635.965.28:581.145.1

MEDEDELINGEN LANDBOUWHOGESCHOOL
WAGENINGEN • NEDERLAND • 74-15 (1974)

DEVELOPMENTAL STAGES OF FLOWER FORMATION IN TULIPS, NARCISSI, IRISES, HYACINTHS, AND LILIES

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(Received 13-III-1974)

ABSTRACT

The developmental stages of flower formation in tulips, narcissi, irises, hyacinths, and lilies are described and compared. Common terminology is applied to similar stages of flower formation in each species.

INTRODUCTION

The developmental processes of bulbous crops can be accelerated or retarded rather easily by temperature treatments provided that the required temperature changes are applied at the right time during the sequence of these processes, which must be accurately known for experimentation with flower bulbs. BLAAUW and his co-workers published many drawings illustrating the various stages of flower formation, i.e. WATERSCHOOT (1927) for the hyacinth, MULDER and LUYTEN (1928) for the tulip, HUISMAN and HARTSEMA (1933) for narcissus, BLAAUW (1935) for the iris, and KRIJTHE (1939) for the lily.

In addition to morphological investigations, SASS (1944), UHRING (1973), and PFEIFFER (1934) made histological studies of the tulip, iris, and lily, respectively. The interpretation of their data would be difficult without exact information about the external morphological phenomena. Following some provisional papers (BEIJER, 1952b; 1953; 1954), the publication of a collection of photographs showing the stages of flower development in tulips, hyacinths, daffodils, lilies, and irises may contribute to our understanding of the developmental processes in monocotyledonous crops. The advantage of photographs is that they represent the stages as they are actually observed, in contrast to drawings, which can give a certain interpretation.

MATERIAL AND METHODS

Because of the differences between the crops under study with respect to time of flower formation and treatments to achieve regular development, the material was collected as follows:

1. *Tulips*: Bulbs of cv. 'Apeldoorn' (12 to 13 cm in circumference) from commercial stocks were stored at 20 °C after lifting in the middle of June. From then on until the middle of August, samples of 10 bulbs each were collected 2 to 3 times a week.
2. *Narcissus*: Bulbs of the cv. 'Spring Glory' were used. Because flower formation starts during the spring, bulbs were collected from the field in the period from the middle of April until lifting at the end of June. After lifting, sampling was continued during the period of dry storage at 17 °C until the end of July when the flowers were complete.
3. *Irises*: Bulbs of cv. 'Wedgwood' (10 to 11 cm in circumference) were used. Since flower formation does not take place during dry storage, the bulbs were planted at different times (starting at the end of November) in a greenhouse at 15° to 18 °C, after a treatment at 17 °C for 6 weeks in addition to a dry storage at 30 °C from lifting in the middle of August (BEIJER, 1952a; de MUNK, 1965). Sampling of growing points was done at the beginning and end of the 6 weeks' treatment at 17 °C and 2 to 3 times weekly during the first month after planting.
4. *Hyacinths*: Bulbs of cv. 'L'Innocence' (19 cm in circumference) were lifted at the beginning of July and stored at 25.5 °C. Samples of bulbs from this material were collected weekly until the end of August, when flower formation was completed.
5. *Lilies*: Bulbs of cv. 'Enchantment' (weighing 23 to 27 g) were selected from a commercial stock of bulbs with a circumference of 12 to 14 cm, after lifting at the end of September. Since, as in irises, flower formation does not take place before planting, the bulbs were planted in a greenhouse at 10° to 15 °C after dry storage at 1 °C for 8 weeks. Growing points were collected weekly in the period from planting up to 12 weeks after planting.

To observe the apices, the bulb scales were cut away such that the main bud with the central growing point was freed (BEIJER, 1952b; 1953; 1954; de HERTOGH and AUNG, 1968). After dissection of superfluous tissue and young leaves, the apices, always still fixed on the stem initial and a piece of disc tissue, were stored in 96% ethanol until they were examined and photographed. To increase the contrast between the different organs, the fixed material was stained in a solution of 3 g/l J2 and 12 g/l KJ for 10 to 15 minutes. The photographs were made, after submergence of the apices in water, within some minutes after the staining.

