methods are indicated, nor have any been employed in making preparations, which are beyond the reach of the 'elementary student'; and at the same time a general 'elementary' acquaintance with the subject on the part of the reader has been assumed.

Since it is necessary to draw the line somewhere, and the difficulty in writing up an elementary account of any flower is to know where to stop and what to leave out, and the present work is admittedly of only a general and elementary character, histological details are omitted; but since the objects are often small, and the use of a lens of some sort is obligatory, it has been decided to stop at the 'Low Power', with which the tissues and general features of cells may be visible. A lens which does not admit of convenience in drawing is useless, and the Zeiss $a_2$ and A have been taken as the most generally useful.

An attempt has been made to strike a mean between the prosy abstruseness of the academic systematist on the one hand, and the imaginative flights of the enthusiastic adaptationist on the other, and to distinguish carefully what are the facts of observation and what deductions may have been read into them. The more abstract conceptions and ideas, however suggestive they may be, which are not always fully warranted by the facts at one's disposal, are thus relegated to a special end section.

Biological and numerical data, unless otherwise stated, have been collected for specimens grown at Oxford, and represent the result of observations extending in many cases over several years; and the Oxford Garden, being not only the oldest in the country, but also occupying a fairly central position, may well establish its claim to be regarded as a standard for English grown plants.

All diagrams and figures are entirely new: the Eichlerian Convention has been followed in the floral diagrams, as being still sufficiently accurate for general purposes, and the sectional elevations have been constructed for a plane accurately referable to the diagrams and drawn, in at least one case, to a definite scale; these being architectural requirements which have not been carefully observed in the past. Developmental figures are given as exact camera lucida drawings of sections also cut in a given direction, or in the case of larger structures also drawn to scale. Although the imperfections of the present work are often startlingly obvious, and no one can read through a single type without being struck by the many lacunae existing in the account of even the commonest form, it has been felt that the time has come for a beginning to be made in the direction of accumulating under appropriate headings the general facts regarding individual types, and it is clear that much remains to be done, not only in connexion with the vast multitude of flowering plants, but even in the more restricted range of the British Flora.

*Oxford*, 1907. A. H. C.

'Verus Botanicus ubique Scientiam Botanices excolit:
Oculis propriis quae singularia sunt observat;
Nec sua solum, ex Auctoribus, compilat.'

(LINNAEUS, 1750.)

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# I

## Helleborus niger[1], L.

*Christmas Rose.*
Black Hellebore.

A HARDY herbaceous plant with perennating subterranean rhizome, and short foliage and flower shoots, sending up flower-stalks to the height of 6 inches to 1 foot. Indigenous to South Europe and Eastern Asia, especially the forest region of the S. and E. Alps; and long cultivated in English gardens, being mentioned by Gerard[2] in 1596. It was introduced from the mountains of Austria and Italy,[3] and is grown for the sake of its showy white flowers produced in the winter months, more particularly in December and January, being the most attractive of the genus, and probably owing its large size and clear colour to its evolution in Alpine districts, where insects are few and floral competition keen. The fruits shed their seeds in May and June, but are not commonly produced in this country in open situations.[4]

*H. niger* also grows in Greece as a mountain form, but the original Black Hellebore is generally agreed to have been a commoner woodland form with a taller branched inflorescence and purplish flowers, which was collected by Tournefort (1702) as *H. orientalis*, and later by Sibthorp (1787) as *H. officinalis*. A form of *H. orientalis* with whiter flowers was introduced from Mt. Olympus as *H. olympicus* (1840): the oriental forms, as also *H. atro-rubens* from Croatia, have a closely similar habit and hybridize readily; many common garden forms[5] are descended from them, and present the habit of the true Black

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[1] *Helleborus* founded as a *genus* by Tournefort (1700), established by Linnaeus (1735); the specific name established by Linnaeus (1753). The name *Helleborus niger* is a Latinized form of the Greek Ἑλλέβορος μέλας (Black Hellebore), and was given to it under the impression that *H. niger*, as a common German and Italian Alpine form, was the plant referred to by Dioscorides for its medicinal value; the description by Dioscorides being sufficiently vague, with the exception of the point that the flower was purplish. That the common Hellebore of the Greek woods had a purple flower and not a white one was also noticed by the French traveller Belon (Bellonius, 1549).

[2] Gerard's description is very apt:—'It beareth Rose fashioned flowers upon slender stemmes, growing immediately out of the grounde an handful high, . . . sometimes very white, and often mixed with a little shewe of purple, which being vaded, there succeede small huskes full of black seedes; the roots are manie with long black strings coming from one head.' The plate is, however, incorrect; a good figure appears in Johnson's Gerard, 1633; the same block appears in Lobelius, 1576. It is interesting to note that while Gerard describes the Christmas Rose clearly enough, he figured a form of *H. orientalis*, and similarly Fuchsius (1542) gives a good drawing of a similar oriental form, although he mentions the Christmas flowering period. As Fuchsius gives this plant as growing in German gardens only as a 'planted form', it is clear that the two species must have been at this time in cultivation, and the difference between them was not noticed, or else the drawings were made in later spring, when the winter-flowering form was not obtainable. Brunfels (1530) also gives an admirable drawing of *H. orientalis*, the purple-flowered type, as *Helleborus niger*. The plant originally called *H. niger* was thus actually the Greek woodland form and the mistake arose later.

[3] The larger form grown in gardens as *H. niger*, var. *major* or *maximus*, is the same as *H. altifolius* (Reich.), and grows wild in Carniola.

[4] The plant grows wild in mountain regions, preferably in rocky situations, and being thus an alpine form it requires abundance of pure air and humus in the soil. Manure other than leaf-mould would be injurious, and the plants do not flourish in the neighbourhood of towns.

[5] An extensive series of hybrids of the 'oriental' section was first formed by Sauer at the Berlin University Garden as early as 1851, and many beautiful forms are now in cultivation, especially hybrids of the handsome spotted Caucasian plant *H. guttatus*. Hybrids of *H. niger* and *H. purpurascens* have been produced by Randonnet, but not being remarkably beautiful do not appear to have been kept in cultivation.

Hellebore; as they flower usually somewhat later than the Christmas Rose they are sometimes called Lent Roses.

The black rhizome had a commercial value as a drug: according to Pliny, Hellebore was used medicinally as far back as B. C. 1400. The poisonous substances have been localized as two glucosides, Helleborin and Helleborein, distinguished by their relative solubilities in alcohol. *H. niger* is much less poisonous than *H. orientalis*: the poisonous qualities are not removed by desiccation or cooking, and the fact that cattle have been killed by grazing on *H. foetidus* has doubtless led to its extermination in many parts of the country.[1]

## Description.

INFLORESCENCE: a simple racemose type with terminal flower, reduced to 5–2 large flowers, or most commonly to one only. Lateral flowers possess normal subtending bract and two prophylls.

FLOWER: hermaphrodite; approximately actinomorphic, being spirally constructed throughout.

RECEPTACLE: elongated, cylindrical (Hypogyny); a distinct internode between androecium and gynoecium.

PERIANTH differentiated into:—

(1) *Calyx* of 5 free sepals, ovate, averaging 40 mm. long by 30 wide, white or pinkish with green at base.

(2) *Corolla* of 13 free members (varying 10–21) functioning as slipper-shaped nectaries; shortly stalked (2–3 mm.), green and tubular (8–10 mm.), 2-lipped, the lower lip larger (4 mm.) than the small upper one (2 mm.); slightly saccate on the lower surface.

ANDROECIUM typically of about 90 free stamens (varying 80–110);
*Filaments* up to 15 mm. long, white, and slender;
*Anthers* yellow, oval, and compressed, introrse (2 mm.);
*Pollen* abundant, yellow.

GYNOECIUM typically of 5 free carpels (varying 6–10): apocarpous above, but apparently syncarpous at the base owing to insertion on conical end of axis.
*Ovary* unilocular, 10 mm. long, green externally, with anatropous ovules in two rows along the ventral suture, 16–20 in each carpel, and lying raphe to raphe in the horizontal plane.
*Styles* free, marked with a groove on the inner surface (ventral suture), and bearing
*Stigmatic papillae* at the extreme tip, about 15–18 mm. from the base of the ovary.

NECTARY: honey is secreted by a glandular region at the base of the cavity of the tubular 'petals', and rises in the tube 2–3 mm.

**Variations** include—

(1) The smaller size of the members of flowers which have been impoverished, or are the last laterals of the inflorescence.

(2) The variable number of members constituting the androecium, gynoecium, and corolla; the calyx segments are remarkably constant, a sixth member being comparatively rare, when present it falls in the theoretical position (cf. diagram, Fig. 7). Starved flowers and the laterals of the inflorescence may give only half the typical measurements; i. e. sepals less than 20 mm. long, stamen filaments 8 mm. only, and other lengths in proportion. The number of parts is most variable in the androecium, and may here fall to 60–70 members.

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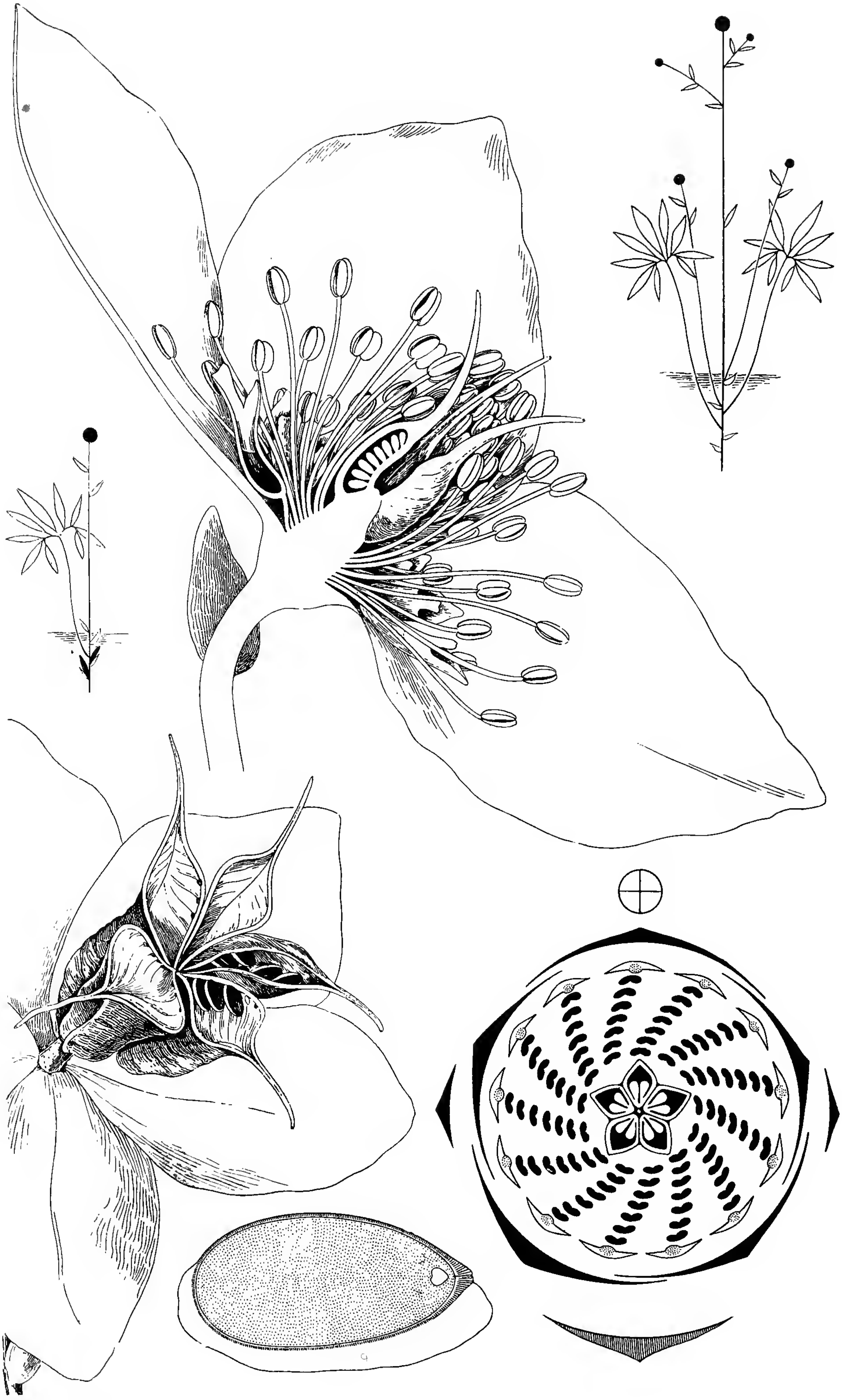
[1] On the other hand it is interesting to note that the illustration (Ἑλλέβορος μέλας) in the Vienna MSS. of Dioscorides (fifth century) has no resemblance whatever to any species of Hellebore.



**Helleborus niger:** Floral Diagram and Sectional Elevation in the median plane, of a typical right-hand flower; Scheme of inflorescence-shoots; dehiscing Fruit, and section of the Seed in the plane of the raphe.

## Floral Diagram.

I. Scheme of Branching. The reduced terminal racemose inflorescence is partly subterranean, and only seen clearly after digging up an entire plant and washing the soil carefully away from the rhizome (plants of the larger cultivated varieties—*H. niger*, *major*—are to be preferred), and the manner of reduction is intelligible when the plant is afterwards compared with *H. foetidus.*

The flowering axis terminates a shoot which has borne leaves in the previous summer, and these persist more or less throughout the winter months, until the new foliage is produced towards the end of April. Above the foliage-leaves, massive leaf-base scale-leaves continue a normal spiral series, which ultimately includes the members of the terminal flower. The 2 uppermost scale-leaves (rarely 3) are carried up with the terminal flower and protect it as $\gamma$ bracteoles during its passage through the soil; that is to say, the elongation of the axis which carries up the flower is largely restricted to an intercalary growth in the internode below these 2 uppermost scale-leaves. The lower scale-leaves remain subterranean, and 2–3 may produce solitary flowers in their axils, as also normally do the 2 higher ones. These lateral flowers all possess 2 large prophylls ($\alpha$ and $\beta$) which protect them in turn. *Note* that the terminal flower is protected by $\gamma$ bracteoles, its $\alpha$ and $\beta$ being at the base of the foliage-shoot; the lateral flowers by $\alpha$ and $\beta$ prophylls; this being the normal type of construction for racemose inflorescences with terminal flowers.

In smaller forms (*H. niger*, type) the flowering shoot reduces to 1 foliage-leaf only, 1–2 scale-leaves at the level of the soil, and a solitary terminal flower with 2 protective bracteoles. Further development of the shoot system takes place by means of vegetative buds produced annually in the axils of leaves lower than the existing foliage-leaves, i. e. well below the surface of the soil. The rhizome thus ultimately assumes a short irregularly branched sympodial appearance.

II. Orientation. Owing to the fact that the prophylls of the flowering shoot are below the foliage-leaves, and above these again a variable number of reduced foliar members intervenes below the terminal flower, the *orientation* of this flower is not constant. The diagram, as in the general case, is therefore drawn for a lateral flower in which the subtending bract and 2 normal prophylls are clearly present, and normal orientation obtains. The floral members develop along either a right-handed or left-handed spiral, in a normal spiral series; the odd sepal 2 being approximately posterior and the sepals clearly quincuncial in prefloration. *Note* that the median position of sepal 2 is a conventional representation which is generally accepted, but the reason for such accurate orientation has not been strictly proved: in the same way the position of the two prophylls $\alpha$ and $\beta$ in the transverse plane is a convention, since the law which controls their exact position is not apparent. As a matter of fact, in a lateral flower, which (as is often the case) has been somewhat flattened in the axil of its bract, sepal 2 is apparently median, while $\alpha$ prophyll is distinctly postero-lateral and only $\beta$ approximately transverse.[1]

III. The whole flower is spirally (asymmetrically) constructed, and as it is not easy to express a spiral construction on a small scale, the *Conventional* diagram, constructed on concentric circles, sufficiently expresses the facts most readily observed in the adult flower.

The stamens fall into 13 slightly oblique rows, a nectary being associated with each row, and these rows are *antidromous* to the ontogenetic sequence of the calyx members.

The actual relation may be better presented on a curve-construction-diagram in which

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[1] The attainment of radial symmetry is often distinctly marred by the fact that the perianth segments are unequal in size; the innermost, 4 and 5, being larger than the others, and 1 and 2 distinctly smaller. This is often the result of exposure to frosts while the buds are coming above ground and the outer members are checked in their last growth expansion. In such case it is obvious that the curvature of the flower-stalk has no relation to the floral orientation.

the intersections of a number of asymmetrical spiral curves plot a similar asymmetrical construction (Fig. 7). The phenomena observed are due to (1) the peculiar properties of the Fibonacci series of numbers normally utilized by flowering plants in the arrangement of their lateral leaf-members, and (2) to the geometrical properties of intersecting spiral curves. In the young vegetative bud of *H. niger* the succulent bud-scales constitute a system in which, owing to the great size of the sheathing bases, 2 members completely wrap the stem, while too few members are developed to enable any definite constant to be ascribed to their spiral phyllotaxis. The upper bracteoles and calyx members being smaller, definite curve-systems become apparent, and five members make a complete investment of the bud. Since these members when numbered up show contact-relations differing by 2 and 3 respectively, the construction may be here defined as a (2 + 3) type (Fig. 3) (July bud); although, on the other hand, the number of members produced is insufficient to indicate any distinction from a (3 + 5) type which will be found to imitate the general effect much more closely (Fig. 7). The curves observed in the androecium of an older bud (October) are 8 and 13. These numbers all belong to the Fibonacci series (1 . 2 . 3 . 5 . 8 . 13 . 21, &c.), and owing to the fact that members of successive pairs of these numbers are only divisible by unity, a single 'ontogenetic spiral' appears to control the actual sequence of development, so long as these rules are obeyed: i. e. the members may be all numbered up in the theoretical order of their appearance. In such spiral curve-systems, any member of the Fibonacci series will give an equally well balanced uniformity of distribution around the axis, and thus make an equally good approximation to radial symmetry. Thus 5, 8, 13, or 21 members selected along the genetic spiral would be fairly equally arranged around the floral axis (cf. Fig. 7). One is therefore justified in accepting 5 sepals, 13 petals, and 13 rows of stamens and 5 carpels as a typical floral construction, and the occurrence of any other number in the flower as implying some irregularity in the attempt to approximate radial symmetry, although the occurrence of 8 carpels or 21 nectaries would again be equally satisfactory. Such a curve-construction may be readily plotted out (Fig. 7), and it will be noted that on selecting a scheme with a right-handed genetic spiral, the curves must so cross that the 13 shorter curves wind in to the centre as left-hand curves, and are thus *antidromous*, as the rows of stamens have been observed to be, this being a geometrical necessity of the construction. Where the transition takes place from the larger perianth segments to smaller sporophylls, 13 members are selected to form a complete contact-cycle of nectaries, but the number may vary from 8–21, giving at these numbers an equally regular distribution around the floral axis. The same (8 + 13) phyllotaxis is continued into the androecium, and may be readily checked in buds taken in October, the intersecting curves being counted on the young anthers. The '13' curves become more obvious as the flower becomes adult, and these constitute the 13 rows of stamens which, when the anthers all become the same size, may be almost straight. On old flowers from which the stamens have been shed, the curves may again be traced on the receptacle by checking the spiral series of scars. *Note* that the phyllotaxis is not absolutely constant; at the apex of the system some of the curves may be lost, and irregularities are thus produced; but owing to the properties of the numbers it is possible to deduce a mathematically mean type. A system of 7 members in each row, or a total of 91 stamens, is here selected as an average form, but is not necessarily expected to occur; for example, 10 well-grown flowers gave the following numbers of stamens—95, 92, 95, 90, 81, 88, 81, 92, 109, 96.[1] Finally, a variable number of end members become carpels, typically 5–8; and these bear no accurately determinable relation to the orientation of the perianth, but vary from flower to flower. But it is conceivable that if the cycles of stamens were completed as in the figure, the carpels forming the first members of a new cycle would be approximately antisepalous.

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[1] In fact 89 as a Fibonacci number would give the most even radial distribution.

## Development.

New flowers commence to be developed as soon as the seeds of the preceding crop are ripe, and the earliest stages are thus to be looked for in June (Fig. 1). Sections of buds taken in July show all the floral members already laid down in their natural contact-relations. A longitudinal section of such a bud (Fig. 2) shows the great contrast between the large perianth members (sepals) and the smaller structures which comprise the rest of the flower. The nectaries are distinctly smaller and more delayed in growth than the stamens, and are clearly formed in the same series with them, so that it is often said that they represent *sterilized* stamens. The primordial carpels are equal in bulk to the stamens, and continue the series of young sporophylls on a very long and markedly conical receptacle. The naked end of the axis remains between the young carpels, and the whole structure closely resembles in composition not only a developing staminal cone of *Pinus*, but still more closely a vegetative shoot of *Abies* or *Picea*—pointing to the fact that structurally a flower-shoot is identical at first, as a phyllotaxis system of lateral appendages, with an ordinary assimilating shoot and its leaf-primordia.

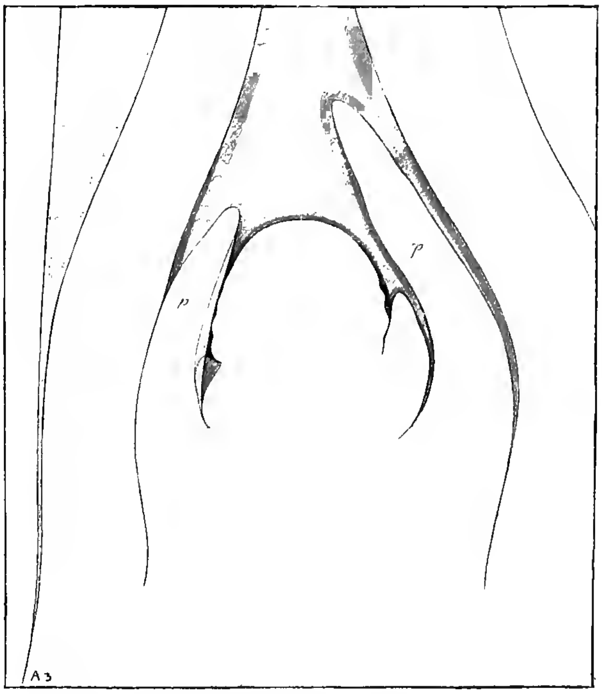

Fig. 1. *H. niger*; June 26, bud showing commencement of the formation of sporophylls.

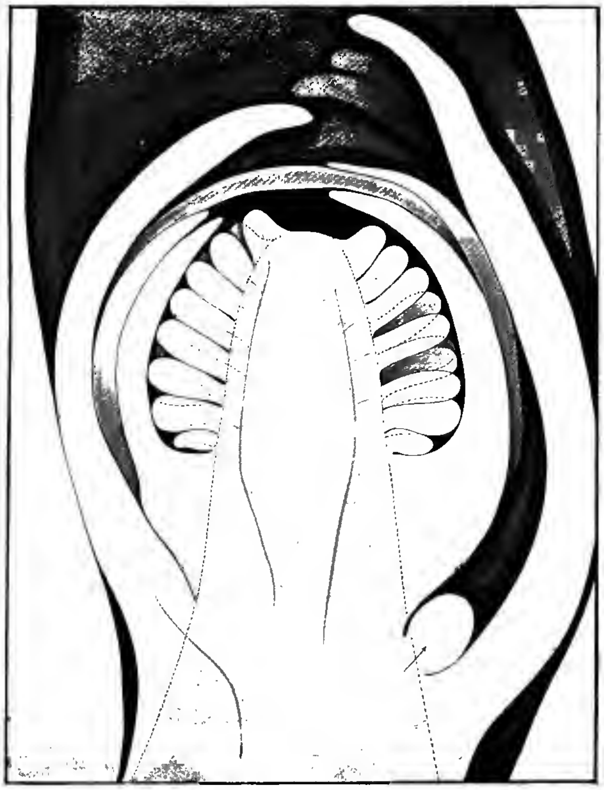

Fig. 2. *H. niger*; July bud; longitudinal section of flower-bud, all the members being laid down. The outline of the conical receptacle is indicated by drawing a line through the insertion of all the members.

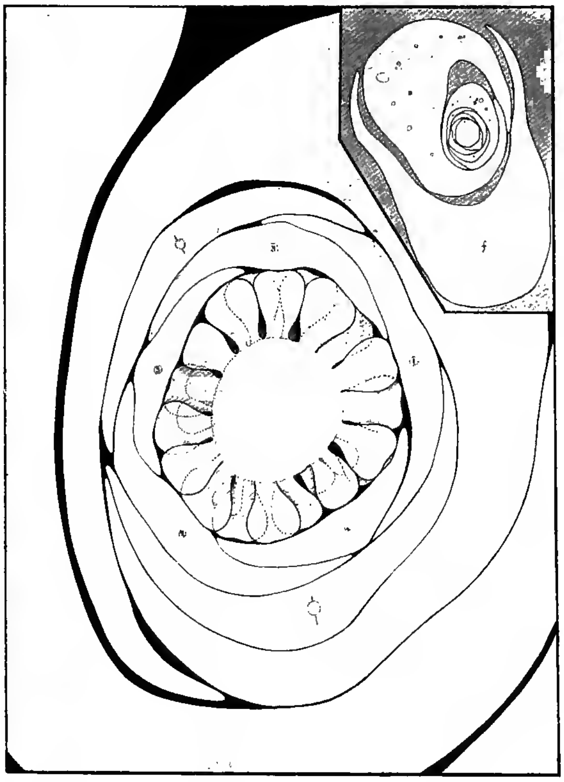

Fig. 3. *H. niger*; transverse section through a similar bud taken at the level of the lowest stamens: a smaller figure gives the entire section on a reduced scale.

Transverse section shows small stamen-primordia, of which about 13 make contact, enclosed by perianth segments of which 5 form a complete investment. In the section figured, cut at the level of the lowest stamens, some of the smaller nectaries are seen through these members (Fig. 3).

Buds taken in October and November show fully developed anthers, with undeveloped filaments, arranged in a compact cone-like mass. The essential points to note are:—

I. The practically unmodified development at first as compared with a foliage-shoot.

II. Certain members are subsequently set apart as sporophylls, and have a special development of their own.

III. The development and structure of the individual sporophylls are as near the theoretical ideal as possible; the filaments of the stamens, for example, being clearly late secondary growths.

All phases of growth and peculiarities of development other than those included in this phyllotaxis construction are to be included under the phenomena of *special mechanism* as indicating adaptations to ensure the pollination of the flower.

## Sectional Elevation.

An elevation of the same type flower may be constructed for the median plane of the conventional diagram: this will then show sepal 2 cut on the left, and the whole of sepals 5 and 3. Seven almost vertical rows of nectaries and stamens and 3 carpels may be represented with difficulty, some of the members being hidden; again, since the actual representation of a spiral series is not easy on a small diagram, for practical purposes the 13 rows may be assumed more nearly vertical. A posterior carpel (antisepalous) is cut open, and shows one series of 8 horizontally placed ovules. A posterior nectary is also cut, and shows the height to which the honey usually rises in the tube.

*Note* the perfect hypogyny of the flower, the distinct *tassel*-type in the arrangement of the essential organs, the commencement of practical syncarpy (as seen in transverse section) at the base of the gynoecium, the projecting styles, the growth curvatures of the stamens during dehiscence, and a correlation between the distance of the stigmatic papillae and pollen-bearing surfaces from the centre of the flower.

## Special Mechanism.

The phenomena thus included may be considered under the heads:—

I. The formation of a receptacular internode, 2–3 mm. long, between the androecium and the gynoecium, which takes the massive ovary well beyond the filament bases.

II. A special type of development in the tubular nectary members; these being also subsequently carried out on short stalks.

III. A long intercalated filament to each stamen; added late in development, only just before the buds expand.

IV. A similar intercalated style, taking the stigmatic surfaces well away from the ovary cavities.

The last two zones of growth are clearly correlated, the distance of the pollen-covered anthers, and of the stigmatic papillae, from the axis of the flower being about equal, although the actual length of the new growth in the two cases is not.

*Note* also that if these two last growths were not put in, the anthers would be practically in contact with the stigmatic surfaces, and self-pollination would be unavoidable on dehiscence. The addition of these zones of growth, which remove the essential surfaces and yet maintain them in correlated positions in space, affords structural evidence of an attempt to secure cross-pollination of different flowers, just as the special coloration of the perianth segments and the formation of special receptacles to collect a secretion which might in itself be unimportant afford evidence of adaptation to insect visits.

## Pollination.

The flower is fully developed beneath or at the level of the soil, protected by a strong hooded scale at the base of the foliage-leaf (September, October), and commences to appear above the soil early in October. The curvature of the flower-stalk prevents the damage of the floral members in passing through the earth, and this curvature persists more or less throughout the flowering and fruiting season. The flowers are rendered conspicuous by their large size and the coloration of the sepals and stamens; the comparative absence of foliage-leaves and the inclination of different flowers lending a certain amount of assistance to this end. The oblique inclination is not constant, but very frequently agrees with the median plane of the flower (cf. diagram). There is no marked scent. The pollen supply is abundant and freely exposed; honey is also secreted abundantly, but is concealed, although readily accessible to insects with short (2–3 mm.) proboscides. As the sepals expand the styles stand erect, pointing outwards with receptive stigmatic papillae; the nectaries being still closely pressed, as in the bud, against the corresponding rows of stamens, the tip of the slipper just fitting the anther of the outermost series. The flower is thus markedly *protogynous*, and this condition may last for a week or more in the half-blown flower. The stigmas are very susceptible to cold dry winds, and often wither and turn black before the stamens begin to dehisce; but in mild seasons, or if protected in a damp chamber, they will remain receptive as long as the stamens are shedding, and even after their complete fall. The outermost stamens shed their pollen first, but rarely in strict theoretical order; dehiscence proceeding acropetally along the 'vertical rows'. Each stamen as it matures elongates from 10 mm. to 15 mm., becoming erect and then bending slightly outwards; a subsequent increased rate of extension on the upper side of the filament produces a reverse curvature, and ultimately the filaments straighten out and lie horizontally along the sepals, the anthers being bent upwards almost at a right angle. This double curvature, which reaches much greater perfection in *Nigella*, results in the path to the nectaries being fringed above and below by circles of stamens presenting their pollen-covered surfaces to any insect passing between them. Young stamens successively erect, dehisce, and bend over, while exhausted ones are flattened down out of the way, wither, and soon fall off; in this manner the pollen supply is extended over 3–4 weeks, a single flower in cold months often remaining functional for from a month to 6 weeks, though the stigmas are typically only receptive for the first week or so. In late spring the duration of a single flower is much less; for example, late stragglers in May last about one week only. The compressed anthers dehisce along their edges, and of the 4 valves thus formed the 2 most external bend outwards, taking on them the whole mass of pollen in a moist cake. The pollen is thus presented peripherally and only becomes powdery in dry weather. The anthers readily close again when wetted; but, owing to the oblique position of the flower, the uppermost anthers are usually shielded somewhat from rain by the perianth segments.

The mechanism is clearly adapted for insects seeking both pollen and honey; the insects alighting on the tufted essential organs, especially the rigid styles, and then walking round on the perianth segments, insert their proboscides into the nectaries, and so come into contact with the fringing pollen masses. The relative size of the members suggests that fairly large bees and Lepidoptera are the normal pollinating agents, and these in passing round from nectary to nectary would get thoroughly dusted with pollen and thus readily transfer some to the projecting tips of the styles of other flowers on which they may alight. At the same time no special care is taken to prevent the approach of small bees and flies which might take pollen without going near the stigmas; and honey, again, is often stolen by useless green aphides. Observations on *H. niger* in its native habitat are still incomplete: in this country it may be visited by various early bees (*Bombus*, *Anthophora*) when flowers delay opening till March; as also by Hive-bees which appear on the first warm sunny days of February; but owing to the optimum flowering period being the early part of January, when insect-visitors are practically out of the question, insect visits are comparatively rare, and as a rule plants left to themselves produce no fruit. Self-pollination in absence of insects is rendered impossible by the protogyny, which is increased by climatic factors, and by the fact that the stigmas are always raised above the level of the anthers, this being specially marked in the larger varieties (*H. major*), and they usually wither as the first outer stamens dehisce.

Artificial cross-pollination is readily effected by means of a small brush, or by removing a pollen-covered stamen, and should be carried out as soon as the sepals expand, as the stigmatic surface is very small, and many pollen-grains are required for each carpel. Artificial self-pollination is also possible in protected flowers, and in isolated blossoms which open in late spring (May). The flowers are freely fertile to their own pollen, and strict experimental data as to the benefit of crossing are still wanting for this type. As seedlings flower in their third year experiments would be tedious. The advantage of crossing is therefore inferred—(1) from analogy of other floral mechanisms, (2) from the nature of the special mechanism. *Note* that symmetrical fruits will not be produced unless all the stigmas are carefully pollinated, and that owing to climatic reasons pollinated flowers may set apparently fine full-sized fruits which, however, fail to mature their seeds and suddenly wither away: few fruits survive a spell of hard frost.

The large flowers of *H. niger, major* expand early in November or even late in October, and last till after Christmas; the main crop of the commoner small form usually opens in the first week of January, and blossoms may remain functional well into February (six weeks), if the weather be mild and favourable. Few remain out in March. The flowers can stand a slight frost, but 10–15° F. of frost produce complete collapse of flowers and foliage, the foliage being killed in exposed situations. The flower-stalks lie along the surface of the ground, and the perianth segments may be completely frozen. The flowers recover after heavy snow, and when frozen recovery is rapid after a thaw, the stalks standing up as stiff as ever; but the stigmatic papillae are blackened and the ovules affected, so that the recovery is only apparent.

As the flowers become older they acquire an increased pink tinge, and when all the nectaries and stamens are shed, the perianth segments present quite a deep pink colour and then gradually become green as the fruits develop.

### Fruit and Seed.

As the stamens become exhausted and wither they are shed, and when all have gone the nectaries are also thrown off. Flowers which have not been pollinated wholly wither away. In pollinated flowers the sepals persist, but turn green and assist in assimilation. The ovaries commence enlarging early in March, and by the end of the month have attained full size as green pods 15–20 mm. long surmounted by the persistent 10 mm. style. The developing fruits are inconspicuous, and are protected and concealed by the new crop of foliage-leaves. Flowers pollinated in January ripen their fruits from May to June, development of the seeds being slow and taking 5–6 months. Later May flowers ripen in July. The ripe fruits dehisce along the free edges of the sutures and form a basket-like cluster of (typically) 5 follicles united at the base. The syncarpous portion does not further dehisce, and thus the 5 follicles when dry and shrunk to 10–15 mm. form a structure about 10 mm. across, from which the whole of the seeds are freely shed as soon as dehiscence takes place. Owing to the unaltered curvature of the flower-stalk the seeds merely fall out on the soil below; when wetted the follicles close more or less completely, but the seeds are shed at the first dehiscence, and, as in similar cases (cf. *Viola*), note that the phenomena of closing are merely the expression of the same hygrometric tensions which induce dehiscence. These are not highly specialized in *H. niger*, since its habitat is usually moist. In fact longitudinal and transverse sections of the wall show that while the leaf-like form of the carpel is perfectly retained, and the vascular bundles run out at right angles from a strong midrib, there is no special fibrous layer in the wall, and the fibrous mechanism is restricted to a sheath of fibres accompanying each of the bundles of the vascular framework.

The seeds are ovoid and compressed, 5 mm. by 2, smooth and black, with a membranous ridge along the raphe, which at first is white and succulent, but soon dries up. Whether this crest has any dispersal significance is still doubtful; more probably, being along the course of the vascular bundle, it is used as an aqueous tissue water-reservoir for the developing seeds (cf. *Viola*, *Galanthus*).

The embryo is small, the 2 cotyledons being laid out in the plane of the raphe, while the food reserves are stored, mainly as fatty oil and a small amount of proteid, in the thin-walled cells of the endosperm.

*Note* that the embryo is protected by the thin testa and the endosperm, supplied with food as fat and proteid stored in the endosperm; but beyond the very doubtful use of the succulent raphe as a food-body for small beetles or ants, there is no arrangement for wider dispersal, and the seeds fall close around the mother plant. Note again that this is the rule for plants growing in situations where the action of drying winds is eliminated (cf. *Viola odorata*). Observations on the white 'food-body', which, however, does not store fat, would require to be made in localities in which the plant is indigenous.

## Monstrosities.

In large forms (*H. niger*, *major*) the carpels are sometimes considerably increased and arranged in a crested double row (cf. *Ruta*) of 15 or more members (26, the highest number observed). The phenomenon is included under the term *Fasciation*, the normal centric type of growth being replaced by an elliptical construction.

Fig. 4. *H. niger*; monstrous flower, viewed from above.

Fig. 5. *H. niger*; monstrous flower, side view.

A very beautiful monstrous form, a terminal of *H. niger*, *major* (B. G. O., 1903), presents a feature of great morphological interest, in that after producing in normal sequence 5 perianth segments, 16 nectaries, and many stamens, two complete cycles of carpels were formed (27 in number) in the same spiral system, and beyond these a further formation of stamens commenced, 15 members being produced: in this case, therefore, the floral axis was not closed with the production of carpels (macrosporophylls), but the whole construction may be brought into line with the heterosporous strobili of certain vascular cryptogams (Figs. 4, 5).

### Comparison with allied Species.

*H. foetidus*, L. The Oxheele, Bearefoot, or Setterwort of Gerard and Parkinson, though these names are applied indifferently to other forms, is a green-flowered form indigenous in many parts of the country, and extends over Western Europe from England to Austria, while the oriental forms range from Austria to the Caucasus.

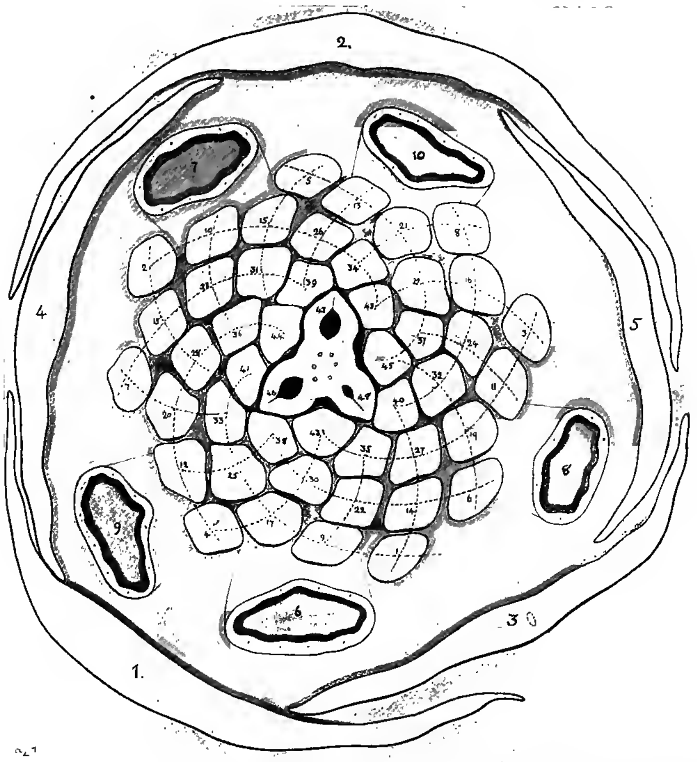

Fig. 6. *H. foetidus*; section of breaking bud (January), showing relative position of perianth segments, 5 nectaries, and (8 + 13) contact-series of 45 stamens.

*H. foetidus* produces wholly aerial flower-shoots from January to May, which terminate in a large panicled inflorescence, 2 feet high or more, containing numerous smaller and less specialized flowers; and in these respects it appears to represent a more primitive type of the genus. The inflorescence terminates a shoot which has produced numerous foliage-leaves in the preceding summer, above which in autumn a bud-region is constituted by progressively reduced leaf-members which continue the normal spiral phyllotaxis, the construction curves of which, as seen in a section of the apex, are (2 + 3). The inflorescence commences to expand in November and December, and the system is closed by a terminal flower, which expands early in January. Below this flower as many as 10 of the upper reduced leaf-base members may be fertile and subtend lateral inflorescence-branches. These are normal *symmetrical dichasia*, which continue their ramification to the fourth degree; they are remarkable for the great development of the prophylls, which form the protective investment of the young flower-buds and are carried up on the axes to the close vicinity of the flowers.[1] The sepals are green, large, and clearly quincuncial in prefloration, and, owing to their persistence in the fruiting condition, the whole inflorescence may be studied throughout at any time from January to May. Theoretical heterodromy is perfect, $\alpha$ and $\beta$ prophylls are readily distinguishable, the ramification tends to be stronger in the axil of the $\alpha$ prophylls, and it is the flower in the axil of $\alpha$ which each time shows the reversed spiral construction.[2] The reason for such a mechanism of symmetry is still far to seek, but it can be readily checked on an old inflorescence. From such an inflorescence

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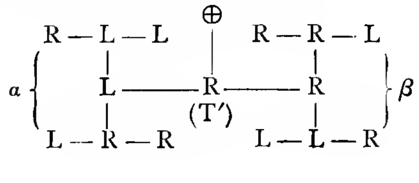
[1] Or, more correctly, internodal elongations between the prophylls and the perianth members are at first less pronounced than those between the lowest prophylls and the subtending bracts.

[2] Type of symmetrical dichasium:—



Consideration of such a scheme, in which the letters R and L are used to express the easily-checked direction of the genetic spiral of the perianth, shows that there can be little advantage in such an arrangement for the lateral branch-inflorescence as a whole. Lateral T′ flowers are also R or L with no reference to T, and the symmetrical relationships of such a dichasium would appear to be restricted to the actual three flowers concerned at each ramification, the two lateral being twin images.

as that of *H. foetidus*, with its panicle of possibly over 100 flowers, the type of *H. niger* is clearly produced by extensive reduction; the dichasial branches being limited to their terminal flowers, and these again very few in number, while the shoot system largely remains below ground. In the structure of the flower itself the same general relations obtain, but the parts are fewer. The nectaries range from 5 to 10, 6 or 7 being the most usual condition, and the asymmetry of such a number is obvious on looking at the flower; while it should be noted that the ones which are present always occupy the theoretical positions so far as they go (Fig. 4). The stamens vary from 30 to 54, the average in good terminal T and T′ flowers being 45; the carpels 2–5, but most commonly only 3. The total number of floral members thus approaches 60, while *H. niger* more nearly averages 120.

Although the floral construction is somewhat simpler than that of *H. niger*, the mechanism of the flower as a whole exhibits a considerable advance. The flower-buds are developed more or less erect on the divergent branches, but the functional flowers are inverted, so much so that the best flowers are easily selected by taking those which hang vertically downwards. The flower-stalk is compressed in the plane of sepal 2, and a definite growth curvature takes place during the flowering period. Correlated with the drooping position, the relatively small perianth segments do not diverge, but form a close bell which just covers the essential organs. The green colour is relieved by a crimson pigment on the inner face of the segments, which, being associated with underlying green tissue, appears as a purple blaze on the inner side of the segments, especially 4 and 5. To what extent this is utilized as a means of attraction is very doubtful—the net result being to slightly darken the interior of the floral cavity (cf. *Arum*). The importance of these characters is rendered obvious by the comparison of withered flowers in which the stalk straightens out, the perianth segments widely diverge, and the purple coloration is greatly increased, especially at the tips of the segments, as a deep purple blotch on both sides; the withered flowers being, in fact, the most conspicuous from a distance. To what extent this can be utilized as a conspicuous coloration, the functionless perianths of older blossoms from which the stamens have been shed subserving a means of attraction to the less conspicuous pendulous blossoms, remains purely conjectural; since, though as a matter of fact the expanded purple-tipped blossoms are readily noticed, there is no evidence that they are equally striking to an insect.

The pigment is a red 'anthocyan' derivative, localized entirely in the epidermal cells, as may be readily observed on peeling the tissues. When arranged as a screen over green chlorophyll-containing cells a purple-brown effect is produced (*H. foetidus*), while in *H. niger* a small production of the same pigment in the epidermal cells becomes responsible for the pink colour of the perianth segments and the dull crimson of the flower-stalk. The growth movements of the stamens are also clearly modified by the adoption of a bell type of flower; the outward movement is wanting, though the elongation of the filaments is considerable; each cycle of stamens elongates and sheds its pollen definitely outwards, with the result that the androecium, which at first forms a compact cone, gradually becomes a tassel group of anthers, and serves as a landing-stage for insect visitors. The pollen supply is very abundant, and the nectary cups fill to the brim. Bees with proboscides of medium length have no difficulty in reaching the honey when holding on to the stamens, and readily collect pollen and honey. The flowers are again markedly protogynous, the styles curving out over the cone of stamens with the stigmatic papillae receptive as the perianth expands. A first chance is thus given to cross-pollination by insect agency, but as the stamens elongate and shed their pollen, the anthers inevitably brush past the styles, and self-pollination is apparently unavoidable. It is of interest to note that this special curvature of the styles is again corrected in the developing fruits.

The earliest flowers (T, T′) opening in January are often imperfect in their mechanism adjustments, owing to the growth regions being affected by inclement seasons; the mechanism is seen at its best in March, more particularly in the T‴ flowers. The structure is thus adapted for large insects which seek pollen and honey. They are also visited by all early bees and *Eristalis*; the Hive-bee is in gardens the most active visitor, collecting pollen rather than honey. Green aphides are also abundant in the sheltered interior. The fruit-pods resemble those of *H. niger*, and these turn yellow as they ripen and shed their seeds about midsummer. The plants fruit freely. The shoots are similarly affected by frost, but recovery is also rapid. The first flowers (T) open in January, T′ rapidly follow, while T″ and T‴ are out in March, when the January flowers show full-sized fruits; the last stragglers may even be found in June.

*H. orientalis*, Lam., and garden hybrids of the various forms of this type, show in some respects an intermediate condition between *H. foetidus* and *H. niger*; the inflorescence is 3–7-flowered, 2 lateral dichasia only being produced in the last case: the flowers are adapted for the same insects, but are slightly more specialized in mechanism. The nectaries are nearer 21 in number, the stamens often over 100, while their contact-curves, especially as seen in sections of the filaments, are (13 + 21). The growth curvatures are better marked, and resemble those of *Nigella*.[1]

## Theoretical Considerations.

Few types are so admirably suited to serve as an introduction to the study of the flower as that of *Helleborus*.

To begin with, it is clear that the floral construction is that of a normal spirally constructed vegetative shoot in which the smaller relative bulk of the sporophylls results in a change in the phyllotaxis system, which, however, follows normal rules. The normal Fibonacci sequence is utilized, and the remarkable mathematical properties of these numbers admit of the deduction of an average type, while a geometrical construction in terms of these numbers shows that radial symmetry must be a definite aim on the part of the organism in the construction of these floral shoots, although absolute symmetry cannot be attained in any asymmetrical (or spiral) construction. The geometrical scheme (Fig. 7) probably represents, so far as knowledge goes at present, the actual relationship of the members as an average construction: the details of the precise method of varying the phyllotaxis system at the point of transition between perianth members and sporophylls cannot be accurately given, and possibly vary in different shoots. The fact remains that the organism 'selects' cycles of members to subserve different functions, one full cycle of protective and attractive segments, one full cycle of smaller nectaries, but several cycles of stamens, and usually one cycle, or less, of carpels. These are isolated according to the rules of the Fibonacci systems from a relatively simple phyllotaxis construction, with the object of attaining the nearest attempt at a radially symmetrical (or actinomorphic) mechanism.

It is interesting to note that a single cycle of members of different value is generally sufficient, and that the production of several cycles of stamens may be correlated with the

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[1] The curve-construction systems of these flowers can be most easily checked by taking transverse sections of buds which are just breaking. In young buds the filaments are short and the anthers are liable to displacement when packed between the enlarging nectaries and bulky carpels. As the filaments commence elongation in the flowering stage, they retain their mutual relation, and it becomes possible to hit off a stage at which they may all be cut in one section: owing to the want of curvature movements in *H. foetidus*, the preparation of such specimens is easy for this type, while *H. officinalis* is better than *H. niger*.

In *H. foetidus* (Fig. 6) the curves of the androecium are very fairly (8 + 13), the '8' curves are most clearly marked, and the system of 45 stamens and 3 carpels may be numbered up from these alone. On so doing the points at which the '13' curves have undergone displacement become quite clear, while the fact that the 3 carpels continue the construction is shown by their close approximation to the theoretical 'divergence-angle' of 137½°. The flower in question works out 'right-handed', and it is clear that the '13' curves are spirals in the opposite sense (antidromous). The 5 nectaries, again, do not accurately alternate with the sepals; their agreement with the theoretical position is shown on comparison with the general scheme (Fig. 7) (cf. *Aconitum*).

In *H. officinalis* with a (13 + 21) construction the same phenomena obtain, but note that here 21 members would form a contact-cycle, and thus an average of 21 nectaries would be expected.

functional period of the flower. In the less specialized flowers of *H. foetidus*, again, the isolation of a complete cycle is noticeably deficient in the case of the nectaries.

From a comparison of the inflorescence of *H. foetidus* also, which is itself a specialized reduction type, it is clear that the ancestral form probably possessed still smaller and less conspicuous flowers on a still larger and fuller panicled inflorescence, which, again, terminated the leafy shoot of the season in which it was produced: the change in the flowering period being due to a slow rate of development of the vegetative growth. It thus becomes easy to connect the extremely specialized habit and shoot-construction of *H. niger* with herbaceous plants of much more normal habit—as, for example, *Aquilegia* and *Delphinium*; though the fact that these, again, are specialized from a still more general type of growth will be discussed under those types.

While the phyllotaxis system and the floral elevation show that the flowering axis retains a simple and primitive condition, the special mechanism is not of an elaborate character. The essential features include the production of peculiar nectaries, and the serial growth movements of the stamens. Both these features are more elaborate in *H. niger* than in *H. foetidus*, and they will be seen to attain a still more elaborate development in *Nigella*. At the same time, as these specializations are correlated with insect visits, the elevation of the stigmatic surfaces and the practical protogyny put self-pollination out of court; and here, again, to a much greater degree in *H. niger* than in *H. foetidus*, with the drooping flowers. The subsequent construction of the fruit is again of the simplest and most primitive order conceivable; the carpels, which are clearly folded 'leaf-base' members, opening when the seeds are mature by a simple desiccation-arrangement along the edge by which they originally closed before producing the ovules.

On eliminating the details which are clearly secondary, the progressive shoot and inflorescence reduction, the special nectary mechanism, and the secondary intercalary zones of growth, the flower reduces to a simple strobilus of sporophylls terminating a vegetative shoot with a normal phyllotaxis construction; the only distinction being between perianth members and sporophylls. These latter are present in relatively large numbers, and this fact may possibly be taken as indicating a primitive type of construction. The boundary-line between the protective perianth and the sporophylls appears to be clearly marked in early development (Figs. 1, 2), the fact that the nectary members must be regarded as homologous with sporophyll members becoming still more clear when allied forms are compared in which the number is more variable, but always varies at the expense of the stamens. If they are few (*H. foetidus*), stamens fill the places of the missing ones: at the same time there is no evidence of actual sterilization of a reproductive appendage. The delayed growth of the primordia suggests that they only attain a secondary nectary function after a period of degeneracy, and this is a general phenomenon in the case of more normal 'corolla' members. It is interesting to note that they occur at a transitional period in the phyllotaxis mechanism, though why such a change should take place with the prophetic view of a production of sporophylls is beyond the range of observation.

In its essentials, therefore, the flower of *H. niger* represents a remarkably simple floral construction, and in all probability is as near the ancestral type from which the bulk of modern Angiosperm flowers have been derived as may be found. The *Helleborus* type possesses well-marked idiosyncrasies of its own, but it is easy to isolate these from the fundamental facts of construction.

From the standpoint of such primitive construction the genus *Helleborus* with the numerous forms conventionally included in the genus (about 15 species) is included in the still more conventional group *Ranunculaceae*, a somewhat heterogeneous collection of about 27 genera and 1,000 species of mainly herbaceous types growing in the North Temperate Zone, which present somewhat similar relations in the fundamentally simple floral construction which includes a relatively large number of free floral members (cf. *Ranunculus*, *Paeonia*, *Clematis*, *Aquilegia*, *Aconitum*, *Delphinium*, *Nigella*).

## **Eranthis**[1] **hiemalis,** Salisb.[2] *Winter Aconite.*

One of a small group of 7 species inhabiting the Mediterranean district and Central and East Asia.

*E. hiemalis* from the Mediterranean district (especially Alpine regions of Italy, Austria, and Switzerland) is in common cultivation, owing to its being one of the earliest spring flowers to bloom in the open (January, February). The flowers are borne singly and terminate the aerial shoot which bears 3 foliage-leaves. This shoot represents an even greater reduction phase than that of *H. niger*, but along identical lines. The *stem* is an underground rhizome, now reduced to a small tuberous body sending up one or more shoots from its upper surface. Each annual foliage-shoot bears 2 sheathing subterranean scale-leaves and 1 (or 2) deeply-cut foliage-leaves which arise above the surface of the soil for about 2 to 6 inches.

*Flowering shoots* are also produced, one or more, according to the strength of the plant. Each consists of a shaft-axis closely resembling a leaf-stalk, and bearing at its apex a cycle of 3 green segmented leaf-members, closely imitating again the lobes of an ordinary foliage-leaf.

*Floral members* follow in close succession, that is to say, no internode is intercalated between the assimilating cycle and the floral structures. The phyllotaxis is apparently (2 + 3), in which system 3 members constitute a contact-cycle. Hence the 3 foliage-leaves approximately alternate with the 3 outer perianth segments, and these again with the 3 inner. The flower only differs from that of *H. niger* in the number of members retained for each special function, and comprises about 50 in all. Thus 6 *perianth segments* are yellow and conspicuous (varying 5–7–8); 6 nectaries, also varying 5–9; about 30 stamens (range 24–39), and finally 6 (range 3–11) carpels. These last are pod-like, wholly free from each other, and of theoretical simplicity, each possessing a distinct stalk (2 mm.).

It is not possible to give an orientated diagram, as the terminal flower is alone produced, and the relation of this to its parent axis varies with the number of leaves on the shoot. *Note*, however, that the involucral leaves are not prophylls, and that so long as constant Fibonacci relationships obtain in the phyllotaxis construction, the arrangement of the parts may be approximately imitated by plotting successive divergence-angles of $137\frac{1}{2}^\circ$. For example, when 6 nectaries are found they have the relation of groups of 2 and 4 as in *H. foetidus* (cf. Fig. 7), and thus do not accurately alternate with the perianth-segments.

All the floral members may occasionally be found grading into each other, i. e. *involucral leaves* occasionally become yellow, while *perianth-segments* may be green and leaf-like; the

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[1] The plant was called *Aconitum hyemale* by the old herbalists (Camerarius, Gerard, Parkinson, Ray), the foliage-leaves closely resembling the first spring shoots of the Monkshood, which are contemporary with the Eranthis flowers (cf. *Aconitum uniflorum luteum bulbosum* of Bauhin's Pinax). Linnaeus gave it the name *Helleborus hyemalis* (1753), and the genus *Eranthis* was founded by Salisbury in 1807, and has been since accepted. Salisbury gives his etymology of the name as ἐράω, ἄνθος; the suggestion being 'floribus tempestate inclementi amabilibus'.

It was grown by Gerard (1597), and appears to have been as common in gardens in his time as it is now. It was known as the *Winter Wolf's Bane* or *Yellow Aconite*, and Gerard draws attention to the fact that it lasted longer the more inclement the weather, and with warm sunny days the flowers soon faded.

[2] The founding of the genus *Eranthis* by Salisbury gives an interesting idea of the reliability of much accepted Systematic work; his standpoint would seem rather remarkable when he goes so far as to state that he was 'unable to find any affinity whatever in it to that in which it has hitherto been placed (*Helleborus*) beyond the common characters of the order *Ranunculaceae*'. The elevation of the flower sufficiently indicates the closeness of its agreement with *Helleborus niger*, and so far as floral structure is concerned there would appear to be no necessity whatever for separating *Eranthis* from *Helleborus*. In fact if floral structure and biology be made essential features in classification, the cleavage line would seem to rather separate off such a type as *H. foetidus*, in which the floral mechanism is being adapted to a pendulous bell type which gives the clue to the evolution of such a form as *Aquilegia*. Salisbury, on the other hand, was impressed by the vegetative habit of the plant—the difference between which and that of *H. niger* is much less than the range between *H. niger* and *H. foetidus*—and more especially by the deciduous nature of the perianth segments, a very subsidiary biological detail, and the fact that he had never seen 5 perianth segments as in allied forms.

number of *nectaries* again increases or diminishes at the expense of the outermost *stamens*, while the number of *carpels* also varies at the end of the series, thus giving a distinct suggestion that all these lateral members are secondary modifications of a primary appendage whose secondary function is determined by the needs or even idiosyncrasies of the flower-shoot.

The structure of the flower is thus practically identical with that of *H. niger*, but on a smaller and somewhat simpler scale.

The floral mechanism also agrees with this conclusion. The stigmas are receptive when the bud opens, and the stamens dehisce in order of formation, i. e. the outer ones first, so that a first chance would be given to cross-pollination, although the last stamens, on dehiscence, may possibly pollinate the stigmas, which are little longer than the filaments.

The flower remains functional for about a week, but is very susceptible to extremes of weather, the delicate perianth segments becoming discoloured and shrivelled both by hard frosts and dry winds. The mechanism is simpler than that of *H. niger*, but there is still a tendency to structural protogyny; self-pollination is not entirely eliminated, and the growth movements of the stamens are less elaborate, so that the pollination mechanism is much on a par with that of the Buttercup.

In gardens the flowers are visited by the first Hive-bees, which take both pollen and honey, and they subsequently set fruit freely. The fruits ripen and shed their seeds in May, when the whole aerial portion of the plant soon withers and disappears. The rhizomes thus perennate through the summer and autumn months; the main crop of foliage-leaves only coming up after the flowers are over.

An additional feature of interest not present in *Helleborus* is observable, in that the delicate perianth segments are here susceptible to small changes of *temperature*, and open like those of the Snowdrop and Crocus on a rise of a few degrees above 10° C.: thus on being brought into a warm room the flowers expand widely in about an hour at a change from 7°–14°, but these perianth movements are not so sensitive as in the case of the Snowdrop.[1]

The movements, as due to phenomena of unequal growth extension, are accompanied by an increase in the size of the segments, which when fully distended are more than twice the size they were when the flower first opened. They are subsequently definitely shed with the stamens, and are useless for any assimilative function.

There is again no arrangement for distant seed dispersal, the follicles opening by their suture and allowing the seeds to be shaken out by the wind, or by decay of the shoot: at most they only appear to roll out for a few inches from the parent plant. When ripe (first week in May) the follicles diverge in a beautiful star-like form, and the suture being thus directed upwards, the ripe fruits present an admirable basket-like contrivance from which the yellow seeds are rolled out. The foliage-leaves soon wither and disappear, and the plants perennate from the end of May onwards till the succeeding January.[2]

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[1] Closed in the morning at 9°, the flowers were half open in the afternoon at 11°: brought from the open air at 9° to a warm room at 16°, they were well expanded in a quarter of an hour. Owing to the delicate nature of the perianth segments, extreme experiments soon injure the tissues, and the expansion movements can rarely be repeated (Feb. 9).

[2] Older interpretations of the flower are often conflicting, owing to the bias of the observer in favour of some particular theoretical conception of floral construction; for example, (1) an attempt to give an interpretation in terms of the assumption of a symmetrical relationship of the floral parts; thus Payer (1856) described a developing bud as a true hexamerous symmetrical construction; (2) an attempt at reading into the flower a complex asymmetrical construction in terms of a single ontogenetic spiral: Eichler (1870) gives the stamens as 12, 13, or 14 spiral rows, and these again sometimes straight, the rows being the product of varying divergence fractions according as required. But it must be remembered that phyllotaxis systems can only be ascribed a *formula* when they contain a sufficient number of members produced in such a rhythmic sequence that they give a definite pattern, and the mechanism of pattern-construction is sufficiently constant for all individuals of the species. Once, therefore, the subject is freed from theoretical bias, the construction appears to be fundamentally that of *H. niger* with the addition of slight irregularities which confuse the phyllotaxis system and undoubtedly indicate a degeneracy in the construction-mechanism. Thus the spirally arranged involucral leaves clearly represent a complete contact-cycle of 3 members of a (2 + 3) Fibonacci system which then changes to (5 + 8) or (8 + 13) as in *H. niger*. To isolate a perianth, 6 members at the region of change are com-

monly taken, the exceptional case of *Helleborus* and *Ranunculus* being here the rule, and 5 less frequent, though as in *Ficaria* the number may rise to 8. That is to say, 6, as a doubled 3 of the Fibonacci series, represents practically as good a type of distribution as 5, and this even becomes characteristic of whole allied families (cf. *Magnoliaceae*). These 6 members thus constitute two cycles of 3 (cf. Fig. 7), the inner 3 being wholly within the outer 3. Similarly 6 (or 5–8) succeeding members are isolated for nectaries and practically alternate with the preceding, although 6 members do not give equal spacing (cf. 6 nectaries in *H. foetidus*). The androecium is the part which presents difficulty; but it is clear to begin with that in a system such as that of *H. niger* (Fig. 7), 30 members are not sufficient to give a very definite pattern—50 stamens in *H. foetidus* are only just enough to be convincing (Fig. 6): hence the difficulty of counting radial rows accurately. When to this is added the fact that the system commonly breaks down or becomes irregular, i. e. rows are often omitted or put in without definite order, the pattern becomes completely thrown out, and it is impossible to give any formula for imitating it. It is possible that the error is introduced in the expansion series, and that 6 perianth segments may be correlated with a failure to adjust the Fibonacci expansion, so that 12 is produced instead of 13. Such irregularities are more obvious to the eye in other Ranunculaceous types (cf. *Nigella*, *Nymphaea*), but their occurrence here is a point which, like the isolation of 6 perianth segments, leads to the conclusion that the strict Fibonacci phyllotaxis construction is becoming less clearly defined, and the construction system may be therefore said to be deteriorating as a mechanical growth system quite apart from the subsequent 'mechanism' of the flower. To what extent such degeneration in the construction system may be correlated with the extensive reduction of the plant in its assimilative system and ramification may be left for the present, but the suggestion certainly is that degeneration in the elaboration of one phase will generally be associated with deterioration in another, even though the organism as a whole is becoming more 'adapted' to its special environment.

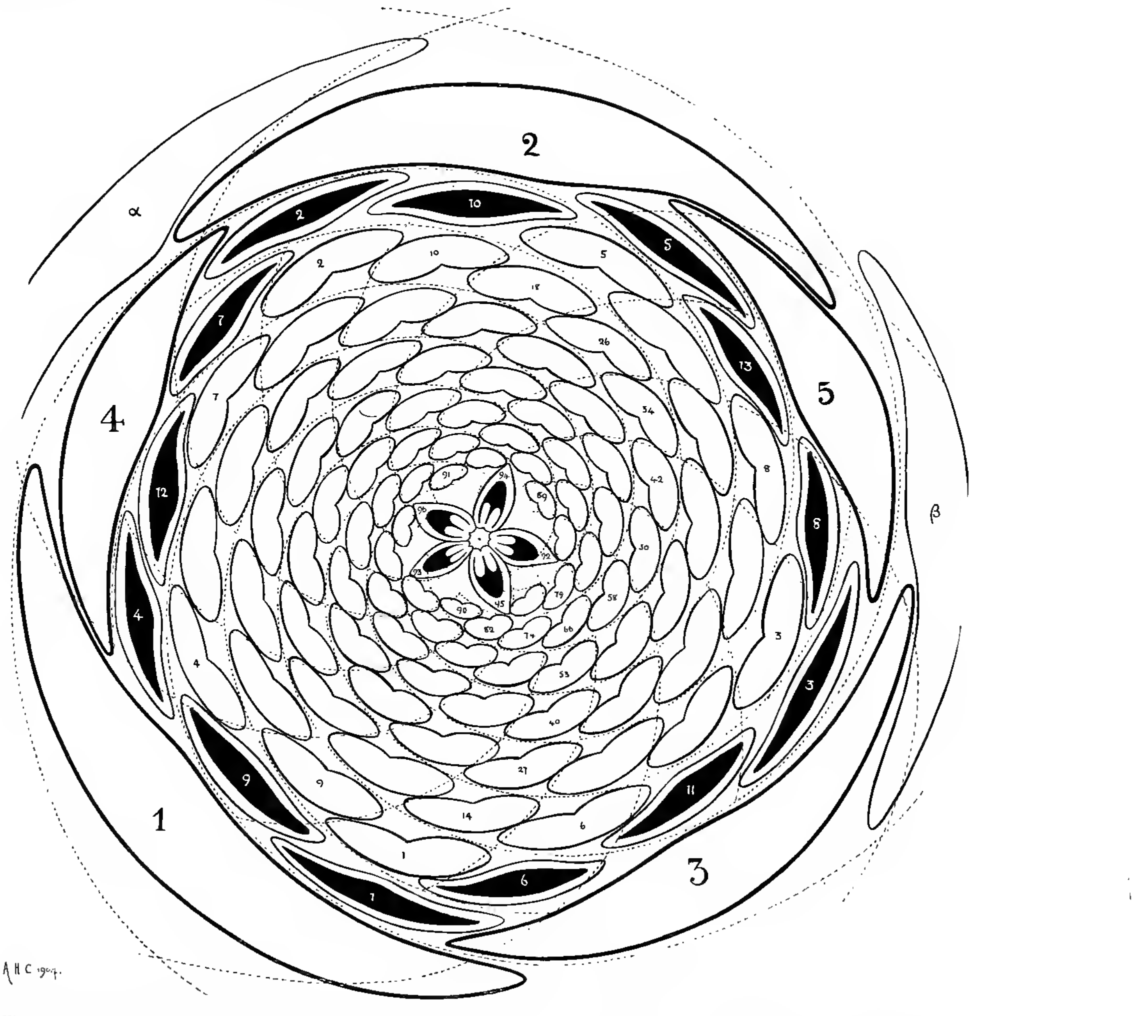

FIG. 7. *Helleborus niger.* Theoretical Floral Diagram in terms of spiral construction (right-hand flower).

The figure illustrates a gradual transition from a (3 + 5) quincuncial system in the perianth to (8 + 13) in the essential organs; the transition being completed in a contact-cycle of 13 members which subsequently become specialized as nectaries. The members may thus be given a theoretical number, and the relation of the different curves, the course of the 'genetic spiral', and the contact-relations of the overlapping members are thus readily exhibited.

Although details of the construction may be omitted, there is reason to believe that the figure represents, as clearly as may be done in a plane diagram, the actual method employed in the construction of the appendages of such a floral shoot. By the isolation for special function of members in terms of other numbers of the Fibonacci series, the diagram becomes applicable to a large number of allied Ranunculaceous types.

# II

## Galanthus[1] nivalis, L. *The Snowdrop.*

A HARDY herbaceous plant, perennating by means of an underground bulb, and sending up an annual flower-shoot with one flower to the height of six inches, or one foot in the case of larger garden forms. The Snowdrop is not indigenous to Great Britain, though an escape in many localities or a survivor of old gardens and now quite naturalized.[2] It is an alpine form, extending along the mountain ranges of South and Central Europe from the Pyrenees to the Caucasus, the centre of distribution for the genus being found in the Eastern Mediterranean district.

It has long been cultivated in English gardens, being mentioned by Gerard in 1597[3]: larger garden forms are now in cultivation and include the fine variety *G. Imperati* (Matthiolus, 1575), and the closely allied forms *G. plicatus* from the Crimea, 1818, and *G. Elwesii* from Asia Minor, 1875. A large number of varieties which show interesting minor deviations from the type, either in shoot-construction or colour-markings of the flower, have been either found growing wild, or isolated in cultivation by florists, and are indicated by special names. The finer cultivated forms present no essential differences, but are larger in all their parts, and the details of construction are often more pronounced than in the wild form.

The flowers are produced from the end of January to March, the optimum flowering period being the middle of February: the fruits ripen and shed their seeds in June.

### Description.

INFLORESCENCE reduced to a solitary flower, borne laterally on the flowering shoot; a membranous sheathing 'spathe' with 2 strong green ribs, and 2 unequal claw-like free tips, is carried up on the flowering axis, and beyond this the flower is pendulous on a special stalk which is about equal to the spathe in length.

FLOWER: Hermaphrodite, actinomorphic, trimerous throughout.

RECEPTACLE markedly crateriform, constituting the outer wall of the ovary cavity, 6 mm. long by 4 mm. in diameter; bright green externally. ('Epigyny' of the flower.)

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[1] *Galanthus,* a genus founded by Linnaeus (1735), and the specific name (1753).

The name *Galanthus* or 'milk-flower' was given by Linnaeus; the name 'Snowdrop' is not old, it comes from the German Schneetropfen, which refers to the pendants or ear-drops worn in the sixteenth and seventeenth centuries. The older Pre-Reformation English names are Candlemas Bells, Fair Maids of February, White Ladies, all connected with the Church festival of Candlemas Day, Feb. 2, and refer to the procession of white-robed maidens which took place on the Feast of the Purification: hence also the French name Violette de la Chandaleur, and Purification flower, Italy. The modern German name is Schneeglöckchen, or little snowbell. It will be noted that Candlemas Day, old style, agrees with the optimum flowering period, which now more nearly coincides with St. Valentine's Day. Old English herbalists all call the plant the White Bulbous Violet.

[2] There is little doubt that like some other valued spring flowers, the Yellow Crocus, the Daffodil and the Periwinkle, the Snowdrop was introduced from the Mediterranean during the centuries of Roman occupation.

[3] The *Leucoium Bulbosum Precox* of Gerard (1597), or 'Timely flowering Bulbous Violet, wild in Italy and places adjacent, notwithstanding our London Gardens have taken possession of it many yeeres past.'

Perianth of 6 free segments, inserted on the rim of the receptacle-tube, in 2 dissimilar series (3 + 3).

*Outer set* of 3 elliptical segments with narrower stalk portions, averaging 20 mm. long by 10 mm. wide; clear white in colour; the edges in larger forms are slightly wrinkled in the lower portions.

*Inner set* of 3 obcordate segments, alternating with those of the outer series 12 mm. by 8 mm.; white, with a green band following the notch on the outer surface, and furrowed on the inner surface, with 8 longitudinal ridges appearing as green lines.

Androecium of 6 free stamens (3 + 3), in normal trimerous alternation with the perianth segments, inserted on the closed receptacle-tube.

*Filaments* slender, 2 mm. long, white.

*Anthers* introrse, orange-yellow, 5 mm. long, tapering to slender points, overtopped by a divergent filamentous process of the connective. *Dehiscence* takes place by pores extending as slits the whole length of the anther, and the 6 anthers are grouped to form a conical cluster closely surrounding the style.

*Pollen* orange-yellow, dusty when dry.

Gynoecium of 3 carpels.

*Ovary* syncarpous, 3-locular with axile placentation and 2 rows (3–6 each) of obliquely ascending anatropous ovules in each loculus.

*Style* simple, slender, 9 mm. long, overtopping the anthers and bearing a tuft of *Stigmatic papillae* on its pointed extremity.

Nectary: the tissue around the base of the style and staminal filaments is more or less swollen and secretes freely. The secretion accumulates in the grooves left around these members, and when abundant fills the cage formed by the 6 filaments and may run down the furrows of the inner perianth segments.

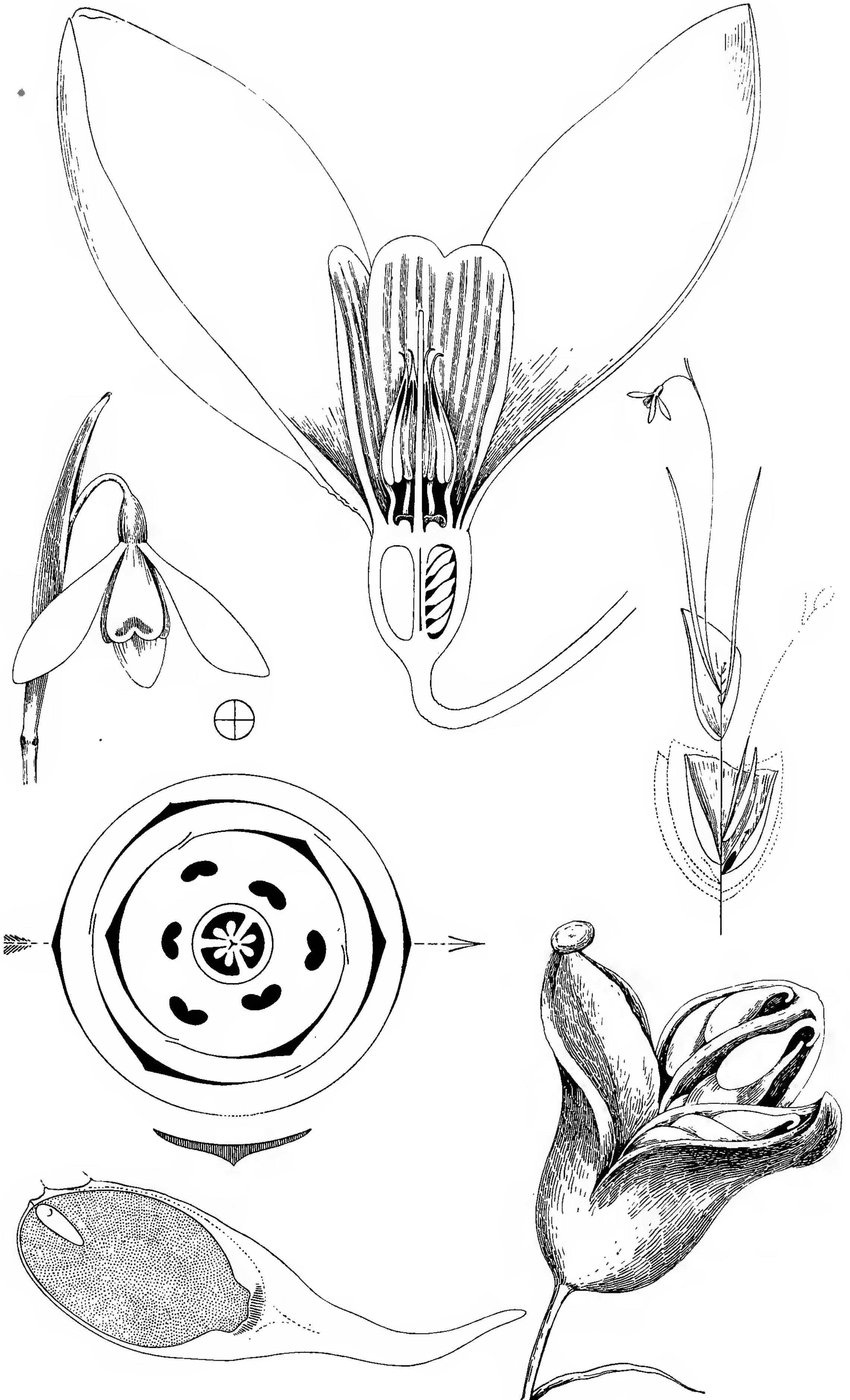
(The furrows between the green lines have a glistening appearance and apparently also secrete; on putting a fresh segment under water it will, however, be seen that the glistening appearance is increased, and is due to the fact that they are not wetted. The tumid character of the 'disc' is more obvious in the larger forms, *G. Imperati*.)

## Variations.

Large garden forms (*G. Imperati*) average 30–35 mm. in length for the outer perianth-segments, and in extreme cases 40 mm. The largest flowers are recorded for *G. plicatus*, 'nearly 2 inches' long. *G. Elwesii* has the lower half of the inner perianth-segments green on the outside, and is thus readily identified. All other parts are correspondingly increased and the disc is almost lobed. (The most specialized nectary of the alliance is found in the closely similar alpine form *Leucojum hyemale=nicaeense*.)

## Floral Diagram.

I. Shoot Construction. The specialized shoot takes the form of a *Bulb*, the constitution of which may be readily observed on digging up a plant in the flowering season. After careful washing, the bulb is seen to be surrounded with brown scale leaves, which represent the remains of the leaves of the preceding year but one. The bulk of the bulb consists of the thickened leaf-bases of the 3 leaves of the previous year: of these 2 are tubular; while the innermost is scale-like and retains in its axil the thickened base of the flower stalk of the previous season. By its side arises the flower-shoot of the current year, consisting of 1 sheathing and 2 green foliage leaves, the bases of all 3 being already thickened with reserve storage. On peeling off the membranous protective sheath-leaf, note that it extends just to the surface of the soil, and acts as a guide for the enclosed foliage leaves and flower in boring up through the soil; it is usually slit for about 10 mm. on one side. Opposite it a flat green foliage leaf may be traced to the base of the bulb, the lower 8–10 mm. only also forming a sheath around the remaining parts. These comprise a second foliage leaf opposite



**Galanthus nivalis;** Floral Diagram and Sectional Elevation in the transverse plane; Scheme of Flowering bulb, dehiscing Fruit and section of Seed in the plane of the raphe.

to the first, which is not sheathing at all, and apparently bears a solitary flower in its axil: on the side of the flower-stalk, remote from this leaf, is seen a small bud formed by the rudiments of the 3 leaves of the next season and the apex of the shoot.

The phyllotaxis is thus a symmetrical (1 + 1) construction, and each annual growth includes 3 leaves and a terminal bud. The uppermost leaf subtends a solitary axillary[1] flower, while a vegetative bud in the axil of the lowermost sheath leaf provides for the ramification of the shoot and becomes in time a new bulb. The construction is practically constant for successive seasons, and traces of 4 years' growth are thus to be seen in a flowering bulb. The storage of food reserves in the old fruit stalk, the base of which persists in the bulb, is a point of special interest.

II. ORIENTATION. The spathe is composed of 2 leaf-members, these being indicated by the 2 claw-like processes at its apex, 5 mm. long, and thus represents a case of gamophylly in vegetative members; the 2 original primordia being carried up by a secondary zone of growth which here produces a protective investment for the flower bud. This, when young, stands erect between these two members, and on expansion ruptures the membranous portion on one side. If the flower is axillary these will therefore be regarded as 2 prophylls; in such case note that the flower-stalk is mainly due to a secondary growth constituting an internode below the first of these members, while the special flower-stalk is an internode between the upper one and the receptacle.

The flower is apparently a strictly symmetrical (3 + 3) construction throughout, and so far as can be seen in the flowering stage the orientation is not at all obvious; also the prefloration of the perianth segments is not constant, owing to the fact that to overlap they need extend more than 120° of the circumference, and as they do not do this when young, or at their bases when adult, the overlapping of the wider upper portions is secondary. On examining a bud just shooting from the soil, and still enclosed in the transparent spathe, it is easy to distinguish the two spathe leaves as $\alpha$ and $\beta$, since one ($\alpha$) is longer and is hooded over and encloses the inner ($\beta$). The insertion of the perianth segments is seen between these members, the extension of which constitute the green ribs of the spathe: and on one side one outer perianth segment is seen, and on the other two outer perianth segments and an inner just showing between them. The position of these, however, varies slightly, sometimes it appears quite symmetrical, at others more or less oblique, suggesting that the bud is twisted inside the spathe. As the symmetrical arrangement might just as well have been attained by secondary twisting, investigation of the developing members will be required.

III. THE FLOWER. Beyond the 3 outer perianth segments, the succeeding whorls of 3 follow in normal alternation. A transverse section of the ovary shows 3 loculi, axile placentation, and 2 rows of ovules in each loculus. A tri-radiate stylar canal permeates the style, and is continued down the axile placenta; this is developed to such an extent that the placenta readily divides into 3 on cutting a section, especially in shrunk spirit-material, and gives the impression of a unilocular ovary with 3 T-headed placentas just meeting in the centre, and thus affords an idea of the readiness with which 'parietal placentation' may be

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[1] The fact that the flower is axillary rather than terminal is not beyond dispute; and *a priori*, from the analogy of a large number of common Monocotyledonous types (cf. *Iris*, *Crocus*, *Hyacinthus*), it might be expected to be terminal, the vegetative bud being the axillary one, and the annual growths of the shoot thus constituting a *sympodium*. The figure illustrates the 'axillary' standpoint which seems clearest when the bulb is examined in the flowering condition and is supported by the greater number of facts. The data are simple, but they may admit of different interpretations: the short axis ends with two opposite leaves and two buds between them; one is vegetative and the other reproductive; the latter is wanted first, grows strongly and appears to terminate the axis. According to the 'sympodial' standpoint, the apex directly grows into the flower, while the vegetative bud is a later lateral development. It is, however, always difficult to prove the origin of such a 'dormant-bud'; and on the other hand interesting evidence is afforded by the case of especially strong bulbs in which two flowering axes may be produced side by side with the vegetative bud between them. In such case it is difficult to reject the conclusion that both the foliage leaves subtend axillary flowers, since the two flower-shoots cannot both be terminal and one is quite as much so as the other (Fig. 5).

acquired (cf. *Orchis*). The secreting receptacular gland (*disc*) may also be indicated in the diagram. Further details can only be ascertained from the study of early stages of development, as by cutting sections of the bulbs during June and July.

IV. DEVELOPMENT. The 2 spathe leaves ($\alpha$ and $\beta$) arise as wholly independent primordia, one after the other on fairly opposite sides of the axis, and crossed with the plane of the two foliage leaves. The first 3 members of the perianth also arise serially. The first 2 approximately crossing the plane of $\alpha$ and $\beta$, while the third is fairly superposed to $\beta$. The exact positions cannot be accurately determined, but it is so far clear that these 5 members are produced one at a time in an asymmetrical (spiral) construction, while beyond them the remaining floral members arise in alternating whorls of 3, showing that the construction thus attained is a symmetrical (3 + 3) type. It is thus possible to assume that the primary asymmetrical formation was a (2 + 3) construction at approximate divergence angles of $137\frac{1}{2}^\circ$, the angle of normal asymmetrical phyllotaxis; but the number of members produced in such a system is too few to give a result which can be accurately checked. These contact relations of the perianth segments are retained in the young growing bud (Fig. 1): the special point of interest being the fact that a plane of symmetry passing through an odd perianth-segment does not appear to coincide with that of the distichous series of vegetative leaves, but one such plane is much more nearly transverse to it.[1] Sections of similar buds show that the prefloration of the perianth segments is wholly secondary. The orientation may thus be conventionally treated as *transverse* since a plane of symmetry passes more nearly in this direction than in any other, and a conventional diagram can thus be drawn which will be sufficiently accurate for the purpose of constructing the correlated sectional elevation. The two prophylls are also conventionally regarded as transverse, $\beta$ being placed on the right-hand side.

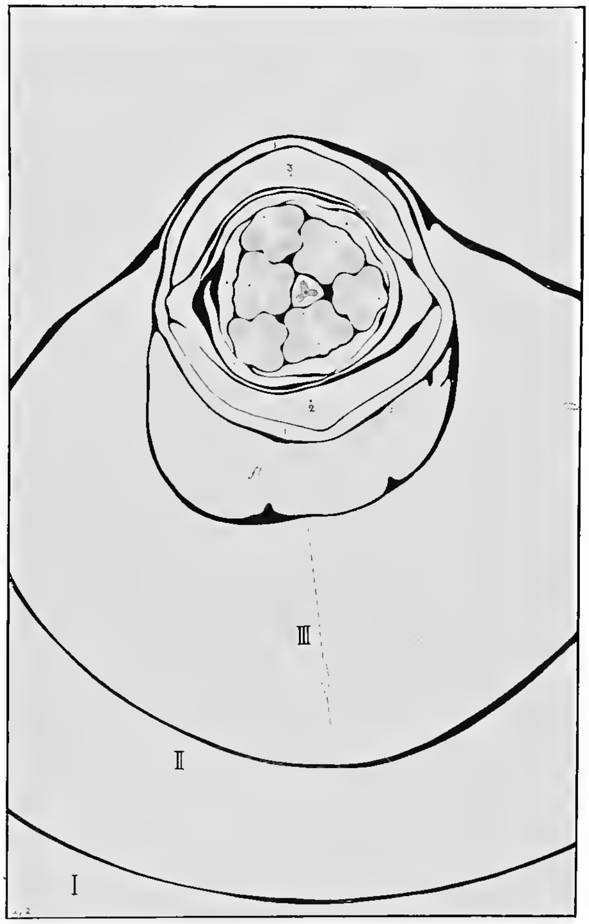

FIG. 1. *G. nivalis, var. Imperati*, Sept. 1 bulb, cut in transverse section to show orientation of flower-shoot with regard to the plane of distichous phyllotaxis.
I, II, III, storage leaves of bulb; *fl'*, old flower-stalk; 1, sheathing leaf; 2, 3, foliage leaves of ensuing season.

## Elevation.

Sectional elevation may be thus constructed for the transverse plane of the conventional diagram, which passes through one of the outer perianth segments on one side, and one of the inner segments on the other, the posterior half being selected for illustration. The flower is erected in its primitive position. The plane of the section therefore passes through 2 stamens, showing two others in face view, also through one loculus of the ovary and one of the ovary septa. Note the relative proportions of the members, the cone-like cluster of anthers raised on short stalks and dehiscing by slit-pores, the very slender style, and the

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[1] A similar oblique orientation is shown in other trimerous Monocotyledonous types, cf. *Lilium, Canna, Gladiolus.* The orientation of a second flower in the inflorescence is not certain owing to the difficulty of obtaining material.

lobed disc. The 'epigynous' character of the flower is very marked, and there is little trace in the adult flower of the manner in which this has been produced.

The relative development and arrangement of the floral parts from this standpoint of elevation is most readily observed in longitudinal sections of bulbs taken from June to October. To secure uniformity, the tops of the bulbs are trimmed down until the arrangement of the bulb scales is seen, and longitudinal sections are then cut in the plane of the distichous phyllotaxis system, since this gives the clearest view of the structure of the flowering shoot as a whole; it must be noted, however, that the flowers themselves are cut obliquely in the plane, and the developmental diagrams will not coincide exactly with the sectional elevation arranged for a conventional transverse plane. The first stages in the development of the flower take place in June and July (Figs. 2, 3, 4).

Section of bulbs taken at the middle of July and commencement of August, shows all the floral parts already laid down, and the general construction of the floral shoot is very clear (Figs. 2, 3). The relation of the vegetative members of the system is easily recognized; the first leaf, wholly sheathing, is seen cut on both sides; the second leaf, sheathing just at the base, shows a small portion on the side opposite to the main portion of the member; the third leaf subtends the flower, and on the other side of this is the rudimentary bud, which marks the end of the plant axis. The flower stem, beyond the two prophylls which form the thin spathe, dilates to a very distinct cup-like form, the *receptacle-crater*; the perianth segments arise from the top of the rim towards the outer edge, the stamens just on the rim, while the carpels arise from the whole of the inner slope, and are so pressed together that they fill the cavity and only leave a small slit between them. The point at the bottom of

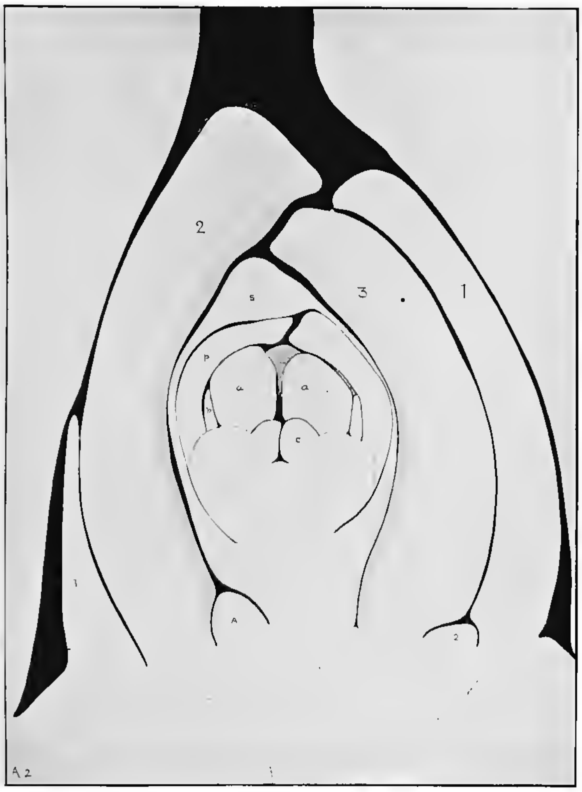

FIG. 2. *G. nivalis*, July 12 bulb; development of flowering axis. 1, 2, 3, the leaf members of the ensuing season; *s*, the prophyll-spathe; *p*, outer, *p'*, inner perianth members; *a*, anther; *c*, carpel rudiments; *A*, end of plant axis.

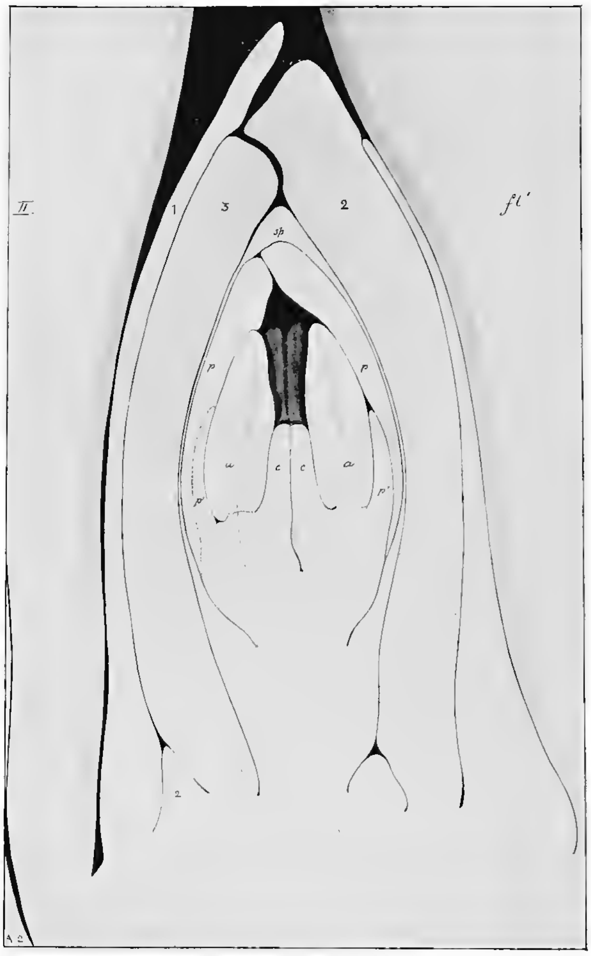

FIG. 3. *G. nivalis*, August 8 bulb; development of flowering axis showing the crateriform receptacle filled by the carpels: lettering as before.

the slit is therefore the apex of the floral axis, and the outline of the crater is obtained by drawing a line through the points of origin of all the members. The stamens are the largest and most rapidly growing members; the inner perianth-segments have a retarded growth, while the stylar portions of the carpels soon grow up between the anther lobes, the slit between them persisting as the style canal (Fig. 3). Note the markedly crateriform receptacle, the distinct origin of the members from it, and the absence of secondary zones of growth.

In subsequent stages the crateriform receptacle grows considerably, the cavities of the carpels broaden out as the loculi of the ovary, and the fused style grows up between the stamens. In a similar section cut in September all the floral parts are fully formed, including the pollen grains in the anthers and the embryo-sacs in the ovules. The growth regions of the floral axis and the flower-stalk proper are already being laid down by active cell-division with a view to subsequent rapid cell-extension, while the anthers are still in contact with the receptacle, and tend to impress on it the outline of their lobes (Fig. 4).

It will be noted that if the floral structures retained their relative positions as seen in the August bulb (Fig. 3), the flower would be a normally self-pollinating mechanism, since the anthers would shed directly on the style tips. The fact that the original arrangement is not retained, but becomes complicated by a secondary special mechanism, thus becomes a proof of the fact that cross-pollination is considered desirable if possible.

### Special Mechanism.

The succulent crateriform axis completely filled by the ovary portions of the carpels gives a special character ('epigyny') to the floral construction, but beyond affording protection against mechanical damage, this scarcely enters into the working machinery of the flower regarded as a mechanism to subserve pollination. Its significance, on the other hand, appears more obvious from the standpoint of subsequent fruit-formation, which includes the protection of the ovules from the desiccating effects of cold winds.

The special mechanism may be considered under the following heads:—

(1) Intercalary growths in the stamens giving rise to slender filaments which remove the anthers from the immediate vicinity of the secreting disc.

(2) A much longer zone of growth in the fused stylar portions of the carpels which takes the stigmatic surface well beyond the anthers, and would eliminate self-pollination if the effect were not somewhat neutralized by the drooping of the flower.

(3) Special colour markings on the perianth segments, limited to the 3 inner segments; a spot following the notch on the outer surface and green lines on the inner surface. These certainly seem to subserve no other purpose than that of a colour-contrast, and may be so far perhaps regarded as 'honey-guides'; on the other hand localization of pigment in spots and bands is usually associated with a decadent coloration, and it is possible that the original flower was wholly green. It is interesting to note that the pigment utilized is only chlorophyll, and that no yellow derivatives have been produced.

The specialization of the inner segments is also indicated by the terminal notch in the margin which also tends to recurve, especially in the larger forms (*G. plicatus*, *Elwesii*), the apparent aim being the production of a bell-type of corolla with a crenulated margin comparable to the bell of *Polygonatum*, *Hyacinthus*, *Convallaria*, &c., in which insects hang on to the margins of the pendulous flowers.

(4) A special glandular region is produced on the receptacle, more especially between the androecium and the gynoecium, and being wholly receptacular may be included as a 'disc' nectary.

(5) The pendulous character of the flower is produced just before expansion by a definite growth-curvature of the internode between the spathe-leaves and the crateriform portion of the axis.

(6) While growth-extension movements of the outer perianth-segments commence after

expansion, and continue so long as the flower is functional; these constitute a protective adaptation since they are absent in allied forms (*Leucojum*).

(7) By the retention of the anthers in a close cone around the style as they were packed in the bud, with the tendency to limit the shedding of pollen to a terminal portion of the anther, the slit widening at the apex to constitute a pore, a 'powdering mechanism' is arranged, the effect of which is increased by the slight extension of the sporophyll-lamina as a slender pointed trigger (for a similar sprinkling mechanism, dusty pollen, slender extruded style with minute receptive surface, cf. *Erica carnea*).

## Pollination.

The flowers emerge above ground in January with all their parts perfect, erect and enclosed in the spathe, and pressed between the 2 flat foliage leaves which bore through the soil. The spathe is ruptured on one side, and the flower-stalk bends so that the flower hangs vertically, the flower-stalk presenting a rather sharp curvature immediately below the ovary.

Observation of the spathe as it first appears visible at the level of the soil shows that the elongation of the flower-stalk takes place while the flower is still enclosed in the spathe, with the result that the stalk is thrown into a loop of a spiral. This may account for the sharpness of the curvature just below the ovary in the pendulous flower, but it is not the cause of the curvature since, if the spathe be slit open while the flower-stalk is still quite straight and the flower floated on water, a definite curvature of about a right-angle will be produced in a few hours, so that the curvature is not only intentional, but is independent of gravity. The original curvature is about equal to that found in the Daffodil, but the weight of the floral members plays a slight part in increasing the droop, as may be readily seen on removing these from a young flower. At the same time the *direction* of the curvature is affected by light (cf. *Narcissus*), and Snowdrops planted in the open tend to droop towards the south, while against a wall the majority droop away from it towards the most strongly illuminated side.

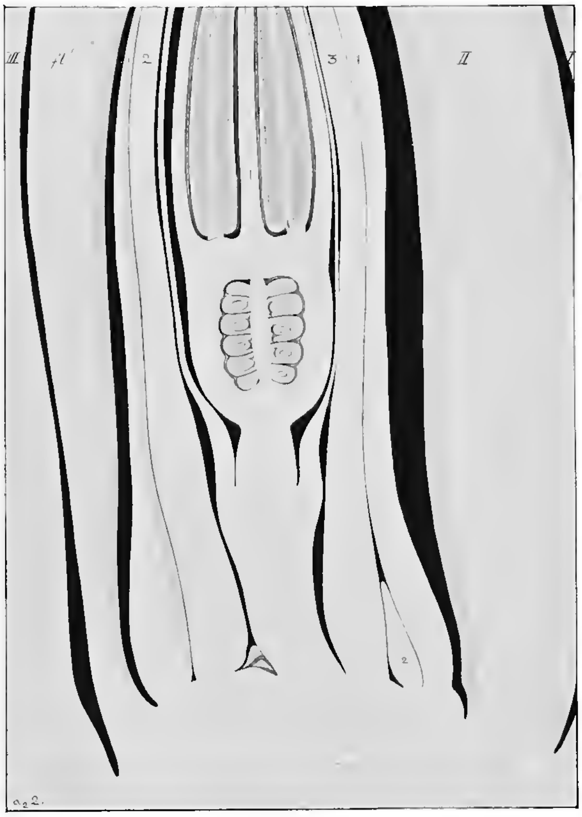

Fig. 4. *G. nivalis*, September 1 bulb; Flowering shoot cut in the plane of symmetry of the (1 + 1) phyllotaxis construction. All floral parts formed, and intercalary zones of growth commencing in the stalk region.

The three large white outer perianth-segments are at once protective and conspicuous; as a rule they do not expand unless the temperature reaches 10° C., and close again below this temperature. The opening and closing movements, as in *Crocus*, are dependent on variations in temperature alone, and may be readily observed in plants or cut-flowers brought into a warm room in the evening. They are due to unequal rates of growth-extension in the cells of the enlarging perianth-segments, the responding zone being limited to the lower third of the segment; these are prolonged into narrower claw portions with slightly wrinkled edges, and growth throughout the life of the flower is considerable; the outer segments of the pendulous buds increasing from 12 mm. to 20–24 mm. before they wither.

A rise of 5° C. affords a stimulus sufficient to open the closed flowers in about half an hour; while in an hour growth-extension may be sufficiently great on the inner surface of the segment bases to produce a recurvature of the segments. By this means the flowers open in February and March in the morning about an hour after the sun reaches them, and close in the afternoon as it leaves them. In cold rainy weather they remain closed, as also during frost and snow which hardly damage the flowers. They expand in bright sunshine while surrounded with melting snow. The capacity for response lessens as the flowers get older, until it ceases before they wither, and thus older flowers are recognized in that they do not close when the others do. Observations made on flowers in the evening when the temperature is falling are more conclusive than those made in the morning on flowers which may have already been slightly stimulated with a rising temperature, and they open in a gas-lit room in the evening with great readiness.

At a low temperature, near the freezing-point, the flowers become too inert to respond to any great extent; thus after a change from 2° to 15°, the flowers were only half-open after an hour, and no further response took place. The same flowers kept overnight at a temperature of 11° opened rapidly and well next morning on a further rise to 18°. With a rise of 8–9°, starting from 8–10°, definite movement may be observed in 5–10 minutes.

*Note* that a comparatively slight expansion is sufficient to expose the bell-shaped inner perianth, and render the flower both attractive and functional; while the same rise of temperature which opens the snowdrop flowers also brings out the first hibernating insects; and thus Hive-bees will emerge in numbers on the second day that the temperature rises beyond 10° C., especially if the sun shines on the hives. The same bees staying out on the flowers in the afternoon, become curiously inert at the same time as the flowers close up again.

The stamens dehisce and the stigma is receptive as soon as the buds unfold; the pollen supply is very abundant, and sufficient to repay collection by bees, while the honey supply may be considerable in freshly-opened flowers in warm weather, but is readily affected by cold dry winds and often appears wanting in the first flowers to expand, as also in older flowers: in large garden varieties the secretion around the base of the style is usually conspicuous enough.