Photography was done with a Leitz Aristophot apparatus equipped with a bellows; the lenses were Zeiss Microtar F1:3.2/2 cm or Leitz Photar 1:1.9/1.25 cm or 1:2.5/2.5 cm and the film Ilford Pan F.

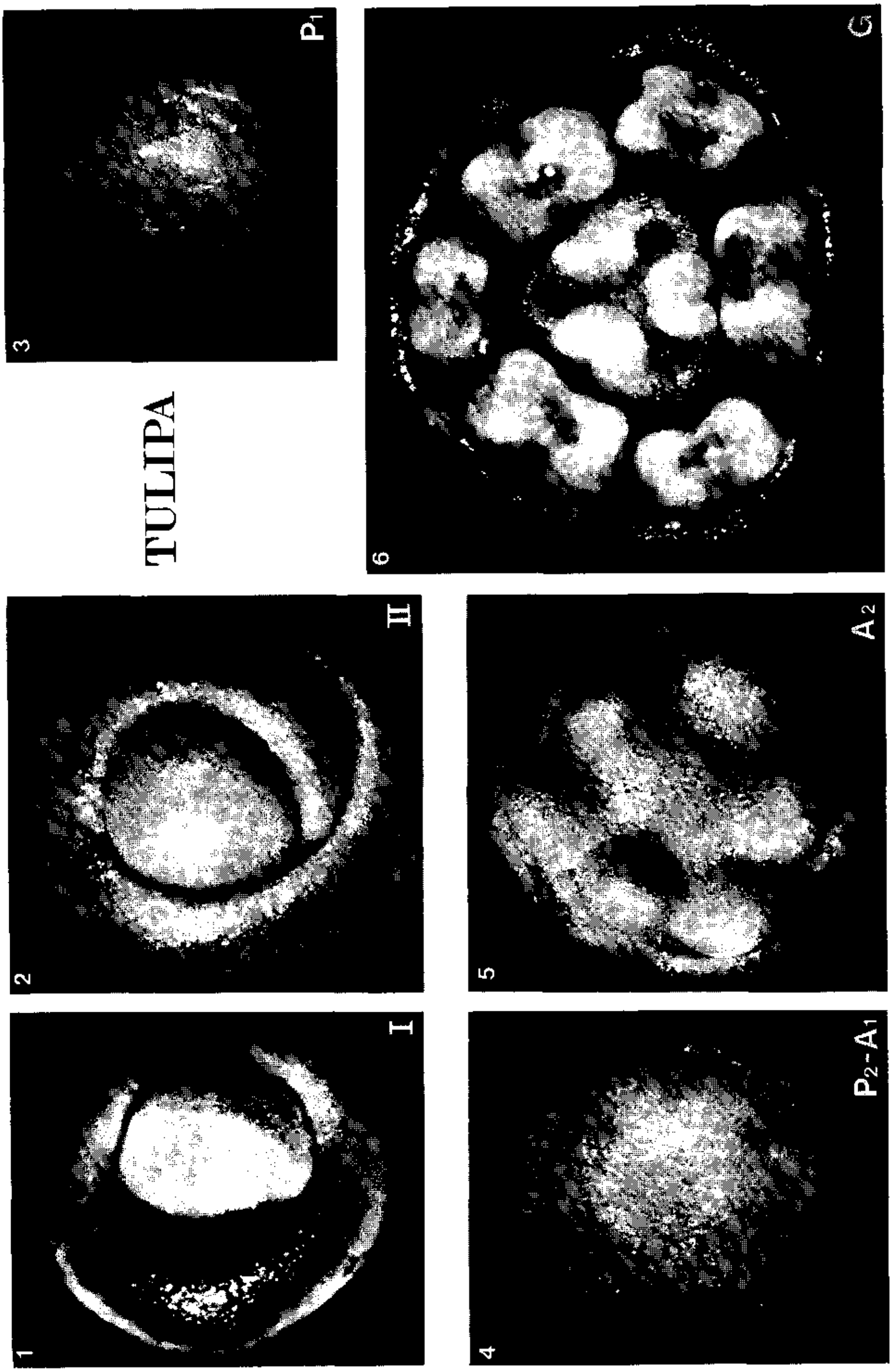
To indicate the stages of development of the flowers, the terminology proposed by BEIJER (1942) is used (Table 1), each stage being indicated by the initial letter or an abbreviation of the name of the last organs to be formed. When similar organs are formed in two groups or whorls, the successive stages are indicated by a number (1 or 2) placed after the letter.