Pollen and honey are only available to insects which hang on to the inner perianth segments of the pendulous flower, but no great length of proboscis is required, as the honey when abundant may slip down the groves of these segments, and drops collect between the anthers and the style. The flowers are thus adapted to the visits of small bees, but larger ones are not excluded. In gardens the flowers are visited chiefly by the Hive-bee, which takes both pollen and honey, but chiefly pollen. Observation of the method employed by the Hive-bee shows that the tips of the outer perianth-segments afford a landing-stage, and grasping the inner ones, which, in larger forms, have slightly recurved edges (*G. plicatus*, *Imperati*), the bee pushes its head into the bell and inserts its 6 mm. proboscis between the anthers, or lower, between the filaments. In displacing the stamens, which form at first a close cone around the style, pollen is freely dusted on its head parts and is thus conveyed to the stigmas of other flowers; the receptive surface projecting 2–3 mm. beyond the anthers. The tendency towards porous dehiscence in the anthers, and the connective tips which recurve as triggers, indicate increased specialization of the powdering apparatus: at the same time it will be noted that the pollen is remarkably dusty, and a dry stamen of a large form on being touched with a needle will set free a yellow cloud of pollen which is visible for 2–3 inches and deposits pollen thickly on all the floral parts. In dry weather, pollen is also shed in a small cloud on shaking the flowers, and pollination may be thus readily effected by the wind (cf. contemporary *Erica carnea*); as in *Erica*, however, the stigmatic surface is very small, and the number of ovules large, so that for effectual pollination the application of a large number of pollen grains on the small stigmatic surface is only likely to be effected by contact with a pollen-covered surface as presented by a visiting bee. Self-pollination is thus not eliminated, and the special features of the flower, its pendulous habit, and sprinkling cone of stamens, thus allow a chance of self-pollination quite as much as they are adapted for the visits of such insects as bees. On the other hand, the special differentiation and coloration of the perianth segments, the honey supply, and the special length of the style which is, from the standpoint of self-pollination, a wholly unnecessary feature, indicate that insect-agency is specially sought by the plant. That bees will also largely effect self-pollination is also clear; the flowers are freely fertile to their own pollen, but as self-pollination in absence of insect-visits would have been better effected with a much less elaborate special mechanism, it may be inferred that cross-pollination is desirable, though it has not been more definitely proved in the case of the Snowdrop.

Even in total absence of insect-visits it is possible that a few grains of pollen may become attached to the stigmatic papillae, owing to the agency of slight air currents as the pollen falls from the anthers, and in cold weather, when no insects are available, every flower is normally self-pollinated, and many set fine fruits.

Individual flowers persist for a relatively long time; during cold weather with snow on the ground they remain unopened, although otherwise functional, for 2–3 weeks. They are only susceptible to damage from cold dry winds, under which conditions they may wither in 3 weeks and do not set fruit. In a cool moist environment individual flowers remain fresh for 6 and even 8 weeks when protected under trees: a month is a good average period, but less in dry weather whether mild or cold.

*Note* that special features of the mechanism may have more than one advantage; so that it is not possible to say which may be the actual aim: thus the opening and closing movements which are evidently correlated with insect-life, also afford protection to the essential organs from wind and rain. The opening may thus be related to insect-visits, and the closing represent a protective adaptation wholly independent of insects, with reference to the protection of the stigma and slender style with germinating pollen-grains from desiccation; but it becomes more difficult to account for the differentiation of the perianth members and the special colour-markings: thus the size and white coloration of the outer perianth members renders the flower eminently conspicuous, and the green markings appear admirably suited as 'honey-guides', but the pointed shape and the dilated curve of the outer segments, which are not easily wetted, has probably quite as much to do with the throwing off of rain-drops or condensed moisture from the closed flower, while the green coloration, which is considerably increased in some forms (*G. Elwesii*), is assimilative and occurs in streaks because it is localized around the vascular bundles. The green spot at the apex of the inner segments is possibly inherited from an ancestral *Leucojum* stock; but it is again interesting to compare the effect of the bilobed segments with that of a typical 6-parted bell-flower as in *Convallaria* and Solomon's Seal.

## Fruit and Seed.

Non-pollinated flowers wholly wither away, and the aerial portion of the flower-shoot follows; but non-pollination is probably rare, and withering of the young fruit is more often due to death by cold. In pollinated flowers, the perianth-segments, stamens and style all wither, the outer perianth-segments being the first to fade, but these parts are not directly shed. The upper surface of the ovary is protected by a zone of cells with cuticularized walls, which may be seen in section of an old flower; these constitute a diaphragm over the top of the ovary, beyond which all tissues dry up, the free members drop away and a circular scar is left at the apex of the fruit. The green ovary slowly enlarges about the end of March, to form an ovoid, green berry-like fruit, until it is about 15 mm. long by 10 mm. in diameter. The fruits of the larger garden forms attain the size of small plums. As the fruits increase in bulk the flowering axis becomes lax, and by a considerable growth in the portion still included in the sheathing leaf it attains a length of over a foot in the typical form, so that the berries are carried well beyond the foliage leaves and lie on the surface of the ground. Where the plants are growing among grass the subsequent growth of the grass stems completely enwraps the green fruits and they become buried in the turf and so protected. The fruits attain their full size in April, about four weeks after the withering of the perianth; they ripen in June and then turn pale yellow. Although succulent and extremely berry-like, they still retain the capsular structure of the *Narcissus* type, and dehisce along lines corresponding to the median plane of each of the 3 loculi; that is to say, by three special lines of dehiscence in the wall of the receptacle-tube. The walls remain succulent, and dehiscence is confined to the upper part of the capsule; no sclerosed tissue is present, and the opening mechanism is provided by the living parenchymatous cells of the inner layers of the fruit-wall. These, as an apparently last vital effort, become turgid, and by expansion rupture the capsule along three lines which open up the cavities of the loculi, and then collapse; water is discharged, and the smooth, dry berry-like fruit is converted into a pulpy and somewhat slimy capsule, on the three gaping valves of which lie the white-tailed seeds, in two rows on either side of the ruptured placental septa, to the number of usually 4–6 in each loculus. The tissues of the wall are full of air as well as discharged sap, and the open capsule floats on water and does not close again (cf. *Nymphaea*). That dehiscence is a vital effort is also shown by the fact that fruits picked only slightly before they are ripe, shrivel up and do not shed. Beyond the secondary elongation of the flowering axis there is apparently no special modification for distant dispersal, and the seeds simply fall out in a clump much resembling that found in the case of *Viola odorata*. The ripe *Seeds* are ovoid, white, 4 mm. by 2 mm., with a long 5 mm. succulent chalazal tail, which owing to want of room in the fruit is often definitely hooked. The micropyle is marked at the opposite end by a slight dot. The seeds are very slightly compressed in the plane of the raphe, and section in this plane shows a very thin testa of two thin unmodified layers continuous with the parenchymatous cells of the chalazal tail, which possess no food material and possibly function only as an aqueous tissue for water-storage during maturation. The bulk of the seed consists of endosperm of very elaborate structure, while at the micropylar end lies a spindle-shaped embryo with a single terminal cotyledon and rudimentary plumule. The endosperm consists for the most part of beautifully pitted cells, the thick walls of which represent a reserve of a form of cellulose (pinkish with Iodine, and purple-brown with Schulze's Sol.), and are penetrated by delicate connecting strands of protoplasm. The mesh-work of protoplasm includes starch grains and a few oil-drops. Starch is absent from the proteid-storing peripheral layer of the endosperm, while the cells of the chalazal process of the endosperm are usually not pitted, contain proteid matter only, and are multinucleate.

*Note* that the embryo is protected mainly by the thick-walled endosperm layers; it is provided with food stored in the endosperm in the visible form of proteid, starch, and oil, as well as cellulose, and beyond the elongation of the flower-stalk shows no modification for dispersal.

## **Variations and Monstrosities.**

Owing to the fact that the whole plant shows special adaptation to a winter and alpine environment, and that forms have been sought out by florists, the number of variations on the type is extremely large. As many as 20 varieties of *G. nivalis* alone have been distinguished by special names; those which present features of morphological or biological interest may be arranged under the following heads:—

(1) VARIATIONS IN SHOOT CONSTRUCTION.

(a) 3 foliage leaves in addition to the sheathing leaf of the flowering shoot, not uncommon in strong cultivated plants (var. *trifolius*).

(b) Two flowers on a common stalk, the second being a lateral flower produced in the axil of one of the prophylls (var. *biflorus*). The orientation of this flower and whether it arises in the axil of $\alpha$ or $\beta$ prophyll is not known.

(c) Two flower-shoots in the axils of 2 foliage leaves (var. *biscapus*). Like the last this occurs commonly in strong plants grown in rich soil (*G. Imperati*). Since such plants vary from year to year according to conditions of cultivation the use of a special name is of doubtful value.

(2) VARIATIONS IN FLOWER CONSTRUCTION.

(d) The normal trimery of the Monocotyledonous (3 + 3) type varies readily in strong cultivated specimens to pure tetramery of the (4 + 4) type throughout.

(e) Similarly a reduction-variation to true dimery of the (2 + 2) type also occurs; thus giving 4 stamens only and 2 carpels.

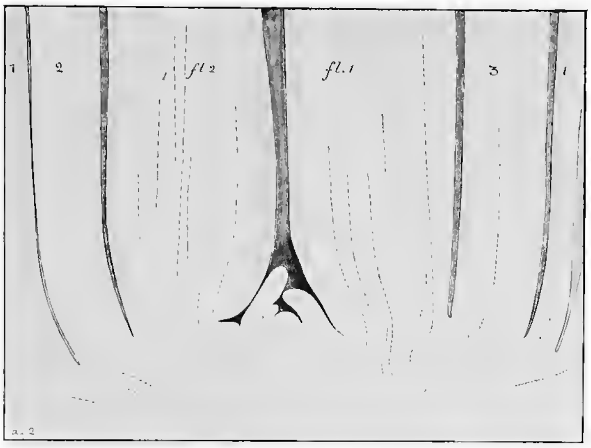

FIG. 5. *G. nivalis, var. Imperati,* Feb. bulb; section of apex of shoot between two flower-stalks.

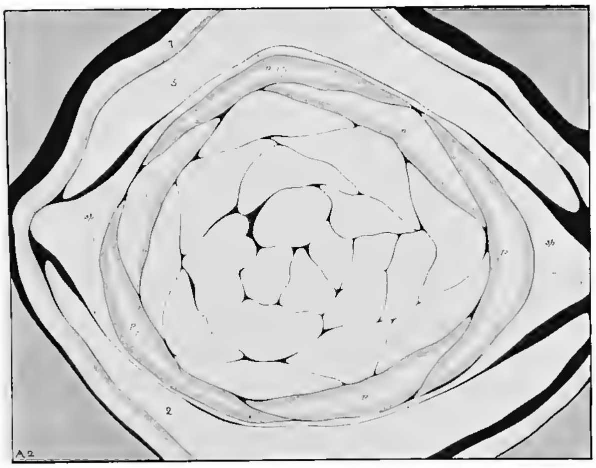

FIG. 7. *G. nivalis*, double form, Aug. 15; transverse section of developing flower just above the edge of the crater, showing irregular asymmetrical phyllotaxis construction.

FIG. 6. *G. nivalis*, double form, Aug. 15; Longitudinal section of developing flower, showing anomalous and irregular production of appendages over the entire surface of the crater.

(f) Still further irregularities present all intermediate conditions, as for example, 5-parted perianths, with 3, 4 or 5 stamens; in such case 2 outer members of the perianth are large, and 3 inner of the bilobed form.

(g) Similar irregularities lead to the presence of perianth-segments of peculiar form; both intermediate conditions between those of the normal outer and inner segments, as also instances of gamophylly among some of the inner ones. The case of 'slit-segments' may also be included here.

(h) In extremely reduced forms the gynoecium may be wholly absent.

(i) Malformed perianth-segments lead on to malformed sporophylls; portions of the stamens becoming petaloid.

(k) These conditions lead on by slight gradations to the typical monstrous cultivated 'double-form', in which the phyllotaxis system is continued for a great many members (20–30), and these, beyond the usual 3 outer perianth-segments, are developed into a miscellaneous collection of normal and malformed members, forming a central rosette to the flower and impeding the normal closing movements. These flowers are sterile in the gynoecium; the development is a vegetative degeneration of the flower-shoot, while the occurrence of normal 'outer' perianth segment forms among the rudimentary and normal stamens is an interesting example of anomalous development, in that it is wholly inexplicable. The developmental stages of such double forms are of interest from the standpoint of a degenerating construction system: thus bulbs cut in August show in longitudinal view (Fig. 6) an irregular production of leafy members over the entire surface of the receptacle-crater. The lack of a gynoecium, although the green ovary-like receptacle is normally apparent in the adult blossom, is thus readily explained; the cavity of the crater being filled with small abortive members.

A transverse section of a similar flower (Fig. 7) taken just clear of the rim of the crater shows that the construction-system remains wholly asymmetrical: that is to say, the transition to a symmetrical (3 + 3) arrangement has been forgotten in the ontogeny of the flower, and it is at this point that the first error possibly appears.

(l) Such doubled monstrosities again lead on to other anomalous phyllotaxis constructions of the '*fasciation*' type, in which the centric development of the flower-shoot is replaced either by several centres, or by a crested growing point. The floral members thus present a double-crested series of as many as 12 outer and 12 inner perianth segments, 20–30 stamens and 10–12 carpels.

(m) Of a different type again are those variations which indicate an imperfect development of the crateriform axis in the production of the 'receptacle-tube': in such case 1–2 of the outer perianth segments may get left on the outer slope of the crater, and in the mature flower thus present the appearance of being 'inserted' on the sides of the green ovary away from the other members (such phenomena afford again an interesting confirmation of the spiral construction of the outer members, the receptacle-tube thus presenting a phenomenon of internodal elongation comparable to that of *Cactus*).

(3) COLOUR VARIATIONS IN THE PERIANTH SEGMENTS include florists' varieties, obtained, from isolated wild specimens, or as sports under cultivation.

(n) The green coloration fading to yellow (cf. *Leucojum vernum*); var. *Sandersii pallidus*.

(o) The coloured spots and stripes reduced to very small extent and even wholly absent; var. *albus*.

(p) The green colour increased, until the inner segments are almost wholly green; var. *viridans*, *virescens*.

(q) Green lines on the outer perianth segments; var. *virescens*, *Scharloki*.

(4) VARIATIONS IN THE SPATHE.

(r) The spathe becomes white and petaloid (var. *candidus*).

(s) In var. *Scharloki* (Caspary) the spathe is only slightly gamophyllous, the 2 constituent members developing as long linear leaves.

(5) NO DIFFERENTIATION IN THE PERIANTH, all the segments being white and similar, the inner ones only slightly shorter than the outer.

(t) var. *hololeucus*, discovered by Celakowski in Bohemia, a still further advance on var. *poculiformis*, found wild in two places in Great Britain, in which the inner perianth segments are long and pure white.

Further garden varieties are distinguished by possessing wider foliage leaves than the type, as also by slight differences in the relative shape and dimensions of the perianth segments.

## Comparison with allied Types.

*Leucojum vernum*,[1] L. The Snowflake, indigenous to Central Europe from France to Bosnia, and occasionally found wild in this country as an escape, is of great interest in that it evidently presents parallel earlier stages in the evolution of the Snowdrop. It flowers a little later (February–April), the distichous foliage leaves are (3–4), the flower-stalk and spathe are identical, but 2 flowers are frequently borne on one flowering axis. The 6 perianth-segments are all alike, of the same general form as those of the outer perianth of the Snowdrop, but all have a greenish spot at the tip on the outer surface. The flower is again often only half-pendulous and presents an open bell-type; the perianth exhibits no closing movements, and the stamens, although possessing a much more perfect porous dehiscence, soon diverge widely instead of forming a conical cluster around the style. A further peculiarity of the *Leucojum* flower is the large club-shaped style. The flowers have a shorter duration period (2–3 weeks), they are similarly homogamous and visited by bees. Variations to perfect tetramery and dimery occur in garden specimens. A somewhat nearer approximation to the Snowdrop type is seen in *L. hyemale*, DC. (= *nicaeense*), from the Maritime Alps (Nice and Mentone at 1,800 ft.). It is a smaller form, with a 2 or more commonly one-flowered shoot, with 6 delicate perianth segments, all pure white or slightly streaked with green externally: the inner 3 segments are, however, slightly blunt, while the outer 3 are pointed. The staminal cone group is present, but there are no 'triggers'; the style is little longer than the anthers, and the receptacular disc is represented by 6 bilobed nectary scales. As an Alpine form it appears to represent the limit of reduction and specialization in the *Leucojum* series.

On the other hand the large summer-flowering *L. aestivum* presents a vegetative development which brings the group into line with such types as that of *Narcissus*. The leaves are numerous (6–8), the plant flowers in May, June, and the inflorescence contains several flowers (4–8), constituting a compound cymose type.

## Theoretical Considerations.

The general reduction sequence in the inflorescence which can be traced from the summer-flowering *Leucojum aestivum*, with the vegetative habit of a Polyanthus Narcissus, to *Leucojum vernum* and *hyemale*, with the habit of a Snowdrop, leaves little doubt that the forms of *Galanthus* represent the present day end-result of a closely similar, though still more pronounced series of shoot-reduction, accompanied by increasing floral specialization. While, again, the specialized forms of *Leucojum* are essentially confined to the Western basin of the Mediterranean, the *Galanthus* section tends to be equally restricted to the Eastern basin; only the least modified *L. aestivum* reaching as far east as Asia Minor. Several of the cultivated varieties of *G. nivalis*, especially those induced by over-feeding, are now seen to represent reversions to earlier stages in the phylogeny of the type, or else irregularities in

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[1] *Leucojum* of Linnaeus 1735, also written *Leucoium* (Linnaeus 1737, and by old writers), from the Λευκοίον = Viola alba of Theophrastus: *vernum*, the Linnaean name established 1753. The plant was figured by Brunfels (1530) with the Daffodil as *Narcissus*; a good drawing is also given by Fuchs (1542) as *Viola alba*, while the form *Leucoion* was retained for the Crucifer *Hesperis*. Cf. also *Leucoium bulbosum hexaphyllon* of Dodonaeus (1616); *Leucoium bulbosum primum* of Tabernaemontanus; and *Leucoium bulbosum praecox majus* of Gerard (1597), the first record for this country, 'The Bulbed Stocke Gilliflower'. The name *Leucoium* was long applied to Stocks (Tournefort, 1700) as also to the Snowdrops. Bauhin (*Pinax*, 1623) distinguishes *Leucoium bulbosum* as a genus opposed to the Cruciferous *Leucoiums*, and Tournefort (1700) improved the section to *Narcisso-Leucoium*.

the present construction, as, for example, plants with more than one flower, and more than two foliage leaves; while the form *hololeuca* is of interest in presenting a practically undifferentiated perianth comparable to that of *L. hyemale.* No amount of cultivation, on the other hand, adds anything essentially new to the type. It appears permissible then to trace the phylogeny of the Snowdrop from a *Leucojum*-like ancestor, with full vegetative habit and abundantly flowered inflorescence of more or less pendulous flowers with green-tipped perianth segments, flowering in the cool wet season and resting in the form of a perennating bulb through a hot and dry summer. The Snowdrop alliance is, however, essentially alpine, and increasing limitation to an alpine environment, with short vegetative period, in which the wet flowering season becomes that of the melting of the snow, impoverishes the plant as a whole; the vegetative shoot is reduced and the inflorescence limited to solitary flowers which may be shot up suddenly, as soon as conditions become at all favourable, and even before the assimilating leaves are fully developed (cf. *Helleborus niger*). The characters of the *Galanthus* type, which indicate specialization beyond that of the *Leucojum* form, include:—

(1) Reduction of the vegetative shoot to a minimum.
(2) Specialization of a single large flower: the advance taking the form of—
  (*a*) The differentiation of the perianth into two series; an outer protective, attractive, and motile cycle of segments, an inner closer protective bell immediately surrounding the essential organs, and also of biological utility from the standpoint of insect-visitors.
  (*b*) The increasing efficiency of the 'sprinkling apparatus'.
  (*c*) The localization of special colour markings.

With regard to (1), it is not clear how reduction could go farther, bearing in mind the correlation of the flat foliage members and the protective sheath with the enclosed flower-bud; while the single flower becomes the type, and more than one a rare exception, the form *biscapus* being, however, readily produced by cultivation in rich ground under non-alpine conditions.

The phenomenon of unequal extension of the growing perianth-segments is a new feature, and is identical with that presented by the perianth segments of *Crocus vernus.* The increased protection afforded to anthers, nectary, style, and stigma by enclosing them in a fairly close bell-type of corolla appears to be of greater influence than any direct modification for insect-visits, and the special shape of the inner perianth segments is apparently connected with a cessation of apical growth with a compensating increase behind the tip, thus producing two lobes and rendering the mouth of the bell more even at a level well clear of the stigma. The localization of the green colour is of special interest, the outer segments lose the characteristic *Leucojum* spot, but this is retained on the inner, and is now extended in that it follows the two lobes and appears as a double spot or a definite V-shaped mark. The chlorophyll-containing tissue also occurs on the inner side of these segments, and in some varieties (cf. *virescens*) may be still further increased as if it had a special assimilatory significance. It is clear that an increase of assimilating tissue in such a form will be an advantage in the case of a flower shot up into the warm air and sunshine, when conduction of food from the leaves and bulb will be at a minimum owing to the low temperature of the soil, as at the period of snow melting, since the excretion of nectar and the feeding of the pollen tubes has to be provided for: the hypothetical utilization of some of these green lines as 'honey-guides' does not necessarily explain the origin of the green stripes; it is probable that the reverse is the case, and the green colouring matter is only eliminated completely on the parts seen externally; the 3 outer perianth segments being produced as large white 'flag' members.

While the essential Snowdrop characters as deduced from *G. nivalis* are quite definite, it is interesting to note that any further specialization would be expected to follow along these lines before initiating any new or striking departure. Further adaptation to

alpine environment should, therefore, act on the flower rather than on the vegetative shoot; the flower might be increased in size and attractive features, or shot up more quickly, i. e. before the leaves, and so appearing to flower earlier in the season; the differentiation of the perianth segments should be more marked, and possibly there might be an extension of the green assimilating-tissue. It is interesting, therefore, to compare in these respects the large type *G. Elwesii*, which is becoming increasingly cultivated, since in many details it appears to represent the present climax of the *Galanthus* alliance. This handsome form, discovered by Balansa in 1854, is indigenous to the mountains of Asia Minor at 2–5,000 ft., and was introduced into this country by Elwes, who collected bulbs from the mountains around Smyrna in 1874. The flowers are of the largest Snowdrop size, and it is the favourite Snowdrop of the florist, owing to the fact that it flowers somewhat earlier than the others.[1] The outer perianth-segments are well over 30 mm. in length, they are very concave, giving the flower a balloon-like appearance when expanding, and possessing a definite motile stalk portion about 6 mm. long, which, on expansion, becomes quite concave outwards. The inner perianth-segments wrap each other closely and constitute a perfectly compact bell-shaped investment to the essential organs, the effect being that of a tubular Hyacinth-bell, rather than that afforded by the almost flat segments of *G. nivalis*. The lobation is more pronounced, the edges distinctly recurved, and the furrows more marked and wrinkled, giving the entrance to the bell a frilled appearance. This last is again so constricted that it is the exact width of the base of the anther cone, and the stigma is exactly adjusted to the centre of the bell-mouth. The green coloration is remarkable; the usual V spot is retained on the outer surface of the inner perianth segments, but the green stripes are now localized, being retained inside the bell, deleted just at the entrance, and a portion of them left at a position corresponding to the outer V spot. The suggestion that these are intentionally localized from the standpoint of insect-visits is certainly strengthened, but a new departure is seen in the presence of a large blotch of green, which is the characteristic feature of the flower, and covers the whole of the lower half of the inner segments, and shows externally even when the flower is closed. This spot can scarcely be regarded in the light of a honey-guide, and its most obvious function, apart from assimilation, appears to be the darkening of the cavity of the bell; it will also be noticed that the green coloration now corresponds on both sides of the segments, the striped effect on the inner side being the expression of the ridge and furrow structure.[2] The triggers of the sprinkling apparatus are again more pronounced as pointed, recurved triangular processes; so that in almost every detail of the flower *G. Elwesii* shows an advance on the type of *nivalis*; points which are obscure in the latter becoming obvious when checked by comparison with the former. On the other hand, the phenomenon of the flowers appearing before the functional foliage is most nearly approximated in the large-leaved form *G. plicatus* from the mountains of the Crimea.

Beyond such an ancestral stage as that indicated by the present-day *L. aestivum*, the

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[1] In a greenhouse it will flower at Christmas, while imported bulbs planted in a sheltered position in August have been known to flower in November.

[2] The simplest solution of the problem would appear to be that the perianth segments of the ancestral form were comparatively small and wholly green, of the relatively insignificant type seen in an undoubtedly primitive form in the *Narcissus* alliance, the autumn-flowering *N. viridiflorus*; and that the modern representatives of the *Leucojum* section represent types in which the more or less perfect elimination of the chlorophyll has resulted in the production of a conspicuous pure white flower; the spots and blotches indicating a decadent coloration, which in the special habitat of these spring flowers may prove more effective as a colour contrast in the mechanism itself. It is interesting to note that no addition of yellow pigments has taken place as in the *Narcissus* section, and that while the *Leucojum* type with six equal perianth segments loses the chlorophyll equally in all, the differentiation of the perianth members in *Galanthus* is correlated with a complete loss of pigment in the outer and more conspicuous members, while the inner more concealed series retains a larger amount of chlorophyll than is found in any *Leucojum*; and the type (*G. Elwesii*) with the greatest amount of differentiation in the perianth also shows a greater contrast in its pigmentation. Note therefore that there is no evidence that these green spots have been placed on primitively white segments as 'honey-guides': they are rather to be regarded as relics of a once diffused pigmentation which have proved useful as affording a simple colour-contrast.

history of the type merges into that of the characteristic Narcissus and Amaryllis plan of plant-structure, which became the centre around which the varied types at present included in the group *Amaryllidaceae* have been segregated; and as a bulbous Liliaceous form with marked epigynous construction in the flower, *Galanthus* is included with about 70 other genera, comprising about 730 species in this very conventional family, which includes a large series of similar epigynous floral forms of very doubtful relation; since it is very possible that the evolution of similar crateriform construction has taken place in several distinct lines of descent among Monocotyledons, just as it certainly has done among Dicotyledons, among which its value as a classificatory feature has been very generally discounted.

Taking the *Amaryllidaceae* at their present valuation, the range of type of vegetative structure covered by these forms is a very wide one; the extremes being represented by the common Snowdrop, with annual shoot reduced to two green leaves and one flower, and *Fourcroya longaeva*, a Mexican Agave-type, which is said to grow for centuries, producing a 30 ft. shaft with 3,000 leaves, ultimately terminating in a single season in a 30 ft. panicle of a million and a half blossoms.

# III

## **Jasminum nudiflorum,**[1] Lindl. *Winter Jasmine.*

A PERENNIAL woody shrub with deciduous leaves and long, straggling, assimilating branches, growing to the height of 20 ft. or more, introduced from Nankin, China, by Fortune in 1844, and commonly grown in gardens, trained as a wall-plant, for the sake of its abundant yellow flowers produced throughout the winter and early spring (December–April), stragglers lasting as late as June, while the first ones may be found early in October. The fruits, which are somewhat rarely produced in the open, ripen at the end of June and July.

### **Description.**

INFLORESCENCE: reduced to single flowers borne terminally on short dwarf-shoots which arise in the axils of the foliage leaves of the preceding summer. At the base of these dwarf-shoots 2 lateral prophylls are present, and above them 3–4 decussating pairs of scale-like bracteoles.

FLOWER: hermaphrodite, actinomorphic, dimerous in the essential organs.

RECEPTACLE: slightly crateriform.

PERIANTH differentiated into:—

(1) CALYX: Gamosepalous of 6 sepals; segments almost free, green, lanceolate acute, 8 mm. by 2. Two are quite external to the other 4, which are usually bent in pairs more or less underneath them.

(2) COROLLA: Gamopetalous, tubular, with deeply cut, almost horizontally expanded limb; segments of the limb typically 6 (varying 4–8); prefloration variable, but 2 segments are wholly inside the others and usually directed upwards at a steeper angle. Corolla-tube 17 mm. by 2; free petal-segments 12 mm. by 8; the whole a clear pale yellow.

ANDROECIUM of 2 stamens, attached 8 mm. up on the corolla-tube;
*Filaments* very short;
*Anthers* yellow, introrse, nearly 4 mm. long: the 2 anthers completely embrace the style and almost block the narrow corolla-tube.
*Pollen* pale yellow.

GYNOECIUM of 2 carpels;
*Ovary* syncarpous, 2-locular with axile placentation, each loculus containing 2 obliquely placed anatropous ovules;
*Style* slender, rising to the entrance of the corolla-tube, 17 mm.;
*Stigma* capitate, of 2 adpressed lobes.

NECTARY: the whole free green surface of the ovary secretes, and honey rises 2 mm. or more in the corolla-tube.

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[1] The name Jasmine is taken directly from the Arabic name (Ysmin), and was applied originally to the scented white-flowered *J. officinale*: this Oriental form is said to have been introduced from Syria by the Moors into Spain, and from thence has spread over South Europe and has been cultivated in this country from very ancient times: the term *nudiflorum* indicates, though not very happily, the fact that the flowers are borne on branches without foliage leaves. The name was given to it by Lindley in 1846.

*Jasminum*, a genus of Tournefort (1700), continued by Linnaeus (1735).

## Variations.

The number of corolla-segments is variable; often 5, less commonly 4; or on strong shoots they may increase to 7, less frequently 8. The percentage of 5–4-parted flowers often increases as the season advances, and is higher on starved plants.

Impoverished flowers have corollas only half the typical size. The stamens are remarkably constant, 3 being comparatively rare.

The style often projects 2–3 mm. beyond the corolla-tube, and the 2 lobes may become widely divergent.

## Floral Diagram.

(1) Shoot Construction. The foliage shoots are symmetrical and exhibit a strictly decussate (2 + 2) phyllotaxis; as is commonly the case in this type of construction (cf. *Fuchsia*, *Fraxinus*) a variation to (3 + 3), giving alternating whorls of 3 members, is occasionally met with, on single shoots or even characteristic of the entire plant.

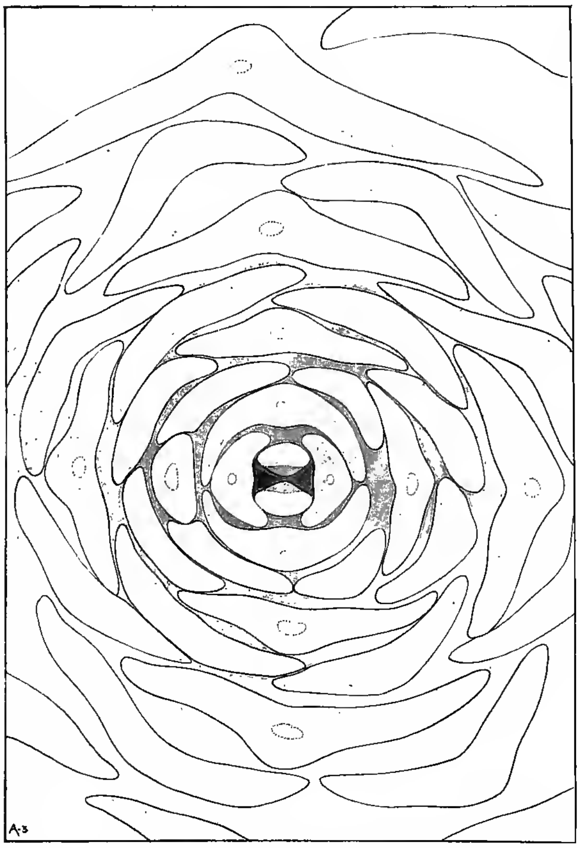

Fig. 1. *J. nudiflorum*; apex of vegetative shoot, August; decussate (2 + 2) phyllotaxis system.

A similar construction is continued into the dwarf flowering-shoots, and orientation is normal and symmetrical (Fig. 1).

(2) Orientation. The prophylls (α and β) are small and pointed, and opposite in a strictly transverse plane; above these, 4 or 3 pairs of bracteoles continue the decussate construction; 4 pairs appear to be typical, 2 of them being small and purplish, and 2 pairs light green. The prophylls have dormant axillary buds, which possibly under certain circumstances would develop into lateral flowers of the inflorescence shoot.[1]

The orientation of the terminal flower, separated by a varying number of leaf-whorls from the basal prophylls of the shoot, has no necessary connexion with the leaf which subtends the shoot; but as the whole construction maintains symmetrical relations, it must coincide with either the transverse or the median plane. A typical construction may be taken as comprising 4 pairs of bracteoles beyond the prophylls, and in such case the calyx, orientated with regard to the preceding leaf-whorl, presents a similar orientation with regard to the median plane of the shoot. At the calyx members the (2 + 2) construction of the vegetative leaves is suddenly changed to typically (6 + 6); and both calyx and corolla are produced in this hexamerous construction; 2 of the members crossing the plane of the 2 preceding bracteoles, and in this special case thus falling in the median plane. (For an identical phyllotaxis phenomenon compare the perianth of *Clematis Jackmanni*, &c., in which, however, only one whorl of the hexamerous formation is utilized; but, as in *Jasminum*, the same variation to 4, 5, 7, 8-parted flowers is possible, according to circumstances of nutrition.)

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[1] A drawing in Paxton's Magazine, made from a plant grown at Chiswick (Hort. Soc.) in 1848, shows dwarf shoots with two flowers each.

Beyond the corolla-whorl, the decussate construction (2 + 2) is resumed, and 2 stamens and 2 carpels represent 2 alternating whorls of this formation; the 2 stamens crossing again with the 2 transverse members of the corolla whorl, and in the type diagram thus falling in the median plane while the carpels are transverse.[1]

The symmetrical relations of the construction, which is thus definitely changed twice in the course of the floral development, are most clearly shown on a curve-construction diagram, in which it can be seen that since a construction by hexamery implies smaller primordia, gaps are necessarily left in the formation at the points of transition, and with subsequent packing as the members become adult, two median sepals will tend to be thrust outwards, and the two transverse petals inwards, the latter thus alternating with the large anthers.

The floral construction is thus remarkably simple and symmetrical; but three distinct phases of member production may be isolated:—

(1) The (2 + 2) system of the vegetative shoots and inflorescence axis.
(2) The (6 + 6) of the perianth whorls, and
(3) The (2 + 2) of the essential organs (sporophylls).

A hint that the (6 + 6) formation is rather to be regarded as a specific anomaly is afforded by the readiness with which the construction varies to 4 and 5, or even 7 and 8. Mixed types are also common, as, for example, flowers in which 6 sepals are succeeded by 5 petals or even by 4.

## Sectional Elevation.

Since the diagram has been orientated for a typical flower with 4 pairs of sterile bracteoles beyond the prophylls, so that the odd pair of sepals falls in the median plane of the axis, the elevation may be constructed for the same median plane. A flower cut in this manner will thus show parts of 4 sepals, 3 whole petals, and the section also passes through the attachment of both stamens and through the median septum of the ovary. In the latter case it is convenient to go slightly off the line and show the 2 ovules of the loculus; these being obliquely arranged are not seen clearly in either plane.

The shape of the corolla-tube varies slightly, it is frequently more open in the throat, or again somewhat compressed in the plane of the stamens, and thus wider in the transverse plane of the diagram.

The receptacle is slightly crateriform, but owing to its relatively small size the flower would be usually classed as 'hypogynous'. The chief point of interest is the relatively enormous size of the corolla-tube and free segments as compared with the essential organs; this being a sign of high specialization, and general among gamopetalous types.

The 'corolla-tube' is seen to consist of two sections which may be conveniently included under special names:—

(1) A *Gamopetalous Zone*, 8–9 mm. long above the point of attachment of the stamens, which represents a distinct zone of growth which has carried up the petal-segments to form a cylindrical or funnel-shaped tube.

(2) A lower section, which represents another secondary growth, which has elevated the

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[1] The relation of the androecium and gynoecium to the perianth members is most readily observed when the sepals and bracteoles diverge widely in the spring months, especially after the fall of the corolla, when the 2-lobed ovary remains enclosed in a calyx, the segments of which diverge like a 6-pointed star, and their orientation may be also compared with that of the decussating bracteoles.

This further applies to the interesting cases of pentamerous and tetramerous construction in the perianth whorls. In the former case a tendency to median symmetry is observable, an odd sepal falling into the plane of decussate symmetry, but either posterior or anterior in position. Similarly in the case of tetramery, the calyx is cruciate in the median and transverse planes, and the corolla, as is also the general case in all tetramerous flowers derived from pentamerous ancestors, is thus diagonal. In both types of construction the median position of the stamens and the *transverse* arrangement of the carpels appears unaffected.

stamens on a second tube, 8 mm. long. As a term is wanted for this region, the name *Zona Mediata* may be utilized.[1]

The long slender style is clearly correlated with the extension of this tubular corolla, but no special growth takes place in the filaments of the stamens.

It may also be noted at this point that the sepals are erect during the colder months, but as the weather improves they tend to expand horizontally, as also do the small leaves on the flowering shoot.

## Development.

The early stages of flower development are to be observed in July and August, but a considerable number of buds are arrested in growth and may be found on the plants during January.

Since the symmetrical phyllotaxis plan of construction is readily deduced from the adult flower, special interest attaches to the production of the secondary zones of growth. Buds taken in August show the earlier stages of development (Fig. 2). The apex of the

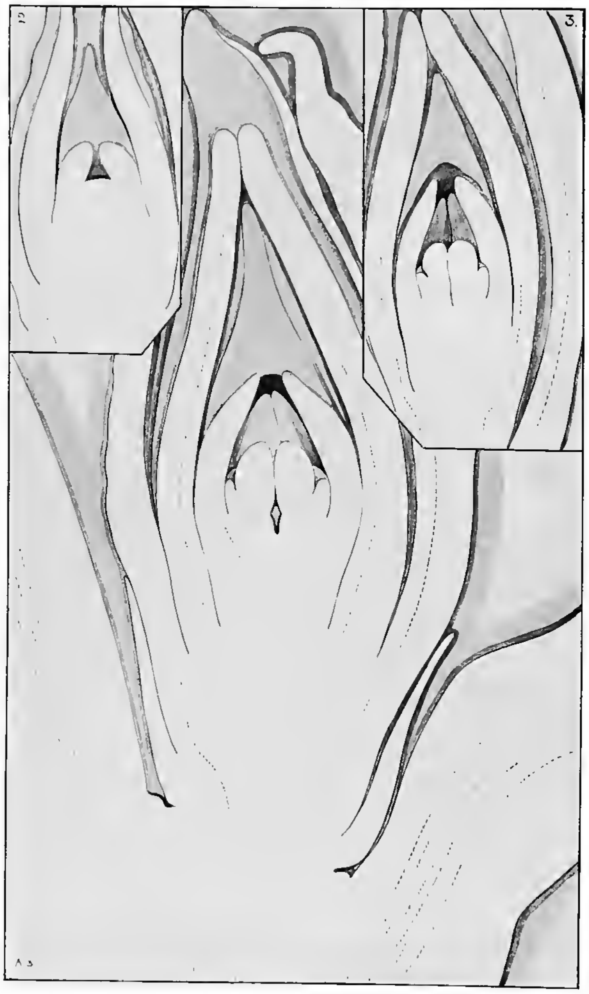

Fig. 2. *J. nudiflorum*; August 25, development of flower. (1) Origin of sepals, petals, stamens, and carpels; (2) apex of vegetative shoot; (3) section of bud before the origin of the carpels: all cut in plane of sectional elevation.

Fig. 3. *J. nudiflorum*; August 25, section in plane of sectional elevation to show formation of ovary and ovules.

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[1] The morphological importance of the attachment of stamens (*insertion*) was first discussed by A. L. de Jussieu (1789), to whom the terms *perigyny*, *epigyny* are due. Jussieu also distinguished the cases of *insertio immediata*, when the stamens were attached directly to the floral receptacle, and *insertio mediata* when they were attached through the intermediary of the corolla. The expression *Zona Mediata* gives the same construction a developmental interpretation.

vegetative shoot is conical (Fig. 2, 2), that of the floral axis slightly crateriform; the sepals arise first, and are well-marked members enclosing the succeeding structures; the petals remain small, while the stamen-primordia increase rapidly (Fig. 2, 3), pressing close together in the median line. The carpels alternate with these last, and all the floral members continue their growth without any special increase in the concavity of the receptacle (Fig. 2, August 25).

The protection of the essential organs in the earlier stages of development is thus effected by the sepals and the bracteoles external to them. (The commencement of the elevation of the petal and stamen-primordia, almost as soon as they appear, is of interest as indicating that the Zona Mediata may be also regarded as a specialization of the receptacle region; a special name is, however, convenient, since other intercalary zones of growth may similarly be ascribed to 'axial' formations.)

In a slightly older bud the formation of the syncarpous ovary, and the elevation of the stylar region, as also the commencement of the ovules, may be observed (Fig. 3), and the buds slowly develop throughout the autumn months; subsequent stages may be found when the first flowers are expanding (November), and may be even delayed till January.

*Note* that these August buds show that the construction is at first a perfectly simple floral structure, which would be a normally self-pollinating mechanism if no further growth regions were intercalated (Fig. 3).

A flower-bud 3 mm. long (January) shows all the essential features of the flower already laid down, and the structure only differs from that of the adult in the absence of the proper adjustments. Thus the receptacle is clearly crateriform, the corolla has a well-marked gamopetalous zone, but the Zona Mediata is no further advanced, although the anthers are fully formed. These latter again are in direct contact with the stigmatic lobes which are being carried to the tip of the bud by the growth of the style. The relative proportions of the parts are those of a comparatively simple type of flower. Subsequent stages may be conveniently plotted out to scale from measurements of successively older flowers, as, for example, from 6, 9, 12, 15, 18, 21, 24, 27 mm. buds. From such a series of figures it will appear that the growth in the Gamopetalous Zone and the Zona Mediata is fairly equal, but the growth of the style is at first much more rapid, so that the stigmatic lobes are pressed into the tip of the bud; in the latest stages the corolla passes the style and the stigmatic lobes remain at the entrance to the tube. *Note* that the adjustment is thus made by perfectly independent growth regions, and the fact that the adjustment is not always accurate is readily accounted for, and thus implies a certain degeneracy in the floral mechanism. The sepals and anthers grow very little after the 6 mm. bud stage, the tip of the yellow corolla showing beyond the sepals in the 9 mm. bud.

## Special Mechanism.

This may be included under the heads:—

(1) A gamopetalous zone of growth constituting a narrow-bored tube 8 mm. long.

(2) A Zona Mediata increasing the length of the tube to 16–18 mm.

(3) Coloration of the entire corolla-formation a clear and conspicuous yellow; the pigmentation being of a simple nature: the colouring matter is localized in small plastids, and is thus probably due to xanthophyll derivatives of chlorophyll.[1]

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[1] Yellow flower buds exposed to intense sunlight, after snow and during frost (January), or with cold winds (March), may produce red anthocyan-derivatives in the epidermis of the outer surface of the exposed petals, giving with the subjacent yellow pigment a deep bronze-crimson patch of colour. *Note* also the crimson coloration of the lower (i.e. outer) bracteoles of the inflorescence buds: that is to say, the plant retains the faculty for forming anthocyan compounds both in its vegetative members and flowers, but the Jasmines do not make any secondary use of this pigment in the floral mechanism (cf. *Syringa*), although it again appears in quantity in the purple black berry fruits of *J. fruticans* and *J. officinale*.

(4) A tendency to gamosepaly is not further utilized, but if it were increased the calyx-tube would protect and support the corolla-tube.

(5) The long stylar-growth which takes the stigmatic surface to the entrance of the corolla-tube, and well above and clear of the anthers with which this was originally in contact.

(6) From this last it would appear that definite means are employed to limit, if not to entirely prevent, self-pollination, the elimination being perfect in absence of insect-visits.

(7) From the total length of the corolla-tube, with the stigmatic surface at one end and the nectary at the other, it is possible to deduce the 'working-distance' of the flower and the character of the insects with which it has evidently been specially correlated. That is to say, an insect standing on the expanded corolla limb will require a proboscis practically equal in length to the corolla-tube in order to extract honey.

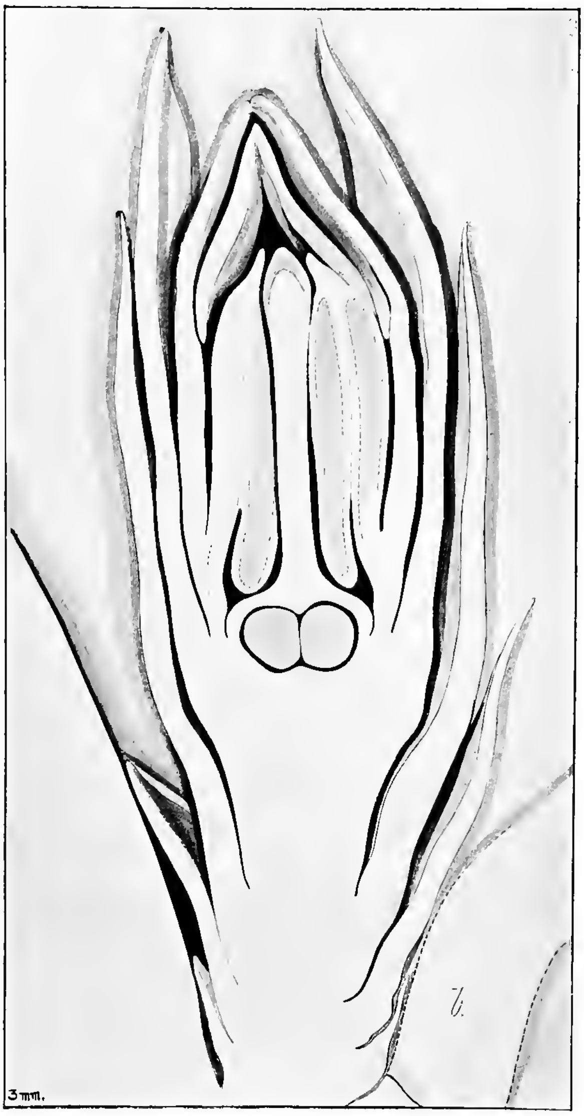

Fig. 4. *J. nudiflorum*; January bud, 3 mm. long. Section in plane of elevation.

(8) The flower is thus essentially adapted to the visits of Lepidoptera with suctorial proboscis of at least 15–16 mm. Large bees are, however, not entirely excluded, but the collection of honey by a licking proboscis is greatly hindered by the manner in which the anthers block the bore of the corolla-tube: it will also be noted that the flowers are not very strong, they do not readily support the weight of a large insect, there is little hold-fast when the corolla is dragged over, and the whole corolla is readily dropped. The flowers thus appear to be most readily pollinated by insects on the wing. The same blocking of the tube by the anthers will have the effect of eliminating small licking insects (unbidden guests), while the pollen supply is also protected and concealed.

While, however, the mechanism may be thus clearly correlated with pollination by certain insect visitors, it must be carefully noted that there is so far no evidence that any of these modifications has been directly produced in the first place as a definite adaptation to this end. All the structural peculiarities are already present in the 3 mm. bud, which would be an effectual self-pollinating mechanism: and it is interesting to note that the same modifications which adapt the flower for the visits of moths, &c., are equally well arranged to secure the protection of the essential organs, more especially the ovules in the ovary, from the effects of desiccation and intense light: for example, the blocking of the corolla-tube by the anthers may be regarded as an ingenious device to ensure a relatively dark and damp chamber for the ovary. While the fact that a simple modification may have several advantages thus militates against its association with one factor alone, it still remains possible that a type of construction, originally evolved in correlation with quite unknown agencies, has been not only utilized by insects, but rendered accurate by natural selection; and thus while it is not possible to state that a special type of insect has been instrumental in evolving any structural detail, it remains clear that the *exact secondary adjustment* of the lengths of the zones of secondary growth can have no other object than that of rendering the mechanism of cross-pollination increasingly efficient.

## Pollination.

The flowers are rendered conspicuous by the bright yellow coloration of the corolla, and attraction is increased by the abundance of flowers produced simultaneously on the leafless shoots. The foliage leaves do not expand until the middle of April, when the maximum flowering-period is well over, and they fall late in October, just before the buds begin to show colour. The yellow petals are thrust out of the buds at an early stage by the elongation of the corolla-tube, and flowers usually commence to expand towards the end of November. They possess no scent, and are evidently built on a very simple gamopetalous principle. The pollen supply is small, and fairly concealed by being placed 5–6 mm. below the entrance to the corolla-tube; the honey supply again is only accessible to long-tongued insects; the working-distance, as already noted, being 15–17 mm. The narrow entrance to the tube practically precludes the admission of anything beyond the proboscis of the insect visitor, and where the anthers block the tube still narrower channels are left on either side between them, the corolla-tube at these points dilating slightly; on looking into the entrance of the tube it will be seen that these pores correspond in position with superposed stigma lobes, so that any fine proboscis passing down the only available path must necessarily brush the stigmatic surface. Cross-pollination, including practical self-pollination when the insect is confined to the blossoms of one specimen, will thus be readily effected by long-tongued bees or Lepidoptera, though the extremely narrow passage suggests that the latter are the insects for whom the flower is specially adapted. On the other hand, self-pollination in absence of insect-visits is quite eliminated by the relative positions of the stigma and anthers.

The flowers are homogamous and persist for 6–10 days during the optimum flowering season (December, January) if the weather is mild. They are completely killed by frost, 10° F. being sufficient to kill all blossoms and unexpanded coloured buds; and few blossoms expand during spells of dry cold weather. The flowers are fertile to their own pollen when this is artificially applied to the stigma, and this should be performed as soon as the corolla expands, since the pollen-tubes have to traverse the whole length of the style (18 mm.) before the corolla falls off, breaking the style at its base as it drops, and in cold weather growth is slow, and the chance of the corolla being shed early considerably greater. Frozen flowers wither on the plant and are not shed. The rarity of fruit-formation is this country, owing to climatic reasons, even when the stigmas are carefully pollinated, renders satisfactory observations in the open air very difficult. Observations on the plant in its native home are wholly wanting, and in gardens the flowers are rarely visited, owing to the lack of insect life at the optimum flowering period. The plants occasionally set fruit, however, showing that the flowers may be satisfactorily worked by insects, but the number of fruits formed is greatly increased by artificial pollination, which is readily effected with a small brush or bristle. The only visitors appear to be early Hive-bees, who search every flower visible in the early months of the year for pollen. The tips of the anthers are just 5 mm. down the corolla-tube, but the Hive-bee just manages to reach the pollen, pushing both its proboscis and fore legs into the corolla-tube; in so doing it definitely pollinates the stigma, though usually, in its struggles, with pollen from the same flower. Plants thus visited by the Hive-bee have been observed to set a considerable number of fruits, but it is quite clear that such pollination is accidental, and that the Hive-bee is by no means the type of insect with which the floral mechanism has become correlated: the same applies to chance visits by hibernated *Eristalis*.

## Fruit and Seed.

The corolla withers and is normally shed, taking with it the stamens and also the style which is held by the anthers. The sepals persist and function as assimilating organs,

bud-scales, succeeded by 2–6 pairs of foliage leaves; simpler leaf-forms (5–3 lobes) may be found on weak branches and at the bases of these shoots. The inflorescence is terminal, a reduced decussate panicle branched to the second degree (T, T′, T″) with terminal flower. Accessory flower-buds often occur in the case of lower members, and a vegetative accessory bud may be found beneath the insertion of the inflorescence shoot. In the case of the primary flower-shoot being damaged, similar shoots may be produced in the axils of the prophylls. The *flowers* are white, very fragrant, and typically 4-parted varying to 5, and 6 petals exceptionally. The mechanism is simpler and self-pollinating; the flower-tube 18 mm. in length. The flowers are visited by considerable numbers of long-tongued bees and moths. Fruits rarely set; a 2-lobed berry, the lobes 10 mm. long, is produced, which becomes green but does not usually ripen to a black berry-like fruit, nor does the plant commonly set fruit even in Spain and Italy. The foliage is eaten by the caterpillars of Sphinx moths which pollinate the flowers.

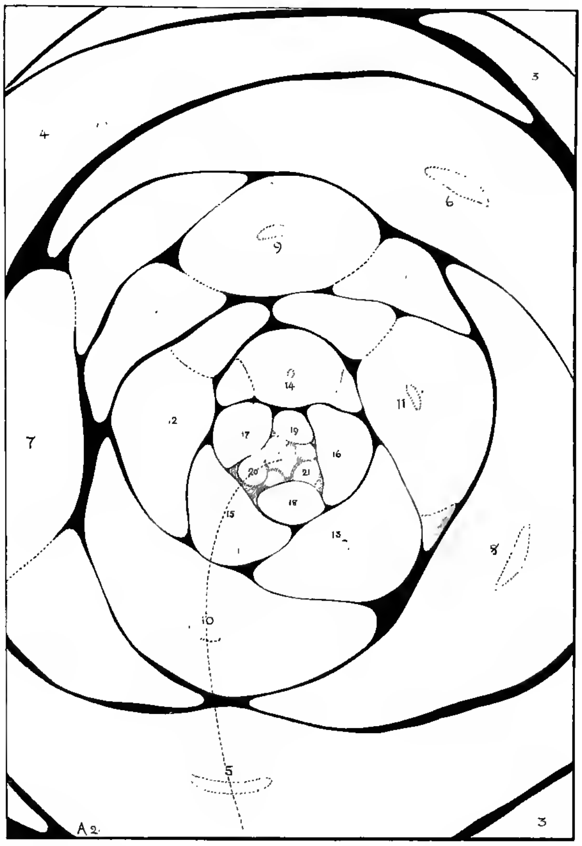

Fig. 5. *J. revolutum*; asymmetrical phyllotaxis system (2 + 3) of vegetative shoot; January bud.

Structure of the Fruit. The ovary wall is membranous, transparent and undifferentiated. The special columnar layer found in the seeds of *J. nudiflorum* now becomes definitely succulent, and is thus adapted as a means of dispersal by the agency of birds. The fruit thus appears as a bilobed berry, but the succulence is a product of the testa of the seeds and not of the ovary wall. The embryo is relatively larger and the endosperm less than in *J. nudiflorum.*

II. Jasminum revolutum (Sims)[1], a form with large fragrant yellow flowers, produced from May to October, is also in general cultivation in gardens.

Indigenous to tropical Asia, it was introduced from Nepaul in 1812, and China in 1814; it forms a woody shrub 10–15 ft. high or more, and is usually grown as a wall-plant. It is equally hardy with the preceding, though at first only grown in the conservatory, and is readily propagated by cuttings. The optimum flowering period is in June, and it shows no tendency to produce seed in this country, at any rate in the open. The leaves are evergreen in sheltered localities, but are killed by hard frosts. It bears 7-lobed pinnate leaves, twice as large as those of *J. officinale*, in a normal *spiral* Fibonacci phyllotaxis, the curve-construction at the apex being most readily expressed by the formula (2 + 3) (Fig. 5). The *inflorescence* shoots are also branches of limited growth, borne in the axils of the foliage leaves (shed) of the previous season. Each continues the asymmetrical Fibonacci phyllotaxis, bearing about a cycle of bud-scale leaves (3–5), succeeded by 5–12 foliage leaves. The terminal inflorescence with terminal flower is a reduced panicle branching to the third degree: lateral branches are subtended by small scale-leaves, and the usual bracts are present at the ramifications; but as in *J. officinale* the prophylls are usually wanting to the

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[1] This garden form, the *J. revolutum* figured in the *Bot. Mag.* of 1815, has been regarded as a larger form of *J. humile* of Linnaeus, a native of tropical Asia, with smaller and fewer flowers on shorter inflorescence shoots, growing as a shrub 3–4 feet high, and long cultivated in this country as Italian Jasmine. It was cultivated by Tradescant in 1656, and is probably the Sweet Yellow Indian Jasmine of Parkinson (1640), supposed to have been introduced from the East Indies or China.

last flowers (T″, T‴). An inflorescence may contain as many as 23 flowers, but usually only half this number. Vegetative buds in the axils of the leaves of these flowering shoots continue the ramification, the uppermost often making a strong shoot after failure of the flowers to set fruit. In the case of such a summer shoot the lowest leaves are often progressively more complicated (1–3–5–7 lobed) (cf. Fig. 6).

The flowers are typically 5-parted in the perianth whorls, but garden forms vary freely to 4–6 and 7 (even 8)-petalled corollas; the calyx is more constant. The stamens possess large anthers (7 mm. in bud), more or less exposed at the entrance to the corolla-tube, while the style grows up between them.[1]

The mechanism thus remains more or less self-pollinating, and the flowers are visited freely by long-tongued bees and many moths; the length of the corolla-tube (working-distance) being 20 mm. Minor irregularities are also frequent, e. g. 3 stamens in a pentamerous flower, and one or both stamens may be petaloid.[2] As in *J. nudiflorum* the nectary-gland continues to secrete copiously after the fall of the corolla.

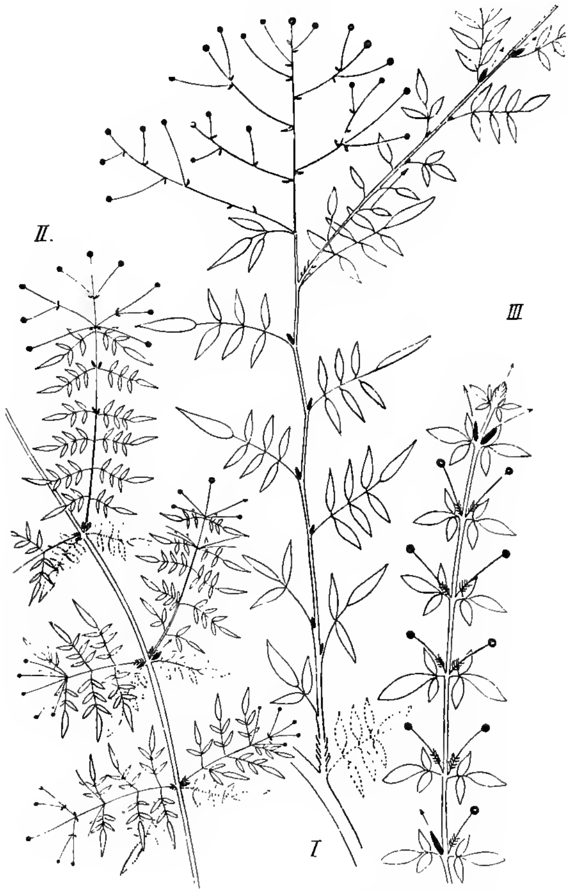

Fig. 6. Schemes of inflorescence shoots:—

I. *J. revolutum*, summer-shoot; asymmetrical construction and reduced panicle with T flower.

II. *J. officinale*, summer-shoot showing further reduction; symmetrical decussate construction.

III. *J. nudiflorum*, delayed flowering period, extreme reduction phase with decussate construction.

## Theoretical Considerations.

From these three types it is possible to isolate the primitive characters:—

I. The persistent pinnate *foliage* of *J. revolutum* is undoubtedly the full type, and the spiral Fibonacci phyllotaxis is again a more generalized type of construction. This becomes symmetrical and decussate in *J. officinale*, and decussate with reduced pinnation in *J. nudiflorum*. This last is also the most perfectly deciduous, and hence has the most specialized vegetative habit; in fact, it shows extensive xerophytic adaptations, and the angled stems are largely assimilatory in function.

II. The *Inflorescences* form a good series; that of *J. revolutum* is again not only the fullest panicle, and terminates special leafy shoots of the current year, but in construction it follows the same normal spiral phyllotaxis, the lateral branches again reducing to dichasia, &c., in the usual manner. In *J. officinale* this system reduces to similar but decussate shoots of the current year with only a few flowers (T, T′ and T″); while in *J. nudiflorum* the shoots bear no foliage leaves, a few sterile scales and a solitary terminal flower, which is, however, no larger than that of *J. revolutum*. The expansion of the flowers of these reduced shoots is further delayed until after leaf-fall

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[1] According to Pirotta (1885), *J. revolutum* at Rome exhibits phenomena of heterostyly. English specimens appear to agree with the figure in which the anthers are at the mouth of the corolla-tube and in practical contact with the stigma lobes. In such case the occurrence of two lengths of style would not appear to present any particular advantage, nor would it constitute the true phenomenon of heterostyly which, however, occurs in the Jasmine alliance in *Forsythia*. (Cf. *F. suspensa*, short-styled; *F. viridissima*, long-styled: only one form of each plant having been introduced.)

[2] A good example of such variation was afforded by a flower which possessed 6 sepals, 6 petals, 3 stamens, and 3 carpels, each containing an ovule. (1904.)

(October onwards), probably implying a habit of perennation over a dry summer season. In the construction of its inflorescence-system, therefore, *J. nudiflorum* also shows extensive reduction, which is apparently correlated with other xerophytic peculiarities (Fig. 6).

III. The *flowers* all agree in their essential organs, as in the character of the mechanism as a narrow tube adapted for pollination by Lepidoptera. The possibly primitive colour, yellow, occurs in both *J. revolutum* and *J. nudiflorum*; the reduction of pigment to white in *J. officinale* being usually correlated with the visits of night-flying moths, although the scent of *J. revolutum* is quite as powerful: as a matter of fact, the pale yellow flowers are almost as conspicuous at dusk as the small white stars of *J. officinale.* The segmentation of the corolla is remarkable; all three types show considerable variation in this respect, but curiously enough, *J. officinale* is typically 4-parted, *J. revolutum* 5-parted, and *J. nudiflorum* 6-parted. When it is noted that *J. revolutum* has with greater constancy a 5-parted calyx, which, though very degenerate, is undoubtedly the old quincuncial calyx correlated with the spiral phyllotaxis of the vegetative shoot, it becomes clear that the ancestral form must have been a normal pentamerous Dicotyledonous type, and that the two forms *J. officinale* and *J. nudiflorum* represent the retention of irregularities of a degenerating construction which become different specific constants in the two cases.

In the floral mechanism, again, *J. revolutum* would appear to have the simplest organization, in that although the floral tube may be 20 mm. long, the stigma is below or between the anthers (cf. *Syringa*), and self-pollination appears inevitable. The elimination of self-pollination by the great development of the style in *J. nudiflorum* thus again marks out this form as being the most highly specialized type.

On the other hand in its fruit, *J. nudiflorum* appears to be most primitive, the aqueous layer of the testa attaining a secondary dispersal significance in the other types.

(*J. fruticans*, a yellow-flowered evergreen form indigenous to the Mediterranean district sets fruit freely in the form of dark purple 'berries'.)

There can thus be little doubt that the ancestral form of the *Jasmine* group was a woody shrub or small tree, with asymmetrical phyllotaxis and pentamerous flowers of the normal Dicotyledonous reduced type, arranged in full panicles of possibly yellow blooms. The general habit of the plant and its floral mechanism as a self-pollinating tubular flower being very much that of the Common Lilac (*Syringa vulgaris*). The reduction variations from such a type, which have produced the different species of *Jasminum*, follow intelligible lines, morphologically speaking, although the causes which may have induced such changes may be still obscure. Of these perhaps the most obscure is the reason why hexamery should, as a specific constant, be so clearly marked in *J. nudiflorum*, when it does not seem to confer any benefit whatever on the flower.[1] Similarly it is extremely doubtful how far the transition to a symmetrical (2 + 2) phyllotaxis system may be correlated with increasing adaptation to xerophytic environment. The special reduction of the essential organs to one whorl each of a symmetrical (2 + 2) construction is again clearly another form of expressing the essential organs in the smallest numbers possible, a general principle throughout all specialized floral series; but there can be little doubt that such a reduction-phase in the sporophylls is wholly independent of the changes in the phyllotaxis of the vegetative shoot, since *J. nudiflorum* distinctly shows the double break in the construction mechanism, while in *J. revolutum*, the dimery of the essential organs is associated with an otherwise pentamerous

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[1] The transverse position of the carpels as a generic factor (cf. *Syringa*) is also of interest, though no reason can be given for such a phenomenon.

As already described, the essential organs of the flower take on a symmetrical (2 + 2) construction which implies a break in the construction mechanism between the corolla and the androecium. Granted this, it is interesting to note that the new symmetrical system of the sporophylls is also symmetrically orientated, two positions being possible: the two stamens may be either transverse or median, and the carpels vice versa. In *Jasminum* one position is the rule, while in other genera the other position is equally a constant: the median position for two carpels only appears more normal because it is so general in other non-decussate flower types. There is clearly no necessity to consider the *Jasmines* as a separate group on this account. In *J. officinale* the two carpels may be found obliquely placed with regard to the cruciate sepals.

flower and Fibonacci phyllotaxis throughout. While other features are more intelligible, therefore, the reduced dimery of the sporophylls constitutes the most marked feature of the series, and it is this which has been always regarded as the character which will serve to isolate the special *Jasmine* group from other plant phyla.[1]

About 140–160 species from the tropics and sub-tropics of the Old World are included in the genus *Jasminum*, which together with 19 other genera and an aggregate of 230 species make up the family *Oleaceae*. The entire series comprises a small and somewhat isolated phylum of the larger gamopetalous section, the essential character being this reduced dimery of the essential organs, which is so remarkably constant, and presumably advantageous as a form of a mean type of construction, that traces of the undoubted ancestral pentamerous type are somewhat scarce (cf. also *Syringa*, *Fraxinus*).

[1] As a suggestion bearing on the evolution of such a reduction-phase, it is interesting to consider the flower of the common Holly (*Ilex Aquifolium*). The flower has here a tetramerous (4 + 4) construction and a tendency to dicliny which is clearly associated with an ancestral pentamerous and hermaphrodite form; while in addition the staminate flowers tend to become gamopetalous with the formation of a distinct Zona Mediata. Exceptional flowers of the Holly *reduce to dimery with 2 stamens and 2 carpels*, and a staminate flower in this condition closely approximates the type of the *Oleaceae*. The genus *Ilex* is a somewhat isolated group probably related to a large tropical phylum, *Icacinaceae*, which includes the very Holly-like form *Villaresia*; on the other hand the genus *Osmanthus* of the *Oleaceae* is quite as Holly-like in appearance and its small white gamopetalous flowers with dimerous sporophylls are structurally closely comparable with those of these exceptionally reduced blossoms of the Holly; while the apparently independent evolution of gamopetaly in the latter shows that it is not necessary to postulate for the *Oleaceae* an ancestor that was gamopetalous before it became dimerous.

# IV

## **Crocus**[1] **vernus,** All.[2] *Blue Garden Crocus. Wild Saffron.*[3]

A HARDY herbaceous plant, perennating by means of a subterranean corm 4–5 inches below the surface of the soil, and sending up one or more annual flowering-shoots 10–12 inches long, which thus project about 6 inches above ground. The blue Spring Crocus is the common vernal species throughout Southern and Central Europe from the Pyrenees to the Carpathians, ascending to an altitude of 5–6000 ft.; it is the parent stock of the great majority of the blue and white Spring Crocuses in garden cultivation. Very doubtfully indigenous to Great Britain, although established locally, and in several parts of the country (Nottingham, Suffolk) meadows may be blue with it in spring, it has been cultivated from time immemorial, together with closely allied species and many varieties; thus Gerard describes several sorts of blue, white, and yellow Spring Crocuses as grown in London gardens in 1597.

The violet, lilac, or white flowers are produced in late February and March to about the first week in April; the fruits shed their seeds in June, and the plants perennate through the hot summer months as well as through the succeeding winter cold: like other Alpine spring flowers they are timed to vegetate and flower at the period of the melting of the snow.

On the other hand, the *Common Yellow Spring Crocus*, imported in large quantities from Holland, and hence often known as the Dutch Crocus, and also cultivated in numerous varieties, is a form of *C. aureus* (Sibth.)[4], which extends throughout Turkey and Asia Minor

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[1] The Greek κρόκος, Latin Crocus, applies strictly to the violet *autumnal*-flowering Saffron Crocus (Dioscorides, Theophrastus), the name being possibly connected with κρόκες (threads), the saffron threads being the aromatic stigma-branches of the flower. Similarly the Crocus of Ovid in the myth of Crocus and Smilax also applies to the autumnal Saffron Crocus.

The Κροκος of Dioscorides is figured in a recognizable condition in the Vienna MSS. An excellent drawing of the Saffron Crocus is given by Fuchs (1542) of plants both in flower and in fruit with great accuracy; a copy of the same figure appears in Turner's Herball (1551) as the Medicinal Crocus.

[2] The systematic generic use of the word *Crocus* dates from Bauhin's *Pinax* (1623) and Tournefort (1700). The latter first described 34 kinds growing in the Paris Botanic Garden (1719). Linnaeus continued the name (1735) but regarded all Crocuses as varieties of the Saffron Crocus (*C. sativus*). Although numerous forms were in cultivation, all Spring Crocuses were included under *C. vernus* by him as late as 1762, probably because they were regarded as garden forms, and only known in cultivation. However, travellers in South Europe and the temperate parts of Asia soon added truly wild species, and the yellow Crocus was first isolated as a distinct species by Lamarck (1791). He called it *C. luteus* (1804) and it had also been termed *C. maesiacus*. The use of *C. vernus* for the blue spring form was thus reached mainly by a process of elimination of other forms, but the more exact definition of the species is usually referred to Allman (1785).

[3] The Saffron Crocus (*C. sativus*, L.) is of immemorial cultivation in the East for the sake of its yellow dye, and in later times the cultivation of this plant appears to have spread throughout Central Europe through the agency of the Moors in Spain. The modern name *Saffron* being the French *Saffron*, German *Saffran* (Fuchs, 1542) and this again from the Moorish *Azafran* and Arabic Zaʿfarān. By the older herbalists, all cultivated forms of Spring Crocuses were thus described as *Wild Saffrons*; cf. Gerard (1597): 'All these Saffrons are unprofitable, and therefore they may be truely said to be *Croci sylvestres*, or Wilde Saffrons: in English, Springtime Saffrons'.

Parkinson (Paradisus, 1629) gives 27 forms of 'Spring-blooming Saffron Flowers'. Miller (1731) gives 20.

[4] Sibthorp gathered the wild *C. aureus* in Greece in the spring of 1795.

and is a common vernal species in Greece. The flowers closely resemble those of *C. vernus* in size and structure, but are of a somewhat simpler type: they are produced in February and March, being usually a week to a fortnight in advance of those of *C. vernus*; when both are planted together the first flowers of *C. aureus* are over before the blue and white forms come up.

## Description.

INFLORESCENCE: usually reduced to a single flower terminating the leafy axis of the current year. The last two leaves are membranous investing 'spathes'; the lower one is attached at the base of the flower-stalk, the upper just below the bottom of the ovary.

In strong plants a second (lateral) flower is also produced; this arises within the lower membranous spathe of the T-flower, and possesses two similar membranous spathes of which the lower therefore represents a prophyll structure.

FLOWER: hermaphrodite, actinomorphic, trimerous.

RECEPTACLE: forming the outer wall of the ovary cavity (Epigyny) for 10 mm. and produced beyond it in the form of a narrow tubular portion, the apparent 'stalk' of the flower; coloured violet in the upper portion like the perianth segments; averaging 120 mm. in length (80–150) and 4 mm. broad; 20–40 mm. of this length is normally below the surface of the soil.

(*Note*, the ovary remains underground while the rest of the flower is carried above ground by late intercalary growth in the flower-stalk and receptacle-tube. Measurements refer to plants growing in good garden soil undisturbed for at least 10 years. In the case of bulbs planted near the surface the length of the intercalated zone is very variable and is readily adjusted to varying conditions.)

PERIANTH of 6 free segments, in 2 series (3 + 3) arising from the rim of the receptacle-tube; obovate, averaging 55 mm. (40–60) long and 25 mm. (20–30) wide; coloured violet-blue or mauve with lighter or darker shades, the colour being often confined to the larger veins (striped forms), or almost entirely eliminated (white varieties).

ANDROECIUM of 3 free stamens, superposed to the outer perianth segments and inserted on the rim of the receptacle-tube;
*filament* 10 mm.;
*anthers* 15–20 mm., extrorse, yellow;
*pollen* yellow, abundant.

GYNOECIUM of 3 carpels, also superposed to the outer perianth segments.

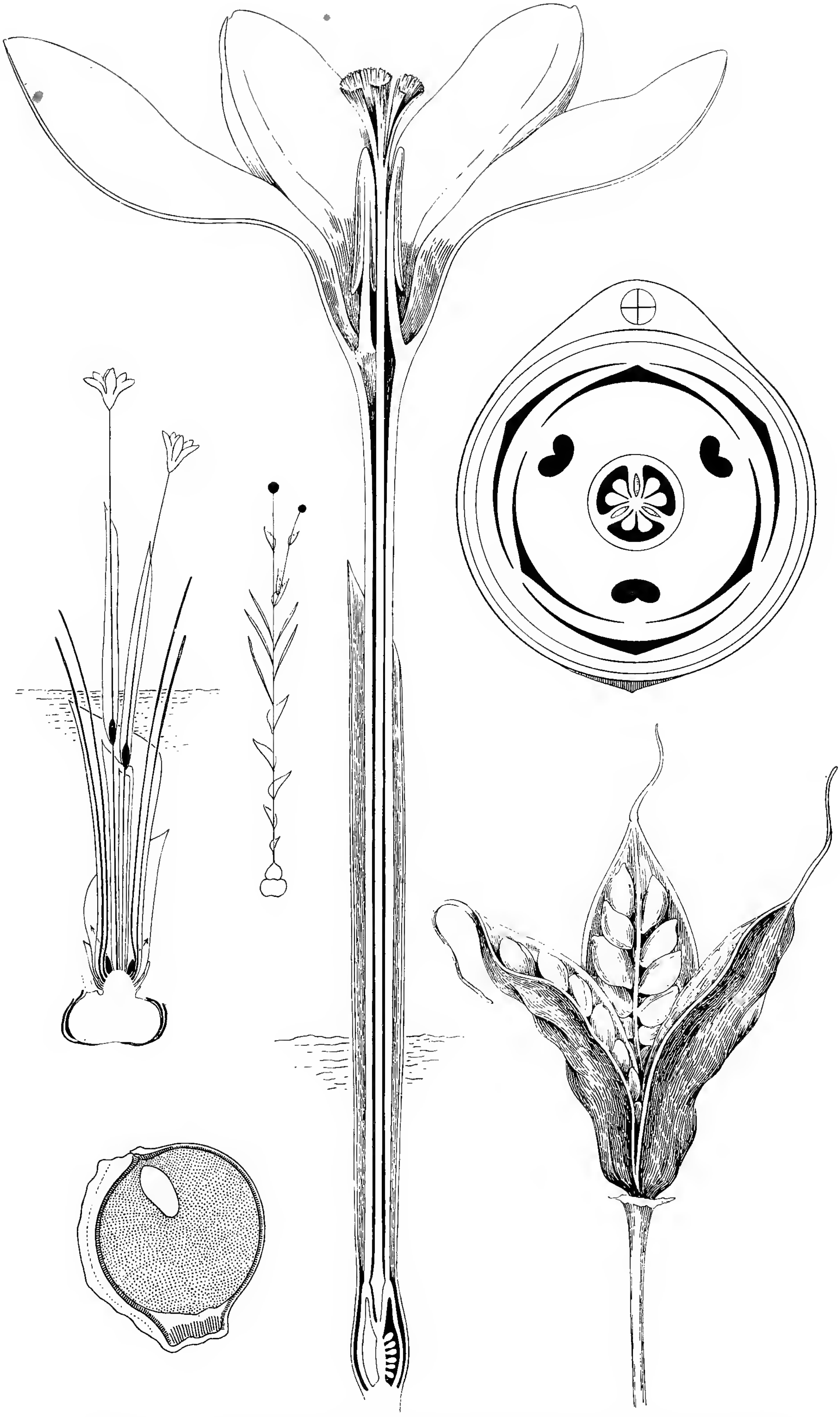
*Ovary* syncarpous at the base of the receptacle-tube ('inferior'); 10 mm. long by 4 mm. in diameter, 3-locular with 2 rows of 6–8 obliquely ascending anatropous ovules in each loculus.

*Style* slender, 140–180 mm. long, 3-branched at apex into bright orange-red stigma-lobes. These broad lobes 6–8 mm. long are each inrolled to form a funnel-shaped tube the edges of which are deeply slit into a fringe of slender segments.

NECTARY: honey is secreted by 3 depressions around the base of the style which are continued into *slits* in the septa of the ovary (septal glands) to a depth of 3 mm. The secretion rises in the narrow receptacle-tube to the free end, the approach being guarded by fringes of hairs at the level of the attachment of the stamens.

## Variations.

Garden varieties differ only (1) in colour markings, or in the distribution of the violet pigment in the cells of the perianth-segments and receptacle-tube; (2) in relative size of parts, the perianth-segments being half as large again as in the type in florist's forms which



**Crocus vernus;** Floral Diagram and Sectional Elevation in the median plane: schemes of Flowering-shoot, dehiscing Fruit and section of Seed in the plane of the raphe.

have been selected to this end. Such large coarse flowers are, however, usually conspicuously deficient in the grace of the undeveloped type.

The wild type is characterized by the production of the solitary terminal flower, and the foliage leaves are 3 and may often reduce to 2 only.

A garden variety with white stigma-branches has been described (Ellacombe, 1873).

## Floral Diagram.

I. Structure of Flowering-shoot. The greater part of the plant is subterranean. On digging up a specimen during the flowering period, it will be seen that the *corm* is an erect but thickened and almost globular axis of the previous season's growth, from which the flowering-shoots of the current year arise as lateral branches in the axils of membranous sheathing leaves. The extreme bases of these axes have already commenced to enlarge to form the perennating corms of the ensuing dry season.

The flowering-shoot bears 3–5 membranous sheathing leaves, the uppermost of which is large and its tip usually just reaches the surface of the ground. This encloses 3–5 slender foliage leaves and forms a protective investment to these members, guiding their passage upwards through the soil. A tubular membranous leaf surrounds the terminal flower-stalk, reaching as far as the ovary, constituting the lower protective *spathe* leaf; while a last leaf affords an additional protecting membranous investment to the receptacle-tube, ultimately showing above ground as a white *upper spathe.* It is thus interesting to note that the elongation of the axis between these 2 spathe leaves which constitutes the special 'flower-stalk' is the only internodal formation in the Crocus plant.

When a lateral flower is present, this arises within the membranous lower spathe of the terminal flower, and 2 similar spathe leaves are present on the lateral axis: or one only may be present. In such case the lower spathe of the terminal flower constitutes the subtending bract (*b*) of the lateral flower; while the lower spathe of this flower is a 2-keeled product of two prophylls, the upper spathe an anterior bracheole. It is clear that in such an inflorescence considerable reduction has taken place, and that the *spathe* leaves are only retained owing to their special biological protective function. Even now the basal spathe is sometimes absent in both terminal and lateral flowers; while developmental history shows that the spathes replace the perianth as protective investments for the essential organs (Figs. 8, 10). Further, such retention of

Fig. 1. *Crocus vernus*, April 1; section of apex of young vegetative shoot arising in the axil of a scale leaf of the corm showing crateriform type of axis.

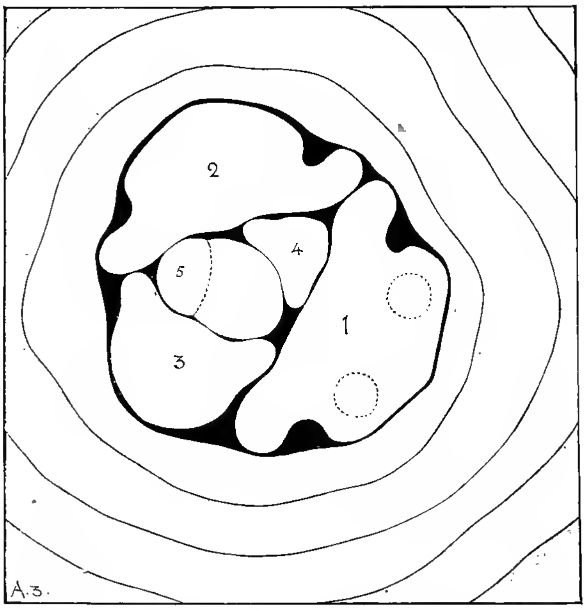


Fig. 2. *C. vernus*, July 1; transverse section of young shoot showing phyllotaxis of 5 leaf-members with the contact-relations of a (2 + 3) system.

leaves on the floral-shoot, which are themselves no longer fertile, points to an older condition in which the inflorescence would have been fuller owing to the production of buds in the axils of these members.

The reduction limit to a solitary terminal flower is very fairly attained in the ordinary type.

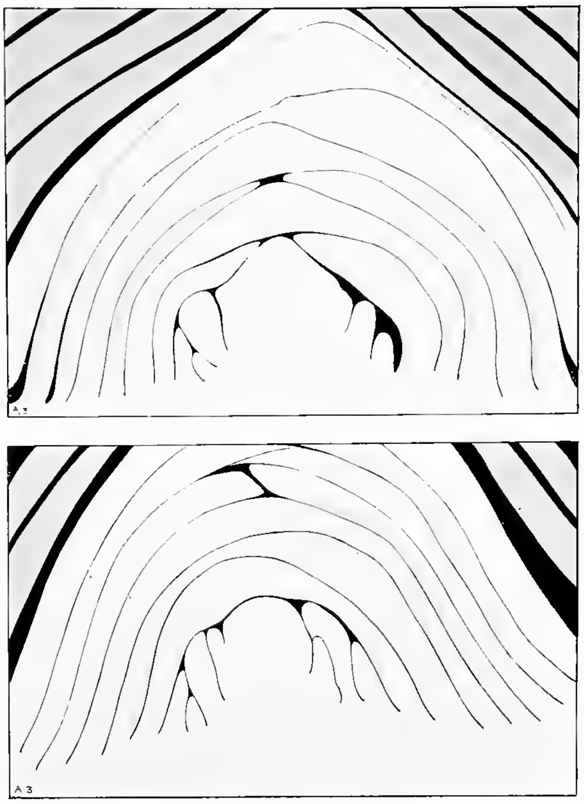


FIG. 3. *C. vernus*, June 24; commencement of flower formation.

II. PHYLLOTAXIS. The leafy shoots are asymmetrically constructed (spiral) throughout. The first formed leaves are so entirely sheathing and succulent that no special formula can be given for their arrangement (April). But when the primordia of the foliage leaves appear, it is clear that they follow a normal Fibonacci system, with a divergence angle of $137\frac{1}{2}$°, though the number is too few to give a marked pattern. The fact that 3 members suffice to make a contact-cycle suggests that the construction may be indicated by the formula (2 + 3), and the full number formed, 5 leaves, would thus represent a double cycle (Vegetative-shoot, July bud, Fig. 2). The spathe-leaves continue the spiral series, and it would appear that as in other Monocotyledonous types the change to symmetrical construction is initiated during the formation of the first perianth members. From the inner perianth onwards the construction is a normal (3 + 3) system; broken, however, by the fact that the primordia of one whorl of stamens, *the inner one*, do not appear to the eye. The existing stamens and carpels thus become superposed members, and are again approximately accurately superposed to the 3 outer perianth members.

III. ORIENTATION. The exact relation of the terminal flower to the axis from which it once sprang cannot be given, since the number of intermediate scale and foliage leaves is variable. The case of the *lateral* flower, however, admits of greater precision. Section of a young bud in which the members are all laid down, but have not undergone any growth displacements, shows that the orientation is fairly exact (transv. sect. of perennating bud, September 15, Fig. 9); the odd carpel and superposed stamen being median anterior.

FIG. 4. *C. aureus*, July 26; section of young flowers in the plane of the elevation-scheme, showing the formation of the crateriform receptacle and growth of the stamens and perianth-segments.

The floral diagram may thus be constructed for the lateral flower and will illustrate these relations. It may also be noted that the presence of a definitely symmetrical plan of orientation for a lateral flower which is hardly typical, and produced in a construction-system which is asymmetrical, must be considered as pointing to a more primitive condition in which the inflorescence of the Crocus was not only fuller, but also a highly specialized shoot-construction (cf. *Iris*). *Note* also that no trace of the 3 missing stamens appears in *Crocus*.

Transverse section of the ovary shows 3 loculi, with 2 rows of ovules in each loculus; while in the upper region of the ovary, septal-glands are cut, as narrow slits in the septa bounded by glandular cells. Their distribution is most readily followed by cutting serial transverse sections of the ovary. Similar sections of young buds (September) show that, as in allied forms, they represent chinks left between the carpels as they fold and fuse together in the production of the 'axile placenta' (Fig. 9). Prefloration is variable, as the 3 members of each perianth series are only brought into contact in the later stages of development.

FIG. 5. *C. aureus*, July 26; developing flower with well-marked crater showing the origin of the carpels (storage leaves white, exhausted scales tinted).

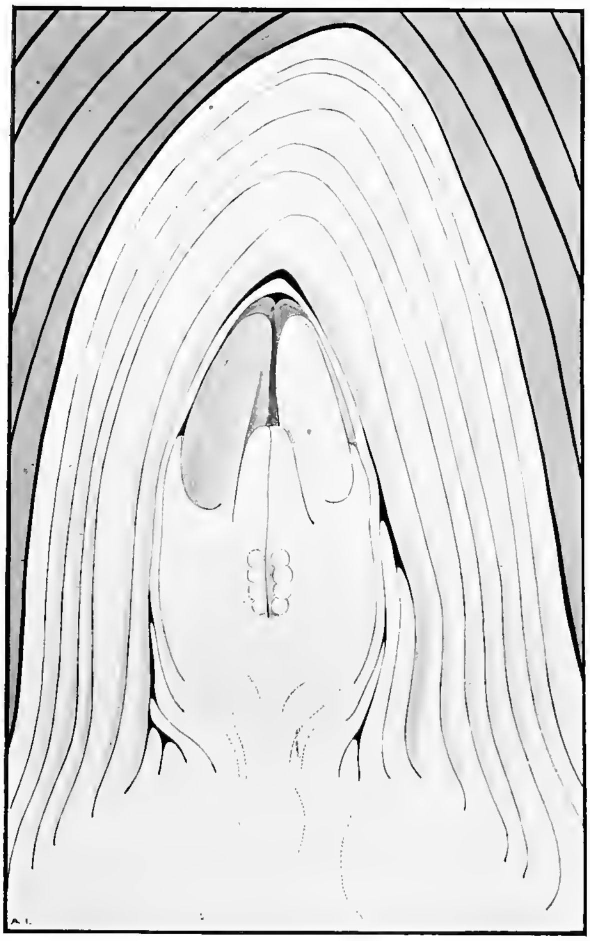


FIG. 6. *C. vernus*, August 15; developing flower showing formation of the ovary and commencement of ovules, also relatively large anthers and small perianth-segments.

## Elevation.

As in the case of the floral diagram, sectional elevation may be constructed for the median plane of the lateral flower. An outer perianth-segment is thus halved on the right, an inner one on the left. The section passes through the insertion of the anterior stamen and anterior carpel. The loculus of this carpel is cut open, showing a series of ascending ovules, while on the opposite side the section passes through the septal-gland which descends to the level of the uppermost ovules.

The most remarkable feature of the flower is the enormous extension of the receptacle-tube as a stalk to take the pollination-mechanism well above the surface of the ground, and however much such a tubular production may have been initiated as a nectary reservoir, it is clear that it is now beyond the range of any insect-proboscis, and can no longer be taken as an indication of the 'working-distance' of the flower. The origin of this special growth-zone, and the very marked epigynous construction of the flower, require to be studied in earlier stages.

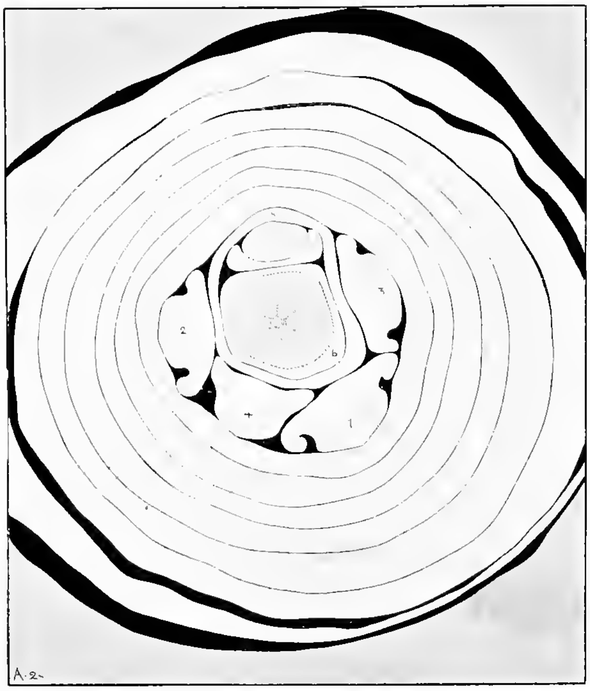


Fig. 7. *C. vernus*, July. Transverse section of a young flowering-shoot showing investing storage-leaves, foliage members, spathes, and origin of a lateral flower.

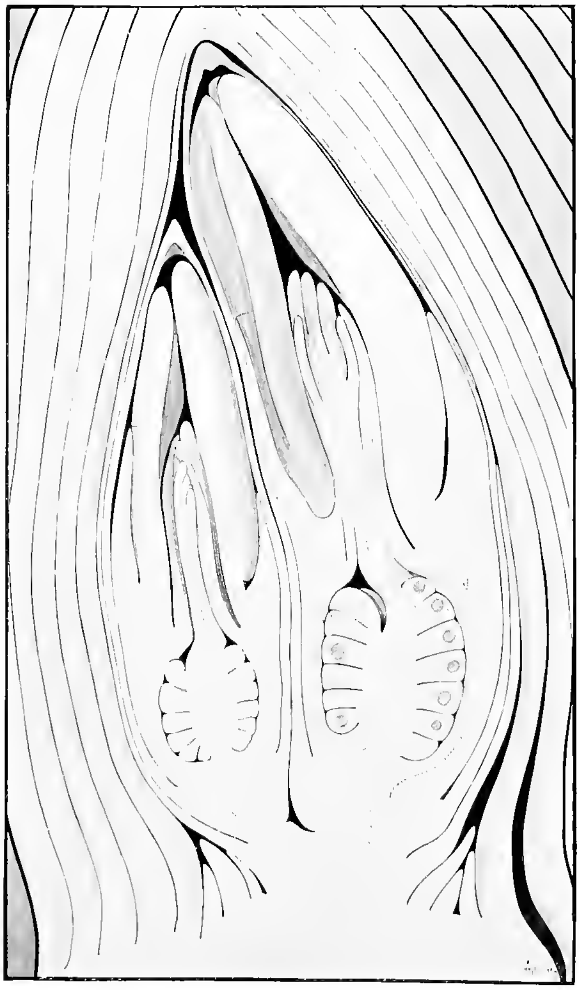


Fig. 8. *C. vernus*, September 15; perennating dry corm; section of terminal and a lateral flower enclosed in investing spathes and storage leaves, at the end of the first phase of development.

## Development.

As a phyllotaxis system the flower-shoot agrees with the construction of many allied Monocotyledonous types. The asymmetry of the shoot in its vegetative condition changes before the production of sporophylls to a special symmetrical (whorled) construction. The transition here also appears to be indicated as a change from a $(2+3)$ to a $(3+3)$ system, and the point at which the change is effected marks the commencement of the perianth cycles. Exact confirmation of the ontogeny of these segments is difficult owing to the shape of the floral axis at this stage, and also to the remarkable delayed growth of the perianth members as compared with that of the stamens.

While transverse sections of young flower-buds thus afford little further information than can be deduced from older stages, the special construction of the crateriform shoot and its special mechanism is easily studied in longitudinal sections of buds at different stages. As in the case of other spring bulbs (*Galanthus*, *Narcissus*), which present specialized perennating shoot-systems, and reduced types limited to a few leaves and flowers, with a tendency to the minimum, the developmental stages of the *Crocus* flower come very fairly true to time in successive years, and may be followed throughout the non-flowering months.

Section of the young shoots on a plant which has just finished flowering, shows the succulent scale-leaves arising around the sides of a well-marked crater, of which the stem apex occupies the base (Fig. 1). The crateriform axis is thus found in the vegetative shoot as well as in the special reproductive region (April bulb).

These scale-leaves are produced in considerable numbers, and the older ones progressively empty and pass into the condition of chaffy investing wrappers to the young corm. About half a dozen of the innermost persist as succulent sheaths to the central flower-bud, and constitute the membranous scales of the shoot in the flowering period (Figs. 2–8).

The foliage leaves are laid down in June; and about Midsummer the special floral axis arises in the centre of the bud. At first conical, it rounds off as the first perianth members appear, and with the production of the stamen primordia it is rapidly converted into a well-marked crater form (Figs. 3, 4). Bulbs taken about the middle and end of July show these and successive stages. The crater form becomes more pronounced, and the stamens rapidly increase and thus give the impression that they are the oldest since the largest members. The perianth-segments are seen to be just on the outer rim of the crater, as the stamens are just on the inner rim, and the carpels extend over the whole of the inner face of the cup, their edges meeting at the bottom, which thus represents the end of the floral axis (Fig. 5, July 26).

As the edges of the hooded carpels grow in to form the septa of the ovary in the cavity of the crater, the free lips grow upwards, uniting to form the style shaft (Fig. 6, August 15), and the flower assumes a construction practically identical with that of the elevation of the Snowdrop. The stamens take their definite form, ovules appear as projections on the carpel edges, but the perianth members remain relatively small and unimportant, the bud being closely invested by the inner spathe-leaf. Growth of all parts continues fairly uniformly, and by the end of August the floral parts assume their definite character and functions. The ovules develop their embryo-sacs, the stamens the mother-cells of the pollen grains, and the stylar branches grow out into a multitude of lobes. The bulbs are now at their optimum perennating stage, and are sold in this condition; the new supply coming in about the beginning of September (Figs. 8, 9).

Sections of flower-buds from such perennating bulbs (Figs. 8, 9, September 15) thus show clearly the *primary* state of differentiation of the Crocus flower. All the parts are developed, they remain in their original close contact, and their relative growth has remained fairly correlated throughout the whole developmental period.

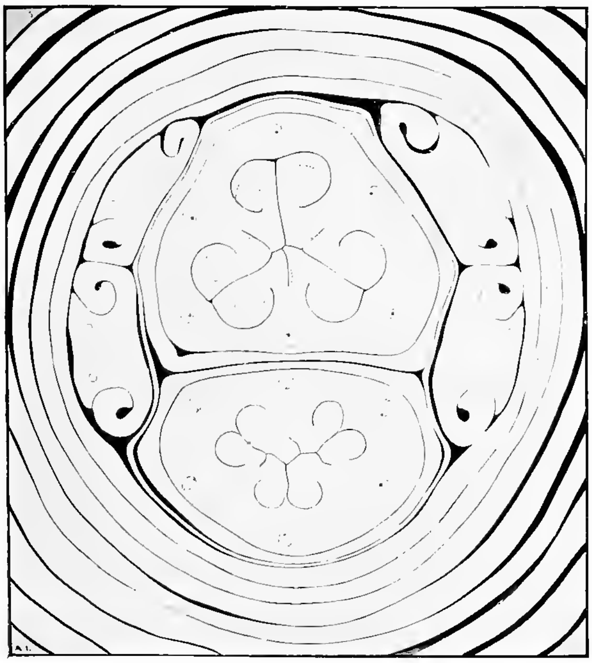


Fig. 9. *C. vernus*; September 15; transverse section of flowering shoot of a perennating (dry) corm, showing orientation of the lateral flower, and origin of septal glands in the terminal; cut at the level of the ovaries in the preceding figure.

The flowers, so far, present little more than a normal bud-construction based on a simple phyllotaxis scheme; certain members have been isolated to produce anthers, others have become carpels; but this interferes but little with the general plan. The great development of the crateriform receptacle produces the definitely epigynous character of the construction, but as already seen this is no very new departure, as the vegetative shoot is also crateriform. It may also be noted that this primary floral-structure yields a simple type of flower which has, so far, no special mechanism, but is a simple self-pollinating arrangement.

All further changes superimposed on this primary construction are thus to be included under the heading of *Special Mechanism.* These comprise secondary growths of intercalary nature, which are put in at certain points, and result in the isolation of different parts of the flower; and the co-ordination of these growths results in the production of a floral mechanism devised to seek means of cross-pollination.

## Special Mechanism.

The elaboration of the secondary zones of growth is most obviously seen in the later stages of the development of the buds, although it may quite readily be deduced from study of the elevation of the functional flower. All stages in the growth of the flower, from the mere perennating bud to the adult structure, may be found in the early part of the flowering period (March). Interesting stages are obtained by taking specimens about the first week in February when the green leaves first show above ground. The flower-buds are now slender colourless bodies about 30 mm. long, from the ovary to the tip of the spathe. Elevation of such a bud is drawn in Fig. 10. From this it will be seen that the new growths which collectively constitute the special mechanism of the Crocus flower are four in number:—

(1) An internode is intercalated between the insertion of the 2 spathe-leaves. This constitutes the *flower stalk*, and ultimately attains a length in the flowering period of about 4 inches; growing to a further length of 10–12 inches in the fruiting stage. As already indicated, it is interesting as representing the only true internode in the Crocus plant (cf. *Richardia*). It is largely responsible for shooting the flower above ground, although it remains wholly underground.

(2) The intercalated *filaments* of the anthers are comparatively short growths, they serve to carry the pollen-bearing anthers well above the throat of the flower, but their function is not preeminently important.

(3) The most remarkable growth is the intercalated extension of the top of the receptacle-tube; it is this growth which takes the 'flower' above the soil and adjusts its length above the surface to a height of 4–6 inches, which is just enough to clear grass and low vegetation (cf. *Galanthus*, *Eranthis*); while it gives the special character to the floral-structure.[1]

(4) Lastly with these two intercalated zones, another and perfectly independent growth region is initiated in the *stylar shaft*, resulting in the extension of this member to a length of 140–180 mm., with the further provision that such growth is *correlated* with the preceding phenomena, so that a certain amount of adjustment is effected; the stigmatic surfaces being carried clear of the pollen-bearing anthers, and sufficiently far from them to eliminate self-pollination under ordinary circumstances.[2]

The result of these new growths is thus not only to convert a self-pollinating type of construction into a mechanism admitting of cross-pollination, but it also provides for the elevation of the mechanism above the surface of the ground. Further, as details in the subsequent elaboration of this mechanism, there may be included:—

(1) The slow and long-continued growth-extension of the perianth-segments during the flowering period, which in virtue of special irritability admits of opening and closing movements of the flower.

(2) A slight intercalation of growth in the ovary, in the region of the septal glands, which increases the length (2 mm.), and therefore possibly the efficiency of these secreting organs.

(3) The special growth of the connective of the stamens which

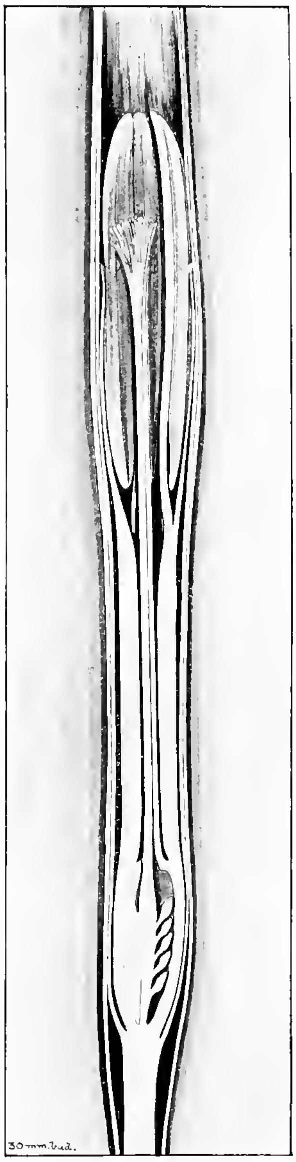


FIG. 10. *C. vernus*, February 1; development of the floral mechanism, showing the elongation of the style-shaft, filaments and Zona Perigyna.