TABLE 1. List of developmental stages distinguished.

Stage symbol	Radical word	Signification
I	–	Stages during the period of leaf formation, apex usually flat or little convex
II	–	Onset of flower formation; swelling of the growing point, which becomes domed
Pr	Primordium	First flower initial of inflorescence formed
Sp	Spatha	Spathe leaf of flower or inflorescence formed
Br	Bractea	Bract initial formed
Bo	Bracteola	Bracteole initial formed
P1	Perianthium	Petals of the first whorl initiated
P2	,,	Petals of second whorl initiated
A1	Androecium	Stamens of the first whorl initiated
A2	,,	Stamens of the second whorl initiated
G	Gynoecium	Primordia of the carpels are formed
Pc	Paracorolla	Primordium of the trumpet formed in narcissi

If gradations in the described stages should be distinguished, a plus or minus sign can be added to the stage symbol when the observed apex is more advanced or not so far, respectively.

PLATE I



Results

Tulip (Plate I; all figures: $\times$ 50)

Fig. 1; Stage I. One or more foliar leaves have been formed. The apex, which is rather flat, can be seen through the opening of the leaf initials.

Fig. 2; Stage II. All foliar leaves are formed; normally, the maximum number of leaves is 3 to 4. The apex bulges and the diameter is increasing.