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[1] It is now seen that the conventional expression 'Receptacle-Tube' includes two regions which might with advantage be distinguished by separate names:—

(1) The *crater* of the receptacle, which ultimately constitutes the outer wall of the ovary-cavity, and is a feature of the *primary* development of the shoot system.

(2) A wholly *secondary* zone of growth, which is a new biological departure, carrying up the perianth and androecium and resulting in the production of a long tubular region. For such a new growth the original nomenclature of A. L. de Jussieu (1789) may be utilized, and it will thus be distinguished as the *Zona Perigyna*.

[2] Of all these intercalated zones, the *rate* of growth is most active in the style-shaft, since it is evident that this, in the same time, has to grow to a length exceeding that of the *Zona Perigyna* and the stamen filament put together. Measurements of flower-buds render this even clearer and serve to emphasize the point that the correlation of these growth-zones is the essential feature of the mechanism.

results in the loculi of the anthers facing outwards (extrorse) and thus shedding their pollen away from the stigmatic segments.

(4) The distribution of a violet pigment in the perianth members, and the upper portion of the receptacle-tube. In veined forms it will be noted that the pigmented streaks follow the course of the vascular bundles of these leaf-members, and thus converge to the point of attachment, while the coloration may be more intense in the basal portions and the tube.

The colouring matter (neutral 'anthocyan'[1]) is localized entirely as a solution in the cell-sap of the epidermal cells of both sides of the leaf and the epidermis of the receptacle-tube. This can be readily seen on peeling off the epidermis from the succulent petal-bases; even in the darkest varieties the exposed inner tissues are perfectly white. In fading flowers the pigment may be also precipitated as a flocculent mass in the centre of each violet cell.

*Note* that this pigment is conspicuously deficient in the vegetative members of the plant, although a trace of it may occur in the upper spathe-leaf. It reappears in the development of the seeds, which are coloured bright rose-red by a deposit of an allied derivative in the cell-sap of the epidermis of the growing ovules.

(5) The pollen grains, anther walls, end of the style-shaft, and the stigmatic branches, contain in their cell-sap a soluble yellow pigment, which when aggregated in mass, as in the stigmatic fringes, appears as a bright orange-red coloration, and may be regarded as affording a protective screen against intense violet rays to the delicate pollen-grain, and more especially to the germinating pollen-tubes in the stigmatic branches.[2]

*Note* that the two brilliant colouring matters of the Crocus are thus to be referred primarily to factors in the metabolic processes, and have not been *initiated* in response to any insect agencies, however useful the contrasting orange and violet may now be in this particular flower. Note also that either colour may be completely eliminated without affecting the distribution of the other, just as chlorophyll has been eliminated in these members without affecting the other colours. Thus violet Crocuses vary freely through all decadent stages of veined and 'feathered' types of pigmentation to pure white, while the white-styled form (Ellacombe) is of interest as indicating the possibility of the loss of the yellow substance.

## Pollination.

The flowers are obviously rendered conspicuous by the bright violet colour of the perianth-segments, to which the large erect lemon-yellow anthers overtopped by bright orange-red tufted stigmas present a striking contrast. They offer a considerable amount of honey and large quantities of pollen to insect visitors, but possess no particular odour.

They may be described as homogamous, the anthers dehiscing and the stigmas being receptive as the buds expand. In warm weather, growth of the flower is extremely rapid,

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[1] The term 'anthocyan' is used merely as a general expression for what is probably a wide range of colour pigments which give a rose-red colour with acids, and a blue changing to green with dilute potash. The view that the red acid-derivative, when localized in epidermal cells of assimilating members, may act as a protective screen pigment, admitting only the rays utilized in the chlorophyll mechanism, brings anthocyan-derivatives into connexion with the metabolism of the assimilating leaf; and the general suggestion with regard to its occurrence in similar situations in the case of floral members would therefore be, that it remains as a relic of the assimilative mechanism which may now be utilized to subserve an attractive function (cf. *Viola*); just as chlorophyll itself, for example, is retained in the flower of the Snowdrop, and yellow derivatives in the case of the Daffodil and many other yellow flowers.

[2] This pigment (which in *C. aureus* becomes diffused throughout the whole of the exposed floral members), is probably allied to the *Crocin* of the true Saffron Crocus, which reaches a still greater degree of concentration in the stigma-branches (Commercial Saffron). On rubbing up a few moistened threads of Saffron on a piece of white filter-paper, the bright orange dye diffuses out, and the addition of a drop of conct. $H_2SO_4$ (or $HNO_3$) gives a deep *blue* coloration, changing later to brown. If the style branches of *C. vernus* be similarly rubbed on paper, $H_2SO_4$ gives a green coloration changing to brown, a transient blue flush often appearing at the first contact of the acid. The pigment in the petals of the Yellow Crocus gives identical reactions.

and buds which shoot above ground one day will expand the next, and may be effectually pollinated by bees the first day they open. In such young flowers the perianth-segments may be only 35 mm. long, or even less in special cases, although ultimately reaching a length of over 50 mm. As in the case of the Snowdrop, growth-expansion is accompanied by phenomena of dissimilar curvatures of the perianth-segments which have the peculiarity of responding to variations of temperature.[1] The same general statements previously given for *Galanthus* apply equally well to the *Crocus.* The flowers remain closed below 10° C., and a rise of 5° will open them well in half an hour. Old flowers lose the power of movement and remain half open. The lower third of the free perianth-segments is the responding region, and all six perianth members respond equally. The wild forms may open out to an almost flat star in bright warm sunshine, and in a warm room the segments will even reflex. Larger garden varieties assume a broadly open cup-form. As in the case of the Snowdrop, observations made in the evening are more satisfactory for eliminating the effect of light, but experiments with extreme temperatures are less reliable owing to the more delicate character of the tissues. The movements are therefore to be regarded as the sign of a redistribution of water in the cells of the different surfaces under the stimulus of heat, and they have evidently a definite biological utility, as in the case of the spring flowers *Eranthis* and *Galanthus*, but it is not yet clear what the precise advantage may be.

Individual flowers remain functional for an average of ten days: they are, however, very sensitive to cold dry winds, snow and rain, and in cold weather may remain stationary for over a week. Under extreme conditions they may shoot above ground but never expand, if the temperature does not rise sufficiently to open them. They usually expand on sunny mornings about an hour after the sun strikes them, and they close again by 4 or 5 o'clock; it is only in very mild weather that they open without direct sunshine. The same rise of temperature above 10° C. which acts as a stimulus to the Crocus flowers, also brings out hibernating insects, the Hive-bee emerging when the sun falls on the hives. The flowers are visited in gardens by bees. The Hive-bee is the most frequent visitor, but it is doubtful whether the flower is at all modified to suit such insects. Hive-bees take both pollen and honey, but although a few may be seen squeezed head-down in the angle of the flower, the majority take pollen only. Since the secretion rises freely in the receptacle-tube to the level of the perianth fringe of hairs, it is clear that the honey is available to insects with quite short proboscides. Hive-bees usually sweep the extrorse anthers clean one by one, and frequently adopt a characteristic action. The bee clutches at the orange stigmas, biting the turgid papillae which fringe them, and then proceeds downwards to sweep the anthers. The whole ventral surface of the insect becomes dusted with the yellow pollen, and cross-pollination will be very readily effected as the bee passes quickly from flower to flower.

Other bee-visitors are *Anthophora pilipes*, taking honey, and *Bombus terrestris* also taking honey. The method adopted by such a large bee, as it grasps the anther column and crawls down it to the nectary pores, closely recalls its behaviour in a Daffodil flower, and suggests that the type of *C. vernus* is possibly differentiating along somewhat similar lines as a 'bell' mechanism.

In normal strong flowers in which the stigma-branches are well above the level of the anthers, self-pollination is evidently eliminated. It is clear, however, that this adjustment, since it depends on the correlated growth of receptacle-tube and independent enclosed style, is a rather delicate one. Under certain conditions, especially in starved blossoms, the growth of the style is less[2] than usual, and thus the stigmatic branches diverge between the

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[1] *Note*, that although the growth of the perianth-segments themselves is capable of response to temperature, the growth of the receptacle-tube is directed to a certain extent by light, and thus plants growing in the open erect their flowers accurately, while with unilateral illumination the flower-tube bends towards the most strongly illuminated side.

[2] The converse case may also be found: the growth of the style may be relatively so great that it protrudes from the unopened bud; an anomalous condition induced by unfavourable environment similar to that occurring in *Oenothera biennis*.

anthers, and as these latter dehisce pollen inevitably falls on the adjacent stigmas (also seen in late stray blossoms, April 15). The flowers are freely fertile to their own pollen, and a large number will thus set fruit in complete absence of insect-visits.

## Construction-variations and Monstrosities.

As in the cases of the Snowdrop and Iris, flowers exhibiting perfect *tetramerous* symmetry, i. e. 8 perianth segments, 4 stamens, and 4 carpels, are not uncommon in strong cultivated forms, and mixed systems may also be found; cases of *pentamery* are also described.

In such examples the tetramerous construction (4 + 4) is to be regarded as a variation in the phyllotaxis system, which is subsequently normally affected by the secondary mechanism, and is an indication of a certain amount of degeneration in the construction-mechanism.

With regard to the alternative reduction construction to true *dimery*, it is interesting to note that such a form with only 4 perianth-segments (2 + 2) is given in the figure of Fuchs (1542) for a lateral flower of *C. sativus*, while the terminal flower is normally six-parted. There is no reason to doubt the accuracy of Fuchs' remarkable draughtsmen, and the figure being copied by Turner (1551) thus appears in the first English illustration of the plant with any claim to scientific treatment.

*Double flowers*, in which the stamens are sterilized to members resembling perianth segments, also occur in cultivated plants, but have not beens pecially selected: of greater theoretical interest are the rarer cases in which a member of the missing inner whorl of stamens is present as a functional sporophyll.

These variations and other occasional more marked anomalies are common to the Yellow Crocus (*C. aureus*), and forms in cultivation which may not be specially designated by name when the peculiarity is noticed. They are thus characteristic of the *Crocus* genus rather than of any particular species (cf. Masters; Penzig, 1894).

Such peculiarities include :—

(1) Union of the perianth-segments by their edges or midribs.

(2) Segmentation of the perianth in the form of deep lobes.

(3) Elevation of stamens on perianth-segments, and their more or less petaloid character.

(4) Sterilization of half the anther of each stamen, the sterile portion taking on petaloid characters.

(5) An interesting dimerous flower (Masters) produced 4 stamens; a (2 + 2) perianth and (2 + 2) stamens, this being the full dimerous variation of the ancestral form.

(6) Union of anthers to form an anther-tube.

(7) Development of stigmatic-papillae and branches from anthers, or even perianth-segments (cf. the beards of *Iris*).

(8) Production of vegetative leaves for spathes.

## Fruit and Seed.

The withering of the flower is marked by the fall of the aerial part of the blossom on the surface of the soil; this being the result of the loss of turgidity in the cells of the floral tube which is not otherwise strengthened. The rest of the flower may be apparently perfectly fresh, but withers in the course of the day. Ultimately the whole of the overground portion shrivels up, remaining attached to the stalk, and is only shed at a later date when the great development of the ovary bursts the spathe. The ovary rapidly enlarges, and the flower stalk elongates sufficiently to bring the young fruit to the level of the soil, so that it is just hidden but is yet within reach of the sun's rays. A length of 15 mm. is reached within 2–3 weeks of the close of the flowering period. All the ovules usually develop as seeds; they increase greatly in size at first, and the epidermis acquires a crimson coloration which is possibly protective in nature although the seeds are now somewhat sheltered. When the seeds are ripe and dry this pigment gives them an orange-brown colour which is characteristic. The fruits ripen in June, that is to say about 13–15 weeks after pollination, and about the end of May they begin to appear above the surface of the soil, being pushed up, especially after rain, by a further extension of the flower-stalk internode. This elongates from a length of 70–100 mm. in the flowering stage to an ultimate length of 200–250 mm., so that the ripe capsules are exposed at about the same height as were the flowers above the surface of the soil. The dry capsules are ovoid, somewhat 3-angled and pointed, about 20–25 mm. long by 8–10 mm. in diameter, and retain at their apex the relic of the subterranean portion of the style. Dehiscence takes place along lines corresponding to the cavities of the loculi, which are thus secondary in nature, since the wall of the ovary is the side of the receptacle-crater, and these open up the cavities of the carpels in the simplest and most direct manner. Three 'valves' thus produced separate to the base, taking with them the septa of the loculi, and widely diverge; when quite dry they become recurved and shrivelled.

The important part of the mechanism of dehiscence is a simple layer of thick-walled sclerosed transverse fibres on the inner surface of the ovary wall. The outer layers are of unmodified cellulose, and as they shrink pull on the inner wall. The fibres contract most in the direction of their length, and the valves thus separate along the previously prepared lines of cleavage. The same hygrometric mechanism necessarily closes the capsule when it is wetted. The sudden elevation of the fruit-stalk is a last expiring effort of growth, since the cells soon lose their turgidity, and under desiccation of a hot sun the fruit-stalks fall over on the soil, and the rounded seeds fall out and are thus carried sufficiently far from the parent plant. There is no special modification for distant dispersal, but the seeds are quite as light as sand-grains and would be carried considerable distances by strong winds; so when the plants are growing in sandy localities the seeds readily drift.

The ripe seeds are ovoid, rounded, or slightly triquetrous by pressure into the 3-angled space allotted them in the fruit, and average 3 mm. by 3 mm. They are reddish-brown in colour, and present a slightly winged raphe terminating in a pointed chalazal extremity. The hilum is marked by a slight scar. Section in the plane of the raphe shows a small monocotyledonous embryo embedded in abundant endosperm, the thick-walled cells of which are filled with reserves in the form of oil drops and a few starch grains. The testa is thin and composed of crushed layers; there is a well-marked chalazal plug.

Development. Fruits taken towards the end of April have reached their full size (about 20 mm. by 10), and mature just at the surface of the soil in the layers heated by the sun. The succulent ovary wall is white, and consisting of cells with watery contents only is fairly translucent. Within it are enclosed the bright crimson seeds.[1]

In these the testa is relatively highly specialized :—

The outer epidermal layer becomes papillose and deeply pigmented with crimson colour-material dissolved in the cell sap; in the ripe seed this degenerates to a brown tannin substance.

The few (6–8) layers beneath this remain undifferentiated, function in the young seed as a starch reservoir, and ultimately shrivel up. An inner layer of large cells apparently functions as an aqueous tissue; in the ripe seed these appear as a brown tannin layer. External to this a columnar series of small cells exhibits a marked thickening, confined to their inner walls, and thus acts as a protective investment. The structure of the fruit-wall and seed-coats thus present undoubted adaptations affording protection to the enclosed endosperm and embryo from extreme conditions of desiccation.

*Note* that the small embryo is protected by a thin testa and hard endosperm; provided

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[1] *Note.* At this time, and early in May, the white translucent succulent fruits are just showing at the surface of the soil, and are embedded in the top inch of the surface layers. They are thus exposed to considerable desiccation when the surface layers are heated by an intense sun, a temperature of 30° (C.) being attained when the air temperature is 17°.

with food reserves, as cellulose, starch, oil, and proteid stored in the endosperm; and beyond the lengthening of the fruit-stalk and the utilization of the agency of the wind to a certain extent, there is no special provision for distant dispersal.

## Comparison with allied Types.

**I. Crocus aureus,** Sibth. The Yellow Garden-Crocus, or Dutch Crocus, differs in a few minor points. It undoubtedly presents a slightly more primitive type of Crocus, in that: (1) The vegetative shoot is less reduced, since the foliage leaves are more numerous (6-8) and usually longer in the flowering period, though not at the first beginning of flowering; while on the other hand the flowers are really more precocious than those of *C. vernus* and commence flowering about 2 or 3 weeks earlier in the season; (2) the inflorescence is less reduced, comprising a terminal and 2 lateral flowers in a flowering shoot; (3) the floral mechanism is less specialized.

Each flowering stalk bears 2 membranous spathe-leaves attached close below the ovary, the outer of which is the tubular protective spathe, and the special internode which constitutes the flower-stalk is thus a different one from that of *C. vernus*. The colour of the perianth is uniformly golden-yellow, although a slight trace of the violet pigment is found along the 3 chief veins of the outer surface of the perianth-segments, and may be continued down the receptacle-tube, producing with the orange colour a green or brown streak.[1] The flowers are somewhat smaller in all their parts, the perianth-segments increasing after the first expansion from 25 mm. to 40 mm. They last just about the same time, are identically sensitive to changes of temperature, and when fully expanded produce a flat star-shaped blossom very conspicuous from a vertical point of view. The anthers diverge and arch outwards (owing, that is to say, to a growth-extension on the inner faces of the filaments) instead of being pressed against the style (this being a marked specific character); and the stigmatic branches are less dissected and often hardly fringed at all. They are typically always below the level of the top of the anthers, and hence self-pollination normally takes place. The septal-glands are smaller (1 mm.), and there are no hair-fringes at the entrance to the nectary tube. The flowers are chiefly visited by early bees (the Hive-bee being the most frequent visitor, and taking pollen only), but also by humble-bees and hibernated butterflies (Small Tortoise-shell), as well as by *Anthophora*. The flowers are much more susceptible than those of the Blue Crocus to damage by sparrows; these bite the top of the receptacle tube at the point where it is most succulent below the attachment of the stamens (noticed by Curtis, 1787).

Seeds are rarely produced in these cultivated yellow forms, though the reason for this, seeing that self-pollination appears inevitable, is still obscure (noticed by Sabine, 1805).

**II. Crocus sativus,** L. The Saffron Crocus, cultivated from time immemorial, from England throughout Europe and Asia to the Himalayas; was formerly grown commercially at Saffron Walden, the aromatic stigma-lobes being used medicinally as saffron and yielding an orange dye. The structure of the plant is closely similar to that of *C. vernus*, but it flowers in the Autumn (September, October), the leaves appearing as the flowers begin to fade, and

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[1] On peeling the epidermis from these perianth segments it will be observed that the soluble *violet* colour is the same as the anthocyan derivative of *C. vernus*, but is here reduced almost to a minimum, and that the other epidermal cells are a colourless aqueous tissue. The inner tissues, however, contain a soluble yellow pigment, the same as that of the style branches of *C. vernus*, and the coloration of the entire flower is now restricted to a general diffusion of this secondary yellow pigment, no contrast being afforded. As a flower conspicuous in itself against a background of soil, the orange Crocus is, however, even more effective than the violet one.

*Note*, that the coloration of the yellow Crocus is thus a secondary one, and has been superimposed on an older violet type. In allied yellow forms, the violet pigment may remain localized in the epidermal cells of the outer surface of the perianth segments, giving a chocolate-brown effect (cf. *C. susianus*, the Cloth of Gold Crocus, which flowers even earlier than the Common Yellow).

remaining green throughout the winter months. The foliage leaves are more numerous (5–15), and the flowers 1–2 on a flowering shoot. The floral mechanism agrees with that of *C. vernus*, the chief difference being noted in the style-branches. These are present as 3 strap-shaped bright scarlet segments,[1] about an inch long, which project far above the anthers and may even hang out of the flower. Seeds are not produced in the cultivated form, though the reason for this is still obscure; apparently the pollen is not matured, since hybrids may be raised by pollinating the stigmas with pollen from wild varieties. According to Maw, many wild species tend to sterility after only two or three years' cultivation.

*C. nudiflorus*, Smith. A beautiful pale-violet autumnal-flowering form, indigenous to the Alpine regions of France, the Pyrenees, and Northern Spain to an elevation of 6,000 ft., also occurs in certain localities (Nottingham, Warwick), in this country. The plants produce solitary flowers in the months of September and October, but the foliage leaves (2–4) do not begin to appear till December, and vegetate most freely in the Spring months. The vegetative shoot is of further interest owing to its production of *stolons* giving new corms at a distance of several elongated internodes. The flowers are clear violet-blue with delicate veins of a darker shade, closely resemble those of *C. vernus*, but the stigma branches, 10 mm. long, are still more freely dissected into a branch-system of very fine divisions; each primary lobe may be twice trifid, the ultimate segments being further inrolled and fringed at the tips. Seeds are produced in May. In its marked precocity of the flowering-period, and its more complex stigmas, this type of Crocus is more highly specialized than *C. vernus*; on the other hand, the retention of distinct rhizome-like shoots may represent a more primitive feature of shoot-construction.[2] The bulbs throwing out several bud-like shoots, just like a sprouting potato, are thus readily identified.

Good specimens (Warwick) are about 10 inches long (over all), the flower-stalk 2 inches, and the perianth-tube 6 inches long. There are 5–6 sheathing leaves on the flowering shoot, and the flower itself, 2 inches long, is carried about 4 inches above the soil. The general appearance and habit is therefore just like that of the smaller wild forms of *C. vernus*, only one flower again being produced in a season by one bulb. The main crop is in perfection towards the end of September. The flowers expand widely in bright sunshine, and show a temperature relation to a slight extent; blooms which had remained closed all day opening in a warm room at 10 p.m.

**III. Crocus speciosus,** Bieb. A handsome species indigenous to the Eastern Mediterranean district, Austria to the Caucasus, Persia, and Afghanistan, is cultivated in gardens and flowers from September to November.

It is one of the largest and handsomest forms of Crocus, and may be taken as an example of the highest development of the group. The main crop flowers at the end of September and first week of October; while in shady places and shrubberies flowers last as strays well into November.

The bulb, of the ordinary size, presents a point of interest in that it is found in Spring covered all over with a crop of small bulbils, which detach from the parent corm and look like germinating seeds.

The flowering axis is ensheathed by 5 leaves, the uppermost of which just clears the surface of the soil about 8 inches from the corm. The foliage leaves (3) are only represented at this time by small ½ inch green members. They appear above ground during the winter months, and may be 20 inches long in April. The length of the whole plant is over

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[1] This is readily checked from a sample of Commercial Saffron, uninjured styles with 3 long bright-red branches, each 25 mm. in length, being readily obtained by soaking the threads in warm water or dilute potash. Note the colour test (pure-blue with conct. $H_2SO_4$) for the dry stain (*Crocin*).

[2] *Note* that *C. aureus* and *C. sativus* are oriental forms, while *C. vernus* and *C. nudiflorus* are indigenous to the Western half of the Mediterranean district.

*C. aureus* and *C. vernus* are spring-flowering, but differ in every other special feature (colour, spathes, hairy throat, anthers, stigmas, &c.).

a foot, about 6 inches being below the ground, and the flower stands 6 or even 8 inches above the soil level. The main flower-axis possesses 2 membranous spathe-leaves arising just below the ovary, one inside the other; there is no basal spathe, and a second flower may arise directly from the corm. In a good specimen the perianth members are 50–65 mm. long by 25–30 broad, a beautiful blue-violet (distinctly blue as compared with *C. nudiflorus*), while the segments, especially the inner ones, are delicately 'feather-veined'. The anthers are of the erect *vernus* type, and the floral mechanism is essentially similar; the style-branches are, however, still more complex, nearly 20 mm. long, and each 3-times trifid. The flower-tube (Zona Perigyna) may be 8 inches in length, and the diameter of the expanded perianth 85 mm.

The relation of the perianth-segments to temperature is of interest, since *C. speciosus* appears to present a case intermediate between the behaviour of the ordinary Crocus and that of a great class of flowers whose members expand in direct relation to light alone.

During late September and the early part of October, the flowers are at their best at a temperature of 15°–16° C., and they open widely and rapidly when the sun shines full on them; they close again towards evening at 18°–16°. Nor do they open again in the evening on being placed in a warm room, only showing a slight tendency to half open on being placed near a fire. The main crop is thus apparently much more sensitive to light than heat.

Later in the year, however, after the first frosts, a few stray flowers left in November at a temperature of 9°–10°, and remaining semi-closed out of doors, again showed the usual *Crocus* characteristics, and opened on being brought into a warm room at 18° in a quarter of an hour; and after closing opened again in the evening on being brought near the fire, exactly as would *C. vernus.*

The flowers thus appear to be more sensitive to light at a higher temperature, more sensitive to heat at a low one.

## Theoretical considerations.

The most important points of interest in the *Crocus* may be comprised under the heads:—

(1) The extreme reduction of the whole plant as seen in both foliage and flowering shoots; in each case a short axis being present, including 3–5 green leaves and 1–2 flowers, or in the true wild type, 3 foliage leaves and 1 terminal flower.

(2) The protection of the subterranean ovary, and the development of both ovules and seeds beneath the surface of the soil.

(3) The reduction of the androecium.

(4) The great development of the crateriform receptacle, a secondary growth in which plays the essential part in the mechanism of the flower as a tubular Zona Perigyna.

All other peculiarities are correlated with these factors; and their special interest is that they clearly point to a much more generalized Monocotyledonous ancestral type which must have possessed a normal aerial shoot-system, more numerous foliage leaves, and more flowers; and that the extreme modifications observed are to be correlated with special seasonal environment, in which a dry summer season extending from the flowering period onwards is succeeded by winter cold: the vegetative period being limited to March–May. Again, the existence of autumnal-flowering forms points to the fact that the dry summer is a more important factor than the cold winter, and the evolution of the spring-flowering types appears connected with their isolation as alpine forms, in which the vegetative period corresponds with the time of the melting of the snow. On the other hand, it is difficult to establish such close correlations for the various species; for example, the flower of *C. vernus* is as complete in all its parts in the early part of September as it is in January, but cultivation in a mild climate will not induce autumnal flowering; while *C. nudiflorus* is equally alpine in its distribution, and flowers precociously in the Autumn. There are thus specific peculiarities to be taken into consideration, and the same environment may affect different species differently.

The only special feature which does not appear to be connected in some way with seasonal conditions is the reduction of the androecium, as implying a further degree of reduction-specialization in the floral mechanism. The phenomenon here observed, in which lateral centres of growth are checked at an early stage without affecting the rest of the construction, rather than a reduction of the entire mechanism from the commencement, is important since it may afford a clue to similar reduction-phenomena in other forms. This feature, together with the specialized crateriform receptacle which produces the marked epigyny of the flower in its primary condition, before the appearance of the secondary Zona Perigyna (which is correlated with the subterranean position of the ovary), constitute the two factors which may be isolated from the other more obviously biological characters affecting the vegetative part of the plant as two points of fundamental significance. They thus become utilized as distinguishing characters to delimit the group of plants known as the *Iridaceae*, which comprises one of the main lines of evolution from a still simpler generalized Liliaceous ancestor which possessed 6 functional stamens (3 + 3), continuing the alternating floral construction, and a more simple conical receptacle (cf. *Iris*, *Gladiolus*).

Under the title *Iridaceae* are now classed about 57 genera and an aggregate of about 750 species (Pax, 1889), of which the genus *Crocus* comprises about 60 forms (Pax); (67, Maw, 1882; 66, Baker, 1892); a group of plants of closely similar type whose centre of evolution appears to have been limited to the Mediterranean basin (especially Greece to Asia Minor), and a possible relic of an ancient North African flora, the extremes of which extended into temperate Asia on the east and to the Cape on the south (cf. *Romulea*, Mediterranean West and South Africa; *Galaxia* and *Syringodea* from the Cape [1]).

[1] In *Romulea* the flower is wholly aerial and the floral tube short (50 species), and in *Syringodea* the stigma is simple (3 sp.).

One species of *Romulea* extends northwards as far as the south coast of Great Britain. *Galaxia* (2 or 3 sp. of Cape plants) possesses a staminal-tube such as may occur in *Crocus* as a monstrosity.

# V

## **Richardia africana,** Kth.[1] *The White Arum Lily.*

(Calla aethiopica, L.
Zantedeschia africana, Spreng.)

A PERENNIAL herbaceous plant, with fleshy subterranean rhizome, a native of Cape Colony and St. Helena, being very common around Cape Town, where it grows in rich soil by the sides of streams, and is generally known as the 'Pig Lily'.

It was introduced into Europe by the Dutch; living plants being received by Commelin, who kept the Amsterdam Botanic Garden in 1687, and is first recorded as being cultivated in this country by Miller in 1731.

Although sufficiently hardy to withstand mild winters in water-courses and deep ponds which are not frozen, it is commonly grown indoors, in conservatories or as a window-plant, and under these conditions produces flowers from January to May, ripening its fruits in June. Out-door plants flower in August.

As seedlings take three years to flower, it is usually multiplied by means of off-shoots which are abundantly produced. A dwarf variety, much smaller in all its parts, has been in cultivation for several years (1894), under the florists' name 'Little Gem'.

### Description.

INFLORESCENCE: The long inflorescence-axis (3–4 ft.) terminates in a finger-like *spadix* completely covered by sessile flowers, and invested by a white funnel-shaped *spathe*-leaf; the latter being broadly ovate (200 mm. by 150 mm.) with a recurved tapering filamentous process about 30 mm. long. The spadix (80–100 mm. in length) bears sessile carpellary flowers below, for 20 mm., and staminate flowers in the upper portion, 60–75 mm. All bracts and prophylls are entirely wanting.

FLOWERS: Diclinous (monoecious) and much reduced; more or less trimerous; actinomorphic.

I. *Staminate flowers.* The 1,000–1,500 sessile stamens represent about 300 flowers, wholly destitute of perianth-segments and containing no trace of the gynoecium.

ANDROECIUM of 3–7 free stamens; filaments negligible; anthers large (2 mm.), yellow, extrorse, of typical structure, but dehiscing by fine terminal pores from which

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[1] Commelin, who first grew the plant at Amsterdam, called it *Arum aethiopicum.* The name was changed to *Calla aethiopica* by Linnaeus (1735), owing to its general resemblance as an aquatic aroid with a white spathe to the European *Calla palustris.* The structure of the flower is, however, different, since *Calla palustris* still produces hermaphrodite flowers; again, though African, it does not grow in Aethiopia. Hence also the florists' names for the plant—'Calla Lilly' and 'Lily of the Nile'!

A new genus was therefore originated for it by Kunth (1818), and the plant became *Richardia africana*; the generic name being intended to commemorate a French botanist, Louis Claude Marie Richard (1754–1821), who is best known for a work on Fruits and Seeds which was translated into English by John Lindley in 1819. The title *Richardia* had, however, already been utilized by Linnaeus (1737) for a genus of the *Rubiaceae*, in honour of his friend and correspondent Richard Richardson, an English botanist of the early eighteenth century (1663–1721). It thus remained either to change the Linnaean genus to *Richardsonia* (Kunth), or to make a new name for the aroid; this being done by Sprengel (1826), who called it *Zantedeschia* after a contemporary scientist, Francesco Zantedeschi, Professor of Physics at Padua.

the pollen emerges in fine silky, white, filamentous masses. Connective very broad.[1]

II. *Carpellary flowers.* Also completely destitute of perianth, but the *androecium* is represented by 3–6 club-shaped yellow staminodes, with very slender stalks, closely packed between adjacent flowers, nearly 2 mm. long.

GYNOECIUM of 3 carpels, less frequently 2 or 4. *Ovary* syncarpous, ovoid, 2 mm. by 2 mm., with axile placentation and 2 rows of 2 superposed, half-anatropous ovules in each loculus. *Style* short and stout, 1 mm.; *Stigma* capitate, a tuft of long stigmatic-papillae a little over 3 mm. from the base of the ovary.

NECTARY. The lower surface of the ovary secretes a small amount of honey as the spathe completely unfolds, and this rises between the staminodes, rendering the surface of the ovary glistening. A slight exudation also occurs on the surface of the staminodes and young anthers.

## Variations.

As the plants only exist in this country under cultivation for their decorative or commercial value, *Richardia* is of interest as an example of a type in which the efforts of the florist, which are mainly controlled by the demand for the white inflorescences for the elaboration of funeral-wreaths, tend to produce a smaller and weaker form rather than a larger structure, the normal inflorescence being already too bulky to be generally useful as a ‘cut bloom’.

Florists’ varieties thus tend to the production of a smaller and really depauperated form with a relatively large flag-like, pure-white spathe, but with impoverished spadix and fewer flowers (cf. var. ‘Little Gem’).

A variety in which the spathe is tinged slightly pink is also in cultivation.

## Floral Diagram.

The main axis of the shoot is a more or less vertical rhizome which sends up annually a flowering shoot, the growth of which is closed by a terminal inflorescence; two lateral and axillary inflorescences are also usually produced each season. A vegetative bud in the axil of a still lower leaf of the main shoot continues the growth in the succeeding year, the general development of the plant being thus sympodial. Small vegetative buds borne on older portions of the rhizome increase the lateral development of the plant. A flowering shoot consists of an abbreviated axis, the apex of which is little above the surface of the soil, and 2–5 foliage leaves arranged with Fibonacci phyllotaxis (Fig. 1). The curve-construction is not clear owing to the extreme development of the sheathing leaf-bases, and the number of leaves is also too small to give a reliable pattern, but the plan is suggestive of the relations of a $(2+3)$ construction. The normal divergence of $137\frac{1}{2}^\circ$ may be clearly seen on cutting a whole shoot across at the level of the soil (Figs. 1, 2). A plant which produces many (5) leaves usually terminates in an inflorescence of which the spathe leaf is the highest leaf-member, and thus on the opposite side of the stem to the uppermost green leaf. A very long internode is put in between these two leaves, which has the biological function of taking the inflorescence beyond the equally long-petioled foliage-leaves. It is interesting to note that this 3–5 foot internode is the only one developed in the entire plant; all other lateral members maintaining the contact relations they had when laid down.

When only few (2) foliage leaves are produced, a terminal inflorescence closes the shoot-development early in the season, and further ramification takes place, lateral axes arising in the axils of these upper leaves. Each of these commences with a large two-keeled, and often

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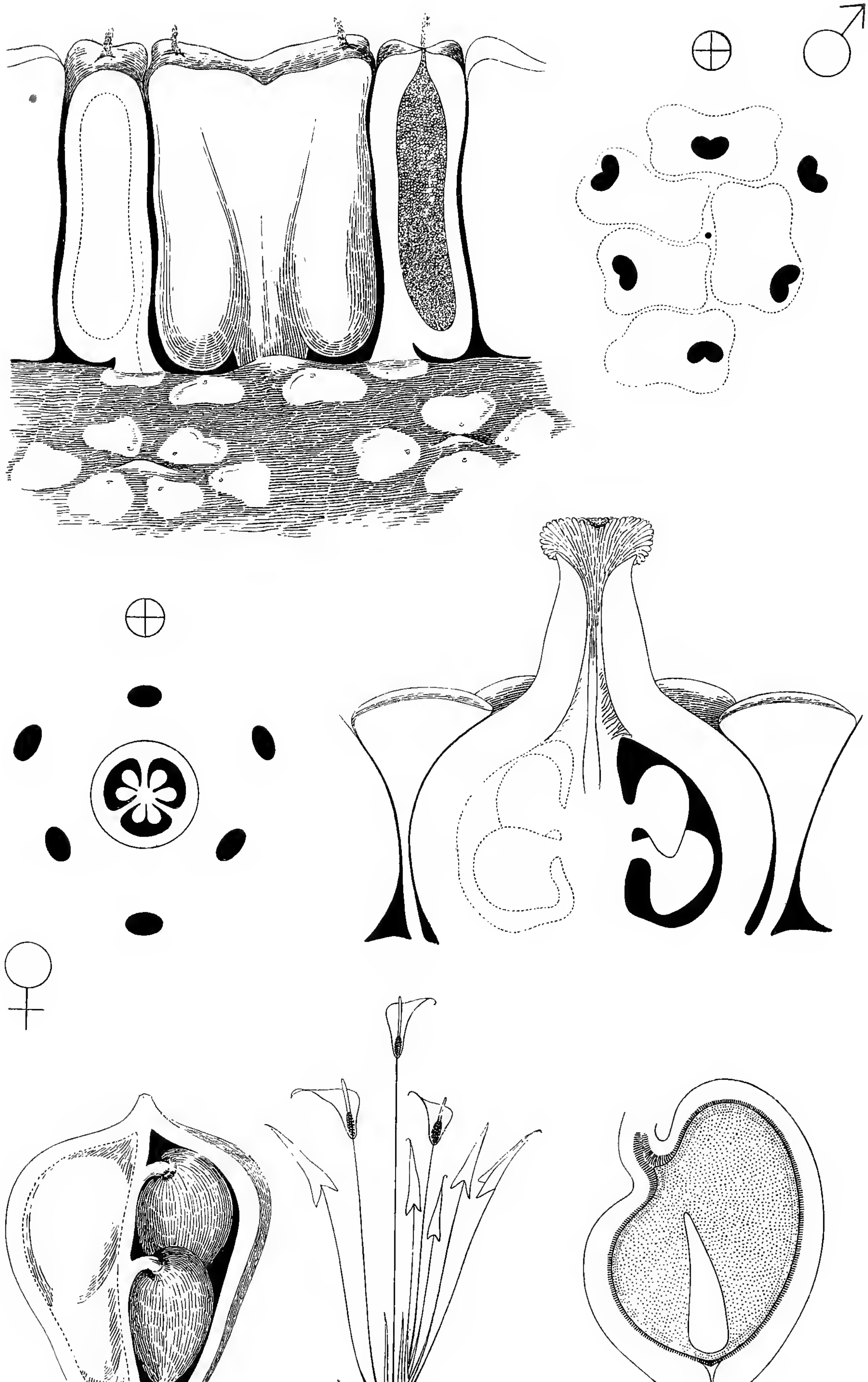
[1] To see the structure of a staminal flower, harden a spadix in spirit, and remove the brittle stamens. The scars left on the axis will be seen to be arranged in groups, most commonly of 4–5 or 6. Seven stamens sometimes occur in one flower, and this has led to the classification of *Richardia* in the *Heptandria Monogynia* of the Linnaean system.



**Richardia africana;** Floral Diagram and Sectional Elevation in the median plane of Staminate (♂) and Carpellary (♀) flowers; Scheme of Flowering-shoot, ripe Fruit cut in plane of elevation, and section of Seed in the plane of the raphe.

two-horned, prophyll structure, about a foot long, enclosed in the sheath of the leaf, and representing two leaf-members,[1] and the branch either terminates directly in an inflorescence, or may produce a cycle (2–5) of foliage-leaves first, the terminal inflorescence being thus delayed till later in the season.

A strong seasonal shoot will thus produce one terminal and two lateral inflorescences, which are so adjusted in relation to one another that the next one comes on as the older one withers. Within the spathe-leaf, the inflorescence-proper continues its development without any production of internodes, and the phyllotaxis system is wholly changed.

No trace of subtending bracts, nor again of prophylls, for the individual florets remains: the construction can therefore only be deduced from the contact relations of the adult members.

Curve-constructions may be counted for the exposed stigmas, and for the individual staminate flowers by observation of the groupings of the scars left on the spadix when the stamens are rubbed off. Irregularities in the construction are frequently observable, curves being broken or lost in both staminate and carpellary regions; so far, however, as it is possible to give any formula for the construction, it will be noted that the arrangements are anomalous, i. e. asymmetrical without being Fibonacci series, and that a marked tendency to equality in the ratios indicates an approach to a symmetrical construction. Curve systems of the form (8 + 9), (9 + 10), (10 + 11), and (11 + 12) may often be traced; but irregularities are very general, and often occur in one set of curves more than the other, and different appearances may thus be found at different levels: in many cases the construction becomes wholly irregular. Such irregular arrangements may be taken as indicating a certain amount

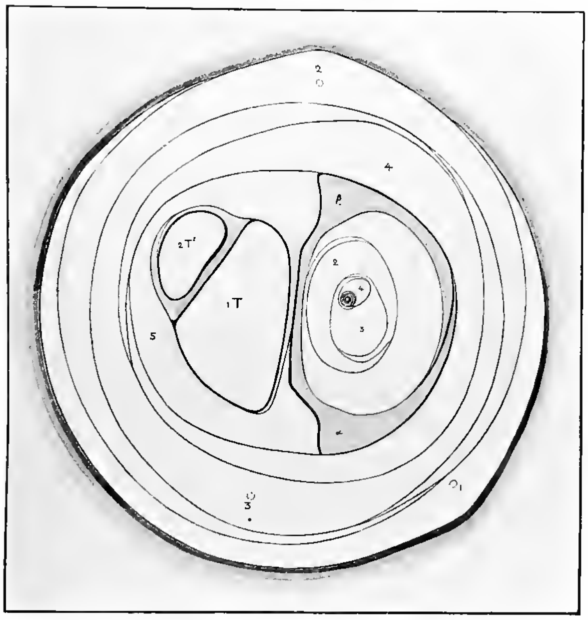


Fig. 1. *Richardia africana*, November; whole shoot cut across ½ inch from soil level; 1 T, terminal inflorescence; 2 T′, first lateral; α, β, tinted prophyll structure of lateral shoot.

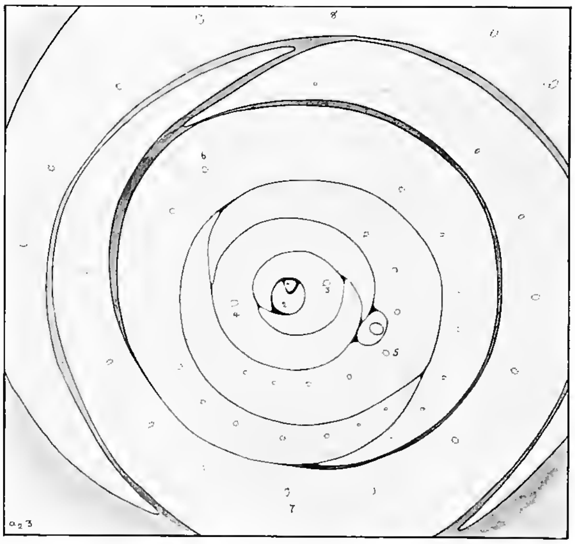


Fig. 2. *Richardia africana*, November; lateral vegetative bud cut in section showing Fibonacci phyllotaxis.

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[1] This enormous two-keeled prophyll structure is of interest since it is clearly at present functionless, being wholly enclosed within the sheathing leaf-base, and not appearing outside it, while the axillary bud is also protected within the series of sheaths throughout its entire development. The 2 'horns' of the prophyll clearly indicate the original 2 leaf-members, while the foot-long gamophyllous region can only be a growth comparable with that of the greatly elongated leaf-bases and probably correlated with the aquatic habit; the extension of the leaf-bases being the method here adopted to take the assimilating laminae well above the surface of the water, and at the same time lend support to the main shoot-system. The prophyll shares in the tendency to basal elongation which is quite useless to it, but it remains possible that the gamophylly of the 2 component members may have been essential at a period still earlier than that of the assumption of an aquatic mode of life.

of degeneration in the construction-mechanism,[1] a view which is supported by the fact that there is again no transitional period between the definite phyllotaxis-construction of the vegetative leaves and that of the floral structures, and the subtending bracts of these, which are the appendages immediately concerned, are also missing. Further, the commencement of the new system is more or less one-sided, owing to the relatively enormous size of the attachment area of the spathe-leaf.

Orientation of the Flowers. Subtending bracts and prophylls are wholly absent; although it is obvious that the former at least must have been mapped out in the shoot system, since their axillary buds as flowers occupy definite positions; that is to say, the origins of the subtending bracts never grew any faster than the shoot-tissues, and so never become visible to the eye as definite primordia. The orientation of the individual flowers is not constant, but exhibits a tendency to symmetry in the direction of the long axis of the spadix, which thus represents as closely as can be seen the median plane of symmetry of the floral diagram. Thus 6 stamens are arranged with 2 in the median plane; 5 with an odd one either posterior or anterior; 4 with 2 median and 2 transverse; while in the case of (3) carpels, an odd one is posterior or anterior, and 4 carpels are arranged as 4 stamens. The floral diagram is thus treated on conventional lines. The 6 stamens of the staminate flower represent two whorls of 3, a construction of the normal Monocotyledonous (3 + 3) type; while 4 stamens represent normal (2 + 2) dimery as a reduction-system, and 5 would constitute a mixed system, as also would the extreme case of 7. While 6 stamens as (3 + 3) undoubtedly represents the theoretical case, groups of 4 and 5 are most frequent and afford further evidence of structural degeneracy in the flower-shoots. The diagram illustrates the conventional arrangement of 6 stamens, and superimposed on it a packing arrangement of 5 anthers as found in the adult spadix.

Fig. 3. *Richardia africana*, November shoots; vegetative apex, and commencement of young inflorescence-system showing the first flower-primordia at the base of the spadix.

In the carpellary flowers the staminodes which represent the stamens of the flower are also irregularly arranged; orientation of the 3 carpels which must again represent the theoretical condition is variable, and 2 or 4 carpels are of frequent occurrence, indicating construction variations to dimery and tetramery as in allied Monocotyledonous types (cf. *Galanthus*). A transverse section of the ovary shows the 3 loculi, axile placentation, and 2 rows of anatropous ovules in each loculus. There is no special nectary-structure, no trace of gynoecium in the staminate flower, but the apex of the floral axis may be traced as a slight papilla between the anthers.

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[1] *Note* that the attribution of numerical formulae to phyllotaxis constructions is only rendered possible by the general occurrence of phenomena of *rhythm* in the growth of plant-shoots; that is to say, a continuation of a certain sequence of events results in the production of a pattern which may be treated geometrically. When the pattern is wholly irregular, this rhythm must have been wanting, and the construction becomes wholly unintelligible; nothing can be said about it beyond indicating the arrangement as seen on any given specimen. The important point to distinguish is, that when the rhythm which appears to be a normal attribute of growth phenomena is broken, it implies a degeneration-effect in the construction-mechanism *phylogenetically*, although ontogenetically and biologically the shoot may be quite as capable of performing its special work as ever it was.

## Elevation.

Section of the flowers in the theoretical median plane, which is taken as represented by the long axis of the spadix, cuts the adult staminate flower irregularly owing to the mosaic of the oblong anther-lobes. One stamen in face view and two in section are figured, and the scars of the remaining members of a group of 5 as represented in the floral diagram.

*Note* the large connective, rudimentary filament, and large anther-lobes, each with a terminal pore on the flat exposed surface. The anther has taken on a shape comparable with the 'peltate' form of packed anther found in many lower types. In the carpellary flower, a conventional case is illustrated in which the odd anterior carpel is halved on the right, showing 2 superposed hemi-anatropous ovules.

## Development.

Little further information than can be deduced from the adult form can be traced in development, so far as the essential construction is concerned. Confirmation is, however, interesting, and developmental stages are readily followed in a conservatory plant taken early in November, when the vegetative shoots are in vigorous growth and proceeding to develop the inflorescences which expand indoors in early spring.

Such a plant presents a stout erect subterranean rhizome portion, from which adventitious roots are given off in great numbers, and in the axils of old rotten and vanished leaves arise small vegetative buds which increase the lateral ramification of the plant to a 'clump' condition.

Section of the apex of such a small vegetative bud (Fig. 2) gives a good idea of the asymmetrical phyllotaxis-construction, the sheathing and hooded leaf-bases not affording any definite pattern, but suggesting by their angular divergence that the Fibonacci type of construction was utilized. Each leaf sheathes around the apex, and overlaps on itself almost as soon as it appears; and as the hooded leaf-base primordium elongates, succeeding leaves slip up inside its cavity, and all the members of the system are thus sheathed one inside the other. Axillary buds may also be noticed (Fig. 2).

Owing to the abbreviation of the axis itself, while the apparent shaft really consists of these long sheathing leaf-bases, a section taken across the main vegetative shaft about ½ inch from the uppermost roots, and the same distance therefore from the surface of the soil, gives practically the whole construction of the shoot (Fig. 1). The axis of the T inflorescence is cut across in the centre, and the sheaths of a full cycle of 5 leaf-members closely invest it; axillary buds belonging to leaves 4 and 5 produce lateral inflorescences (T′); of these, 2 T′, the second to flower, develops immediately beyond the 2-keeled prophyll, the spathe being the next leaf-member. In the axil of the next lower leaf 4, the leafy shoot is continued beyond the 2-keeled prophyll ($\alpha$–$\beta$) to a full cycle of 5 leaf-members, the uppermost of which becomes the spathe of 3 T′ inflorescence. A vegetative bud in the axil of one of the upper leaves of this branch (Fig. 3) will continue the growth of this shoot in the succeeding season; the rhizome is thus sympodial in structure.

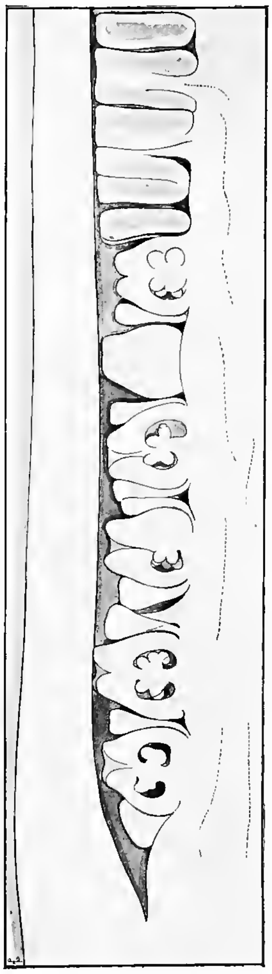

FIG. 4. *Richardia africana*; development of ♀ and ♂ florets as a layer of structures with uniform height along the spadix.

The same shoot will suffice to show all stages in the development of the flowers. The T inflorescence is already well-developed, the anthers containing pollen-grains and the ovaries including ovules on which the integument is just commencing (Fig. 4). The second inflorescence (2 T′) shows much earlier stages; the ovaries are rudimentary with placental growths, and the anther lobes are being differentiated; while the 3 T′ inflorescence is only just commencing to lay down the carpellary flowers (Fig. 3), and the naked apex of the spadix projects far ahead. These flowers arise as low circular elevations in fairly alternating rows and come into lateral contact. The apex of the vegetative bud is shown in the same figure, the shape of the apex being slightly crateriform: the internode which will constitute the inflorescence shaft is also beginning to elongate.[1]

### Special Mechanism.

In the individual flowers this is conspicuously deficient, and there are practically no secondary growths within the inflorescence region. On the other hand, it is clear that the inflorescence, as a whole, is now utilized as a floral organ, and in this connexion note that :—

(1) A remarkable secondary growth is found in the relatively enormous 'stalk' internode which elevates the spathe above the green foliage-leaves.

(2) Conspicuous coloration (white) of the spathe-leaf, implying an elimination of chlorophyll as the spathe develops and unrolls, at any rate on its upper exposed surface.

(3) The anthers present their usual yellow colour (xanthophyll derivatives), but this is intensified and with the white spathe constitutes a colour contrast.

*Note* also :—

(4) No trace of crimson pigmentation (anthocyan) in the type; but the occurrence of a small amount in the spathe of a cultivated variety is of interest as indicating the possibilities of the plant, or even a tendency to revert to a less conspicuous form.

(5) The position of the carpellary flowers at the base of the spadix inclines the inflorescence to structural protogyny, if the flowers become functional in the natural sequence of their development.

(6) The pollen and small honey supply are freely exposed to any insect visitor, and the spathe functions as a protective and attractive perianth-investment.

(7) Of all these points it is difficult to interpret (1) and (2) otherwise than in the light of special features connected with a demand for insect assistance in pollination.

### Pollination.

The inflorescence develops in August and September, and is wholly concealed and protected within the sheathing leaf-bases of the shoot; the spathe-leaf again being closely rolled round the spadix until it is shot up to its full height by the elongation of the stalk internode. It is rendered extremely conspicuous by the pure white coloration of the trumpet-like spathe-leaf, and the contrasting yellow of the aggregated stamens and staminodes of the spadix gives a central 'eye' to the structure.

The pollen supply is very abundant; the honey scanty, being secreted by the carpellary flowers, though a moist exudation may be present over the entire spadix.

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[1] A feature of special interest in the development of such an aroid type as *Richardia* is found in the abbreviation of the developmental phases of the gynoecium. Thus while in *Acorus* the development of the 3-locular syncarpous ovary is still practically normal, and three folded lobes definitely indicate three carpellary leaf-members, arising as distinct primordia and soon becoming gamophyllous, the development of a gynoecium of identical construction is hastened in *Richardia* to such an extent that the three definite primordia are not observed. The ovary arises as a protuberance which becomes hollowed to a crater form, and three slight lobes are expressed on its margin; these incurve and meet to produce the placental lobes, and the ovary retains a blunt slightly 3-lobed apex for some time (Fig. 4); a stage which is in fact the adult condition of *Acorus*, while *Richardia* adds a slight stylar elongation. With a further reduction of the placental lobes and the development of the ovules from the base of the cavity only, a *radially symmetrical unilocular* ovary will be produced, in which no trace of the three component carpels can be observed. Such a structure is, however, not necessarily monocarpellary (*Arisarum*). Further, if the ovules develop constantly in an eccentric manner, on one side of the cavity only, a condition is reached in which a monocarpellary condition may be still more nearly approximated (*Arum*): such a series of reduced ovary-formations, which are phylogenetically undoubtedly derived from three normal carpels, and probably ontogenetically also, though the separate carpel-origins cannot be determined, is of interest again since a similar reduced ovary, containing now only a single ovule laterally placed, is characteristic of the reduced flowers of Grasses, although here also there may be supporting evidence of the structural existence of three carpel-origins (cf. *Cyperus*).

Protogyny is very marked; that is to say, it occurs to a much greater extent than is warranted by mere developmental sequence of the carpellary and staminate flowers. The stigmatic papillae are receptive as soon as the spathe-leaf unrolls, while the staminate region of the spadix remains smooth and level with the staminodes. After about 6 days, in a conservatory at a temperature of 60° F., the stigmatic papillae commence to wither. Increase in bulk of the anthers is due to extension in length and breadth of the stout connective. The stamens are closely packed, and the anthers possess normal structure with 4 loculi and a fibrous 'dehiscence-layer'. The latter is, however, no longer used, the lateral pressure of the turgid connectives squeezing the pollen-grains, in the form of a fine thread 3–4 grains wide, through 2 minute pores on the exposed terminal surface of the anther. These threads of pollen continue to be expelled as the anther tissues dry up and the whole stamen shrivels. The amount of pollen produced is relatively very great, the threads of pollen-grains hanging down on the spadix in a white woolly mass which may be detached like a fleece. These, when falling into the bottom of the spathe, completely cover the carpellary region; pollen continues to be shed for 6–8 days. Self-fertilization of the inflorescence is rare; the stigmas usually completely wither before the pollen falls on them, and the mass of pollen mildews. Detailed observations on the plant in its native habitat are wanting; comparison with allied forms suggests that the flowers are visited by comparatively small flies, which crawl down the spathe and rub off pollen from a previously visited inflorescence against the stigmatic papillae which almost touch the walls of the cavity, while on emerging at a later date they crawl up the spadix, becoming dusted with the pollen-filaments. In this country the spathes are visited by small flies and green aphis, for the sake of the honey secretion, but these do little good, and, as a rule, plants left to themselves only produce occasionally 1–2 fruits on a spadix.[1]

The plants may be cross-pollinated with absolute certainty by means of a camel's-hair brush; pollen from an older inflorescence being dusted over the stigmas of one which is just expanding. In this case all the carpellary flowers set fruits and fertile seeds with surprising readiness. Self-fertilization from pollen of another inflorescence of the same plant is avoided by the succession of the lateral axes, a single shoot rarely possessing more than one functional inflorescence at a time.

Individual flowers last about 6–8 days, and owing to simultaneous dehiscence of the anthers throughout the spadix, the staminate and carpellary stages are of approximately equal duration; the whole inflorescence being functional for 14 days at 60° F., or 20 days at a lower temperature (50° F.).

### Fruit and Seed.

The close of the flowering period is indicated by the withering of the tip of the spathe. No definite detachment of floral members takes place, the staminate flowers shrivel up and turn brown as they decay; the pollinated ovaries rapidly enlarge, the carpellary region of the spadix attaining a length of 35 mm. in a month, and 70 mm. in 2 months. The fruit heads develop symmetrically, the ovaries retaining the same relative arrangement as in the flowering period, and when full-grown present a cylindrical cluster of orange-yellow berries about 90 mm. long by 50 mm. in diameter.

The upper half of the spathe-leaf withers over the spadix, while the lower greener portion retains its protective function and also assimilates. It persists over the green developing fruits for some time as a means of checking transpiration, but is ruptured as the

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[1] The inflorescences are visited for pollen by early Hive-bees, who take all they can find anywhere; and the occasional setting of a few fruits in a greenhouse is probably due to the visits of such bees. I have seen Hive-bees taking pollen from cut blooms in wreaths placed on graves (Feb. 24).

Plants growing out of doors in water may even fruit freely (West Cornwall), pollination having been probably effected by bees during the summer months.

fruits attain their full size; the dead and withered staminate region usually persists at the end of the stem.

The *fruits* take about 4 months to mature their seeds; they are ultimately somewhat ovoid, smooth, golden-yellow berries, 20 mm. long by 15 in diameter, obscurely 3–4 ridged in correspondence with the septa of the component carpels, or more or less irregular by pressure; each is terminated by a black point, the remains of the withered stigma.

The whole of the ovary wall, septa, and stout funicles of the seeds becomes succulent and constitutes a yellow pulp with sweet taste, in which the seeds are imbedded.

The fruits are thus of the simplest structure, as indehiscent 'berry' forms, and they are presumably utilized for dispersal by the agency of birds, though these again are not recorded.

All the ovules, typically 12, may develop good seeds; these, when ripe, are heart-shaped, often irregular by pressure, about 5 mm. by 4. The micropyle is at the pointed end, while near the broader end a lateral scar indicates the broken funicle, and the seed is practically orthotropous.

Section in the plane of the hilum shows a thick pulpy testa, a thin inner layer of which is protective and more marked at the chalazal end, a copious endosperm and a monocotyledonous embryo with broad radicle-end opposite the micropyle. The thin-walled cells of the endosperm contain abundant starch-grains and fat-granules: a peripheral zone of 2–3 layers is characterized by the absence of starch, these cells containing fat and proteid granules only. Ripe seeds sink in water.

*Note* that the embryo is protected by an inner (sclerosed) layer of the testa; provided with abundant reserve food, stored as starch, fat and proteid in the endosperm, and is probably dispersed by the agency of birds: the conversion of the parenchymatous tissues of the ovary wall into a sweet pulp being possibly to be regarded as a special adaptation to this end, although, as in the case of the yellow coloration, it is difficult to draw a distinction between definite adaptations and phenomena of decay.

## Monstrosities.

Anomalous structures are very general in cultivation, and may be attributed to irregularities in cultivation methods, over-manuring, &c. As the plants are large and kept under observation, variations are readily noticed.

Such irregular forms may be classed as:—

(1) *Disturbances in the growth-mechanism for producing appendages* (*Fasciation phenomena*), including 'twin-spadices', branched and 'fingered' forms, also forked spadices in which dichotomy takes place in either the carpellary or the staminate region.

(2) *Disturbances in the mechanism of spathe-production*, including 'double-spathes'; green-spathes by failure of chlorophyll elimination; additional spathes by repetition of the mechanism in the next leaf, or even more (2–3); elimination of chlorophyll in the next leaf without special change of form.

(3) *Disturbances in the internode-mechanism*, including apparent production of flowers down the stalk, or in patches more or less isolated from one another.

(4) *Accessory buds*, giving paired lateral inflorescences in the axil of a single leaf.

*Note* that none of these can be regarded as *reversions* to an older type; they are all indications of a degeneracy of parts of the constructive machinery of the organism, such as is frequently observed in plants under a high state of cultivation.

Degeneration phenomena in the individual flowers, including tetramerous and irregular forms, have been already included as floral variations which conform to broader morphological laws.

## Comparison of Allied Forms.

**I. Acorus Calamus,** L.[1] Sweet Flag. A perennial herbaceous aquatic plant with creeping rhizome and *Iris*-like foliage, indigenous to the southern portion of Great Britain and widely distributed in the Temperate regions of the Northern Hemisphere (Central and South Europe, East Asia, and North America).

The foliage leaves are arranged with (1 + 1) phyllotaxis, in lateral rows on the 'dorsiventral' rhizomes. The shoots produce terminal inflorescences, and the vegetative ramification proceeds sympodially from the axil of a lower leaf. The spadix is finger-like, about 80–90 mm. long by 12–15 mm. in diameter, and is elevated, as in *Richardia*, on a stalk 2–3 feet long: the spathe-leaf, however, is not rolled round it, but produced in the same *Iris*-like leaf form (1 to 1½ ft. long) below the spadix, so that it looks like a continuation of the stalk, and the spadix itself appears lateral.

While the phyllotaxis of the vegetative shoot is of a special symmetrical type, the arrangement of the inflorescence presents, as in *Richardia*, an abrupt change to an irregular formation in which construction-curves, as indicated by the contact-parastichies, approximate a symmetrical arrangement indicated by (15 + 15) or (14 + 15). Irregularities occur at the base and apex of the inflorescence which covers the whole of the spadix.

The flowers, 600–700 in number, arise in the axils of small subtending bracts, which are quite visible in early stages. The special point of interest is that they are all *hermaphrodite, trimerous* flowers of the strict Liliaceous type, in which (3 + 3) perianth segments are succeeded in normal (3 + 3) construction by (3 + 3) stamens and 3 carpels. In the adult condition the flowers are closely packed, and the perianth-segments are small and thin, 2 mm. long by 1 wide; they have no special function and are obviously survivals of a once much more perfect floral shoot. The stamens possess normal 4-locular anthers, dehiscing by slits, and are elevated beyond the 2 mm. ovaries by very slender 2 mm. filaments. The development and general structure of the ovary is quite normal, but slight variations are found in the interior in the adult condition.[2]

The flowers are markedly protogynous, the stigmatic surface withering and turning black before the stamens send up their anthers to the surface of the compact inflorescence. It is interesting to note that the protogyny is apparently intentional in each individual *flower*, and that all the flowers function approximately simultaneously on one spadix; so that the protogyny of the *Richardia spadix* must be equally a secondary phenomenon. Similarly such marked protogyny, which is apparently wholly a secondary modification, by eliminating self-pollination, implies a definite adaptation for pollination by external agencies. There is no particular evidence that this is left merely to the wind, and pollen-seeking flies would appear to be invited. Such insect visitors have not been observed, and as a matter of fact *Acorus* does not produce its berry-fruits in this country, nor on the continent, although it

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[1] The name established by Linnaeus (1753).

Two reed-like plants known to the Greeks as *Acorus* and *Calamus* (Dioscorides, also Pliny), occasioned considerable confusion amongst earlier herbalists who tried to identify them with plants of their indigenous flora. Thus Brunfels (1530) and Fuchs (1542) give *Acorus* as an Iris (the Yellow Flag, which Gerard also figures as *Acorus palustris*); and *Calamus aromaticus* of Tabernaemontanus (1588) is a reed (*Arundo*). The figure of Ακορος in the Vienna MSS. of Dioscorides is sufficiently vague to have been meant for an *Iris* as much as *Acorus*, being unlike either.

*Acorus* became fixed as the name of the present plant by Matthiolus (1562), Tabernaemontanus, and Lobelius; and in Bauhin's Pinax (1623) its full title is given as *Acorus verus* or *Calamus aromaticus officin.*

A good figure with flower-spikes is given by Tabernaemontanus (1588) as *Acorum cum suo iulo*, and the same block was used by Gerard (1597) as *Acorus officinis falso Calamus*.

Gerard grew the plant in his garden, but did not know that it was wild in this country, nor did old English writers; Morison gives it in 1699. It is very common in some parts (Norfolk), and is probably indigenous, as notwithstanding the use of its aromatic leaves for strewing floors, &c., it does not increase sufficiently rapidly to repay planting; while it does not produce fruit on the continent any more than in this country. On the other hand, as a valued aromatic and medicinal plant it may well be only a relic of the Roman occupation.

[2] As in *Richardia*, 'fasciation' monstrosities have been recorded in which one shaft bears 2 or even 3–4 spadices; and a similar phenomenon in the case of the individual flowers (twinning) has been observed in the upper part of the inflorescence.

does so in India and Japan. Artificial pollination experiments have so far been unsuccessful, and it is quite possible that failure to produce fruit is dependent on cultural conditions as an aquatic. It is interesting to note that the *Iris*-habit of the rhizome, phyllotaxis-construction and foliage-leaves of the vegetative shoot, must be as secondary a production as it undoubtedly is in the highly specialized *Iris*-series; and that the peculiar form of the spathe-leaf in *Acorus* cannot therefore be regarded as a primitive character of the group, although the floral-region and individual floral-construction undoubtedly present the essentially fundamental characters of the family, since they come into line with the generalized form of Monocotyledonous floral mechanism.

**II. Arum maculatum,** L.[1] The Cuckoo Pint,[2] represents one of the higher stages of development among modern Aroids, in that the inflorescence, though consisting of extremely reduced flowers, is so correlated that as a whole it imitates the mechanism of a single zygomorphic floral-structure. The spathe becomes a fly-trap, and protogyny is well marked. Special modifications proceed along the lines already marked out in *Richardia*, but to a much greater extent; thus reduction is more extensive in the individual flowers, the end of the spadix is bare and constitutes an apparently attractive organ, while the originally protective green spathe is constricted above the flower region of the spadix to produce what is primarily a damp, shaded chamber, access to which is, however, secondarily guarded by a fringe of filamentous processes derived from sterilized floret-primordia.

The Common Arum is indigenous to Great Britain and the whole of Central and South Europe; in this country it flowers in May. The general morphology of the plant is also closely similar to that of *Richardia*; the subterranean rhizome, a small tuber about the size of a walnut, is situated at a depth of 6–12 inches below the surface of the soil, and produces an annual flowering shoot of 2–5 net-veined spotted foliage-leaves in normal spiral phyllotaxis; the shoot terminates in an inflorescence invested by a bottle-shaped, pale-green spathe-leaf 8–10 inches long, a constriction in which delimits a basal chamber, 35 mm. by 20 mm., the entrance being 10–13 mm. in diameter.

The *carpellary flowers* are few (30–50), and are arranged in irregular phyllotaxis sequence, curve-constructions of such type as (6 + 6), (6 + 7), (8 + 8) being approximated, and thus again indicating an approach to symmetrical construction. No bracts, prophylls, perianth, or androecium-members are present, and the gynoecium is reduced to an ovoid, pale-yellow ovary (3 mm. by 2), the unilocular cavity of which bears 2 rows of 2–3 ovules on its posterior margin.

Above the carpellary flowers a few (8–15) aborted florets, with swollen ovary-like bases, bear filamentous processes up to 5 mm. in length.

The *staminate region* is sharply defined as a collar of purple anthers, 5–6 mm. high, and 8 mm. in diameter. Each anther is normally 4-locular and about 1 mm. each way; dehiscence takes place normally by two slits, a slight growth of the axis and general shrinkage of the anthers as they shed, allowing the pollen to be freely discharged. From the fact that the 90–120 anthers are often grouped in pairs on short stalks, it would appear that loss of all other parts is here associated with extreme reduction to dimery in the androecium.

Above the zone of anthers a few (30–40) sterile floret-primordia bear long filamentous

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[1] *Arum* the Latin name, Greek ἄρον, probably applied by the Greeks to Arums and species of *Dracunculus*; *Aron* of Brunfels, *Arum* of Fuchs, a form without spots; the spotted form figured by Lobelius (1576) as *Arum officin.*: *Arum maculatum* the name given by Tabernaemontanus (1588), Bauhin (1623); the genus *Arum* founded by Tournefort, and retained by Linnaeus (1735) as also the specific name.

[2] An excellent figure of the whole plant in flower and fruit is given by Fuchs (1542) under the name *Pfaffenpint*; the drawing given by Gerard (1597) is clearly founded on this, and the old English names are Wake Robin, Cockowpintle, Starch-wort; the last name being associated with the use of the rhizome for starching linen, before wheat-starch came into common use (Parkinson). Gerard describes the spathe as being 'like a hare's ear' in form 'with a clapper of dark murrie colour'. The figure given by Brunfels (1530) is quite good. The mediaeval name Pfaffenpint indicates a phallic origin.

processes (4–5 mm.), which just reach the side walls of the spathe and so constitute a guard-fringe 2–3 members deep. The bare end of the spadix projects as a club-shaped mass, 50–60 mm. long, coloured dull purple externally, but yellowish within, the purple pigment being restricted to the papillose epidermal cells. In some cases the purple pigment is entirely absent, and the spadix is thus left pale yellow; hence the common name 'Lords and Ladies'.

The nodding-club constitutes an effective contrast to the pale-green trumpet of the spathe, which is usually flushed with purple, especially around the edges, and again in some plants spotted like the foliage-leaves. Note that the pigment increases with exposure to light, and also becomes more marked in older tissues, e. g. the guard filaments.[1]

To what extent such coloration is intended to be attractive to insects is doubtful, or that insects are attracted by it. The inflorescence possesses a rather unpleasant odour, and flies are attracted to it as soon as it expands: large brown dung-flies (*Scatophaga*) have been observed to alight on the spadix, but not going farther down. Other stray visitors include small beetles and green aphis. The spathes are visited in great numbers by small 2 mm. flies (*Psychoda*), which may collect inside the chamber to the number of several hundreds, in extreme cases filling the entire cavity (Knuth). These flies crawl down the papillose spadix, and once inside the guard-fringe make little effort to escape; the fringe of filaments does not entirely prevent their exit, and on sharply picking the inflorescence, the insects being disturbed crawl out again; under ordinary conditions they fly about in the cavity, and the guard fringe is an effectual bar to them when on the wing: many die and a layer of dead flies may accumulate at the base of the chamber. So that any hypothetical 'symbiosis' is not at all a success from the point of view of the *Psychodae*. These small flies, attracted by the peculiar odour, probably enter the chamber for shelter and warmth, since during the night the temperature of the cavity may be 2–3° C. higher than that of the external air, and in early Spring this may be a consideration. On the other hand, on a hot sunny day the internal temperature is only that of the shade, and it may be noted that the presence of air in the intercellular spaces of the chamber-wall, which produces the peculiar velvety-white appearance, will also tend to keep the internal temperature constant; though, on the other hand, the cavity being open above would not appear to be able to get very much warmer than the surrounding air.

Such remarkable accounts have been published for the closely similar *A. italicum*,[2] that the temperature relations of *A. maculatum* require very careful investigation. The following data refer to plants growing at Oxford (B. G. O., 1905). The opening spathe possesses a singularly penetrating and disagreeable odour, which is given off by the

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[1] The exact localization of the crimson pigment to the functional stamens may, in addition to any protective significance, be connected with the production of an attractive wheel-pattern as seen from the entrance to the chamber; an effective contrast and appearance of depth being produced when this dark zone is seen through the pale fringe of filaments; similarly the abrupt termination of the pigment at the base of the spadix is a feature which is not entirely explained by suggestions of a protective surface coloration. On the other hand, there is no evidence to show that the forms with the pale spadix are any less successful as floral mechanisms than the purple ones, or that the large form *A. italicum* is any the worse for having no externally visible crimson pigmentation.

In *Arum italicum* no purple coloration is visible externally, though a purple flush is constantly present on the inner wall of the chamber. From this it might be argued that the purple coloration is more useful as a screen to darken the inner chamber than as a means of attraction.

[2] Arcangeli (1883) gives *Arum italicum* as opening the spathe at 9 o'clock in the morning and reaching perfection at 3–5 p.m.; the internal temperature rising to 40° C. between 6 and 8.30 p.m.

Kraus (1882) gives an internal temperature of 40–44·7° C., when the air temperature is 17·7° C., the rise of temperature commencing at the apex of the spadix. Note that such a temperature is considerably over blood-heat.

*A. italicum* (B. G. O., June 1–6, 1905). A similar method, in the case of a plant living under similar conditions in the open, gave a rise from 17° air temperature, to 36·7°, or nearly 20° C.; this being the highest recorded from several spathes. Poor specimens on an open bed gave a rise of only 14–15°. The rise of temperature was again confined to the spadix, which became distinctly warm to the touch, and was similarly associated with complete elimination of starchy reserves. The optimum conditions were usually found between 5 and 7 p.m.; the temperature falling again to that of the air by midnight. Spathes removed from the plant and packed with cotton-wool give results little below those obtained from the plant *in situ*.

spadix apparently as an oily excretion, since if the club-shaped end be rubbed by the fingers, the sickly scent adheres to them for some time. This naked end of the axis, being entirely destitute of appendages, is in itself an extraordinary production; and its metabolism, which is sufficiently energetic to be expressed by a rise in temperature during spathe-expansion, is even more striking.

The inflorescences expand late in the morning, 10–12 noon, or even late in the afternoon, and give off the penetrating odour which is especially noticeable when the spadix is smelt at close quarters, in the opening of the spathe-funnel. The rise in temperature is apparently confined to the spadix end, and does not affect the temperature of the inner chamber to any great extent, and this is usually only 1–2° higher than that of the external air (early May: shade temperature 17–18°). The temperature rises to a maximum towards the evening (5 p.m.), and may be several degrees above that of the air and green foliage, the spadix being appreciably warm to the touch, and readily tested by a thermometer, although more exact methods are still needed. The effect is considerably greater in strong inflorescences than in smaller ones, and a difference of as much as 13° C. has been observed.

The following experiments may be taken as a guide :—

Experiment 1, May 10, 5 p.m. A fine inflorescence, which began to expand during the morning of a close cloudy day, was tested with an ordinary chemical thermometer. Shade temperature among foliage-leaves 16° C.; a green foliage-leaf wrapped around the bulb gave no change (16° C.); the bulb was pressed right down to the base of the spathe-chamber and kept there some minutes, the temperature did not rise above 17·5° C.; the bulb was held in contact with the end of the spadix and the mercury rose to 20·5°, indicating that the emission of heat was proceeding. The spadix was then loosely packed with cotton-wool, and the thermometer placed so that the bulb was in contact with the spadix-end and retained in position by resting against adjacent twigs. Under these conditions, the plant being in its natural habitat, growing among bluebells and grass, the temperature rose slowly to 25°, and ultimately to 29° C. At 7 p.m. the temperature had fallen to 20°, and at 10 a.m. next morning the spadix was cold and flabby.

Experiment 2, May 12. Plants growing in the open, exposed to bright sun, producing small spathes, with a poor water supply. Temperatures taken as before :—

10 a.m., spathe just expanded, foliage in sunshine 20° C., chamber-cavity 20° C., spadix cold, 19°.

1 p.m., air temperature 17·5°, cavity 18°, spadix 18°.

4 p.m., cool wind; air 15°, chamber 17°, spadix in contact with bulb of thermometer 18° and rising: closely packed with cotton-wool rose to 25°, i. e. 10° C. above the temperature of the air.

5 p m., flowering shoot with leaves picked and brought into a room with temperature 17°, spadix temperature rose 26·5°.

5.30 p.m., spadix 27°.

7 p.m., 26·5°.

8 p.m., 23·5°.

9 p.m., 19°.

10 p.m., 17·5°.

11 p.m., 17°, the temperature of the air; the cavity of the chamber being 18°.

While fine inflorescences have been observed to heat their spadices to 25–29° C., small ones give 21° only; and the usual rise appears to average 10–12°.

The extremely energetic metabolism of the spadix-tissues is thus localized in the naked club-shaped end, and has nothing to do with the individual florets: the action may thus be compared to the heating effect of a hot poker: the work is done apparently at the expense of the reserve starch material; thus section of the spadix of an inflorescence about to unroll shows all the tissues gorged with starch-grains, even the epidermal papillae being full, and on treatment with iodine solution a thin section goes dead-black. Section of a spadix taken at 10 a.m. next morning, however, gives no starch reaction, only a trace of granules remaining in the epidermis and near the central bundles.

Thus the spadix recorded in Experiment 2, was put into spirit at 11 p.m., and when examined showed that the club-region was almost entirely emptied of starch, while a certain amount still remained in the stalk-portion. In a contemporary spadix, kept fresh till next morning, this amount of starch had also disappeared, and though considerable storage still remained in the vicinity of the florets (stamens and filament processes) the whole spadix had been completely emptied. Examination of the spadix during the period of maximum heat also shows a definite deterioration in the amount of starch present. The whole of the starch reserves in the yellow tissue of the swollen spadix-head thus appear to vanish in the course of a few hours.

It will also be noted that the clean bright colour of the spadix, with a soft bloom on it, also coincides with the period of active metabolism, the structure becoming more or less flaccid and mottled when its function is over. Although, again, the increased metabolism may have been originally correlated with the opening movements, it is difficult to associate it with any other interpretation than that of its attractive significance, since it otherwise implies a considerable waste of reserve starch.

The inflorescence is only functional for a short period: the main crop of spathes being over within a week when the plants are growing in masses under uniform conditions; this being normally the second week in May. The duration of a single spathe varies according to exposure in the open, or shelter in moist, shady situations. On an open bed, exposed to sun and wind, the spathes open one day, the anthers shed on the second day, while on the third the spathe commences to wither. In cool, shady situations, even during dry, sunny weather, the spathe may remain green and fresh for 5–6 days, and dehiscence of the anthers may not really take place till the third day. Exposure to cold, drying winds completely ruins the inflorescences, and these may never even unroll.

The plant would thus appear to require a warm and moist environment for favourable development, and the spathe is intended to slowly expand in the morning under the stimulus of a warm sun, become fully expanded, with a purple clapper extremely conspicuous against a whitish-green background, throughout the day, with an increasing temperature in the spadix reaching its maximum before dusk, and so attracting small flies as a means of shelter. As the pollen begins to be shed next morning, they are only required for one night; the temperature-mechanism hence only works once, and is correlated with the increasing bulk of the spadix, and the exhalation of a pungent odour which has also practically disappeared on the second day. Many flies are killed, possibly suffocated owing to the abstraction of oxygen from the atmosphere of the chamber and accumulation of $CO_2$ on the floor of the cavity.

The yellow pollen is shed in abundance, and falls on the floor of the lower chamber and on any imprisoned insects: with the general desiccation of the anthers the sterile guard-filaments also lose water and droop, so that those flies which have not died are free to make their way out and pass to other expanding spathes with receptive stigmas.

The plants are thus freely pollinated, and set fruits in the form of large clusters (80–100 mm. by 30) of bright-scarlet berries which ripen in July and August, when the foliage has died down. These are extremely conspicuous, and are devoured by many species of birds, particularly pheasants,[1] and the seeds may be dispersed in this way. Those which are not thus eaten decay on the surface of the soil when the succulent axis becomes killed by early frosts (October).

The ripe fruits, as scarlet ovoid berries (12 mm. by 10), more or less irregular by mutual growth-pressures, possess an undifferentiated wall of red pulpy tissue, the intense coloration being, as usual, localized in the smooth epidermis. The seeds are closely similar to those of *Richardia*, 1–2 being produced in a fruit; they are heart-shaped (6 mm. by 5), with a brown testa of dead parenchymatous layers, a brown protective non-lignified layer, and a large mass of endosperm, the cells of which are gorged with small starch-grains; a well-marked aleurone layer of cubical cells surrounds the starchy mass.

*Arum* as a type presents an advance on *Richardia* in that the spathe is not merely a protective wrapper with a secondary attractive function, but it constitutes a chamber in which insects may be retained. This is correlated with a decrease in the number of flowers,

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[1] Also Chaffinch (Scott).

and more particularly in the pollen-producing members, and the exhibition of a long leafless end to the shoot-axis, a most anomalous condition when compared with other plant-phyla. The decrease in the number of the flowers may be associated with an improved chance of pollination by insect-agency, and may thus be regarded as a reduction-specialization; but observation of developmental stages (Fig. 5) shows that it is the limitation of the flower area on the lower portion of the spadix which induces the constriction of the spathe, and not vice versa; so that when the flowers project on the spadix, and the spathe grows to fill all the available space in the bud, it becomes pressed over them and follows the irregular outline of the flower-producing surface. On subsequent growth-expansion it retains this dilated form, whereas where the flowers are produced throughout at a uniform level (*Richardia*, Fig. 4) no such constriction is initiated.

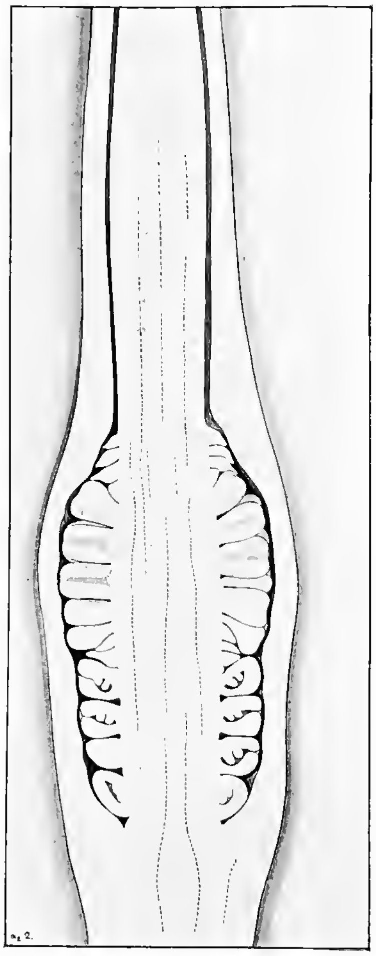

Fig. 5. *Arum maculatum*, November shoot; young inflorescence showing ♂ and ♀ flowers, rudimentary structures, and spathe following the contour of the primordia borne in the spadix.

Since the inflorescence as a whole now approximates a protogynous floral-mechanism, the general rules of reduction-specialization should also apply to subsequent developments of such a line of evolution; i. e. the stamens may become still fewer, and the ovaries be similarly reduced until they approach the limit which obtains in the majority of modern flower-shoots; such reduction being also associated with further progression in the elaboration of a protected cavity, which not only shelters the essential organs from injurious environment, but may be also utilized as a shelter for insect visitors.

A type which grows readily in English gardens, under identical conditions of cultivation, may be selected as one which presents a much nearer approximation to such a hypothetical structure.

**III. Arisarum proboscideum**[1], Savi. A plant identical in habit with the common Arum, but with smaller though closely similar foliage, indigenous to the Apennines and mountains of Albania. In this country it grows in gardens equally well with *A. maculatum* in shady borders, and also flowers during May, though it does not appear to produce fruit. The *inflorescence*, completely hidden beneath the foliage, is still more highly specialized, though along very similar lines. The *spathe* is much smaller, constituting a nearly closed chamber, 20 mm. long by 14 wide, hood-like, and opening by a small orifice (10 mm. by 7) on one side, while the tip of the spathe-leaf is prolonged into a long slender 'tail', 6–8 inches long; this tail projects upwards among the foliage-leaves. The spathe-chamber is further much more bilateral, and the purple coloration is strongly marked, the interior of the hood being deep purple with small lighter spots, the colour also projecting down into the white wall of the lower chamber as 8 streaks which follow the principal veins.

The pale yellow *spadix*, which is wholly enclosed, and is the only structure seen on looking in at the orifice of the spathe, is club-shaped, and the upper portion is relatively greatly developed as a whitish tongue-shaped mass, 20 mm. long by 10 wide, with a peculiar

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[1] *Arisarum*, a genus of Tournefort (1700). The plant was included as an *Arum* by Linnaeus. The present name dates from 1816, being established by Gaetano Savi of Pisa. Arisarum, the Latin form (Pliny) of 'Αρίσαρον of Dioscorides; the typical form *A. vulgare*, Targ. being common throughout the Mediterranean district, though lacking the extreme specialization of *A. proboscideum*.

irregular cancellated surface and soft spongy texture, containing only a moderate supply of starch grains. The mimicry of the mechanism of a zygomorphic flower is much more nearly approximated than in *Arum*; the *carpellary flowers* are reduced to 1 ovary only (less frequently 2–3) at the extreme base of the spadix, on the side away from the insertion of the spathe, and thus immediately beneath the orifice. The ovary-cavity is unilocular, and contains many erect orthotropous ovules (50–60).

The *staminate flowers* reduce to about 15, each being represented merely by one solitary stamen (less commonly 2), 2 mm. high, possessing a 2-locular anther, the loculi of which are bent round on the filament in such a manner that dehiscence has the appearance of taking place by a circular slit.

There are no sterilized florets as a guard-fringe, although the structural constriction in the spathe is still noticeable, but an advance on the *Arum* type is seen in the limitation of the orifice and the upper entrance chamber. The spadix-head again acts as a platform for entering insects[1]; the inflorescence is similarly protogynous, and the chamber presents the characters of a fly-trap in that the way out is not directly obvious to a crawling or flying insect. The long tail apparently acts as a guide to the chamber from the upper air, and it is difficult to credit it with any other function. No increase of temperature is observed in the expanding spathe, the temperature of the inner chamber being on a warm bed only ·5° higher than that of the external air (17·5°, May): the small supply of starch in the spadix disappears in older specimens when the pollen has been shed.

It is interesting to note, that the extreme degeneration of the originally spicate inflorescence (*Acorus*), the ultimate reduction of the carpellary-flower region of *Richardia* to a single ovary, and that of staminate flowers of the full type (*Acorus*) to solitary stamens, is here associated with a progressive specialization of a secondary pollination-mechanism, and has reached such an extreme phase, that if all intermediate forms had been eliminated, it would have been extremely difficult to trace what the line of descent might have been, or to establish any connexion whatever with the full type of the trimerous hermaphrodite Monocotyledonous flower-construction.

## Theoretical Considerations.

The European *Arum maculatum*, the one first figured by Brunfels (1530), and Fuchs (1542), became a centre around which have been segregated a number of unmistakable *Aroid forms* which are like nothing else in the vegetable kingdom, and which now include a great series of 105 genera and over 800 species, the vast majority of which are tropical forms (over 92 $^{\circ}/_{\circ}$); while comparatively few extend to Northern Europe, *A. maculatum* being the only really common indigenous species. The range of *Aroid form* is marvellous, and the most highly specialized ones are far in advance of even such a type as *Arisarum*; yet the most generalized form (*Acorus*), and the highest reduction limit (*Pistia*), are about equally widely distributed as aquatics; while the only two types which exhibit their superiority by great capacity for variation, and so become emphasized by systematists as comprising a large number of forms entitled to 'specific rank', are *Anthurium* (200) and *Philodendron* (100)—more generalized forms which retain inflorescence-regions of a comparatively simple type; the former being in the *Acorus*-stage, but reduced to *dimery*; the latter approximating the condition of *Richardia*. On the other hand, the ancient position of the group is shown by the survival of a great number of curious monotypes; 40 genera being monotypic, and nearly 30 more comprising only 2 or 3 species; and even in these cases, as in that of the species of *Arisarum*, the differences might be well considered to be of 'generic' importance.

The group of Aroids stands almost alone in the Monocotyledonous series, though

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[1] Arcangeli (1893), from observation of the plant in its native habitat, suggests that the peculiar spongy texture of the end of the spadix is a mimicry of fungoid tissue, and that the plants are adapted for visitation by fungus-eating insects of the fly series (*Nemocera-Fungicoli*); but this does not appear to have been further established.

within its own limits it is clear that the vegetative habit presents normal methods of shoot-construction, while the floral-constructions are clearly based on a trimerous hermaphrodite type identical with that of the great Liliaceous phylum. No Aroid, however, presents a more generalized inflorescence-system than that of the close spike of *Acorus*; there is no trace of a branched panicled floral-region, so that the phylum at its commencement already labours under very considerable restrictions. Otherwise the structure of the sporophylls is quite normal in these earlier types (*Acorus*), and the syncarpy of the ovary proceeds along normal lines, while the loculi are typically many-seeded.

The biological utilization of a protective spathe-leaf, which as a wrapper to the inflorescence becomes so intimately connected with the secondary mechanism of cross-pollination, is comparable with a similar phenomenon in the group of the *Palms*; and these two series are very generally grouped together as a wider phylum, the Spadiciflorae (Eichler and Engler).

These two series are by no means alike, but rather so different that it becomes of interest to consider the points of dissimilarity rather than those of agreement, in that they are probably to be regarded as the modern divergent branches of a common ancestral stock which presented the generalized characters of both groups.

In fact just those primitive structural features which are lacking in one phylum are found to be retained by the other; so that while it is clear that neither can be descended from the other, both may be equally derived from a generalized Monocotyledonous form, which might again be equally the ancestral stock of the great Liliaceous group of families.

Thus the inflorescence, which among Aroids is from the first a simple spike, showing by the remarkable break in the phyllotaxis construction, that a long series of phylogenetic stages may have been omitted, presents among Palms a typically branched condition which in some forms reaches an immense bulk [cf. *Corypha* (Palm) and *Fourcroya* (Amaryllidaceae)]; all transitions to the reduced spadix-condition may be traced in the group. On the other hand, the Palms exhibit a general tendency to retain the simple Liliaceous flower-type, largely unmodified except by secondary dicliny, since these forms are essentially anemophilous, and the Palms represent a great tree-phylum, of which the smaller forms are reduced vegetative types. The Aroids, on the contrary, are essentially herbaceous, and typically comprise the inferior vegetation of tropical forest-regions, many being shade-plants, epiphytes, and dwellers in swamps and streams, while the trees occupy the best ground. The decadence of the flower is immediate, and the pollination-mechanism which is evolved in correlation with low-grade creeping, and low-flying, insects becomes established, not in the individual flower, but in the inflorescence as a whole. One generalized feature the Aroids retain which is not found in any Palm, that of an ovary with many ovules in each loculus. No Palm has more than 1-seeded loculi, and the tendency of the group is to reduce to 1 seed to each flower; although again some Palms may present a still earlier condition in the gynoecium by retaining apocarpy. It cannot thus be claimed that the Palm series is wholly more primitive than that of the Aroids, nor are they again more primitive than generalized forms of recent Liliaceae; it appears best to regard the Aroid and Palm series as two great *Complementary Phyla*, derived from a very ancient and much more generalized Monocotyledonous prototype, which comes very near the generalized arboreal forms of the Lily alliance; while the curious types *Pandanus*, *Typha*, *Sparganium*, which combine characters now divided between these two main series, suggest the stray survivors of the intermediate lines of evolution, which have become gradually eliminated with the progression of these two great main branches.

# VI

## Daphne Mezereum[1], L. *The Mezereon*[2].

A PERENNIAL woody shrub, growing to the height of 4–5 feet, possibly indigenous to English woods, and extending over the forest-regions of the whole of Europe, and from the Caucasus to the Altai Mountains in West Asia. It was not known in the wild state to early English botanists (Ray), and was first cultivated in this country by Gerard, in 1597, who states that he received the plants from Elbing in Poland.

It is now commonly grown as an ornamental shrub for the sake of the abundant fragrant purple flowers produced from January to April; the optimum flowering period being early in March before the leaves unfold. A variety, *autumnale*, commences to flower early in November before the old leaves fall, and remains more or less in bloom until the new leaves unfold in April. Another variety has white flowers succeeded by yellow berries. The fruits of the type are scarlet berries, and are ripened in June; they may remain on the bushes till August. All parts of the plant are poisonous; twelve berries being stated to be sufficient to kill a small child. Owing to these active properties it has at all times been regarded as a valuable medicinal plant, and its nomenclature and literature have been discussed at length by older writers.

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[1] It is remarkable that the name Δάφνη, applied by the Greeks to the Bay-tree (*Laurus nobilis*), should now denote a relatively insignificant shrub. An excellent drawing of the plant in bloom was given by Fuchs (1542) under the title *Daphnoides* or *Laureola*, with the impression that the plant was the *Daphnoides* of Dioscorides. The plant described by Dioscorides had white flowers and black berries, and some confusion would appear to have existed in Fuchs' time, as he mentions that the flowers are generally reddish, but sometimes white, and the berries *black*.

Hence Turner, as a student of Fuchs, in his 'Names of Herbes' (1548), gives *Daphnoides* (Lauriel, Lorel or Laureola) for the wild English green-flowered species (*Daphne Laureola*) which has black berries.

Lonicerus (Frankfort, 1569) calls the plant *Chamelea* or *Mezereon*, the former name being identified with the Χαμελαια of Dioscorides, while he states that the 'Barbary Arabs and Physicians' call it *Mezereon*. Lobelius (Antwerp, 1576) describes two plants, with good figures both of flowers and fruit: (1) *Daphnoides* or *Laureola*, the green-flowered form; (2) a red-flowered *Mezereum Germanicum* or *Chamaedaphne* of Dioscorides, also *Chamelea Germanica*, and Mezereon as one of its popular names. Hence Gerard, who was largely indebted to Lobelius, follows (1597) and calls the Mezereon *Chamelea Germanica*, the *Dutch* Mezereon or German Olive Spurge; while the green-flowered form is the *Daphnoides* or Latin *Laureola*, the English Spurge Laurel, Lauriell or Lowry.

This terminology is usually followed by the herbalists: thus Parkinson (1640) still retains the name *Chamelea Germanica* or Mezereon, the Dwarf Bay.

It is interesting to note that of the three plants described by Dioscorides with which *Daphne Mezereum* has been identified, comparison of the figures given in the Vienna MSS. of Dioscorides (fifth century) shows that: Χαμαιδαφνη is obviously not a Daphne but *Ruscus hypoglossum*; Χαμαιλαια is a shrub that cannot be identified, as it has no flowers or fruit; and Δαφνοειδες might very possibly be meant for *D. Laureola*, but is obviously not the Mezereon.

Among the later herbalists (Parkinson, 1640) a curious idea arose that *D. Mezereum* and *D. Laureola* were male and female forms, although which plant was which sex was in dispute; thus the full names as given by Tournefort (Paris, 1700) are:—*Thymelaea Lauri folio, sempervirens seu Laureola Mas*, and *Thymelaea Lauri folio deciduo, sive Laureola foemina*; the latter being the Mezereon.

The name *Daphne* was given by Linnaeus (1735), and the old generic names *Mezereon* and *Laureola* are thus maintained as specific designations and retain the capital letter.

[2] The name *Mezereon*, introduced into Europe through the agency of Arabian physicians, is probably of Persian origin, a medicinal Persian shrub being called ماذريون *māzeriyūn*. In country dialects the word is corrupted into *Mesilion*.

## Description.

INFLORESCENCE: much reduced lateral racemes forming clusters of (1–3) flowers, surrounded by an investment of partially-coloured bracts and bud-scales, are borne in the axils of the foliage-leaves of the previous year. (More than one such bud may be present; the accessory buds being formed (1–2) in descending series below the primary bud.)

FLOWER: hermaphrodite, actinomorphic, tetramerous.

RECEPTACLE: a cylindrical tube, coloured purple like the sepals, averaging 8 mm. in length and 2 mm. in width. (The tubular portion of the flower is to be regarded as a receptacle of a highly specialized crater-form, though the evidence for such a view may not be apparent at first sight.)

PERIANTH: undifferentiated, usually regarded as representing a *Calyx* of 4 free sepals, inserted (2 + 2) at the rim of the receptacle-tube. The outer pair are larger, and completely enclose the others in the bud; ovate, acute, purple-red; outer pair 5–6 mm. by 4–5 mm., inner pair 5 mm. by 3–4 mm.

ANDROECIUM of 8 free stamens, arranged (4 + 4) in two whorls, and these are attached at two levels, about 5 and 7 mm. respectively from the base of the tube on the inner slope of the receptacle-crater.

The uppermost whorl is antisepalous, and the inner and lower whorl alternates with the first.

*Filaments* very short; *anthers* yellow, introrse, 1 mm. long; *pollen* yellow.

GYNOECIUM: reduced to a solitary carpel. *Ovary* ovoid, green, 2 mm. long, unilocular with a single anatropous ovule completely filling the cavity, suspended from one side, with its micropyle directed upwards and pressed against a descending process of the ovary wall.

*Style* short; *Stigma* capitate with long papillae, 3 mm. from the base of the receptacle-tube, and obscurely 8-lobed by pressure between the anthers in the young bud.

NECTARY: around the base of the ovary which is practically stalked, a distinct receptacular, ring-shaped *disc*.

## Floral Diagram.

INFLORESCENCE. The foliage-leaves follow a normal spiral phyllotaxis of the asymmetrical Fibonacci type. Section of a vegetative bud (Fig. 1) shows that the curve-construction is most readily expressed by the formula (3 + 5), since 5 leaves make a contact-cycle, and the most conspicuous construction-curves are those drawn through members which when numbered up differ by 3. On the adult shoot with equally-spaced nodes this would become a $\frac{3}{8}$ phyllotaxis, according to the Schimper-Braun notation, and the line drawn through a series of members differing by 8 would be a vertical one. The flowering-shoots arise laterally in the axils of the foliage-leaves of the previous season. Hence flowers will only be found on shoots one year old. Each bud consists of 2 small, brown, approximately lateral prophylls succeeded by 2–3 brown scales grading into coloured scales. There are in all typically 5 of these bracteoles above the prophylls, comprising a cycle of an asymmetrical construction similar to that of the foliage-shoot, and these constitute a protective investment to the flower-buds (cf. *Ribes*). The number varies (4–8), and the phyllotaxis is not always clear, since these members are few, and also fall off as the flowers expand. None of these scale-leaves are fertile, and above them 1–3 sessile flowers are produced which, since they do not necessarily correspond to the scale-leaves, may be regarded as the flowers subtended by higher bracteoles which have not been visibly developed. These flowers further present no prophylls. The posterior one often opens first, and the others almost simultaneously; but owing to the evidently much reduced character of the inflorescence shoot, it is not possible to give stricter rules for their position.

A feature of special interest is found in the presence of *Accessory Buds* in the inflorescence region. These are in structure identical with the usual axillary bud, and are formed in

descending series, 1–2 in number; if they are flowering-buds they produce the same cluster of (1–3) flowers, but 1 may be a vegetative bud and in such case is usually formed above the primary bud.[1]

Orientation. As there are no prophylls, and the subtending bract is doubtfully present in all cases, orientation of the diagram follows theoretical rules which are only to be accurately checked in the developmental history, although they may again be deduced from the comparison of closely allied forms in which these members are present.

The dimerous calyx is orientated with the outer pair of sepals in the median plane, and the inner pair transverse; the construction-system, allowing for the missing prophylls, thus following a normal symmetrical decussate (2 + 2) system. Beyond the calyx, or outer perianth-cycle, the construction changes to a doubled form, i. e. to (4 + 4). The first series of these new members, which should have produced a diagonal *corolla*, is, however, here absent, although a gap is left in the construction-system where it should have been found. (It is present in an allied S. African genus *Gnidia.*)

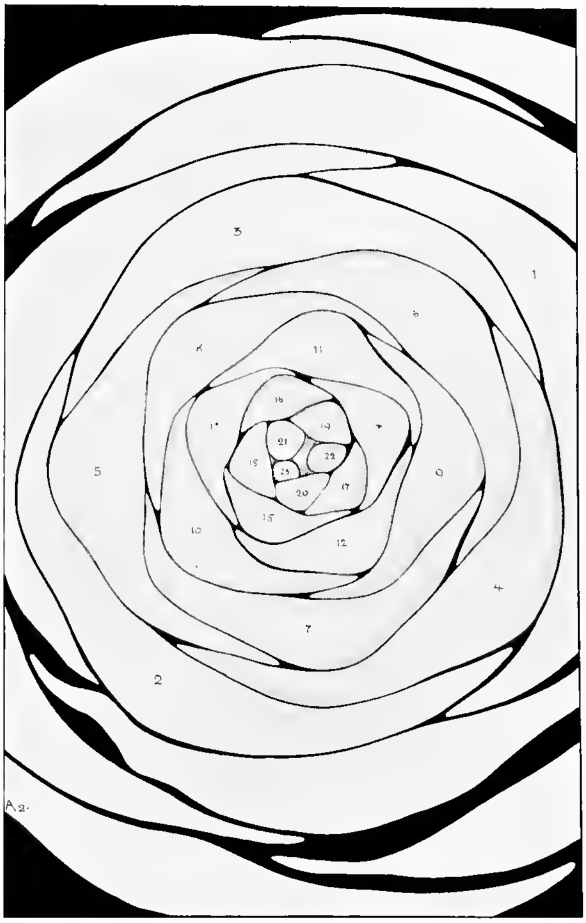

Fig. 1. *Daphne Mezereum*, January bud; apex of vegetative shoot showing phyllotaxis-system (3 + 5) at the centre.

Evidence that the plant once produced a corolla is based on—(1) structural evidence deduced from morphological rules; (2) comparative evidence taken from the study of allied types. The (4 + 4) arrangement continues normally for 2 alternating whorls of 8 stamens which constitute the androecium, the first whorl being thus median-transverse, the second diagonally arranged. The gynoecium again shows great reduction, and is formed apparently from one carpel which

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[1] *Note.* In the shoot-construction of higher plants it has become a rule, for some reason hitherto unexplained, that the ramification of the shoot bears a definite relation to the leaf-arrangement. This is not a law, but a rule deduced from the study of plant-forms; the special fact of observation being that one growth-centre capable of giving rise to a new branch arises at a spot in the primary construction-system which subsequently appears as the *axil* of a leaf-member. The fact that one such lateral centre is normally related to each leaf is thus a generalization based on the observation of the great majority of higher plant-forms. But there is no reason why, if one such centre may so arise, others may not equally well do the same. Such occurrences are, however, less general, with the result that a second axillary-bud is conventionally described as a supernumerary structure: such buds are not uncommon in inflorescence-systems in which the first bud becomes a flower-bud directly, and a second bud would serve to continue the vegetative ramification (cf. *Fuchsia*). They also occur in inflorescence-systems in which (from the fact of their presence) it might be suggested that one lateral flower would not exhaust the available food-supply at that spot. (Cf. *Jasminum officinale*, *Euonymus europaeus.*)

Where several such buds occur, in no particular sequence, or of varying function, as in *Daphne Mezereum*, the formation of two or three axillary growth-centres, where one would be usually expected, may be regarded as in a sense homologous with the production of several centres of growth in one flower (cf. Double Daffodils). While these phenomena are thus somewhat anomalous, it is clear that they do not in any sense represent a more primitive construction, in that a fuller inflorescence-scheme along perfectly normal lines, and hence probably a nearer approximation to the real ancestral condition, is found in *Daphne Laureola* and other species. The production of such accessory buds points rather to a deterioration in the construction-system of the shoot, and may possibly be correlated with other special adaptations to environment, which include, for example, the reduction of the number of flowers, loss of perianth members, bracts and prophylls, and the abnormal flowering period.

contains only a single anatropous ovule. This is represented as being posterior in position, though the orientation is variable.

An annular nectary-collar (disc) around the base of the gynoecium is also indicated in the floral diagram.

## Sectional Elevation.

The elevation is constructed for the median plane of the flower, which passes through the two larger outer sepals. The most conspicuous feature is the highly specialized crateriform character of the receptacle, expressed as a well-marked Zona Perigyna; this being at first sight indistinguishable from the gamophylly of a 4-parted perianth (the difference in the terminology being only a matter of definition according to the nature of the members elevated). The special feature of the floral-tube is that the whole of the perianth and androecium whorls are affected, and that the Zona Perigyna may be regarded as an elongation corresponding to three distinct internodal formations about 5, 2 and 1 mm. long respectively. Note also the nectary, and the peculiar ovary with capitate stigma and single anatropous ovule completely filling the cavity: the inner integument of the ovule is closely pressed against the upper wall, and a projection from this fits into the micropyle, so that the pollen-tube never crosses a free space in entering the embryo-sac, the ovary being practically solid. The length of the perigynous zone of growth gives the working-distance of the flower—from the anthers to the nectary—as 6–10 mm.

Fig. 2. *Daphne Mezereum*, origin of axillary inflorescence-buds.

## Development.

Buds begin to be formed in the axils of the foliage leaves about the end of April, and by May 1 the first bud is well-formed, and rudiments of a second and third can be seen in longitudinal section of the shoot. Flowers are laid down first in the uppermost axillary buds, and all early stages in development may be found on an annual shoot early in June; the buds at the base of the growth being well advanced, those in the upper portion just commencing the floral members. (Fig. 2, descending series of buds, June 12.)

The floral axis becomes markedly crateriform as soon as the perianth-segments are laid down, so that the outer series of stamens arises definitely from the inner side of a steep crater (Fig. 3, 2). The second whorl follows in alternating (4+4) construction, but is not so readily seen owing to the rapid growth of the gynoecium. This arises as a protuberance filling the base of the crater (Fig. 3, 3, 4) so exactly terminal that it is difficult to regard it as a single leaf-member; it grows up and hollows out, producing one rounded ovule-primordium obliquely at one side, though not necessarily always posterior as conventionally represented in the diagrams (Fig. 4). The members thus arise in close contact, and the crater continues its elongation to form a tubular structure: buds taken in July show the zones of secondary elongation definitely marked.

It is only important to note that this tubular flower is the simple development of a crateriform type of receptacle, which is here restricted to the floral-shoots, and which assumes this special characteristic at an extremely early date. The true structure of the gynoecium is again very doubtful; the assumption of a single carpel is a mere conventional way of describing it, since there is no direct evidence of more than one being concerned (cf. *Arum*, *Aucuba*). If it is the product of one carpel only, the flower would be apocarpous, and this fact would be of assistance in determining the systematic position: but the gynoecium develops as a ring-wall which may be eccentric in its growth, thus increasing more rapidly on one side than on the other; and in Fig. 2 it is seen that such increased growth on the anterior side may be correlated with a greater development in the anterior perianth-segment as well, since this overlaps the posterior one. Such eccentricity is frequent in lateral buds. There is no indication of a suture, or of a stigma-lip, and in fact no trace of either one or more leaf-members which may be homologized with carpels. As a somewhat similar type of ovary-development occurs in other forms (cf. *Viola*) in which indications of component carpels may subsequently be found, there is no necessity to call in question the carpellary theory in the case of *Daphne*. It is easy to correlate the loss of bract, prophylls and petals, the reduced tetramerous construction, and the reduced type of gynoecium limited to only one macrosporangium, with extreme degeneracy in floral-construction, and here, as in *Arum* and *Viscum*, mere ontogeny has little to say. Nor would the question become any clearer by stating that the gynoecium or the ovule is derived directly from the apex of the floral axis: such may be a matter of description but is not interpretation.

FIG. 3. *Daphne Mezereum*; development of flowers, June buds.

## Special Mechanism.

This is practically limited to the construction of a tubular flower by secondary zones of growth in the primarily crateriform receptacle; the result being the isolation of two whorls of stamens, both enclosed in the tube-growth, at the levels of 5 and 7 mm. respectively from the base of the crater.

The flower thus ultimately becomes a narrow-bored tube, 8–10 cm. long, blocked near the entrance by the anthers, so that the pollen is more or less hidden, and can with difficulty be collected. The honey-supply is also protected and hidden from sight. The mechanism is thus evidently adapted more particularly for honey-taking bees and Lepidoptera, and the short working-distance of 6–10 mm. renders the honey available to a large range of insects of these types. An additional factor in the attraction of such insects is found in the powerful scent. On the other hand it must be noted that zones of growth of very general occurrence are here wanting, or not utilized; thus there is no production of a flower-stalk internode; the filaments of the stamens are not extended, and the stylar growth is insignificant. In the distribution of pigment again, while the anthers present the usual yellow coloration due to xanthophyll derivatives of chlorophyll, the exposed portions of the perianth-segments and outer surface of the floral-tube is simply coloured deeply with a dull purple-red anthocyan pigment which is limited to the epidermal cells. The same pigment is also widely distributed, with or without chlorophyll, in the bracteoles and even leaves and stalks of the vegetative shoot.

*Note* also, that the specialization of the floral-tube, and the absence of other zones of growth, admirably adapt the mechanism for protection against desiccation, and also, as seen in the pigmentation of the tube, against the effect of intense light. Although in fact the final adjustment of the floral mechanism to a structure with certain definite relations between its parts, which remain fairly constant, and render it a successful arrangement for securing pollination by insect-agency, has thus undoubtedly been evolved in correlation with the habits of certain insects, there is every reason to believe that the actual causes which induced the original lines along which subsequent evolution has taken place, were the stimuli of the action of light and desiccation on the delicate reproductive-cells, and that the key to this floral-structure is to be found in the same xerophytic adaptation which is well expressed in the relations of the vegetative shoot and inflorescence.

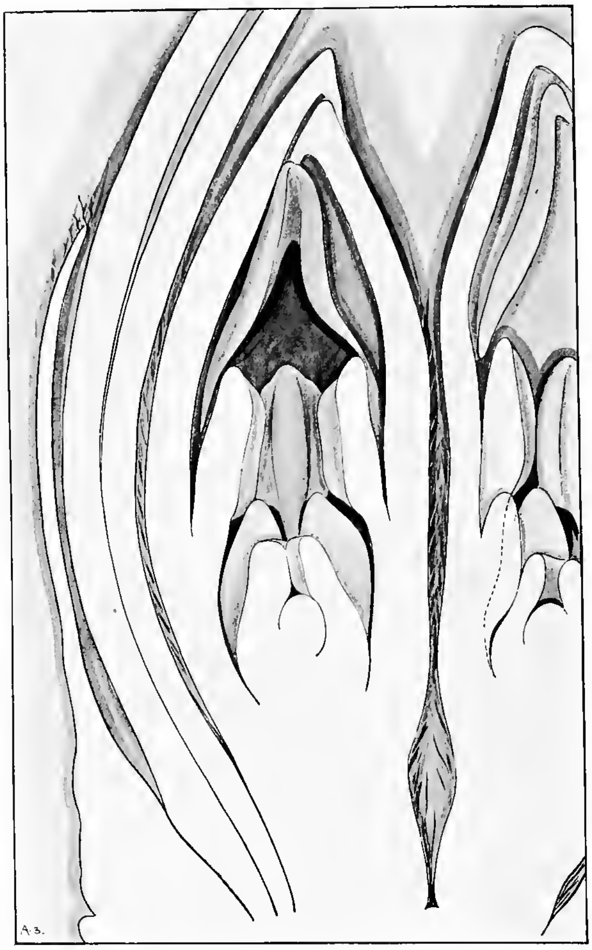

Fig. 4. *Daphne Mezereum*; flower bud with all its members laid down; cut in the median plane

## Pollination.

The flowers are rendered conspicuous by the purple-red coloration of the sepals and receptacle-tube. This again is considerably increased by (1) the close aggregation of the clusters, and the simultaneous expansion of a considerable number of flowers; (2) the absence of foliage leaves during the flowering period, as also of competing plants: in mild seasons var. *autumnale* commences to bloom early in October and November before the old leaves fall off (Nov. 3–18), and the last flowers remain until the expansion of the new foliage in the early part of the succeeding April; (3) the flowers emit a strong fragrant odour. Individual flowers persist for about a week, or even 3 weeks in mild seasons. They are damaged by severe weather, filled up by rain, and killed off by severe frosts.

The uppermost flower of the uppermost bud of a cluster usually opens first, but this is not constant; and the first flower of a lower bud usually expands before the last of its predecessor; so that a constant succession of blossoms is thus fairly maintained in each cluster during the flowering period.

The flowers are homogamous; the stigmatic-papillae being receptive as soon as the sepals diverge, and the anthers dehisce immediately as they undergo slight desiccation. The working-distance of the somewhat narrow tube practically limits the flower to fairly long-tongued bees and Lepidoptera. These in taking honey can scarcely fail to come into contact with the anthers, and to rub off pollen-grains on the stigmatic-papillae. Cross-pollination is thus likely to occur when plants grow near together, but pollination by means of pollen from other flowers of the same plant is likely to be the most frequent result. The arrangements for eliminating the self-pollination of the individual flower are thus, possibly in correlation with this fact, extremely vague; and the chance of the single pollen-grain which would be required to pollinate the solitary ovule falling from the anthers directly on to the stigma appears to be very considerable. Flowers isolated from insects set fruit freely; although net experiments are not satisfactory owing to the danger of extreme damp. A slight tendency to eliminate the chances of such self-pollination is seen in the horizontal or oblique presentation of the flower tube; a feature which becomes still more prominent in *D. Laureola* and *D. pontica.*

The flowers are visited in gardens by a varied collection of hibernated insects; flies, bees, and butterflies (*Vanessa urticae*). The Hive-bee is the most frequent visitor, and can only take honey with considerable difficulty. That smaller insects which may also effect self-pollination are not excluded, is shown by the fact that in mild seasons green aphides may be found sheltering inside the tubes.

Flowers pollinated in the autumn do not set fruit, the ovaries being killed by later frosts.

## Monstrosities and Variations.

The flower is already so reduced that little variation can be expected from it.

Structural variations include a further reduction to *trimery* observed in the case of starved specimens; in such case 3 perianth-segments are succeeded by 3 + 3 stamens. Mixed cases may also be observed. Abnormalities which come under the head of meaningless monstrosities occur on garden plants in the form of fasciation-phenomena, in which the floral-shoot includes two centres of growth: such cases include perianths of 7–8 segments, numerous stamens more or less irregularly arranged, and twin gynoeciums of the normal pattern. (Similar monstrous forms may be observed in *D. Laureola.*)

## Fruit and Seed.

Non-pollinated flowers wither away and are wholly shed. In the case of fertilized ones, the ovary rapidly enlarges within the flower-tube; this withers with its attached members, and being stretched by the developing fruit is ruptured at the base, and thus carried up on the young berry and soon thrown off.

The green fruit reaches full size, as a smooth ovoid berry, about 8–9 mm. long, by 5 in diameter, in about 6 weeks, or early in May. These ripen in June, and by about the first week in July are ready for dispersal; the maturation being indicated by a conversion of the pigment in the epidermal cells to a bright scarlet, due to the addition of the crimson pigment to yellow xanthophylls. Thus the white-flowered form, which is deficient in this protective pigment in its flower-shoots, and also grows best in a shaded situation, produces yellow berries. The main crop ripens from July 3 to July 10. The whole of the ovary-wall becomes succulent; this consists of a red skin with sweetish watery pulp, which possesses a disagreeable taste, and encloses the large black seed, 7 mm. by 5. The inner part of the pulpy fruit-wall presents a delicate network of vascular bundles. The seed is rounded below with a pointed micropylar end: beneath a thin white film, the outer integument, with the vascular bundle running down one side, a black sclerosed layer becomes visible; this constitutes the protective seed-coat. Section in the plane of the raphe, indicated by the vascular bundle, shows a large embryo enclosed in a testa of which the protective coat is a single series of thickened and lignified prismatic cells, the outermost layer of the inner integument; this is not completed around the chalazal end, a well-marked chalazal plug being present.[1]

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[1] In the flowering stage the ovule is remarkable for the great specialization of the integuments, which extend as separate investments almost to the base of the ovule. The vascular bundle is also obvious, coiling down one side to the chalazal end. The outer integument, three cells thick, appears to be less important than the inner, which is closely related to the ingrowth at the top of the ovary cavity. The outermost layer of this, (the fourth cell-row)

Both cotyledons are cut in the section, and a small amount of endosperm is present as a thin film over the bulky embryo.

At the tip of the fruit a small withered style-relic persists, and at the base a broken ring indicates the point of abscission of the floral-tube; the remains of the nectary are also still distinguishable.

*Note* that the large embryo is protected by the lignified layer of the inner integument, a region which was already well-marked in the flowering stage; and is provided with abundant food in the form of oil and proteid stored in the cotyledons, a small supply left in the scanty endosperm being negligible and chiefly restricted to the 'non-digestible' layer. The fruit is dispersed by the agency of birds; the special adaptations to this end comprising (1) the succulence and sugar-storage of the ovary-wall; (2) development of an attractive colour as the cells cease their connexion with the assimilative functions; (3) the strongly-marked sclerosed prismatic layer of the testa.

The birds which more especially take these berries during the summer months are the Robin and the Blackbird; but many trees in gardens are never visited by birds at all, although sparrows often destroy the green fruits, picking out the seeds before they are grown and leaving the green husks.

In absence of bird dispersal-agents, the fruits remain on the plants throughout the summer, and are shed from the end of August; a few persist until November, when they are shed with the fall of the foliage-leaves. Seeds germinate freely.

## Comparison of Allied Forms.

I. *Daphne Laureola*, L. A small evergreen shrub 1–3 ft. high, indigenous to England but not extending to Scotland and Ireland. It flowers in March (February to first week of April), and bears drooping clusters of pale apple-green blossoms succeeded by blue-black berries. The flowers possess a structure identical with that of *D. Mezereum*, but the tube is longer (8–10 mm.), and relatively narrower, the working-distance being 10 mm., and suited for humble-bees and early moths.

The inflorescence is suggestive as exhibiting a much fuller type; as many as 100 flowers being crowded together, and all may be out simultaneously. In the axils of several (10–15) of the persistent upper foliage-leaves of the annual shoot of the previous season, lateral racemes are borne. Each commences with 2 prophylls, an investment of 5–6 sterile scale-leaves, about 3 fertile bracts subtending flowers, and finally 2 or 3 flowers without bracts or prophylls. Some of the fertile bracts again may subtend 2 flowers. No prophylls are present to the individual flowers, although the node at which they should appear is marked. The flowers are distinctly pendulous.

In addition to the increased development of the inflorescence-region, it is interesting to note the presence of subtending bracts to some of the flowers but not to others; and it is clear that *D. Mezereum* represents a stage of the still greater reduction of a type like this. *Note* also that the crimson pigment is entirely absent from the leafy shoot and flower shoot of *D. Laureola.*

II. *Daphne pontica*, L. An evergreen shrub, 5–8 ft. high, commonly cultivated in gardens and shrubberies, indigenous to Asia Minor and Siberia, and introduced in 1759. It flowers later than the preceding, in April and May, but does not produce fruit in this country. The flowers are olive-green or yellowish in colour; the flower-tube is long and slender (10 mm.), so that the flower is practically limited to Lepidoptera, and the perianth-segments are also slender and recurved. The inflorescence is the most interesting feature,

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forms a columnar sclerosed layer at an early date after fertilization, and the nucellus is also greatly developed. The endosperm digests this and extends outwards to the sclerosed layer, leaving ultimately only a thin film between. The sclerosed layer is not continued at the extreme base, since food supplies have to enter by the vascular bundle, and this opening is subsequently closed by the chalazal plug.

as a variation on the *D. Laureola* type: the flowers are borne on the shoots of the current season as the new buds expand; and the inflorescences are both terminal and lateral, bearing flowers below, and continuing the vegetative structure of the plant above. The flowers are produced wholly in twin pairs, without bracteoles or prophylls, in the axils of small subtending bracts, so closely alike and simultaneous in flowering that it is difficult to say whether one is a branch from the other, or an accessory bud from the same bract; what is found exceptionally in *D. Laureola* here becoming the rule.

III. *Daphne Cneorum*[1], L. A small trailing shrub, growing about a foot high, widely distributed over the Alpine regions of S. Europe, is also in general garden cultivation. It flowers in late April and throughout May, or even throughout the Summer if kept moist. It rarely ripens its whitish berries in this country, in which it has been grown since 1739.

The flowers are borne in terminal clusters without bracts or prophylls; they are bright rose-purple in colour, and possess a much narrower floral-tube (1 mm. across at the orifice), which is further increased in length to 13 mm.; these last two factors suggesting that this Alpine form is becoming restricted to the visits of Lepidoptera, although such visitors will still promote self-pollination when once the anthers have dehisced. The flowers are also strongly scented; and though bright rose-coloured, appear white at dusk when the foliage is invisible, thus suggesting further correlation with the visits of moths.

From comparison of these types it is clear that *reduction* is the key to the structure of the inflorescence in all of them; and that in the secondary mechanism of the individual flowers, the tendency of the tubular structure is to become relatively still longer, and that the ultimate types will be specialized for Lepidoptera alone. *Daphne Mezereum*, which possesses the most reduced inflorescence-construction, retains on the other hand a more generalized floral-mechanism which can be worked, though with difficulty, by the Hive-bee with a proboscis of 5–6 mm.

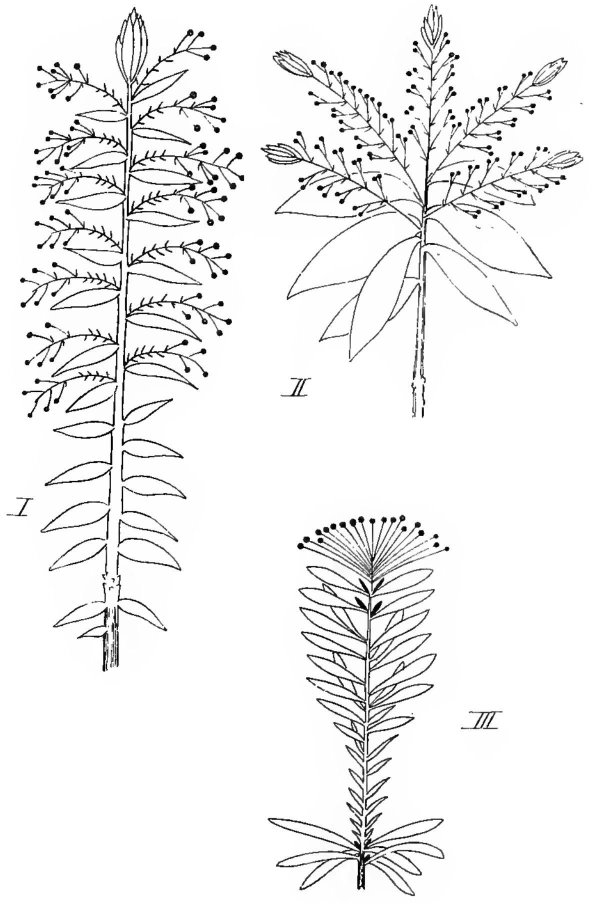

Fig. 5. Inflorescence-schemes of *I*, *Daphne Laureola*; *II*, *D. pontica*; *III*, *D. Cneorum*.

## Theoretical Conclusions.

The peculiar structure of the gynoecium and its resultant berry-fruit is so definite, and so evidently the outcome of a long line of reduction-specialization, that there is no difficulty in referring any plant whose flower possesses this special ovary to a position close to the Daphnes, that is to say, to the same family. On the other hand, the succulence of the ovary-wall may be a secondary character of a structure which once dried, and might thus appear as a dry nut.

The flower is of greatest interest, perhaps, as a reduced type in which symmetrical tetramery has become established in the floral-shoot of an otherwise asymmetrically

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[1] *Cneoron* of Matthiolus; *Cneorum Matthioli* of Clusius, the name Cneoron being used by Pliny for a plant unidentified.

constructed plant-body. That the flower is really a case of tetramery is inferred from the presence of 8 stamens, arranged (4 + 4), the inner whorl being diagonal; in fact, if this last whorl was not present, the proof of tetramerous construction rather than dimerous (2 + 2) would be difficult. As it is present, the loss of a diagonal corolla-whorl is also inferred from the structural relations of tetramerous flowers; and this becomes confirmed by the fact that the petals are present and functional in the S. African genus *Gnidia*, *Struthiola* (Cape Colony), *Dicranolepis* (Tropical Africa), *Linostoma* (Further India), *Lophostoma* (Amazon).

As already indicated, it would appear that the full ancestral type was a shrub or small tree, with panicled inflorescences of 4-parted flowers with apocarpous gynoecium, and a tendency to further reduction in all its parts. Once the full tetramerous condition is established, analogous examples in other lines of descent (cf. *Ruta*, *Fuchsia*, *Oenothera*, *Alchemilla*, &c.) strongly support the view that a still earlier type was of the normal pentamerous construction characteristic of a majority of petaloid Dicotyledons.

The extreme reduction of the inflorescence-region in *D. Mezereum* is associated with an anomalous production of accessory buds; while the older, since more universal, reduction of the ovary to the ultimate condition of one carpel and one ovule is rather of the nature of a reduction-specialization; since it may be pointed out that one of the apparent ideals of the higher flowering families is to devote the entire mechanism of each flower to the production of a single, preferably cross-pollinated, seed.

The special mechanism added to the tetramerous construction is very simple; it consists merely of a single zone of growth, included under the term Zona Perigyna; and the further development of the idea can do little more, it would appear, than continue to make the tube either longer, or more perfectly adjusted to the length of the proboscis of some particular type of insect. The mechanism is simple, and by no means perfect for any claims of cross-pollination; and the fact that it is not to be regarded as a particularly successful line of flower-development is probably to be concluded from the comparatively feeble development of this particular type in modern flora. Thus 40 species are included in the genus *Daphne*, which together with 37 other genera, and a grand total of about 400 species, constitute the modern family termed the *Thymeleaceae* (Gilg, 1894).

Of the entire group which is widely distributed over the whole world from Norway (*Daphne*) to New Zealand (*Drapetes*), and from Canada (*Dirca*) to Patagonia (*Drapetes*), two genera only besides *Daphne* reach any great specialization, as indicated by the number of species described by systematists. Thus the S. African genus *Gnidia* (80–90 forms), presents a full type of flower, with well-marked petals; while some species present the original 5-parted flower; on the other hand *Pimelea*, including 70–80 forms from Australia, Tasmania, and New Zealand, shows a degree of reduction even greater than that of *Daphne*; the androecium being reduced to dimery, and consisting only of 2 stamens. Between these extremes the European *Daphne* occupies a fairly medium position.

With regard to the wider relationships and phylogeny of the group, but little can yet be said; since it is clear that, once reduction sets in, all phyla which are extensively reduced must come to resemble each other, more or less, in the absence of distinctive characters; and the general features of the reduction-phenomena[1] exhibited by *Daphne* in its inflorescence and general floral-structure are so normal, that it is still possible that the modern grouping of the Thymeleaceae contains different lines of phylogenetic reduction. Thus the present arrangement of the group (Gilg, 1894) includes a few forms with syncarpous ovaries and axile placentation; while in others (*Gnidia*, *Pimelea*), the solitary carpel has the peculiar

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[1] These reduction-phenomena, which are characteristic of the *Daphne* type, and thus of the entire group of the *Thymeleaceae* which has gradually been collected around it, are probably to be regarded as induced as the result of exposure to xerophytic environment. Thus the group consists characteristically of steppe plants; and although this can hardly be said of the English *D. Mezereum* and *D. Laureola*, suggestions of such protective adaptation against desiccation and intense light have not been wanting in the former case; and here, as in other types, the present habitat of a plant is often as little guide to the ancestral evolution of the structure, as the fact that it will grow in an ordinary garden.

lateral style familiar in the Strawberry and other Rosaceae. Further, once it is made clear that no wide phylogenetic significance can be attributed to a tetramerous type of construction, which is a structural variation common to most lines of descent; nor again to the specialization of a Zona Perigyna on a crateriform receptacle; it is exceedingly doubtful what is left to base generalizations upon: this being again the ever-present difficulty in determining the lines of evolution of recent flowering-plants. The deduction from *Daphne Mezereum* of a petaloid, pentamerous, possibly apocarpous type of floral-structure takes us at once almost to the limit of floral-structure as it is found in the majority of Dicotyledons. The combination of these characters with a tendency to a development of Perigyny, is suggestive of the general features of the Rosaceae (cf. *Alchemilla*, *Poterium*); but any connexion with this ancient series would have to be almost as ancient as the group itself, so that little progress is made, and the series still remains isolated, and is usually conventionally grouped with other series which resemble it most closely in a general convergence to a simple type of tubular floral construction, correlated with simple clustered inflorescences.

# VII

## **Viola odorata,**[1] L. *The Violet.*[2]

A hardy herbaceous plant with short prostrate perennating woody stem, and terminal rosette of more or less evergreen foliage leaves, growing about 6 inches high; probably indigenous to Great Britain and Ireland,[3] and extending over the whole of Central and Southern Europe, N. Africa and Asia to Siberia and Japan; present in N. America only as an escape from cultivation.

The Violet has been cultivated in gardens from time immemorial[4] for the sake of its fragrant 'violet' flowers produced in the early Spring months (March, April).

A large number of varieties, hybrids and florists' forms are in cultivation, and specimens of the larger varieties are obtainable throughout the winter (October–March).[5] In a wild state the flowers vary in colour to pure white,[6] and a red-purple; the fruits ripen and shed their seeds in the first weeks of June.

The plant is further remarkable for its production of self-pollinating *cleistogamic* flowers which ripen fruits throughout the summer months.

### Description.

Inflorescence: reduced to solitary flowers borne in the axils of a few of the last foliage-leaves of the preceding season. Two lateral prophylls are present as small scale-leaves (5 mm.), placed close together at a point about half-way up the flower-stalk.

Flower: hermaphrodite; zygomorphic, and bent over on its stalk; pentamerous type of structure.

Receptacle: very slightly crateriform and eccentric.

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[1] The Ἴον of Dioscorides, Ἴον πορφύρον or ἴον μελάνιον, the purple-black violet, or *Viola purpurea* of Theophrastus. The figure in the Vienna MSS. of Dioscorides is distinctly recognizable as meant for a tufted *Viola*. Good figures under the same names are given first by Brunfels (1530), *Viola nigra*.

Fuchs (1542) gives an admirable drawing of the whole plant as *Viola muraria* or *purpurea*, and Gerard (1597) illustrates ten different sorts, of which four are varieties, white, and double, of the March Violet, *Viola nigra* or *purpurea*; cf. also *Viola Martia* of Tabernaemontanus (1588), and Bauhin (Pinax, 1623).

The name *Viola* was also applied by old English writers (Turner, 1551, and Gerard, 1597) to the Snowflake (*Leucojum*) and various purple and white-flowered Crucifers (*Hesperis matronalis*, *Lunaria*); cf. 'Stock Gilloflowers, Wallflowers, Dame's Gilloflowers, Marian's Violets' of Gerard, while Bauhin (1623) still maintains *Viola matronalis* and *Viola Lunaria*. As the name had been applied to these plants from the erroneous idea that they might be the one referred to by Dioscorides, the word was gradually restricted to the *Viola*-types as we now know them: *Viola* being established as a genus by Tournefort (1700), and the specific name *odorata* being the Linnaean designation (1753).

[2] Violet through the French Violete (Maignan, 1549; Tournefort, 1700), Violette (Jussieu, 1789).

[3] Generally distributed in Great Britain, reaching its northern limit in Forfarshire, and by some (cf. Watson) regarded as a relic of cultivation: also rarer and a still more doubtful native in Ireland.

[4] Gerard (1597) cultivated white varieties, single and double, as well as the double-blue one, in addition to 'Pansies'.

[5] Plants being cultivated in the open on a large scale in fields for this purpose (West Cornwall, &c.), as they cannot be grown in greenhouses.

[6] The white variety is more common on chalk or limestone soils.

PERIANTH differentiated into :—

1. CALYX of 5 free sepals, green, tinged violet, ovate, 5 mm. long by 2–3 mm. wide; two at the front are separated by a petal-spur, and all 5 have basal flap-extensions nearly 2 mm. long, which together form an investment around the base of the flower. The sepals are slightly larger forwards.
2. COROLLA of 5 free petals, alternating with the sepals; the odd one in front is produced into a relatively large hollow spur. The 5 petals are somewhat dissimilar :—
   (1) The two back petals, 13–14 mm. by 6, oval, with narrow stalk-portion and unequal-sided, are sharply recurved in the flower.
   (2) Two lateral petals, 14 mm. by 6, more asymmetrical, diverging in the flower and possessing a small tuft of white hairs about 4 mm. from the base.
   (This last is absent in some wild forms: var. *imberbis*, Leighton.)
   (3) An anterior petal, 14 mm. by 8, oval, slightly notched at the apex, and produced at the base into a pouched spur-sac 5 mm. long, with a rounded end. The petal is symmetrical, and the spur is compressed in a vertical plane, to a breadth of 3 mm. All the petals are coloured violet-blue, the colour being fainter or absent at the base of the members, but emphasized over the veins. The veining is rendered still more striking on the front petal, which has 3 strongly marked central veins, while the asymmetrical lateral petals only show 2 towards the front margin.

   *Note* that the curvature of the upper petals is sufficiently strong to force back the sepal beneath them, and that the coloration of the veins converges to the centre of the flower, and more particularly, since it is strongest on the front petal, to the orifice of the spur.

ANDROECIUM of 5 free stamens, in normal alternation with the petals; *filaments* negligible; *anthers* introrse, 2 mm. by 1½, cream-coloured, with a broad triangular *connective* flap, 2 mm. long, coloured orange; *pollen* pale, or white.

The whole staminal group constitutes a cone, 4 mm. high by 3 mm. in diameter, of which the apex is formed by the orange connective-flaps closely pressed against the style.

Two of the stamens, those over the front petal, possess *nectary*-tails which converge into the petal-spur as green, blunt, compressed processes 4 mm. in length.

GYNOECIUM: syncarpous of 3 carpels. *Ovary* green, conoid, 2 mm. long, level with the anthers; cavity unilocular, with a nearly flat floor and 3 parietal placentas bearing anatropous ovules in 2–3 rows. *Style* 2 mm. as long as the connective flaps of the stamens, hooked at the end (1 mm.), the point projecting over the orifice of the petal-spur, and slightly papillose at the tip, which is about 4·5 mm. from the base of the ovary and 8 mm. from the end of the nectary-lobes.

The total number of ovules in the ovary averages 30.

NECTARY: the tailed processes of the 2 front stamens secrete, and the spur of the front petal acts both as a protective shield and storage reservoir.

## Variations.

Being a highly specialized floral-mechanism, the flower of the Violet is remarkably constant under cultivation. Improved garden-forms and florists' varieties differ only in the larger size of the plant-parts as a whole, and of the petals of the flower; the essential organs remaining practically unaffected.

Violets commonly sold in the streets during the winter months give measurements nearly twice as great for the perianth members, but little more for the stamens and ovary, e.g. :—

*Sepals* 12 mm. by 5; *petals* 23 by 10–14; *spur* 8 mm. by 3–4; *anther* 3 mm. long, flap 2 mm.; *nectary*-lobes 5 mm.; *ovary* 3 mm., style 3 ('Czar' Violets, cf. also 'Princess of Wales').

A still larger form, also commonly sold in Spring ('La France'), produces a flower as large as a small Pansy, 30 mm. in diameter. The petals are broader and flatter than the proportions of the type (20–22 mm. by 16–18), the essential organs being the same as those of the preceding case.

The variety 'Admiral Avellan' is a good red-purple coloured form. A common *double* form of perfectly irregular construction is included under the head of a monstrosity ('Marie Louise').

## Floral Diagram.

The vegetative shoot presents normal spiral phyllotaxis of the Fibonacci series, but the pattern seen in transverse section of the apex is confused owing to the great development of the stipular-segments of the leaf-primordia (Fig. 1). These stipules subsequently act as a protection for the developing flowers in the perennating rosettes. The main stem is more or less procumbent on the surface of the soil; the development of long internodes and rudimentary leaf-members distinguishing the production of 'stolons' from the assimilating rosettes in which the leaves are well developed and internodes not formed.

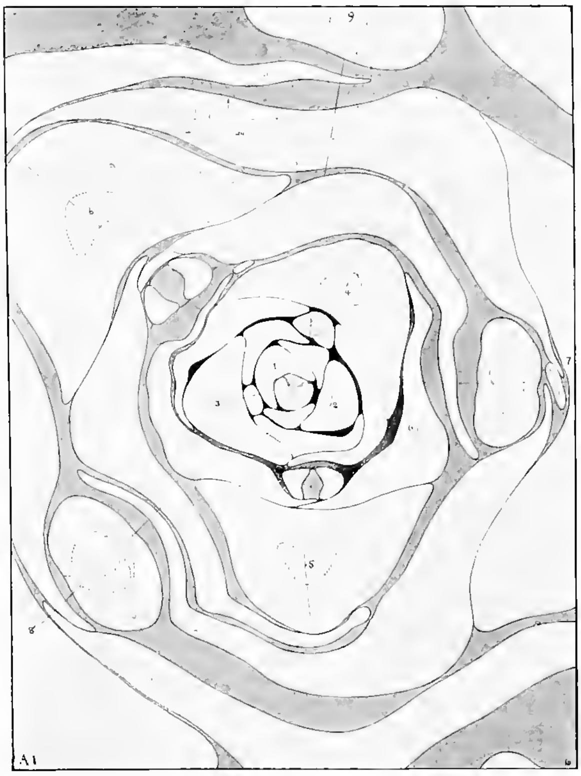


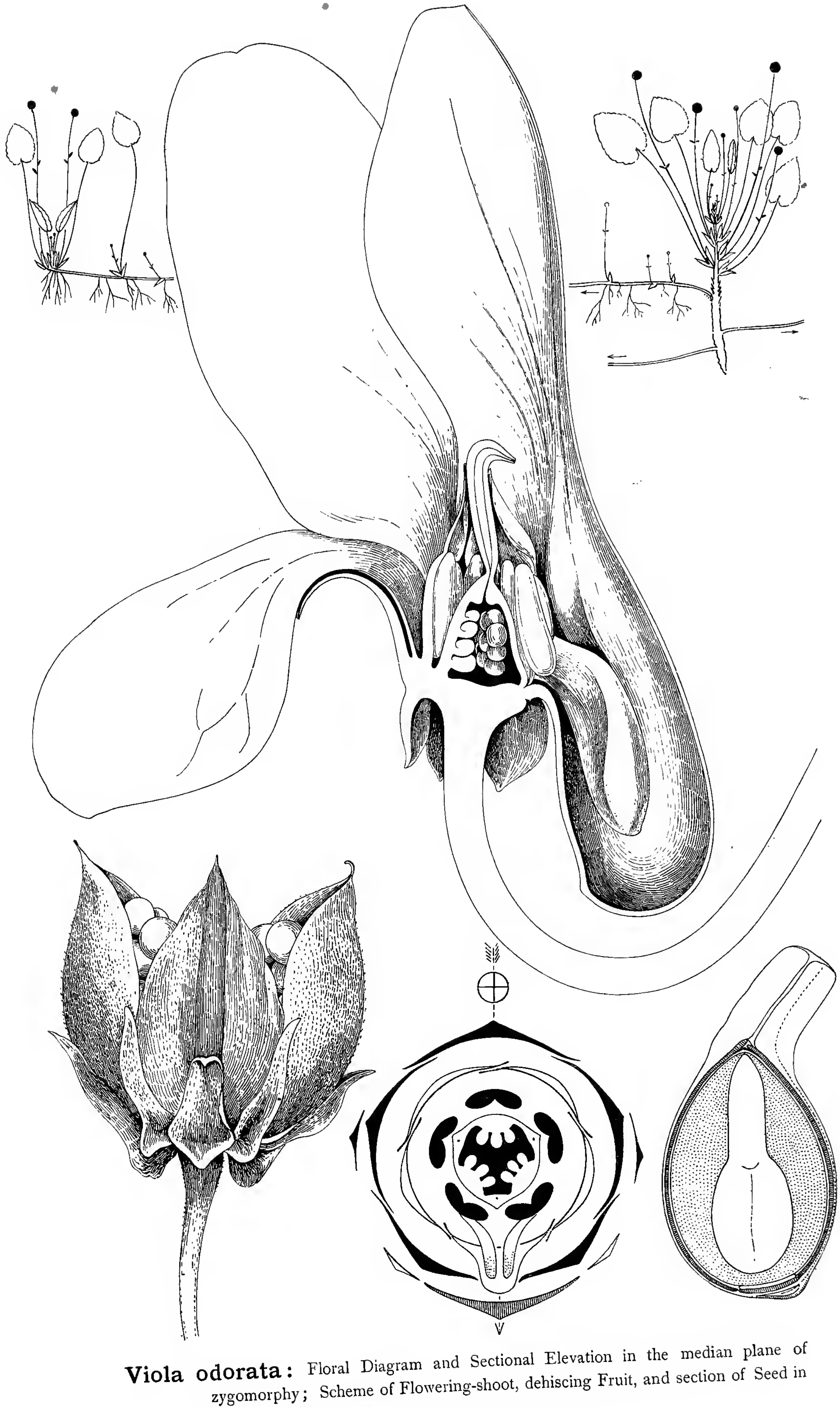
Fig. 1. *Viola odorata*; section of shoot-apex, phyllotaxis (2 + 3) complicated by stipular formations.

Every leaf subtends a lateral shoot-axis which is either a new vegetative branch (stolon) or a flower. (Figs. 1, 2.)

The foliage leaves produced each season are few in number (5–6). They are rapidly developed towards the end of the flowering period (April). Flowers are produced in the axils of the upper foliage leaves of the preceding season, and also in the axils of the scale leaves of the stolons. They develop in the autumn and perennate over the winter, when the foliage in exposed situations may be more or less killed.

Plants taken during the flowering period thus show stolons ending in rosettes, each consisting of 3 or 4 old leaves, 2 or 3 of which subtend perfect flowers, and above these the cycle of new foliage-leaves commencing active growth. Flower-buds in the axils of these new leaves, and also some in the axils of older ones, are never perfected, but become the *cleistogamous* flowers observed during subsequent months.

The youngest flowers are protected by the stipules of the subtending foliage-leaf, and also by their own prophylls ($\alpha$ and $\beta$). These are relatively large at first and quite enclose the flower (Fig. 2). Note that the 2 prophylls are not exactly opposite, and that an internode is put in below $\alpha$ and above $\beta$, but not between them. The structure of the flower is of the general pentamerous form characteristic of the majority of Petaloid Dicotyledonous Types, and commences as an asymmetrical phyllotaxis-construction which attains symmetry before the production of the sporophylls. The primary construction is that of the *Mean Dicotyledonous Type* with the exception of the gynoecium, which is only reduced to 3 carpels instead of 2; and superimposed on this is a marked degree of eccentricity which renders the flower zygomorphic in the plane of sepal No. 2, which is so approximately the median plane of the diagram, that for general purposes it is taken as being a useful convention (Fig. 2). No definite law appears to control the orientation of an asymmetrical (spiral) shoot, but as a fact of observation sepal 2 is, as near as can be judged by the eye, median posterior, and $\beta$ prophyll is equally near the transverse plane; $\alpha$ prophyll is distinctly postero-lateral.



**Viola odorata:** Floral Diagram and Sectional Elevation in the median plane of zygomorphy; Scheme of Flowering-shoot, dehiscing Fruit, and section of Seed in the plane of the raphe.

The sepals of the calyx present the normal quincuncial type, the odd member being No. 2 and thus conventionally taken as median posterior. Prefloration of this spiral system is very obvious in the bud condition. As in the general case, it is convenient to take a right-hand flower for illustration. It is probable that the quincuncial calyx is the relic of a (3 + 5) asymmetrical construction in the floral shoot, which was once common both to this and the vegetative buds. Beyond the calyx, however, a true symmetrical construction is attained, and the rest of the flower is clearly based on a system (5 + 5) which would give alternating whorls of 5 members. The corolla thus appears as a cycle of members in the vicinity of the change of system.

This phyllotaxis-construction is affected by the further assumption of a marked degree of eccentricity, the effect of which will be traced in the visible ontogeny of the members, and also in their shape—since in an eccentric construction only those members growing in the plane of eccentricity can be truly symmetrical in the sense of being equal-sided. This plane of eccentricity passes through the centre of sepal 2, which is the posterior member of the quincuncial calyx. The petals of the corolla thus alternate with the sepals, but the 2 posterior and 2 lateral are unequal-sided; it is the anterior symmetrical petal which is produced backwards to form the spur. Zygomorphy also affects the prefloration, the posterior members being extended outside the lateral, and these again below the anterior member. The stamens continue the normal alternation; the two which produce nectary-growths being now described as the anterior pair: the gynoecium is reduced to 3 carpels which are orientated in the plane of zygomorphy, the odd member being here median anterior. A transverse section of the ovary shows a triangular unilocular cavity with 3 rows of ovules on each of the 3 placentas. The nectary-process of the stamens, and the spur of the anterior petal, being really the controlling features of the floral-mechanism, are also indicated in the floral diagram. The history of this construction as traced in actual development adds little to the information deduced from the adult flower. The calyx-members arise in a spiral sequence which also includes the prophylls; but the development of the other members is affected by the secondary eccentricity, with the result that of the 5 theoretically equal petals, the anterior member becomes visible first and the others in so-called 'ascending order'. That is to say, the anterior side of the flower grows at a greater rate at this period than the posterior, and the centre of growth is thus apparently displaced posteriorly towards sepal 2. The same eccentric formation is seen in the development of the androecium, of which the 2 anterior members again are the first to become visible.

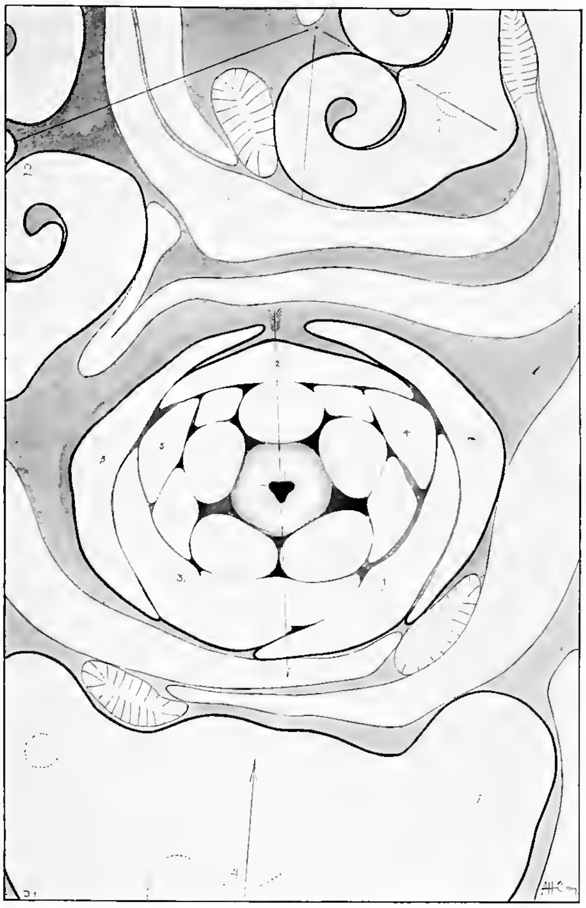


FIG. 2. *Viola odorata*; development of flower, all the members laid down in a slightly eccentric system. Assimilating members drawn with a bolder line than the stipular lobes.

## Sectional Elevation.

The elevation is constructed in the median plane of zygomorphy; as the flower is sharply bent over on its stalk it requires to be so placed that the essential organs are erected.

Such a section passes through the recurved sepal 2 on the left, and the anterior spurred-petal on the right. The spur is cut open along its length, and one of the nectary-processes exposed. The position of the other members is checked from the diagram.

The ovary, being cut along the posterior placenta, shows the anatropous ovules bent towards the apex of the ovary; the style with hooked stigma-tip is hollow, being only just closed at the basal region in which it is slightly kinked.

*Note* the peculiar shape of the receptacle, which is slightly crateriform, and hollowed over the apex of the floral axis. It is also eccentric, since much more pronounced on the posterior side (the outline of the receptacle being taken by drawing a curve through the insertion of the members). *Note* also the very rudimentary filaments, the large introrse anthers, and the large connective-flaps, that is to say the well-developed *laminae* of these sporophylls, which press closely against the style; the function of the style being obviously to take the stigmatic-hook just beyond these processes, while the hook projects over the entrance to the spur. Development along one plane of symmetry is thus associated with the production of one spur, and the essential organs are also modified in connexion with this spur.

## Development.

While the primary construction of the flower can be readily deduced from the adult structure, and the facts of ontogeny checked by means of transverse sections of flower-buds, the chief interest attaches to the development of the eccentric construction and the production of special mechanism, which is much clearer in longitudinal sections of the young flower-buds.

Owing to the fact that young flowers are produced in the axils of the new season's foliage leaves during the flowering period, all stages in development may be obtained from plants as they produce their first flowers in March. As already stated, every leaf normally subtends a foliage shoot or a flower-bud, but relatively only a few come to perfection, these being the flowers in the axils of the perennating foliage leaves.

Development commences almost immediately behind the growing apex, and the flower stalks soon commence to elongate, so that even most rudimentary flowers are definitely stalked. Two lateral prophylls ($\alpha$ and $\beta$) are well developed at first, and enclose the young bud between them; additional protection is afforded by the large stipules of the foliage leaves.

With the assumption of eccentricity in the construction-system, the receptacle soon becomes slightly crateriform, and longitudinal sections to show the relation of these phenomena may be taken in the median plane of the buds, which is the plane of eccentricity.

Thus young flower-buds on stalks about $\frac{3}{4}$ mm. long (Fig. 3, I), show the commencement of the hollow crater-formation while the eccentricity is already quite definitely marked —the *anterior* side of the receptacle being nearly twice the size of the posterior, and the anterior members of the calyx, corolla, and androecium whorls distinctly larger than the posterior. The apex of the floral axis is situated at the base of the slight crater-depression. *Note* that the flower-stalk at this stage consists only of a secondary internodal extension below $\alpha$ prophyll.

In a slightly older bud, on a 1 mm. stalk (Fig. 3, II), it is clear that another internode is commencing above $\beta$ prophyll; the crater is larger and more obvious but the eccentricity is less, the anterior side of the receptacle being now but little larger than the posterior. The gynoecium is also being laid down, the carpels arising as low elevations on the inner slope of the crater.

A somewhat older stage, stalked 2 mm. (Fig. 3, III), shows the floral members all clearly formed. The sepals are beginning to overlap; the stamens commence their anther-lobes, while the carpels fuse laterally and grow up to form the wall of the syncarpous ovary, without leaving any marked free tips. The eccentricity of the axis has been fairly equalized, and would now escape observation if earlier stages had not been seen. The outline of the crater is well marked, and the apex of the axis is the flat floor of the ovary cavity. Subsequent growth of the primary structure entails the development of the pollen-sacs in the anther, 2 being produced in each lobe quite normally, and the formation of ovules in the ovary.

A bud about 1·5 mm. long shows these modifications completed (Fig. 4), and the floral structure begins to assume its characteristic form; the stamens are differentiated, and the sepals, which are now the protective investment of the flower, commence to form their basal projecting flaps as an exaggeration of the peculiar basal asymmetry of all lateral appendages. Observation of the receptacle shows, however, that, though the crater does not become any more pronounced than it was before, the eccentricity of the axis is now *reversed*, and the posterior side of the floral-receptacle is now distinctly larger than the anterior.

Section of a still older bud, 2 mm. long and stalked 10 mm., gives the full differentiation of the primary condition of the flower (Fig. 5). The posterior development of the crater-wall is now very marked, and the flat apex of the floral shoot along the floor of the ovary very striking. The stamens are fully developed, the ovules are turning upwards and forming their integuments, while the apex of the syncarpous gynoecium becomes extended as a hollow style-tube.

*Note*, however, that the style does not extend beyond the connective-flaps, and that the flower is so far a self-pollinating type. On the anterior side of the flower, at this late stage, the spur is only now commencing as a pocket-like depression of the anterior petal-base, while simultaneously an emergence is arising from the filament at the back of the anterior anthers, which will be the nectary (Fig. 5).

FIG. 3. *Viola odorata*, March 5; development of flower, successive stages drawn to the same scale, cut in the median plane of the elevation.

The primary structure of the flower may therefore be summed up as a fairly normal Dicotyledonous Type, approaching the mean construction-system, in which the receptacle has only a very slight tendency to a crateriform condition; while a marked degree of eccentricity which commences at a very early stage shows a tendency to reversal at a later period, though again neither of these phenomena is further emphasized in the adult condition.

Special attention may also be paid to the development of the *Gynoecium*: the 3 carpellary members never exist as independent leaf-primordia; developmental stages are abbreviated; the gynoecium arises as a ring-wall with slightly triangular outline, the only trace of the component carpels being a slight elevation of the edge of the cup at 3 points—i. e. the carpels are not so much 'syncarpous' as *gamophyllous* from a very early date.

Similarly, the placentas are not derived from incurved carpel-edges (sutural), but from continuations corresponding to the original positions of these along the gamo-carpellary region. Hence the ovules are no longer seen to be arranged in two rows along each placenta, 3 being usually cut in transverse section (*V. odorata*, 6–7 in *V. altaica*).

*Note* that such gamophylly of carpels is as secondary a phenomenon as the gamophylly of any other floral cycle; also that the development of the ovules on an intercalated zone of growth, which is not necessarily therefore 'receptacular' (cf. Corona of *Narcissus*), does not make the ovules 'axial', although such views may have been put forward. Nor does the case of *Viola* present any objection to the carpellary theory; the carpellary theory being a phylogenetic conception, and not necessarily an ontogenetic one; nor can any necessity for absolute recapitulation in development be reasonably postulated. The case of the *Viola*-gynoecium is thus of interest, in that, while the floral development of *Viola* is recapitulatory to a remarkable extent, the gynoecium presents abbreviated conditions which may serve as a guide to the phylogenetic history of other types.

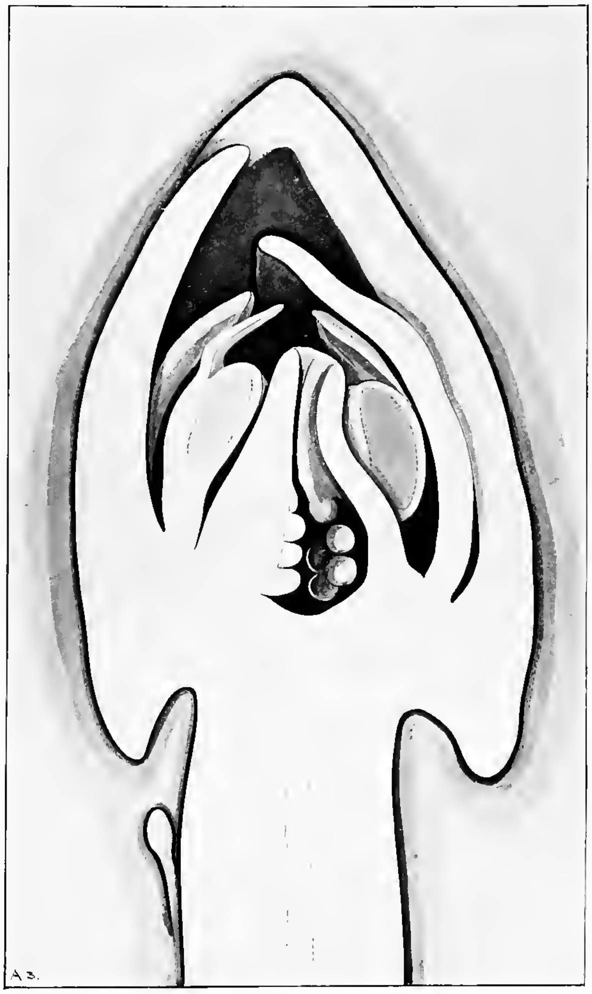


FIG. 4. *Viola odorata*; median section of flower-bud 1·5 mm in length.

## Special Mechanism.

The special growths which differentiate the flower as a mechanism, from a mere phyllotaxis-construction of leaves and sporophylls, may be included under the following heads:—

(1) Elongation of the internode below *α* prophyll to an ultimate length of 40 mm. as the special flower-stalk.

(2) Elongation of the internode above *β* prophyll to the ultimate length of 40 mm. as an additional section of the flower stalk, which moreover effects a curvature in its upper region, this being directed by the stimulus of light. Flowers thus bend over towards the most strongly illuminated side, or in the open all face South. The amount of curvature is also variable; the majority of flowers turn sufficiently to place their long axis at an angle of about 135° with the vertical; in some cases flowers become quite doubled over by the extreme activity of this growth phenomenon, and the spurs thus project almost vertically upwards. When growing under sheltered conditions, the curvature is often less, and the flower points horizontally. The position in which the spur is directed obliquely upwards appears to be the normal one (cf. *Delphinium*).

(3) Elongation of the petal-spur and the included nectaries, which only takes place as the buds become full-sized.

(4) *Recurvature* of the posterior petals, a growth-extension phenomenon only attained on the expansion of the bud. In a newly opened flower the strength of this curvature is not only sufficient to roll back the posterior sepal, but if this be removed the petals bend back to a much greater extent.

(5) *Elongation of the Style* and bending of the apex to a hook at right angles with the

shaft: this growth-zone is of the greatest importance, since it is clear that it at once produces a cross-pollinating mechanism when the stigmatic-tip is definitely carried beyond the anthers, and outside the chamber roofed in by the large connective-flaps, while the direction of the curvature is controlled by the zygomorphy of the flower. The flower bud, originally differentiated as a structure in which self-pollination would naturally ensue, thus becomes a mechanism inviting cross-pollination by the aid of insect agencies.

(6) *Distribution of pigment.*[1] The main portion of the petals is coloured intense 'violet'-blue by a soluble pigment (anthocyan-derivative) localized in the epidermal cells of both surfaces: it is especially abundant over the main veins, and thus gives an elaborate veining to the anterior petal, at the base of which the pigment is concentrated over the veins and lessened in the intervening spaces. To what extent this is an intentional production of guide-lines is here doubtful (cf. *V. tricolor*). The anthers are yellow (xanthophyll-derivatives); the gynoecium and nectary-tails retain chorophyll, and a bright orange pigment is localized in the connective-flaps. The latter undoubtedly affords a useful contrast with the violet of the petals, whatever may have been its primary significance.

(7) *Development of hairs.* As a *Viola*-type, *V. odorata* presents a feeble development of hair-structures; the stamens, style, and nectary-lobes being smooth, and only in the last case a few small papillae may occur on the outer surfaces.

The *ovary*, however, produces simple hairs on its upper surface, where it becomes exposed between the connective-flaps; and these 'packing-hairs', which are undoubtedly protective in function, are continued down the ovary wall in 10 more or less marked lines corresponding to the gaps between the anther-lobes.

Hair-fringes occur in the form of a few simple hairs on the lateral petal-bases, which also protect the inner members, and have the additional function of preventing lateral access to the spur (cf. var. *imberbis*, in which they are wanting).

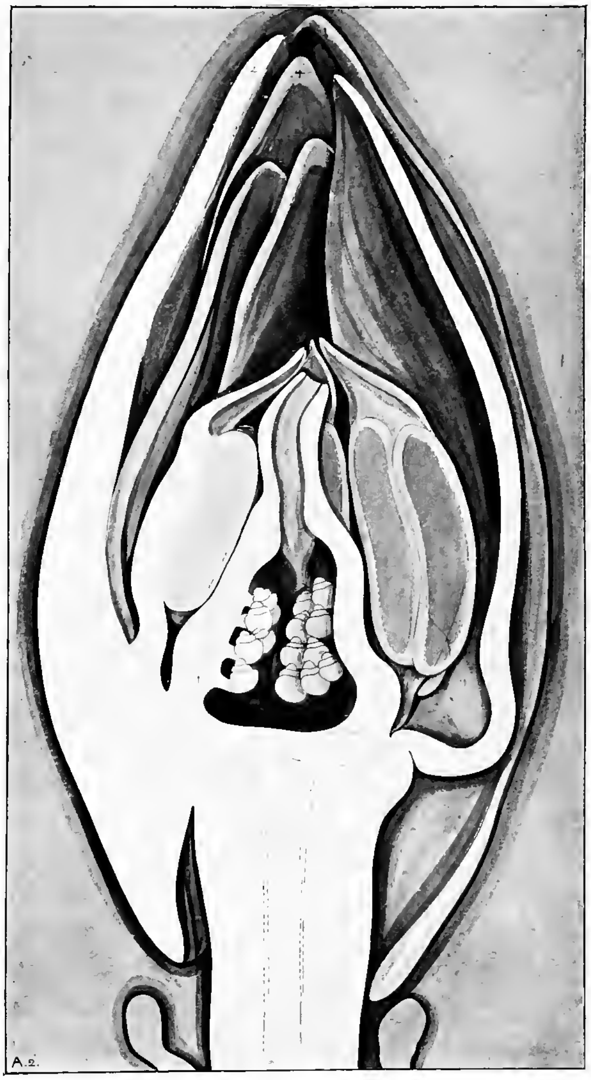


Fig. 5. *Viola odorata*; 2 mm. bud showing commencement of final specializations, nectary and spur, filaments and style.

The floor of the entrance-groove is also covered with papillose hairs with smooth rounded apices, the meaning of which is not

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[1] Previous to the introduction of litmus, this violet pigment was used as a colour-test, the change to red with acids, and green with alkalies, being very delicate. For this purpose the plants were formerly grown in large quantities at Stratford-on-Avon, a 'syrup of violets' being prepared, or strips of paper dyed with the colouring matter.

The analogy of the familiar litmus-reaction is apparently responsible for the idea that the colours seen in so-called 'anthocyan-pigments' are to be also regarded as indicating the acid (red), neutral (violet), or alkaline (blue) nature of the cell-sap of tissues presenting these colours. Note that there is no reason to believe that this is the case; consideration of the exactitude of the processes required to produce in such a manner the exact violet, lilac, or mauve tint peculiar to many flowers, in all the cells of a petal, is alone sufficent to indicate the deficiencies of the older conception. Many of the red derivatives are undoubtedly present in acid sap, but the blue tints are more probably to be regarded as oxidation-derivatives.

clear: they may be possibly utilized as footholds by insects which insert their fore-feet into the tube, or by being slightly rough serve to direct the proboscis to the upper side of the tube. Differentiation of these hairs, the primary function of which remains uncertain, is much more important in allied forms (*V. tricolor*).

From the general features of the adult flower the following conclusions may be drawn:—

The bright colour, strong scent, and special storage for a secretion which might otherwise be aimless, indicate adaptations for insect-guests.

The honey is concealed, and the pollen supply also is difficult to obtain. Pollen-seeking flies and bees thus appear to be eliminated. To obtain honey a proboscis will be required sufficiently long to reach from the style-tip, which blocks the entrance to the spur, as far as the secreting surface of the nectaries.

This distance, which may be termed the *working distance* of the flower, is here 6–8 mm.

The asymmetry of the flower thus appears to be correlated with a spur-mechanism adapted for the visits of insects seeking honey; these being provided with a proboscis at least 6 mm. in length. Other insects are practically excluded; hence the flower may be described as a 'bee-flower'.

## Pollination.

The curvature of the flower-stalk in response to the directive agency of the strongest light is effected before the bud expands; and it is clear that the strong recurvature of the posterior petals is an exaggerated form of the growth-extension which constitutes the 'opening' of the bud. The flowers offer honey only, the pollen being protected from collection by the position and close fitting of the anthers around the ovary.

The stamens shed as the bud expands, and the stigma being at the same time receptive to pollen, the flowers may be described as *homogamous.* The honey is concealed in the spur, and the whole flower is evidently arranged to be looked at from one particular point of view. To an insect, for example, facing the flower as it is suspended obliquely forwards in the vertical plane, the anterior petal appears as a spoon-shaped landing-stage; the lateral petals assist in limiting the sides of the entrance, while the posterior are recurved well out of the way; the entrance to the spur appears as a dark hole, fringed above with the white hairs at the base of the lateral petals, while in its upper part the hooked style projects down like a fang. Access to the honey must necessarily be under this style-hook; pollen is shed on to the floor of the groove leading to the spur, and any attempt at licking the nectaries must result in pollen being rubbed or shaken on to the base of the proboscis. Cross-pollination is thus readily effected when other flowers are visited, and the base of the proboscis in passing the stigma-hook will scrape off pollen-grains into the cavity of the stigma. This is less likely to be done with the pollen of the same flower in the act of withdrawal of the proboscis, and so cross-pollination will tend to be most usual. Self-pollination by insect-agency does not appear to be absolutely eliminated, and the flowers are freely fertile to their own pollen. It must be noted again that the fact of the projection of the style-hook beyond the anthers at a late stage of development is a structural feature which tends to eliminate self-pollination and increase the chance of crossing, apart from any experimental observations on the value of such a process.

The flowers are functional for 6–8 days, and are industriously visited by several early bees. Large Humble-bees, although clumsy, and too big for the flower, take honey and pollinate the flowers successfully in the correct position, their proboscides being well over the required length. The Hive-bee is perhaps the most frequent visitor in gardens: as its proboscis is little over 5 mm. long, it has considerable difficulty in working the flower. The time taken is also considerable; it may take half a minute or more to struggle with a single flower. The Hive-bee is evidently not the insect whose visits are most sought; alighting on the back or side petals, the bee forces its head into the entrance to the spur with great violence, rolling over as it does so, until it is standing on the recurved posterior petals and working the flower upside down; the stigma and anther-cone are thus pressed out of place, but the bee manages to get its head within working distance.

The most active and at the same time most elegant worker is the bee *Anthophora*, which pollinates so many spring flowers. Having a proboscis of 21 mm. it hovers over the flower, with proboscis half extended, just alighting and grasping the edges of the anterior petals with its fore legs; in this position it can probe the base of the spur with its long slender proboscis with the greatest accuracy; and it may be timed passing from flower to flower, and taking less than a second to examine a blossom, though it stays longer when honey is abundant. It is evidently this class of medium-sized insect with long proboscis which is correlated with the evolution of the special-mechanism of the Violet flower. Further, when it is seen how delicately the mechanism can be worked by *Anthophora*, as opposed to the clumsy manœuvres of the Hive-bee, it begins to be clear that the placing of the anthers in a compact conical group, closed above by the large orange connective-flaps, is a means of affording a delicate powdering-mechanism; the pollen being dusted out through the small open end of the cone on to an inserted proboscis, when the cone or the style-hook is gently touched. The precision of the mechanism when well worked may be thus greatly increased, while it is obvious that such a powdering-mechanism will be greatly improved if the anthers unite laterally to a definite anther-tube (cf. *V. altaica*).

*Note* that it does not follow that merely because a given insect is observed to visit a flower, that it has had any necessary connexion with the evolution of the floral-mechanism, even though this may be clearly adapted for insect-visits. Mere enumeration of all the insects seen to visit a flower is not so much the point to be aimed at, as the consideration of how each may be fitted to work the flower. The adaptations between insects and flowers are mutual, and a highly specialized floral mechanism is usually correlated with a high degree of specialization on the part of the insects which visit it.

The Hive-bee is a clumsy visitor so far as the Violet is concerned, but it visits every possible flower in spring in the hope of getting something; *Anthophora*, on the other hand, is a delicate worker, beautifully adapted for such a floral-mechanism (cf. *Primula*, *Vinca*), and similarly it is equally possible that Lepidoptera have been largely concerned in the evolution of *Viola* forms (cf. *V. altaica*).

### Cleistogamy.

The flower-buds are practically fully developed in the cool moist autumn months after the summer dry season, and perennate through the cold winter, being ready to grow and open as soon as the weather becomes mild.

Hence plants kept under favourable conditions flower directly (October, November). The foliage and some of the more developed buds which are freely exposed are apt to be damaged by frosts, and thus relatively few of the flower-buds laid down during the autumn produce functional flowers. Each of the leaves of an autumn rosette may subtend a flower-bud, and a full cycle of 5 good buds is commonly observable (November).

In the spring (March) the flowers arise in the axils of the old surviving perennating leaves, which now lie close to the ground and have been more or less damaged by frosts. The whole flowering-period lasts about 4 weeks. The first week (end of March or early in April) the flowers open with very short stalks (1–2 inches) just clear of the old foliage; the new leaves being very small. Patches of plants now look quite blue as the flowers curve to face the light. The first crop may consist of as many as 3 flowers to a rosette, and all may be out simultaneously.

At the end of the second week, the flowers are still more abundant, but they now possess much longer stalks, and the new leaves are becoming bright green and stand erect on the rosettes; the leaf-stalks 1½ to 2 inches, and the flower-stalks 3 inches: the fact that the prophylls are still half-way up the flower axis shows that both internodes are concerned in this last elongation. At this time the flowers of the first series are faded, or are setting fruit; and in the third week the foliage-leaves are growing to such an extent that they completely cover the flowers, the leaf-stalks being 80–100 mm. or 4 inches long, and the laminae large and bright green. Only late stray flowers are now available, buried in the foliage, and thus quite hidden from sight (middle of April).

The vegetative growth of the plant becomes still more vigorous and reaches its maximum in May, the leaf-stalks being then fully 6 inches long. About the middle of May the foliage is the most conspicuous portion of the plant, and the first fruits have reached their full size, and lie along the surface of the soil; on the other hand, the flower-buds arising in the axils of the new leaves are checked in development by the extremely active vegetative growth; they are in addition out of sight, and practically in the dark when the plants grow closely together, as is their habit. Such arrested flower-buds are found in all conditions, from nearly full-grown buds with coloured petals, to small 1–2 mm. buds. These flowers never develop the full floral-mechanism of secondary growths, and remain in the primary self-pollinating condition (Figs. 4–5). Being hidden by the foliage and kept in a fairly damp, sheltered environment they become *cleistogamic*, and the pollen-grains germinate *in situ* and come into immediate contact with the stigma.

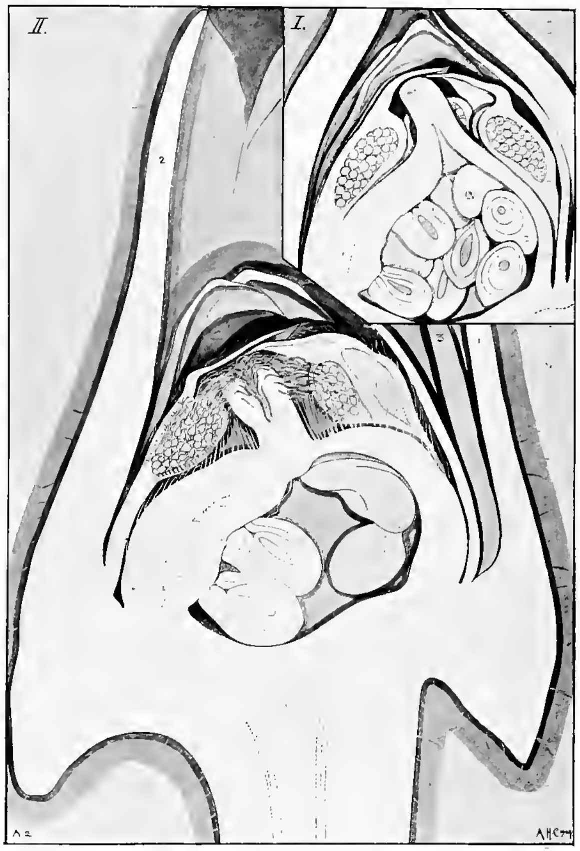

Fig. 6. *Viola odorata*, summer buds showing cleistogamy. I, before the germination of the pollen; II, after pollination has been effected. (3 mm. buds.)

*Observations* of the details of the cleistogamic pollination are readily made on material collected during May–September; the 2–3 mm. reduced flowers are borne on slender flower-stalks, and may be cut in median longitudinal section (Fig. 6).

The floral-construction remains as a whole at a stage near that figured (Fig. 5), with the addition of fully matured pollen-grains and adult ovules. The pollen-grains are, however, fewer in number than in normal flowers, and the ovules are also fewer (about half the normal). The anthers lie against the ovary wall, and the distance from the uppermost pollen-grains to the end of the rudimentary style is extremely small (about 5 or 6 diameters of the pollen-grain). The style is crumpled against the connective-lobes which completely roof in the gynoecium, and is thus brought into direct contact with one or more of the anthers. The pollen-grains germinate within the pollen-sac; and the stamens, although possessing a well-marked fibrous layer, being kept moist, do not dehisce normally. The apex of the loculus is ruptured (cf. *Richardia*), probably merely by the pressure of the germinating spores within it, and the pollen-tubes pass directly on to the style, and may be traced in the ovary cavity (Fig. 6). All the ovules in the ovary may be pollinated, but as these are few (10), fruits produced in this manner do not develop anything like the number of seeds in a normally cross-pollinated fruit. It is curious to note that practically every pollen-grain inside the loculi of the anthers of these flowers germinates.

Not only do the young flower-buds developed in the axils of the new crop of foliage-leaves (March) remain in a rudimentary condition and so become cleistogamic (May, June), but the buds borne in the axils of the rudimentary leaves of the stolons may also similarly degenerate (August). The vegetative part of the plant is at a standstill over the dry season, but the flower-buds developed in the axils of the next young leaves produced in autumn will be the normal flower-buds of the succeeding spring. It is possible that a reason why such flowers, which are not wanted for the optimum flowering season, should continue to develop self-pollinated seed instead of aborting, may be found in the fact that they are borne in the axils of vegetative leaves which are vigorously assimilating, or on vigorously growing stolons, so that although they are shaded and kept moist under the crop of foliage-leaves, the food supply will be abundant and close at hand. Violets obtained in November ('Czar' Violets, forced in a warm frame) show all the anther-loculi filled with germinating pollen-grains, just as in cleistogamous flowers. This ready germination of the pollen may thus represent the first stage in cleistogamy, which, however, only becomes of physiological importance when occurring in a floral-mechanism still capable of a direct method of self-pollination. Adult mechanisms in which the stylar-zone has been added can never become cleistogamic, even if the pollen-grains do germinate *in situ*.

For a closely comparable phenomenon cf. *Oxalis Acetosella*, which will, however, continue the production of cleistogamic flowers and fruits during the summer months on a hot exposed garden bed, when the foliage is very feebly developed.

There is no reason to regard the production of cleistogamic flowers as at all an act of *compensation* for a lack of normal fruits, owing to failure of the mechanism of cross-pollination.[1]

Plants of *Viola odorata*, growing in good soil on a sunny bank, or in an exposed garden-border, produce large quantities of flowers in April (main crop), and every flower may set good full capsules; the soil being covered with fruits during May: similarly, observation of the working of the flower by insects (cf. *Anthophora*) shows that there is no failure either in the mechanism of pollination or in the number of insect-visits or visitors; while not only are the cleistogamic flowers degenerate as mechanisms, but they are also degenerate from the standpoint of spore-production, and the resultant fruits are smaller and contain much fewer seeds than the normal capsules.

### **Monstrosities.** (Cf. Masters, 1869; Penzig, 1890.)

Since the flowers have been so long and so extensively cultivated, an enormous number of variations and irregularities have been recorded, and an attempt may be made to reduce such aberrant forms to some sort of a system. The more usual variations and interesting exceptions may therefore be included under the following heads:—

(1) '*Fasciation*' *phenomena*, including the multipolar growth-system of the vegetative shoot which may occur in almost any type; and '*Synanthy*' of the flower, in which commonly the apex of the floral axis becomes bipolar, and each centre produces some members; a curious type of doubled flower being thus generally produced (Masters, 1869).

(2) *Variations in the phyllotaxis-construction scheme of the flowering shoot.*

- (α) Substitution of *tetramery* for pentamery; flowers of the form 4 sepals, 4 petals, 4 stamens and 2 carpels being found, with or without peloric additions (Forbes, 1848, (?) *Viola canina*).
- (β) Partial production of *trimery*, with peloria (Forbes); 3 sepals, 3 spurred petals, 5 stamens.
- (γ) Partial *Dimery* with peloria; 2 sepals, 2 spurred petals, 4 stamens, 2 carpels (Hildebrand, 1862).
- (δ) Incomplete substitution of *Hexamery*; 6 sepals, 7 petals (Bode).
- (ε) Flowers possessing 4 carpels with cruciate orientation (diagonal placentas) are common among cultivated varieties ('Czar' violets).

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[1] On the other hand, there can be little doubt that the 'cleistogamic habit' is more constant in some individuals than others, but to what extent it is induced by unfavourable cultivation, or becomes a varietal factor, requires further investigation.

(3) *Indefinite extension of the Floral members*, more particularly as petaloid forms, representing the general case of 'Double-flowers'.

These are of very ancient origin; they are described by Theophrastus; and in more recent times figured by Lobelius (1576), and Tabernaemontanus (1588), as *Viola Martia purpurea* and *alba multiplex*; cf. Gerard and Parkinson. The primary (3 + 5) construction is continued indefinitely beyond the calyx, and instead of a symmetrical (5 + 5) system being attained in the corolla, petaloid-segments are produced in cycles of 5, and the arrangement may be continued for over 50 members.

In such cases spurs may be present or absent on the outer members of the series, or in a rudimentary condition.

Such flowers are always sterile, and at best have only a rudiment of the gynoecium.

A simple type (A. de Candolle, 1841) gave 5 + 5 + 5 petals and 5 carpels.

(4) *Prolification* of the floral axis; a new flower-bud continuing the growth, and growing up inside the ovary which may even contain perfect ovules (Clarke, 1866). (Cf. *Helianthemum*.)

(5) *Irregularity in the mechanism of spur-production.*
- (α) More spurs than one; 2–3–4 being found on as many petals ('Irregular Peloria'), a very common case: symmetrical development of 5 spurs on all 5 petals ('Regular Peloria'), De Candolle (1827), Hildebrand (1862), Pasquale (1877).
- (β) No spurs at all, hence regular flowers.

(6) *Confusion between members of different functions.*
- (α) Green petals (general in double-forms).
- (β) Petaloid (more or less) stamens (= sterilized sporophylls).
- (γ) Rudimentary ovules on green members (Henslow, 1882 (?) 'papilliform structures on margins and midribs', possibly = marginal glands).
- (δ) Segmented dwarfed posterior petals (Camus, 1885).
- (ε) Sepaloid petals with no spur (Camus, 1888).

Of these, the attempts at Tetramery, Dimery, &c., are of theoretical interest, as indicating a radical change in phyllotaxis-construction comparable to that obtaining in Tetramerous and Dimerous families.

*Note* that loss of spurs, as also regular forms, suggests an ancestral condition, not by any *reversion*, but simply owing to failure in adding a new feature to the mechanism.

Similarly (6, δ) also suggests a phase found in recent allied genera, in which the primary eccentricity is alone present, with the result that the anterior member is far larger than the others.

With the exception of the doubtful case (6, γ), there is really nothing very *monstrous* in any of these multitudinous variations; they may all be referred to failures in the adjustment of certain features of the floral-construction or mechanism, and again are of no phylogenetic assistance except in so far that some of them often suggest the elimination, more or less perfect, of a single construction factor.

## **Fruit and Seed.**

At the close of the flowering-period the petals wither, tend to lose their violet colour, and are soon shed: the ovary rapidly enlarges and the anther-cone is pushed off; the developing fruit being protected by the persistent green sepals which close up over it, and retaining at its apex the withered stigma and style.

The fruit attains full size in 2 weeks, as an ovoid green capsule which presents no particular peculiarities; it is merely the ovary-portion of the gynoecium grown large; the upper portion of the flower-stalk also becomes more bulky, and the weight of the fruits on the slender stalks renders them more or less procumbent. They are thus completely hidden from sight under the new crop of foliage-leaves, and kept moist on the surface of the soil.

The main crop of capsules mature their seeds in mid-June, or about 8–9 weeks from pollination.

The green *fruits* are slightly 3-angled, fairly globular capsules, 12–10 mm. long by 8–10 mm. in diameter; they are covered with short downy hairs, and the blue pigment (anthocyan) reappears in the epidermal cells of the wall when they are exposed to direct sunlight. When ripe they dehisce along 3 lines which alternate with the placentas.

*Note* that, since the ovary is entirely a gamocarpellary structure, and there are no sutures in its wall, these lines of dehiscence are wholly new formations, put in where they will be least in the way, since the massive placentas carry up all the food to the developing seeds (cf. Snowdrop, Crocus).

Section of the ovary-wall shows a mass of large, elongated, horizontally radiating, sclerosed and pitted cells backing the 3 placentas; the cells of the placentas themselves being mainly of cellulose, and their walls slightly collenchymatous. The bulk of the capsule-wall is unmodified parenchymatous tissue, but the sclerosed bands of the placentas are continued outwards as 2–3 horizontal rows of sclerosed-fibrous cells, and these constitute an inner lignified lining-layer to the 3 valves, and enable them to retain their shape, while at the same time the enclosed seeds are protected from desiccation.

The capsules open in the form of 3 valves which diverge from the base, and each valve, in virtue of the collenchymatous placenta, tends, as this dries, to fold in on itself.

This hygrometric action is not sufficient to flip the seeds off, as in allied forms (*V. tricolor*), but it is enough to loosen them from their point of attachment, and they all fall out in a cluster on to the soil.

Since all the ovules may produce good seed the number in one capsule may be 20–36.

The *seeds* themselves, derived from ordinary anatropous ovules, are ovoid, nearly 3 mm. long by 2 in diameter, with a well-developed white 'aril' as a projection 2 mm. long at the micropylar end. The raphe can be traced down one side, and terminates at a slight chalazal knob. Section in the plane of the raphe shows a thin brown testa, of which one layer of oblique, columnar stone-cells is beautifully lignified and pitted, and evidently protective; a copious endosperm, the cells of which have slightly thickened walls, abundant fat, and crystalloidal aleurone-grains; and a well-developed embryo, lying straight down in the endosperm from the micropylar end; the orientation of the 2 cotyledons, as seen in the circular transverse section, being inconstant.

There is also a chalazal patch of brown tannin-containing cells; and a chalazal plug of sclerosed pitted cells continues the oblique lignified layer of the wall across the base of the nucellus.

The 'aril' process around the micropyle consists of thin-walled cells with frothy protoplasmic contents, and represents the greatly-developed lips of the outer integument. Development also shows that the special oblique sclerosed layer of the testa is derived from the outermost layer of the inner integument (cf. *Daphne*); external to this the outer integument remains undifferentiated and thin-walled, only at the chalazal end does it become lignified. There is also a small cuticularized nucellar plug under the micropyle.

*Note* that the embryo is supplied with reserve food in the endosperm cells in the form of cellulose, fat, and proteids; it is highly protected from desiccation by the lignified testa-layers of special origin; and that there is no modification at all in connexion with distant dispersal: the white succulent-aril tissues being probably a relic of an aqueous storage tissue in the developing seed; and although it contains a certain amount of proteid matter, there is no evidence that it is intentionally provided as a food-body for hypothetical seed dispersal by the agency of ants, although these insects are partial to such juicy plant structures.

## Comparison of Allied forms.

### I. Viola tricolor, var. arvensis, L.[1] Corn Pansy.[2]

A small herbaceous corn-field weed, with prostrate trailing shoots a foot or more in length, flowering freely throughout the summer months (May to November), usually growing as an annual, being cut down by severe frosts, but perennating in sheltered situations.

Indigenous and abundant through Great Britain (to Shetland) and Ireland, and widely distributed over Europe, Asia, including Siberia and Japan, though only in North America as an escape from cultivation.

This varietal form (*V. arvensis*,[3] Murray, 1770) was early separated as a definite species; but it is probably better to regard it as one of the forms of the very variable *V. tricolor*: its special point of interest being that it is distinctly the most depauperated variety of the very definite *tricolor* type,[5] though the reason for its remaining so remarkably constant is not apparent.

*Structure of the Vegetative Shoots.* In *V. odorata* the short woody stem, which in old plants reaches a length of 3–4 inches, has a terminal cluster of a few leaves (double cycle = 5), and the growing-point continues its growth indefinitely over succeeding seasons.

Each year's growth is about $\frac{1}{2}$ an inch long, and the lateral axillary branches are all of the form of stolons which elongate a few (4–6) internodes, and then produce a vegetative rosette which may root and constitute a new 'plant'. The stolons do not immediately die away, but may remain connected with the parent axis for 3–4 years, 1–5 being produced each year; their age may be checked by counting back the series on the shoot, and by observation of the annual rings in the poorly-developed xylem bundles. Their length is not great, and competition in the centre of a Violet patch is keen, hence younger shoots tend to choke out older ones; the average length is about 6 inches, but in the large cultivated forms (cf. var. 'Princess of Wales'), in which the vegetative portions and flowers equal the type, × 2, they may be over a foot long.

In *V. tricolor* the arrangement of the vegetative shoot is very different, and possibly more generalized than that of *V. odorata* in some respects, though not in all.

The main axis continues its growth throughout the summer, easily reaching a length of $1\frac{1}{2}$ ft. in good ground, and growing quite as strong as the Garden Pansy, from which it may be difficult to distinguish it (var. *arvensis*). The leaves possess large dissected stipular lobes, and the leaf-stalks are not well differentiated; internodes are elongated between the leaves throughout the shoot, and the phyllotaxis-construction is similarly a Fibonacci type (2 + 3).[6]

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[1] The *Herba Trinitatis* of Brunfels and Fuchs[4] who gives a figure of it (1542), less satisfactory than usual, and doubtfully the form now called *tricolor*, as grown in gardens at that date. The figure given by Brunfels (1531) is quite good. 'Trinitatis et herbam et florem vocatam vulgo estimo, ob flosculos quos habet tricolores, quibus nihil iucundius, nihilq; magis admirabile.' It was named *Viola tricolor* by Dodoens (1583), and the name was continued by Clusius and Gerard (1597); cf. *Viola trinitatis* of Tabernaemontanus (1588), and *Viola tricolor hort. repens* of Bauhin (1623).

[2] Gerard gives *V. tricolor* in four varieties, as Hartes ease and Paunsies. 'The three-colored Violet' or 'Herb-Trinity'; French, Pensées, and thence to Low-Countries and England as Pansies; other old English names are 'Love-in-Idleness' and 'Three faces in a hood'.

[3] The form *arvensis* was separated by old writers at an early date; cf. *Viola tricolor arvensis* of Bauhin (1623), and *Viola trinitatis minor petraea flore albo* of Tabernaemontanus (1588); the block of this latter figure being afterwards used by Gerard.

[4] A much better figure is given by Matthiolus (1563) as *Viola trinitatis*; his figure of *V. odorata* is also excellent.

[5] Thus De Candolle (1824) included var. *arvensis* with fifteen other sub-varieties of the *tricolor* type; the large-flowered garden-form being indicated as var. *hortensis*.

[6] (B. G. O., 1904.) Plants were observed in which the internodal elongation was intercalated only between *every other leaf*; leaves being thus isolated with their axillary flowers in pairs diverging at an approximate angle of 137° at each apparent node. Section of the apex confirmed the construction, and that it was not, as at first appeared probable, a variation to (2 + 2) or (2 + 4). The two flowers were functional simultaneously.

Beyond a seedling stage, represented by the first series of 5 or 6 leaves, *every foliage-leaf subtends a flower*; and as the growth of the shoot proceeds, new flowers are produced in acropetal series, and the shoot goes on developing and pollinating flowers, and shedding seeds, as long as the weather is favourable (November). Thus the flowers had been continued to 20 members on a main shoot by the middle of November; the apex was still active and half a dozen flower-buds were in sight; the lateral axes also having proceeded as far as 10 flowers.

Vegetative ramification takes place from the axils of the first seedling leaves, from the axils of the prophylls of these branches, and from *accessory buds* developed behind the flower-stalks. These last usually grow only after the shedding of the seeds, but will develop branches when the plants are propagated by layers or cuttings.

Similarly branches from the lower region of the shoot increase the ramification of the plant in the same summer, and some of their axillary buds may persist over the winter when the long trailing shoots are killed (cf. *V. altaica*).

*Note* also that the stipules are but basal-lobes of a primary leaf, and the elongation of the central portion alone on a new growth is certainly secondary; thus the subsequent specialization of the median-lobe alone for assimilation-purposes may be a later adaptation (*V. odorata*). The first leaves of the stolons in *V. odorata* are also reduced to a form resembling that of the stipular lobes of the same plant, and this also is clearly secondary. The marked distinction between the assimilating-lamina and membranous 'stipules' of *V. odorata* may thus be as secondary a modification of an older type approached by *V. tricolor*, as is the structure of the shoot-system itself. *V. tricolor* represents a more generalized form so far as the internodal structure of its non-perennating leafy shoot is concerned, and possibly in its foliage also. *V. odorata*, on the other hand, has the perennating woody stem and permanent growing apex, but differentiates its vegetative shoots as foliage-rosettes and runners. So far as the vegetative system is concerned, the two types may possibly be regarded as divergent, biologically-adapted, forms arising from a perennial woody type of growth (or shrub), which presented a normal appearance of internodes and foliage-leaves; the adaptation again being required to enable the plant to withstand periods of winter-cold, especially in the form of cold winds. *V. tricolor* has thus become practically an annual, i. e. perennating only in the seed stage, and still repeats in summer weather the free construction of a milder climate.

*Note* also that the free and continuous flowering condition of *V. tricolor* evidently represents an earlier condition of the abbreviated floral period of *V. odorata*; and that the latter still maintains, almost perfectly, since with the exception only of a few stolons, the general idea of producing a flower in the axil of every assimilating leaf. Similar accessory buds may also be produced in *V. odorata*, and these may give rise to stolons. But comparison of the two types suggests that the limitation of flower-production to a short spring season has not yet been fully attained; and the older habit of continuing the production of flower-buds represents an imperfect adjustment in the economy of the shoot, which thus induces the subsequent phenomena of *cleistogamy*: still this does not wholly explain why later flower-buds should become cleistogamic and produce seeds, since they might simply abort, as in the more general case when more flowers are laid down than will be required.

*The Flower* possesses a structure essentially similar to that of *V. odorata*, but presents a few features of further elaboration.

I. Development of the corolla members (*V. arvensis*) is less considerable; they are smaller and less differentiated, and the coloration is deteriorating; the violet pigment (anthocyan) may be wholly wanting; reduced to lines following the 3 main vascular-bundles of the anterior petal for a short distance only, and the central bundle of the lateral petals; or again a faint trace of violet may be present on the posterior petals, or less frequently on the whole corolla.

On the other hand, with the suppression of the violet pigment, a yellow chlorophyll-derivative appears, and the petals may be yellowish ; especially so at the base of the anterior member where it is concentrated as a prominent orange 'eye'. Coloration is very variable; and when compared with that of typical *V. tricolor*, in which these blue and yellow pigments are both strongly developed, it becomes evident that all parti-coloration, blotching, and reduction of pigmentation to lines over the vascular bundles, must be regarded as a sign of deterioration in a once uniform coloration; although it is possible that the ultimate minimum phase, which gives an effect of radiating lines, and emphasizes the 'eye' of the flower, represents the portion which is really of significance from the standpoint of insect-visits.

The flower of *V. arvensis*, in which all other violet pigment is completely eliminated, while some is left in a concentrated form on the 'black' lines, carries with it the suggestion that such a restriction of pigment is intentional as a true reduction-specialization, and is a definite biological adaptation, as a part of the attraction-mechanism; the lines being undoubted 'honey-guides' in which the vascular bundles, which necessarily converge to the 'eye' of the flower, have been secondarily utilized. In the type *V. tricolor* there are 7 lines on the anterior petal, and 3 on each lateral; the posterior petals are violet, the anterior bright yellow, with or without blotches of violet: all stages of deep violet and pure yellow may be found, while superposition of the two pigments results in bronze coloration. The large-flowered garden varieties similarly increase to 9 lines on the anterior petal.

II. The tufts of hairs on the lateral petals, wanting in var. *imberbis*, are here much more prominent; they constitute definite guard-fringes which limit lateral access to the spur-cavity, and thus directly assist the pollination-mechanism by preventing illicit visits.

III. The anther-lobes have lateral hair-fringes which interlock as they develop, and not only bind the anthers into a close ring, but by preventing the pollen from falling between the anthers, may improve the powdering-mechanism ; the pollen being shaken out between the connective-flaps of the anterior pair of anthers, which are adjusted to form a distinct pore.

IV. The stigma is no longer hooked, but dilated to a hollow globular form (1 mm. in diameter), in which the tips of all 3 carpels are concerned. Hairy patches on the sides of this stigma-head face the fringes of the lateral petals, and further assist in preventing lateral emission of pollen.

The globular cavity affords shelter to the germinating pollen-grains, it is true, but it also implies that the pollen-grains must first be placed in the cavity; an operation which is impossible without very accurate insect-working. The orifice is somewhat triangular, in correlation with the component carpels, and in the type *V. tricolor* the region corresponding to the anterior lobe becomes reflexed as a stout recurved ridge of cells which acts as a scraper to an inserted proboscis which may be dusted with pollen taken from another flower. On the other hand, when the proboscis is withdrawn, the pollen removed from the anther-cone will tend to accumulate on the other side of this scraper, and only that from other blossoms will accumulate on the orifice side, and so be gradually pushed into the germination-cavity. The knee-like bend at the base of the style is apparently connected with this as a hinge-adjustment working in the median plane. As the proboscis of an insect-visitor enters the narrow orifice below the style-head, this latter is canted upwards on its hinge, and the stigmatic-opening is thus directed forwards.

In several respects, therefore, the adjustment-mechanism for a chance of cross-pollination by insect-agency has been considerably improved; the path to the honey is still further delimited, and the elimination of self-pollination from the same flower is made apparently absolute. And not only do the new improvements aid in blocking the access to the nectary by any other path except that which takes a straight course from the stigma-lip between the two secreting spurs, but warning guard-hairs cover other points of approach.

V. The differentiation of *hairs* on parts of the floral-mechanism becomes much more elaborate.

1. The tufts on the lateral-petal bases, which block the lateral approaches, are strongly developed, and constitute the most conspicuous feature as white marks in the eye of the flower. They overhang the style-head, and afford a grasping hold to insect visitors.

2. The ovary is destitute of protective hairs; it being now completely invested by the anthers which themselves develop packing-hairs, and these by means of irregular projections take on an interlocking function; there are also small tufts of simple hairs on the sides of the style-head, and a few similar hairs on the posterior edges and tips of the connective-flaps of the anterior stamens only.

3. Hairs on the anterior spurred-petal differentiate into three varieties: (1) the papillae at the approach to the orifice are sharp-pointed, possibly warning in function, and directing the proboscis to the entrance-pore; (2) immediately beyond the angle, and inside the pore-cavity, these are replaced by a simple type (cf. *V. odorata*); while (3) a dense grove of peculiar hairs, $\frac{1}{2}$ mm. in length, best described by the word 'knobbly', fills the cavity of the groove for 2 mm. at the base of the petal and entrance to the spur. These peculiar hairs apparently function as guard-fringes to the spur-cavity. They do not injure a delicate proboscis, but may serve to keep out small injurious insects (e.g. Thrips).

4. Definite warning-papillae are developed on the upper surface of the stigma-head; these are absent on the back, but increase gradually forwards, until at the projecting end they become definitely spine-like; similar small papillae occur on the nectaries and increase in number toward the secreting tips.

5. (In var. *hortensis*; tufted hairs, similar to the patches on the lateral petals, are produced at the entrance-orifice on the anterior petal, arising among the sharp-angled ones of the yellow lip.)

*Note.* The function of the guard-fringes of the lateral petals may be checked in the case of an old flower: that attempts at illicit visits are frequent is shown by the very considerable accumulation of pollen-grains wiped off behind the fringes; pollen-grains in various stages of germination by 3–4 pores being found in the angle behind them and on the petal-bases.

That the style-head with globular germination-cavity is a successful piece of mechanism, may be observed by cutting median sections of the dried head persisting on a developing fruit: the cavity will often be found *full* of germinating pollen-grains, the tubes of which may be traced down the style-canal (very marked in treatment with Schulze's sol.; the pollen-tubes, turning dark blue, may be readily traced through the tissues).

Among other points of interest, note:—

1. The elongation of the flower-stalk is now practically limited to the internode below $\alpha$ prophyll; so that the 2 prophylls appear close up to the flower.

2. The upper internode, above $\beta$, is alone concerned in the curvature which points the flower as a whole fairly horizontally, at an angle of 90° to the stalk (in large forms, var. *hortensis*, the lower internode shares the curvature and 'nyctitropic' movement).

3. The posterior sepal is less reflexed than in *V. odorata* (only 90°, *V. arvensis*), though fully reflexed in the larger varieties.

4. The axis is slightly more crateriform; and a slight eccentric Perigynous zone is noticeable on the posterior side.

5. The full 'working-distance', as given by the distance from the stigma-lip to the tip of the nectary-spurs, is between 5 and 6 mm. (*V. arvensis*); so that a Hive-bee should work the flowers without much difficulty: though it does not necessarily follow that the more exact adjustment of the floral-mechanism is correlated with this type of insect; since its methods in the case of *V. odorata* have been seen to be clumsy, rather than suggestive of increasing accuracy.

In the type *V. tricolor* the working-distance is also 6 mm.; and in the large 30 mm. flowers of garden varieties, 6–7 mm.

6. *V. arvensis* has often so feebly developed a lip to the stigma-cavity, that it appears to be negligible, and self-pollination is effected by insect visitors. The mechanism, although more elaborate in some details than that of *V. odorata*, is evidently a slightly degenerated form of *V. tricolor*; and thus other reduction-phenomena, such as decrease in the pigmentation, and in the size of the corolla-members, are possibly correlated with increased chances of self-pollination.

Degeneration of the floral-mechanism may be even carried to a further extent in plants growing in damp shaded situations; as also in flowers produced in late cold months (November). In such cases the flowers never reach full adult status, and remain in more or less imperfect stages of the mechanism; so that if the pollen-grains germinate, they remain self-pollinating mechanisms, which are described as *cleistogamic*, although it is not essential that the flower-buds should be *closed*. All degeneration-stages may be observed in *V. arvensis* under the action of unfavourable environment (usually enfeebled light-supply), and the mechanism of cleistogamy is clear on reference to that of *V. odorata*.

It may be noted that one of the most important factors of such cleistogamy is the extreme readiness with which the pollen-grains germinate, so long as they are kept in moist air; thus, as previously noticed, they will germinate freely when lying on the basal surface of the lateral petals.

7. Three special growth-movements connected with the floral mechanism;—(1) the stalk-curvature, (2) the curvature of the posterior sepal, (3) that of the posterior petals,—being phenomena of unequal growth-expansion of turgid cell-layers, present phenomena of daily *periodicity*, which are observable during the first half of the flowering-stage: the turgidity of the active cells being greater by day (morning), and less at night (evening), with the result that the curvatures are slightly modified towards night, and the flowers thus tend to droop forwards and half close towards evening. Such movements have been described as *nyctitropic*, but there does not seem to be any reason for regarding them as anything more than subsidiary phenomena of the mechanism of growth extension.[1]

8. Note also that in *V. tricolor*, and to a less extent in *V. arvensis*, the colour which depends on different amounts of pigment may vary from flower to flower, even on the same plant, or in adjacent flowers of the same shoot; such variation being a further sign of deterioration in the pigmentation-mechanism.

9. In *V. tricolor var. hortensis* the flowers may be 30 mm., by 25 mm. across; the larger they become, however, the more marked do their differences from *V. altaica* appear: the habit is relatively more graceful and slender, and the flower is always more oblong than circular. The lower internode of the stalk shares in the growth-curvature; the stigma-lip is more pronounced, and the hairs on the orifice of the flower more differentiated; the working distance is increased to 7 mm., and the nectary-tails are distinctly papillose, especially at their tips. All the data agree closely with those given for the type *tricolor*. They are pollinated by long-tongued species of *Bombus* and by *Anthophora*.

Pollination. The general idea of the mechanism is sufficiently clear: the pollen shed from the introrse anthers no longer falls between the anthers and connective-flaps, but is directed into a *pollenic chamber* formed by the latter; the anthers being interlocked by their hair-fringes. From this chamber the pollen is dusted on the head of a visiting insect through a small round orifice between the connective-flaps of the two anterior

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[1] A peculiar phenomenon of reduction of the type may be noticed in late strays of *V. tricolor* (as also *V. altaica*) when produced in cold weather at the end of the season (Dec.–Jan.), the primary eccentricity of the flower alone obtaining; then while the anterior petal forms a large lip, the posterior and lateral petals remain small and closely applied to one another. The erection-curvature of the posterior petals also fails, and the whole mechanism thus takes on an appearance strongly suggestive of an ancestral form by the elimination of some of the final adjustments of the floral scheme.

stamens, this orifice being immediately below the stigma-orifice and only separated from it by the stigma-lip.

The mechanism of pollen-dusting is thus extremely precise if the flower is delicately worked; and cross-pollination will be readily effected by an insect which approaches the mechanism in the requisite manner: on the other hand, rough treatment is likely to disarrange the mechanism, and result in pollen from the same flower being pressed into the stigma-cavity. The fact that the mechanism is so beautifully adjusted conveys with it the impression that accurate workers will eventually be encouraged at the expense of clumsy ones; in other words, that such a mechanism must be passing on to exclusive pollination by long-tongued insects alone.

Again, possibility of the failure of the adjustments is not wholly eliminated. The pollen is shed from its chamber on to the lip of the anterior petal, and the style-head may easily come to rest on practically the same spot: in the normal condition of the flower it is only kept away from it by a correlation of the turgidity of the cells of the style-shaft, and the petal midrib. Similarly, the stigma-lip is the only boundary between the cavity of the pollenic-chamber and that of the stigma. If the stigma-lip is badly differentiated, or the style droops on to the surface of the anterior petal, pollen-grains have not far to send their tubes in order to enter the germination-cavity. This appears to occur in the depauperated blossoms of *V. arvensis*; and a loophole for *autogamy* is thus still left in the mechanism.

Insects with proboscides of 6 mm. in length, by struggling with the flower, usually promote self-pollination (cf. Hive-bee, 6 mm.). A bee with even a 4 mm. proboscis can with difficulty get a certain amount of honey, and similarly promotes self-pollination (*Andrena* 2–3). The flowers are less adapted for bees with short proboscides and bulky mouth-parts, as the entrance beneath the stigma-lip is extremely narrow.

The flowers are freely visited by such long-tongued bees as *Anthophora* (21 mm.), *Bombus hortorum*, and several other Humble-bees; the terminal portion of the proboscis of these insects being sufficiently slender.

Similarly, butterfly visitors can readily obtain honey (Cabbage-white, 16 mm.); and the mechanism is successfully worked by these insects with a minimum chance of self-pollination, owing to the fact that the flowers expand in series on each shoot.

A flower lasts about 1 week in hot summer months, 2 weeks in the spring, and even 3 weeks in cooler months and late autumn; as one flower withers the next expands, and the series is continued as long as the weather is mild (November).

Flowers isolated from insect-visits do not set good seed; but they are freely fertile to their own pollen if this is applied artificially.

Fruit and Seed. Details of fruit-development agree with those of *V. odorata*; the ripe capsules being very similar in structure, small, ovoid, 8 mm. long by 5 in diameter, retaining at their apex the withered style-heads.

The seeds are numerous (50–60), or as many as 20 on each valve. The differentiation of the fruit-wall is also further specialized, in that the sclerosed pitted-cells are more abundant and have thicker walls; in addition to the radiating pitted-elements grouped along the length of the placentas, a zone of transversely elongated, much thickened and pitted, fibrous-cells forms a complete investment external to these and surrounding the whole wall. The parenchymatous cells of the placental-region become still further collenchymatous, and on desiccation constitute a strong placental hinge on which the firmer portions of the wall fold together. Dehiscence is thus associated with two hygrometric movements; (1) the general divergence of the valves, produced by the contraction of the outer unmodified cellulose layers of the wall; (2) the folding in of the valves individually. The latter phenomenon results in the expulsion of the smooth seeds under pressure of the strong valve-edges, and they are thus flipped out for a distance of several (5–6) feet. In that these movements are hygrometric, wetting the capsule produces the reverse effects; the separate valves open, and then they all close up again. It is interesting to note that the collenchymatous tissue soon decomposes, and in a short time the capsule-valves being reduced to lignified skeletons open out flat. The lignified cells of the inner ovary-wall again undoubtedly afford considerable protection to the developing seeds, so that the utilization of these in the dehiscence-mechanism may, as in other types, be largely secondary; the high specialization of the collenchymatous hinge-mechanism can, however, be only regarded as a definite adaptation intended to discharge the seeds; and it is again correlated with further adaptations in the testa, which do not occur in *V. odorata* which does not thus propel its seeds.

The *seeds* are small ovoid ($1\frac{1}{2}$ mm. by 1), with a brown, polished surface, and a small white 'aril' growth on the *hilar* region.

Section in the plane of the raphe shows essentially the same structure as that of *V. odorata*; a straight well-developed embryo being embedded in a copious endosperm, the cells of which contain abundant fat and proteid. The testa is beautifully specialized; several distinct cell-layers being observable; of these the lignified layer (as in *V. odorata* but still more thickened), derived from the outermost layer of the inner-integument is the specially protective zone, and is continued across the chalazal end by thick-walled lignified cells; at the micropylar end there is also a lignified nucellar plug. The peripheral layer consists of special cells which under their thin smooth cuticle present a remarkable cellulose thickening of the outer wall. Scattered among these cells are others with a special reticulate-thickening only. It is this highly-thickened outer layer which responds to the pressure of the closing valves, and gives the seed a polished elastic coat. The hilar aril consists of thin-walled cells, the contents of which are fat and abundant proteid-matter: the structure is thus that of a 'food-body'; and such a storage of food wholly outside the protective layers of the seed-coat can hardly be essential to the embryo.

## II. **Viola altaica,**[1] Pall. **The Garden Pansy.**[2]

A hardy herbaceous plant similar in habit to *V. tricolor*, but much larger and stouter in all its parts; the trailing shoots are 1–2 feet in length, and though these are usually killed by frost, the roots and lower portions of the stems are perennial.

The plant is a native of Siberia, where it is frequent in sub-alpine, and even high alpine situations, and flowers in May and June (Ledebour). The flowers vary in colour from deep violet-purple to pale yellow, streaked and blotched colour-forms also occurring as in the case of *V. tricolor*; in the wild state the flowers are 40 mm. in diameter, and represent the largest alpine type of *Viola*.

On the continent large-flowered forms from Alpine regions of Central Europe were also brought into cultivation, including the species *V. sudetica*, Willd., which also varies with violet to yellow long-spurred blossoms (25 mm. by 20), and the Alpine *V. grandiflora*, Vill. with large yellow flowers (40 mm. by 30).[3]

Garden races produced from such forms are slenderer in habit than the *V. altaica* stock, and the flowers are always more oblong than circular (cf. *Viola tricolor*).

Considerable crossing has undoubtedly taken place between such mixed races and

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[1] The plant was thus named by Chevalier Pallas who collected it in the Altai Mts. 'on the confines of Chinese dominions'.

The first good figure is that in the *Bot. Reg.*, 1815, of a pale yellow flower with a few dark veins. At that time it is said to have been still rare, and only grown in frames, and it was also noted that the first spring-blossoms were much larger than those produced later in the year.

It is said to have been introduced into English gardens about 1805.

[2] The large-flowered varieties of *V. tricolor*, which under generations of garden-cultivation reached quite a considerable size, constitute the *Pansies* of old English gardens; and selected varieties of these intermixed with forms of the indigenous mountain species *V. lutea*, Sm., which was cultivated as far back as 1629 (Parkinson) constitute the native stock.

[3] These three Alpine forms are closely allied and have all been included in the species *V. lutea*, Huds.; *V. sudetica* being practically a form like the English *V. lutea*, Sm., with violet posterior petals; *V. grandiflora* resembling the former, but twice the size (cf. Reichenbach). The species *V. lutea*, Huds., is again sometimes regarded as only one of the many forms of *V. tricolor*; and no sharp line of demarcation either exists or need be drawn between 'specific forms' which only exist as useful conventions.

*V. altaica*, but modern garden Pansies show no trace of it; and the general run of garden forms may be regarded as variations on the *altaica* type alone.

The flowers are produced in profusion in early spring (April–June), the earliest being out in February, while late strays last on well into November. The fruits shed in series also, from the first week of June onwards. Cultivated garden forms present an almost infinite range of colour-markings and tints of yellow-violet, purple-red, browns, white, and even black.

The structure of the vegetative shoot is identical with that of *V. tricolor*, and the plants regularly perennate. The shoots are readily propagated as layers or cuttings, in which case the accessory vegetative buds develop as branch axes, as in *V. tricolor*. The floral diagram is identical, and the flower differs from that of *V. tricolor* (type) only in the increased size and vigour of all its parts, the more pronounced character of details of the floral mechanism, and most of all in the *flat circular* form of the corolla-expansion, which is projected in an approximately vertical plane, affording much less foothold to an insect visitor. This flat circular corolla, in which, that is to say, zygomorphy is apparently less pronounced from an external point of view, is correlated with a much less degree of structural eccentricity in developmental stages; while it is interesting to note that the florists' ideal, in attempting to produce larger and still flatter and more circular blooms, is but the continuation of the line of evolution along which the plant has been long proceeding.

The detailed description refers to a medium-sized garden flower, about 50 mm. in diameter; the largest blooms attain a diameter of 80 mm., while impoverished ones may be even less than 30 mm. In these cases the difference is noted chiefly in the petals, the essential-organs remaining practically constant.

## Description.

INFLORESCENCE reduced to solitary flowers borne in the axils of the foliage-leaves of the current year. Two lateral prophylls, small and 3-lobed, are carried up on the flower-stalk to the vicinity of the flower.

FLOWER: Hermaphrodite, zygomorphic, pentamerous in the outer whorls.

RECEPTACLE slightly crateriform, and eccentrically so; the back of the flower being carried up $\frac{1}{3}$ the height of the ovary cavity (slight eccentric perigyny).

CALYX of 5 free sepals, ovate-acute, 18 mm. by 5, green, with a backwardly directed basal flap, 5 mm. long, projecting over the spur. The odd sepal at the back of the flower is recurved, and is smaller than the others (10 mm. by 4).

COROLLA of 5 free petals, alternating with the sepals, slightly unequal and very variable in colour markings: at the back of the flower, 2 petals roundedly obovate, 25 mm. by 35 mm. wide; two side-petals, rounded, 25 mm. by 30 mm., with papillose fringes near the base; a median front petal, broadly obovate, 30 mm. by 30, channelled at the base and produced backwards into a blunt spur 8–9 mm. long by 2 mm. in diameter. Coloured lines or blotches on the 3 front petals converge to the grooved entrance to the spur on the front petal which lies over the lateral ones.

ANDROECIUM of 5 free stamens, alternating with the petals; *filaments* extremely short; *anthers* 2–2$\frac{1}{2}$ mm. long, in close lateral contact around the ovary, being held in position by marginal series of interlocking hairs of special structure: the connective is continued as an orange-yellow triangular flap 1 mm. long, and these 5 flaps complete the cone-arrangement around the style, except for a short space in front. From the outer surface of the filaments of the 2 front stamens, tailed processes, 5 mm. long, project into the petal-spur as green secreting nectary-lobes.

GYNOECIUM of 3 carpels; *ovary* syncarpous, ovoid, green, 3–4 mm. long, unilocular, with 50–80 anatropous ovules in several (3–6) rows along 3 large parietal placentas. The micropyles are directed towards the apex of the ovary. *Style* kneed below, expanding upwards, and dilated to form a rounded style-head, containing a stigmatic cavity guarded by a projecting lip, at a distance of 6–7 mm. from the base of the ovary.

NECTARY: The glandular appendages of the 2 front stamens secrete freely, and the secretion is protected from desiccation, and also collected, in the projecting spur of the front petal, which is directed obliquely backwards and upwards; the liquid may fill the spur beyond the tips of the secreting appendages.

### Floral Diagram.

Identical with that of *V. odorata*, the back of the flower is now seen to be the posterior side, and the nectaries and spur are derivatives of anterior members; the flower having developed its zygomorphy as structural eccentricity in the plane passing through sepal 2, which is approximately median.

### Sectional Elevation.

This, taken in the plane of zygomorphy, shows the increased importance of the petals; the essential organs being now relatively small (contrast *V. arvensis*). The mechanism remains practically identical, but the working-distance of the flower is increased to 10 mm. (stigma-lip to nectary-lobes): insects with proboscides of 5–6 mm., which can work the other types with difficulty, are thus entirely excluded.

The whole mechanism is much larger and stronger in all parts than that of *V. tricolor*; the details are better differentiated, and can be more readily checked by the unaided eye, while features which were obscure or doubtful in *V. tricolor*, and especially so in var. *arvensis*, now become obvious and are seen to acquire a definite meaning.

As elaborated details, *note*:—

(1) Recurvature of the posterior sepal is complete, and the spur is completely invested by the sepal-flaps, being thus protected from boring.

(2) The circular character of the flower, with a central eye and general 'target' character, there being no definite landing-stage when the flower is projected in a vertical plane: these features suggest adaptations for the visits of Lepidoptera (cf. *Pelargonium*).

(3) The papillose fringes of the lateral petals, as prominent tufts of simple white hairs, form broad (5 mm.) patches overarching the entrance groove; these hairs afford a holdfast to an insect-visitor, in addition to their primary function of limiting lateral access. Similar papillose hairs are greatly developed over the yellow base of the anterior petal at the entrance to the groove (cf. var. *hortensis*).

(4) The anther-cone fits the space between the petal-bases so closely that lateral access to the honey is prevented, the only exposed member being the style-head hanging immediately over the entrance-groove. Warning-hairs are prominently developed on the front of the style-head, becoming definitely spiny immediately over the orifice to the stigmatic-chamber. Rough cells with irregularly thickened and cuticularized walls also cover the base of the anterior petal on either side of the median groove.

(5) The lip is strongly marked as a recurved ridge-outgrowth of cuticularized cells with irregularly thickened walls; it does not move freely as a hinge, although it can be pushed backwards or forwards on the soft subjacent tissue once or twice without being damaged. It constitutes a rough scraping surface.

(6) The anthers on dehiscence gape widely at the apex of the lobes, suggesting a transition to porous dehiscence as a further improvement of a neat powdering mechanism.

(7) Adjacent anthers are held closely together by interlocking hair-fringes; the connexion between the anterior anthers being sufficient to prevent any pollen-grains from passing between them.

*Note* also the presence of small rough papillae on the edges of the connective-flaps, though the anterior edges of the flaps of the anterior anthers are quite smooth and bare; these are anisophyllous, and overlap in front, leaving a (1 mm.) fairly circular orifice between their tips, immediately below the stigmatic lip: this orifice may be termed the *pollenic-pore* of the *pollenic chamber*.

The posterior edges of these same anther-flaps are fringed, and bear tufts of simple hairs, while these come into contact above with the similar small lateral hair-tufts on the sides of the style-head. Lateral emission of pollen between the anther flaps of the lateral stamens is thus provided against, while pollen is not likely to be shed in the drooping flower between the lateral and posterior flaps, and these have practically no fringes (only small papillae). Further, as the style-head is moved upwards on its basal hinge, it presses against these flaps while the pollen escapes below.[1]

(8) Note that the *pollenic pore* is immediately below the orifice of the germination cavity of the stigma, and only separated from it by the stigmatic lip: also that these two orifices are practically identical in size (1 mm. each way) and their centres only 1 mm. apart.

This therefore represents a final perfection of the pollination mechanism, the object of which is here to deposit on a special region of an insect a patch of pollen exactly equal to the area of the opening of the stigmatic-chamber; and this implies an extremely delicate adjustment, and demands an approach in the exact median plane (cf. *V. tricolor*, the same details all present but on a smaller scale).

(9) The groove of the anterior petal, which follows this median plane, is compressed and almost closed in by the great development of the side walls; its cavity is roofed in by the anterior anthers, and it thus constitutes a practicable tube leading to the spur. From the side walls, along the whole length of this entrance tube, from the papillae at the entrance to the insertion of the stamens (5 mm.), a great development of the peculiar 'knobbly' hairs which converge to the central line loosely fills the entire cavity of the groove. These afford no obstacle to an entering proboscis in the median line, and they are again lacking along the median line at the base of the groove, so that a proboscis feeling its way along the surface is not affected by them. They also evidently exclude minute insects (e. g. Thrips) whose presence in the spur-cavity might deter an insect from inserting its delicate feeding-organ into a recess with unknown occupants. These hairs have also been regarded as *pollen collecting hairs,* under the impression that they receive pollen which falls through the pollenic pore. It is clear, however, that only those hairs at the extreme front of the series will ever

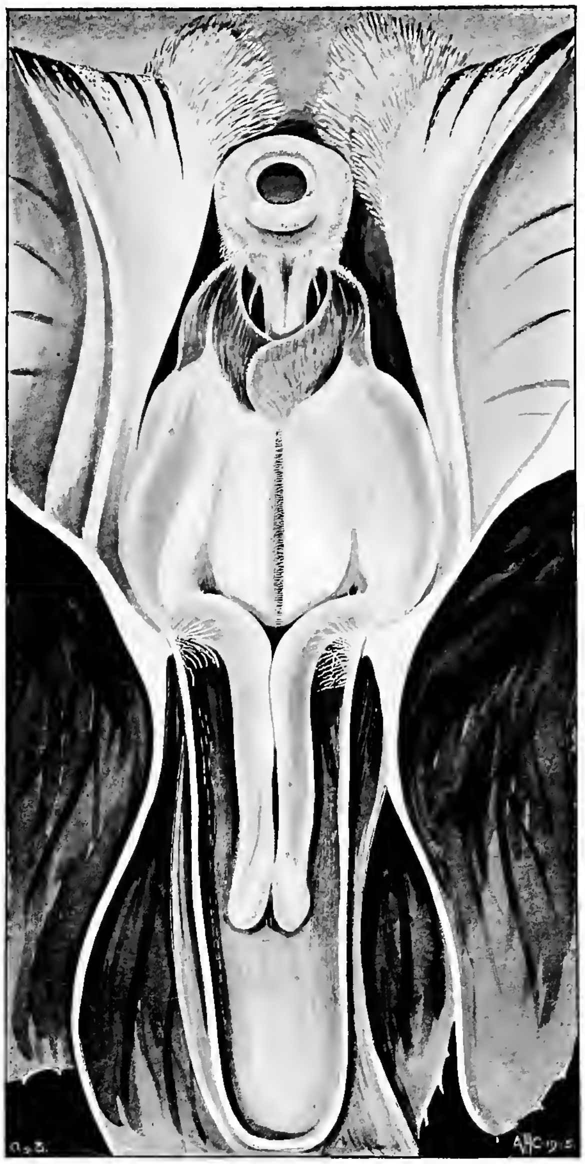

Fig. 7. *Viola altaica.* General view of floral mechanism from below, after removal of anterior petal lamina, showing orifice of stigma, pollenic-pore, and nectary-lobes projecting into the spur.

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[1] *Note* that the mechanism of a sprinkling apparatus is mainly controlled by the special development of the 'connective flaps' which are in fact the upper portions of the laminae of the microsporophylls, and not as in the case of the nectary-lobes, new emergences. The stamens of *Viola* have thus retained a distinctly earlier type of structure than that of the more general Angiosperm type, in which this portion of the sporophyll is usually only represented by a small point.

receive such pollen, and pollen is found here, and may in addition be wiped off here by insect visitors; but the same hairs extend for a distance of 5 mm. further back. In character they represent an exaggerated 'knobbly' development of the interlocking hairs of the anthers, which in *V. tricolor* appear to replace the packing hairs which in *V. odorata* grow directly from the ovary they were originally intended to protect. It is more probable that these are here a protection for the nectary and its secretion, and serve to keep this from desiccation and so maintain it in a fluid condition. Added to this may be the apparently minor point of the development of small warning-papillae on the nectary-lobes, and the fact that these increase towards the secreting tips which are quite rough (cf. *V. tricolor*). The nectary, that is to say, is not intended to be *licked* by a licking proboscis (bees), so much as to be pumped in a fluid condition by a suctorial proboscis (larger bees and Lepidoptera). These deductions may afford further light on the presence of hairs loosely blocking the entrance of a gamopetalous flower-tube (cf. *Vinca*); a primary significance as a xerophytic adaptation being always preferable to any hypothetical protection against 'unbidden guests' of whose existence the plant is unaware, though undeniably they may be excluded as a secondary and subsidiary result of the same modification.

As the floral mechanism is relatively small, and the details cannot be represented in the sectional elevation with sufficient clearness, a general view of the mechanism, as seen from below, after removal of the front of the anterior petal, is represented in Fig. 7.

The flowers are homogamous, and are functional as soon as the corolla expands; they remain so for 10 days or a fortnight, in cool seasons still longer (17–21 days).

A proboscis of 7–9 mm. will suffice to take honey from the secreting surfaces with a little difficulty, while one of 10–14 mm. will be required for draining the spur: the flowers are therefore not visited by the Hive-bee (5–6 mm.), but by various humble-bees;—from *Bombus terrestris* (7–9 mm.), a clumsy visitor, to *Bombus hortorum* (18–21 mm.).

Other bee visitors are *Anthophora* (19–21 mm.), always a delicate worker; while several butterflies may be observed taking honey with their suctorial proboscides; cf.:—

Small Tortoiseshell (*Vanessa urticae*, 14–15 mm.).
Cabbage White (*Pieris rapae*, 13–15 mm.).
Painted Lady (*Vanessa cardui*, 13–15 mm.).

*Note* that *V. altaica*, which shows a close approximation to radial symmetry in development, retains a zygomorphic design owing to the possession of 2 nectary lobes and a spurred petal, and may be regarded as a zygomorphic flower which is regaining an outward appearance of radial symmetry. It is interesting to consider how far this may be correlated with adaptations for pollination by the agency of Lepidoptera, as indicating a 'target' type of attraction: for similar external appearance of radial organization combined with structural irregularity, cf. *Pelargonium zonale*, *Phlox decussata*, and garden forms of *Verbena*.

*Note* also that *V. altaica* with a short broad spur (8–9 mm. by 2 mm. wide) still remains adapted for a wide range of insects, while other alpine forms exhibit a progressive limitation of visitors by a correlated increase in the length of the working-distance, more especially as indicated by a longer and slenderer spur.

Thus the Alpine *V. calcarata*, with similar floral-structure and flowers 40 mm. by 30, blue, or yellow with violet streaks, possesses a slender spur 13–25 mm. in length, the working distance from the stigma-lip to the ends of the nectaries being about the same, so the flower can only be pollinated by butterflies, and the longest by the Humming-bird Hawk Moth (25–28 mm.).

## Fruit and Seed.

As the petals wither they become inrolled, and protect the developing ovary for a few days: they are soon shed, the anther-cone is pushed off in one piece, and the green ovary rapidly enlarges to an ovoid green fruit protected by the re-erected sepals which continue their assimilative function; the remains of the style also persist at the apex. The fruits are half-grown in a fortnight, and attain full size in a month, as ovoid capsules 10 mm. in length and 7–9 mm. in diameter; they stand erect on their stalks and ripen in 6 weeks. The first crop sheds in the beginning of June, and fruits are matured throughout the summer months. Few flowers and fruits are developed in the dry season, but a second crop comes on again in cool autumn months, and the last strays may be found late in November.

The ripe fruits open under desiccation, and the 3 valves lie back along sepals 1, 2, and 3, exposing the seeds in several rows filling the entire inner surface of the valves; all the ovules normally set.

Section of the ovary-wall shows essentially the same structure as in *V. odorata*, but specialization is more pronounced; the longitudinal bands of radiating cells are thicker, and the lining-layer of fibrous-cells is also many-layered; the collenchymatous structure of the placental tissue is much more pronounced, so that while the whole wall is firmer and stronger, the shrinking collenchymatous layer is also more efficient. The divergence of the 3 valves which lie out flat over the sepals is probably due to desiccation in the outer cellulose tissue of the capsule wall, and is a distinct and primary feature of dehiscence; the valves thus come to lie straight back with all their seeds in position. The folding in of the valves on the seeds then gradually takes place, and may be delayed over 2–3 days, the seeds being flipped off one by one as the valves close in. Ultimately the valves are folded closely on the placental hinge; but as in *V. tricolor*, on the decay of this soft collenchymatous layer, the woody skeletons again open out. The seeds are thus violently ejected for distances up to 6 feet.

The seeds are small ovoid and pale brown, with smooth polished coat, 2 mm. by 1½ mm.; the rounded chalazal end is raised as a small tubercle, while the pointed micropylar end bears laterally a pronounced hilar scar in the form of a cushioned growth of tissue; the vascular bundle passes down on one side, but the raphe does not form a distinct ridge. As many as 75 seeds may be ripened in one capsule. Section in the plane of the raphe shows that the seed is essentially of the *V. tricolor* type. The hilar-scar tissue contains proteid in thin-walled cells, and as this character extends to the cells on the other side of the micropyle, this mass of tissue may be described as an 'aril', though smaller than in the case of *V. odorata*, and equally doubtful as a 'food-body'.

## Theoretical Considerations.

The flower of the *Violet*, when considered from the standpoint of the primary floral construction, reduces to a comparatively simple floral structure.

Taking into consideration those features which are undoubtedly secondary departures, and secondary modifications of the primary construction-system, it is evident that the following phenomena may be abstracted from the adult mechanism.

(1) The eccentricity of the flower shoot, expressed in the adult form as Zygomorphy associated with one spurred-petal and two spurred-stamens. This eccentricity is, however, shown in developmental stages to consist of two opposed phases, one of which is more recent than the other; i. e. when the secondary growth of the posterior side of the flower is eliminated, a primary anterior eccentricity is revealed, which, if it had continued its normal course, would have resulted in the posterior petals being smaller than the others. Eliminating this first eccentric phase, the floral shoot returns to a *radially symmetrical* pentamerous type approaching again that of a normal centric shoot-system.

(2) The small amount of *perigynous* growth may be also eliminated; and the type thus reduces to a primary normal condition of *hypogyny*, with a conical growing apex similar to that persisting in the vegetative shoot.

(3) The floral axis now appears as a simple floral phyllotaxis-construction, indicated by a floral diagram in which an asymmetrical (quincuncial) protective calyx is succeeded by a symmetrical (5 + 5) construction in the sporophylls; 5 'petals' being isolated as rudimentary

members at the cycle of transition; a floral construction of the simple Type II, found at the present time in such a form as *Aquilegia* is thus outlined.

(4) From such a phyllotaxis-construction, itself a complicated advance on a still more generalized wholly asymmetrical construction, a floral-formula approaching that of the 'Mean Type' has been attained by reducing the floral members to a single contact-cycle of each kind, with a still further reduction in the case of the gynoecium. The approach to what has been elsewhere termed the *Mean Type* of floral-construction (cf. *Ribes*) is so close, that the fact that *Viola* stops at 3 carpels, which continue the median symmetry of the construction, suggests that complete reduction to the bicarpellary gynoecium of the Mean Type is not far off, while the full ancestral form would be 5 carpels.

Otherwise the floral shoot is 'normal' in construction; the prophylls and quincuncial calyx being orientated as in the most general case for Dicotyledonous Angiosperms, and these members again presenting the usual characters of asymmetrical Fibonacci construction; so that, as already indicated, a shrubby ancestor with normal Fibonacci phyllotaxis throughout all its shoots may be postulated.

The *Inflorescence* scheme presents a point of difficulty; the system of single axillary flowers showing no sign of any more panicled inflorescence-system terminating the vegetative shoots, and no terminal flowers occur.[1]

It therefore becomes necessary to find homologous cases in other phyla; and if these exist it may appear that such an inflorescence-system as that of *Viola* is to be regarded as a wholly secondary or alternative construction-scheme, which may possibly be associated with special habit or conditions of environment. Such homologues are in fact general, and among them may be cited the unique case of *Vinca* among other Apocynaceae (cf. *Amsonia*, *Nerium*), the case of *Lysimachia Nummularia* among the larger forms of the same genus, and the case of *Linaria Cymbalaria* as compared with *L. vulgaris* and the larger Snapdragons.

There thus appears to be sufficient evidence to warrant the hypothesis that *V. odorata* is the modern highly-specialized representative of a shrubby, or even arboreal, plant-phylum which produced normal foliage-shoots and panicles of regular flowers, which had already passed from an asymmetrical vegetative type of construction to a symmetrical pentamerous condition, along lines characteristic of a vast proportion of modern flower-types, and sufficiently indicated in the form *Aquilegia*. From such a floral-form evolution has proceeded along lines of reduction similar again to those which have produced the great preponderance of flower shoots of the 'Mean Type'; and from this in turn, by the development of a degree of structural eccentricity which has affected the development of secreting-glands and spur-receptacles. Two distinct phases of eccentricity occur, and all subsequent specializations of the floral-mechanism are correlated with the visits of cross-pollinating insect agents in the form more particularly of bees; the best types showing increased adaptation to the visits of long-tongued bees and Lepidoptera. It is important to note that these conclusions have been arrived at mainly from the fact that such phases are definitely presented in the recapitulation-phenomena of the floral ontogeny: in only one feature is the developmental phylogeny abbreviated, as already noticed, in the early gamophylly of the carpels, and failure of the gynoecium to present absolute evidence of the carpellary theory.

Such deductions receive further confirmation from the study of those allied forms which systematists, for generations, and often from quite different considerations, have agreed to unite with *Viola* in the special group termed the *Violaceae*.

Thus arboreal forms are abundant in the genera *Paypayrola*, *Isodendrion*, *Rinorea*, *Gloeospermum*, *Leonia*, *Melicytus*, &c.

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[1] Exceptional cases for *Viola tricolor* (?) have been described in which the prophylls on the flower-stalks subtended lateral flowers (Kirschleger, 1845).

Panicled inflorescences of a compound type, *Paypayrola*, *Rinorea*; and in many reduction phases (often cymose) *Amphirrox*, *Leonia*, *Melicytus*.

Centric flowers are characteristic of the genera *Paypayrola*, *Amphirrox*, *Rinorea*, *Leonia*, &c., without secondary nectaries on the stamens, or again with such emergences on all *Melicytus*.

The full gynoecium of 5 carpels obtains in *Leonia*, sp., *Melicytus*, sp.; or is reduced to the dimerous form of the Mean Type in *Hymenanthera*, which again possesses only 1–2 seeds.

The primary eccentricity obtains alone in *Calyptrion*, *Hybanthus*, *Anchieta*, *Agatea*, &c., in which the anterior side may be so greatly developed that the odd petal is far larger than the others.

While the nectary is present without its secondary protecting and collecting spur in *Hybanthus* and *Agatea*.

In conclusion, *Viola* stands out as the crowning genus of the entire group; the type, that is to say, in which the various modifications of the original construction are present in the greatest number, and combined to make a most efficient form of floral mechanism.

This conclusion is further supported by an examination of the numerical relations of the genera.

The family *Violaceae* (cf. Reiche and Taubert) comprises 15 genera and about 320 species, of which *Viola* itself is the only type attaining any great specific variation at 200 species,[1] and world wide distribution throughout the whole of the North Temperate regions, South American mountains, Cape and Tropical Africa, New Zealand and Sandwich Islands.

The survivors of the more generalized forms belong to Tropical America, while the interesting genus *Melicytus* belongs to New Zealand and Norfolk Island.

The distribution of such an essentially narrow series of types gives therefore no definite information as to the centre of origin for the whole family; just as the construction readily reduces to a simple character approaching the 'Mean Type', about which nothing definite can be said, beyond the fact that similar generalized forms can be postulated as the basis of other phyla; and the stages behind these are completely lost.

From such a standpoint it is interesting to compare the essential regular primary construction as presented in the floral diagram with such a regular type as *Passiflora*; while on the other hand alliance has been suggested with the ancestral form of the *Cistus* phylum (cf. *Helianthemum* with somewhat similar 3-carpelled unilocular gynoecium, and stamen groups uniting to 5 leaf-trace bundles).

On the other hand it is just as reasonable to regard these forms as approaching the same comparatively simple construction scheme by convergence to a mean type, on which they proceed to erect a wide scheme of subsidiary specializations; representatives of these secondary devices being met with in most diverse lines of descent. In any natural system of classification the *Viola*-alliance will be necessarily placed among the obviously more primitive Polypetalous and Hypogynous series; while among these there will ever be a tendency to associate it with those which present common structural features, quite apart from any standpoint as to whether these latter are to be regarded as accidental resemblances or definite affinities.

Thus by Jussieu (1789) the genus *Viola* was placed in the order *Cisti*, next to the genus *Helianthemum*; De Candolle (1805, Prodomus, 1824) first separated a distinct family from the *Cistineae* as the *Violarieae*, pointing out resemblances ('affinities') with *Polygala*, *Drosera*, *Passiflora*; Lindley (1829 and 1836) used the term *Violaceae*; while Bentham (Genera Plantarum, 1862) continues the family as *Violarieae*, a prejudice in favour of the importance of the structure of the gynoecium retaining them near the *Cistaceae* in the

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[1] *Hybanthus* 50, *Rinorea* 40.

artificial cohort *Parietales*. Eichler (1878), with a clearer view of the series of the *Cistiflorae*, takes the *Violaceae* as one of the simpler groups; and the same general understanding is continued in Engler and Prantl (1895). The small family of the *Violaceae* thus owes its isolation as a distinct group to the wide distribution of the *Viola* forms in temperate parts of Europe, where it became known to the earliest botanists, and by them was made a type around which tropical genera have been subsequently segregated. It is not too much to say that had this type been lacking, there would have been little difficulty in placing the simpler tropical genera of the family in other tropical series (cf. *Flacourtiaceae*); and in this case, as in many others, our view of the grouping of the plant-kingdom is largely influenced by European bias.

## I. NOTE ON FIBONACCI PHYLLOTAXIS SYSTEMS.

The Phyllotaxis pattern at the apex of a shoot of *Viola odorata* was described as being not a good one, owing to the rapid development of the leaf-stipules, so that contact cycles were obscured; the ratio was given as approximately (2 + 3).

On a section-drawing, made carefully with camera lucida, the median points of the young leaf-members can be indicated with a fair amount of accuracy, by taking the median vessel of the protoxylem of the central bundle when this is differentiated, and the members may be given a theoretical numerical value along the course of the 'ontogenetic' spiral. In such a figure the divergence angles show a certain amount of variation, owing to errors of preparation, the most important of which is due to the difficulty of cutting the section in an accurately 'transverse-plane', since this direction must be judged by the eye. In the section figured, for example (Fig. 1), it could be shown by measurement that the section tilted a little in the plane of No. 3: angles being measured between successive members from 1–10. Since errors of levelling may be eliminated by taking an average of angles around the axis, and 3 members are here sufficient for the purpose, the average of the 3 angles between 1-2-3-4 was 138½°, that between 3-4-5-6 138°. Now the theoretical angles of all Fibonacci systems above (2 + 3) only vary within a degree from 137½°, and 1° is also allowable for errors of measurement; it thus follows that a Fibonacci ratio is here utilized, but it is impossible to say which, since subsequent differences in rates of tangential growth may mask the original system. Strictly speaking the divergence angle for a (2 + 3) system is 138°27′42″, and 3 members should constitute a contact-cycle: but if 2 members make contact around the axis, as would be expected for a (1 + 2) system, the divergence angle should be 144°. It thus appears preferable to regard the system as a (2 + 3) form, in which the leaf-primordia show a relative increase tangentially, and so appear to slip further around the axis than is normally the case. That the stipular lobes have an increased tangential rate of growth, when they are isolated, is shown by the fact that they slide between the axillary bud and its subtending leaf, and even overlap in the axil (cf. Fig. 2).

*Note* also that the so-called '*stipules*' are normal segments of the primary leaf-lamina, and thus identical with 'pinnules' (cf. *Jasminum revolutum*, *J. nudiflorum*, Fig. 5, p. 41), the fact thatt he conventional 'leaf-petiole' is put in above these basal lobes, instead of below them, being a wholly secondary phenomenon: conventional views derived from the contemplation of adult structures being frequently inverted in statement.

It may also be observed that the axillary buds are not always in the radial plane of the subtending leaf, and the *prophylls* undoubtedly arise at an approximate angle of 137° from each other, though this becomes less clear in later states. One of them (β) is fairly transverse, but the other (α) is distinctly postero-lateral, though the law which governs their position is still obscure.

## II. ORIENTATION AND ECCENTRICITY OF THE FLOWER.

The flowers of *Viola odorata*, since they can be readily cut transversely in a section of the vegetative shoot (Spring and Autumn), are useful in that they throw light on the evolution of the normal Dicotyledonous Floral Type, and afford confirmation of the deductions obtained from the more generalized forms, *Helleborus* and *Aquilegia*.

A section, taken at a time when all the members have been laid down, and no further growth-regions have been established, exhibits the floral organs in their relative contact positions. In such a section, carefully drawn under the high power (D) for increased accuracy, although all the details are quite clear under the low power (A), on drawing radial planes through the leaf-centres and the apex of the axis, or the spot where this should be, in a section taken at a lower level, it will be noted that the median plane of the flower does not exactly coincide with the radial plane of the subtending leaf (*b*), but lies obliquely across it. On the other hand, the plane of median bilaterality of the floral shoot itself clearly passes through the central bundle of sepal 2; this being rendered obvious by the slight assumption of eccentric growth (Fig. 2).

Hence the flower although definitely eccentric (zygomorphic) in the plane of sepal 2, cannot be said to be also absolutely zygomorphic in the median plane which should also be the radial plane of the subtending leaf, although the approximation is here very close. That is to say the zygomorphy of a flower is established in its own growth-centre, without direct reference to the symmetry of the parent shoot. Sepal 2 is not absolutely *median posterior*, although, since the rule which controls its position is not yet determined, the Eichlerian convention may be retained so long as its accuracy is not accepted too strictly. In the eccentric growth-system, note the increased development of the anterior members, which produces a subjective effect that they are older than the posterior, just as in fact they also appear to arise first as protuberances. This effect is more obvious in the petals than in the stamens, though in the case of these latter the *anisophylly* of the lateral members, as contrasted with the perfect *isophylly* of the median member, is very marked.

The *petals* again are clearly growing at a slower rate than the stamens, and thus appear as degenerate organs (cf. *Helleborus*); although they may be utilized subsequently for a new function, and acquire a rapid growth in the final phases of the flower, it is possible that this check in development is recapitulatory.

The phyllotaxis system of the inner members (petals and stamens) is clearly a symmetrical (5 + 5) construction while observation of the first 5 members ($\alpha$, $\beta$, 1, 2, 3) suggests that these, being a normal quincuncial cycle, represent a contact-cycle of a (3 + 5) construction, as opposed to that of the vegetative shoot which was classed as (2 + 3). While these appearances may in fact be the result of any Fibonacci ratio beyond (2 + 3), the view that the (3 + 5) type is here utilized is further suggested by the readiness with which it would be changed (by adding two more curves) to the undoubted (5 + 5) construction.

Now the 5 members (1, 2, 3, 4, 5) of the calyx do not give such a good contact-cycle, 4 and 5 being distinctly inferior members; so that if a new path is opened up with a single member, these 2 members may be regarded as indicating the changes in the construction; i.e. at No. 4 the system becomes (4 + 5) and at No. 5 (5 + 5), with the result that all subsequent members are symmetrically produced (cf. *Aquilegia*); the transition thus agreeing with the remarkable phenomena which are so largely constant for petaloid Dicotyledons: i.e. the first contact-cycle *after the change* is isolated as a true whorl of 5 '*petals*', while the spiral contact-cycle of 5 members *before the complete change* is isolated as a quincuncial *calyx*. Since the change is initiated only after the minimum production of one complete contact-cycle around the axis, 2 members are now left over, and these remain outside the floral-mechanism as *prophylls*. The reason for such an elaborate design may not be now fully clear, but it is a legitimate hypothesis that it represents a *minimum recapitulation of phylogenetic stages*, and from such a standpoint may be justifiably taken as a *normal type*; while instances in which the transition is delayed (cf. *Malva*), or abbreviated (*Vinca*), may be regarded as the exceptions which prove the rule.

It may also be noted that a similar normal transition expressed in terms of a (2 + 3) construction, acquiring symmetry at (3 + 3), in that it only involves the addition of a single construction-curve, should by analogy result in the isolation of only a single prophyll (cf. *Lilium* type); and that since such a single member would be the $\alpha$ of a Dicotyledonous construction this should also be expected in the postero-lateral position; while the 3 members before the change may be homologized with *sepals*, and the 3 after the change as *petals*, these conventional expressions thus acquiring a morphologically accurate definition.

# VIII

## **Narcissus Pseudo-Narcissus,**[1] **L.**

*Daffodil.*[2]
*Lent Lily.*[3]

A HARDY herbaceous plant perennating by means of a subterranean bulb, and producing leaves and solitary flowers to the height of about 1 foot in early spring.

Indigenous to the whole of South Europe and the Western Mediterranean District, and growing in the open air as far north as Sweden. It also grows wild in many parts of Great Britain, but not in Ireland, in meadows and by the sides of streams, but is very doubtfully native, having in all probability been introduced like other spring flowers (*Crocus*, *Vinca*, Snowdrop) during the Roman occupation.[4]

A very large number of varieties, and hybrids with allied species, as also monstrous forms, are cultivated by florists and others, and are in great demand commercially during the months of March and April. Wild forms are thoroughly established in copses, woods, orchards, and meadows, especially in parts of Leicestershire, Herts, Norfolk, and the south-western counties.[5] The flowers are produced in March and April to the early part of May, and the fruits ripen and shed their seeds in June. The plants then wholly disappear, and perennate during both the hot summer and cold winter.

All parts of the plant contain a narcotic poison, and are not eaten by grazing cattle.

The flower and vegetative organs are both built on a plan closely comparable with that

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[1] The word *Narcissus* is the old Greek name; the Νάρκισσος of Dioscorides being the Tazetta Narcissus, and the term was also applied to *Narcissus poeticus*. The illustration in the Vienna MSS. is the Tazetta form. The name was adopted by Linnaeus (1735), the specific title of *Pseudo-Narcissus* having been applied by the older herbalists to this plant to distinguish it from *N. poeticus*. The word thus retains its capital initial letter, and Gerard in 1597 calls the Daffodil *Pseudo-Narcissus Anglicus*.

The name Narcissus is often associated with the story of Narcissus and Echo (Ovid), but is older than the myth, and has a possible relation to its narcotic properties (Pliny).

Brunfels gives a good figure of the plant and flower as Narcissus (1530).

[2] Daffodil, Daffodillies (Milton), Daffodowndillies (Spenser, Gerard *) have been regarded as corruptions of *Asphodelus*, as the nearest approximation in this country to classical meadows of golden Asphodel. It is quite as likely that the last name as an alliterative term is an old folk-name alluding to the nodding heads of the flowers.

[3] The term *Lent Lily* is of interest from its association with monastery gardens of the pre-Reformation era: large double forms are sometimes termed Lent-Roses. Similarly *N. incomparabile* was called the Chalice-flower.

[4] The plant is usually found growing wild in places where the Snowdrop and Spring Crocus are also found, and most commonly in the neighbourhood of cultivated ground and the site of old gardens. The introduction of all South European plants which would grow in this country by the Roman settlers of the fourth and fifth centuries is most probable when the horticultural proclivities of the Romans are taken into consideration; this applying to the families of soldiers, &c., as much as to the ruling classes; and the readiness of transit is most obvious in the case of bulbous plants. It is true that Roman gardens were mostly 'kitchen-gardens', but flowers were extensively grown for chaplets (Pliny).

[5] Forms of *Narcissus* are grown commercially on a large scale in the Scilly Isles, as also in Lincolnshire (Spalding), Wisbeach.

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* Gerard (1597) gives over a dozen sorts of *Narcissus* in cultivation, including double forms then just introduced; 'The common yellow Daffodilly or Daffodowndilly is so well-knowne to all that it needeth no description.'

Parkinson in his 'Paradisus' drew a sharp line between true Narcissus (*N. poeticus*) and bastard Narcissus (*N. Pseudo-Narcissus*), according as the cup or chalice was shorter than or as long as the perianth-segments. 'The cup doth very well resemble the chalice that in former dayes with us, and beyond the Seas is still used to hold the Sacramental Wine' (1629). He gives nearly a hundred varieties as then in cultivation.

of the Snowdrop, but the former is of special interest owing to the enormous development and biological importance of a new and secondary outgrowth of the perianth-region termed the *corona.*

## Description.

INFLORESCENCE reduced to a single flower borne in the axil of the uppermost of the 2–4 foliage leaves of the annual flowering shoot. The unopened bud is protected by a sheathing membranous spathe-leaf, which wrinkles up as the flower expands, but still closely invests the ovary and lower portion of the floral-tube. This spathe is about 35 mm. long, and is 2-keeled and slightly bilobed at the apex.

FLOWER: hermaphrodite; actinomorphic; trimerous Monocotyledonous type.

RECEPTACLE forming the wall of the ovary cavity (Epigyny), green externally, ovoid, 10 mm. by 4 mm., and produced beyond it as a short funnel-shaped tube 4–5 mm. long (i. e. as far as the insertion of the stamens).

PERIANTH gamophyllous, with 6 free segments: *Perianth tube* funnel-shaped, 18 mm. long, 15 mm. wide at the mouth and 4 mm. at the base, smooth and yellow on both sides. *Free segments* in two series (3 + 3). The outer 3 slightly broader than the inner, pale yellow in colour, ovate-acute. Outer segments 25–30 mm. long, 15–18 mm. wide. Inner segments 12–15 mm. wide.

A cylindrical outgrowth from the margin of the perianth-tube (*corona*) is the most prominent feature of the flower; this forms a tube 30 mm. long and 15 mm. in diameter, of a deeper yellow colour; the surface is wrinkled internally, and the margin is irregularly lobed and frilled (2–4 mm.) and often slightly recurved.

ANDROECIUM of 6 stamens (3 + 3) in normal series alternating with the perianth segments, inserted at 2 levels, 4 and 5 mm. respectively up the floral-tube. *Filaments* stout, pale yellow, 20 mm. long. *Anthers* yellow, 10 mm. long, introrse; pollen pale-yellow, abundant.

GYNOECIUM: syncarpous of 3 carpels, continuing the normal alternation. *Ovary* in the receptacle-tube, 10 mm. by 4, 3-locular; placentation axile, and 2 rows of anatropous horizontally-placed ovules (12 in a row) in each loculus.

*Style* long and stout, 40 mm. *Stigma* 3-lobed, the lobes small and recurved, corresponding to the carpels.

NECTARY: 3 pocket-like glands sunk in the septa between the loculi of the ovary (*septal-glands*) secrete slightly, and open by pores at the base of the style. The scanty secretion thus tends to collect at the base of the floral-tube at a distance of 40 mm. away from the receptive stigmatic-surface.

## Variations.

Measurements refer to average specimens growing wild (Devonshire); and these agree closely with the type grown in gardens, and for imported Dutch bulbs.

A very large number of closely allied forms, varieties, and hybrids are in cultivation, and such forms may be included under the general florist's term 'Trumpet Daffodils'. Such flowers only differ from the *Pseudo-Narcissus* type in slight colour-variations, and in increased size of parts; many have been in garden cultivation for a considerable period; thus several varieties with whiter flowers (*N. cernuus, moschatus,* &c.) were introduced from Spain about 1600.

Species and varieties of *Narcissus*, including chiefly florist's forms, are catalogued to the number of over 500.

## Floral Diagram.

The structure of the whole plant is essentially that of the Snowdrop, but represents a fuller and therefore more primitive type, as in the case of *Leucojum.*

On digging up a bulb in the flowering stage, an average specimen will show the following structure:—

I. *An outer investment* of decomposing brown scales, the relics of the leaves of the preceding season but one.

II. *The thickened bases* of the leaves of the previous season containing reserve food-materials (chiefly starch), together with the base of the old flowering axis which also stores food (cf. *Galanthus*). These are arranged with distichous (1 + 1) phyllotaxis and consist of 4–5 wholly sheathing flask-shaped members; the outer 3 being the bases of membranous scale-leaves, the upper 2–3 of the foliage leaves, one or more of which may possess axillary shoots as new bulbs bearing green foliage leaves. An uppermost leaf does not entirely invest the stem, and bears in its axil the relic of the flower-stalk of the previous season.

III. *The leaves of the current year*, the bases of which are already thickening with reserve food-materials to constitute the new bulb; 3 of these are sheathing tubular leaves, the uppermost of which comes as far as the surface of the soil: they thus protect the foliage-bud, and direct its passage up through the earth. Most commonly 3 foliage leaves (2–4) are produced, the uppermost having the flower-stalk in its axil, and on the opposite side of this the small bud of the next season continues the construction: in section the new leaf-members may be observed. All these leaf-members continue the same (1 + 1) phyllotaxis construction. The general scheme is thus identically that of the Snowdrop, and although the evidence is not absolute, there can be little doubt that in the *Narcissus*, as in the *Snowdrop*, the small bud in the centre of the bulb is really terminal, and the solitary flower is truly axillary (cf. *Galanthus*).

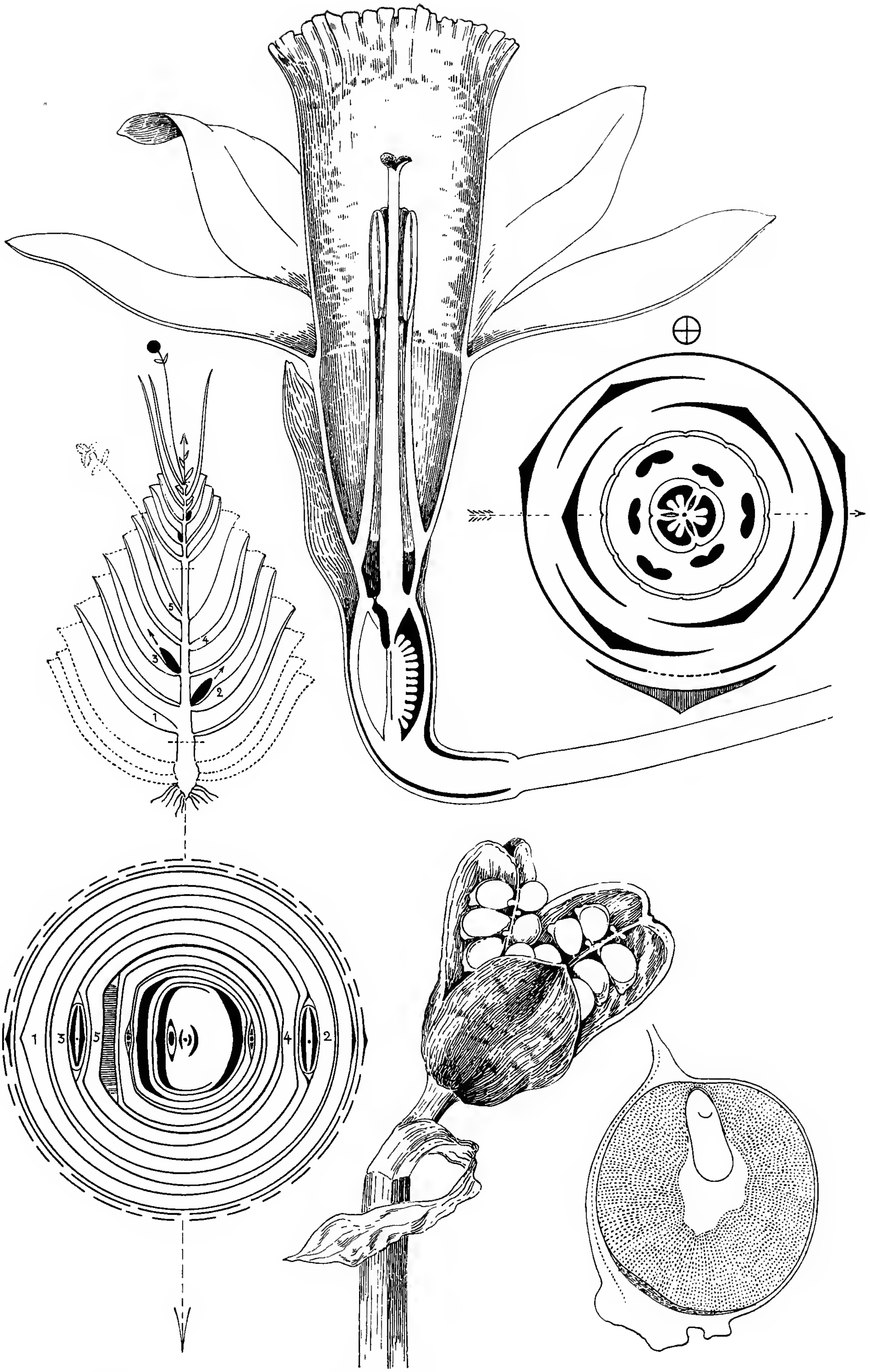
The bulb may thus be planned for transverse section or elevation; and on reducing the construction to an elementary schematic figure, it will be seen that the morphological form is quite normal, and that the 'bulb' is only a biological specialization of the ordinary (1 + 1) phyllotaxis common to many Monocotyledonous types (cf. Grass, *Iris*, *Canna*, *Acorus*). The characteristic feature is the absence of internodal formations, and here, as in the Snowdrop, only one internode is well developed in the plant, namely, the one below the spathe-leaf; the internode *above* the spathe-leaf is less developed, but again, as in the Snowdrop, is the seat of a biological curvature.

A point of interest is found in the orientation of the lateral axes (new vegetative bulbs) which are very freely produced. These arise in the axils of the lower foliage-leaves, and commence with 2 transverse primordia, which unite posteriorly and become gamophyllous to form the characteristic posterior 2-keeled, 2-lipped prophyll-structure: the succeeding foliage-leaves, however, all follow the median plane of symmetry, which agrees with the plane of the (1 + 1) system of the parent axis. The lateral phyllotaxis thus commences as if decussate, but becomes (1 + 1) in the median plane apparently with a definite object. Such a development of the whole leaf-arrangement of the plant in one plane is somewhat rare in aerial shoots, but is more frequent in prostrate stems and rhizomes (cf. *Acorus*). It is thus possible that this construction indicates that the bulb of *Narcissus* has passed through a rhizome-stage in which a dorsiventral shoot-system, with leaves produced symmetrically in the same plane, bore a succession of lateral inflorescences.

The flowering axis is thus regarded as axillary, and it is reduced to a single terminal flower; although in other forms of *Narcissus* (*Tazetta*) the inflorescence may contain 12–20 flowers, cymose ramification taking place in the axils of the prophylls. These forms thus bear the same relation to the Daffodil as *Leucojum* does to *Galanthus*; that is to say, the more primitive condition was a much fuller branch-system.

The spathe-leaf, as in the Snowdrop, represents 2 prophylls, which arise independently in the transverse plane, become gamophyllous and form a protective investing tube 15 mm. long anteriorly, reaching a length of 35 mm. posteriorly. The spathe does not split; but when the bud expands simply wrinkles back. In the bud it is definitely 2-keeled, membranous throughout, and 2 small lobes at the apex indicate the prophyll primordia. The whole structure is thus a very complicated biological production, adapted for a special protective function.

*Orientation* of the floral-members is not obvious in the flowering-stage, and may be conventionally treated: as in other Monocotyledonous types it is probable that the orienta-



**Narcissus Pseudo-Narcissus:** Floral Diagram and Sectional Elevation of Flower in the transverse plane; Scheme of Flowering bulb; dehiscing Fruit, and section of Seed in the plane of the raphe.

tion is not strictly symmetrical in either plane. Young flower-buds in the bulbs take on a definite position, and become somewhat flattened as they squeeze between the flattened bulb scales. The flower thus tends to be symmetrical in a transverse plane[1] (cf. *Galanthus*).

The structure of the flower shows a definite (3 + 3) arrangement: prefloration is inconstant in the individual perianth-whorls; the anthers are introrse in the bud, and transverse section of the ovary shows 3-loculi, axile-placentation, 2 rows of ovules in each loculus, and in the upper region of the ovary slit-like septal-glands.

## Development.

Early stages of the flower are identical with those of the Snowdrop, thus increasing the probability that deductions drawn from one of these plants will also hold for the other.

The flowers commence to be laid down about Midsummer; the prophylls of the spathe arise independently, and fairly in the tranverse plane, and these are succeeded by 3 perianth segments which are formed in a spiral series, and thus undoubtedly represent, as in allied Liliaceous forms, the retention of a still more primitive asymmetrical shoot-construction. Symmetry is acquired with the production of the inner perianth-segments and succeeding members follow in a uniform (3 + 3) system. Two cycles are thus specialized as perianth members, two for androecium and one for the gynoecium. The fact that the outer perianth-cycle is spirally produced indicates that the orientation is probably essentially oblique, and that the prophylls are really in the same spiral sequence, although they become specialized too early, fit into cavities made by succeeding members, and acquire a spurious symmetry in later stages. Similarly the fact that the symmetrical floral-construction attained in the sporophylls is (3 + 3) suggests that the original asymmetrical construction, which was therefore also characteristic of the vegetative shoot, may have been the Fibonacci system (2 + 3) of other Monocotyledonous types (cf. *Lilium*).

Fig. 1. *Narcissus poeticus*, July 20. Development of floral members on a crateriform receptacle; apex of vegetative shoot and rudiment of a second flower in the axil of a spathe member.

Further, as in *Galanthus*, the development of the flower as a phyllotaxis system is considerably masked by the great development of the receptacle as a crater-form.

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[1] The orientation of the flower is best checked when all the floral-members have been laid down, but no secondary growths have been initiated, since these might tend to produce different arrangements. Bulbs at this stage are taken about July 20 (cf. elevation, Fig. 1), and a transverse section cut at the level of the crater-edge will display all the members in their original contact-relations (Fig. 2, I). As in *Galanthus*, an approximation to transverse symmetry is the nearest that can be said of the construction: the system may be further checked by sections at a lower level, which give the orientation of the vascular bundles (Fig. 2, II). Thus the odd carpel is very fairly transverse, and an odd perianth member of the outer cycle is approximately superposed to it, though the odd inner segment is not diametrically opposite it, and the median plane (that of the phyllotaxis of the parent shoot) falls apparently between an outer and an inner perianth member. Such oblique orientation is probably the expression of the fact that the symmetrical (3 + 3) construction of the inner whorls is secondary to a primary asymmetrical construction of the first members, the number of leaf-units laid down in this primary system being too small to give any recognizable pattern. The transverse orientation, though apparently only approximate, becomes definitely established in later bud-stages, as the bud is compressed between the flat foliage-leaves of the shoot.

Sections of buds taken in July show an appearance identical with that of *Galanthus*, and can scarcely be distinguished.

The perianth-members arise from the outer rim of the cup-like axis, the stamens from the inner rim, and the carpels fill the sloping interior; the outline of the crater being obtained, as in other cases, by drawing a line through the insertions of the members (Fig. 1).

All the floral-members are laid down, and have assumed their definite occupations before any trace of the corona appears (July bulbs).

Sections of buds taken in August show that this remarkable structure arises as an outgrowth of the tissues between the bases of the perianth-segments and stamens (Fig. 3); the first trace of it being noticed between the insertions of the filaments: it then becomes continuous as a ring-growth all round the edge of the receptacle-tube, and presents the appearance of an extension of the edge of the crater. There is no need, however, to insist on it being a 'receptacular' formation; it is distinctly a new and secondary feature of great biological importance, which has no relation to the primary structure of the floral-shoot, but is a part of the secondary mechanism. Section of perennating bulbs (September to February) shows all the floral members in position, the elaboration of pollen in the anthers, of ovules in the ovary, the septal-glands, and the corona well-developed and about 5 mm. long, half as high as the anthers. The carpels fuse very imperfectly, and the apex of the floral axis may thus be observed at the base of the ovary, that is to say at the bottom of the crater (Fig. 4).

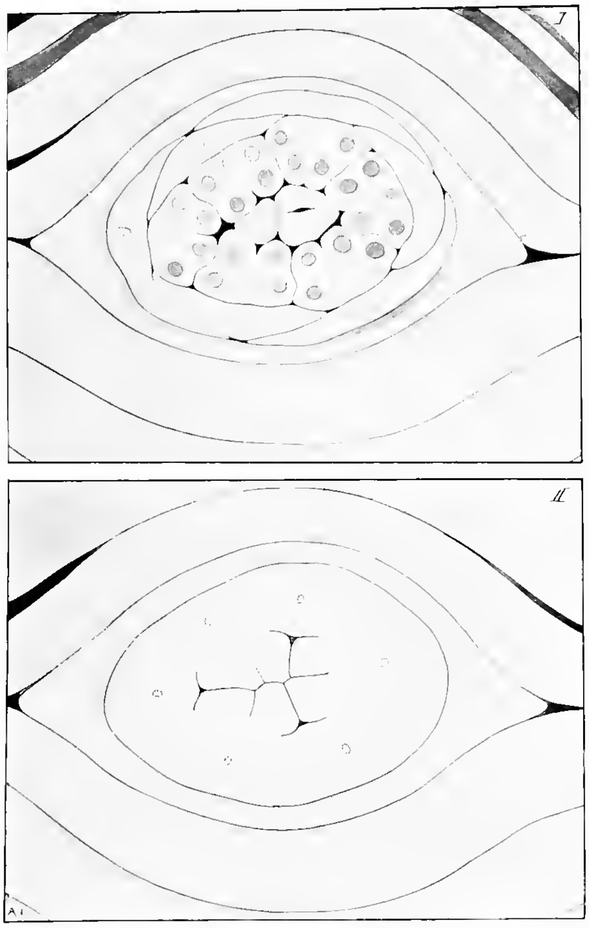

FIG. 2. *Narcissus poeticus*, July 20. Development of the flower; sections I and II taken at the levels indicated (I and II) in the preceding figure.

## Special Mechanism.

While the primary floral-structure thus includes the comparatively simple phyllotaxis system of the Liliaceous Trimerous-type, together with a highly differentiated crater-type of receptacle which gives the flower its characteristic *Epigyny*, the secondary and biological mechanism may be included under the following heads.

(*a*) *Secondary zones of growth.*

I. The production of an internode below the 2 prophylls, constituting the flower-stalk, averaging 11 inches in length, which serves to elevate the flowers beyond the foliage leaves (11 inches long).

*Note* that there is no internodal formation between the prophylls, these being biologically utilized to form a single spathe-organ.

II. A short internode above the prophylls, about 5 mm. in length, which is the irritable region and causes the nodding of the flower. Growth is unequal in this region, and is stimulated by the action of light and gravity. The curvature takes place without any reference to the orientation of the flower, and ultimately the floral-axis points to the direction of strongest light, at an angle with the flower-stalk which varies very little either way from 90°. The trumpet of the flower is thus definitely placed in a horizontal position.

III. The perianth-tube which constitutes the greater portion of the base of the trumpet is a *gamophyllous zone* of growth involving the perianth-segments.

IV. A short zone of growth also takes up the stamens as well as the perianth-tube, and may be regarded as an extension of the receptacle-crater; but better as a new zone of growth, the *Zona Perigyna* (cf. *Crocus*).

(*Note* that in the Daffodil the gamophyllous-zone is very important, and the Zona Perigyna rudimentary: on the other hand in *Narcissus poeticus* the converse is the case.)

V. The enormous development of the new region, the *corona*, which constitutes the trumpet proper, and gives the character of the genus, as a cylindrical chamber, with all the advantages of a bell-type enclosing the essential organs (cf. Gamopetalae).

VI. The growths of the stamen-filaments, which expose the anthers in the centre of the trumpet cavity, 20 mm. from the base.

VII. The stylar-growth of the gynoecium, which carries the stigmatic surface about 5 mm. beyond the tips of the anthers. This again indicates a *correlation of growth* which is of the utmost importance, as it completely transforms the mechanism from the necessarily self-pollinating type of the perennating bud (cf. Fig. 4) to a mechanism which eliminates self-pollination, and that is to say to one which must be adapted for cross-pollination.

(*b*) *Distribution of Pigment.*

Practically the whole of the floral-region is coloured yellow with xanthophylls, the chlorophyll only remaining to a small extent in the receptacle-wall of the ovary, and fading out in the base of the floral-tube. It is interesting to note that the amount of pigment is greatest in the new biological corona-zone, thus giving it a deeper colour, and suggesting that the use of the pigment as an attractive agent is intentional. Cultivated varieties differ in the relative amount of pigment in different parts, but the tendency is to a deep and uniform orange-yellow coloration throughout the whole flower; the yellow chromoplasts being found in the epidermal cells as well as in the subjacent tissue.

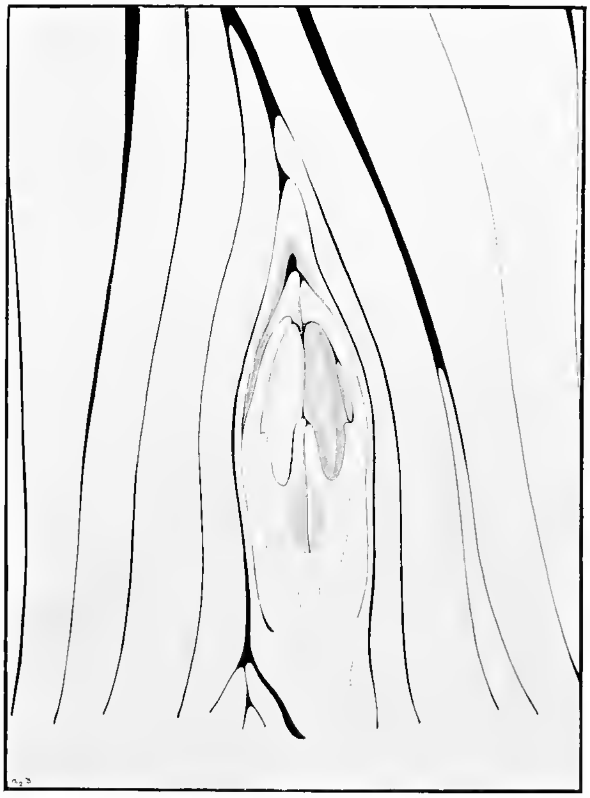

FIG. 3. *Narcissus poeticus*, August 15. Development of flower; origin of corona and ovules.

(1) *Note* that the gamophyllous zone (III) would alone give a flower-tube 18 mm. long: when the Zona Perigyna (IV) is added to this, the tube becomes extended to 22 mm., the length of the longest proboscis of a Humble-bee (or *Anthophora*); the addition of the corona-tube, however, renders the total floral-tube over 50 mm.; a distance beyond the range of any indigenous insect operating from the outside. When to this is added that the diameter of the bell is 15 mm., it is clear that the floral-tube is arranged for insect visitors to enter bodily, whatever may have been the meaning of these tubular growths originally. The examination of the structural mechanism thus indicates that the flower is adapted intentionally, with a correlated series of growth-zones, for cross-pollination by the agency of insects; these enter the tube in search of honey at the base of the trumpet, presumably rubbing pollen off the anthers and against the protruded stigma-lobes as they do so.

(2) *Note* also that the production of the crateriform receptacle, which in the primary

construction resulted in the epigyny of the flower, has evidently no reference to any pollination-mechanism; but possibly has a relation to the *protection* of the ovules, and the subsequent protection of the developing seeds.

(3) The flower-bud is converted from a generalized self-pollinating mechanism to an elaborated cross-pollination mechanism during the last phases of growth-extension known as the 'expanding-buds'.

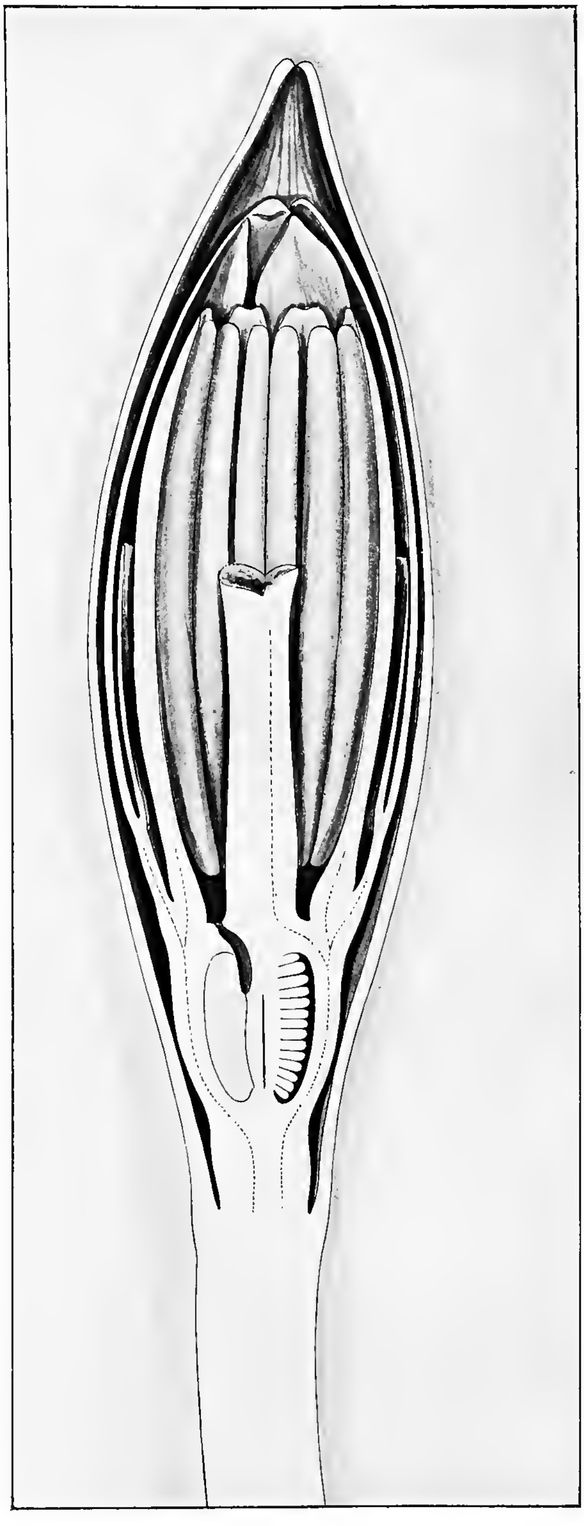

Fig. 4. *Narcissus Pseudo-Narcissus.* Section of perennating flower-bud in the plane of sectional elevation of the flower. Reduced from a drawing (× 10).

## Pollination.

Owing to their large size and clear coloration the flowers are eminently conspicuous at a time when other flowers are scarce, and there is little foliage on plants or trees.

The floral-organs are fully matured long before they appear above ground, and the buds emerge from the soil in an erect position, enclosed in the prophyll-spathe and guided vertically upwards between the foliage leaves, much as in the case of the Snowdrop.

As soon as the floral axis has reached its full length, curvature commences in the upper internode (above the spathe), and takes 2 or 3 days to be completed. The interesting feature of this growth movement is that it is adjusted, though not necessarily caused, by response to light and gravity; the flowers bend over at an angle of 90° towards the most strongly illuminated side, and thus on a slope or bank all face down hill; and in the open, if freely exposed, towards the south or south-west. When growing in clumps the latter is often not at all obvious as the stems are shaded during growth: the best effect is produced by growing a line of bulbs in single file north and south; the exact agreement of all the flowers then becomes very striking. Often also the growth of the internode continues, so that flowers come to point irregularly as they get older.

The biological significance of the movement is evidently that it is a definite adaptation for the visits of low-flying insects, and is of the same nature as the curvature seen in the case of the tall Sunflower heads, though not in the low-growing Daisy.

*Note* that the habits of insects again do not necessarily cause the movement, but may possibly increase by natural selection a tendency to unequal growth, which is the general property of vegetative shoots.

The flowers are homogamous, the anthers shedding as the perianth expands, and the stigmatic-lobes being simultaneously receptive.

On the divergence of the perianth-segments the corona is immediately disclosed, and free access to the interior of the flower is permitted.

The flowers offer both pollen and honey to insect visitors. Honey is secreted by the epithelium of the septal glands, the pores of which are just visible to the eye, but does not produce any visible deposit at the base of the tube. The anthers are grouped in a close ring around the very strong and somewhat spindle-shaped style-shaft, and together constitute a fairly rigid column in the axis of the flower-bell. That this production of a strong columnar group of anthers is a definite feature of the growth of the special mechanism, is shown by the fact that in older faded flowers, the cells of which have lost their turgidity, the filaments tend to diverge again; that is to say, the close pressure of the anthers against the style is effected by a special degree of turgidity in the cells of the outer surface of the filaments. The anthers are introrse in the bud, and dehisce by two slits from the apex downwards, the strongly diverging valves carrying the pollen to the outer face. Any large insect entering the bell must thus rub against the pollen-covered group of anthers, whether it comes to collect pollen or honey; small insects are also free to collect pollen, especially that which falls on to the surface of the corona. But while larger insects must also first come in contact with the projecting stigma-lobes, small insects may take either pollen or honey without effecting pollination at all. In fact, no insects are really excluded from the flower; but no insects with proboscides less than 7–8 mm. can readily obtain honey from outside the filaments.

In gardens, the flowers are visited by early bees; the Hive-bee collects pollen, as from every available spring-flower, and readily effects both self- and cross-pollination in so doing. The larger Humble-bees take honey, and observation of the working of the flower by the large *Bombus terrestris* suggests that the floral organization has become adapted for this insect rather than for any other; and it is interesting to watch a large specimen of this bee in a garden with a varied supply of blossoms, passing from one Daffodil to another and definitely selecting the large-belled forms, both 'Trumpets' and *Incomparabilis* (var. 'Sir Watkin'), with its back smeared yellow with pollen. Thus the flower is quite strong enough to bear the weight of its somewhat heavy body; the bee just fills the bell, forcing the anther column to one side as it violently enters the cavity, while the length of the rather short proboscis of this bee (7–9 mm.) is just adapted to probe the narrow slits between the broad flat filaments which lead to the nectary-pores; that is to say:—

The two newest features in the biology of the flower, the Zona Perigyna and the Corona-bell, are just suited to the measurements of the larger humble-bees.

On the other hand, *Anthophora pilipes*, with proboscis 21 mm. long, can probe the nectaries at a distance, and only just enters the bell; though it readily effects pollination, there is no such exact correlation between its special character and that of the flower. Similarly the large fly *Eristalis*, with 10 mm. proboscis, can readily take honey and pollinate the flower.

To what extent the violent operation of the wind may shake pollen from the anthers on to the corona surface, and back again on to the stigma, is still obscure; but it is clear that there is no definite adaptation to this end. The flowers are freely fertile to their own pollen, but few set fruit in absence of insect visits. Even the 'setting-fruit', as judged by the continued growth of the ovary, does not necessarily include fertilized ovules, and requires to be further checked. Both self- and cross-pollination will be abundantly provided for in the event of insect-visits, and the evidence that cross-pollination is preferable is still based on morphological deductions from the development of special mechanism. The earliest flowers may expand during the last days of February; the main crop extends from the first week of March to the second week of April. Individual flowers remain functional for just three weeks (18–34 days), although the stigmatic surface tends to suffer desiccation from the action of cold dry winds; and here again it is interesting to note that the horizontal direction of the flower helps it to swing like a vane, while the great development of the corona chamber further assists in the protection of the essential organs from desiccation; and here, as in other bell-types, the first evolution of the tubular zones of growth may quite as likely have been first initiated as a protective mechanism for the reproductive organs, and afterwards adapted and further specialized in connexion with insect-visits.

*Note* that as seedlings take 3–4 years to flower, experiments on the value of cross- and self-pollination in such a type are somewhat tedious.

## Fruit and Seed.

In old pollinated flowers all the parts wither and dry up; the ovary rapidly enlarges, but the floral members are not shed for a week or two, when they are all abstricted by one abscission layer from the surface of the ovary, which then becomes protected by a cap as in the Snowdrop.

The fruits attain full size as ovoid green pods in about 2 weeks (May 1st), and when mature (June 1st), form dry capsules which dehisce by 3 valves in the manner general among epigynous Monocotyledonous types.

*Note* that the mode of formation of the 3 valves does not represent any separation into component carpels, since the valves are portions of the receptacle-crater on which the carpels were based. The lines of separation are entirely new productions, and are formed at the most convenient places for opening up the cavities. Hence each valve has a septum along its median line on the inside, and 2 rows of seeds one on each side of it from adjacent loculi.

The valves diverge under desiccation, and consequently close again when wetted, and the shining round black seeds are readily scattered by the accidental agencies of wind, &c., and roll out of the capsules. There is no special adaptation for distant dispersal.

(1) *Note* that the biological curvature of the flower-stalk is again corrected in the fruiting condition, so that the open capsule is more or less upright; also that the structure of the fruit, although similar to that of the Snowdrop, has a simpler organization as seen in its mode of dehiscence.

(2) The mechanism of dehiscence is derived from the shrinkage of outer cellulose layers under desiccation, while an inner sclerosed layer tends to remain unaltered; it is therefore to be classed as hygrometric.

The fruits ripen and shed their seeds during the first weeks of June (8–15), the whole crop being shed within a few days when the weather is hot and dry.

The ovoid capsule (15–20 mm. by 10–12 mm. in diameter), originally green, turns yellowish as it withers, and soon dries up completely. The 3 dehiscence lines are continued about half way down the wall, and the 3 valves shrivel up to half their original size, so that the seeds which at first fill the basket-like cavity of the capsule are slowly pushed off and roll out.

Sections of the fruit show that the bulk of the wall remains undifferentiated parenchymatous tissue, but the loculi possess an inner lining layer of a single series of lignified pitted tracheides, with thick walls and netted cross-bars. This specialized layer serves as a protective ((?) aqueous) layer during the maturation of the seeds, and on dehiscence, under desiccation of the cellulose layers, constitutes the supporting framework of the capsule.

The *seeds*, of which 50 may be produced in one fruit, are black, with a smooth glossy surface, globose and often angular by mutual pressure, about 3 mm. long by 2 in diameter when wet, somewhat less in the dry condition.

The withered funicle persists on the seed, and the raphe is visible as a slight ridge leading to a slightly winged chalazal extremity.

Section in the plane of the raphe shows a small monocotyledonous embryo, with terminal cotyledon and obliquely-placed plumule, embedded in a mass of thick-walled endosperm cells: this latter does not entirely fill the cavity of the embryo-sac, and the cells are arranged in lines radiating from the central hollow.

The walls of the cells are beautifully thickened and pitted (purple-brown with Schulze's sol.), and contain abundant fat and proteid. A chalazal mass of parenchymatous nucellar tissue persists at the termination of the vascular bundle: the testa consists of a few dead layers of brown-black cells.

*Note* that the embryo is protected by the dead testa-layers, and by being embedded in a very solid endosperm; it is provided with reserve food as cellulose, fat and proteid stored in the endosperm cells; and beyond the action of the wind there is no arrangement made for dispersal to a distance.

## Variations and Monstrosities.

The cultivation and improvement of the Daffodil as a florist's flower has made considerable progress during the last twenty years, the object of hybridists being the production of (1) larger blossoms, (2) white coloured forms, and more especially flowers which shall be as large as possible and pure white. The best plant of this description so far has been named 'Peter Barr' (1902) (catalogued at fifty guineas, 1903); the blossoms being about 5 inches in diameter, with a 2-in. bell, and creamy white in colour. The flower has thus been increased to a size which is almost that of the type × 2 diameters, all the floral parts being correspondingly increased. In some of these large forms the texture, however, appears somewhat coarse.

For similar large forms, cf. Barr's:—

'Weardale Perfection', over 5 inches diameter, the stalk 2 ft. high, white perianth and pale primrose corona, 2 inches long and nearly 2 inches across the frilled edge.
'Duke of Bedford', $4\frac{1}{2}$ inches across, $2\frac{1}{4}$ across mouth of corona, yellow.
'Lord Roberts' (1901), golden yellow.
'Madame de Graaf', white, and 'Monarch', full yellow, the parents of 'Peter Barr'.

Older varieties include *major* and *maximus*, deep yellow; *bicolor*, white perianth, yellow trumpet, as also 'Horsfieldii', 'Empress', and more recent 'Victoria' (Barr, 1897), 'Weardale Perfection' (Barr, 1894).

*Diminutive forms* are also cultivated in which the proportions are very nearly reduced $\frac{1}{2}$, var. *minor*, about 3 inches across, with a trumpet $\frac{3}{4}$ of an inch in length: a form *minimus* still smaller (reduced $\frac{1}{3}$) is probably a distinct species; it was found growing wild in Spain by Barr (1887); the plant is only 3 inches high, the flower 1 inch long, about an inch across, the trumpet $\frac{1}{2}$ an inch only; all the parts being fairly reduced in proportion.

*Structural variations* in the primary phyllotaxis-construction giving tetramerous or dimerous flowers are not commonly found; and such irregularities are usually of a mixed type.

Thus Daffodils may be found with 8 perianth-segments, but the androecium is not also (4+4); in the same way, 5, 7, or even 9-parted perianths occur. Dimery is rare: a cultivated form *N. poculiformis*, of doubtful origin, with a short corona of the *N. incomparabilis* type is of interest in that dimery is commonly present. Four perianth-segments being succeeded by 4 (often only 3) stamens, and 2 carpels in the gynoecium giving a 2-lobed stigma.

*Minor Monstrosities* include the production of petaloid-segments from sterilization of one or more anthers, similar petalody of carpels, division of perianth-segments. The same irregularities are common in *N. poeticus* and other cultivated forms.

A variation in the inflorescence region, giving 1 or 2 lateral flowers included in the spathe, may probably be regarded as a reversion (cf. Fig. 1).

A considerable number of cultivated varieties which are objects of general admiration are the sterile monstrosities known as 'double' forms. Many of these are of great antiquity; e.g. *floreplено* in the Isle of Wight, found wild there (1629), *grandiplenus*, *cernuus plenus* (double-white), and the orchard form *Telemonius plenus*, which is probably the *Pseudo-Narcissus luteus multiplex* of Gerard (1597), and obtained by him from Paris. In many localities on the continent (Provence), as in England, this is by far the commonest form found growing in a semi-wild condition.

Doubling follows very simple rules, and as in the most general case represents a disturbance which becomes a *degeneration* in the construction-system; with this being correlated a total sterilization of the reproductive organs. The floral axis commences development normally, so far as the laying down of a (3 + 3) system on a crateriform receptacle is concerned, or remains asymmetrical at (2 + 3), and these constructions may be continued almost indefinitely for 60–70 members. Although it has been usual to record such flowers as continuing the whorled (3 + 3) construction, owing to preconceived ideas as to the structure of the normal flower, there is no evidence of such regularity; and in the vast majority of double forms the construction remains indefinite and asymmetrical of the primary (2 + 3) form.

The segments thus produced afterwards become quite irregularly modified as pale perianth-segments, darker segments with the corona texture, green leaf-like members,[1] and ultimately scale-like members. In one striking variety they attain uniformity, and thus present 6 superposed series (var. *Eystettensis*). Wherever the irregularity commences in the phyllotaxis pattern, it is interesting to note that the whole of the new members are formed on the inner slope of the crater, so that doubled forms may be distinguished into 2 classes —(1) those in which the irregular effect is developed at the rim, and no corona is developed (although irregular corona-formations may be found at isolated regions, and have given rise to suggestions that the corona is a 'ligular' structure); and (2) those in which it is initiated at a later date, and the massed members are included within a normal corona-bell. These phenomena occur together in the same variety. In other cases *fasciation* effects are found, the members being aggregated in groups around 2 or more subsidiary growth-centres (var. *grandiplenus* or *plenissimus*).

*Note* 'double varieties' are showier and last longer, and hence may be preferred as commercial objects.

Under favourable conditions of weather a double Daffodil may remain fresh for 6 weeks (March); 2 weeks in warm dry weather (April).

*Hybrids* have also been obtained between such different forms as *N. Pseudo-Narcissus* and *N. poeticus*. A form grown by Herbert (1843) produced a corona of intermediate dimensions, and was thus curiously like *N. incomparabilis*.

More recently whole series of hybrids have been produced between 'Trumpet' types and *N. poeticus*, *N. Jonquilla* and (?) *N. Tazetta*; all of which have trumpets of intermediate dimensions (*Medio-Coronati*), e.g. :—

Yellow trumpet forms and *N. poeticus* give *Barrii* sections ;
White trumpets and *N. poeticus* give *Leedsii* section ;
Trumpet Bicolor and *N. poeticus* give *Nelsoni* ;
also, Trumpet Daffodil and *N. Jonquilla* the *Odorus* type.

It does not, however, follow that all *Medio-Coronati* are to be regarded as hybrids, since coronas of all lengths might be expected in the wild state, and so *N. incomparabilis* is probably a true species although cultivated for a considerable period. Thus Parkinson cultivated it in several varieties in 1629, but Miller says he received bulbs from Spain and Portugal, and it would appear to be wild there.

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[1] When this production of green members is excessive, the flower is said to 'go blind' and is useless; a similar phenomenon is observed in the case of *N. poeticus* when grown on bad soil.

## Comparison of Allied Forms.

### I. Narcissus poeticus, L. *The Pheasant-Eye Narcissus,*

is naturalized in some parts of the country, and is indigenous to the whole of S. Europe from France to Greece as a common wild plant.

The flower is of great interest, in that while the vegetative structure of the plant and general construction system is identically the same as that of the Daffodil, the floral organization presents a converse and almost *Complementary type of secondary mechanism.* Thus, instead of producing the corona into a wide-mouthed bell 30 mm. deep, while the Zona Perigyna which constitutes the narrow guarded tube of the flower is only 5 mm. long, as in the Daffodil, *N. poeticus* develops the corona as a shallow cup 5 mm. deep, and produces the Zona Perigyna into a narrow-bored tube for exactly 30 mm. All other features are of minor importance, being subsidiary to this essential fact of construction, which thus converts the mechanism into a *Moth*-type of flower, instead of being as in the Daffodil a Humble-bee type.

The structure of the vegetative-shoot is identical with that of the Daffodil, but the bulbs are usually considerably larger and contain more leaf-members. Each season's growth produces 7–8 leaf-members and a single flowering axis: of the leaf members 4–5 are foliage-members, the others investing scale-leaves.

The spathe-leaf is 40–50 mm. in length, and rarely a second flower-bud may arise in the axil of one of the component prophylls; it seldom becomes a functional flower (cf. Fig. 1), though in the allied form *N. biflorus* this becomes the type.

The internode between the spathe-leaf and the ovary (20–40 mm.) bends over at a right angle, which in early spring flowers (April) is very closely approximated, though the angle may be much less in the later main crop (May).

The green receptacular ovary (15 mm. by 4) is surmounted by the perianth-tube, a cylindrical region (33 mm. by 4 in diameter); the 3 mm. bore of the cavity being further limited by ridges corresponding to the stamens, the narrow grooves between these latter constituting channels for the honey, and guides to the entering proboscis.

The free white segments (3 + 3), 30 mm. by 20–25, diverge at a right angle with the tube, and constitute a broad 6-rayed star which is extremely conspicuous by day, and also at dusk. At the orifice of the tube the corona forms a shallow cup, 15 mm. in diameter and 3–5 mm. deep; it is bright yellow in colour, with a wrinkled and frilled edge tinged bright crimson-scarlet.

The androecium consists of 2 whorls of (3 + 3) construction, the filaments being attached 28 and 30 mm. up the tube, just below the orifice; the outer (upper) whorl being above the lower (inner) whorl, and most visible from the outside. The filaments are extremely short (1 mm.), and the anthers present a remarkable phenomenon of shrinkage as they dehisce, from 10–11 mm. in length to 4–3 mm. only. The style shaft, 30 mm. long, just takes the 3-lobed stigma to the level of the lower anthers, and these recurve at the base of the corona-cup, in the immediate vicinity of the stigma-lobes superposed to them. On looking into the cup, 3 entrance-pores are noticed in front of these upper anthers, while the lower ones quite block the tube. The nectary in the form of 3 septal-glands, 4 mm. deep, opens at the base of the style-shaft on distinct papillae.

*The Floral Diagram* is identical with that of *N. Pseudo-Narcissus*, the similar oblique orientation being shown in young flower-buds (Fig. 2); symmetry is most closely approximated in the transverse plane.

*The Sectional Elevation* follows this plane, passing through an inner perianth-segment on the left, and an outer on the right: the relation of the perianth-tube, corona, anthers, and stigma-lobes being thus rendered sufficiently obvious.

From the standpoint of *Special Mechanism*, similar zones of growth are concerned, but the concentration of the essential organs of pollination at the mouth of the floral-tube is very striking, and at the same time comparable with the general tendency of other tubular types as in Gamopetalous Dicotyledons.

The corona has the effect of limiting the entrance to the tube; its wrinkled edges may possibly be regarded as an adaptation as a holdfast for visiting insects, when the perianth segments are flattened back to a target-type of bloom.

In cultivated varieties (cf. var. *reflexus*), this may be exaggerated to a form in which the cup-shaped corona is alone protruded forwards as the functional bell of the flower (cf. also *Narcissus calathinus*). The remarkable shrinkage of the large anthers on dehiscence is also clearly correlated with the necessity for including them within the corona, otherwise they would, even with the omission of a zone of elongation in the filaments, project several millimetres beyond it:[1] and this close aggregation of the anthers is clearly connected also with the arrangement by means of which 3 definite narrow entrance-slits are provided to the floral-tube opposite the outer whorl of anthers, and by passing over these latter and along the sides of the lower anthers an entering proboscis is thoroughly smeared with pollen.

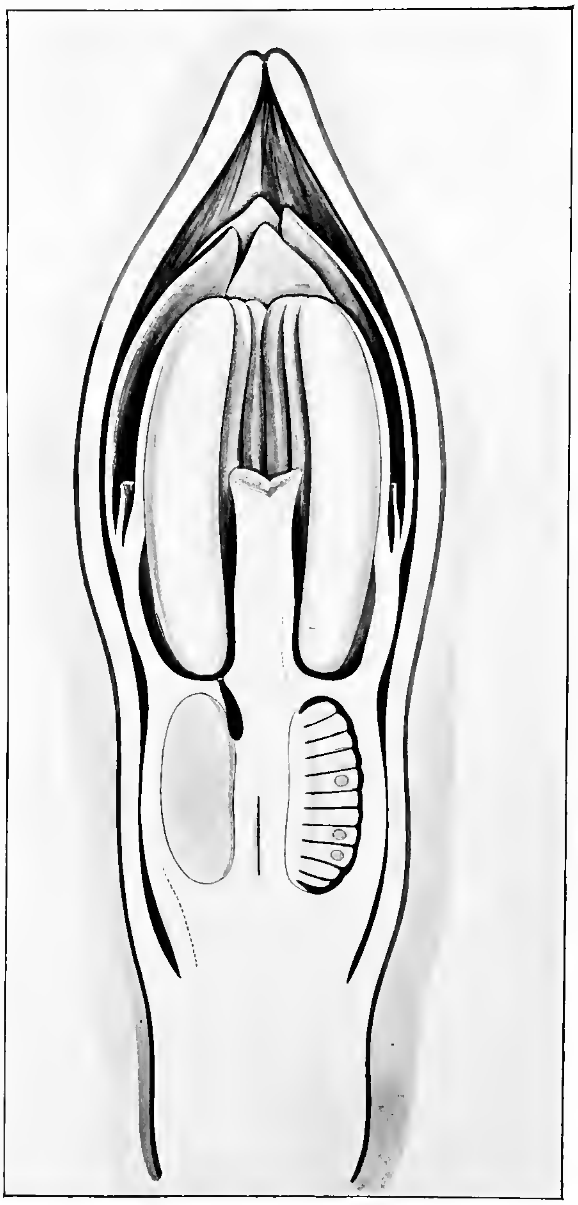

Fig. 5. *Narcissus poeticus*. Section of perennating flower-bud to agree with sectional elevation of the flower.

On the other hand, the 3 lower anthers as they dehisce come into direct contact with the alternating stigma-lobes, and self-pollination by insect visitors, and even in their absence, appears unavoidable. At any rate the elimination of self-pollination is by no means so effectually guaranteed as in the Daffodil; and *N. poeticus*, though highly specialized as a moth-type of mechanism, would appear to be at present in a more primitive phase.

Of the large number of varieties in cultivation, the tendency is to promote the culture of the most early-flowering forms; and while the type flowers in May, early varieties which present no real differences open 3 weeks earlier mid-April (6–15). The flower-buds emerge from the soil in the erect position, and 2–3 days before the expansion of the flower the internode within the spathe-leaf bends sharply over, and reflexes to such an extent that the flower-buds droop vertically downwards (180°). This curvature is corrected to a right angle (90°) with the vertical the day before the perianth unfolds, and remains constant during the flowering stages, to re-erect during fruit development. Later May blooms bend but slightly, and the main crop at the later date may only project at an

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[1] In warm rainy weather the perianth may expand, and the stamens remain unaffected and unable to dehisce for even 1–2 days; the peculiar appearance thus presented of the large anthers projecting 6 mm. from the perianth-tube, or 2–3 mm. higher than the corona is very striking; while at the same time it is clear that if the flowers open during the afternoon in warm moist environment, a first chance will still be given to cross-pollination by moths which have been visiting flowers a day or two older.

angle of 45°; in some cases there is practically no curvature at all. Both light and gravity are utilized as directive stimuli.

As in the case of the Daffodil, the flowers remain functional for about 3 weeks in April, 2 weeks in May. They are not visited in our gardens except by a few pollen-collecting Hive-bees; autogamy appears inevitable, the flowers are fertile to their own pollen, and set fruit freely.

The fruits grow rapidly; their history, form and dehiscence agree with similar phenomena in the case of the Daffodil. Full size is attained in a fortnight (23 mm. by 15), and the green capsules ripen and shed their seeds in June. Structure of the seed again corresponds to that of the Daffodil. Development is often imperfect, and large apparently good fruits may contain no seeds.

*Monstrous* forms occur in cultivation: *Double* forms being here also in great request. The same two cases of doubling may occur; either the abnormality only commences within the crater, so that a few petaloid members are produced within a normal corona; a rather insignificant production from the florists' point of view, and therefore rejected; or the irregularity may occur at an early date, in which case the flower becomes a large rosette of white perianth-members, many of which may have small corona-pieces as outgrowths of the laminae, and below these long stalk-portions which assume the characters of the Zona Perigyna, being green with a tendency to curve round to a tubular form. This double form is widely cultivated (commercially). Instances of Dimery, and such cases as the production of stamens for perianth-members are also recorded; all such examples indicate, as in the Daffodil, irregularities at some point in the different factors of the construction-mechanism.

*Developmental* stages agree with those of the Daffodil (cf. Figs. 1, 2, 3); the perennating buds are essentially similar (Fig. 5), but that of *N. poeticus* already indicates the complementary characters of its corona and Zona Perigyna growths.

One additional feature is found in *N. poeticus*, which does not occur in the Daffodil; the orange coloration, often scarlet in some varieties, of the edge of the corona frill, is due to definite orange plastids of a spindle-shape, different from those of the yellow Daffodil pigments. In hybrid varieties, one of the objects of the florist is to introduce this pigment as much as possible throughout the whole of the corona, and even into the perianth segments.

*Note* that it is difficult to explain the appearance of a new method of pigmentation, which is lacking in the closely allied form *N. biflorus*, except as a definite attempt to concentrate attention on the 'eye' of the target-like flower: yet to prove that this is the case it would be necessary to show that the blossom of *N. poeticus* is a more successful floral mechanism than that of *N. biflorus*.

## II. Narcissus Bulbocodium,[1] L.

## Corbularia.[2]

*Hoop Petticoat Daffodil.*

A small Daffodil with more delicate blossoms, indigenous to the South of France, Spain, and North-west Africa, and long cultivated in this country in many very distinct varieties.[3] The plants are of the usual Narcissus-type, but smaller and slenderer in habit (in one early-flowering form *monophylla* often reduced to one foliage member), and 6 inches to a foot high. The flowers are solitary, and vary considerably in size and colour, from

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[1] *Narcissus Bulbocodium* of Linnaeus (1753). *Bulbocodium*, an old generic name applied by Bauhin and Ray to the Daffodil, = *βολβοκώδιον* of Theophrastus, and used by Linnaeus for another genus (1737).

[2] *Corbularia*, a genus of Salisbury (1812), a useful designation for the zygomorphic forms of *Narcissus*.

[3] Figured by Parkinson (1629) as *Pseudo-Narcissus juncifolius luteus major*; also received later by Miller from Portugal; the latter appears to be responsible for the name 'Hoop Petticoat Daffodil'. The plants grow freely in the open, and flower in May.

$\frac{1}{2}$ inch to $2\frac{1}{2}$ inches in length of trumpet, and from white (*monophylla*) to pale yellow (*citrinum*) or a deep golden-yellow.

The flowers are interesting as exhibiting the corona-formation carried to an extreme, which quite dwarfs the perianth-members: while the corona continues the funnel shape of the perianth-tube onwards for a distance of 16–20 mm., to form a wide-mouthed bell which may be 20 mm. or more across, the free perianth-members are slender and inconspicuous, usually remaining green-veined, while the corona-bell alone assumes the clear coloration of golden-yellow or white. An additional factor is also noted in the floral-mechanism, in that the stamens and style present growth-curvatures which render the mechanism as a whole *zygomorphic*, although the perianth-tube and corona retain their original radial construction almost unaffected. As the buds expand, the stamen filaments and style bend downwards to touch the lower surface of the bell, and then upwards again, so that the anthers and stigmatic surface are presented in the median line of the bell, and an insect entering the flower must pass over them in succession. The stigma is protruded still farther than in the Daffodil, and in some varieties (cf. *monophylla*) may project beyond the bell. The anthers are freely versatile, and the members of the inner whorl a little shorter than those of the outer, so that as all bend upwards the former come to lie behind the latter, and the anther-cluster gains in efficiency by being stretched along the floor of the bell. The Zona Perigyna is extremely short (1–2 mm.); the filaments form a palisade over the approach to the nectaries; it is clear that the flower is adapted for the visits of insects (bees), which crawl right into the corona-bell and take honey between the filament bases. The flowers are produced in April and May (those of *monophylla* in December, February). It will be noted that the zygomorphy, although perfectly definite as a factor in the mechanism, since the growth-pressure exerted by the filaments on the lower surface of the bell may be considerable, is not of a very accurate type, since it is apparently correlated with the growth movement which bends the flower-stalk, and cannot be given an orientation in the floral diagram. Nor is the exact significance of this new factor wholly explicable; the essential feature appears to be that the pollen-supply is more readily available to pollen-collecting insects, and is rubbed off against the lower surface of the insect's body, while in the Daffodil type, the bee which enters the bell is rubbed over its back. The Daffodil and Corbularia may so far be regarded as complementary types of mechanism; and it is interesting to note that both tend to eliminate autogamy by the extreme elongation of the style-shaft. *Note* that in *C. monophylla* this region continues to grow after the bud expands.

## Theoretical Considerations.

The reduction of the bulb-construction to a theoretical diagram illustrates the fact that the morphological structure of the plant-shoot follows normal rules for phyllotaxis and ramification so far as its specialized and symmetrical system is concerned; so that, notwithstanding its extreme reduction and biological adaptations, there is no difficulty in postulating for it an ancestral form on the lines of the more generalized types of the aerial shoots of Monocotyledons. On the other hand, comparison of the floral diagram shows a perfectly normal trimerous Monocotyledonous type, and the recapitulation of the (2 + 3) spiral system in the first perianth-segments, followed by symmetrical (3 + 3) whorls for the rest of the floral members, is of interest, in that it suggests that the phyllotaxis of the vegetative shoot is a secondary phenomenon, and that the ancestral vegetative form, which again had a wholly aerial shoot system, was spirally constructed throughout, as in the case, for example, of *Lilium candidum*.

Comparison of the sectional elevation shows that the peculiarities of the flower are due to secondary growths, the most important zones being the Zona Perigyna and the entirely new development of the corona, to which may be added the correlated stylar growth region. That the corona is a later departure than the Zona Perigyna is suggested not only by its actual ontogeny, but also by the comparison of allied forms; while the great development of the crateriform receptacle being common to all and definite from the first is possibly the most ancient modification of this floral type of structure. The corona as the most recent feature of the flower is relatively small in *N. poeticus* and *N. Tazetta*, and has not in these types attained such importance as to constitute a bell-type of flower; the most primitive case being found in *N. Broussonetii*, a rare form from Morocco, in which it only exists as a mere annular ridge at the end of the perianth-tube. This last form may be therefore regarded as so far the nearest to the primitive stock of the Narcissus-group, while *N. Pseudo-Narcissus* represents the highest forms in which the corona has reached the maximum length, i. e. equalling the protective perianth-segments. *N. poeticus* from this standpoint would come about half-way; but while the great bell-types have become modified in correlation with large-bodied bees, the forms with lesser developed coronas appear to be specialized in a different manner for Lepidoptera; a still further advanced condition is found in *N. Bulbocodium* (Corbularia), the Hoop Petticoat Narcissus, in which zygomorphy has set in.

The corona thus appears to have arisen as a continuation of ridged outgrowths of the rim of the receptacle-tube between the perianth and the androecium, which had the effect of forming a guard, and limiting the entrance to the floral tube;[1] this being in fact a very general phenomenon in other types in which the floral mechanism involves a tube-principle (cf. *Vinca*, *Myosotis*, *Agrostemma*). This growth affording by its special coloration a central coloured eye-spot, became useful as a guide; and in this connexion it is of interest to note that the colour of the corona is always more stable in varieties than that of the perianth-segments.

Only when the corona reaches a relatively very considerable size does it become at all useful as a *bell*, and the first advantage of such an organ is probably the protection of the included anthers and stigmatic papillae from extreme desiccation. When further exaggerated it becomes a *chamber* into which insects can creep, and in the limit, when it equals the perianth segments which cover it in the bud, the beautiful bee-fitting cylinder of the Daffodil is attained. But it must be carefully noted that large Humble-bees did not create or even call forth this mechanism; they have only utilized and perfected a structure which was originated and developed for probably very different purposes. On the other hand, there is a distinct suggestion that the primitive forms were adapted rather for moth-agents, and that the Daffodil succeeds in more northern latitudes, where moths are less plentiful than bees in the spring months: thus the flowering period of the Daffodil is just over when the earliest varieties of *Narcissus poeticus* commence to bloom (first weeks of April).

The genus *Narcissus*, within which there has been included a large number of forms characterized by the possession of this *corona*-growth, thus ranges from *N. Broussonetii* with only a faint ridge, to the great bell-form with eccentric stamen-cluster, *N. Bulbocodium.* Haworth (1831) gave specific rank to 150 forms, while Baker and Burbidge (1875) reduce them to 21; a curious example of the manner in which the value of 'species' varies with the temperament of the systematist.

By a curious inversion of ideas the most highly specialized forms (*Bulbocodium*, *Ajax*) are taken first in the classification of the various types (Burbidge; Pax, 1888), and the smaller and more primitive forms last; and thus *N. Broussonetii* is described as having a 'nearly obsolete' crown (Baker), or a crown 'reduced to a mere rim' (Burbidge), and 'very abnormal'.

Species with only a trace of the corona grade directly into the typical *Amaryllis* construction, and thus the genus *Narcissus* is included in the conventional family of the

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[1] A closely comparable but wholly independent evolution in the North American types *Eucharis* and *Hymenocallis* leads to the production of a zone of growth in the same region, which differs in that it elevates the filaments of the stamens on a similar cup.

Amaryllidaceae, but much still remains to be done with regard to determining the lines of the evolution of the group. This appears to have been localized in the Western Mediterranean basin; the simplest forms[1] as well as the greatest range of type[2] being found as relics on the hills around this district, in Spain (Pyrenees), Algiers, Morocco, and the Canary Islands. It is thus possible that the group of the Narcissus represents the modern descendants of an ancient, sand-inhabiting, moth-pollinated Amaryllis-section of a sub-tropical North African flora.

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[1] Types with comparatively insignificant flowers, several in an inflorescence, and autumn-flowering—

*N. viridiflorus*—Spain and Barbary States.
*N. elegans*—Algiers, Sicily, Italy.
*N. serotinus*—Spain, Barbary States to Palestine.
*N. Broussonetii*—Morocco, Mogadore.

[2] *N. Bulbocodium*—Bayonne, Pyrenees, Algiers.

# IX

## **Erica**[1] **carnea, L.**[2] *Early-Flowering Heath.*

A HARDY perennial low-spreading woody shrub, with evergreen needle-leaves, growing a foot to eighteen inches high, indigenous to the Alpine regions of Central and Southern Europe, from Servia through the Alps to the mountains of Italy, South Germany, and Saxony.

Introduced in 1763, it is cultivated in gardens for the sake of its abundant flowers produced in early spring (March, April). The flower-buds are fully formed in the preceding autumn, and in very mild winters the plants may be a mass of bloom in January and February. The fruits ripen and shed their seeds in June.

### Description.

INFLORESCENCE: Reduced lateral racemes of 1–5 flowers borne in the axils of the needle-like foliage leaves, throughout the upper portion of the previous summer's growth. These racemes are clustered into a panicled aggregation which is more or less unilateral owing to heliotropic curvatures of the lateral axes. Individual flowers possess subtending bract and 2 lateral prophylls: these are all small and are carried up a short distance on the flower-stalk.

RECEPTACLE: conical (hypogyny).

FLOWER: hermaphrodite, actinomorphic, tetramerous throughout.

PERIANTH differentiated into:—

CALYX of 4 sepals, slightly gamosepalous at the base; free segments ovate-lanceolate 3–4 mm. by 1 mm., pink or crimson.

COROLLA gamopetalous of 4 petals, alternating with the sepals, white to pink later; corolla-tube 5 mm. long and 1 mm. wide at the mouth: free segments acute, about 1 mm. long and 1 broad.

ANDROECIUM of 8 free stamens, 4 antisepalous and 4 antipetalous.

*Filament* 6 mm, slender, slightly bent or kneed just below the anther.

*Anthers* deeply 2-lobed, 1 mm. long, purple-black, introrse, dehiscing by slit pores down half their length.

*Pollen* yellowish-gray, in tetrad groups.

GYNOECIUM of 4 antipetalous carpels.

*Ovary* ovoid, 1 mm. long, green, syncarpous, 4-locular with axile placentation, and 8–10 obliquely suspended anatropous ovules in each loculus.

*Style* filiform, 6 mm. long.

*Stigma* capitate, almost imperceptibly 4-lobed, the lobes being surrounded by a slight ridge. The stigma-lobes are commisural, the stigmatic surface slightly concave.

NECTARY: a swollen ring-disc around the base of the ovary, with 8 descending lobes between the bases of the filaments. Secretion is abundant, and rises in the corolla-tube as far as the top of the ovary.

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[1] Erica of Pliny, ’Ερείκη of Theophrastus, applied by old writers to the Heather (*Calluna*). Fuchs (1542) gives a good drawing of *Calluna* as Erice. Gerard (1597) describes 9 (= 6) different sorts of *Erica* as Heath, Hather or Linge; *Erica vulgaris* being *Calluna*. Cf. *Erica vulgaris glabra* of Bauhin (1623).

[2] *Erica* founded as a genus by Tournefort (1700), established by Linnaeus (1737); *carnea* the name finally adopted by Linnaeus (1764) from the colour of the flowers, an old synonym being *E. herbacea* from the colour of the flower-buds which are green in late summer; (*E. procumbens herbacea* of Bauhin's Pinax, 1623).

## Floral Diagram.

The evergreen needle-leaves of the foliage shoots persist into the second summer, and are borne in alternating whorls of 4. This represents a symmetrical phyllotaxis-construction (4 + 4), and in weak shoots the construction commonly varies to (3 + 3), but the (4 + 4) is the characteristic type for this species (Fig. 1).

The apex of the shoot continues the vegetative growth; short flowering-axes of limited growth arise in the axils of the upper foliage-leaves as dwarf shoots of the second degree. The lower foliage leaves do not subtend dwarf shoots.

The dwarf flowering-shoot arises in the axil of a foliage-leaf, and presents normal orientation; 2 minute prophylls are borne laterally, and beyond these 2–3 whorls of small free bracteoles: either 2–3 whorls of an alternating trimerous series, or 4 or more members of a decussate (2 + 2) series. Above these sterile leaf-members occur the few fertile bracteoles which are carried up on the floral axes they subtend: in the case of trimery, 3 flowers are typical, or less by reduction: in the more usual case 4 are present, or less by reduction, and less frequently a fifth belonging to a still higher whorl of bracteoles. There is no terminal flower. In weak shoots the construction reduces to prophylls, 1 whorl of scales, and 1 flower; the scales are so small that such a single flower looks as if it were axillary to the subtending foliage-leaf.

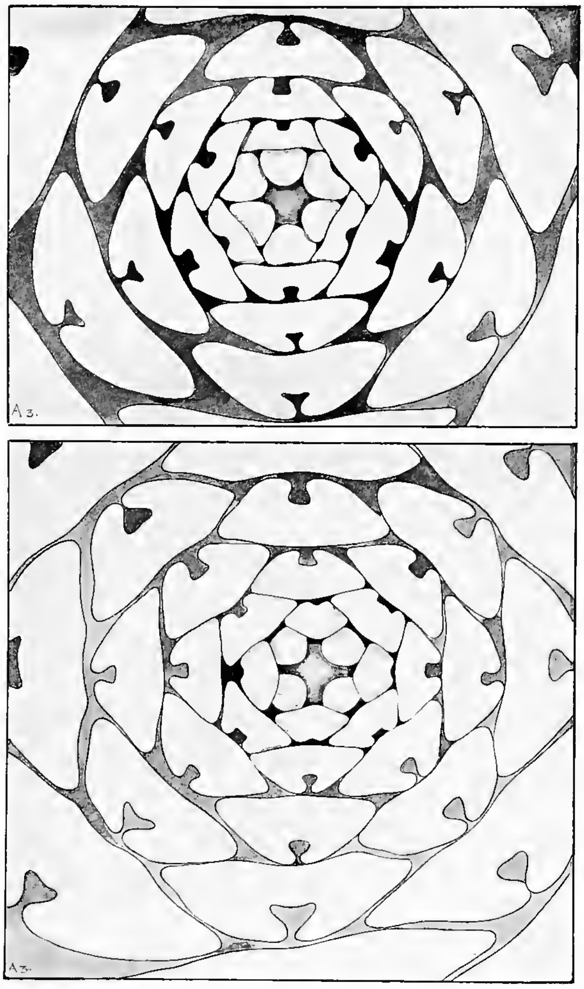

Fig. 1. *Erica carnea.* Phyllotaxis systems of vegetative shoots (3 + 3) and (4 + 4).

The prophylls ($\alpha$ and $\beta$) of the individual flowers are also carried up on the flower-stalk by a special zone of growth, so that $b$, $\alpha$, $\beta$ thus form a 3-leaved involucre to each flower, protecting it in early stages of development.

*Note* that these dwarf flowering-shoots are developed in the summer on foliage-shoots of the current year; the flowers are fully formed in Autumn, but flowering is delayed till after the cold season. The spring flowering-period is therefore secondary, and presents the phenomenon of a delayed flowering function.

The diagram illustrates a typical case of a 4-flowered decussate inflorescence.

*Note* that the vegetative shoots are (4 + 4) or (3 + 3), and the inflorescence axes (3 + 3) and (2 + 2).

*Orientation* of the flower is again normal for symmetrical construction, and the phyllotaxis-arrangements are thus wholly symmetrical throughout the entire plant. The calyx represents a (2 + 2) construction, the outer pair of sepals being median, the inner transverse, but a (4 + 4) construction is regained in the sporophylls. As in other tetramerous types derived from a pentamerous ancestor, the 4-parted corolla is diagonally arranged at the point of departure, between the (2 + 2) system of the prophylls and sepals and the (4 + 4) of the sporophylls. The 4 petals are simultaneous in development, and constantly *right-convolute*[1] in prefloration.

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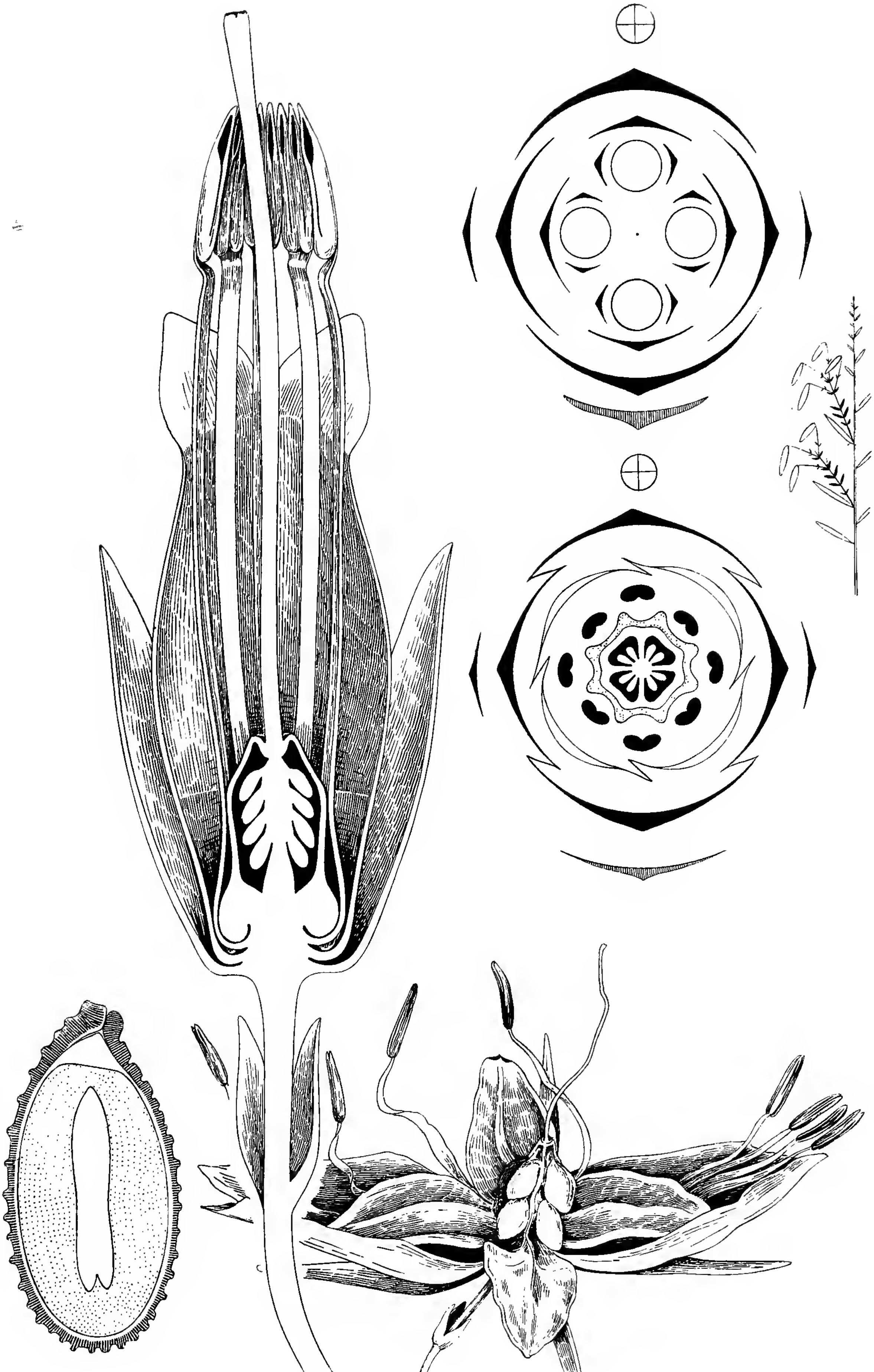
[1] That is to say, on looking at the conventional *Diagram* the petals present an appearance of winding to the centre as *right-hand curves*: or taking the conventional *elevation*, the *right-hand edge* of the petal is inside, and is the one figured when the overlapping is considerable in the flowering-stage (cf. *Vinca*).



**Erica carnea:** Floral Diagram and Sectional Elevation of Flower in the median plane; Inflorescence diagram and scheme; dehiscing Fruit, and section of Seed in the plane of the raphe.

The androecium of 8 stamens continues the (4+4) construction for 2 whorls; and since the strict alternation is not maintained into the gynoecium of 4 carpels, there must be a break in the system somewhere, and the flower is said to exhibit the phenomenon of 'obdiplostemony'. In the open flower the 8 filaments form a perfect circle around the ovary, and the 8 anthers are arranged in a uniformly compact group. Transverse sections at the points of origin of the stamens show scarcely any appreciable difference between the 4 antisepalous and the 4 antipetalous, but if anything the former are slightly lower on the receptacle; and in actual ontogeny there can be no doubt whatever that the antisepalous stamens arise first.

As in other obdiplostemonous types (cf. *Linum*, *Oenothera*), more conclusive evidence of the relative value of the androecium whorls, beyond what is thus deduced from the adult construction, is not available; but it is sufficiently clear that taking the facts as they are, they directly suggest that there is a break somewhere, and that it takes place between the androecium and the gynoecium; that is to say, one cycle or an odd number of cycles has remained suppressed at this point, which becomes subsequently emphasized by the presence of a *disc*-nectary.

A transverse section of the ovary shows that the 4 loculi are definitely antipetalous, and there are 2 rows of ovules in each loculus, the placentation being axile.

Section taken below the cavity of the ovary shows the circular nectary (disc), the 8 glandular lobes of which project between the bases of the 8 filaments. The apparent arrangement of the 8 stamens in a single series may thus be secondary, and the result of slight displacements produced by pressure in early development around the 8-lobed receptacle.

Being a definite and important region the disc-nectary is thus represented in the floral diagram.

## Elevation.

Since the primary phyllotaxis-construction is wholly symmetrical, section follows an accurately median plane, and passes through the subtending bract (*b*) which is elevated on the flower-stalk. One is so used to express the secondary elongation of a shoot in terms of 'internodes' between leaf 'insertions', that there is no exact terminology to express the fact that a secondary growth-elongation here takes place at the point of origin of the bract on the axis, and apparently removes it on to its own axillary shoot (cf. *Cytisus Laburnum*).

The prophyll $\beta$ is also shown, and the plane of the section passes through 2 median sepals which are only very slightly elevated on a gamosepalous zone of growth. On the other hand, the gamopetalous zone is well marked, and alone constitutes the whole of the corolla-tube, the petal-lobes being comparatively small: 2 median stamens are cut, and 3 others represented arising from the receptacle quite independently, and having no connexion with the corolla. The anthers have a peculiar form (2-horned), and just beneath them the filaments are bent. The ovary is relatively large, and section is here taken off the strict median plane which passes through a septum, in order to show the contents of 2 loculi. The style is a simple rod-like shaft, and the stigmatic-lobes are extremely minute, and are surrounded by a low ridge corresponding to the carpel tips. The stigmatic lobes, better seen in allied forms (cf. *Calluna*), are commissural and hence antisepalous. The nectary region is prominent, though the descending lobes are not very clear owing to the filaments being in front of them; they appear to be derivatives of a receptacular region between the androecium and the gynoecium, a point of interest in connexion with the previous suggestion that some members have remained unexpressed at this point.

*Note* the cylindrical basket-like arrangement of the filaments, and the compact conical group of anthers with introrse aspect and porous dehiscence.

## Development.

Developmental stages show little of the essential phyllotaxis mechanism beyond what can be deduced from the adult construction. The symmetrical whorls appear in regular series; as already indicated, the antisepalous stamens arise first, the antipetalous later; but while development in time is no absolute criterion of theoretical value (since a member by growing at a greater rate than an adjacent one may, by appearing larger at any given moment, convey a subjective impression that it is therefore older), nothing is gained by placing the break in the construction-system at any other point, e.g. between the androecium and the corolla, in order to bring it into line with other so-called 'obdiplostemonous' types; since obdiplostemony as a phenomenon of reduction might occur in any line of descent in which reduction stages have become characteristic.

Similarly little more can be traced in the development from the standpoint of the elevation than can be inferred from the adult mechanism. The only point of interest is that of the curious stigma which in the case of *E. carnea* is still more obscure than in other species owing to its small size when adult. The 4 carpels become gamophyllous almost as soon as they acquire any definite bulk, and the tips form a fairly uniform edge to the still open cavity; as the ovary closes in, the placental ridges, continuous with the sutures of the carpels, appear as 4 lobes at a slightly higher level than the tips of the carpellary leaves themselves. Growth in this region practically ceases, and the 4 commisural or placental elevations show above the collar-edge of the carpel-tips which in some cases form 4 obscurely marked lobes (cf. *Calluna*). The 4-locular ovary assumes a 4-angled form, and the 4 angles press outwards against the antipetalous stamens, so that these may even look at certain stages as if on a circle a little outside the antisepalous ones. The disc again appears relatively early, when the ovules commence to form on the placentas; the regions of secondary elongation are also put in at slightly different times, and without any reference to one another, the rate of growth being at first most rapid in the style-shaft.[1]

FIG. 2. *Erica carnea*, June buds. Development of floral members. Stages 1, 2.

*Note* that the prefloration of the corolla is established at a very early date, before the commencement of the Gamopetalous Zone. Though such an arrangement of regular overlapping must be directed by special growth-phenomena in the corresponding edges of the 4 petals, which so far as can be seen are isophyllous, and equal in origin and position in the symmetrical bud, and should by theoretical construction meet at their adjacent edges on exactly equal terms; it is difficult to see what benefit can accrue to the bud from any one

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[1] For good figures of the early stages of *E. cylindrica*, cf. Payer (1857).

form of overlapping rather than another; and the fact that one special case[1] becomes a constant affords a curious suggestion of aim at perfect radial symmetry in the case of certain floral-mechanisms: from another standpoint, it may be the mere survival of a feature which was more prominent before the evolution of the present gamopetalous mechanism, which has apparently led to a reduction in importance of the free petal-lobes.

*Development of E. carnea.* The structure of the flower is readily followed in early stages, as the flower-buds stand erect on their special shoots, and are easily cut in longitudinal and transverse section; while the 4-angled form admits of fairly accurate orientation.

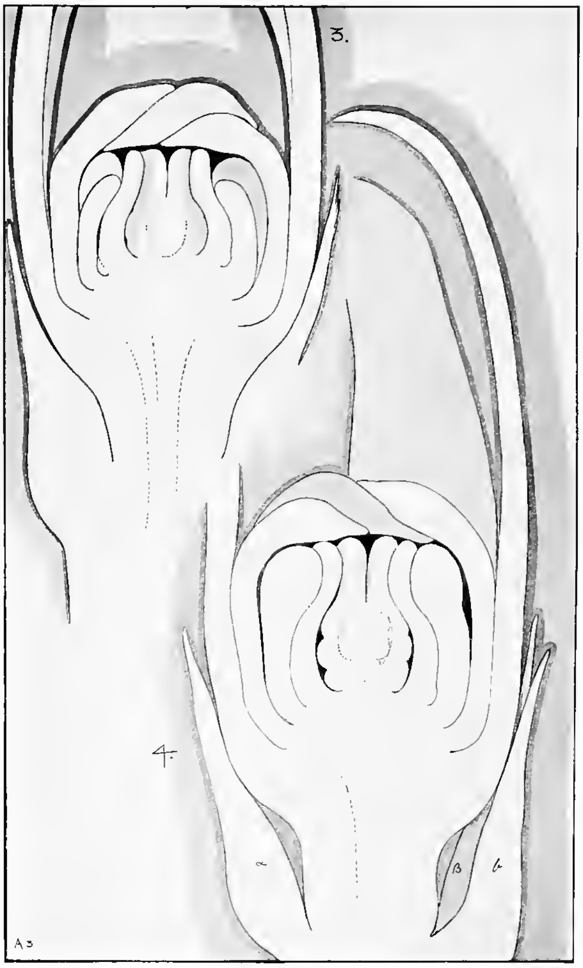

Fig. 3. *Erica carnea*, July buds. Formation of the ovary-cavity and ovules. Stages 3, 4.

The buds commence to develop early in June; and by June 20 (Fig. 2) the stamens are laid down, and the carpels just commencing. The apex of the shoot remains conical or dome-shaped throughout the entire history, so that the flower is a purely hypogynous type, and no trace whatever of crateriform character appears in the receptacle. The bract (*b*) and prophylls (α, β), as also the sepals, are at first in close contact (2); a short zone of growth is put in between the sepals and prophylls as the special flower-stalk, but the growth which 'carries up' the bract takes place later; the manner in which the bract becomes involved being indicated in Fig. 2. The sepals, also at first in close contact with the inner members (2), soon grow out and constitute a damp protected chamber (3–8), in the basal half or third of which the rest of the floral members continue in close contact. The petals are rather remarkable for their early growth-relation to the stamens which they closely invest, becoming convolute at an early date (2–3), all stages showing the overlapping of the free segments. The stamens develop normally; the filaments being soon differentiated, and the anthers becoming bilobed (3) before the appearance of ovules in the ovary. What is more remarkable is that the nectary-lobes begin to differentiate at the same time (3, 4, 5); this being extremely early, previous to the development of definite sporangia in the sporophylls, and as compared with the general case, quite unusual; since nectaries are typically late biological adaptations, and not structural features. The possibility that these lobes represent a lost cycle of sporophylls is thus strengthened, although no more definite proof appears available. The carpels show a great development in the placental region; ovules commence to be formed at the end of June, become anatropous (6, 7) and develop integuments, while the anthers only present undifferentiated archesporial tissue. The style-shaft gradually grows out, and the very slight lobes over the placentas are apparent in July (7). Note that in a median section a placental formation is always facing the observer, and the ovules borne on the former portion are seen by focussing below the

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[1] The mathematical possibilities for tetramery including 4 types of prefloration, and $2^4 = 16$ cases of diagram orientation. Even radial symmetry (convolute prefloration) gives 2 cases of which one is selected (cf. *Vinca*).

median plane which cuts the posterior and anterior placentas. The buds are thus practically complete in July (7), and mature their ovules and pollen throughout August. They were 1 mm. in length by the middle of June; 2 mm. by the middle of July, and 3-4 mm. in August, when they become green and pendulous on the foliage-shoots. As the length of the bud is merely due to the growth of the sepals, little outward change takes place, and the October buds are no longer, though the essential members have gone on extending until the calyx becomes filled with the growing mechanism (8); the ovules being now fully formed and the pollen-tetrads visible in the anthers. Green buds taken at this time present a feature of interest in that the anthers are coloured dark purple with a strong solution of anthocyan localized in the epidermal cells, while the pigment is still practically absent from the rest of the flower, or only traces found in the sepals and bracteoles; the possibility of this pigment being utilized as a protective screen to the developing pollen is most clearly suggested.

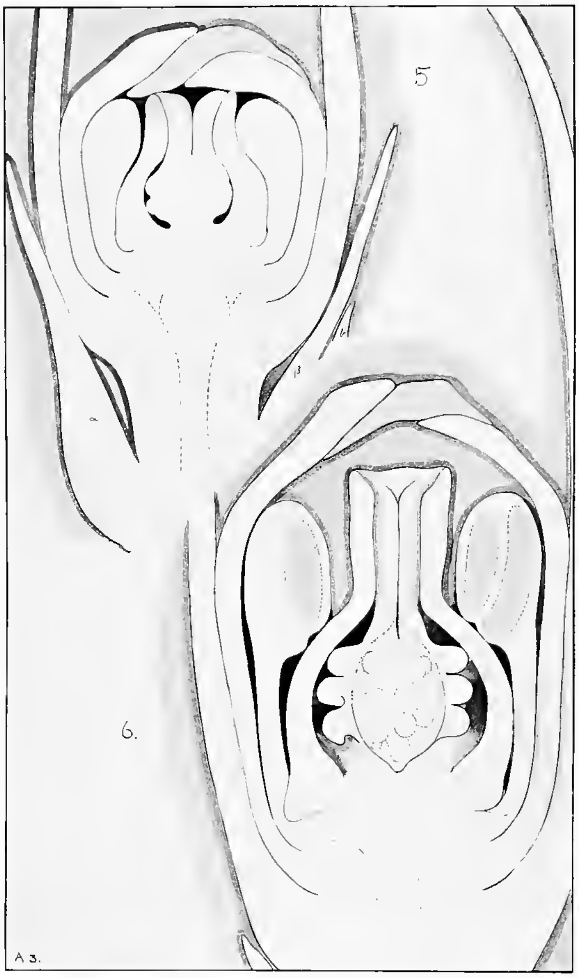

Fig. 4. *Erica carnea*, July buds. Development of flower. Stages 5 and 6.

### Special Mechanism.

From general consideration of the elevation, quite apart from the confirmation in developmental stages, it is clear that this may be comprised under the following heads :—

(1) A definite *Gamopetalous Zone of growth* carrying up a whorl of petals and constituting a flask-shaped flower-tube enclosing the ovary and nectary.

(2) The elongation of stamen-*filaments*; a growth-phenomenon which is equal in both whorls, and has the effect of carrying the anthers beyond the corolla-tube so that they dehisce outside the bell.

(3) The slight growth-*curvature* of the filaments, by means of which they press against the slightly-constricted mouth of the corolla-tube, and so maintain a fairly steady position, at any rate in the early stages of the flowering period; also a more exaggerated curvature in the opposite direction just below the anthers.

(4) A well-marked *stylar*-zone in the gynoecium, which removes the minute receptive surface beyond the anther cone.

(5) An almost negligible *gamosepalous* zone of growth in the calyx, not sufficient to be of any definite use, but suggestive as showing that the sepal-cycles although of slightly unequal value may be elevated together.

(6) A growth-*curvature* in the new flower-stalk zone, which renders the flower more or less pendulous, but does not greatly affect the previous modifications of the pollination-mechanism owing to the minuteness of the stigmatic-surface.

(7) The concentration and localization of a crimson pigment (anthocyan), and correlated loss of chlorophyll.

This red pigment is present in the epidermis of the vegetative shoot, and slightly masked by chlorophyll in the red stalks of the flowers.

In the sepals and corolla chlorophyll is eliminated as the flower-buds enlarge, and a slight coloration is left in the sepals, which increases in intensity as the tissues grow old and the flowers fade. The corolla, practically colourless at first, also turns crimson as the flowers grow old. The pigment is concentrated in the anthers, so that these appear dark purple, turning brown-black as the pigment-cells die: most noticeable also is the pure bright colour of the otherwise white filaments just below the attachment of the anthers. This last coloration appears to be utilized as a 'honey guide'.

The pollination mechanism is sufficiently clear from the standpoint of construction. The flower is essentially a simple tubular form produced by gamopetaly; the honey-supply is relatively abundant, and is secreted at the base of a tube 5 mm. long, the entrance to which is blocked by a palisade of 8 stout filaments crowned by a conical mass of closely-packed anthers, the circular orifice at the end of these being again blocked by the growing style.

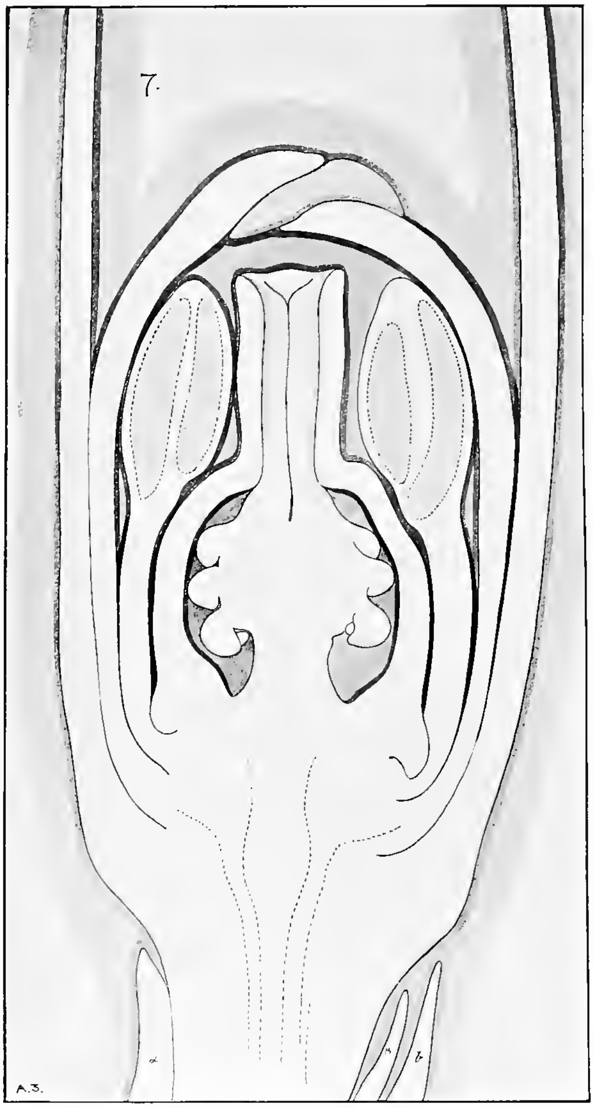

Fig. 5. *Erica carnea*, August bud. Developing flower.

Access to the honey is only possible through the chinks left between the ends of the filaments as they project beyond the petal-lobes, i.e. as 8 narrow slits, not more than 1 mm. long, suitable for the insertion of a delicate proboscis at least 5–6 mm. long; and it may at once be concluded that such a delicate mechanism is suitable for and probably correlated with the visits of Lepidoptera, although again the palisade of filaments is not strong enough to resist the violent attack of bees.

The flower might thus be expected to be visited by butterflies and moths which, in probing the slits between the bright-coloured filaments, receive pollen from the anthers on their heads, and so transfer it in turn to the slightly projecting stigmatic-surface of other blossoms.

*Note* that the special conical aggregation of the anthers, in which normal slit-dehiscence is becoming reduced to terminal pores, recalls a similar sprinkling apparatus in a pendulous flower in the case of *Galanthus*; and here also it is associated with a minute stigmatic surface at the end of a projecting slender style-shaft. *Erica* presents a further complication in the arrangement of the interstaminal slits at a point much farther from the actual secreting nectary; but the Snowdrop and *Erica*, although types from widely distant alliances, present many points of similarity in their secondary mechanisms; and the fact that this may be possible is of interest, in that it shows how little phylogenetic importance can be attributed to mere resemblances in the secondary adaptations of the pollinating machinery (cf. also *Viola altaica*).

## Pollination.

The half-pendulous flowers are bent forward by a growth-curvature of the inflorescence axis, and are rendered conspicuous by the white or pink coloration of the corolla-bell, the pink sepals, and contrasting dark-purple group of anthers at the entrance to the floral cavity. Conspicuousness is considerably increased by the contemporaneous flowering of the clustered inflorescences which, as the flower-stalks bend over to the most strongly illuminated side, present the appearance of a unilateral panicle in which the leaves are too small to diminish the general effect, and thus the whole shrub at the optimum flowering period is a mass of pink colour.

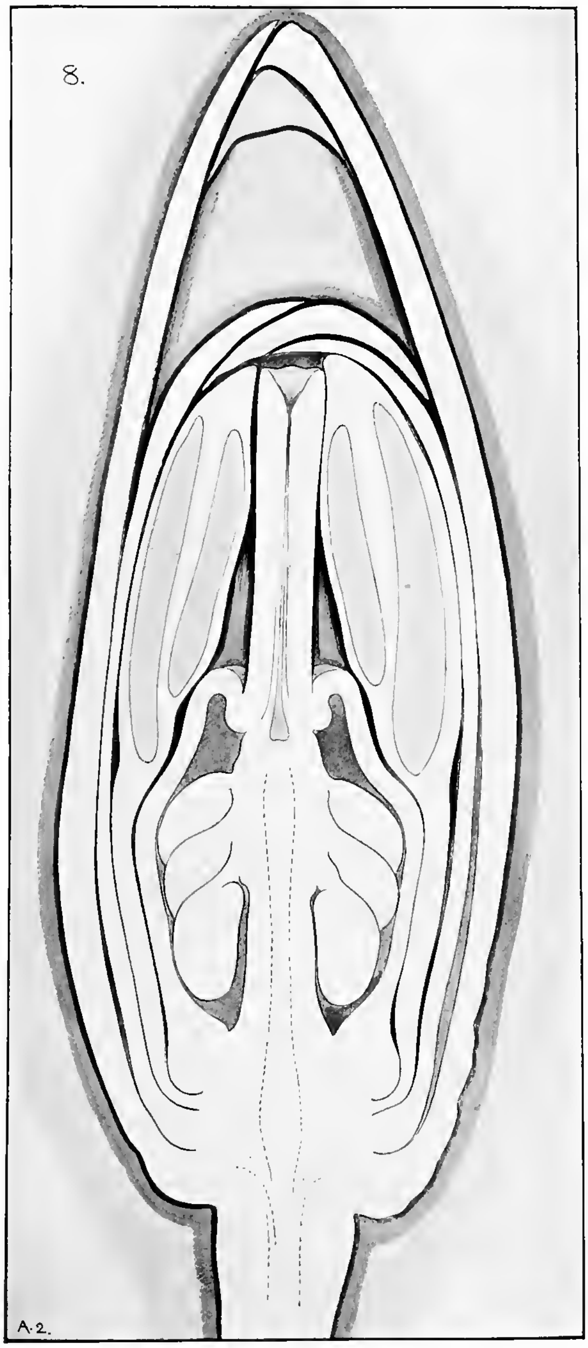

Fig. 6. *Erica carnea,* Autumn bud. Development of flower. Stage 8, perennating condition.

The flowers possess no scent; the pollen-supply is small, and the dusty pollen is not readily collected. On the other hand, the honey-supply is considerable, and the secretion rises in the corolla-tube to the height of the upper shoulder of the ovary.

The flowers are evidently adapted for high-grade honey-seeking insects, and the working-distance of the flower, as indicated by the length of the narrow corolla-tube (5 mm.), suggests that bees with rather short proboscides and Lepidoptera might be welcome visitors. As already indicated, the narrow entrance-slits postulate a fine proboscis, and that Lepidoptera should be the characteristic pollinating-agents, although bees with stouter mouth-parts are not wholly excluded.

Observation of plants in their native habitat (Müller) confirms this view; the flower being essentially a butterfly-visited type, and the most frequent visitors the Painted Lady (*Vanessa cardui,* 13–15 mm.), and an occasional Humble-bee.

Individual blossoms persist for a considerable period, according to external conditions: in cold months as long as 3–4 weeks, in March and April 20–10 days. In the early months of the year the shoots may be covered with snow, and the plants remain apparently at a standstill for 1–2 weeks at any time during a cold spell. The elongation of the style-shaft, which is probably the growth-zone which finally changes the whole mechanism from a self-pollinating one (bud-stage) to a cross-pollinating structure, appears to be most readily affected by these conditions of weather. Thus pink flowers with protruding anthers (January 1, 1900), gave no sign of a projecting stigma until February 6, the pollen having been shed just previously as the stigmatic surface was passing up through the cluster of anthers. A single flowering-shoot may exhibit flower for 4–8 weeks (February 26 to April 24), the first few blossoms even expanding in January (January 1), while the optimum period comes later (March); and as in the general case of Alpine flowers it is correlated with the period of the melting of the snow.

As the corolla expands, the anthers emerge in a compact cone, the stigma-tip pushing its way through them slightly later, but usually before the anthers dehisce. The stigma is receptive from the first, and the flowers are thus practically homogamous, with a tendency to protogyny which may be rendered effective by the action of cold dry winds (cf. *Cydonia*, *Helleborus*). The whole flowering-shoot displays its flowers irregularly in descending series, that is to say, all the inflorescence-shoots have been so long preparing that they are of practically equal age, and the upper buds being the first to feel the sunshine open first. The pollen-tetrads are light and dusty, and any insect seeking honey must place its head in contact with the anthers, and pollen will be thus shaken on to it. On visiting another flower pollen will be rubbed off on the projecting stigma, and cross-pollination will be effected, but it is obvious that a possible majority of flowers will receive pollen from the flowers of the same shoot, and of the same plant. Strict autogamy of the same floral mechanism is only very accidentally effected, since the minute stigmatic-surface is usually clear of the anthers. The flowers are, however, quite fertile to their own pollen.

Owing to the close proximity of the blossoms and their obliquely-pendulous habit, pollen will be readily shaken from the anthers of higher flowers on to the stigmas of lower ones on the same or adjacent branches. Self-pollination of the flowers of the same plant is thus readily effected by the action of the wind, and the plants will set fruit in complete absence of insect visits: on shaking the branches in dry weather the dusty pollen rises in small clouds, just as in the case of a strictly wind-pollinated type.

It is also clear that if the growth of the style-shaft be feeble, as may occur when the flowers grow under unfavourable conditions, the mechanism may remain a self-pollinating one, as in the bud structure.

The slight development of the stigma-lobes, which are well marked in the later stages of the proterandrous allied forms (cf. *Calluna*), may possibly be correlated with the apparent secondary assumption of protogyny in the early-flowering type.

As the flowers grow old the anthers diverge slightly, showing that they were previously held in position by growth-pressures in the filaments, and the corolla assumes a more marked crimson tint; this change of colour (cf. *Weigelia*, *Ribes*) may be taken as evidence that the functional condition of the flower is over, and as a sign of death in the tissues: there is no evidence that it affords any increased conspicuousness to the plant, or any additional attraction to the insect world. On the other hand, since bulk for bulk a white flower is far more conspicuous than a pink one, and gives an impression of a larger size, it might be argued that here as in other cases (cf. *Ribes*) the attempt on the part of the plant is rather to eliminate the pigment from the attractive members (corolla) while retaining it as a protective screen in the outer investment of the flower (calyx) in the bud condition.

In gardens the flowers are visited almost exclusively by Hive-bees, and by these in great numbers. The bees do not take pollen, of which only a small quantity of dusty material is available; but the characteristic tetrads of the plant are thoroughly dusted over their heads. The delicate slit-mechanism is ignored, and since their thick 5–6 mm. proboscides only just suffice to probe the nectary, their method of working is very clumsy from the standpoint of the flower. Hanging on to adjacent blossoms, they push the group of stamens bodily on one side, and force their proboscides into the corolla-tube. Thus, although the flower is now constituted as a 'butterfly-type,' it was evidently originally a 'bee-flower', and the Hive-bee can still manage to work it; although it is more adapted for the visits of long-tongued Humble-bees and Lepidoptera (cf. *Viola odorata*). Plants visited in gardens by Hive-bees set abundant fruits, while those restricted to occasional pollen-showers only produce a few. The earlier flowers (January, February) do not yield fruit; the reproductive organs being injured by frosts.

## Fruit and Seed.

The complete withering of the flower is only indicated by the change of the colour of the corolla to brown, although the mechanism may really have ceased to be functional for some time. The nectary continues its secretion, and none of the floral-members are shed; the withered corolla-bell and calyx-members constituting a protective investment to the developing green fruit. All the members in fact persist until the fruit is ripe and the seeds are shed. The protection thus afforded against desiccation, &c., to fruits developing in situations exposed to strong light and violent winds, is here economically effected by simply omitting what was undoubtedly the more primitive arrangement for such a gamopetalous form.

The *fruit* rapidly enlarges after fertilization, reaching full size in 4–5 weeks (mid April): when ripe, 8–10 weeks after the flowering period (early in June), it presents the form of a small ovoid capsule (3 mm. by 2) dehiscing by 4 valves which open out in the form of a cross, superposed to the sepals, rupturing the corolla-tube as they diverge.

Dehiscence takes place along lines corresponding to the carpel mid-ribs; the septa between the loculi are broken, and the axile placenta remains as a central column to which the seeds are attached. The mechanism is hygroscopic: the inner half of the ovary wall is differentiated into a layer of transverse and oblique fibres; along the septa these become more abundant and pass down longitudinally; the developing seeds being thus further protected by a lignified zone of tissue in the ovary-wall; and on desiccation, the shrinkage of the outer cellulose layers gives the pull which opens back the 4 valves when dry; while they close up again when wetted. The small seeds may be carried for considerable distances by the agency of the wind.

The *seeds* are very small, ovoid, 1 mm. long, brown and finely netted externally; the micropyle is at the pointed end, and the raphe is not marked. As the seeds are slightly compressed in a plane tangential to the ovary, and the raphe is external, a section along the narrow diameter will fall in the plane of the raphe. The testa is thin; an outer layer of thick-walled cells is protective; the endosperm is considerable, and consists of thin-walled cells full of fat. The embryo is cylindrical with 2 small cotyledons, the orientation of which is not constant.

*Note* that the small embryo is *protected* by the testa; provided with *food* as fat and proteid stored in the endosperm; and is *dispersed* by the agency of the wind; to which end the minute size of the seed, possibly a result of the general impoverishment of the plant-form, undoubtedly serves as an aid, though very doubtfully to be regarded as a 'special adaptation'.

## Comparison with allied Types.

### I. Erica cinerea, L. *Common Fine-Leaved Heath.*

A closely similar 'Ericoid' plant-form, indigenous to Great Britain, usually very common on dry heaths, and extending over the Atlantic shores of Europe, Spain, the Rhine Valley to South Norway, being possibly at its best in Great Britain.

The bushes grow 1–2 ft. high; the flowers are bright rose-purple, and are produced in July and August.

The vegetative shoots resemble those of *E. carnea*, both in symmetrical construction and habit; the phyllotaxis-system being characteristically (3 + 3), but strong shoots vary to (4 + 4).

The inflorescence-scheme is somewhat different in details, but with the same general tendency to an appearance of a unilateral panicle. Towards the apex of the flowering shoot (1) flowers are borne singly in the axils of subtending bracts which are again 'carried up' on the flower stalks. (2) Lower down, dwarf shoots are produced, which bear prophylls subtending single flowers, and these also are elevated on the flower-stalks. (3) Still lower the dwarf shoots bear prophylls and 1–2 whorls of foliage leaves, some of the lower members of which (1–3) may be fertile: while (4) the lowermost leaves on the main shoot subtend dwarf vegetative shoots of limited growth bearing 3–4 whorls of foliage leaves in the systems (3 + 3) or (2 + 2). The general arrangements are thus comparable to those of *E. carnea*, whose inflorescence is in the phase of (3). *E. cinerea* presents additional reduction-stages of what must once have been a still more elaborate lateral panicle; while it is interesting

to note that the vegetative leaves on the inflorescence dwarf-shoots remain assimilative members, while in *E. carnea* they were reduced to minute scale-leaves (Fig. 7).

*Orientation* of the diagram of the tetramerous flowers is identical, as also are the general features of the construction and special mechanism, including bract and prophylls, calyx, corolla, androecium and gynoecium, nectary and stigma-lobes.

The corolla, bright rose-magenta in colour at first, with a tendency to go purple when older, is bell-shaped, 6 mm. long by 4 in diameter, and constricted at the entrance to $1\frac{1}{2}$ mm.; the petal-lobes being small (1 mm.) and slightly divergent. As compared with the mechanism of *E. carnea*:—*Note*, (1) the filaments do not elongate sufficiently to carry the anthers out of the corolla-bell; they are wholly enclosed and protected in the interior of the cavity of the flower; the pollen-supply is thus sheltered, and cannot be collected by pollen-seeking insects.

(2) Free access to the interior of the flower is restricted by the narrow orifice, the anthers and style projecting into the aperture.

(3) The anthers possess the slit-pore type of dehiscence, and being aggregated in a group around the style present as effective a sprinkling-apparatus as in *E. carnea* (cf. *Galanthus*, *Viola*), but they are in addition provided with tailed appendages which grow to touch the corolla and thus constitute a delicate trigger-mechanism, since access to the honey is most readily obtained by passing through the slits left between these appendages and the wall of the corolla-tube, and thence between the filament-bases to the descending nectary-lobes: and here as in the general case the proboscis of the insect feels its way along the corolla-wall.

(4) Free access is thus left for a delicate proboscis 6–7 mm. long; while the entrance to the flower-tube is rather narrow for an insect with broad base to its proboscis. The Hive-bee is thus practically excluded from the flower, and the mechanism is again more suited for Humble-bees and Lepidoptera. The pollen is dusty, and the arrangements for cross-pollination agree with those of *E. carnea.* The flowers are bored to an enormous extent by the Hive-bee; often every flower over wide tracts may be found bitten through. By making an aperture about half-way up the corolla, the bee avoids the anthers and their appendages.

*Erica Tetralix*, L. The 'Cross-leaved Heath', with pale rose-pink or white bells, agrees in all essentials with the preceding; the flower is somewhat larger and more hairy, 7 mm. by 4, the entrance to the bell 2 mm. in diameter. The mechanism is that of *E. cinerea*; it is visited by the same bees, and is also frequently bored by the Hive-bee.

The inflorescence is of a reduced type which presents further specialization as an aggregated unilateral system of 10–20 flowers. The phyllotaxis system is (4 + 4), and a few whorls of leaves in the inflorescence region subtend single flowers. These possess bract and prophylls, the former being again found on the flower-stalk (Fig. 7).

In both *E. Tetralix* and *E. cinerea*, no floral members are shed when the flower withers; the young fruits being protected by the withered corolla-bell, which is again much more efficient in the common species.

The ripe fruits and seeds closely resemble those of *E. carnea.* All the floral members persist; the corolla withering to half its size, and fading out to a brown colour. The ovary, which is thus enclosed in a sheltered chamber, enlarges to an ovoid capsule 2 mm. in length, which ripens its seeds early in October. In dry situations the capsules dehisce by 4 valves, which break away from the axial portion which retains the style, and these lie back over the sepals, the broken septa making a distinct antisepalous cross on the basket-like structure. The small purple-black seeds, 1 mm. in length, are scattered out through the orifice of the corolla-tube. In damp situations the fruits may remain closed until the ensuing spring (cf. *Calluna*). The seeds are dark and possess a 'netted-surface' owing to the relatively large size of the superficial cells, but these are not so markedly developed as in the case of *Calluna.* Owing to their minute size the seeds will obviously be carried some distance from the parent plants by the agency of the wind, which, as the character of heath-vegetation indicates, is an important factor in the biology of the plant.

### II. **Calluna vulgaris**[1] (Salisb.) *Ling*[2], *Heather.*

A low woody shrub of Ericoid habit, growing 2–3 ft. high, with numerous minute green evergreen leaves borne in decussate (2 + 2) series. Short foliage shoots and flowering shoots are borne in the axils of leaves of the current year's growth and the pale lilac, rose or white flowers are produced in the summer months (June to September), the optimum period being mid-August. The seeds ripen in late autumn, and are shed under the action of strong drying winds in the succeeding spring.

The plant is the most widely distributed of Ericoid types, extending over the whole of Northern Europe, to Iceland, Greenland, and Nova Scotia on the other side of the North Atlantic Ocean.

The shrubby plant-form is of interest as an extremely reduced biological form adapted to withstand cold winds as the characteristic vegetation of 'Heaths'.

Both foliage leaves and flowers are extremely reduced in size, and the inflorescences are very variable, presenting a wide range of reduction-phases from a well-developed panicled condition. The terminal portion of the annual shoot remains wholly vegetative, and short lateral shoots borne in the axils of the uppermost leaves will continue the ramification in the succeeding season, thus providing a tufted growth-form. In the axils of the leaves of a lower region solitary flowers are borne, and still lower down many-flowered lateral branches are produced. The apex of these may remain vegetative (at base of panicle), but more usually ends in a terminal flower. The lateral flowers may be 10–14 in number, and are borne in the axils of leaves beyond the prophylls, which are usually sterile. In the upper region of the panicle, however, reduced systems of 3 flowers are common, consisting of a terminal and 2 lateral flowers, the prophylls being now alone developed and fertile. A well-developed panicle may possess a flowering region over 6 inches in length; on the other hand, reduced types of inflorescence are more general, and in the weakest shoots a simple raceme of a few flowers, less than half an inch

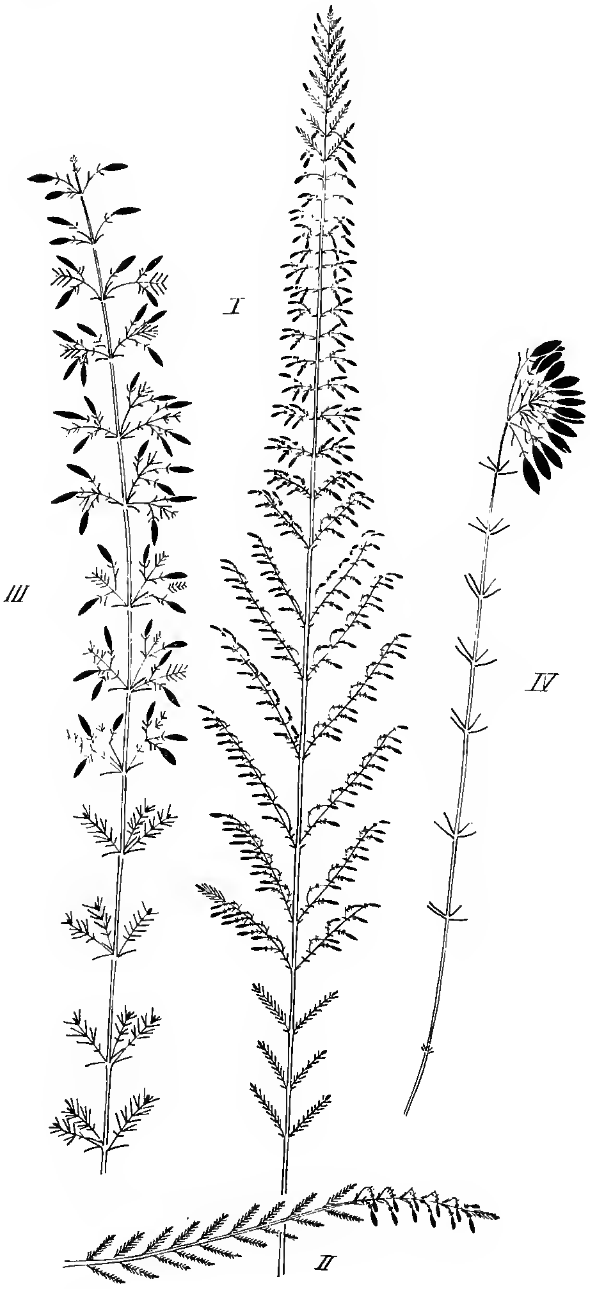

Fig. 7. Inflorescence schemes. I, *Calluna vulgaris*; II, prostrate form of *Calluna*; III, *Erica cinerea*; IV, *E. Tetralix*.

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[1] *Calluna* a genus founded by Salisbury (1801), and separated from *Erica*, L. on account of a different method of fruit dehiscence, = *Erica vulgaris*, Linnaeus. Calluna (καλλύνω) since the plant is used for brooms (Scotland, Sweden). The name *Erica vulgaris* was first applied by Bock (Tragus, 1552).

[2] *Danish* Lyng, *Swedish* Luing, *French* Bruyère.

in length, is reached, the limit being in fact a single lateral flower. When growing in the open, only the strongest inflorescences present radial symmetry, though even here the flowers of the side branches turn towards the illuminated sides, and the branches become unilateral: this condition being characteristic of the majority of the flowering shoots. It is interesting to note, however, that in the case of plants growing under conditions of extreme exposure, when the whole plant is reduced to short prostrate shoots rising as little as one inch above the surface of the ground or rocks, these reduced unilateral flower spikes become prostrate with the flowers directed away from the light towards the soil-surface, so that visiting insects have to crawl beneath them between the flowers and the ground. The relation between such inflorescence-systems is readily shown in schematic form (Fig. 7).

Individual flowers possess a subtending bract and lateral prophylls, the orientation of the flower, and the floral diagram, is that of *Erica*; but two points of special interest are found different from the *Erica*-type. Firstly, the subtending bracts are not 'carried up' on the axillary shoots, and bracts as well as prophylls possess tailed appendages similar to those of the foliage leaves. Secondly, 4 bracteoles constitute a pseudo-calyx to every flower, and are constantly present, however much reduction may take place in leaf-production in the inflorescence-region. Thus the limit of a lateral flower possesses 2 prophylls and 4 bracteoles outside the calyx. Further, the members of this pseudo-calyx differ from other bracteoles in being destitute of tailed appendages, while the true sepals have become petaloid. The fact that 4 such bracteoles may be isolated, and set apart for a special 'calyx' function as the true sepals assume that of a corolla, is of special interest, not only biologically, as the expression of a new adaptation, but morphologically, since they are in development identically the same members which become the sepals of the *Erica* type. Evidence is thus afforded of a remarkable elasticity in the floral construction-formula of even such a reduced type as this, since *Calluna* clearly utilizes more members of the lateral axis in its floral mechanism, the occurrence of a cycle of bracteoles between the prophylls and the calyx being comparatively rare.

The *Floral Diagram* is identical with that of preceding types and so also the arrangement of the members seen in the sectional elevation.

The calyx is relatively large and conspicuous, the free sepals being 6 mm. long and enclosing the other members: the corolla more insignificant, with a short gamopetalous zone $1\frac{1}{2}$ mm. long, and free petal lobes 2 mm., forming altogether an open bell which may be more or less pendulous owing to curvature in the flower-stalk between the bract and the prophylls.

The stamens combine the tailed 2-horned anthers of *E. cinerea* with the kneed filaments and compact anther-cluster of *E. carnea.* The anther-tails just touch the corolla-tube, and on looking into an opening flower, in which the growing mechanisms are still turgid, these tails present the appearance of a 16-pointed star which shows up white against the dark background of the ovary and base of the corolla-bell: access to the honey is thus guarded by this fringe of appendages, and limited to paths between them and the broad filament-bases. The nectary-lobes are well marked, and form descending growths between the filament-bases. The ovary presents a greater placental development than in *Erica*, and the style, with late developing commissural stigmatic-lobes, is identical with that of *E. cinerea*, and again shows a tendency to bend upwards in the drooping flower. The grouping of the anthers, their dehiscence by long slit-pores, and the appendages which act as triggers, constitute an efficient sprinkling-apparatus, and cross-pollination will be readily effected by insect agency. As in *E. carnea* the pollen is dusty, and pollination may also be effected by the operation of the wind.

Owing to the short working distance, from the slits between the anther appendages to the secreting surface (only $1\frac{1}{2}$ mm.), the honey is freely accessible to an enormous range of insects. They are visited by great numbers of flies, bees, humble-bees, butterflies and moths; it is obvious that they can be readily worked by the Hive-bee, and these insects visit the flowers in such profusion that 'Heather-honey' acquires a commercial value, and hives are carried to the vicinity of Heather-moors in August. As in the other *Erica*-forms it is clear that self-pollination between flowers of the same shoot and same plant will be of very general occurrence; true self-pollination of the individual mechanism is quite eliminated by the growth and curvature of the style, and this is further limited by the slight proterandry of the flower; the stigmatic lobes being only fully developed after the pollen has been shed. *Note* that the paired appendages of the anthers (sporophylls) appear comparable with similar outgrowths on the vegetative leaf-members.

As in allied forms, no floral members are shed, but the corolla is inconspicuous and the protective function is afforded by the withered sepals, which bend over the ovary and enclose it in a membranous investment.

The *fruits* ripen in late autumn (November), and the seeds are shed in the succeeding spring when the capsule opens under desiccation; the dead sepals remain on well into the second summer, and the seeds are gradually drifted out by the agency of the wind; some may remain enclosed for 12 months.

The *capsule* opens by 4 valves which are however *antipetalous*, and thus represent the outer portions of the ovary wall which separate at the commissural lines.

The *seeds* are extremely minute, about $\frac{1}{10}$ mm. in length, ovoid and pale brown. Section shows a structure essentially similar to that of *Erica*; a minute straight embryo, including abundant fatty reserves, being imbedded in a mass of thin-walled endosperm, the cells of which also contain fat and proteid, but are only 4-5 deep. The testa is only represented by a few dead cuticularized walls and one peripheral layer of large empty cells, 6-7 of these reaching the whole length of the seed. These are therefore to be regarded as evidence of a definite adaptation for wind dispersal, and the light dust-like seeds are drifted out of the investing perianth-leaves throughout the second summer.

Finally, taking xerophytic reduction as the key to the evolution of Ericoid forms, it is evident that *Calluna* presents the extreme case of reduction-specialization, as it also possesses the widest distribution.

The vegetative reduction is expressed as a (2 + 2) shoot-construction, in the feeble growth of the annual shoot, the small size of the leaves and their special form, as also in the small size of the flowers in which the corolla is distinctly retrograde; while in correlation with this degeneracy of the gamopetalous condition, the calyx-members assume an increasing importance, not only as an attractive series, but as the protective investment of the developing fruits as well as of the flower-buds.

### Theoretical Considerations.

In considering the special characters of such Ericoid forms, it is important to distinguish between primary features, and secondary modifications which may be the result of extreme specialization in connexion with the reduced vegetative habit of the vegetation of Steppes and 'Heaths'. Thus all these types have agreed in presenting types of phyllotaxis-construction of the form (2 + 2), (3 + 3), (4 + 4); the simpler cases of symmetrical shoot-mechanism:—are these constructions to be regarded as primitive features, or are they secondary to a more generalized asymmetrical growth-plan? Similarly the flowers are wholly tetramerous. There is no apparent law regulating the assumption of such constructions, but it may be noted that there are one or two points which may be regarded as suggesting that such special cases of symmetry have been acquired, though the reason for such a change may still be far to seek: e.g. the introduction of the (3 + 3) and (4 + 4) constructions always presents a preliminary production of 2 lateral prophylls, so that the new arrangement is not initiated at the first production of the shoot, but there is a break at the commencement, and the original formation is (2 + 2); secondly, a similar break occurs in the ontogeny of the floral-construction, in which tetramery, commencing in the diagonal whorl of petals, only succeeds a decussate system of 6 members (prophylls and sepals). Further, such a peculiar orientation of a tetramerous flower, giving 4 diagonal petals, is characteristic of the general case of tetramery in flowers phylogenetically derived from pentamerous types; this being constant for such different phyla as the *Cruciferae*, *Onagraceae*, *Rubiaceae*, &c., so that the presence of a diagonal corolla may be taken as a very fair sign of a previous fuller condition of pentamery in the floral formula. Such a construction in the floral shoot is alone sufficient to imply that the vegetative shoot must also at some time have been constructed in a system involving the number 5, that is to say, it must have involved a construction in terms of a Fibonacci ratio (2 : 3 : 5, &c.) (cf. Kepler, 1611). Thus the diagonal corolla affords indirect evidence of an ancestral normal asymmetrical Fibonacci phyllotaxis-construction in the *Erica*-phylum, quite apart from the fact that confirmation of such a deduction is found in the presence of pentamerous flowers and spiral phyllotaxis in many existing genera of the family. Nor is there any evidence to show how it might be possible on the other hand for a pentamerous construction to arise from a tetramerous one. Even in strictly Ericoid types the full ancestral condition may be seen to be retained as a tree-growth, with lateral panicles of flowers of the same general and even special character, and more normal broad petiolate foliage-leaves produced in Fibonacci construction-system (cf. *Arbutus*, *Vaccinum*). The systems (3 + 3), (4 + 4) may also be regarded as enlargements of a decussate (2 + 2) vegetative construction (cf. *Fuchsia*, *Fraxinus*); and it is possible to correlate the assumption of this special case of symmetry with xerophytic habit. Further, there is no reason to regard the converse evolution of tree-like forms from Heath-forms as at all likely; or that such a type as *Arbutus* is to be regarded as an amplified Heath; vegetative reduction is a known characteristic of Heath and Steppe flora, and that Ericoid forms represent decadent lines of evolution exhibiting extreme xerophytic specialization may be taken as established; the morphological evidence only confirming what has been deduced from other standpoints.

Similarly the *inflorescence systems* are extremely reduced, *Calluna* presenting the most marked indications of a fuller condition: on the other hand, though the *flowers* share in the reduction-phenomena of the shoot-system by a restriction to tetramerous symmetry, they retain a fairly full type of *floral diagram* for a highly-specialized gamopetalous phylum. The *Fruits* again would appear to be essentially simple structures, protection being afforded the seeds by a lignified zone which subsequently leads to dehiscence by valves on desiccation. Of the two methods possible, *Calluna* presents one, *Erica* the other, neither being a separation into component carpels or rupture of theoretical sutures; so that dehiscence methods thus appear to be wholly secondary.

When expressed in terms of its fundamental pentamery, i.e. along the lines indicated by comparison of the 4- and 5-merous flowers of such a type as *Ruta*, the floral diagram would appear to be closely comparable with that of such polypetalous types as *Ruta* and *Sedum*—a quincuncial calyx being succeeded by symmetrical sporophylls, a pentamerous corolla-cycle being differentiated at the zone of transition, and 2 complete cycles of (5 + 5) stamens being retained together with 1 full cycle of 5 carpels.

As in *Sedum* and *Ruta*, again, signs are not wanting that this reduction has been accomplished at the expense of members between certain cycles, which constitutes in these types the general phenomenon expressed by the term 'obdiplostemony'. In *Erica*, again, the break is undoubtedly to be placed between the androecium and the gynoecium, and may possibly be associated with the production of a *disc*-nectary at this point; this being the distinctive character of the *Ruta* type, and not that of *Sedum*.

On such a fairly elementary construction *Erica* superimposes a special feature of true *gamopetaly*, which in these types is absolutely a *Zona Gamopetala*, without any trace of the *Zona Mediata* which is usually such a general feature of the evolution of the gamopetalous condition (cf. *Cotyledon*, *Trifolium*); and while a Zona Mediata is found in many branches of the same series, it is this purely gamopetalous condition which is so markedly characteristic of the strictly Ericoid types.

The subsequent elaboration of the special mechanism is concentrated on the evolution of a pollen-sprinkling apparatus in which the essential features are a conical cluster of anthers, dehiscing by apical pores or slits, trigger emergences and pointed stigma-surfaces. Self-pollination may be eliminated by the growth of the style-shaft, and the ovary presents a special feature in its abbreviated developmental phases and the rudimentary nature of the free tips of the gamophyllous carpels. The peculiar formation of the anther-lobes is again a feature common to the whole phylum (Bicornes).

Omitting these special details, the presence of a *disc*-gland at the base of the gynoecium, and the construction-data of the floral members suggest a close alliance, so far as primary construction is concerned, with such a form as *Ruta*; and while the evolution of a sprinkling mechanism is so secondary that it may occur in any phylum (cf. *Viola*, *Galanthus*), the only essentially new modification appears to be the special zone of growth which carries up the corolla-members. The use of such a gamopetalous zone, as a means of protection to the essential organs, nectary-secretion, and finally for the developing seeds, has been already indicated, the ultimate adaptations for visitation by special insects being probably secondary to the original function; and from such a standpoint the *Ericaceae* may be considered as a special branch of a Discifloral stock, in which the progressive reduction of the androecium is associated with the functional importance of a receptacular *disc*-gland; a somewhat parallel case of evolution being met with in the example of *Cotyledon* among the simpler types of *Sedum* and the *Crassulaceae*.

### *Note on Nomenclature.*

The plant *Erice* (= *Calluna vulgaris*, L.) of Fuchs, 1542, and the *Erica vulgaris* of Bock (Tragus, 1552), became a centre around which was gradually collected a group of Ericoid forms, 15 being given by Bauhin (*Pinax*, 1623), though not all of *Erica* genus as now defined. These were definitely cast as a genus *Erica*, increased to 29 species, by Tournefort (1700).

The genus was continued by Linnaeus (1737) who has the merit of first pointing out the great *Bicornes* alliance (1750). By A. L. de Jussieu (1789) the group was extended as an order (*Ericae*), of which *Erica* in the narrow sense remained one of 16 genera; while the Rhododendrons, included by Linnaeus as Bicornes, were placed in an order *Rhododendra* of 7 genera.

By De Candolle (1805, and Prodromus, 1838) the order *Ericaceae* (taken from Lindley, 1836) was enormously increased to 52 genera, and was now made to include the *Rhododendra* of Jussieu; while Bentham and Hooker (*Genera Plantarum*, 1876) advanced another step, and established the order *Ericaceae* as a centre around which to segregate a series of 5 other orders as the 'cohort *Ericales*', which appears to represent one of the most narrowly defined alliances among Gamopetalous Dicotyledons, and the arrangement is generally accepted; the original Linnaean term being, however, revived for the group *Bicornes* (cf. Eichler, 1875; Drude in Engler and Prantl, 1889).

The family *Ericaceae* now includes 67 genera and a total of about 1,350 species, the genus *Erica*, represented by 420, being by far the leading branch. The whole group *Bicornes* includes 6 orders, 108 genera, and a total of over 1,700 species; *Erica* in fact working out as 24°/o of the whole.

# X

## Ribes[1] sanguineum, Pursh.[2] *Crimson Ribes or Flowering Currant.*

A woody shrub with deciduous leaves, growing 2–12 feet high, indigenous to the NW. coast of North America between 38° and 52° N. lat., being common in California and Oregon in rocky situations by the sides of streams. Discovered by Menzies in 1787, it was introduced into this country by Douglas in 1826, and is now very generally cultivated in gardens for the sake of its abundant racemes of aromatic rose-crimson flowers produced in early spring (commencement of April to middle of May) before the foliage-leaves are fully developed. It is quite hardy, and ripens in autumn currant-like fruits with a pale-blue waxy bloom.

### Description.

Inflorescence : Simple pendulous racemes of 20–30 flowers borne terminally, and laterally in the axils of the foliage-leaves of the previous season. Subtending bracts large and coloured ; 2 lateral prophylls present and coloured, or minute and often absent, especially in the upper part of the raceme.

Flower : Hermaphrodite, actinomorphic, pentamerous in type.

Receptacle : markedly crateriform, constituting the outer wall of the ovary-cavity (2 mm.) and coloured green ; prolonged as a free tube, 3 mm. long and 2 mm. in diameter at the mouth, coloured crimson.

Perianth differentiated into :—

(1) Calyx of 5 free sepals, inserted on the rim of the receptacle-tube, 6 mm. by 3, narrowly obovate, coloured crimson (or white).

(2) Corolla of 5 free petals, alternating with the sepals, narrowly obovate, 3 mm. by 2, white at first, becoming crimson in older flowers.

Androecium of 5 free stamens, in normal alternating series, inserted on the rim of the receptacle-tube ; *filaments* 2 mm. ; *anthers* introrse, white ; *pollen* white.

Gynoecium of 2 carpels : *ovary* syncarpous, filling the lower portion of the receptacle-tube, unilocular, with parietal placentation, two well-developed placentas bearing several rows of anatropous ovules (average total 150–200) : *style* simple, forming a stout column 8 mm. long, with short diverging branches terminated by viscid stigmatic surfaces.

Nectary : honey is secreted by the tissue at the base of the free portion of the receptacle-tube, and accumulates around the base of the style.

[1] *Ribes* from a name given to a plant with acid berries by Arabian physicians, which was probably a species of *Rheum* growing in Syria and Persia (*Rheum Ribes* *). The word was applied by the older herbalists to *Ribes rubrum*, the Red-currant of the garden, and an excellent drawing of this plant is given under this name by Fuchs (1542).

The generic name was established by Linnaeus (1737).

[2] The specific name dates from Pursh, Flora of North America (1814).

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* Cf. Bauhin (1623), all species of *Ribes* (L.) are given as *Grossularia*, and the name *Ribes* retained in the same section for *Ribes arabum foliis petasitidis*, = *Ribes legitima arabum* of Clusius.

The forms were also included in the genus *Grossularia* by Tournefort (1700).

## Variations.

Modifications under cultivation are restricted to colour-variations, from a white-flowered form to a dark crimson one (*atro rubens*); (double forms are included as monstrosities).

## Floral Diagram.

The leaves of the foliage-shoots are constructed in a normal spiral phyllotaxis-system of the Fibonacci type: section of the bud-apex shows the young leaf-members making contact in the relations of a (2 + 3) system (Fig. 1).

A similar asymmetrical construction is continued into the flowering-shoots. These are developed in autumn, in the axils of the foliage-leaves of the current year, and perennate over the winter months inside closed buds which expand in March.

At the base of these shoots are 2 small brown prophylls which fall off when the bud first expands; these are succeeded by a varying number (4–7) of bud-scales, the lowest ones being brown, the inner ones more membranous, and more or less tinged with crimson.

An anterior brown scale and a series of 5 coloured membranous scales which constitute a protective investment is most typical.

Beyond these rudimentary appendages 2–3 foliage-leaves are produced in the same spiral series, and succeeding these the coloured bracts which subtend the individual flowers, 20–33 in number. There is no terminal flower, and the contact-parastichies of the flower-buds, clearly observed when the inflorescence emerges from the bud, are (3 + 5), thus giving 8 slightly spiral longitudinal rows of flowers.

The whole series of leaf-members presents an instructive example of leaf-modification and specialization for different functions along a short asymmetrical construction, and good transitional stages in lamina-development are commonly observed.

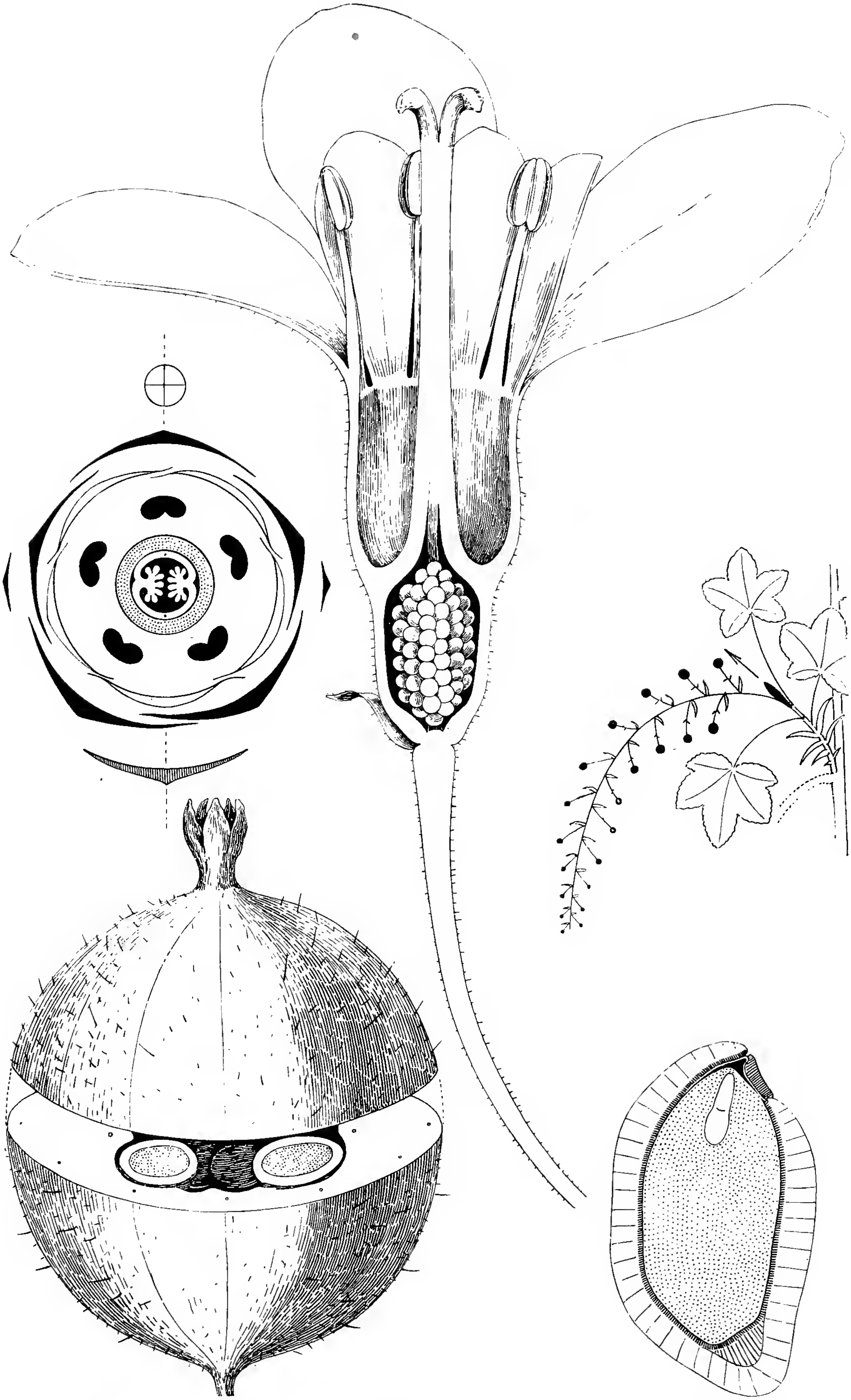
In the axils of the uppermost foliage-leaf a vegetative bud continues the growth of the shoot after flowering; in the case of lateral shoots, short spur-branches are formed which may bear flowers in the succeeding season.

Fig. 1. *Ribes sanguineum.* Apex of perennating vegetative shoot, phyllotaxis system (2 + 3).

The *orientation* of the flower is normal for the pentamerous type; the prophylls are minute, crimson, and often wholly wanting throughout all the flower-shoots of a plant, in other cases they may be constantly present, or may occur on the first flowers only of the inflorescence, or again only one may be developed. Individual plants appear to remain constant to such minor variations in succeeding seasons.

When the prophylls are present they are found immediately below the base of the ovary: the flower-stalk is thus seen to be a development of the single internode below the first one (α).

The *calyx* is of the normal quincuncial type in development, and often in prefloration, though the latter is frequently irregular, showing that overlapping of the segments may be secondary. Sepal 2, is approximately median posterior, though its exact position cannot be given in such a wholly spiral construction-system (Fig. 2).



**Ribes sanguineum:** Floral Diagram and Sectional Elevation of Flower in the median plane; Scheme of Inflorescence, ripe Fruit, and section of Seed in the plane of the raphe.

The *corolla* arises as a simultaneous whorl, indicating a change to a symmetrical (5 + 5) construction; prefloration is wholly secondary and varies, the petals scarcely overlap in the flower, a 'quincuncial' arrangement may be often traced.[1]

The 5 stamens follow the (5 + 5) symmetrical construction initiated in the corolla, and there is no trace of the existence of any other series of these members.

The 2 carpels are typically median in position; the stigmas corresponding to the carpel-tips have the same position, and thus serve as a guide to their orientation; these again by reference to sepal 2, and the prophylls when these are present, will be often found to be oblique, and the plane of their orientation may vary from that of sepal 1 to sepal 3; since section of the ovary shows that the placentas also agree with this arrangement, it would appear that the flower has not yet attained accurate median symmetry (Fig. 2).

A transverse section of the ovary shows the unilocular cavity, and 2 large T-headed placentas, each bearing 5–7 rows of anatropous ovules extended fairly horizontally.

The secreting surface, being of great importance in the development of the flower as an insect-visited mechanism, is indicated in the diagram as a zone surrounding the gynoecium.

## Sectional Elevation.

As in the general case this may be taken in the plane of sepal 2, which is for practical purposes the median plane of the floral diagram. While the floral diagram itself is normal for a pentamerous type which has become reduced to a 'mean type' of structure, differing only from the theoretical ideal in the obliquity of the carpel-orientation, the elevation shows very striking modifications. The receptacle-tube is the most conspicuous feature, and its special development gives the floral axis its peculiar character. With this exception the elevation indicates the normal arrangement, sepal 2 being cut on the left, the odd petal cut on the right, and a full view is given of one of the placentas in the ovary-cavity. The significance of the receptacular modification is best followed in sections of earlier stages of the floral development.

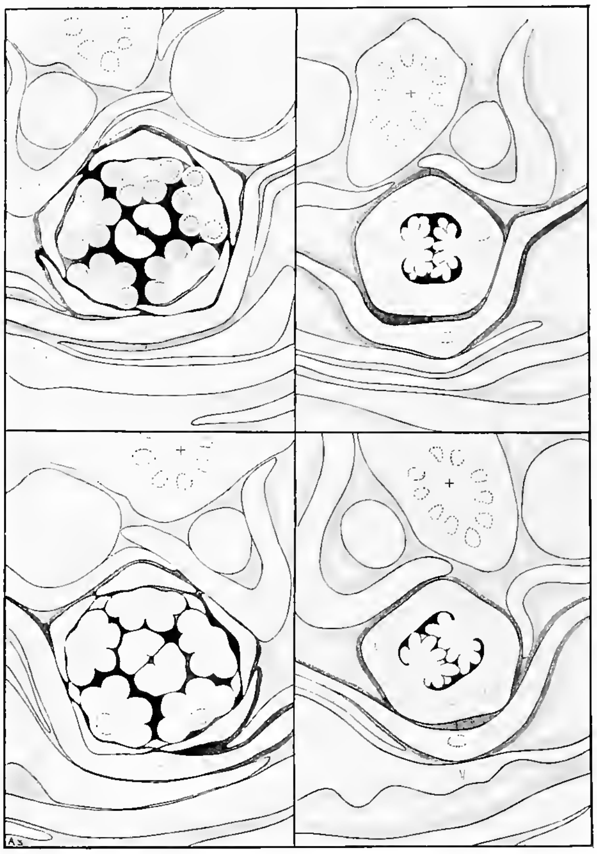


FIG. 2. *Ribes sanguineum.* Development of flower, perennating buds (December); variations in orientation of flower and gynoecium.

The flower-bud develops normally, and the receptacle becomes crateriform at an early date, the 2 carpels subsequently arising at the base of the concavity (Fig. 4).

As the crater enlarges the 2 carpel-primordia fuse laterally in the median line, and an increased growth in this region produces the elongated ovary-cavity as an *Epigynous Zone* of growth, giving rise to what has been conventionally termed an 'inferior ovary'; the sepals, petals, and anthers remaining in their original close contact relations above (Fig. 6).

A bud cut in November (to January) shows this condition, the fully-developed stamens and minute petals being now apparently attached to the rim of the crater, and the ovules arising in rows on the intercalated zone (Fig. 3). As the inflorescence-buds begin to swell

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[1] Cf. Note on Prefloration. *Cydonia japonica.*

(about March 1), and the flower-spikes emerge from the buds and assume a pendulous condition, another intercalary zone, the *Zona Perigyna*, is initiated in the receptacle cup at the level of the internode between the androecium and the gynoecium, with the result that a cylindrical tube is produced which carries up the sepals, petals, and androecium; so that it is only at a comparatively late date that the flower assumes the structure seen in the elevation.

The secondary formation of this tube as a *Zona Perigyna* gives the special character to the flower, which may now be classed as *Perigynous*, and since the honey is secreted by the tissue at the base of the new growth, it is clearly closely connected with the working-distance of the flower.

*Note* that the erect petals and stout staminal filaments constitute a practicable extension of this tube-mechanism, thus increasing the working-distance to 5–6 mm., and preventing any lateral access to the honey. The filaments represent special growths in the stamens, by means of which the pollen-supply is elevated to the mouth of the floral-tube, while a still greater zone of growth in the style takes the stigmatic surfaces even higher than the anthers; though, as the flower is more or less pendulous, this is not really so important as the elevation would seem to imply.

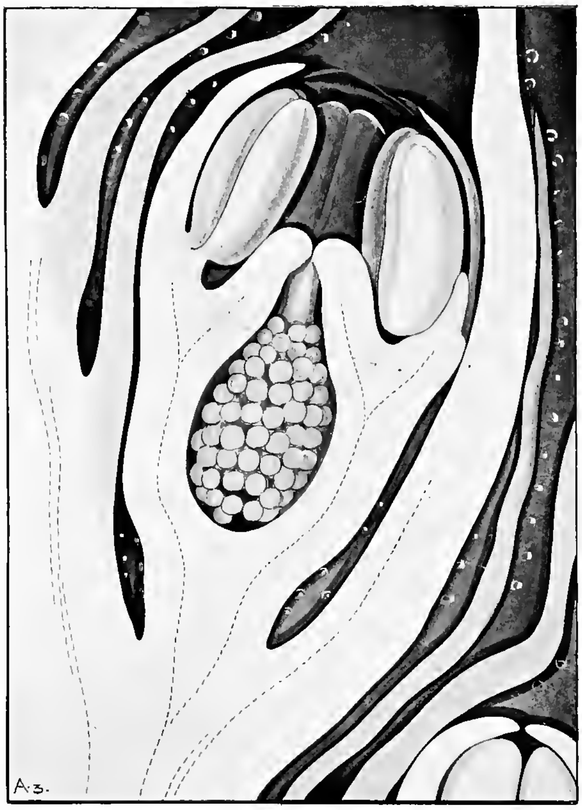

Fig. 3. *Ribes sanguineum*, January 15. Section of developing flower in the median plane.

## Special Mechanism.

The special mechanism of the flower-shoot, which when superimposed on a comparatively simple phyllotaxis-construction converts it into an efficient organ of pollination, may be included under the following heads:—

(1) A *Perigynous zone* of growth constituting the tubular portion of the flower, 3 mm. in length. *Note* that the *Epigynous* zone as an extension of the primary concavity of the receptacle, although utilized later in fruit-production, has no necessary connexion with the pollination mechanism.

(2) Intercalation of *filaments* as long stalks to the stamens, which take the anthers to the level of the petal-tips.

(3) An extension of the *style-shaft*, which is clearly correlated with both the preceding growth extensions, and thus elevates the receptive surface beyond the anthers.

*Note* therefore that the special tubular character of the flower as a honey-containing vessel is due to (1); the protrusion of the essential surfaces to (2) and (3); while (3) tends to eliminate the chance of self-pollination which would inevitably take place if the bud-structure had been retained in the adult condition.

The working-distance of the flower is thus given by the length of the whole tube portion from the stigma and anthers to the secreting surface, or 5–6 mm.; while the flower is thus clearly adapted for the visits of pollen-collecting insects, and also honey-seeking bees and Lepidoptera with proboscides at least 5 mm. in length, though larger insects with longer proboscides are not excluded.

With these floral growths may be included:—

(4) *The internodal extension of the inflorescence-axis* just before the flowering period,

the base of the axis adding a growth-curvature which renders the young inflorescence distinctly pendulous as it pushes out of the bud before the last increased growth of the flowers, which at a later stage renders the inflorescence definitely pendulous by its own weight (cf. Laburnum).

(5) *A flower-stalk internode* between the subtending bract and the first prophyll; after the flowering-stage is over a special growth-curvature takes place in this region (? geotropic), and the young fruits are re-erected.

*Note* also that, although the primary construction of the receptacle, and the epigyny of the gynoecium, is probably to be correlated with the protection of the ovary-contents, this has no reference to the actual mechanism of pollination; while, on the other hand, the secondary extension of the crateriform receptacle as a *Zona Perigyna* has no special relation to the protection of any of the essential organs, since the pollen supply and the stigmatic surfaces are intentionally carried beyond it: its significance as a hollow tube-cavity appears to be restricted to that of a honey reservoir, its length serving to restrict the flower to visits of insects of a certain type.

FIG. 4. *Ribes alpinum*, December 28. Development of flower, showing crateriform receptacle.

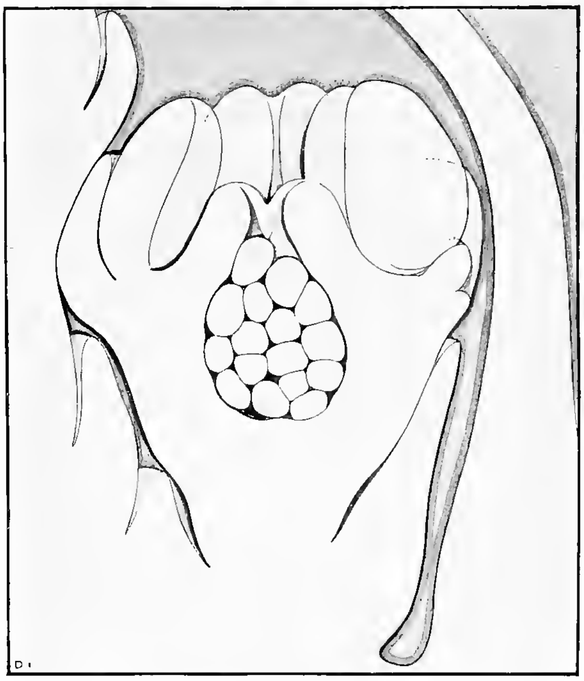

FIG. 5. *Ribes rubrum*, December 28. Development of flower, showing the formation of the ovary-cavity.

(6) *Distribution of pigment.* The epidermis of the receptacle-tube and sepals is coloured bright crimson by anthocyan-derivatives dissolved in the cell-sap, the production of which is by no means limited to the flower. Similar coloration occurs in the epidermis of the flower-stalk, inflorescence-bracts, prophylls and axis, bud-scales and even leaf-stalks of the plant when exposed to strong light. Although its primary significance may probably be that of a protective screen, some facts about it point to its being now definitely correlated with insect-visits, e.g. the purity of the colour in the floral-members, as indicating complete elimination of chlorophyll, and the elaboration of a pure rose-coloured derivative, brighter than the purple fundamental colour which is to be seen in large quantities in the cell sap of the ripe fruit; the lack of pigment in the petals when the flower first opens, as also in the new growths of stamen-filaments and style-shaft, produces a colour-contrast with the brightly-coloured exposed sepals, though all these regions as they become old and of deficient vitality take on the crimson coloration.[1]

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[1] That the formation of the red pigment is a result of the normal metabolism of the adult flower-shoot in which light only plays a secondary part is shown in an interesting manner by picking shoots of *Ribes*, in which the winter

## Pollination.

The flowers are obviously rendered *conspicuous* by the red coloration of the sepals and free portion of the receptacle-tube, whatever the primary significance of this pigment may be; and this is greatly increased (1) by the aggregation into pendulous racemes of almost simultaneously expanded blossoms, (2) by early flowering before the leaves are fully grown, and (3) by similar coloration of the flower-stalks and bracts. The shrubs are thus a blaze of colour in April and early May when few other plants are in bloom. From the standpoint of cross-pollination it must thus appear that special means are adopted to render the shrubs conspicuous as a whole, and attractive from a considerable distance, rather than to emphasize the individual mechanism (cf. Hawthorn).

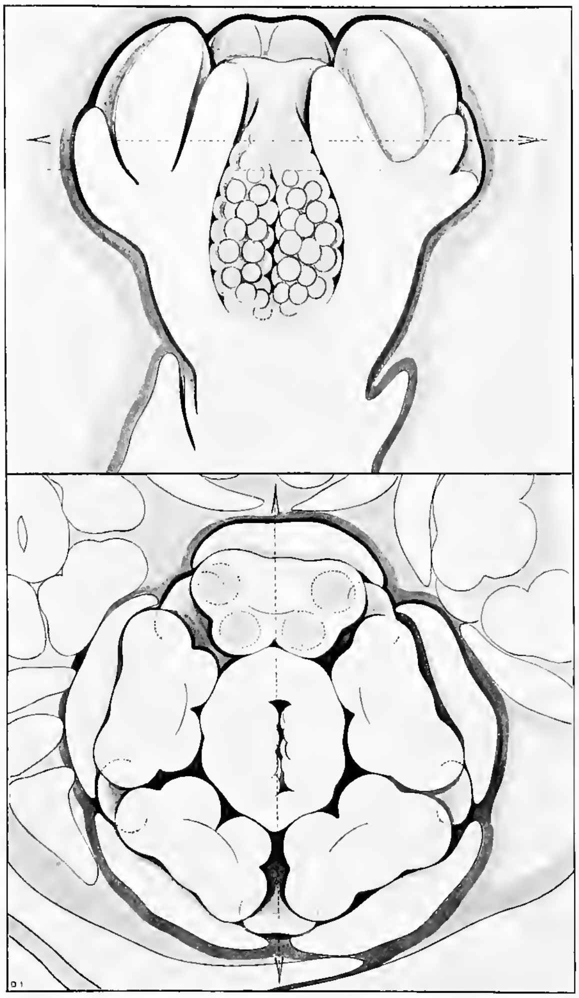

FIG. 6. *Ribes nigrum*, December 5. Development of flower: transverse and median sections in corresponding planes indicated by arrows.

The white petals present an 'eye'-contrast in functional flowers, but as these become old, the petals turn crimson like the sepals, and pollinated flowers have thus been described as subserving an increased means of attraction; but there is no evidence that this can be regarded as an intentional adaptation, since the bushes in fact tend to be most showy when practically all the flowers are over. The coloration of the petals has no necessary connexion with pollination, but is possibly a phenomenon of reduced vitality largely affected by continued exposure to light. (For similar colour relations in sepals and petals cf. *Erica carnea*.) From another standpoint it is the delay in the formation of a generally diffused pigmentation which is utilized to afford a colour-contrast in the opening flower; or it might be said that the flower is really tending to become more conspicuous as a white form; but here again caution is required, since the white-flowered variety with permanently white sepals still exhibits the colour-change in the petals, filaments and style; while in *R. aureum*, in which the rose-colour is replaced by a yellow pigment, the same colour-change is added in the case of the older petals, and the opening flower has no contrasting eye though the withering blossoms have a very showy one. As in the case of other flowers presenting the late colour-change (cf. *Weigelia*, *Aesculus*), it may be noted that the opening functional flowers are increasingly conspicuous at dusk when the older dark-coloured ones soon become invisible.

The flowers possess the strong aromatic scent of the vegetative shoots, due to epidermal glands secreting ethereal oil, which has no necessary connexion with insect-visits, and they provide abundant honey at the base of the receptacle-tube, but relatively small quantities of pollen.

The receptacle-tube is about 3 mm. deep, and the erect petals and stamens constitute

buds are only just breaking, and allowing them to stand in water in a warm room. In a few days both leaves and flowers expand, but the latter are pure white, and no trace of red pigment is seen, the blossoms being small and dwarfed, and all late zones of growth feebly developed.

a serviceable prolongation for nearly 3 mm. farther. Honey rises to a height of nearly 2 mm., and the lower end of the tube being slightly dilated, it holds a large drop of fluid in spite of the pendulous character of the flower. The honey supply is thus freely available to insects with proboscides of 5–6 mm.

The pollen, on the other hand, is somewhat concealed, since the stamens are a little shorter than the petals, and the pollen cannot be readily wiped off by pollen-collecting bees. The Californian insect-visitors are not described, but the flower appears to be adapted for the visits of fairly short-tongued bees and possibly for Lepidoptera (? nocturnal species). In gardens the flowers are visited by large numbers of bees, including the Hive-bee (5–6 mm.) and Humble-bees (*Bombus terrestris*, 7–9 mm.), and the Hive-bee is the most industrious and possibly most important pollinating agent.

*Anthophora pilipes* (19–21 mm.) is by far the most elegant worker;[1] in order to probe the flower it stands off at such a distance that the stigmatic surface and anthers are only lightly touched by the lower portion of the proboscis. The Hive-bee takes honey only, pushing its head well between the stamens, so that individuals may be observed with their heads completely whitened with pollen. *B. terrestris* is an extremely clumsy visitor, and probably does as much harm as good. Since the stigmatic surface is receptive as soon as the buds expand, and the stamens do not immediately dehisce in moist air, the flower is slightly protogynous by construction, and a first chance may be thus afforded to cross-pollination; as in other Spring flowers, such protogyny is increased by the action of cold dry winds, which may spoil the stigmatic surface before the more sheltered anthers are properly shed; on the other hand, sheltered stigmas remain viscid after the rest of the flower has withered, so that there is no evidence of any intentional protogynous adaptation (cf. *Cydonia japonica*). Bees as a rule visit the younger flowers, i. e. the lower ones of the pendulous inflorescence, first, and this fact may co-operate with the tendency to protogyny, and so be useful from the standpoint of cross-pollination. Thus, though there may be no exact correlation in these respects, there is a distinct suggestion as to the lines along which the mechanism might be improved. Note again that the older inflorescence is pendulous mainly by its own weight, and the frequent tendency of the style to bend upwards also gives a hint of the manner in which secondary zygomorphy might become induced.

Individual flowers persist for 5–10 days; a whole inflorescence for 4–5 weeks; at the optimum period in warm moist weather as many as 30 flowers may be out simultaneously, though 20 is a good average. More usually about 12 flowers are expanded at one time; of these 6 are functional and visited by bees, the others are crimsoned and are beginning to wither. From these data it may be inferred that the normal rule is that a contact-cycle of flowers (5 in a $(3+5)$ system) should be always at approximately the same phase.

In complete absence of insects the chance of pollen falling on the small stigmatic surface is very remote, and protected flowers do not set fruit.

The flowers are, however, quite fertile to their own pollen, and isolated bushes visited by insects set numerous berries. Self-pollinated flowers rarely develop fruits, the berries being shed at an early date. Experiments out of doors are usually spoilt by climatic factors.

*Note* that self-pollination (autogamy) is normally eliminated by the growth of the style being regulated as the perigynous zone is put in just before the flower expands, so that the stigma is taken clear of the anthers. When this adjustment is not exact, autogamy becomes

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[1] If flowering specimens of *Ribes sanguineum* are watched for a short time on a sunny day in April, they are almost certain to be seen visited by a small coal-black bee the size of a small humble-bee, and very active in its habits, hovering over the flowers with half-extended proboscis. This is the female of *Anthophora pilipes*, it possesses a very long proboscis (19–21 mm.) and brown shaggy hind-legs, with a great capacity for pollen-carrying, patches of white or yellow pollen being very conspicuous against the black body. The male is similar in size and habits, but of a bright fawn colour with a whitish face and beautifully feathered legs. These bees are the most successful agents for all tubular Spring-flowers (cf. *Vinca*, *Viola*, *Primula*, *Corydalis*).

possible, and flower-buds isolated under muslin often show this irregularity; hence such flowers will pollinate themselves and set fruit, though mature fruits have not yet been obtained from such flowers.

It is also of interest to note that the flowers are often *bored* in great numbers by Hive-bees, and some bushes may be thus affected more than others; large holes, often 2 mm. in diameter, being taken out of the receptacle-tube on the side presented externally in the drooping inflorescence. This is apparently more usual in cold dry weather when the secretion of honey is feeble, the insect being thus enabled to lick the entire secreting surface.

## Variations and Monstrosities.

As a pentamerous type of no extreme specialization, the normal construction-variations to hexamery and tetramery may be expected, and occasionally occur.

Hexamery, as a transition to a (6 + 6) construction, may be perfectly maintained as far as the androecium, giving 6 petals and 6 stamens. And similarly tetramerous construction (4 + 4) gives 4 petals and 4 stamens, the corolla being orientated 'diagonally'. Intermediate and mixed forms are also general.

A large number of such irregular constructions were observed (B. G. O., 1904) in the case of a strong plant which had been pruned so far back that the bulk of the flowering shoots had been removed, and few-flowered inflorescences were developed at a later date from more dormant buds.

A special feature, noticed in so large a number of blossoms that it could not be a mere 'accident', while it also represented the only abnormal detail, was the sepalody of the anterior petal, this being brightly coloured and equal in size to the sepals, and thus very conspicuous in the expanding flower: in some cases one of the posterior petals was similarly modified, so that it became obvious that the odd petal was really the sixth member of the quincuncial system of the calyx, while the posterior member would be a seventh. The explanation being probably that such flowers presented instances in which the assumption of the symmetrical (5 + 5) construction system had not taken place normally at the fifth member of the calyx series, but had been delayed, so that the corolla was partially spirally produced; the fact being only rendered visible by the subsequent modification of the spiral members along similar lines; and such a construction is clearly a first step in the production of a 'double-flower'.

An interesting case is that in which the delimitation of the members on the crateriform receptacle is not adjusted correctly, with the result that in the production of the epigynous zone of growth one or more perianth members may be left isolated on the outer surface of the receptacle-tube: the effect in the adult flower being much more remarkable than the accident to which it is due (for similar phenomena cf. *Galanthus*).

The form in cultivation as a 'double-variety' (*flore pleno*) is of interest from the beautiful manner in which the structure of the crateriform receptacle is emphasized when the floral shoot presents an indefinite assemblage of members growing from its concave surface. The flowers are developed in autumn, as in the normal case, and sections of perennating buds (November to February) show the essential features of the construction; an indefinite number of rounded primordia arising on the sloping surface of a beautifully cup-shaped receptacle. The ultimate floral production consists of a rosette of petaloid segments, of the 'button' type, 20 mm. in diameter; 100–150 petaloid segments being inserted on the rim of the cup, and succeeded by rudimentary stamens and sterile carpel-like members at the base of the concavity. (May.)

## Fruit and Seed.

Non-pollinated flowers wither and fall off early in May; the abscission layer being formed just above the bract. The perianth of fertilized flowers also withers but is not shed;

the flower-stalks bend back, and re-erect themselves on the drooping inflorescence axis, and the sepals close up again, thus indicating that they originally diverged by an intentional growth effect. None of the floral members are shed, the ovary steadily enlarging to an ovoid berry covered with glandular hairs, with green assimilating surface, and bearing at its apex the withered relics of the floral members which may all be identified even when the fruit is fully ripe.

The flowering period is usually completely finished in the first or second week of May, and the new foliage is simultaneously matured; as in other shrubs which bloom during the period of leaf-expansion, the number of fruits developed appears to be affected by the vigour of the vegetative growth, more especially as a result of competition for the available water-supply, and in dry seasons a majority of the young berries will be shed. The significance of the succulent receptacle as a water-reservoir for the young fruit thus becomes apparent (cf. Apple).

The berries attain full size in July and are freely exposed to the desiccation of the hot summer sun (80° F. or more). Section of the hard green berries taken in the middle of July shows protective adaptations in the ovary-wall. The cuticle is thick, and both epidermis and hypoderm function as aqueous layers; the innermost layer becomes converted into a lignified zone of peculiar banded fibrous-cells: the outer layer of the seed-coat is also aqueous, while the innermost layer consists of brown tannin-containing cells.

Ripening of the fruit takes place early in August, and is indicated by the production of pigment (anthocyan-derivatives) in the wall and pulp, and a pale waxy bloom on the whole surface, which may be so well marked that the berries appear quite white or pale blue. The main crop ripens by the middle of August, and the fruits remain on the bushes until October or even November, as they are not immediately taken by birds. They are ultimately shed at the time of leaf-fall, rarely remaining over the winter; they decay on the ground beneath the bushes and the seeds germinate freely in the succeeding spring. Usually only a few (5–14) berries ripen in each inflorescence.

The mature fruit is a globular berry, 13 mm. by 12 in diameter, or less, and bears a few small scattered bristly hairs, the relics of the glandular covering of the receptacle-tube and young fruit. When the waxy layer is rubbed off, the pale-blue berry becomes blue-black, while in spirit-material the 10 vascular bundles of the petals and sepals can be traced as meridional lines.

Transverse section shows a thin succulent wall, of which the epidermal and some of the subjacent layers are filled with an intense purple-red pigment which gives the blue-black effect by fluorescence from concentrated solution. The pigment gives the usual anthocyan reactions, rose-red with acids, and deep-blue with Eau de Javelle. The fruit-wall is about 1 mm. thick, the bulk of the juicy contents being derived from the succulent colourless placental tissue, in which the vascular bundles supplying the seeds can be clearly followed. The remains of the lignified layer can be removed from the pulp.

The berries are insipid in taste, the mucilaginous portions being only slightly sweet; they are not taken with avidity by garden birds, and it is not easy to prove that any intentional modification obtains toward this special end.

The seeds are 10–45 in number in large fruits, so that the majority of the ovules fail to be functional; and still fewer are found in small berries.

They are smooth, brown or black, ovoid or irregular in shape by mutual pressure, about 3 mm. long by 2 mm. wide, the pointed narrower end represents the chalaza, the broader end has a lateral dimple for hilum and micropyle; a lighter ridge along one side marks the plane of the raphe.

Section in this plane shows the seed with a broad testa, consisting of a greatly developed succulent outer columnar layer of cells, containing sugars and tannins, and a narrower non-lignified protective inner zone. Endosperm is abundant, and the small embryo has its cotyledons laid out in the plane of section—though, as usual in cases in which a small embryo is imbedded in a large mass of endosperm, this orientation is not constant. The endosperm cells have slightly thickened walls, and contain granular proteid and abundant fatty reserves.

*Note* that the small embryo is *protected* by the inner layer of the testa; provided with *food* in the form of fat, proteid, and cellulose stored in the endosperm; and is possibly dispersed by the agency of birds, though the birds are not specially indicated for *Ribes sanguineum* in its native home, and the extent to which the water-storage tissue of the ovary wall and outer layer of the testa may be subsequently adapted to constitute a tissue which shall be attractive to birds is not clear, though again it is evident that further improvement might take place along these lines.

*Note* that such an indehiscent *Berry*-type of fruit is here directly consequent on the great development of the crateriform receptacle as the outer wall of the ovary cavity, which in that it becomes succulent, secreting mucilage internally and wax externally, suggests that such modifications have a primary significance in connexion with the economy of the water-supply, and that any reference to the ultimate utilization of these structures for distant dispersal must be wholly secondary. Under ordinary conditions the berries are shed, and the seeds germinate readily under the parent bushes in the succeeding spring.

## Comparison with Allied Forms.

Other species of *Ribes* are common, both wild and in cultivation; they all possess the same vegetative habit and floral diagram, and flower contemporaneously. These, together with *R. sanguineum*, may be arranged in a series of considerable biological interest, as illustrating the progressive specialization of the floral mechanism in correlation with special insect-types, and thus possibly indicating a transition from a small and simple fly-pollinated type to a bright-coloured 'bee' or 'butterfly' type, in virtue of one controlling idea, namely the progressive development of the glandular receptacle-region. On the other hand it must be remembered that the fact that such a series may be arbitrarily arranged, does not in itself prove anything, nor need the simplest cases be necessarily the most primitive. The evidence only becoming satisfactory when it comes into line with deductions made from quite a different standpoint, as for example that of the floral-ontogeny.

### I. Ribes alpinum, L.

A common Alpine form, throughout Europe and Siberia, found wild in parts of Great Britain. In general appearance this shrub presents a very good idea of what may have been the original stock. The racemes are *erect* and consist of very small greenish flowers of typical *Disciflora1* pattern (cf. *Euonymus*), the most important feature of the flower being the relatively large and quite *flat* secreting disc, 2–3 mm. in diameter, in which the ovary appears embedded.

The insect visitors are flies and small bees (*Andrena*), the honey being quite freely exposed.

As a secondary peculiarity, supposing that it is a starved and even degenerate form, it may be noted that it is *diclinous* owing to the imperfect development of the stamens and carpels on separate individuals, though the members themselves are normally present.

### II. Ribes rubrum,[1] L. The Garden Red Currant.[2]

The inflorescence is pendulous and the flowers somewhat flat, and about 7 mm. in diameter. The sepals are greenish-yellow, a faint purple flush appearing in some cases. The petals are extremely small, and remain in their primary rudimentary condition. The

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[1] Linnaeus, 1753. The original *Ribes* figured by Fuchs (1542). The St. John's Berry, since the fruits are ripe about Midsummer.

[2] Currant or Wild Currant; *Currans* of Gerard, from the resemblance of the berries to those of the Currant Vine.

glandular disc is saucer-shaped, 3 mm. in diameter, with an irregular surface, more marked in some specimens than others, owing to the pressure of the anther-lobes in the bud, and thus tending to a formation of antipetalous lobes. The honey is thus freely exposed and the secretion is considerable. The stamens are short, and, being widely spaced at the periphery of the disc, the connective takes on a compensatory extension, the anthers, especially when shed, being curiously hammer-headed. The flower is again suggestive of a depauperated rather than primitive mechanism; all the secondary growth-regions being very feebly represented, and the number of ovules is small. The flowers are visited by small bees *Andrena* (2–3 mm.), and most commonly in gardens by the Hive-bee. Autogamy in absence of insect-visits is rendered improbable by the spacing out of the anthers away from the short curled styles.

### III. Ribes nigrum, L. The Garden Black Currant.

Similar inflorescences of small greenish flowers, about 7 mm. in diameter, are produced contemporaneously with those of the preceding type. The floral structures are better marked; the sepals have a distinct reddish flush (anthocyan), and the petals are larger (2 mm.) and converge to the median line, as also do the stamens; in older flowers the petals are reflexed. The receptacle is now a prominent cup-shaped secreting surface, 4 mm. in diameter and nearly 3 mm. deep, semi-spherical in shape: entrance to the cavity is limited above by the manner in which the stamens converge to the median line, the gaps between them being just covered by the petals. The stylar-zone is so adjusted (4 mm.) that the stigmatic surface is carried in the median line to the level of the top of the anthers and thus stands directly in the only path to the honey. The entrance to the flower is thus restricted to a narrow orifice, and the working-distance definitely fixed at 4–5 mm., both honey and pollen being fairly well concealed and protected. Autogamy is, however, not eliminated owing to the close vicinity of anthers and stigmatic surface, but a first chance is still given to cross-pollination in the opening flowers, especially in damp weather, when the anthers do not dehisce on the first day. The flowers are visited by both the Hive-bee and *Anthophora*, the former being the most active garden visitor. The flowers are freely self-fertile, and during mild weather every flower sets fruit.

### IV. Ribes Grossularia, L.[1] The Gooseberry.[2]

The inflorescence is conspicuously reduced to 2 or even 1 flower, though the individual blossoms are no more specialized than those of *R. nigrum*. The purple coloration of the sepals is more pronounced, and the petals are distinctly white; as the sepals recurve the colour contrast becomes noticeable though not remarkably conspicuous. The general idea of the mechanism is that of *R. nigrum*, but the aperture of the flower is widely open; the petals stand erect, and cover the gaps between the erect stamens (3 mm.). The receptacle is a well-marked cup-form, 4 mm. in diameter and over 3 mm. deep; the palisade of petals and stamens constituting a serviceable prolongation, so that the working-distance becomes 5 mm. The whole of the internal surface secretes, so that the honey-supply is copious, while the pollen is also freely exposed and may be readily collected. As features of further specialization it may be noted that the Zona Perigyna, which constitutes the secreting surface, is now more definitely localized from the Zona Epigyna which constitutes the ovary-cavity, so that the green 'ovary' appears on the outside of the flower as a definite 'inferior' structure. The styles are free, and each adds its own stylar-zone, and both styles and filament-bases produce abundant stiff hairs which serve to block the entrance to the flower-cup. As the flowers are hairy externally, it is possible that the extension of these

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[1] *Grossularia*, from *grossulus*, a small green fig, a genus of Tournefort (1700), and hence retains the capital letter; Linnaeus (1753).

[2] The Gooseberry is said to be wild in England and France (*groseiller*), and has been cultivated in this country from very early times, being given by Turner (1573). Probably originally used as a green sauce for young geese, but apparently eaten as a fruit in Parkinson's time.

hair-formations to the internal cavity had the primary object of protecting the secreting surface from desiccation, since the protection of the ovary is already provided for by the closing in of the receptacle. Being present they also undoubtedly assist in preventing the access of 'unbidden guests'. The flowers are visited by numerous bees, especially the Hive-bee, as also by flies (*Eristalis*). They differ again from the Currant-types in being slightly *proterandrous*; the style growth being usually incomplete when the flower first expands. The sepals curve back again as the flowers become old and faded. As in the preceding cases, autogamy may take place in the case of flowers so obliquely placed that pollen may fall by itself, or assisted by the wind, on to the viscid stigmatic-surfaces, and individual flowers may be found at any angle with the vertical.

The plants flower very early (March) and may be quite over before the Red and Black Currants commence; the latter is again usually a week or more later than *R. rubrum*.

### V. Ribes aureum,[1] Pursh. The Yellow-Flowering Gooseberry.

Introduced from North-west America (Valley of Missouri and Columbia R.) in 1812, this has been almost entirely replaced as an ornamental shrub by *R. sanguineum*. It reaches the highest limit of the series; the flowers are produced in slightly drooping racemes and are contemporaneous with the other forms; they are of a bright yellow colour throughout, and are strongly clove-scented, the vegetative part of the shrub not being aromatic at all. The structure of the flower is essentially that of *R. sanguineum*, and the blossoms are worked in a similar manner; they are, however, remarkable for the increased development of the tube-mechanism which further restricts the number of insect visitors. The receptacle-tube is elongated to 10 mm., and the working-distance is increased by the erect palisade of stamens and petals to 13 mm.[2] The tube is also narrower in proportion (3 mm.), and the secreting surface is limited to the basal region, including part of the outer surface of the ovary which is not so clearly separated off as in the other types. A single style-shaft takes the stigmatic surface clear of the anthers, and autogamy is thus structurally avoided, although it is still possible in drooping flowers. The flowers are of the slightly protogynous type of *R. sanguineum*, and are also extensively bored by bees which cannot otherwise obtain the honey. They are visited by Humble-bees and *Anthophora* in gardens. The petals are remarkable for a very definite colour-change, the exact function of which is not clear; these are pale yellow in the opening flower, but in older ones they take on the same familiar crimson epidermal pigmentation as those of *R. sanguineum*, although this colour substance is not apparently present either in the other floral members or in the vegetative shoot. Older flowers thus present a brilliant colour-contrast which is wanting in the freshly expanded ones. In the case of plants which are freely visited by insects, the flowers are pollinated before the contrast appears; nor can it be said that this coloration of older flowers increases the decorative value of the inflorescence as a whole to any marked extent, nor again are the newly-opened flowers much more conspicuous at dusk. Bees visit both old and young flowers without appearing to differentiate between them, yet if the colour-change is meaningless from the standpoint of the pollination-mechanism, it is curious that it should be restricted to the petals as a corona-like line of colour.

## Comparison of Fruits.

While it is difficult in the case of *R. sanguineum* to directly associate the changes observed in the fruit in its so-called 'ripening' with adaptations to secure dispersal by the agency of birds, since other interpretations may be given to the phenomena, it becomes of interest to compare them with the fruits of these other species of *Ribes*, the berries of which are valued by man, and are undoubtedly not only attractive to birds, but devoured in large quantities, and eagerly sought by blackbirds, thrushes, &c.

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[1] Pursh, Flora of N. America, 1814.

[2] In large-flowered garden forms, the tube may be 11–12 mm., and the total extension 15 mm. The corolla being 23 mm. in diameter.

Thus in *R. sanguineum* the waxy coating is possibly a means of protection against desiccation, and the great development of the purple pigment may be only a change from the large quantity of tannins stored in the green fruit as the tissues become old, and the ripening process be so far regarded as an incipient decay. On the other hand, these same factors may readily acquire a secondary value once they are present; and in this connexion it is interesting to speculate why the waxy coating does not appear earlier in July, or why the pigmentation should tend to be localized peripherally and not be diffused throughout all the ovary-wall or seed-coats. Although possessing the same fundamental construction, there can be no doubt that *R. rubrum* does carry these ripening processes a stage further, and that in this case the berry is designed to be attractive to birds, but only by increased development along similar lines.

*Ribes rubrum.* The berries ripen early in July, the first changing colour about Midsummer. The fruits are 8–10 mm. in diameter, or twice as large in cultivated varieties, and are bright red, juicy, and glistening. As in other specialized succulent fruits, the ripening is indicated not only by a change of colour, the disappearance of the chlorophyll of the green fruit and a localization of red anthocyan-pigment in the epidermal cells and some of the subjacent tissue, but the volume of the fruit is increased to double its previous size, within a day or two, as the expression of an increase in the osmotic properties of the cells of the fruit-wall. The juice of these cells and that of the seed-coat is sharply acid in flavour, and this possibly accounts for the rose-red colour of the pigment. The seeds are again few, and pale yellow-brown: in the white-fruited form in cultivation these pale seeds seen through the transparent fruit wall give the fruit its characteristic yellowish tint. Fragments of the sclerosed lining-layer can also be found, and these give the phloraglucin-reaction, the fruit and seed agreeing in all essentials with that of *R. sanguineum.* The structure of the fruit is distinctly less xerophytic, since the aqueous tissue of the ovary wall, as also the wax of secretion, is altogether absent; while it may be noted that the anthocyan-pigment was wholly lacking in the flower, and appears in the fruit for the first time.

*Ribes nigrum.* The fruits ripen in the early part of July, as black berries 10–12 mm. in diameter. They possess the strong aromatic character of the rest of the plant. The pigment, which is deep red, gives the black appearance as in *R. sanguineum* by reflection from a concentrated solution, and is practically localized in the epidermis which may be peeled off, leaving a greenish pulp. The seeds are 20–30 in number, and agree with the preceding types; the same sclerosed lining-layer is also present.

*Ribes Grossularia* produces fruits of much greater size, which ripen later in July and August. They are full-sized in the early part of July, being 20–30 or 40 mm. in length, and 20–25 mm. in diameter. The epidermis may be smooth or hairy, and pigment may be present in the epidermal cells. In some forms chlorophyll persists in the ripe fruit. The ovary wall in the green fruit is very thick and presents large lacunae.[1] The epidermis is not specialized, and the sclerosed lining-layer is wanting. The great development of succulent tissue apparently renders lignification unnecessary.

Biologically it is interesting to note that the smaller berries up to 10 mm. diameter are readily bolted whole by such birds as the Thrush, and a certain number of seeds pass safely through the alimentary canal; the larger fruits are pecked, and here the mucilaginous layer of the outer testa, which is apparently originally a water reservoir for the ovule, becomes extremely useful, since it may not only supply nutriment, while the rest of the seed passes on, but by adhering to the beak or other parts of the bird may cause the seed to be wiped off, and thus subserve a dispersal function.

It is also difficult to avoid a comparison of the brilliant scarlet fruits of the Red Currant, which are taken by birds as soon as they are ripe, with those of the Mountain Ash, which

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[1] Figured by Grew, 1682.

are equally favoured, in size, form, colour and flavour, as typical bird-dispersed fruits, although their structure and the original significance of the parts may be different.

## Theoretical Considerations.

All these *Ribes* types are woody shrubs with deciduous leaves, developing their flowers at the end of summer, and perennating with protected winter-buds over the inclement winter period of the North Temperate Regions of the Old World and North America.

Correlated with this mode of perennation and the Spring flowering-period, the inflorescence is reduced to a simple racemose condition recalling a catkin-type, borne on a dwarfed shoot with aborted apex, the vegetative ramification being continued from a lateral bud immediately below the flowering region (cf. *Cytisus Laburnum*).

The flowers also exhibit a simple type of construction, the floral diagram being constant for them all; this may be considered in fuller detail, since it is evidently a reduction-derivative of a once much fuller construction, and the reduction appears purposeful and is of the nature of reduction-specialization rather than degeneration.

Taking the different regions of the flower in succession, therefore, it is clear that:—

The *calyx* is a normal asymmetrical Fibonacci construction, identical in all respects with that found in the vegetative shoots, and orientated in the same manner with regard to the sterile leaf-members of the floral-shoot, which do not enter into the mechanism of the flower itself, but are included as prophylls. Why two such vegetative leaves should be isolated on such a shoot is not clear, nor why such members should be limited to two: it must be noted that they are members of the same asymmetrical phyllotaxis-construction as the calyx members, and are not necessarily in any strictly transverse plane. The only suggestion as to the meaning of such members is that deduced from the general study of the inflorescence, that they represent a means of continuing the development of the shoot in case the terminal structure is damaged, and that given the special orientation adopted, two members happen to fall fairly right and left of the shoot, and give a sufficiently approximate balanced symmetrical distribution. Similarly the reason for this special orientation of a Fibonacci system by which sepal 2, or ontogenetically the 4th member of the series, is so approximately median-posterior is still vague, though as a fact of observation it is so widely distributed a phenomenon in all Angiosperm phyla. The result of the isolation of 7 members of a Fibonacci phyllotaxis-system is thus to give 2 approximately lateral prophylls and a *Quincuncial Calyx,* in which the ontogenetic value of the members may be traced in their prefloration as a *single complete contact-cycle*, such as would mathematically follow from a construction by $(3+5)$ intersecting curves.

Beyond these 7 members the phyllotaxis-construction becomes symmetrical, and 5 members arising simultaneously indicate a construction of the form $(5+5)$, in which again 5 members will make contact at their edges as a complete contact-cycle, and any overlapping will be a secondary phenomenon—if wholly irregular, with a mathematical chance of $2^5 = 32$ different methods (cf. *Pyrus*)—or if regular, under the control of some secondary law of growth (cf. *Vinca*). In *Ribes* the former case apparently obtains. The special point, however, being that at this transitional stage of the phyllotaxis-construction *one complete contact-cycle* is again retained for a special (attractive) function as 5 petals.

Similarly, the symmetrical $(5 + 5)$ construction is continued henceforth into the *sporophylls*, and one complete cycle only, i. e. 5 members, is retained as the functional androecium.

By analogy it would be expected that one complete cycle might be isolated as the 5-carpelled gynoecium; but though this is a general feature in many floral-constructions, this is not the case here.

Reduction-specialization is controlled by a tendency to limit the number of seeds produced by one pollinating mechanism; a generalization again deduced from the comparison of what takes place in those phyla which possibly present the highest types of floral

organization (cf. *Compositae*). Such a tendency usually makes itself felt first in a reduction of the number of carpels; and the lowest number possible, which will give a radially symmetrical syncarpous ovary, is clearly 2; that is to say, any 2 carpel-origins out of a contact cycle of 5 may be developed, while the others are suppressed, thus giving a 2-locular ovary without definite orientation. When this phase of reduction becomes fixed, the surviving carpels are developed in a plane of median symmetry, and though at first producing many ovules, the general tendency will be to still further reduce these, the ultimate limit being the production of one seed, and the development therefore of only a single ovule in the ovary (cf. *Compositae*).

Such a type of floral-construction comprising:—

*Two lateral prophylls* (which may continue the ramification of the vegetative shoot or of the inflorescence-system).
*One quincuncial contact-cycle* of protective members (calyx).
*One whorled contact-cycle* of members of transition, subsequently utilized as a corolla.
*One whorled contact-cycle* of stamens, and the
*Symmetrical syncarpous* relic of a whorl of carpels,

represents not necessarily a primitive, since fairly simple-looking form of flower-shoot, but the simplified end-product of a long line of reduction-specialization, phases of which may be traced in types still existing.

Thus the prophylls and quincuncial calyx are clearly the expression of an old asymmetrical Fibonacci phyllotaxis-construction which once persisted throughout the whole of the floral shoot, as in the vegetative shoots of the same plant, and the sporophylls were developed in the same construction-system as the vegetative leaves. Such a type persists for example in *Helleborus* and *Caltha*; while in *Helleborus* may be noted a tendency to change the construction-system for the sporophylls with a consequent isolation of a cycle of transitional members.

The remarkable type *Aquilegia* again points the way to the assumption of symmetry in the sporophyll-region, with isolation of prophylls, a quincuncial calyx, 5 petals at the point of transition to sporophylls, and a definite (5 + 5) construction throughout the whole of the androecium and gynoecium. It appears probable that all flowers of the *Ribes*-type of floral diagram have followed this line of specialization, as indicated in *Aquilegia*, with the further proviso that the androecium is reduced to one cycle, and the gynoecium to less than one. That is to say, with due regard to as symmetrical a plan of construction as possible, the floral diagram of *Ribes* represents a certain *limit* of reduction-specialization in that:—less than 2 prophylls will not admit of a symmetrical continuation of the system; less than a contact-cycle of sepals will not afford a complete investment; less than a contact-cycle of petals will not utilize all the space available; and less than a complete cycle of stamens will not give a radially symmetrical (centric) floral-mechanism, nor can radial symmetry be retained in the gynoecium with less than 2 carpels. With any further limitation of members, the floral mechanism must inevitably become morphologically degenerate, since either some cycles must be missed (cf. *apetaly*, *dicliny*), or the flower may lose its original radial symmetry and become eccentric (*zygomorphic*), or bilaterally specialized.

So strongly is such a standpoint supported by a general review of the floral forms of higher plants, that it becomes convenient to indicate this apparently simple diagram by a special name, since it marks a certain reduction-phase of floral-construction beyond which it is not safe to go without loss of essential characters.

This scheme will therefore be denoted by the term 'MEAN TYPE' of Floral-Construction, as applied to a Pentamerous Petaloid form: homologous reduction-phases being also associated with the production of trimerous and tetramerous flowers, as also again in the case of phyla which may be apetalous (*Urticaceae*, *Chenopodiaceae*).

That is to say, the possession of a *Mean Type* of Flower by any plant cannot be regarded as a necessary mark of 'affinity' with any other: it may represent a reduction-phase which may be reached in many diverse phyla, and such forms would then resemble each other only by convergence of type; the significance of this diagram being purely biological, in that it represents a certain balance between modern floral organizations and the external environment on which they are dependent for their successful development, protection and pollination. On the other hand it is equally possible to regard it as indicating a definite generalized biological stage in the main line of phylogenetic evolution on which different phyla have superimposed different secondary devices of their own. It therefore becomes of interest to accumulate evidence for one or the other of these points of view, since it is evident that if the type is widely distributed its correct interpretation will throw a strong light on the systematic study of the flower.

The prevalence of this Mean Type Diagram throughout the modern flora is one of the remarkable features of the vegetable kingdom. It is characteristic in its pure form, or as readily recognizable derivatives, of over 30,000 species of Dicotyledonous flowers, or about *one third* of all the flowers known on the world at the present time.

It is equally characteristic of the vast group of the *Compositae* (11,000 sp.) and the polypetalous *Umbelliferae* (1,300); of the centric types of gamopetalous construction *Rubiaceae* (5,000), *Apocynaceae* (1,000), *Asclepiadaceae* (1,500), and the eccentric types *Scrophulariaceae* (2,000) and *Labiatae* (2,600).

So striking is this convergence of higher plant phyla to a mean type, so far as the floral diagram is concerned, although subsequent developments of the floral mechanism may be extremely complex, that one is justified in regarding all more extended floral types as survivals of more primitive conditions (cf. *Helleborus*), notwithstanding the fact that some of these again may present peculiar lines of development of their own (cf. *Cydonia*, *Malva*), and the term *Mean Type* is selected in that it may not only be taken as an indication of the fact that the construction is a mean between a more primitive stage, in which the sporophylls were produced in greater abundance on the floral axes, and floral mechanisms of extreme specialization, but it also includes the biological idea of the economy of the construction.

In *Ribes* the mean type is associated with an ovary-structure in which parietal placentation obtains, a relatively large number of ovules being developed on the bulky placentas; and the tendency to a reduction in seed development is traced rather in the number of seeds matured than in the number of ovules laid down. The special development of the bulky placentas is again consequent on the development of the *Zona Epigyna*, an entirely new growth-zone in which the placentation, although it follows the plan of the primary carpel-edges, is no longer sutural (cf. gamocarpy of *Viola odorata*).

Further marked construction-changes become apparent in the elevation, and include the localization of other distinct zones of growth: the special character of the floral mechanism as a tubular structure, with a secreting glandular surface which may protect the ovary and style from desiccation, and also becomes associated with insect visitors, is due to a definite and new growth-region, the *Zona Perigyna.*

Although this may have been small at first (*R. rubrum*, *alpinum*), it ultimately assumes much greater prominence as a factor which determines the type of insect visitor (*R. aureum*), and different species of the genus *Ribes* thus represent different phases of the same construction-mechanism.

No new construction feature is really added, beyond the details already indicated as common to all these types, and the *Zona Perigyna* may thus be isolated as the essential character of the *Ribes* construction.

The general scheme of the flower thus reduces to a Mean Type of a Pentamerous Petaloid floral-shoot based on a crateriform type of receptacle, and further specialized in correlation with the production of a *Zona Perigyna,* originally only a glandular region between the androecium and gynoecium (*discus*), which subsequently becomes exaggerated to a tubular form, and thus renders the flower as serviceable for the function of cross-pollination by insects of advanced type as any analogous growth-form in gamopetalous phyla. The presence of the crateriform receptacle, in that by the special epigynous growth-extension it comes to form the whole of the outer limit of the ovary cavity, leads on naturally to the production of an indehiscent fruit, with a tendency to remain parenchymatous or even succulent during seed-maturation, and this again may ultimately acquire a secondary significance in connexion with later phenomena of seed-dispersal by the agency of birds.

Although the genus *Ribes* represents a fairly distinct type of plant-form when vegetative habit, flowers and fruit are all taken into consideration, it still remains on the whole a somewhat generalized type about which nothing very definite can be said, and hence its position in schemes of classification has always presented difficulty.

Thus among the older herbalists, the single plant *Ribes rubrum*, figured by Fuchs in 1542 as *Ribes*, became extended to a group of 11 kinds of *Grossularia* in Bauhin's *Pinax* (1623). Tournefort (1700) increased the number of species to 19, grouped in a definite genus *Grossularia*, and placed among the shrubs such as Roses and Myrtles. In the Linnaean artificial system *Ribes* falls naturally in the *Pentandria Monogynia*, a large and miscellaneous collection of plants of obviously very different alliances, but all with flowers of the Mean Type. In the Natural System of Linnaeus *Ribes* appears in the *Pomaceae* (1751): Jussieu (1789) rather curiously placed *Ribes* and *Cactus* in a separate order *Cacti*, being clearly impressed with the perigyny of the flower, and the berry-fruit with unilocular cavity, rather than by any other features, but arranged them as the next family to the Saxifrages. It is interesting to note that Jussieu considered the elevation of the flower of greater importance than the ground plan. De Candolle (*Prodromus*, 1828) separated the *Ribes*-type as an entirely distinct order, the *Grossulariae*, but really follows Jussieu in locating it between the Saxifrages on the one hand and the *Cactaceae* on the other; the group having now risen to an aggregate of 53 species.

Similarly Bentham and Hooker (*Genera Plantarum*, 1865) made the family *Saxifragaceae* wide enough to include *Ribes*, which then appears as the end-group of the family with 56 species, while the *Cactaceae* are removed to another series.

In this conventional position, which really shows little advance on the original arrangement of Jussieu, the group still remains; the Eichler-Engler system being unable to suggest anything more definite (cf. Engler, 1890), and the large and conventional series of the *Saxifragaceae* being maintained sufficiently elastic to include a miscellaneous collection of types, as a matter of convenience rather than actual phylogeny (cf. *Philadelphus*).

# XI

## **Cydonia[1] japonica,** Pers.
## (Pyrus japonica,[2] L.)

*Scarlet Cydonia.*
Japanese Quince.[3]

A HARDY woody shrub or small tree with deciduous leaves, indigenous to China and Japan, growing to the height of 12–15 feet. It was introduced from Japan by Sir Joseph Banks in 1796, and is commonly cultivated in gardens for the sake of its brilliant scarlet flowers produced in the early months of the year (February–May), and to a great extent before the expansion of the foliage buds.

In sunny sheltered situations it produces large green to golden-yellow inedible apple-like fruits which ripen in September and October.

### Description.

INFLORESCENCE: a few-flowered (2–8) raceme with terminal flower. Subtending bracts, the lowest of which are stipulate, the upper ones much reduced, as also 2 claw-like lateral prophylls are present in the case of the lateral flowers; but these usually fall off before the corolla expands. The terminal is similarly protected by 2–3 reduced leaf-members.

FLOWERS: Hermaphrodite, actinomorphic, pentamerous throughout.

RECEPTACLE: markedly crateriform, constituting the wall of the ovary cavity for 5 mm., and extending beyond it as a cup-like structure about 7 mm. wide and 4 mm. deep.

PERIANTH differentiated into :—

(1) CALYX of 5 free sepals, inserted on the rim of the receptacle-tube, broadly ovate, green, and slightly unequal in size (4–6 mm. long, by 3–4 mm. wide).

(2) COROLLA of 5 free petals, alternating with the sepals, bright rose-scarlet, with a short claw (4 mm.) and rounded lamina, 15–20 mm. long and broad; the colour varies to red, pink, or white in garden varieties.

ANDROECIUM: of typically 50 free stamens inserted in 5 alternating whorls of 10 down the inner slope of the receptacle-tube (rarely exactly 50, the range being 40–65).

*Filaments* slender, 10 mm. in the outer whorl to 8 mm. in the innermost.

*Anthers* introrse, freely movable on the pointed end of the filament, yellow 2 mm. long.

*Pollen* pale yellow. (To see the attachment of the stamens, remove them carefully and note the position of the scars on the sloping receptacular surface.)

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[1] *Cydonia,* the Latin form of the Greek Κυδωνία, the name of the common Quince, which is said to have been introduced into Greek cultivation from Cydon in Crete.

[2] *Pyrus,* founded as a genus by Tournefort (1700) and established by Linnaeus (1737). *Cydonia,* also a genus of Tournefort, regarded as unnecessary by Linnaeus. The plant was originally called *Pyrus japonica* by Thunberg (*Flor. Japon.,* 1784). C. H. Persoon restored the genus *Cydonia* in 1807, and it is retained for *Pyrus* forms with more than two ovules in each loculus (Focke, 1888).

[3] The Japanese name is given by Thunberg as *Atsuma Kaido* or *Buké*; in its native home the plant also flowers from February to April; it is a very variable form as shrub or tree, and the varieties in cultivation may possibly differ slightly from the type; the first figure in the *Bot. Mag.* of 1803, of a semi-double form, flowered at Vauxhall in August, is very distinct. Garden-varieties vary in the intensity of the rose-coloration, from dull red to dark crimson; white-flowered forms and semi-double varieties are also grown. The summer habit and flowers may be somewhat different from the spring condition.

Gynoecium of 5 antisepalous carpels.

*Ovary* syncarpous, within the basal portion of the receptacle-tube, 5-locular, with axile placentation and 2 rows of 10–14 horizontally extended anatropous ovules in each loculus.

*Styles* long, fused at base for 6–8 mm., and zoned with white hairs; free branches 12 mm., expanding upwards and crowned by the lobed stigmatic surfaces.

*Stigmatic lobes*, one large (2 mm.) descending the inner side, and 2 bifurcated lateral lobes, the branches of which are shortly coiled.

Nectary: below the attachment of the stamens, the sloping surface of the open receptacle-crater forms a well-marked reddish disc for nearly 2 mm., apparently roofing in the ovary. This secretes copiously, and as may be particularly well seen in older flowers, the honey fills the cup.

*Note.* In old flowers the stamens may increase to 12 mm., the innermost anthers do not always dehisce, and are frequently malformed, while they usually remain permanently bent on their filaments.

Flowers in which the whole or part of the stamens are not functional are frequent, and the gynoecium may be ruined in development by frosts, and thus appear wanting.

Cultivated varieties vary somewhat in the size of petals and stamens; the measurements refer to a fine garden form. (B. G. O.)

The best flowers are found late in May. The petals are now intensely scarlet; they open flat back as in the Apple, Pear and Quince, and the flowers reach 50 mm. in diameter; the petals being 25 mm. by 25, and the tips of the styles 27 mm. from the extreme base of the flower.

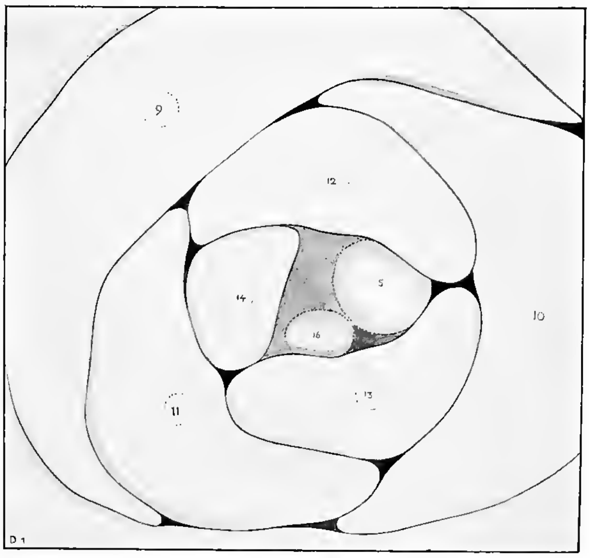


Fig. 1. *Cydonia japonica*, August bud. Apex of vegetative shoot showing the contact relations of a (2 + 3) system.

## Floral Diagram.

Inflorescence. Flowering-shoots are borne on branches which are two years old. A majority of the buds borne in the axils of the foliage-leaves of the first year become short spur-branches in the second year, and then develop flowers in the winter months (Dec., Jan.). These unfold in the succeeding spring. A flowering-shoot presents, above the brown winter bud-scales, 3–8 stipulate foliage-leaves arranged with normal spiral phyllotaxis, the apex of the leafy shoot showing contact-parastichies in the system (2 + 3) (Fig. 1); the uppermost leaves which may be very reduced in structure subtend lateral flowers. Internodes are not developed, and the terminal and lateral flowers together form a compact cluster of blossoms.

The inflorescence commonly consists of a terminal flower, which develops and opens first, surrounded by 5 lateral ones which thus constitute a complete cycle round the axis: the lateral flowers develop in normal ascending series, and should open in the same sequence, but this is very inconstant. The prophylls and reduced bracts (*b*) fall off as the buds enlarge, and are thus usually absent when the flowers are expanded.

Orientation of the flower is quite normal, the 5-parted calyx being quincuncial in development and prefloration; sepal 2 is approximately median-posterior, and usually readily distinguished by being larger than the adjacent members 4 and 5. The petals alternate with the sepals, and arise as a true pentamerous whorl. Prefloration is irregular, and owing to the presence of a broad lamina with a narrow 'claw' base, largely secondary, and in later growth petals may be even found overlapping sepals. Observation of opening buds shows that there is often an apparent tendency to median symmetry, the anterior members being wholly within or wholly without the others. The diagram only illustrates a common case. More exact data may be obtained by careful observation of a large number of buds, and the percentages compared with the mathematical chances of possible forms (cf. *Note on Prefloration*).

Beyond the petals, the construction system which in the whorled pentamerous corolla would appear to be symmetrical (5 + 5) becomes doubled, and thus the androecium is clearly constructed in a (10 + 10) system, of which 5–6 whorls are produced. In the first whorl 2 stamens arise right and left of the insertion of each petal, and succeeding whorls of 10 regularly alternate. Slight irregularities may occur, the last whorl being often imperfect or absent, or a few members of a 6th whorl may be formed. In large-flowered garden varieties further irregularities may be due to the presence of whorls with more than 10 members, and the number of members in the androecium reaches the higher limit; thus 6-parted corollas may be succeeded by a (12 + 12) construction in the androecium.

The five carpels have a definite position, and are antisepalous; the fact that the androecium whorls may be imperfect at the close of the series has no effect on the position of the gynoecium. A transverse section of the ovary shows 2 rows of ovules horizontally arranged raphe to raphe. The number varies from 10–15 in each row, and the total average is thus about 120.

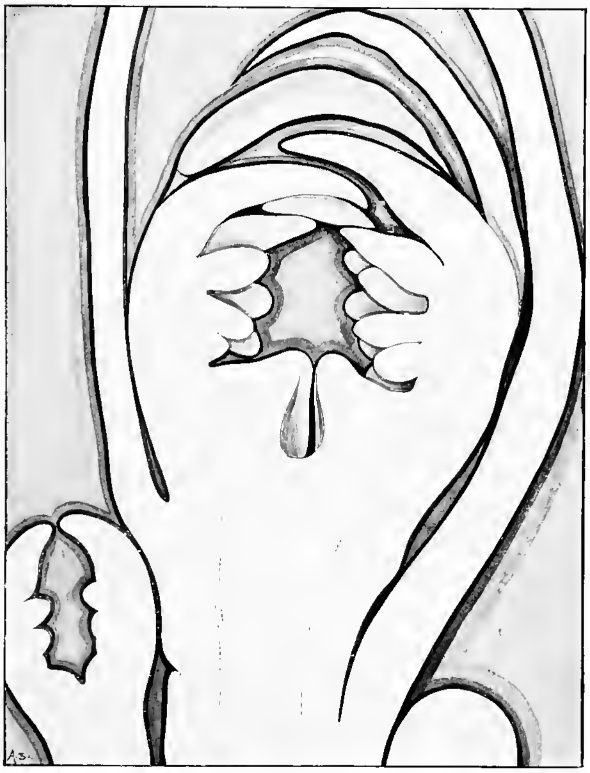


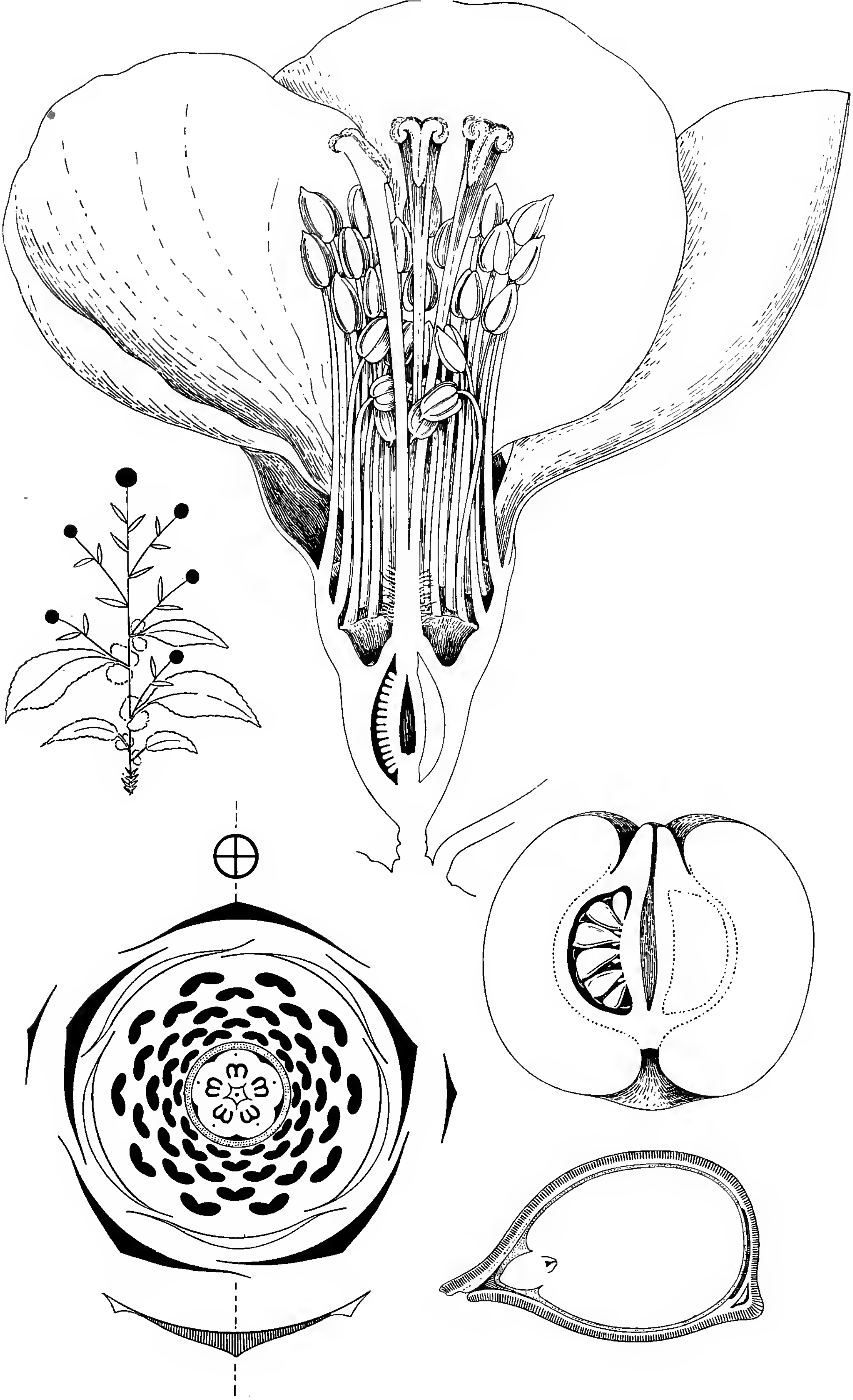
Fig. 2. *Cydonia japonica*, January bud. Development of flower; all the floral members laid down on a crateriform axis.

Fig. 3. *Cydonia japonica*, January 1. Differentiation of stamens and carpels.

The ovules are interesting for their comparatively late and rapid development in the first expanded flowers; section of ovaries at different periods of the expansion of the corolla showing various stages of development very clearly, owing to the horizontal direction of the ovules. Breaking flowers may thus show the first formation of the integuments.

*Variation* to 6 styles and 6 carpels, showing 6 more or less perfect loculi in the ovary, occur in garden forms; further irregularities are often shown in an anomalous production of style branches (7–8), even when 5 carpels remain constant in the ovary.

The *nectary* is indicated as a zone of secreting tissue between the androecium and the gynoecium, and is clearly a wholly receptacular gland (*disc*).



**Cydonia japonica:** Floral Diagram and Sectional Elevation of the Flower in the median plane; Scheme of Inflorescence; section of ripe Fruit to correspond with that of the flower, and section of the Seed in the plane of the raphe.

*Note* that the carpels fuse laterally in the ovary portion of the gynoecium but not in the axial region ; transverse section thus shows a fairly broad axial cavity.

## Sectional Elevation.

Section of a typical flower, taken in the approximately median plane passing through sepal 2, shows this sepal cut through on the left, the anterior petal on the right, while 27 stamens are included in the figure. The posterior carpel is also cut through on the left. The filaments of the stamens constitute an erect palisade around the nectary, and the unopened anthers of the innermost whorls of the androecium pack the approach from above. The styles are fused laterally to a stout shaft below, and a style-canal, which may be more or less blocked by fusions, leads to the open space between the ovary-portions of the carpels, at the base of which the apex of the floral axis may still be distinguished. The chief interest centres in the formation of the receptacle region, and the constitution of the 'epigynous' growth-form.

The axis presents a strongly marked *crater* formation which in the adult flower is distinctly vase-shaped, the sepals being attached on the extreme edge, and the petals just inside them; the androecium whorls remain in practically close contact on the inner descending slope, and the 5 carpels are attached by long sloping bases which constitute the 'outer-wall' of the ovary cavities. The loculi of the carpels become slightly involved in the growth of the receptacle, and thus appear slightly sunk beneath the apex of the floral-shoot, but there is no very decided intercalation of a new zone of growth at this point, so whether the flower may be termed *epigynous* or not remains optional. On the other hand, a short zone of growth is intercalated between the androecium and the gynoecium, and this increases the length of the receptacle-cup by 3–4 mm.; it may therefore be included under the term *Zona Perigyna*, and the relation of these zones of secondary growth is thus seen to be essentially similar to the construction found in *Ribes*, though on a somewhat less differentiated scale.

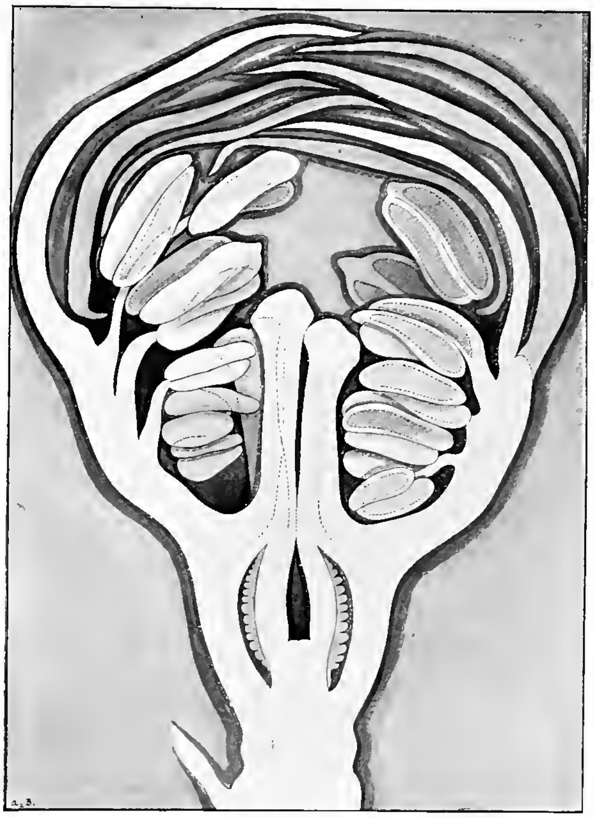


FIG. 4. *Cydonia japonica*, March 1. Development of flower, showing differentiations of zones of special growth.

## Development.

The very simple construction may be readily followed in developmental stages. Flower-buds collected during the first weeks of January, when cut in longitudinal section, show all the essential features; and since the terminal flower develops more rapidly than the next below it, several stages may be seen in sections of one perennating-bud (Fig. 2).

The apex of the axis forms a well-marked crater before the androecium is fully in evidence; the primordia of the stamens appear on the descending slope, and the 5 carpels arise independently at the base, the carpels being larger members than the stamens immediately preceding them.

A well-marked cup-shaped receptacle is thus produced, the stamens being situated above the carpels, but in close contact with them, while the outer perianth members (sepals) overarch and protect the central cavity of the flower-bud (Fig. 2).

As development proceeds the carpels erect at right-angles to the crater surface and their edges become infolded: as they come into contact in the middle line, they erect in the central cavity of the flower and fuse by their adjacent sides, an axial space over the apex of the shoot axis still remaining unenclosed (Figs. 2, 3). The anthers commence differentiation into sporangial lobes, and a short stalk portion (filament) begins to appear; the petals are still small and rudimentary, though the sepals are well developed and overlap as a protecting cover to the flower (Fig. 3). Differentiation of the regions of the flower now rapidly proceeds throughout all the structure.

The basal portion of the receptacle-cup extends as the carpels grow sufficiently to block the axial space, and the cavities of the loculi are produced along a sloping base which finally appears as the outer wall of the 'inferior' ovary: the stylar elongations of the carpel-tips fuse where the carpels are brought into contact in the middle line, and thus an axial space is left below, while the free stylar portions elongate into the hollow cavity of the bud, and produce highly-specialized stigmatic lobes. The stamens also elongate freely into the bud cavity, the anthers and developing filaments fitting into and filling the space available under the overarching petals and sepals. The ovules also commence as primordia arranged in rows along the carpel-edges (sutures) (Fig. 4). In such a bud, the commencement of the *Zona Perigyna* is also indicated as an extending region between the lowest stamens and the point at which the stylar fusion takes place; and the construction as a whole is already practically that of the adult flower; the relatively enormous development of the petal laminae and the great extension of filaments and styles being only added during the 'unfolding' of the buds.

### Special Mechanism.

So far as the development of this simple crater-type of flower is concerned, the construction is clearly self-pollinating, as the anthers would normally shed directly on to the stigmatic tips of the carpels, if growth were uniform throughout the entire bud. Modifications of the construction may therefore be considered under the following heads:—

(1) The floral members not only grow at unequal rates, but new growth-regions are put in; the *Zona Perigyna* functioning as a secreting layer, the surface cells of which are colourless, the subjacent ones pigmented.

(2) The sepals, at first a protective cycle, remain small and are unimportant in the adult flower.

(3) The petals, at first rudimentary members with a slow rate of growth, become greatly hastened later, and assume a red pigmentation in their epidermal layers. The increase in area is confined to a broadly circular lamina-region, while the basal attachment region remains small and tends to differentiate a short stalk-portion ('claw'): as the laminae extend they come into new and irregular contact-relations which are responsible for the different methods of 'prefloration'.

(4) The filaments of the stamens are intercalated after the full formation of anther-lobes and pollen.

(5) The stigmatic surfaces are carried up by still longer stylar growths.

(6) And it is clear that the last is the most important feature of the mechanism, since self-pollination (*autogamy*) in absence of insect visits thus becomes eliminated, and the stigmatic surfaces are carried well above the anthers before the bud expands.

The flower is thus differentiated as a non-pollinating mechanism, which requires the assistance of an external agency, and while *wind* is not suitable, since the pollen is moist, and wind is injurious to these spring blossoms, it is clear that insects are invited, and that—

(1) the pure concentrated coloration of the petal surfaces,

(2) the glandular region of the receptacle,

(3) and the correlated growth-adjustments of filaments and styles must be regarded as modifications to this end.

The construction-mechanism therefore suggests that the flower is definitely adapted for the visits of fairly large insects which may take the freely exposed pollen or concealed honey; and further observation of the protective investment of a palisade series of filaments around the secreting surface, suggests that fairly high-grade insects with long proboscides are the chief pollinating agents, with whose structure and habits the development of this flower has become co-ordinated.

(For similar phenomena of intercalation of Zones of Epigyny and Perigyny, correlated growths of filaments and style region, as also special localization of a pure pigment-derivative cf. *Ribes sanguineum* which has, however, an entirely different primary construction.)

## Pollination.

The flower-buds enlarge during January and February, and by the beginning of February the first flowers may be ready to unfold. The optimum period depends on warm weather—March and April. Stray flowers last till June, and solitary blossoms may occur at any time during the cool autumn months (October, November). The blossoms are very conspicuous owing to the brilliant rose-scarlet coloration of the large petals with contrasting yellow anthers and styles, and conspicuousness is greatly increased (1) by the absence of foliage-leaves, due to the non-development of assimilating members on the spur-shoots, (2) the contemporaneous opening of members of the same inflorescence, and of the great majority of shoots.

The plants present a blaze of colour when few other shrubs are in bloom and may be distinguished at a distance of 100–200 yards.

As the flowers become older and exposed to light, as also with a warmer temperature, the rose-coloration becomes more intense on the petals and spreads to other members; the secreting surface becomes deep-red, while the filaments of the stamens and the exposed portions of the styles may also be intensely coloured. The stigmatic surfaces and anthers, however, do not change, the pigment thus only appearing in the intercalated zones of growth as these regions become old. (For similar extension of pigmentation, cf. *Ribes*.) Similarly summer and autumn blossoms are deep-crimson, while the first February blooms on the same plant may be only a bright rose-pink. The colour is due to anthocyan-derivatives, but it may be noted that the clear effect produced in the petals is much more brilliant than the ordinary crimson pigmentation seen in the filaments and styles, and that the same pigment occurs over the chlorophyll-containing tissues of the sepals and flower-stalks.[1] In sections also, the extent of the glandular secreting layer of the nectary is readily traced owing to the fact that these cells are not pigmented, although the subjacent tissue may be. The primary significance of such a pigment may still be doubtful, but there can be little doubt that the presence of such a body attains a secondary significance from the standpoint of insect-attraction, though there is again no reason to believe that any other bright pigment, if it had been present, might not have been equally useful for this purpose, or that a white flower would not be almost as efficient. In the case of early spring flowers, however, it is important to note that white flowers are of little value against a background of snow, and pigmented forms may in such environment have an advantage, apart from any primary use of the pigment in the economy of the tissues.

As the corolla expands, the receptive stigmatic lobes project beyond the stamens and the flower thus structurally inclines to protogyny, since in cool moist weather the anthers do not immediately dehisce on exposure to the air. The stigmas are very susceptible to the action of cold dry winds, and they often wither before the anthers fully dehisce; the flower may thus become definitely protogynous under conditions of environment (cf. *Helleborus*

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[1] In the opening flower the rose-red anthocyan derivative is localized in the epidermal cells of both surfaces of the petals, and to a slight extent of the nectary tissue; while on the outer surfaces of the receptacle-tube and the sepals, where these are exposed to light, a deep-crimson coloration masks the chlorophyll of the subjacent tissue. As the later flowers are aggregated in close clusters, the posterior side (sepal 2) against the axis is thus often conspicuously pale-green when the anterior side is blazed with crimson.

*niger*); under more favourable conditions, and in the case of protected flowers, the stigmatic surfaces remain receptive and viscid even after the anthers have shed and become withered.

The stamens dehisce centripetally, that is to say in the normal sequence of development, the filaments of the inner whorls straightening out in turn; though the innermost remain more or less inclined against the styles, thus blocking direct access to the honey. The outer filaments again are sufficiently stout and closely packed to prevent lateral access.

The flowers offer abundant freely-exposed pollen to pollen-collecting bees and flies, and the secretion of honey is also abundant under favourable climatic conditions (March, April); the secreting surface of the earlier blossoms is often found to be quite dry. The honey is concealed from sight, and the only path to it lies along the stylar branches, and it is thus only accessible to insects with proboscides longer than the shorter central stamens, the anthers of which are 10–12 mm. from the honey. Hive-bees (6 mm.) are thus excluded[1]; they take pollen with avidity, and in so doing effectually pollinate the flowers, but they are useless when they alight on the petals and try to probe the palisade of filaments. The flowers are evidently more adapted for Humble-bees with long proboscides, and the plants are again abundantly visited by all such bees which may be out in the spring months. The most successful visitor is *Anthophora pilipes*, with proboscis 18–20 mm. in length. As these bees lightly pause on the tassel of essential organs, the slender proboscis is guided along the curve of the style-branches to the nectary-cup, a distance of 20 mm.; a zone of hairs on the main style-shaft forms a delicate investing screen over the nectary, and although this presents no obstacle to an inserted proboscis, it may serve to keep out small useless insects, while it also prevents desiccation of the secreting surface. These hairs are often absent in early spring flowers, but are usually well differentiated when the blossoms reach their optimum development (April). The exact significance of a zone of hairs in the throat of a tubular floral structure is somewhat vague, but it is clear that so many functions may be served by such a production that it is difficult to establish any one factor as being essentially of primary importance (cf. *Viola*, *Vinca*).

Individual flowers persist for 10–14 days; a single clustered inflorescence may exhibit bloom for 3–4 weeks. Self-pollination (autogamy) in absence of insect visits is eliminated by the elevated position of the styles, while even in obliquely-placed flowers pollen does not readily fall from the anthers. The flowers are, however, freely fertile to their own pollen, and self-pollination is largely effected by visiting insects; though here again it may be noted that the best worker (*Anthophora*) by accurately pointing its proboscis along the stylar curve will also be the most efficient agent of cross-pollination from the standpoint of the flower; on the other hand, in the case of isolated plants, the crossing will be only effected between blossoms of the same individual. The flowers are so abundantly visited by bees that it appears very unlikely that any blossom will escape pollination, and as a rule enormous quantities of young fruits commence development, though few may be ultimately ripened. Unfertilized flowers wither and fall away. In the case of starved plants (readily observed in the case of freshly transplanted specimens) the last growth zones may be injuriously affected, and thus imperfectly co-ordinated, the styles elongating insufficiently to take the stigmatic surfaces beyond the anthers. Self-pollination (autogamy) thus becomes possible, and the floral mechanism deteriorates to a condition which recalls that of the Apple.

## Variations and Monstrosities.

These include only the semi-double forms in cultivation, in which additional petal-segments are produced at the expense of the outer members of the androecium,[2] and irregularities in the construction-mechanism in which hexamerous conditions may be more or less perfectly maintained. Tetramery has not yet been observed. As previously

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[1] Instances of 'boring' are occasionally met with, large holes being bitten right through the wall of the receptacle-tube. As few insects are out at this time of year, this is probably the work of the Hive-bee.

[2] Such florist's blossoms show considerable increase in bulk, and resemble small roses, being 50–60 mm. across.

indicated, anomalous branching of the carpels may give a number of functional, perfectly formed, style-branches in excess of the number of loculi in the ovary.

Flowers are often found with the whole of the gynoecium missing; such a variation is, however, possibly referable to injurious climatic action.

### Fruit and Seed.

After fertilization the flower continues its growth; the ovary enlarges considerably (10 mm. by 6); the filaments go on increasing to 12 mm., and the style-branches elongate considerably (20 mm.) The petals are soon shed, and the sepals, filaments, and styles all tend to turn crimson. The enlargement of the ovary continues, and affects more particularly the base of the style-shaft and the sides of the receptacle-cup. Ultimately, when about 20 mm. by 15, abscission of the whole of these members takes place by a line of separation below the nectary-region. The fruit thus assumes a characteristic appearance, the 'eye' being filled by a mamilla-like protuberance, which represents an enlargement of the style-base, and no trace of any of the floral members remains (June 1).

The round apple-like fruits reach their full size in September, and average 50 mm. by 55 mm. in diameter. They are hard and sour, but become fragrant, golden-yellow, and covered with a waxy film when ripe in October. In warm sheltered situations, when the weather during the optimum flowering-period has been favourable, the plants may produce large crops of fruit.[1] In the majority of years relatively few fruits are ripened, and young stages are shed in great abundance; as in the case of the allied Apple-forms, and other spring-flowering shrubs in which fruit-development proceeds simultaneously with the production of the new season's vegetative shoots, this may be due to competition for the water supply, and the young fruits are shed under desiccation. The fruits are quite inedible when ripe, and do not become more agreeable by being kept.[2]

Asymmetrical forms are produced if the loculi are not all pollinated, and a considerable proportion of the ovules may set seed; as many as 20 may be found in a single loculus, and 75 in the entire fruit.

The bulk of the ovary-structure, including the broad septa, remains parenchymatous; only the lining layers of each loculus are converted into a thin horny sheet of non-lignified fibrous cells, which probably represents a retention of the fibrous lining layer which in allied forms (cf. *Spiraea*, *Lathyrus*) becomes subsequently utilized as a dehiscence-mechanism. In addition to this smooth lining investment, a more or less continuous zone of lignified stone-cells is differentiated externally to the loculi and forms a well-marked 'core' to the fruit, and thus represents a stage in the complete sclerosis of the inner part of the ovary-wall, which in some allied genera gives rise to a 'stone-fruit' (cf. *Crataegus*).

The seeds are ovoid (8 mm. by 5), and slightly and irregularly angular by mutual pressures to 3 mm. in thickness: the micropyle and hilum are situated at the pointed end, a distinct raphe along one straight side or edge of the seed terminates in a chalazal knob.

Median section in the plane of the raphe shows a thin testa, composed of a uniform band of brown non-lignified fibrous cells; the peripheral layer has a glistening cellulose thickening of the outer wall, almost obliterating the cavity, and this on being wetted tends to become somewhat mucilaginous.

A small amount of endosperm, the thin-walled cells of which contain fat-granules and proteid matter, forms a thin film of 2–3 layers around the large embryo, the two cotyledons of which constitute the main bulk of the seed, and are flattened out in the plane of compression; these also contain abundant food-reserves of fat and proteid. The fibrous layers of the testa-wall give no reaction with phloroglucin, though the mucilaginous layer often gives a faint pink colour; a well-marked chalazal patch of brown tannin-containing cells is also

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[1] As much as 10 gallons of fruit were produced on one wall-shrub in a favourable season (B. G. O., 1904).

[2] Attempts have been made to utilize the fruit for preserves. The resultant product, however, is no better than may be obtained from very inferior crab-apples.

present (nucellar tissue). *Note* that the embryo contains the great bulk of its *food-reserves*, abundant fat and proteid being stored in the cotyledons; it is *protected* by the testa layers, and doubtfully *dispersed* by the aid of animals which devour the decaying fruits. The fruits are non-dehiscent, and fall off on to the ground at the base of the plant at the time of leaf-fall (October, November). To what extent any definite modification towards dispersal by animal agency can be traced in the production of such a fruit-mass is very vague.[1] The parenchymatous development of the ovary-structures, which subserves the function of a storage reservoir for the young fruit, may be regarded as quite as much a 'xerophytic' adaptation as the production of the investing zone of stone-cells around the young seeds; similarly, the yellow coloration of the fruit is nothing more than the colour change in the chlorophyll also noticed in decaying foliage leaves. Comparison with the case of the Apple suggests that such animals as pigs may take the decaying fruits on the ground, and thus disperse the seeds; but although the basis of such a dispersal-method may be present, there is no evidence that it is in any way intentional. *Note* that, as in *Ribes*, the ovary of such a crateriform type has by construction no sutures externally, and could therefore only dehisce by new arrangements; and that when such an ovary remains without further differentiation it readily passes on into a succulent (i. e. parenchymatous) indehiscent fruit-stage.

## Comparison of allied types.

### I. **Cydonia vulgaris,**[2] Pers. (**Pyrus Cydonia,**[3] L.). The Common Quince.

A deciduous tree with straggling branches, growing 15–20 feet high, indigenous throughout the whole of South Europe to the Caucasus and Japan; doubtfully indigenous to Great Britain, but being extensively cultivated by the Romans was probably introduced during the Roman occupation. Gerard (1597) describes it as cultivated in gardens and orchards, and often planted in hedges, &c. Still grown for the sake of its large pear-shaped golden-yellow fruits, used for making preserves (*Cotiniate*, *Marmalade*[4]) and Quince-wine. Flowering spurs are developed on shoots in the second year, and produce usually solitary terminal flowers which are relatively large and conspicuous. The flowers expand in May, after the foliage leaves are developed, and the fruits ripen in October and are shed with the fall of the leaves.

The sepals are large, green, and recurved, and the large white or pinkish petals (35 mm. by 25) give the opening flower a globular appearance; at a later stage the petals open out flat, and the flowers are 50 mm. across. The filaments project and turn lilac. The floral mechanism resembles that of *C. japonica*, but is much simpler, both from the standpoint

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[1] Examination of the half-grown green fruits, 25 mm. in diameter, exposed freely to the intense heat of the July sun, on plants trained against a stone wall, suggests most clearly the extreme importance of protection for the developing seeds and the delicate endosperm and embryo-tissues from desiccation. The ovary-wall constitutes a succulent parenchymatous mass, in which a zone of irregular patches of lignified stone-cells occurs just below the epidermis and subjacent assimilating layers, while the inner zone of stone-cells is fully formed and lignified as well. The testa is thick and succulent, and the endosperm consists mainly of aqueous-tissue enclosed in a thick cuticle. Note that with the special development of stone-cell masses the lining layer of the loculi does not lignify. The succulent tissue is very acid. Note also that the mucilaginous testa-layer contains starch, but has not yet developed its outer wall: in a larger fruit (35 mm.), taken at the same time (mid-July), the wall is seen to be thickening. The peculiar characters of the fruit are thus produced at an early date in its development, and the 'ripening' process adds nothing to its peculiarities beyond the decadent colour-change in the outer assimilating layers.

[2] Μηλέα Κυδωνία of the Greeks, from Cydon in Crete, where it was probably cultivated and thence introduced into Greek horticulture (possibly 'golden apples' of the myth). *Cydonia vulgaris*, the name given by Christian Hendrik Persoon (1807).

[3] *Pirus* of Pliny: a good botanical figure of the whole plant, including flowers and fruit, is given by Fuchs (1542) under the name *Cotonea Malus*. *Cydonia*, founded as a genus by Tournefort (1700), hence retains a capital letter: *Pyrus*, the Linnaean genus (1737), continued from Tournefort and always so written; if the Linnaean nomenclature is taken as a standard quantity there is no advantage in returning to the spelling *Pirus* (Focke, 1888). The floral structure being more distinct from that of *Cydonia japonica* than it is from that of the Apple, the generic value of *Cydonia* itself is doubtful (cf. *Chaenomeles*, Lindley).

[4] From *Marmello*, Spanish name for the Quince.

of construction and that of special adaptations. Thus the stamens reduce to the first two whorls of 10, as a complete cycle of 20 members, the filaments being of 3 different lengths, and the styles do not elongate sufficiently to carry the stigmatic tips beyond the anthers of the innermost and shortest stamens; the stigmatic lobes are much less elaborate and would hardly be noticed. The nectary (Zona Perigyna) is 3–4 mm. deep, and the loculi of the ovary contain only few ovules (3–4 pairs).

Pollination may be effected by insect agency, the general visitors being bees (Hive-bee and various humble-bees); access to the nectary is scarcely limited by the filaments which constitute a single palisade around the approach to the honey, though the general method of visiting the flower is similar to that found in the case of *C. japonica*, and more clearly understood after a consideration of that type. The flower otherwise remains a self-pollinating mechanism, though a first chance may be given to cross-pollination as the corolla expands before the stamens shed. The large pyriform fruits possess a normal 'eye' of the Apple type, and the large sepals persist when the fruit is ripe. The specialization of *C. japonica* is wanting in this respect as well. When young the fruits are covered with a velvety coat of woolly hairs, and an enormous amount of lignified stone-cell tissue is produced in irregular masses around the ovary-region (cf. Pear); young fruits (July) may thus consist more than half of woody tissue.

The fruits ripen in October, and are the size of large pears; the rounder 'apple' form however occurs as a variation, and may characterize the whole tree: they turn golden yellow, possess a peculiar strong odour, and a waxy film gives them a greasy character when handled. They are hard and bitter, and remain so on keeping (November). The loculi are bounded by oblique fibrous-cells which constitute the 'horny layer', and the inner part of the fruit mass is full of hard groups of stone cells. The seeds, in 2 rows in each loculus, overlap each other (9 mm. by 5), and are very similar to those of *C. japonica*. They present a special feature not noticed in allied types, in that the outer layer of the testa is markedly mucilaginous, as a columnar layer of cells with enormously developed outer walls, hyaline and stratified, the peripheral ends of which on being wetted disintegrate to a mass of mucilage (pink with Schulze's sol.) to such an extent that the seeds appear embedded in a mass of colourless mucilage. The endosperm is further protected by a thick cuticularized wall (i. e. of macrospore). The fruits are shed at the period of leaf-fall, and rapidly rot on the ground beneath the tree, the seeds being set free by decay of the fruit-mass. The significance of this special layer of mucilage-cells, which is wanting in the Apple and Pear, and only very feebly indicated in *C. japonica*, is still doubtful: it cannot be intended to keep the seeds moist, since it normally decays at the same time as the succulent fruit-tissues; it is therefore probably to be correlated with the increased necessity for protection of the developing seeds; and taken into connexion with the thick cuticular membrane around the endosperm, may be regarded as the expression in the seed-coat itself of those xerophytic adaptations which in the fruit-wall are indicated by woody stone-cell masses, aqueous tissue, and external covering of woolly hairs. On the other hand, it is interesting to note the almost complete suppression of anthocyan-compounds in *C. vulgaris*, the petals alone presenting a faint pink coloration, and the stamen-filaments turning slightly violet as they become old.

### II. Pyrus Malus.[1] *The Apple.*

A deciduous tree with open branches, growing 20–30 or in extreme cases 40 ft. high, indigenous to Great Britain, rare in Ireland, and extending over the whole of Europe and Central and Western Asia, preferring good ground and abundance of moisture.

The wild form, Crab or Wilding, represents the original stock; cultivated varieties were introduced by the Romans: the fruits of the wild stock are relatively small and extremely sour (*Verjuice*).

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[1] *Pyrus*, the Linnaean genus 1737 = *Pirus* of Pliny. *Malus*, as specific name established by Linnaeus (1753); since used for a genus by Tournefort (1700), it retains the capital letter.

Flowering spurs are borne on woody shoots one year old, and the inflorescence resembles that of *Cydonia japonica.*

Individual flowers present the reduced characters of *Cydonia vulgaris*, the petals, 20 mm. by 15, are white, coloured crimson externally where exposed to light in the expanding buds: the stamens are 20 in number, and the carpels produce only one pair of ovules each, these being anatropous with the micropyle directed downwards. The pollination-mechanism is identical with that of the Quince; cross-pollination may be effected by bees (Hive-bee, humble bees, &c.), but the flower remains in a self-pollinating condition. The apex of the floral axis is plainly shown between the bases of the carpels, and as the flower withers the petals are shed, but the remains of the closed 5 sepals, stamens, and styles persist as in the Quince to form the 'eye' at the apex of the succulent fruit.

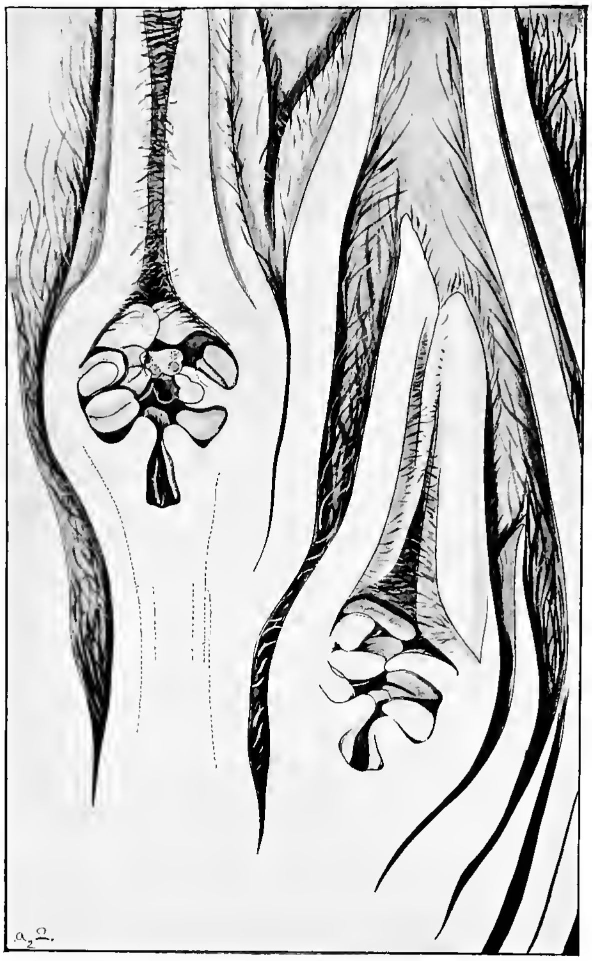

Fig. 5. *Pyrus Malus*, March 1. Developing flower-buds, showing crater-formation and origin of the carpels.

Cross section of the fruit shows that the 5 loculi of the ovary are again superposed to the sepals, and an axial cavity persists as in the other types. The ripe fruit, also matured in October, as the flowers are produced in May, differs, however, in possessing no stone-cells; each loculus of the ovary possesses a horny lining-layer of lignified oblique fibrous-cells,[1] and the bulk of the fruit consists of a parenchymatous development of the receptacle-crater on which the carpels are very obliquely inserted: 10 vascular bundles corresponding to the sepals and petals are very obvious in transverse section. Note that the loculi only produce 2 seeds each, and that the Apple is so far the most reduced member of the Quince series; and that this reduction is not correlated with increased specialization, since *Cydonia japonica* not only retains the fullest androecium and many-ovuled carpels, as also elaborated stigmatic surfaces, but alone presents a special mechanism to promote cross-pollination and more or less eliminate self-pollination (autogamy). Also that if the generic rank of *Cydonia* and *Pyrus* be in dispute, the differences between *Cydonia japonica* and *Cydonia vulgaris* are much more essential from the standpoint of floral-construction and mechanism than those between the latter and *Pyrus Malus.*

As in all these allied forms, the flowers commence to be developed during the Autumn months; and buds cut when the foliage leaves are being shed (October) will show all the floral members already laid down. These buds perennate over the winter months, and will be found but little advanced in early spring. Buds of the Apple taken about the 1st of March show the well-marked crateriform construction, and the independent origin and oblique insertion of the carpels on the inner wall of the crater (Fig. 5). In a somewhat older bud (April 12)

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[1] The fact that this parenchymatous secondary growth in the receptacle may be sometimes initiated in cultivated forms, independently of any fertilization of the ovules, gives rise to the very general accounts of 'coreless-apples'. In such cases there is no lignification in the lining-layer of the loculi, and the cavities become obliterated; the general result being closely comparable with that found in the cultivated Banana.

the floral-mechanism is receiving its final adjustments, while the ovary has become syncarpous by lateral, but not axial, fusion of the carpels, and already presents a good approximation to the construction of the mature fruit-form, the sides of the fruit being clearly formed by the oblique carpel-bases.

Observation of young green fruits, an inch in diameter, taken during the hottest part of July, confirms the impression gained from *Cydonia* that the protection of the ovary is the point of fundamental importance. The whole of the ovary-wall is acid and succulent, and the testa presents a broad zone of tannin-containing cells. The lignified tissue is, as in the mature fruit, restricted to a layer of fibrous-cells lining the loculi. In the more xerophytic Siberian Crab this region becomes 3 layers thick. The cells of the epidermis produce red anthocyan-compounds where exposed to light, this being exaggerated in many cultivated forms. The brilliant scarlet of the Mountain Ash is only found in the Siberian Crab.

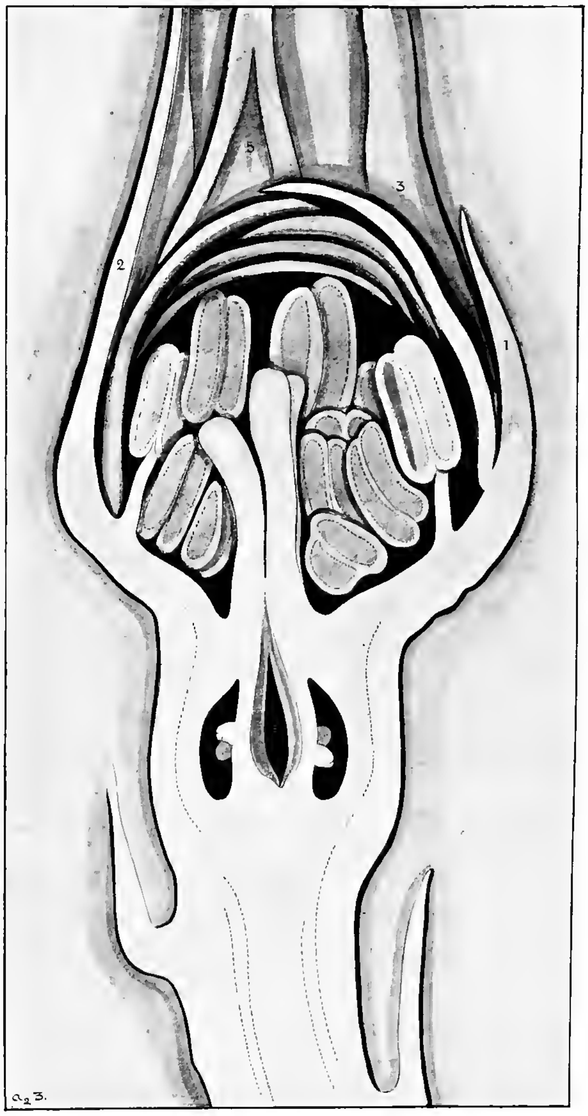

Fig. 6. *Pyrus Malus*, April 12. Development of flower showing intercalation of special zones of growth.

## III. **Pyrus communis,** L. *The Pear.*

Similarly a deciduous tree, indigenous to Great Britain, the whole of Europe, and Central Asia to Japan. Found growing on poor dry soils, as a tall upright tree 20 ft. or even 50 ft. high, with dense branch-system and spiny shoots in the wild type; clearly therefore much more xerophytic in habit than the Apple. Also cultivated in an immense number of varieties for the sake of its fruits which in the wild state are very small and quite inedible. It also flowers a week or two earlier in the spring (Mid-April to early May), and ripens its fruit in October and November, the fruits being shed at the time of leaf-fall.

In inflorescence-structure, flowering spurs on the preceding year's growth, as also size and general character of the flowers, the Pear closely agrees with the Apple; it presents a similar 20-stamened, self-pollinating type, there is, however, only a trace of crimson coloration in the petals (buds), and usually a larger number of flowers in an inflorescence. All structural features are so clearly marked that it presents the best example of the series. The inflorescence-shoots, flowering-spurs on the wood of the previous year, are well-developed, bearing a cycle of (5) foliage leaves below, and a cycle of reduced members which subtend large flowers on long stalks, and ending in a terminal (T) blossom. Slender filamentous stipular-lobes, prophylls, &c., are shed as the buds expand, and the inflorescence thus presents a terminal flower surrounded by a cycle 5 (often 6 or more) lateral flowers; the T flower opens first and the T′ in the ascending order of their development, though the lower T′ may often expand as soon as the T. The flowers are an inch across (cultivated forms), the sepals woolly on the inner face; the pure white petals (only pink externally in the bud stage) constitute a cup-shaped blossom, and afford an excellent contrast to the crimson-purple anthers; the anthocyan-pigment thus reappearing in the epidermis of the anther-lobes, and eliminated elsewhere (cf. Hawthorn). The flowers further resemble those of *Crataegus* in their faint scent. The 20 stamens are widely spaced as a single palisade-fringe around the nectary, and the order of their insertion is quite obvious. The nectary appears in surface view as a green saucer-shaped disc, 4 mm. in diameter; but section shows that it is 2 mm. deeper, and here so pressed against the styles that these, although wholly free, are held in close apposition and thus appear as if fused. There is no common style-shaft, or fringe of hairs, and the stigmatic surfaces are not definitely lobed but covered with large papillae. In these respects the Pear represents a type of structure quite different from that of both the Quince and the Apple, and externally is in many respects curiously like the *Crataegus* type. The carpels, though fused laterally, are wholly free in the axial line, and the loculi each contain 2 large anatropous ovules. In mild weather the anthers do not dehisce on the first day the corolla is expanded, and they may remain closed for several days in wet weather; a first chance is thus offered for cross-pollination.

As presenting a feature of more pronounced reduction of the *Cydonia* type, it is interesting to note that the carpels frequently reduce to four only.[1] The fruit resembles the Quince in size and form in cultivated varieties, but that of wild stock is very small and almost solid, owing to the enormous development of groups of lignified stone-cells around the loculi of the ovary. In cultivated forms the same stone-cells are produced, but their presence is rendered less obvious owing to the still greater development of succulent parenchymatous tissue. The shape of the fruit, which resembles that of the Quince rather than the rounded form of that of the Apple and *Cydonia japonica*, shows that the stimulus of secondary growth passes farther down the floral axis; the 'core' of the fruit being no longer in the centre, but much nearer the 'eye' of the fruit. The horny lining-layer of the loculi (= core) is also present, but the cells are not lignified.

Fruits fall from the tree at the same time as the foliage, with the first early frosts (October), and rapidly rot as they lie among the decaying leaves; in this position they may possibly be devoured by such animals as swine. The seeds are identical in structure with those of the Apple, and there is thus no special adaptation for distant dispersal.[2]

### IV. **Pyrus Aucuparia,**[3] Gaertn. *The Mountain Ash* or *Rowan.*[4]

A low tree with deciduous pinnate leaves, growing 20–30 ft. high, indigenous to Great Britain and all parts of Europe and N. Asia, preferring a moist cool climate and good soil. In this country it reaches the greatest perfection in the Western Highlands of Scotland; it is also largely cultivated as an ornamental tree, and was well known to classical writers[3]; the berries are eaten as food in some parts of Europe; while the fact that they have been used from time immemorial, wherever the plant grows, to bait traps for birds accounts for its being known as the Fowler's Service Tree, or Bird Service Tree.[5]

This plant is of interest in that while it presents still further reduction-phases of the flower, it retains a compound panicle which represents a fuller and therefore more primitive condition of the inflorescence-system. Flowering shoots are borne in the axils of the leaves of the shoots of the preceding season, and foliage and flowers are produced in May.

The *Inflorescence* is a compound panicle with corymbose aggregation, ramifying to the third and fourth degree: normal bracts and prophylls are present, but these fall off as the

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[1] Similar reduction to 4 carpels is general in the case of the small fruits of the Siberian Crab (*Malus prunifolia*).

[2] The Wild Pear = *Pyrus sylvestris* of old writers, the Choke Peare of Parkinson (1640); Gerard (1597) notes that the fruits are bitter and sometimes have a choking taste and *even hogs will not eat them.*

[3] *Fraxinus montana* of Theophrastus, *Fraxinus aucuparia* (Gesner, 1541), *Sorbus aucuparia* (Clusius, 1576), *Aucuparia* being the Latin name. Linnaeus classified the plant as a *Sorbus*; the present title dates to Gaertner (1844).

[4] The Wild Ash, Quick Beame or Quicken (Gerard, 1597).

[5] French, Sorbier des Oiseleurs; German, Vogel Beerbaum.

inflorescence attains the adult condition, and the whole mass takes on a white colour by the reduction of the chlorophyll-containing members to a minimum.

The flowers are small, only 12 mm. in diameter, and the petals white; the inflorescence closely resembling that of the Hawthorn. In structure and mechanism the individual flowers essentially agree with those of the Apple and Quince, the same 20 stamens with filaments of three lengths (successively 5, 4, and 3 mm. long) being present; but further reduction is found in the gynoecium, the number of carpels commonly falling to 4 and 3.

Individual carpels still produce a symmetrically placed pair of ovules, i. e. one from each edge of the suture, the anatropous ovules having the micropyle directed downwards; but as a rule only *one* develops as a seed in each loculus. The carpels fuse laterally as in preceding types, but the styles remain wholly free, and the central canal is open to the apex of the axis.

The fruits ripen in August and September, as spherical bright-scarlet berries (12–13 mm. by 10), and the seeds are undoubtedly largely dispersed by the agency of birds (Thrushes, Redwings, Fieldfares): Thrushes greedily devour the berries in large quantities, the berries being bolted whole. They are sharply acid in flavour, and remarkably juicy as compared with other *Pyrus*-types: as in other very succulent fruits the ripening process, indicated by the production of the scarlet pigment, is also associated with a rapid increase in the volume of the fruit: the green unripe berries being comparatively small and hard.

The seeds resemble in structure those of the Apple and Pear, but are much smaller; the outer layer of the testa is not mucilaginously thickened, and the endosperm is relatively more abundant. The fibrous non-lignified lining-layer of each loculus of the fruit is very thin, but lignified stone-cells occur at the free edges of the carpels adjacent to the central cavity, and further sclerosis takes place at the periphery of the loculi in the ovary-wall. In the ripe fruit the seeds readily separate from the pulp, covered by the sclerosed layers which constitute a nearly continuous investment, and each retains the withered style of the carpel concerned.

The berries in form and general appearance may be regarded as the typical fruit adapted for dispersal by the agency of birds in this country; and special modifications to such an end may probably be traced in:—

(1) the production of an intense-scarlet pigment in the epidermal cells of the fruit, and to a lesser extent in the pulp: the pigment being undoubtedly the same which occurs in the fruit of the Apple, but here it is localized and present in concentrated form, when the berries attain a condition of 'ripeness', which does not obtain either in the flower or in the vegetative shoots (cf. *Ribes rubrum*). The berries in the aggregated inflorescence-clusters are thus rendered remarkably conspicuous during August and September, and they are taken by Thrushes, &c., as soon as they commence to turn colour (cf. *Viscum*) (July 22).

(2) The almost complete protection afforded to the individual seeds by the secondary sclerosis of the ovary-wall around each loculus, as an advance on the irregular production of groups of stone-cells in the other types. As in the general case, the primary function of such sclerosis was undoubtedly a quite different one, and the utilization of the protective investment in dispersion by bird-agency wholly secondary. The seeds would probably be equally efficiently dispersed without injury without any such sclerosed investment (cf. *Ribes* and *Viscum*, non-lignified testa); the importance of the modification lies rather in the absence of a distinct *core*, and the isolation of the individual seeds. *Note* also that the more exact localization of the sclerosed cells of the ovary-wall indicates an approach to what has been known as the *Drupe* type of fruit-construction.

## Theoretical Considerations.

In comparing the types *Cydonia* and *Pyrus*, it may at once be noted that all these forms are deciduous woodland-trees perennating over a cold winter-season,[1] during which

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[1] Perennation may be said to commence about the middle of October, and is marked by the fall of the leaves: these turn brown and fall off, leaving the protected winter-buds which enclose the developing flowers of the succeeding season.

All these forms agree closely in their relations toward time the flower-buds laid down in the previous autumn are being slowly developed on the ripened wood, usually of the now year-old shoots, to flower in the second season, or exceptionally another year is required for the process (*C. japonica*). That is to say, the flowering-axes are not produced on the shoots in the same summer as that in which these vegetate, but are delayed over a resting period.

*P. Aucuparia* presents the fullest inflorescence as a multibranched panicle; a whole region of the plant shoot-system being devoted to the function of reproduction; and this becomes reduced considerably along normal lines to T and T′ flowers (*C. japonica*, *P. Malus*), and ultimately to T only in the Quince. Such reduction of the inflorescence-system is a direct consequence of this type of aerial perennation. When an inflorescence-region has to be developed, and the individual flowers brought to a considerable degree of perfection while they are wholly enclosed in a winter-protected bud, in order to produce functional blossoms at the onset of spring, one of two things must happen:—either a few flowers only can be produced of a relatively large size, or a large number of very small ones may be retained in a ramified inflorescence-system; and such small flowers may be expected to present extensive phenomena of reduction; that is to say, reduction must take place, it may be either in the inflorescence or in the floral axes themselves; and some types pursue one path and others the other, even in the same phylum; and not only is this probable, granted a necessity for such economy of construction can be adduced, but it becomes clear that the ancestral type of the phylum probably combined the full characters deduced from its specialized descendants.

Thus it does not follow that, since *P. Aucuparia* retains a more primitive copiously ramifying inflorescence-system, its small white fly-pollinated flowers are also to be taken as the primitive form from which the larger more attractive blossoms of *Cydonia* have been evolved; the flower of *C. japonica* is in fact the one which presents the more complete structure in both androecium and gynoecium, from which the *Pyrus*-forms are clearly reduced derivatives. The Quince and the Mountain Ash are thus to be regarded as so far complementary types along diverging lines from a common stock, in which a large inflorescence of relatively bulky floral-shoots, developing in a warmer climate on shoots of the current season's growth, may well be considered the ancestral form. A similar production of large inflorescence-systems, with reduced fly-visited or even wind-pollinated flowers, becomes the general case in all tree-phyla which in cold latitudes have to develop their flowers inside perennating buds (cf. *Fraxinus*). The fact that *C. japonica* has the most primitive flower of the series thus affords a valuable suggestion that the extensive reduction-phenomena observed in the majority of trees in these latitudes is largely due to climatic factors, and that small feebly-differentiated flowers are by no means to be regarded as necessarily primitive types (cf. *Viscum*, *Corylus*).

Analysis of the floral-construction shows that the phyllotaxis system presents different phases. The calyx continues the Fibonacci phyllotaxis characteristic of the vegetative shoot, and is therefore observed to present serial development along a 'genetic-spiral'. The corolla on the other hand arises simultaneously, and indicates a different type of construction. Another variety is found in the androecium; and lastly, the gynoecium does not follow directly on from the androecium, but the carpels are apparently orientated in relation to the external floral members, or independently with regard to the parent axis. This is less obvious in the reduced forms which only produce 20 stamens, and of which an inner series of 5 shorter members may alternate with the carpels, but the flowers of *C. japonica* show that the difficulty which is only suggested in the case of the Apple is a phenomenon of importance,

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leaf-fall, and all fruits not previously shed also fall away at this time. The inflorescence-buds developed in the axils of the leaves afford useful material for the study of developmental stages. Thus the Apple and Pear (Oct. 20) have all their flowers laid down and well-developed, the terminal flowers having stamens on a well-marked crateriform receptacle, and the first trace of carpels commencing. The Mountain Ash also has the inflorescence laid down, and the carpels are just appearing in the terminal buds.

since it marks a definite break in the construction-system between the androecium and the gynoecium. Now whatever interpretation be given to phyllotaxis-phenomena, it is clear that while it is easy to conceive that, granted a definite construction-system, such a system should continue to be laid down; any change of system must indicate a structural effort on the part of the plant which may be 'accidental', or on the other hand may be evidence of a structural design. The facts suggest, therefore, that the gynoecium is constructed in constant relation to the arrangement of the sepals on the receptacle-crater, without reference to the preceding androecium-cycles which may even be incompletely finished off; and similar orientation obtains in allied Rosaceous types (Apple, Quince) in which the androecium members have been reduced to a minimum as a single complete-contact series. Such a break in the construction is, therefore, not only of phylogenetic significance, but is comparable to somewhat similar phenomena observed in other phyla (cf. *Aquilegia*, *Geranium*).

The construction-system of the flower of *Cydonia japonica* thus presents four distinct stages:—

(1) The quincuncial calyx, a retention of the asymmetrical Fibonacci construction of the vegetative shoot.

(2) The assumption of symmetrical (5 + 5) construction at the corolla-members.

(3) A doubled (10 + 10) system in the androecium.

(4) An independent gynoecium-construction of the (5 + 5) type again, which does not follow on directly from the preceding (10 + 10) type.

These phases, since they represent distinct efforts at a change of construction, thus indicate stages in the phylogeny, in that they must have been in all probability initiated at different points in time. It is sufficient at present to note that the first phase coincides with the structure of such a flower as *Helleborus*; the attainment of the second phase only is represented in *Aquilegia*; while the later phases are those which mark off a very considerable group of plants which have been segregated around this 'Apple-type' as one of the simplest sections of the great family of the *Rosaceae* (Pomoideae).

The floral mechanism is simple in the *Pyrus* section; and in *Cydonia vulgaris*, the flowers, though showy and freely visited by insects, still remain fundamentally self-pollinating mechanisms. Only in *C. japonica* is self-pollination eliminated by a vigorous and correlated growth in the styles. The suggestion is again that the other forms are reduced types in which the mechanism has become imperfect by degeneration, rather than that they are to be regarded as more primitive; since if the growth of the style-branches and stamen-filaments is not correlated in this manner, little is gained by putting it in, beyond the production of a diffused group of essential members, in which, though a chance may be given to cross-pollination, autogamy becomes the rule. All agree again in the possession of an intercalated gland between the androecium and the gynoecium as a tubular Zona Perigyna; the succulent sides of which may be pressed against the style-base in order to narrow the cavity (*C. vulgaris*, *Pyrus communis*); while a zone of hairs on the style-shaft protects it and keeps the flower-tube and upper surface of the ovary from desiccation (most exaggerated in *P. Aucuparia*). The tubular character of the working mechanism is emphasized by the close contact of the stout stamen-filaments which have been described as constituting a palisade; and given that the construction is here (10 + 10), in which 10 members would normally form a contact-series, though not quite touching if rounded at the edges, a curious light is thrown on the presence of 20 members in two cycles, the inner ones just filling the slits between the outer ones, and thus securing a full cycle of complete contact with a minimum number of members, i. e. 20, as the smallest number which will suffice to constitute a working palisade; and reduced flowers can reduce so far in safety. From such a standpoint, the reduction of the androecium in these forms may be also regarded as a reduction-specialization, it being evident again that the innermost anthers of *C. japonica* are often quite functionless.

Great interest also attaches to the structure of the receptacle, which gives the special crateriform character to the flower, and by involving the gynoecium affects the character of the subsequently produced fruit. The developmental diagrams sufficiently illustrate the relation of the crater to its superimposed members, and not only so, but the figures of young buds in which the corolla and stamen-filaments have not yet attained their adult volume present very fair theoretical figures of the structure of the ripe fruits (Fig. 4); and apart from the actual number of ovules present, the structure of the receptacular ovary is common to all these forms. The figure of the Apple-bud (Fig. 6) is especially interesting as a testimony to the remarkable uniformity of growth in the ovary-region on the whole, from a stage 2 mm. in diameter; and it indicates the theoretical relation of the obliquely placed carpels to the crateriform receptacle, the true apex of the shoot being at the base of the axial cavity between them. Further, the utilization of a crateriform floral axis, when such an apex is not present in the case of the vegetative buds, undoubtedly implies that the object in view is the more perfect protection of the ovary-contents from injurious environment, particularly loss of water; and that it is necessary to economize the water-supply to the developing fruits is evident when it is borne in mind that these spring flowers are contemporaneous with the young energetically transpiring spring foliage, and that the fruits commence to grow while transpiration is still at its greatest activity, and the young vegetative shoots are growing with great rapidity. Such a type of gynoecium may therefore be reasonably expected to be produced in such tree-types, quite apart from any prophetic instinct as to any subsequent relationship of the resulting fruit to the animal kingdom. So also the receptacle, further developed as a mass of succulent parenchymatous tissue, affords an admirable protective investment to the developing seeds, and also acts as a water-reservoir; becoming all the more efficient in these respects as it increases in bulk, and this again without any reference to its future employment. The same observations apply to the alternative method of protection by means of lignified masses of tissue in the ovary-wall; and here again it is interesting to note that the moisture-loving Apple possesses only a trace of such sclerosis, while the xerophytic Pear may be almost solid throughout (wild form), and the fruits of the latter become succulent under cultivation in more favourable soils. If no further growth-modification ensues—such a mass being indehiscent by construction, since the carpel-sutures are on the inner surface of an axial cavity, and more or less fused in above—dispersal of the seeds can only be effected by shedding the mass as a whole; and the seeds will be set free by the decay of the parenchymatous tissue which further affords a source of nutriment to the developing seedlings: there can be little doubt that this is and was the ordinary fate of generations of Wild Apples, the fruit of which while on the tree is usually by no means attractive or conspicuous. On the other hand, the small fruits of the Siberian Crab (*Malus prunifolia*) are brilliantly coloured, and may possibly present a transition-stage to animal-dispersal (birds). In a state of decay the fruits may have become an article of food to such animals as swine; and that birds and animals do now disperse the seeds of the more specialized types thus becomes a phenomenon of secondary and very subsidiary adaptation which has so far affected the character of the fruit but little.

Similarly the seeds are by no means conspicuously protected for such methods of dispersal, being deficient in lignified investments. The factors which have led to the evolution of the apple-type of fruit are thus probably wholly unconnected with the fate of the structure, and Apple-trees may have existed and multiplied by seeds for millions of years before the evolution of any animals who devoured their fruits: the action of the wind and the shape of the small rolling fruit-mass being quite as satisfactory dispersal factors as the majority of common trees possess (cf. *Quercus*).

The diminution in the number of ovules traced from *C. japonica* to the Apple, and to a still smaller number in *P. Aucuparia* by further reduction in the number of carpels, though undoubtedly morphological reduction from a primitive condition (*C. japonica*) may also be viewed as a phase of reduction-specialization, in that here as in other phyla, the general aim may be taken to be the development of one crossed seed from one act of pollination; and from this standpoint, the possession of a vast number of flowers which each produce few seeds may be regarded as an approach to the most satisfactory reproductive mechanism:

just as a more generalized and even degenerate type of pollination-mechanism appears to answer all the needs of the plant sufficiently well. It is thus interesting to regard *P. Aucuparia* with the most 'reduced flowers,' as being both in androecium and gynoecium a somewhat more highly specialized type, though *C. japonica* clearly possesses the most highly differentiated pollination machinery. Similarly *P. Aucuparia*, with its multitude of small flowers, passes on to a multitude of small fruits which are much more useful for dispersal by the agency of birds than the more bulky apple-types: and not only so, but these fruits, which are now devoured by birds in large quantities, present what to a certain extent may really be correlated adaptations, as secondary modifications in structures which had originally a different significance. Thus the epidermal scarlet colour, absent in the floral stages, becomes intensely brilliant and concentrated as the fruits mature, the tissue becomes more succulent, and the enclosed seeds are much better protected for a passage through the alimentary canal as small easily isolated 'stones'. It thus becomes a point of interest to contrast the ultimate consequences in the two diverging types of the series.—*P. Aucuparia* retaining, as far as possible, a primitive panicled type of inflorescence, and becoming limited to small flowers and small few seeded berries—and *Cydonia vulgaris* in which the large solitary flowers produce relatively enormous fruits; while more elaborate and probably earlier conditions of the floral mechanism are retained in *C. japonica*, which as a distinct type may well be placed in a separate genus (*Choenomeles*,[1] Lindley, 1822).

The familiar types of the Apple and Pear have formed a centre around which have been grouped 50–60 species to constitute the genus *Pyrus*, which may without much straining include *C. vulgaris* and *C. japonica*; the separation of the two last as the genus *Cydonia* being based on a fruit character (∞-ovuled loculi) of no very essential importance. On the other hand the floral mechanism of *C. vulgaris* is identical with that of the Apple, while *C. japonica* differs in such important respects that it, as already noted, might well be placed in a genus by itself.

The genus *Pyrus* again becomes a centre for the isolation of a large sub-group *Pomoideae*, which includes Rosaceous types exhibiting the special features of this receptacular flower and fruit.

This group was first isolated by Linnaeus[2] (1750) as Order 37, *Pomaceae*, of his Natural System. His arrangement was, however, not wholly satisfactory, since it comprised with *Pyrus*, *Crataegus*, *Mespilus* and *Sorbus*, the genera *Ribes* and *Punica*. In the more perfect Natural System of Jussieu (1789) the *Pomaceae* appear as the first section of the order *Rosaceae*, *Malus* and *Cydonia* being added as genera; while by De Candolle (*Prodromus*, 1825) the *Pomaceae* constitute Tribe VIII of the *Rosaceae*, the number of genera rising to 14. The systematic position has since remained practically unchanged; cf. *Pomoideae* of Focke (Engler and Prantl, 1888), including 14 genera and about 200 species.

## NOTE ON PREFLORATION.

Since the phenomena presented in the overlapping of the corolla-members afford several points of interest, and may often attain the significance of a specific or even generic constant, it will be useful to have the general facts included under the term *Prefloration*[3] briefly summarized.

In an *asymmetrical* (spiral) construction, the paths for the sliding of any members which tend to grow beyond their original areas are provided in the geometry of the pattern, and no difficulty arises: the sepals of a (3 + 5) calyx, for example, if they meet and overlap, will always show the 'quincuncial' type of prefloration.

On the other hand, if the arrangement of the members is *symmetrical*, no sliding effect is allowed for in the primary construction; such members should exactly and symmetrically meet at their edges. When this remains as

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[1] Lindley's genus for this plant (*Choenomeles japonica*) has not been accepted, since Lindley was under the erroneous impression that the fruit split into five valves when ripe, and the fruits have been made the chief point of consideration in the classification of these allied forms.

[2] Hermann of Leyden (1690), an early 'Fructist,' distinguished *Angiospermae-Carnosae-Pomiferae* as his 18th class.

[3] *Aestivatio* of Linnaeus (1751). The term Prefloration being an improvement due to Richard.

the adult construction, the prefloration is conventionally termed ***valvate*** (Linnaeus): and conversely a valvate prefloration affords suggestive evidence of symmetrical construction.

If sliding growth of the edges of laterally extending petals takes place in a whorled system, it commences without any reference whatever to the primary construction, and hence its interest when it becomes a floral constant. The general geometrical properties of the construction therefore require to be established as a standard of reference from which further consideration of the phenomena may be approached.

Thus if *n* members be arranged around a circle, there will be *n* ways of overlapping their edges: in the case of five petals, therefore, these arrangements have been recognized and have received special names as types of ***imbrication*** (Fig. 7, I–V).

In order these may be distinguished as:—

| | | |
|---|---|---|
| I. Left Contorted. | cf. Eichler (1871). or | *Left Convolute.* |
| II. Quincuncial. | | *Quincuncial.* |
| III. Ascending, and its reverse Descending. | | *Bilateral.* |
| IV. Cochlear. | | *Cochlear.* |
| V. Right Contorted. | | *Right Convolute.* |

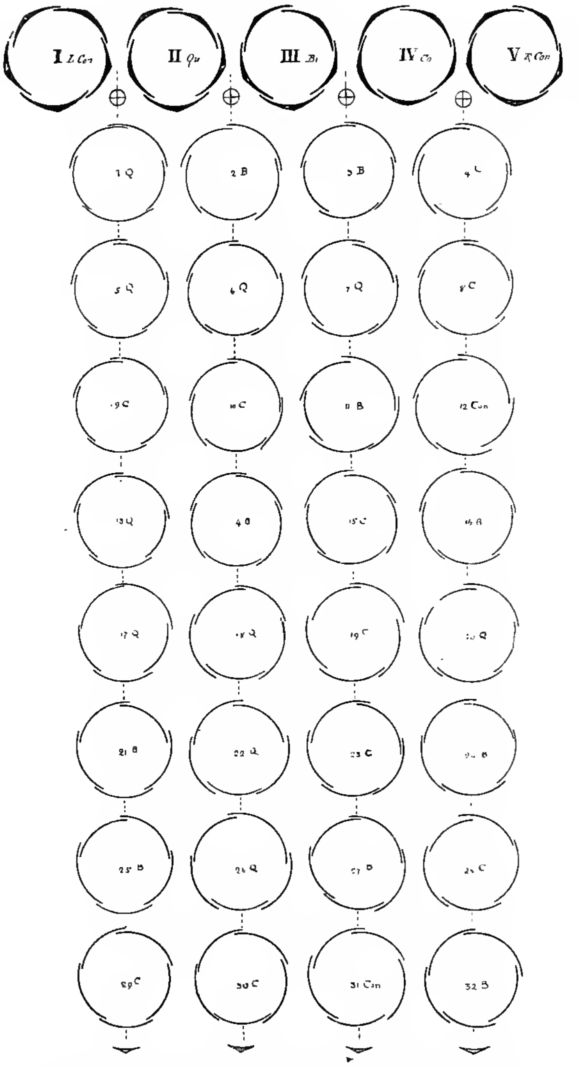

FIG. 7. Types of prefloration of a pentamerous corolla.

The types I and V present little difficulty; the only doubtful factor being the secondary convention required to distinguish 'Left' from 'Right' (cf. note on *Vinca*). The term *contorted* is open to objection, in that it contains the idea of *torsion*, which is really non-existent, and may be preferably changed to the more harmless '*convolute*'; a word which was used by Linnaeus (1750) for the rolling up of the edge of a foliage leaf, and has already been admitted by Eichler into the question of prefloration (1878).

Of the other 3 types, II has two members wholly outside and 2 wholly inside; III has one wholly outside and one wholly inside on opposite sides; i. e. separated by one or two members: IV has one member wholly outside, adjacent to the one wholly inside.

All these irregular arrangements (II, III, IV) were rather vaguely included by De Candolle (1827) under the term *quincuncial;* but with the introduction of clearer views on spiral constructions by Schimper and Braun (1835), No. II became isolated as the true quincuncial spiral pattern of Bonnet, and the term *cochlear*, applied to a labiate corolla with a lip-member either wholly inside or wholly outside, became applied to the others (St. Hilaire, 1840). Eichler, in adding the precision of orientation to the subject, selected the *ascending* and *descending* methods for those flowers which present bilateral symmetry; and *cochlear* thus became restricted to anything left over, the origin of the term being now unimportant. While the term *cochlear* may therefore be used for IV, if it is of any value, it may be noted that *bilateral* covers all cases of III, without taking reference to the median plane.

The subject may, however, be regarded from another standpoint, since though in a symmetrical construction the general probability would be that the arrangement would be a matter of chance, it is this very fact, whether the arrangement is really left to chance, or is the consequence of some definite growth impulse, which is the point of special interest.

Thus if *n* members, arranged in sequence like a whorl of petals, overlap with a regular method of orientation with regard to the parent axis and subtending bract of the flower, the number of possible methods of imbrication will be $2^n$; i. e. when the floral diagram is considered as a pentamerous type, there are $2^5 = 32$ possible methods of prefloration, and these may be readily plotted out as a scheme for purposes of reference (Fig. 7), and the general facts further considered.

For example, out of these 32 types, 10 are quincuncial (31 %), 10 bilateral, 10 cochlear, and one each of right and left convolute; while 8 have the odd petal wholly inside, and 8 have it wholly outside; i. e. 50 % have a 'lip' petal.

On checking these results for *C. japonica*, in which the orientation is very fairly clear for lateral flowers as the buds are breaking:—Sepal 2 is usually a large pale-green sepal at the back of the flower between 4 and 5, which are smaller, while 1 and 3 being external in the inflorescence are coloured red: select only flowers in which the relations of the sepals are clear; put a pin through No. 2, and plot the pattern observed in the breaking petals. A hundred flowers is probably much too small a number to afford a reliable result. But as an example, 100 flowers from the same plant gave:—

45 % quincuncial,
31 % bilateral,
22 % cochlear,
1 was convolute,

while 53 % had the odd anterior petal wholly in or wholly out. The agreement with the theoretical numbers is already sufficiently clear to indicate that *C. japonica*, including the Apple-type of flower, presents a corolla-prefloration which is a matter of chance, and no definite terminology can be ascribed it. For types in which the corolla-prefloration becomes a special constant, cf. *Erica*, *Vinca*, &c.

# XII

## Vinca[1] major, L. *The Greater Periwinkle.*[2]

A HARDY perennial low shrubby plant, with glossy evergreen leaves and trailing foliage shoots, growing to the height of 2–3 feet; indigenous to Western and Central Europe, extending from the north-west of Africa and Spain to Asia Minor and the Caucasus; now long thoroughly established in many parts of the southern portion of Great Britain, as also in Ireland, with a rather sporadic distribution, suggesting that at some time it has escaped from cultivation.[3] It was first described as growing wild in 1650,[4] and apparently was not known to be indigenous by Gerard, Parkinson or Ray (1688); Gerard (1597) states that it was in general garden cultivation at that time. It is now commonly grown in shady gardens and shrubberies for the sake of its low covering foliage, and violet-blue flowers produced on erect shoots in the spring months (April–June). The fruits which are somewhat rarely produced ripen and shed their seeds in August.

### Description.

INFLORESCENCE: Flowers borne simply in the axils of the decussating foliage leaves to the number of 1–4 on one shoot at successive nodes.

FLOWER: hermaphrodite; actinomorphic; pentamerous type.

RECEPTACLE: slightly crateriform; flower stalk with a right-handed twist.

PERIANTH consisting of:—

(1) CALYX: gamosepalous of 5 sepals; calyx-tube 2 mm.; free segments linear acute, green, slightly unequal, 10–12 mm. long; each with 2 small marginal glands near the base.

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[1] *Vinca* founded as a genus by Linnaeus (1737), Tournefort (1700) calling it *Pervinca*; *major* in contradistinction to *V. minor*, the Lesser Periwinkle. *Vinca* is the Roman name of the plant, *Vinca pervinca* of Pliny, though the latter full form applies rather to the smaller species *V. minor*. The two forms were not always separated by older writers, even Linnaeus regarding *V. major* as a form of *V. minor*.

By old herbalists the name *Clematis Daphnoides* of Dioscorides was very generally associated with *Vinca*, and a figure of *V. minor* is given under this name by Fuchs (1542), although Brunfels (1530) had figured it quite satisfactorily as *Vinca pervinca*.

Lobelius (1576) figures *V. major* as a distinct form under the title *Clematis* or *Pervinca major*; cf. also *Clematis Daphnoides major* of Bauhin's Pinax (1623).

The word *vinca* is probably related to *vinculum*, the flexible trailing shoots of the smaller form having been in general use for forming wreaths, a custom said to still obtain in parts of Italy to the present day ('The Funeral Flower'): the name presents an analogy to the old English term *bine*, and *Vinca pervinca* might be thus translated 'Bine-thorough-bine.'

[2] The English form *Periwinkle* comes from the same source *pervinca*, by the confusion of the letters V and U, and thus *Peruinca* becomes *Peruinkle*, *Pervinkle*, *Periwinkle*, these names being given by Gerard (1597). The name *Pervinké* occurs in Chaucer, probably applied to the lesser form, which is again mentioned as growing wild by Turner (1551).

[3] From the general use of the flexible leafy shoots for a basis of wreaths and chaplets, its funeral associations, and the fact that no very special medicinal value was attributed to it, there can be little doubt that the presence of both species of Periwinkle in this country is to be regarded as a relic of the Roman occupation; such a view throws light on its distribution in isolated spots which may be now far removed from cultivation, as it grows freely from suckers, and the prostrate shoots root freely at the ends, but owing to comparative failure of seed production, and the entire absence of mechanism for wide fruit dispersal, it cannot rapidly spread over a large area.

[4] How (1650); also for Oxfordshire, Plot (1677).

(2) Corolla: gamopetalous of 5 petals, alternating with the sepals; corolla-tube funnel-shaped, 5-fluted in the upper part; violet-blue, 18 mm. by 8 wide at the mouth, with antipetalous tufts of hair in the vicinity of the anthers; free segments violet-blue or white, 20 mm. by 15, somewhat asymmetrical, the series resembling the blades of a propeller, and the straight edge external in the bud; the broader half has a wavy edge, and a minute tuft of hairs is present at the tip of the segment. The entrance to the corolla-tube is emphasized by a ridge-outgrowth, 2 mm. high between the bases of the segments, forming a bridge holding the petals firmly in position, and rendering the entrance a sharply defined pentagonal orifice.

Androecium of 5 antisepalous stamens, attached 7 mm. up on the corolla-tube.

*Filaments* sharply kneed below the level of the stigma, and bearded, recurved to touch the corolla-tube and then overarched above the stigma-head 2 mm. higher.

*Anthers* introrse, 1 mm. surmounted by a broad hairy connective-flap, 1 mm. by 1 mm.

*Pollen* white, shed in masses on the stigma head.

Gynoecium of 2 carpels, apocarpous in the ovary region.

*Ovary* of each carpel a small green pod, 2 mm. long, unilocular, with 2 rows of 3–5 anatropous ovules along the ventral suture.

*Styles* fused to a column, slender below with enlarged spindle-shaped head, 8–9 mm. long, and surmounted by a 5-lobed plume of white hairs, 2 mm. in diameter. Around the broadest diameter of this style-head a broad zone of viscid *stigmatic papillae* represents the receptive surface, and below this an orange-coloured collar-piece overhangs the knees of the stamen-filaments.

Nectary. Alternating with the carpels, 2 green glands, equal in bulk to the ovaries, secrete freely, and honey fills the corolla-tube to the level of the ovary.

## Variations.

Hexamerous flowers, with 6 petals and 6 stamens also occur, the (5 + 5) construction being replaced by (6 + 6). In such cases the gynoecium and calyx usually remain normal. Similarly tetramerous construction is also found (4 + 4). These being the general variations of advanced pentamerous types.

*Note* the great size of the corolla and tube-mechanism as compared with that of the essential organs, so that these are small even on a large diagram: this feature is characteristic of highly specialized attractive types, and very general among Gamopetalae.

Stunted blooms produced in cold, dry weather (under exposure) do not attain such dimensions: in such blossoms the expanded corolla may be only 20 mm. in diameter or even less, and the tube 15 mm. only, the tips of the stamens being only 10 mm. from the honey: in this case the flowers are no larger to look at than those of *V. minor*, though the mechanism still remains on a larger scale, and they are almost as easily worked by bees.

Similar small flowers are again often found in late autumn (November) as the last of the second crop produced in a cooler season.

## Floral Diagram.

The lax foliage-shoots bear simple evergreen leaves in decussate series (2 + 2), and become woody at the base. These lower portions persist over the winter, and in the axis of the more or less persistent leaves new spring shoots arise and bear flowers in April–May.[1]

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[1] In the middle of the bush such shoots arise in autumn (October), and commence flower production, and are sheltered over the colder months. The long trailing shoots do not branch, but act as runners, rooting freely at their tips and developing new tufts of shoots.

Transverse section of the apex shows a perfectly normal decussate, symmetrical (2 + 2), phyllotaxis system (Fig. 1). The flowers are produced singly in the axils of certain of the foliage leaves, but in only one of a pair, and thus in passing up the stem the series gradually gives the subjective impression of a R. or L. spiral. Variations are, however, frequent, especially in weaker shoots with few flowers, in which case the flowers may be spaced out with nodes between them. *Note* that a similar limitation of lateral axils is general in the case of decussate systems (cf. *Agrostemma*), and the alternating effect has most probably to be correlated with the symmetrical growth and nutrition of a bud-construction containing only a limited number of flowers which are required to function in series one at a time.

The *orientation* of the flower with regard to the subtending bract is not the one which usually passes for *normal*: there are no prophylls on the flower-stalk, either in the flowering condition or in developmental stages, and the quincuncial calyx is not arranged so that the second member falls as near as may be seen in the median posterior position. This may be readily observed in the case of very young buds which stand erect and parallel to the main axis; while in buds about 5 mm. long the orientation of the calyx is quite obvious. In such a bud the sepals vary in length, according to the usual quincuncial system of development, and while Nos. 1 and 2 may be 5 mm. long, 4 and 5 are only 4–3½ mm. and also narrower; sepal 2 falls laterally with regard to the subtending foliage leaf, and a section through the bud at the level of the top of the ovary shows that the 2 carpels are also placed approximately in a *transverse* plane, and the nectary-lobes are median with regard to the bract.

FIG. 1. *Vinca major.* Transverse section of the apex of a vegetative shoot, decussate (2 + 2) phyllotaxis.

Transverse sections of shoots bearing very young developing flowers (October–February) confirm these observations. Strict evidence as to the plane of orientation is difficult to obtain, owing as in the general case, to the fact that the floral axis arises at an angle in the axis of the subtending bract; in a section transverse to the parent shoot the flower-buds are cut slightly obliquely, while in a section cut transversely to the young flower-axis the members of the parent shoot are cut obliquely (Fig. 2).

Observation of sections of the young floral axis, in which the flower-stalk has not commenced to elongate, agrees with the facts deduced from the comparison of older buds, and from the study of the vascular bundles in the base of the floral receptacle (Fig. 4, 2).

One sepal is always as near as possible in the transverse plane, but it cannot be said that either a sepal or a petal falls exactly in the median plane either posteriorly or anteriorly (Figs. 2, 3, 4).

It will also be noted that the odd sepal in this approximately transverse plane is always sepal 2, and that the quincuncial character of the calyx is quite obvious in early stages (Fig. 2, 2), the spiral in which the members are numbered being either R. or L. hand.[1]

Hence the orientation of the quincuncial calyx is apparently *transverse* rather than *median*, as in the general case. Further confirmation is obtained by noting the prefloration

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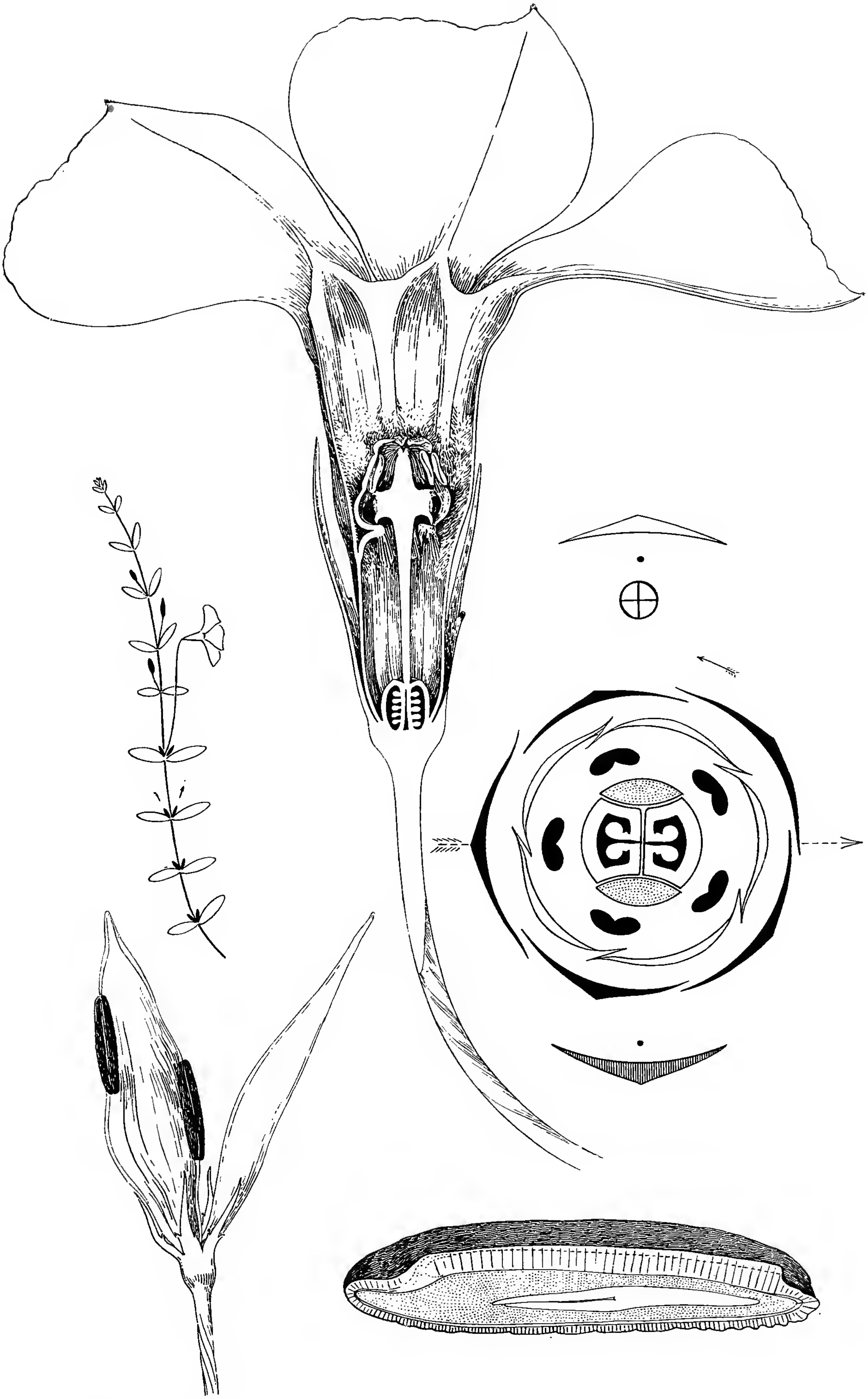
[1] (The left-hand case is taken in planning the diagram and elevation as a matter of convenience.)



**Vinca major:** Floral Diagram and Sectional Elevation of Flower in the transverse plane: Inflorescence Scheme; dehiscing Fruit, and section of Seed in the plane of the raphe.

of the sepal-segments in very young buds, and careful drawings show that the transverse symmetry is, so far as can be judged by the eye, as nearly established as is the more general case of approximately 'median' symmetry.

In the case of older buds the pentagonal corolla-tube so fits in the bud that one flat side (corresponding to a petal) is applied to the bract, and one angle fits between the next pair of leaves, so that the appearance is ultimately presented of a posterior sepal and an anterior petal: even in such old buds, however, sepal 2 may be usually distinguished by being broader and longer (1 mm.) than its adjacent members 4 and 5.[1]

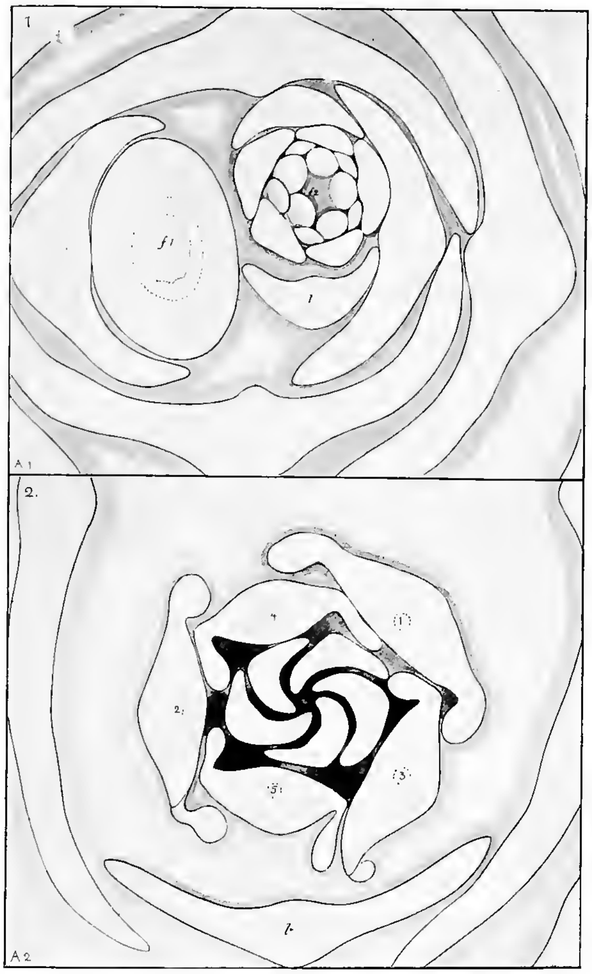


Fig. 2. *Vinca major*, October buds. (1) Transverse section of shoot-apex showing the origin and orientation of a flower-bud ($f^2$) obliquely placed in the axil of the subtending bract (*b*). (2) Older bud showing quincuncial prefloration of calyx, sepal 2 being approximately transverse, the glands of the sepals and left convolute prefloration of the petals.

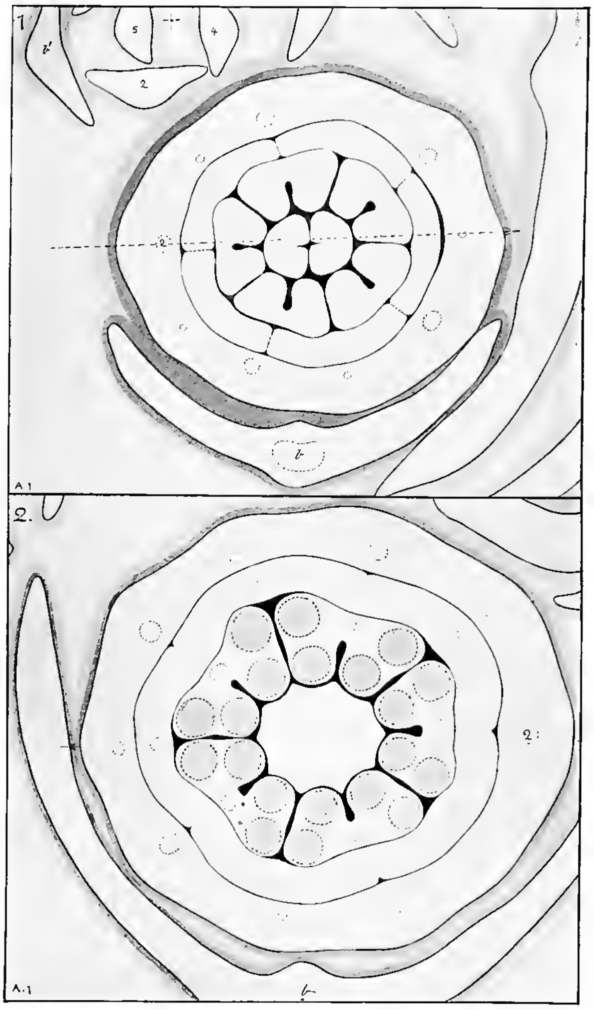


Fig. 3. *Vinca major*. (1) Section through all the floral members: calyx-tube with vascular bundles, petals valvate below; the arrow indicates the plane of sepal 2. (2) Slightly older bud, drawn to the same scale; vascular bundles indicated in calyx-tube, corolla and style-head: section passes through the pollen sacs of the anthers.

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[1] A curiously artificial interpretation was put forward by Wydler (1851), and adopted by Eichler (1875): by regarding the main axis as a sympodium, and the flowers as terminating the component axes, each flower would be orientated normally with regard to the leaf below the node from which it really springs, and the two foliage leaves at this point would be the α and β prophylls: the sympodium would be continued through α, and the flower would thus appear to be falsely in the axil of its own β prophyll: this would imply that the flower-shoot was to be regarded as a homodromous monochasium, which however did not attain the symmetrical construction of a scorpioid cyme, while the last ramification was continued as a vegetative shoot.

There is, however, absolutely no trace of any such construction at the growing point at any stage of development, the decussate symmetrical phyllotaxis being perfectly definite: in all respects the shoot behaves exactly as if the flowers were axillary; vegetative buds forming in the axils of all the foliage leaves, and even accessory buds in the axils of the leaves subtending flowers when these latter are shed. The sympodial theory is founded on purely academic reasoning, following the phyllotaxis conceptions of Schimper and Braun, and is perfectly gratuitous, since

The facts admit of a sufficiently simple interpretation: the isolation of the first 2 members on the floral axis as lateral protective prophylls has been eliminated, and the spiral sequence of members is from the first directly developed as the floral perianth; the result being that the 2 members, which in the more usual construction become $\alpha$ and $\beta$ prophylls, are now sepals 1 and 2. That is to say sepal 2 is exactly in the place of $\beta$, and therefore as nearly transverse as can be judged by the eye, although there is yet no proof that it is mathematically so. Number 4 sepal should now be the member which is normally sepal 2 and be posterior, but the position of this member cannot be accurately estimated,[1] since at this point the phyllotaxis system must be changing, as almost immediately the floral construction becomes again symmetrical at the normal (5 + 5) type of the whorled pentamerous flower.

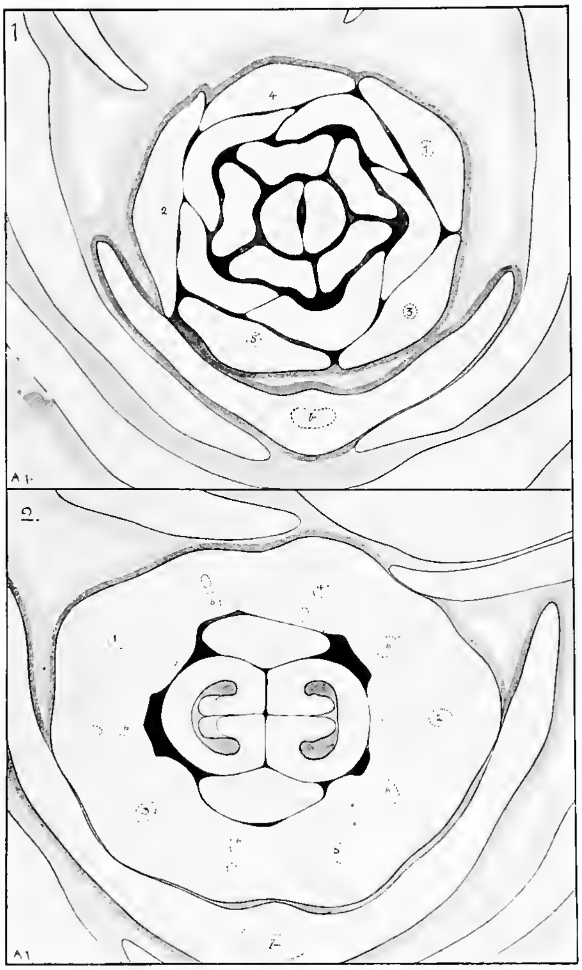

Fig. 4. *Vinca major*. Development of flower. (1) Section of young bud showing the commencement of the prefloration of the petals. (2) Section of a similar bud through the crateriform portion of the receptacle, showing developing ovules, nectary-lobes, and vascular system of stamens, petals, and sepals.

It is to be noted that the foliage leaves are all constructed in a symmetrical system, and the floral axis shows therefore at first a reversion to a presumably older asymmetrical construction, similar to that in other types of pentamerous flowers; and the fact that at this point, where the continuity of the construction system is broken, *Vinca* should have adopted a less usual type of formation becomes an interesting example of generic variation; the tendency to vary in this respect being possibly connected with the causes which have led to the very special habit of the plant, and the biological production of procumbent decussate vegetative shoots, which in fact represent a type of plant body also quite distinct from that which is usually regarded as the normal case (for a somewhat similar construction in the floral axis, cf. *Primula* and its allied trailing forms *Lysimachia* and *Anagallis*).

While the corolla and androecium follow in normal alternating series, indicating a continuation of the (5 + 5) construction for two whorls of members, the 2 carpels are orientated in the plane of sepal 2, i.e. also in the transverse plane (Figs. 3, 4). It is this point in the formation of the flower which renders *Vinca* of special interest, in that the

although it may afford a means of bringing all the peculiarities of the construction into line with what is still a hypothetical general type, it remains wholly incapable of further proof. The value of Wydler's suggestion is not so much that it explains the case of *Vinca*, which is admittedly unique among closely allied forms (*Apocynaceae*), as that it brings into prominence the fact that the normal quincuncial type must be remarkably preponderant as a type of floral construction, when such elaborate cooking has been accepted as admissible for an occasional and isolated exception. Instead of trying to force the facts into one general scheme, it now becomes of interest to take them as given by the plant, and endeavour to find the reasons why the ordinary construction should have been as it were forgotten in the phylogeny of *Vinca*; while the possibility is not eliminated that what is regarded as the general type is not after all so accurate a construction as accepted by Wydler and Eichler. The case of *Vinca* is further seen to be somewhat abnormal when it is noted that it presents an example of an asymmetrically constructed floral shoot arising from and orientated with regard to a perfectly symmetrical type of construction in the main shoot.

[1] It is in many cases approximately so, and the error would be still less noticeable if the construction of the parent shoot was also asymmetrical (cf. *Primula*).

2 carpels which are normally in the median plane when sepal 2 is median, here follow the odd sepal; that is to say their orientation is connected with the construction of the floral axis, and is not related to that of the parent shoot. Genera which are most closely allied to *Vinca* retain both the normal orientation of the calyx and the median carpels. *Vinca* is thus to be regarded as an interesting exception which helps to prove that there is a *rule* in the general type of flower-construction; but it must be noted that the rule has been evolved, and must represent a certain optimum method of construction, taking all things into consideration, which may have been followed in many diverse lines of descent (cf. the 'Mean Type'); it must be distinguished from the working of a morphological *law* which remains a purely academic abstraction.

The transverse position of the carpels is not absolutely constant,[1] and they may occasionally be found to be oblique; a phenomenon again general in pentamerous flowers in which the limitation of the construction to two carpels indicates so far only a failure in the phyllotaxis system, and the retention of two members only in any particular plane of symmetry has not yet become specialized as a part of the floral mechanism (cf. *Ribes*). The well-marked nectary-lobes alternate with the carpels, and are also placed in the diagram. A transverse section of the ovary shows the two carpels of simple structure, quite free from one another, and bearing anatropous ovules on their incurved margins (sutures).

*Prefloration*: while the sepals, though quincuncial in development and prefloration in early stages (Fig. 2), are never sufficiently broad to overlap in the older buds in the very definite prefloration of a R. or L.-hand spiral flower, the petals are remarkably developed, and the free segments are asymmetrical with regard to a median line, one side of the petal being developed considerably more than the other, and this is constant all round the corolla, giving the expanded portion somewhat the appearance of a screw-propeller. The petals overlap in a definite over-under series which may be termed *convolute*, but the direction is constant; that is to say, whether the calyx is right or left-hand, the petals always fold one way, and a convention is thus required to distinguish one direction from the other. As a matter of fact the case of *Vinca* has been distinguished as *Left-hand*, and there is perhaps no advantage in altering the expression, although the convention adopted may not appear very satisfactory.[2]

FIG. 5. *Vinca major*. Development of flower; section of young bud in the plane of the elevation, showing all the floral parts laid down on a slightly crateriform receptacle.

This phenomenon of convolution in the corolla, which is constant, and clearly has nothing to do with the phyllotaxis spiral of the calyx, is thus a secondary phenomenon due to anisophylly in the petal-segments, and must be regarded as another construction-idiosyncrasy of *Vinca* as a genus, since it can have no conceivable utility in the floral mechanism, and closely allied types may be equally constant as right-convolute forms (cf. *Nerium*). Nor, since it is a phenomenon of growth-overlapping, does it appear to have

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[1] In *V. minor*, which is a somewhat more reduced form of the genus, the 2 carpels may have any position.

[2] Cf. *Note on 'Contorted' corollas*.

any relation to the appearance of a twist which is found as a growth-phenomenon in the flower-stalk as a right-handed twist (cf. *Note on 'Twists'*).

*Note* that in the *convolute* corolla it is the half of the petal which falls inside in the bud which undergoes increased development, the smooth sharp edges of the other halves constituting the projecting ribs of the flower-bud which is otherwise considerably lacking in projecting adaptations. (For similar secondary anisophylly of convolute corollas cf. *Hypericum*, *Oxalis*, *Althaea*.)

## Sectional Elevation.

To show the floral parts to the best advantage, section of the flower is taken in the plane of sepal 2, and thus passes through the two carpels. As a matter of convenience, since the flower is thus cut across the transverse plane of the diagram, both diagram and elevation are drawn for a flower with a left-hand calyx; sepal 2 is thus represented halved on the left of the figure.

*Note* the small slender sepals, protective only in the earliest stages (Figs. 5, 6), and not now overlapping; in the expanded flower they reach to the level of the essential organs and form a guard to the lower corolla-tube. The gamophyllous region is just sufficient to cover the ovary and the nectary. The large corolla and corolla-tube are remarkable for the asymmetry of the petals, and the well-defined guard-ridge which limits the entrance to the functional tube, although gamopetaly extends slightly farther. Note that in a left-convolute flower the left-hand side *as seen in the sectional elevation* is the inside and most developed half of the petal.

The corolla-tube comprises two well-marked zones of growth:—

I. That of the *Gamopetalous Zone*, 11–12 mm. in length, forming the outer chamber of the tube, bearing the guard-ridge, fluted lower down, and hairy in the region of the anthers.

II. A perfectly smooth lower chamber formed by a second zone of growth taking up the stamens, *Zona Mediata*, 6 mm. in length.

The peculiar kneed structure of the filaments is apparently correlated with the manner in which they overarch the stigma, and the connective-flaps form a complete investment over the essential organs as seen from the entrance to the corolla-tube. The large style-head blocks the aperture in the median line, and the paths to the honey lead along the 5 fringed grooves of the outer tube between the anthers and stamen-filaments.

The filaments are very strongly curved; the 5 knees are sharply bent forward and embrace the style, holding the lower rim of the style-head firmly in the centre of the tube, and then curved back again until they press against the wall of the tube; from these points the anthers bend inwards, and are thus held fairly rigidly in position. These filament curvatures play an important part in maintaining the working stability of the floral mechanism, so that the entrance-slits between the anthers maintain their proper shape and resistance to penetration, and as the curvatures are largely sustained by the turgidity of parenchymatous cells, the tension naturally tends to be relaxed in older and fading flowers. The ovary is distinctly apocarpous, and the crateriform receptacle fairly well marked; the apex of the floral axis appears between the bases of the two carpels.

The ovules are anatropous, 2–3 or 4 as seen in vertical series, and the micropyles are directed upwards.

The stigmatic portion is remarkably specialized; the carpels are completely fused in the stylar shaft, and there is evidently not only a correlation between the length of the fused styles and that of the Zona Mediata, but this is required to be extremely exact: even in starved flowers with impoverished corollas this part of the mechanism remains perfectly adjusted, in fact it cannot apparently get out of order owing to the manner in which the knees of the filaments embrace the style-head, and as the Zona Mediata expands, these necessarily pull the style up with them; it might be longer, but cannot be shorter.

The style-head is spindle-shaped, with a broad zone beneath the terminal conical portion differentiated into 3 bands; an upper guard-band of short hairs, the true stigmatic region with viscid surface, and a lower frilled ridge with sharp edge which constitutes a lower guard to the stigmatic surface.

The distribution of *Hairs* is of special interest:—

1. *Note* minute tufts on the petal-tips, which pack the aperture at the apex of the unopened bud.

2. The great development of silvery hairs, downwardly directed along the entrance-slits on the wall of the corolla-tube, these ceasing below the filaments.

3. A great development of upwardly directed hairs on the connective-flaps, which almost block the aperture of the corolla-tube.

4. The central portion where these last meet is further filled with a plume-tuft on the style-head itself; this tuft is somewhat 5-angled, and the downward drooping silvery hairs form the inner boundary of the entrance-slits. These slits are thus clothed on all sides with downward pointing hairs.

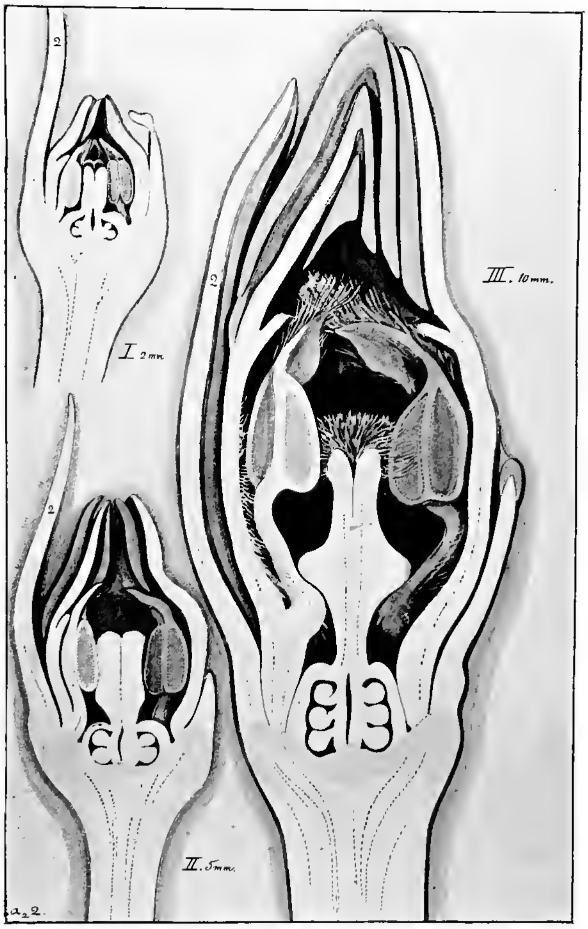

Fig. 6. *Vinca major*, February buds. Development of flower. Elevations in the plane of sepal 2 for 2 mm., 5 mm. and 10 mm. buds.

5. While these hairs are mostly above the level of the stigmatic surface, the filament knees show a beautiful growth of strong downwardly projecting hairs which also pack the centre of the tube around the upper portion of the style.

The hairs are thus collected in the vicinity of the stigma and anthers, and almost close the aperture of the tube; the point of interest is that they should definitely point downwards, since if their function were solely to block the tube the formation would be irregular or felted.[1]

*Note* that owing to this development of hairs on the essential organs and corolla-tube, the ovary, nectary, and pollen are perfectly protected from the effects of desiccation and intense light, as well as from small insects.

The honey is perfectly concealed, as also the pollen-supply; access to the honey is limited to certain narrow paths, while the pollen cannot be collected at all.

It is also interesting to note that the bright orange colour of the style in its lower hidden portion may possibly be a retention of a pigmentation protective against intense light[2]; but it can have no relation to insect visits, as it is wholly out of sight from the entrance to the flower which only presents a small central white 'eye'.

The *Development* of the special type of corolla and tube-mechanism is readily studied in

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[1] The cells covering the upper surface of the conical style-head, although hidden below the long white hairs of the terminal plume, are produced into minute tooth-like points; as these hairs occur nowhere else in the flower, and would tend to divert an inserted proboscis from the apparent median orifice between the connective flaps, they are probably to be included under the heading '*Warning-hairs*.' *Note* that the softer hairs of the connective flaps being also upwardly directed in the median line of the tube, as also the short stiff hairs of the guard-ridge over the stigmatic surface directed upwards and outwards, may possibly be also included in this category.

[2] *Note* that the orange pigment is present throughout the whole tissue mass of the upper portion of the style-shaft, being most intense just below the stigmatic region, and curiously absent in the portion of the style-head (green) above the level of the stigmatic surface.

sections of buds at successive stages. Buds require to be taken during February and March, and when cut in the transverse plane of the diagram scheme will give sections of the flower in the plane of sepal 2. (Cf. elevation.) (Fig. 6.)

Section of a bud 2 mm. long shows the receptacle with a distinct crater-form, and the members placed on it are still of quite simple character. The stamens are now on the receptacle, and the carpels distinct, though fusing at their tips and already laying down the ovules. The only special feature of the flower present at this early stage is the emergence-ridge on the developing corolla-tube, and this is especially well marked behind the anthers (Figs. 5, 6).

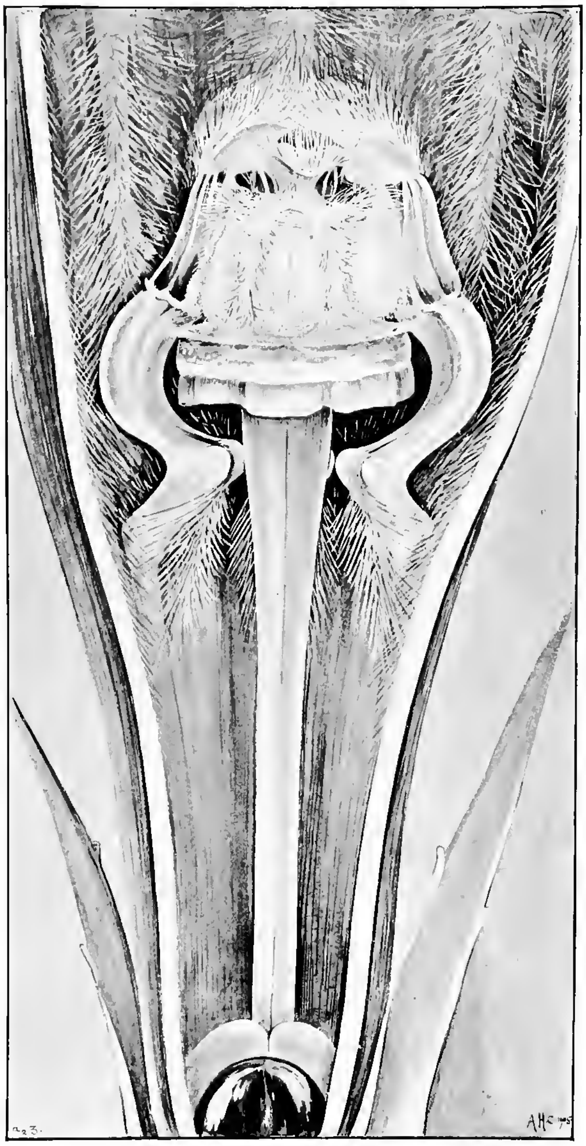

Fig. 7. *Vinca major.* Floral mechanism in the opening flower: the corolla tube is cut down, and 2 stamens have been removed leaving pollen-masses shed between the hairs of the stylar plume.

In slightly older buds (2·5 mm.) the styles commence to grow up; and in a 5 mm. bud (Fig. 6, II) they form a definite stigmatic-head of 2 lobes very similar to that of *Heliotropium*; the Zona Mediata commences to elongate at this stage and the connective-flaps arch inwards. The corolla is still shorter than the sepals, but in a 10 mm. bud the petals begin to appear beyond the sepals, and much of the subsequent mechanism becomes clear. The knees of the stamens are put in, and these press against the style-head which is developing a ridge in connexion with them (Fig. 6, III). The tufts of hairs begin to appear, and the anther-flaps form a protective chamber. The Zona Mediata and style-shaft are still short, but it is clear that as the style-head increases it will fill the space between the anthers, and its conical end and terminal plume of hairs will fill the gaps between the anther flaps (Fig. 6, III). These being in fact the only features required to perfect the mechanism, and only added in the rapidly growing coloured flower-buds.

The hairy knees of the filaments, the anther-flaps, and even the guard-ridge on the corolla-tube appear to be all connected in the bud-stage with the protection of the inner chamber of the flower, and these features may be so far correlated with the feeble development of the calyx and the absence of prophylls; the sole external protection of the buds being due to the fact that only a few are contained between the closely packed leaves of the young flowering shoots which again appear at the bases of the shoots in the interior of the bushy plant.

Observation of the developmental stages thus confirms the view that the essential feature of the mechanism is the exact adjustment of the style-growth to that of the Zona Mediata, by the intermediary of the knees of the stamen-filaments.

*Note* that the crateriform receptacle is not further utilized, being no better marked proportionately in the 10 mm. bud than in the 2 mm. one.[1]

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[1] The nectary lobes are well differentiated at the stage represented in Fig. 5, but in a section cut through sepal 2 the lobe is hidden behind the ovary; this also applies to the figures in Fig. 6.

## Floral Mechanism.

As previously indicated, the flower develops simply as a pentamerous type, along familiar lines, on a slightly crateriform receptacle, and the subsequent specializations include gamophylly of the perianth cycles, the corolla whorl being carried up at an early date by a well-marked gamopetalous zone, while the calyx cycle is elevated only slightly, and subserves no very obvious function.

The Zona Mediata is added later, although a trace of this development may be noticed at a comparatively early date (Fig. 5), and the special mechanism then commences to be differentiated. The stamen-filaments are added, and a well-marked stylar zone takes up the tips of the carpels: these modifications are all usual phenomena among allied gamopetalous phyla; the peculiarity of *Vinca* consists rather in the addition of subsequent specializations in the stamen-filaments and style-head. Other details are noticed in the special localized production of hairs and emergences, the guard-ridge of the corolla-tube and the nectary lobes coming under this latter head.

The corolla-tube and free petal-segments are coloured violet by a localization of an anthocyan derivative in the epidermal cells only. Anthocyan compounds are conspicuously deficient in the green vegetative leaves, but traces of a red derivative may be found in the epidermis of exposed shoots, and occasionally in the sepals and flower-stalk.

The mechanism may be regarded as comprising a tube-structure constituted by the gamopetalous zone and Zona Mediata; the former making an outer chamber which is remarkable for its depth. At the junction of these zones the essential parts of the mechanism admit of the isolation of three chambers:—

(1) The *pollenic chamber* roofed in by the flaps of the anthers and the stylar plume; the centre being occupied by the conical style-head, on the surface of which the pollen masses are shed.

(2) The *stigmatic chamber* which contains the stigmatic surface as a broad viscid band around the style-head, guarded above by a slight ridge, and below by a descending collar; the upper ridge preventing the direct fall of pollen on to the receptive surface, although, as in an ordinary self-pollinating mechanism, this is situated below the level of the anthers.

(3) The *nectary chamber* below the attachment of the anthers, roofed over by the arching filament bases, with the two nectary-lobes at the bottom of the tube.

Free communication into all 3 chambers is afforded by the chinks between adjacent stamens, and these are thus antipetalous, but the sides of the passages are fringed with descending hairs.

Although the flower commences as a simple self-pollinating mechanism (Fig. 5), it is clear that subsequent modifications tend to practically eliminate self-pollination (autogamy) in the absence of any external agency: and it is clear also that this external agency can only be that of insects of a considerable size and intelligence. Thus the *working distance* of the flower must be greater than the distance of the anthers from the honey, since pollen-collection is out of the question, and cannot be much less than that from the nectary to the outer guard-ridge of the corolla, i. e. not less than 10 mm. and probably nearer 18 mm. Small bees and flies are thus eliminated, and the flower is restricted to the visits of long-tongued bees or Lepidoptera. The morphological structure and development of this flower thus shows that it is intended as a cross-pollinating mechanism to be visited by long-tongued insects (over 10 mm.), and that these visit the flower for the sake of the honey secretion only.

That much of the mechanism, and especially the production of localized patches of hairs, will also subserve protection of the ovary-contents and germinating pollen from the effects of intense light and desiccation is sufficiently obvious, and it is not clear which factor, if any, may have been the prime determining cause in their initiation; but there remain some details, as for example the exact relation of the style to the stamen-knees, the production of guard-ridges to the stigmatic surface, and the fact that the hairs point in definite directions, which can only have been originated from the standpoint of insect visitation.

**Pollination.**

The mechanism receives its final adjustments in the rapidly enlarging buds which stand erect on their stalks in the axils of the green leaves of the erect young shoots.

The corolla acquires its violet colour, and as it expands, as if by a left-hand twist, a curvature of the flower stalk is added, which bends the stalk at a right angle, so that the flower-tube is projected horizontally. This curvature is influenced by light, and the flowers are thus turned toward the side of strongest illumination (cf. *Narcissus*); when growing in a hedge-bank this exposure of the flowers is very noticeable, but less so when the plants grow as bushes in the open. The growing flower-stalk also exhibits apparent torsion, and this is constantly right-hand, and the original orientation of the flower is quite obscured (cf. note on apparent twists).

The expanded corollas present the form of a 5-pointed star, 40 or even 50 mm. in diameter, the pale-violet colour rendering them very conspicuous among the dark green foliage leaves. Normally only one is functional at a time on the same shoot, and the blossoms possess no scent or other adaptation to render them attractive: on the other hand, the pale star-like blooms are very fairly conspicuous at dusk. The 'eye' of the flower is not at all conspicuous at a distance, and there are no so-called 'honey-guides'; the flowers are visible to the eye for a distance of 35 yards.[1]

*Note* that the violet colour is identical apparently with that of *Viola*, but the pigmentation is not so intense; it is confined to the epidermal cells, and turns bright rose-red with dilute HCl. (anthocyan compounds).

Single flowers persist for 8–10 days, and as one withers the next above expands, so that a flowering-shoot is in working order for a period of about six weeks in spring.

The flowers require a certain amount of warm weather to develop well: in cold springs, with night frosts and dry winds, they remain very stunted, and the colouring matter is only feebly developed, so that they have a sickly appearance (early April). They only attain good condition when the weather is sufficiently favourable to admit of abundant insect-life (late May), and the violet colour becomes more intense towards the close of the flowering period.

The flowers are homogamous, the stigmas being receptive as soon as the corolla expands, while the pollen is shed as soon as dry air is admitted into the breaking bud, and in warm weather the pollen will be found to be shed in buds which are just about to expand.

The pale pollen masses are shed from the two lobes of the anther in definite coherent aggregates, 1 mm. long; those of adjacent pollen-sacs often lightly cohering as well, and the pollen may be thus deposited on the sloping surface of the style-head in 10 moist cake-like masses adhering to 5 paired *pollinia* which, however, are not viscid.[2]

These pollinia thus alternate with the stamens, and lie on the inner floor of the 5 paths leading to the inner chambers of the flower. So complete is the shedding that it is easy to obtain an estimate of the number of pollen-grains included in one pollinium by pressing it with a cover-slip. The number is 1,000–1,500 for a double mass, or 3–400 for a single loculus (sporangium) of an anther. It may thus be computed that the number of microspores produced by one flower is 5–7,000, while the number of macrospores, as indicated by the number of ovules, is less than 20: this proportion, though apparently widely divergent, is really far less than that of more undifferentiated types, and the relative number of pollen grains may here be said to be low owing to the efficiency of the pollination mechanism.

*Note* that the formation of these 'pollinia'-like masses is not of special interest from the standpoint of *Vinca*, since it is largely the natural effect of shedding moist pollen into

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[1] At this distance flowers growing in the open become lost to the eye among the foliage leaves (B. G. O.). Those of *Vinca minor* under similar conditions were lost sight of at 14 yds.

[2] These masses of pollen on desiccation readily break up, and pollen grains become entangled in the hairs of the stylar plume, which to this extent may be regarded as 'collecting hairs': the stylar guard-ridge only just keeps them from coming in contact with the stigmatic surface and clumsy working by an insect may very possibly promote self-pollination.

a damp protected chamber, but it points the way to a further development of the idea, and the evolution of a true pollinium in closely allied forms (cf. *Asclepias*); since if the pollen were also adhesive, an insect would tend to carry away the mass as a whole.

As already noted, the pollen is shed within a pollenic chamber bounded by hairs, and the pollen-masses become entangled in the silky hairs of the style-plume, and so lie on the inner boundary of the antipetalous entrance-slits, which are only penetrable by a slender proboscis. It will be observed that an insect which inserts such a proboscis will not remove pollen grains until it has been made sticky, and in this case it is the stigmatic surface which supplies the viscid material. A fine proboscis again will give the neatest effect, and as the proboscis of an insect can only readily bend downwards, the visitor must work from the centre of the flower. The method of pollination may be readily imitated by using a fine bristle, or even a pin, and the amount of viscid matter and pollen accumulated on the latter after probing a few flowers is very striking.[1] Proboscides of the requisite length are only found among a few bees and Lepidoptera; and it is probable that *Vinca*, though still worked by bees, is really specialized for the visits of moths. In this connexion it is interesting to note the tendency to a distinct horizontally projected 'target-type' of flower; the effect being produced by a flat expanded corolla without special 'landing-stage', the central 'eye', and the special growth curvature of the stalk. (For similar details cf. *Narcissus poeticus* and *Viola altaica.*) As a matter of fact, the flowers are very little visited in this country, since Lepidoptera are scarce in the spring months; in its natural habitat it is contemporary with the moth-visited *Narcissus* (*N. Tazetta*).

The flowers in this country are visited by species of *Bombus*, but generally accidentally, or in mistake for the smaller form (*V. minor*), which is easily accessible to many bees.[2]

The flowers can only be said to be satisfactorily worked by the bee *Anthophora pilipes* (19–21 mm.) which pollinates so many tubular spring flowers (cf. *Primula*, *Ribes*, *Cydonia*).

On a sunny morning these bees work the flowers at considerable speed, and may be seen hovering over the plants with half-extended proboscis, passing freely from flower to flower, and working them with the precision of a Hawk-moth, only lightly resting on the corolla segments and dipping their proboscides into the flower-tube (cf. *Viola odorata*).

As the bee rarely visits or probes a flower more than once, since the honey supply only requires one visit, self-pollination even by insect agency is uncertain, since the pollen is not moved down by the inserted proboscis, and the viscid portion of this latter is well covered by pollen from the abundant supply when it was being withdrawn from a previous flower. The mechanism as adapted for crossing rather than self-pollination has thus reached a considerable degree of perfection, though it is still evident that various little accidents may be suggested which would really result in the self-pollination of the same flower, while pollination between flowers of the same plant is necessarily extremely frequent, free intercrossing being only likely to obtain when plants are growing in considerable numbers. Even in this country the flowers are apparently never visited in many localities, though the value of such negative evidence is extremely small. Flowers which have been watched in vain for many days may at one particular time be found to be abundantly visited; for example 2 or 3 *Anthophorae* may visit every blossom on well-covered plants in half-an-hour or so in the morning as the sun gets warm.

*Note* also that it is clearly difficult in treacherous spring weather to exactly co-ordinate the life-periods of both the flowers and the insects; while in the case of *Vinca*, it must be

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[1] The flower was first described as a cross-pollinating mechanism and figured by Sprengel (1793).

Darwin, who never saw it visited by insects, but who obtained both cross- and self-pollinated seeds, was the first to give a correct account of the working mechanism (1861).

[2] (B. G. O. 1902) A large Bombus (*B. lapidarius*), after frequently visiting flowers on patches of *V. minor* and *V. herbacea*, passed on to adjacent clumps of *V. major*. Its proboscis (12 mm.) being only long enough to reach a little beyond the stigmatic surface, unless considerable force was employed to force the mouth parts into the flower, thus became soon clogged with viscid matter: the bee was then observed to alight on the ground, and took 2–3 minutes to clean its mouth parts; it then flew away apparently wiser.

borne in mind that the plant is not indigenous, and still requires to be studied in its native home.

## Variations and Monstrosities.

1. *Variations in the Phyllotaxis Construction* whereby Tetramery is substituted for pentamery occur, the (4 + 4) formation being represented usually by 4 petals and 4 stamens, the rest of the flower being variable. This occurs in impoverished flowers, and generally it is the last flower on the shoot which shows it. Such flowers are commoner in the case of the reduced type *V. minor*. In such case Tetramery may be of the true type, giving a cruciate calyx and diagonal corolla, while a tendency for the two carpels and two nectaries to alternate with the 4 stamens is interesting, but of doubtful value as evidence for the foliar nature of these glandular emergences.[1]

Similarly very fine flowers may vary to true Hexamery, 6 petals being succeeded by 6 stamens, indicating that the (5 + 5) construction may vary equally well to (6 + 6).

2. '*Double' Flowers* are also found in *V. minor*, and may occur as cultivated forms. In these various anomalies obtain, both as irregular phyllotaxis phenomena, giving corollas of 7–8–9 lobes, and a second corolla-tube at the expense of part of the androecium,[2] and also *fasciation*-phenomena, in which the growth-centre undergoes division, with the result that twin styles are present, and 2 sets of carpels more or less perfectly produced.[3] A point of interest in this latter case is the frequent fusion of the style-heads of the 4 carpels into one mass, with one irregular stigmatic zone, while the style-shafts are still distinct. In other cases the floral axis may be continued, and produce a second malformed bud within the first flower.

Simpler malformations include the production of carpels as more or less green leaf members; and in an interesting example observed, one carpel was represented by a green leaf to which the stylar portion of the other one was fused, bearing its half stigmatic zone and half-plume of hairs on one side.

Such malformations are clearly freaks, and possess little morphological value as evidence of phylogenetic stages; as in the general case monstrosities present little that is really new, but in that they indicate that the construction-mechanism has gone wrong at some point, they serve to illustrate the fact that the normal construction must represent the successful outcome of a definite architectural scheme.

## Fruit and Seed.

After an expansion period of a week to 10 days, the corolla withers and is shed, taking the androecium with it and breaking off the style as it falls, leaving the ovary portions of the carpels and the nectary-lobes surrounded by the green sepals. Non-pollinated flowers are soon wholly shed, the flower-stalk being separated at its insertion. The two carpels enlarge until they overtop the nectary-lobes, and the stalk undergoes further twisting and becomes reflexed, the young fruits being thus hidden away among the foliage leaves and protected from desiccation. The green ovaries, separated as soon as the fused stylar portions are lost, grow to form diverging shining green pods, so curiously like folded foliage-leaves that it is often difficult to find them. Either both or only one may be developed, and as in *Asclĕpias*, single pods are even more usual, owing to the unsatisfactory fruiting character of the plant.[4]

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[1] *V. major*, 1902, a good tetramerous flower with 4 sepals, 4 petals, and 4 stamens, presenting a square aperture to the corolla-tube, showed 2 carpels superposed to 2 petals and thus diagonally orientated.

[2] 1902, an excellent fasciation phenomenon observed in a 6-parted flower of *V. major*, twin gynoecia were represented by 2 fully formed sets of 2 carpels, and 4 nectary lobes, the twin style-shafts were only fused in the style-head.

[3] Also a true double corolla of 7–8–9 segments within the first, giving the 'Hose-in-hose' type of monstrosity (*V. minor*).

[4] Fruits are somewhat rarely produced (Oxford). Sowerby (1797) figures good fruits for Norwich, the limit of distribution.

To make plants fruit well, they should be grown in small pots and all new vegetative shoots removed (Loudon).

This appears to be due in the case of *Vinca* to the enormous growth of the vegetative shoots in May and June, and under ordinary conditions the flowers are all shed, even when carefully cross-pollinated. The pods are green, 30 mm. long by 5 in diameter, spindle shaped, and very inconspicuous. When ripe (August 25th), the pod splits along its suture and opens back to the form of a lanceolate leaf, turning brown-black and exposing the seeds, of which in this country usually only 1–2 are produced, attached to the suture one above the other.

The seed, 11 mm. long by 4 wide (10 by 2½ when dry), are dark brown in colour with a netted surface, and in form remarkably like small date-stones, one side, that of the hilum, being deeply grooved, and they are attached to the carpel wall by a delicate funicle. Transverse section shows that the embryo-sac is rolled round along its length to a crescentic section; the raphe forms a well-marked ridge between the lobes. Section in the plane of the raphe shows a fairly well-developed embryo, the two cotyledons of which are arranged in the direction of compression, and thus both cut in section; it is embedded in a mass of endosperm, the cell-walls of which are much thickened, and the contents include fat and proteid. The testa is formed by crushed dead layers, one outermost layer consisting of large pitted elements.

*Note* that the embryo is protected mainly by the cellulose walls of the endosperm and by the testa; supplied with food in the form of cellulose, fat, and proteid, stored chiefly in the endosperm cells and to a less extent in its own tissues; and that there is no modification for distant dispersal; the fruits droop and shed their rather large seeds directly on the soil beneath, in a manner suggestive of some other shade-inhabiting plants (cf. *Viola odorata*).

Section of the ovary-wall shows little modification; the outer half consists of unmodified cellulose-walled tissue, the inner half consists of (2–3) layers of larger sclerosed and pitted cells, an inner lining series becomes a layer of lignified transverse fibres. Such sclerosis of the inner tissue may indicate a certain amount of protective adaptation for the young seeds, and on desiccation the contraction of the outer cellulose walls enables the wall to open out flat; it closes again on being wetted, but the movements are imperfect, and the seeds are not immediately dropped when the pod first opens.

## Comparison of Allied Types.

I. **Vinca minor,** L., a closely similar plant, but smaller in all its parts, much commoner in a wild state in Great Britain, though again rather sporadic in distribution, and extending over South Europe.

Flowers are produced from March to May, and strays may occur in autumn (Oct.–Nov.). The trailing shoots are only 1–2 ft. long, and the inflorescence region is reduced to a single lateral flower (less commonly 1–2). The flowers are of the same violet-blue colour; white forms and 'double' monstrosities also occur. The corolla is about 30 mm. across, and the flower repeats the structure of *V. major* on a smaller scale. The orientation and floral diagrams are similar, but the 2 carpels are much less regular in position. Tetramerous and hexamerous variations are also frequently met with. The floral mechanism is similar, but the working distance of the flower is reduced to 10–11 mm. at the extreme limit, with a minimum of 7 mm., the length of the style.[1]

The flowers can thus be visited by various Humble-bees, e.g. *Bombus hortorum* (21 mm.), *B. lapidarius* (12–14 mm.), *B. agrorum* (12–15 mm.), and even *B. terrestris* (7–9 mm.),

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[1] The flower differs from that of *V. major* in a few minor points: the sepals have no hairs or glandular emergences; the corolla-tube, 10–11 mm. in length, is composed of Zona Mediata for 4½ mm. All details of hair mechanism are identical, but the stylar plume is not so fine, and the guard-ridge (corona) is only just recognizable between the petals; the nectary lobes are yellowish, equal in height to the ovaries, and closely packed with them: the orange-pigmentation of the style-collar and shaft-tissues is entirely wanting. *White-flowered* varieties have no trace of the violet pigment, or only a few lines of purple-red anthocyan cells in the lower corolla-tube, identical with those occurring in the epidermis of the vegetative shoots. (Blue flowers may similarly show a red-purple colour in this part of the corolla.)

as also the fly *Bombilius* (10 mm.). As in the case of the contemporary flowers of *V. major*, *Anthophora pilipes* is by far the neatest worker, and visits the flowers at a much greater rate.

The plants do not fruit any more freely than those of *V. major*, though a few may usually be found on searching carefully. These ripen and shed their seeds in September; the follicles are essentially similar to those of *V. major*, but smaller (25 mm.), and contain as many as 4 seeds (6 mm. by 2). The seeds are identical with those of *V. major*, and the fruit-wall similar, but the sclerosed inner layer is not pitted; the dehiscence mechanism is thus the same, and there is again no modification for distant dispersal.

*Vinca herbacea*, Waldst. and Kit.[1] *The Hungarian Periwinkle.*

Introduced from the Berlin Botanic Garden about 1818, and often cultivated. It grows on sandy chalk hills in Hungary, S. Europe, and Asia Minor, in much more open and exposed situations than the British species. The flowers are essentially similar to those of *V. minor*, but are much more freely produced; the prostrate decussate leafy shoots producing as many as 6–7 flowers, 2–3 of which may be out simultaneously. The plant is not evergreen, but perennates underground, all the aerial portions disappearing in winter and the flowering shoots coming up in March.

The violet-blue flowers are 25 mm. across, the corolla-tube 10 mm., of which the outer chamber comprises 2–3 mm., and the Zona Mediata 7 mm. Otherwise the construction is identical, and the flowers are visited by the same insects as *V. minor*. The ramification of the shoot is more pronounced, and accessory vegetative buds, arising between the flowers and their subtending leaves, continue the growth so rapidly in some cases that the shoots look like dichasial formations. The decussate phyllotaxis is less regular, and may vary to (1 + 1), i. e. alternate leaves. The plants do not appear to set fruit in this country.

### II. **Amsonia Tabernaemontana**,[2] Walt. *Amsonia.*

A hardy herbaceous plant with perennating underground rhizome sending up annual flowering shoots to the height of 2–3 feet. A somewhat variable form, growing in low ground and damp situations in SE. United States, where it flowers in April and May, N. Carolina and Illinois, to Florida and Texas. Long cultivated in this country (1816), but very doubtfully the plant grown under this name by Miller in 1759. It is grown in herbaceous borders as a decorative plant for the sake of the corymbose panicles of pale blue flowers produced in June and July. It is of special interest as presenting the *generalized characters of the group with a much simpler condition in the floral mechanism.* In ordinary garden cultivation it fruits and seeds freely, and these structures again present the general *Vinca* characters, and are readily obtained in large quantities.

Erect strong shoots come above ground towards the end of April, bearing foliage leaves in considerable numbers, arranged with normal asymmetrical Fibonacci phyllotaxis, and terminated by the inflorescence, the flowers of which at this date show all early construction-stages similar to the first phases of *Vinca major*. The inflorescence is, however, a normal terminal racemose panicle with terminal flower, branched to the third degree. (T flower expands about June 1st.)

Smaller shoots on the underground stem, taken at the end of October, when the aerial axes die off at the first frosts, show the leading flowers developed as far as the commencement of the carpels. The phyllotaxis pattern of the vegetative apex is very regular, good examples of Fibonacci system (5 + 8) being found.

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[1] Waldstein and Kitaibel (1802).

[2] The name *Amsonia* was given to the plant by Clayton in remembrance of Charles Amson of S. Carolina (Flora of Virginia, 1762). Linnaeus (1762) placed it in the genus *Tabernaemontana*, a group named by Plumier after the herbalist Tabernaemontanus (*Kreuterbuch*, 1589). The genus *Amsonia* was restored by Walter (*Flora of Carolina*, 1788), and the name has been written *Amsonia Amsonia* (Britton, 1894).

The inflorescence continues the spiral construction, the lateral branches arising in the axils of the uppermost reduced leaf-members. Normal bracts and prophylls are present at the points of ramification, and the orientation of the flower is also normal, the odd sepal, No. 2, being as far as can be seen median posterior.

The peculiarities of *Vinca* are therefore quite wanting, and *Amsonia* presents a perfectly normal type of shoot-construction. Vegetative buds (3–5) in the axils of the uppermost leaves below the inflorescence region continue the ramification of the assimilating shoots and may produce a second crop of flowers.

The floral diagram agrees with that of *Vinca*, and the petals are similarly apparently rolled up with a right-hand twist ( = *left convolute*) in the bud stage, and the 2 carpels are in the median plane (cf. sepal 2). The nectary, however, is only represented by a swollen ring (*disc*) around the base of the carpels. The calyx is gamophyllous as far as the ovary extends (2 mm.), the free sepals being reduced to small teeth; the corolla-tube, 9 mm. in length, 2 mm. wide below, and 3 mm. higher up, is composed of a Zona Mediata (6 mm.) and a gamopetalous zone (3 mm.). The petals are strap-shaped, only very slightly anisophyllous, 10–12 mm. long, and 2–3 mm. wide. They may be widely expanded, or more or less recurved, and are of a pale violet-blue colour, darker towards the 'eye' of the flower. The same pigment (anthocyan derivative) being localized in the epidermal cells.

The entrance to the corolla-tube is fringed with shaggy hairs, and a well-marked wheel-like series of tufts constitutes a guard-fringe to the aperture, 9 mm. from the nectary.

The stamens are quite simple in character, with anthers 1 mm. long, and filaments less than 2 mm.; the anthers converge towards the axis of the corolla-tube and overarch the glandular stigma-head. The anther-lobes are yellow-brown to green, black when shed, and the pollen is loose and dusty: descending hair-fringes from the stamen-insertions line the Zona Mediata, and with the hairs around the gamopetalous zone mark out 5 lines of approach to the nectary, which are thus, as in *Vinca*, antipetalous; and their position is indicated by the intense spot of colour at the base of the petal, which thus becomes a 'honey-guide', though possibly not originally placed here for this function.

The gynoecium is equally apocarpous in the ovary region, but the receptacle is not at all crateriform, and the carpels contain 2 rows of 5–7 ovules in each loculus: the carpels unite in the style-shaft, and the terminal stigmatic head-piece, slightly bilobed at the apex and papillose, is glandular and secreting above, and produced beneath into a recurved distinct *collar*, in the hollow below which is the receptive surface.

The mechanism is homogamous, and depends for its efficiency on the correlation between the growth of the Zona Mediata and that of the style-shaft.

The style-head is thus brought exactly beneath the anthers as they dehisce; but there is no adaptation to maintain it in a fixed position.

The working distance of the flower is between 7 and 10 mm.; and the pollen being concealed beneath the outer guard-fringe, and the honey also hidden at the base of the tube, the flowers can only be visited for the sake of their honey which again can only be reached by a long and delicate proboscis.

As in *Vinca*, note that all the hair-fringes also have the function of protecting the essential organs, including the nectary-secretion, from desiccation; but from such a standpoint alone it is difficult to explain the descending fringes below the stamens, and the fact that between the stamens the corolla-tube is left clear.

The flowers are thus clearly adapted for the visits of bees and Lepidoptera with proboscides over 7 mm. in length, and they are visited by butterflies, moths, and bees in gardens in this country, *Bombus hortorum* and *Anthophora pilipes* being the most assiduous workers.

Since the stamens tend to shed directly on the style-head, and the stigmatic surface is protected by the recurved collar, self-pollination (autogamy) would appear to be eliminated. The working of the mechanism is sufficiently clear; the delicate proboscis of a Lepidopterous insect, being inserted between the black anther-tips, follows the paths marked out by the descending fringes, along the curve of the corolla-tube, to the nectary; and on its withdrawal it comes back in the median line, dragging past the collar of the style-head, and so scraping off any pollen which may be on it brought from another flower. It then again becomes touched with viscid matter as it drags over the style-head (glandular region), and on being pulled up past the anthers it collects more pollen which has remained in the vicinity of the anther-lobes.

Self-pollination of the same flower is thus prevented, but pollination between flowers of the same inflorescence and those of the same plant will be readily effected.

Isolated plants set fruit freely, but only a relatively small number (25) of the whole inflorescence.

The flower is rather small for the accommodation of the bulky mouth parts of most bees, and these insects in trying to obtain honey treat the mechanism with considerable violence, a fact which again suggests that the mechanism is becoming restricted to the visits of the neatest workers (Lepidoptera).

*Note* that the collar of the style-head, which in *Vinca* apparently merely acts as a guide to enable the proboscis to be dragged smoothly over the stigmatic zone when it is pulled up out of the flower, is here definitely functional as a scraper, and the receptive surface is correlated with this action. In this respect *Amsonia* presents a different line of specialization; otherwise its whole mechanism is a much simpler edition of that of *Vinca*, but also presents an approach to more generalized characters, so that it may be clearly regarded as a much closer approximation to the hypothetical ancestral form of the *Vinca* series (*Apocynaceae*).

The fruits produced from the essentially apocarpous gynoecium are long divergent simple pods, 3–5 inches long, a pair to each flower corresponding to the carpels, and completely free from each other, cylindrical, smooth and green (120 mm. by 3 in diameter). Each dehisces when ripe (October) by the original suture; the opened carpel closely resembling a withered foliage leaf: they contain about 10–12 seeds arranged in alternating series, as they grow from either side of the suture.

Structure of the fruit-wall is simple: the epidermal layer is covered with a thick smooth cuticle, the mass of the wall remains undifferentiated (12–15 cells thick), while 1–2 of the innermost layers become longitudinal fibres; and owing to the presence of this lignified layer, the fruits open on desiccation and close again when wetted.

The seeds also resemble those of *Vinca*, being cylindrical with ends bevelled by mutual pressures, the original shape of the ovule being lost, 7 mm. by 2, the testa appearing corky, and the raphe distinguishable down one side. Section shows a fairly large embryo, with 2 cotyledons lying in a plane at right angles to that of the raphe (as in *Vinca*), surrounded by a broad layer of endosperm. The cells of both embryo and endosperm store proteid and fatty oil, and the endosperm cell-walls are also slightly thickened. The testa is composed of three distinct layers, the interior one being pigmented (brown), and a middle layer of dead crushed cells, which become thrown into irregular longitudinal folds. There is again no modification for distant dispersal, and the seeds fall out of the pods around the parent plant.

### III. **Nerium**[1] **Oleander**[2], L.

*Oleander.*
*Rose Bay.*[3]

An evergreen shrub, growing 8–10 feet high, indigenous to the Mediterranean region and East Indies, growing in damp places and by the sides of streams; cultivated in this country in greenhouses, or in sheltered situations in the south, from time immemorial,

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[1] Nerium of Pliny; Νήριον of Dioscorides; the *Nerion* of Bauhin's Pinax (1623), and a genus of Tournefort (1700). *Nerium* as corrected by Linnaeus (1737).

[2] Oleander, the medicinal name of the plant, from the Italian name, Oleandro of Lobelius (1576). The Oleander of shops, Gerard (1597) and Parkinson (1649).

[3] Rose Bay, from the Laurel-like foliage.

having been recorded by Gerard in 1596. The phyllotaxis system is symmetrical of the special (3 + 3) type, which may be regarded as a variant of the decussate (2 + 2), and there is no marked system of perennation.

The inflorescence terminates the vegetative shoots of the previous year, and possesses a terminal flower and a limited system of ramification: the leading branches being in whorls of 3, in agreement with the phyllotaxis of the main shoot, but these reduce immediately to dichasia, the terminations of which are few-flowered monochasia. All bracts and prophylls are normally present, and the system thus reduces along legitimate lines. The terminal flower expands first, and subsequent blossoms in the order of their construction, many being functional contemporaneously.

The flowers are large and showy, and of a bright rose colour,[1] 40–50 mm. in diameter, and of the general *Vinca* type of construction. They are produced from the end of May to July (conservatory). Special interest attaches to the *floral mechanism*, which reaches, along the general plan outlined in *Vinca*, a much greater perfection of specialization in correlation with the visits of Lepidoptera, and thus helps to clear up points which may be vague in these allied forms.

The quincuncial calyx is insignificant, being sufficiently gamophyllous to cover the ovary and base of the corolla-tube, and the receptacle is distinctly crateriform.

The corolla, narrowly tubular below, as a Zona Mediata, 13 mm. long, by 2–3 mm. in diameter, expands slightly upwards and is continued as a funnel-shaped gamopetalous zone 9 mm. long by 10 in diameter, the free petals being 22 by 20; these last again are anisophyllous, the right edge (as seen in elevation) is greatly developed and waved, being folded inside in the bud, and the corolla is thus right convolute, or the reverse of that of *Vinca*, whatever the 'genetic' spiral of the calyx may be, and equally a specific constant for which no reason can be given. (The buds thus appear as if rolled up with a *left-hand* twist.)

The entrance to the corolla is guarded by a strongly marked corona-ridge development, 5 mm. deep, which is irregularly produced into strap or tooth-like segments, 5–6 of which constitute antipetalous lobes, 5 mm. in length, thus emphasizing to a still greater extent the guard-ridge of *Vinca*.

The corona, as also the gamopetalous zone, is marked by bright crimson streaks following the course of the main vascular bundles, and thus serving as 'honey-guides', as they converge to the base of the flower, and mark the usual antipetalous paths to the honey within the inner chamber.

Guard-fringes of hairs are, however, conspicuously absent; but the lines of descending hairs from the filaments of the stamens are continued down the narrow Zona Mediata, the corolla-tube between the filaments remaining smooth to the base; so that the 5 antipetalous paths limited below by fringe-ridges allow access to the secreting surface which is not present as a mere disc-ring, nor as special disc-emergences (*Vinca*), but as a considerable glandular development of the surface of the Zona Mediata, which is wrinkled and corrugated for a distance of 4 mm. from the base, thus affording a greatly increased secreting surface, and implying a greater honey-supply. It is interesting to note that the pink tint of the corolla and the attractive streaks stops at the insertion of the filaments; and the cavity of the Zona Mediata, which is invisible from the entrance to the flower, is a pale yellow colour only (or slightly pink at the base): such a fact points to the conclusion that whatever may have been the origin of the red pigment, it is now definitely localized in correlation with insect attraction, and the special development of colour-stripes is really utilized as a honey-guide. As in the *Vinca* type the special features of the mechanism were concerned with the mutual relations of the stamens and style-head, so in the Oleander these become

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[1] Due, as in the other types, to anthocyan derivatives localized in epidermal cells: white varieties in which this pigment is absent also occur (common in Crete), and 'double' monstrosities were cultivated by Parkinson.

even more complicated, although the fundamental idea of the construction remains the same; this being, as traced in *Amsonia*, that a long delicate proboscis shall feel its way along the curve of the corolla-tube to an invisible supply of honey, and then be withdrawn along the axis of the tube, first touching a viscid surface of the style and then removing pollen from the anthers; pollen from another flower being rubbed off in the process on a stigmatic surface which may have, as in *Amsonia*, a special scraper.

The elaboration of this mechanism is seen in *Nerium* in the structure of the stamens. The filaments are short and stout, and converge toward the axial line of the flower-tube, so that the anthers just come into lateral contact; the loculi of the anthers are extremely small (2 mm. only), but the anthers are produced below into relatively long curved club-shaped tail-processes 2 mm. long, while their apices are prolonged into a long hairy process, 10–12 mm. in length, fringed with silky hairs 2 mm. long. These 5 exaggerated connective processes are at first loosely spirally twisted into a strand as if with a right-hand twist; when uncoiled they serve to block the entrance to the corolla-tube and subserve protection as much from desiccation as from 'unbidden guests'.

The special feature of the stamen is, however, the fact that each filament, at a point immediately below the anther, is *fused with the style-head*, so that the conical cluster of 5 anthers is thus kept fixed and almost rigid; the mechanism for this purpose being in fact simpler and far more effectual than that adopted in *Vinca*.

The pollen is viscid, and is shed in definite masses, remaining in position between the lobes of adjacent anthers, which, being in lateral contact themselves, roof in a 'pollenic chamber' around the glandular style-head.

The gynoecium is again apocarpous below, sunk $\frac{1}{3}$ in the receptacle cup; each loculus contains 2 rows of about 12 anatropous ovules, and the stylar regions fuse to form a stout spindle-shaped style-shaft 15 mm. in length. The rounded style-head is slightly bilobed at the free apex, 1 mm. above a circular ridge, by means of which it fuses with the stamen filaments. The papillose stigmatic surface is situated immediately *beneath* the point of fusion, and thus below and external to the almost closed pollenic chamber.

The flowers are homogamous, and are essentially cross-pollinating mechanisms requiring insect agents to perform the pollinating function.

The minimum length of proboscis required by an insect, which can put its head right down the gamopetalous zone, will be given by the length of the Zona Mediata (12 mm.), so that long-tongued bees may still work the flower by crawling right into the bell. The extreme range for Lepidoptera will be given by the full length of the corolla-tube and corona-processes, since such insects cannot get their wings into the flower (30 mm.).

The entrance to the inner chamber containing the nectary is restricted to 5 narrow antipetalous slits between the stout stamen filaments, and these are still further blocked by the manner in which the curved anther-tails project down into them. It will be observed that these curved processes, which represent a distinctly new departure, are of extreme importance; they bend in on the filaments in such a way that while free access is permitted for a narrow thread-like proboscis to feel its way along the smooth surface of the corolla-tube between the hair fringes, on withdrawal of the proboscis by pulling it straight up in the median line, it is naturally directed into the slits *between the processes of adjacent anthers*, and so rubs against the stigmatic surface left exposed between the points of fusion with the filaments; thus any pollen adhering to the proboscis tends to be scraped off on to the stigmatic surface, while the proboscis then receives pollen from the loculi of the anthers higher up, which remains collected in the narrow slits between adjacent anthers.

One obtains a good idea of the way this mechanism works by remembering that when inserting a long and delicate tactile organ into a long dark cavity, the interior of which is hidden from sight, an insect, just like anybody else, naturally feels its way from a point it can see; and, in this case, the proboscis tip follows the surface of the corolla-tube as it passes down out of sight, and the lines of descending hairs afford a means of keeping it straight on its course. On withdrawal, however, it is pulled straight up, kept off the descending hair-fringes, and tends to follow the line of the smooth axial style-shaft, and is thus unavoidably guided into the slits bounded by the smooth basal lobes of the anthers, since these curve round sufficiently to touch their filaments. A distinct chance for cross-pollination is thus afforded, since pollen brought from one flower is thus rubbed off on the stigmatic surface of another before fresh pollen can be deposited on it; the entering proboscis by following the corolla surface, and possibly assisted by the guide-lines, avoids the anther-cone altogether. Cross-pollination between flowers of the same inflorescence is however possible, since several flowers may be expanded simultaneously: this has the same effect as self-pollination, and the plants are freely fertile to their own pollen under these conditions; an isolated plant in a greenhouse visited only by Humble-bees will, in fact, set fruit freely. Still, so far as each individual blossom is concerned, the mechanism for cross-pollination presents an extremely high degree of specialization, and can have no other interpretation. While an advance on the *Vinca* type is shown, in that the growth correlation of the Zona Mediata and style-shaft is still better effected by a definite cell-fusion between style-head and filaments, the central chamber is also more effectually blocked, since large bees cannot force the entrance; while the working mechanism is maintained with a remarkable degree of accuracy, and being no longer dependent on turgidity-relations of tissues, is as successful in old flowers as in freshly expanded ones.

In South Europe (Riviera) the flowers are visited by the Oleander Hawk Moth (*Deilephila Nerii*), which flies at dusk; the caterpillars of this beautiful malachite-coloured moth feed on the poisonous foliage.

The fruits, freely produced in a greenhouse, though rarely in the open air (cf. Gerard, 1597), are in the form of long paired pods (120 mm.), and ripen in August and September. On dehiscence the brown tufted seeds are drifted out, largely by the distension of their woolly hair covering on drying.

The structure of the fruit-wall is simple; the outer layers are collenchymatous and shrivel up, the inner consist of obliquely transverse fibres, 2–3 layers thick. Opening and closing movements due to hygroscopic tensions are thus well marked. The seeds are numerous and really somewhat small (3 mm. by 1), but in addition possess a stiff stalk (2 mm.) and a chalazal tail (1 mm). They are developed from anatropous ovules, and section in the plane of the raphe which runs down one side is thus spindle-shaped. The testa consists of dead brown layers; the embryo, endosperm, and orientation of the cotyledons agree with those of preceding types, but a new departure is seen in the remarkable development of the epidermal cells into brown hairs which may be an inch in length. These are all directed towards the apex of the fruit, and away from the micropyle and funicle. The hairs on the funicle are short and stiff, those on the seed proper long and woolly; while at the chalazal end they form a plume-tuft 10–15 mm. in length. When shed from the pod it is clear that this tuft of hairs will delay the fall of the seed, and that they will be wafted by the wind, and fall with the barbed funicle-spike pointing downwards. The hair-covering thus combines the advantages of a 'pappus' and a creeping or 'boring tip'. To what extent this hairy covering has been initiated with a view to wind-dispersal, rather than as a xerophytic adaptation in the exposed fruit-structures, remains very doubtful; but having been initiated it is clear that it may have a very definite dispersal significance at the present time, since the arrow-like form of the seed with differentiated regions appears as a secondary improvement of an original merely hairy type.

A semi-double *monstrous* form in cultivation is of interest in that it presents the 'hose-in-hose' construction: two distinct five-parted corolla-tubes being present one within the other, the petals alternating, and the inner tube possessing normal stamens and floral mechanism. (Cf. Hose-in-Hose *Primula* and *Jasminum primulinum*.)

The special feature to note in these cases being the elasticity of the construction plan which admits of 2 cycles of the (5 + 5) corolla formation being laid down before the sporophylls are commenced; or, as some would say, the second corolla series is homologous with primordia which in the normal flower are subsequently developed as stamens. It is also interesting to note that the *outer corolla* puts in a gamopetalous zone, and produces the normal emergences (corona) of the type.

The colour also varies to pale yellow.

## Theoretical Considerations.

As a floral type, and the only native representative of a remarkable group of plants, *Vinca* abounds in points of special interest.

The peculiar vegetative habit, with trailing decussate shoots bearing evergreen leaves and isolated flowers, is clearly wholly secondary: and in this respect the stout erect shoots of *Amsonia*, with abundant foliage leaves produced in normal asymmetrical phyllotaxis, and terminal panicles of a considerable number of flowers, represents a generalized case which comes into line with the ordinary run of vegetation, and is thus undoubtedly nearer the ancestral form.

*Amsonia* itself is, however, modified for perennation over a cold winter, by death of the overground portion and development of lateral subterranean shoots which commence laying down in autumn the flowers of the succeeding summer; so that *Nerium*, which has essentially the same general type of shoot-construction (but with a special case of symmetrical phyllotaxis), is still nearer the original form: the shoots end in terminal panicles, and buds borne in the axils of the leaves immediately below the inflorescence region continue the vegetative growth and bear flowers in the next season. *Nerium* is again a sub-tropical plant, and the group as a whole is a tropical one. There can thus be little doubt that the type dates back to a tropical tree-phylum, and that *Vinca* is highly specialized in connexion with its special mode of perennation in colder latitudes: the apex of each shoot continues its vegetative growth during the season, while the lateral inflorescence branches reduce to the single terminal flower, development of which is so hastened that no prophylls are left to continue the ramification, and the first lateral members of the floral shoot enter into the construction of the perianth. This accounts for the unusual orientation of the quincuncial calyx which alone retains the original asymmetrical Fibonacci phyllotaxis, though, with this exception, the floral construction is perfectly normal as a form of the *Mean Type* of floral organization (cf. *Ribes*), in which 2 symmetrically placed carpels are alone retained after a symmetrical $(5 + 5)$ construction in the petals and stamens.

The floral diagram thus remains constant for all these types; and the more generalized scheme of inflorescence continued as a compound panicle, more or less reduced along successive ramifications, is traced quite clearly in *Amsonia*, and less clearly in *Nerium*. The extreme reduction obtains in *V. minor*, in which the vegetative shoots become limited to a single flower.

While the construction system as plotted in the floral-diagram thus presents remarkable constancy, the only variation being found in the last phase of reduction (*V. minor*), in the irregularity of the orientation of the carpels, the main interest of the type centres in the evolution of the *special mechanism* and its relation to cross-pollination. Of the types considered, *Amsonia* clearly retains the simplest phase, and from the normal character of its stamens is evidently nearest the ancestral state. The primary feature of the mechanism consists in the elongation of the corolla-tube, a feature which may well have been originally initiated as a protective adaptation for the enclosed ovary and nectary, just as the gamophylly of the calyx has still no further function. Similarly the production of hairs closing the orifice of the corolla would be equally protective for the essential organs and stigmatic surface. But the subsequent development of these features, the correlated elongation of the Zona Mediata and style-shaft, and the specialization of hairs in different regions, can only be explained as modifications in connexion with insect visits. Such a condition of affairs is again very generally met with, and may occur in various phyla which are not necessarily at all closely connected, e.g. *Phlox*, *Verbena*, *Primula*, *Jasminum*, *Gentiana*: the common features being a long narrow-bored tube enclosing the ovary at the base, with a long style-shaft carrying the stigmatic surface to the vicinity of the anthers placed near the orifice of the tube. This mechanism is superimposed on a construction of the *Mean Type*, which is further remarkable for the possession of an apocarpous ovary, and this is purely apocarpous in development, and only becomes truly syncarpous (not *gamocarpous*) by a true and wholly secondary fusion, in part, to assist in the production of a firm style-shaft. Just as this tubular mechanism may be reached or approximated, as a certain optimum floral construction in quite different phyla, so that it cannot be taken as a necessary guide to close relationship, so also the presence of apocarpy in a mean type of floral diagram may be taken to suggest that the *Vinca* type dates back to an independent evolution from an extremely ancient stock, and that gamopetaly may have in this case arisen in old apocarpous phyla (cf. *Asclepias*).

The special mechanism of *Vinca* and its allies, however, passes considerably beyond such a generalized gamopetalous condition, and the first path of specialization is noticed in the differentiation of the stigmatic surface. In *Amsonia* this remains bilobed and glandular, and has every appearance of being receptive, but the true stigmatic region has moved away from the apex, and is not only lateral, but covered by a protective outgrowth. Although the stamens remain quite normal, and the anthers dehisce by slits and shed the pollen forwards on the style-head, it is thus prevented from reaching the stigmatic surface, and autogamy becomes eliminated. Entrance to the inner chamber of the flower is also blocked in the median line by the great development of the style-head, and lateral access must follow the walls of the corolla-tube between the converging filaments: the old stigmatic surface then becomes utilized as a gland, and its secretion plays a definite part in connexion with the function of the style-collar as a scraper.

The localization of the paths to the honey to minute guarded grooves at once characterizes the mechanism as specially adapted for Lepidoptera rather than bees (cf. *Verbena*).

*Vinca* again goes several stages further, but although essentially the same in general plan and idea, it does not follow on directly from the *Amsonia* type, but has peculiarities of its own; as seen for example in the different method adopted for blocking the entrance by connective flaps and style-plume, the pollinia-like masses of pollen shed on a non-secreting style-head and the great development of nectary lobes. Improvement is exhibited in the adjustment of the mechanism, and the manner in which the peculiar curvatures of the filaments maintain the top-heavy style in its central position, and emphasize the entrance slits.

Similarly in *Nerium*, although the structure is the same in plan, and additional features are present which increase the complexity of the mechanism, there is no direct connexion with that of *Vinca*; and all three types, although roughly representing progressive phases of specialization, are not necessarily successive ones, but are rather to be considered as divergent branches from a common stock.

Thus in *Nerium*, the filaments of the stamens are again quite simple; specialization here only affects the anther-portions; the rigidity of the mechanism is obtained by direct cell-fusion with the style-head which is again nearer the simpler type of *Amsonia*, it being the collar-ridge which has been fused up with the filaments, and the stigmatic surface is beneath it.

The importance of *Nerium*, however, lies in the fact *that processes from the anther-lobes increase the efficiency of the slits*, and only admit of a delicate proboscis being withdrawn along a very exact and narrow groove, a prolongation, below the level of the stigmatic surface, of the space between the closely applied adjacent anther-lobes. It is clear that if the viscid pollen-masses specialize a little more as definite pollinia, such a 'slit-mechanism' would easily pass on to the type of *Asclepias*.

While so much specialization is thus lavished on the floral mechanism, it is interesting to note that the fruits of all these types remain in a remarkably undifferentiated and primitive condition, and with the withering and shedding of the fused carpellary portions which constitute the style, they develop as typical follicles, and when ripe dehisce by the original suture, and then present a form remarkably like the simple foliage leaves of the vegetative shoots. Only in *Nerium*, in which the developing fruits are freely exposed during a hot summer season, does protective adaptation in the ovary-wall and seed-coat attain any particular complexity, the investment of woolly hairs on the developing seeds, which pack the internal cavity of the ovary, being possibly ultimately utilized to assist the dispersal of the seeds by the agency of the wind.

Around *Vinca*, the first well-known European form, and *Apocynum* of North Temperate America, have been grouped 130 genera and nearly 1,000 species of plants to constitute the family *Apocynaceae* (cf. Schumann, 1895, Engler and Prantl), since the same general lines of floral construction and mechanism obtain in all.

The first conception of such a group was put forward by Linnaeus as Nat. Order 29, the *Contorti* (1750), and founded on the curiously constant anisophyllous convolute corolla. The Contorti of Linnaeus included *Vinca*, *Nerium*, *Tabernaemontana*, as well as genera now conventionally isolated as the *Asclepiadaceae.* The family *Apocineae* was instituted by Jussieu (1789), and included the same types together with others (29 in all) of doubtful relationship.

The group *Apocynaceae* is essentially tropical and ranges over the whole world; thus the largest genera are :—*Aspidosperma* (45), from S. and Central America, *Gymnopogon* (50), Madagascar, Australia, and Pacific Islands, and *Rauwolfia* (45), from the Tropics of the Old and New World. *Vinca* includes 5 species, *Amsonia* 7, and *Nerium* 3, so that none of these types can be said to be remarkably successful at the present day; while *V. minor* again reaches the highest northern latitudes in Europe, and species of *Apocynum* in America. The bulk of the genera have the less specialized type of mechanism; one or two forms only possess more carpels (5 in West African *Pleiocarpa*); thus indicating probably a simpler ancestral condition, in which an apocarpous gynoecium of 5 carpels would seem to suggest as ancient a type as can be found in any other gamopetalous phylum (cf. *Asclepias*).

## NOTE ON APPEARANCES OF TWISTING.

In dealing with the appearances of Twisting observed in plant stems and the corollas of many flowers, certain conventions may be taken as established in common affairs, and these may with advantage be accepted as the standpoint from which to approach the consideration of the growth-twists of plant-forms.

When the right hand is used for doing work, it will be observed that greater power can be utilized in directing a turn outwards away from the body than inwards towards the body, and thus when pressure is brought to bear on a tool, an outward wrench gives the greatest mechanical advantage. As a consequence tools are constructed to be turned in this direction, a familiar example being the use of the gimlet, screwdriver, and corkscrew. This movement becomes the *right-hand direction*, that of 'screwing up' or winding up; the direction of the movement being again that of the hands of a clock (clock-wise), and thus from left to right (sun-wise).

So generally is this 'right-hand twist' recognized as mechanically advantageous, that *screws* which are made to be 'screwed up' with the right-hand motion are termed *right-hand screws*; and unless required for a special purpose, in which the opposite movement will be an advantage, all screws are made *right-hand.*

It must be carefully noted, however, that a right-hand screw is screwed up with a right-hand movement, and back again with a left-hand movement, while the point of insertion must be on the side of the screw away from the operator. It is the ordinary 'screwing home' movement which gives the name to the screw; while since the penetration of the screw may be regarded as due to the fact that the thread does not uncoil, it follows that the thread is twisted in the opposite direction to that of the screwing-up movement.

*Hence a 'right-hand' screw has really a 'left-hand' thread.* Further, spiral twists are commonly produced by torsion on a group of strands constituting a *rope*, and owing to the fact that torsion is the commonest method in ordinary life of producing this spiral appearance, the nomenclature of *torsion* becomes read into the subject of plant-spirals with which it has nothing whatever to do; similar appearances being not necessarily produced by the same cause. No *torsion* exists in the plant, only a subjective appearance of torsion produced by inequality in the movements of growth-extension; just as a snail by growing more on one side than another may give the impression of having been 'coiled-up,' or flower-petals may grow round each other, as in *Vinca*, and thus appear to be twisted (*contorted*). As already indicated, the use of the term *contorted*, in that it contains the idea of torsion, may be replaced by the more neutral expression *convolute*.

On holding a piece of string in the left hand, and twisting it with the thumb and first finger of the right hand, which is the simplest and most convenient method of making a twist for a right-handed person, using again the outward wrench, which is the right-hand movement, the string when its fibre is twisted closer together is said to be *right-hand string*; if, on the other hand, it unwinds with the normal right-hand twist, it is said to be *left-hand* string. All string, yarn, rope, &c., is again normally made with this right-hand twist and is technically termed right-hand. Left-hand yarn, &c., may be made for special purposes, but the convention is recognized and is thus seen to agree with the convention established in the case of screws. A piece of right-hand string may be very conveniently kept for purposes of reference in dealing with the twist effects seen in plant and animal growth-forms.

There is thus no need to go further than the terminology of ordinary affairs to find conventions for dealing with such phenomena fully established. It remains to take them to the plant and bring them into line with any conventions which may have grown up in botanical literature.

(1) The case of a torsion-effect seen in a growing stem (cf. *Vinca*, flower-stalk) is thus readily settled; on holding the base of the stalk in the left hand and twisting the end of it, it winds up like a piece of right-hand string, and may thus be termed *right-hand*, although there was no twisting in the stem itself, but an asymmetrical growth movement.

(2) When the flower-bud is similarly held by its stalk it will also be found to wind up with a right-hand twist and open with a left. The growth movement of the corolla at first imitates the former twist, but as the flower expands it gives a reverse condition, the movements being again the expression of heterauxesis at different periods.

Taken as a twist, however, it is tempting to apply the terminology right-hand to this case, just as in that of the flower-stalk. But unfortunately for such a standpoint the expression *left-contorted* (convolute) has become recognized in botanical literature as expressing the twist effect of the *Vinca* bud, the idea being (Eichler, 1875), that the left edge of the petal was alone seen from the outside of the unopened bud.

Such a convention may not be wholly satisfactory, since there is no obvious criterion for saying which edge of the petal is left rather than the other, it depends on the standpoint and position of the observer. What is meant is, however, fairly clear on the whole, and it would only promote confusion to change a convention once laid down; the only thing to do is to try and bring it into line with the twist terminology.

This may be readily done by noting that the *last movement* of the flower on expansion is a left-handed one, since the bud opens on applying a left-hand twist to it; and the corolla of *Vinca* may thus be called *left-convolute* from this point of view, which is quite as satisfactory as it would be to call it a right-convolute one because it winds up in the bud with a right-hand twist. Some convention is necessary; there are only two choices, and either would do; the one retained is the one which can be brought into line with previous nomenclature.

## CONVOLUTE PREFLORATION.

The same difficulty of R. and L.-hand applies to the appearance of convolution ('contortion'); different standpoints being taken up according to the position of the observer looking at:—

(1) the unopened bud from the outside;

(2) the floral diagram (ground plan) seen from above;

(3) the sectional elevation, seen i. e. from the axial side.

The established convention of *left-hand* has been defined by saying that the left edge is outside in the bud ((1) outside view of Eichler): but as already noted it is assuming another convention to say which is the left edge. There is no left edge in the diagram (2), while in the elevation (3) the left-hand side is the converse one. In order to retain the expression *left-hand* for (2) and (3), it must be noted that in the diagram (2) the petals are expressed as curves winding into the centre as left-hand curves (against the clock), while in the elevation the left-hand side of the petal, as seen from the floral axis which really produced it, is developed to a greater extent than the other.

Again, it may be noted that of the two ways of looking at the question, one is quite as good and legitimate as the other, since the effect seen has not been produced by any physical phenomenon of *torsion*, and the actual nomenclature adopted is a matter of convenience; the general idea in such a case being to retain the terminology which has priority. *Vinca* is thus said to possess a *left-convolute* corolla, although it winds up in the bud on the application of a right-hand twist, while the twist on the flower-stalk is called right-hand, for the reason that it also winds up with a right hand twist: the case of the corolla being more complex, in that it is really reversed when the flower expands, although the method of overlapping still remains the same. *Note* that prefloration is independent of the twist appearance, since it is possible to imagine petals exactly meeting (valvate), and yet exhibiting a rolled-up series (cf. *Ipomoea*).

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