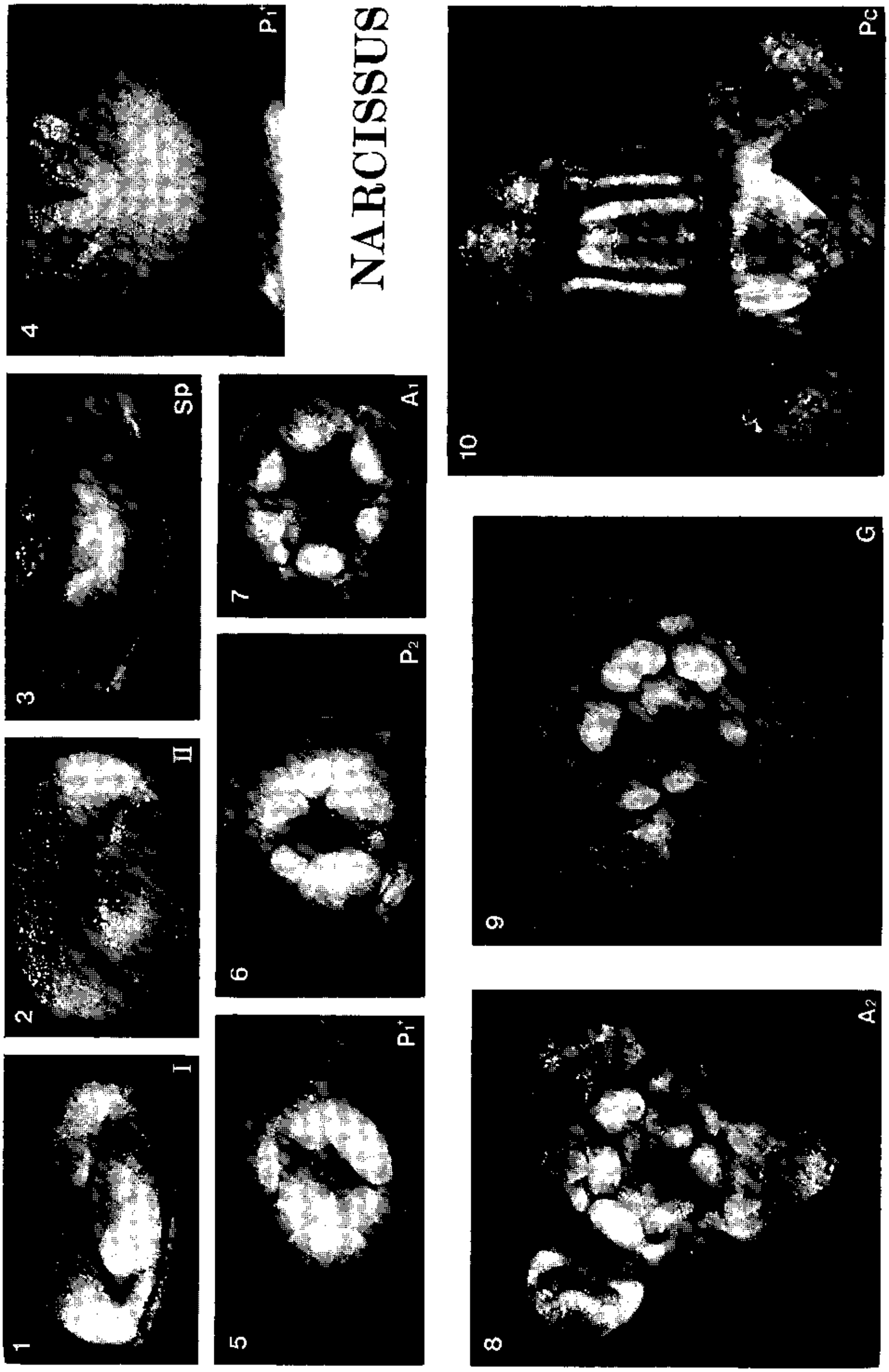
Fig. 3; Stage P1. Perianth members of the first (outer) whorl have been split off from the outer side of the apex, which gives the apex a triangular outline. The young foliar initials have been removed.

Fig. 4; Stage P2 to A1. The size of the perianth members of the first whorl has increased; the perianth members of the second (inner) whorl have been split off between the members of the first whorl; the stamen primordia of the first whorl are just visible adaxially to the perianth members of the first whorl.

Fig. 5; Stage A2. A further increase in size of the perianth initials can be seen. A more adaxial implantation of the second whorl of the perianth is now evident, which explains the terms outer and inner for the first and second whorl, respectively. In addition to Stage A1 (Fig. 4) a second whorl of stamen initials has been formed which corresponds with the inner whorl of perianth members.

Fig. 6; Stage G. All primordia present in stage A2 have increased in size. In the centre of the apex three carpels have been formed, representing the gynoecium.

PLATE II



Narcissus (Plate II; Figs. 1–7: × 27; Figs. 8 and 9: × 22; Fig. 10: × 15)

FIG. 1; Stage I. A small flat growing point is seen splitting off foliar leaves laterally.

FIG. 2; Stage II. After the last foliar leaf has been split off, the apex becomes domed.

FIG. 3; Stage Sp. A spathe leaf characteristic for the *Amaryllidaceae* is formed circularly. The apex is growing upward.

FIGS. 4 and 5; Stage P1+. Three perianth members of the first whorl are split off. To observe this and the following stages well, the spathe leaf must be dissected. Without such dissection, the growing point resembles Fig. 4.

FIG. 6; Stage P2. Six perianth members have been split off. The three perianth initials of the first whorl are larger than those of the second.

FIG. 7; Stage A1. Three stamen primordia are present adaxially to the perianth initials of the first whorl. To observe these primordia, the perianth initials must be dissected.

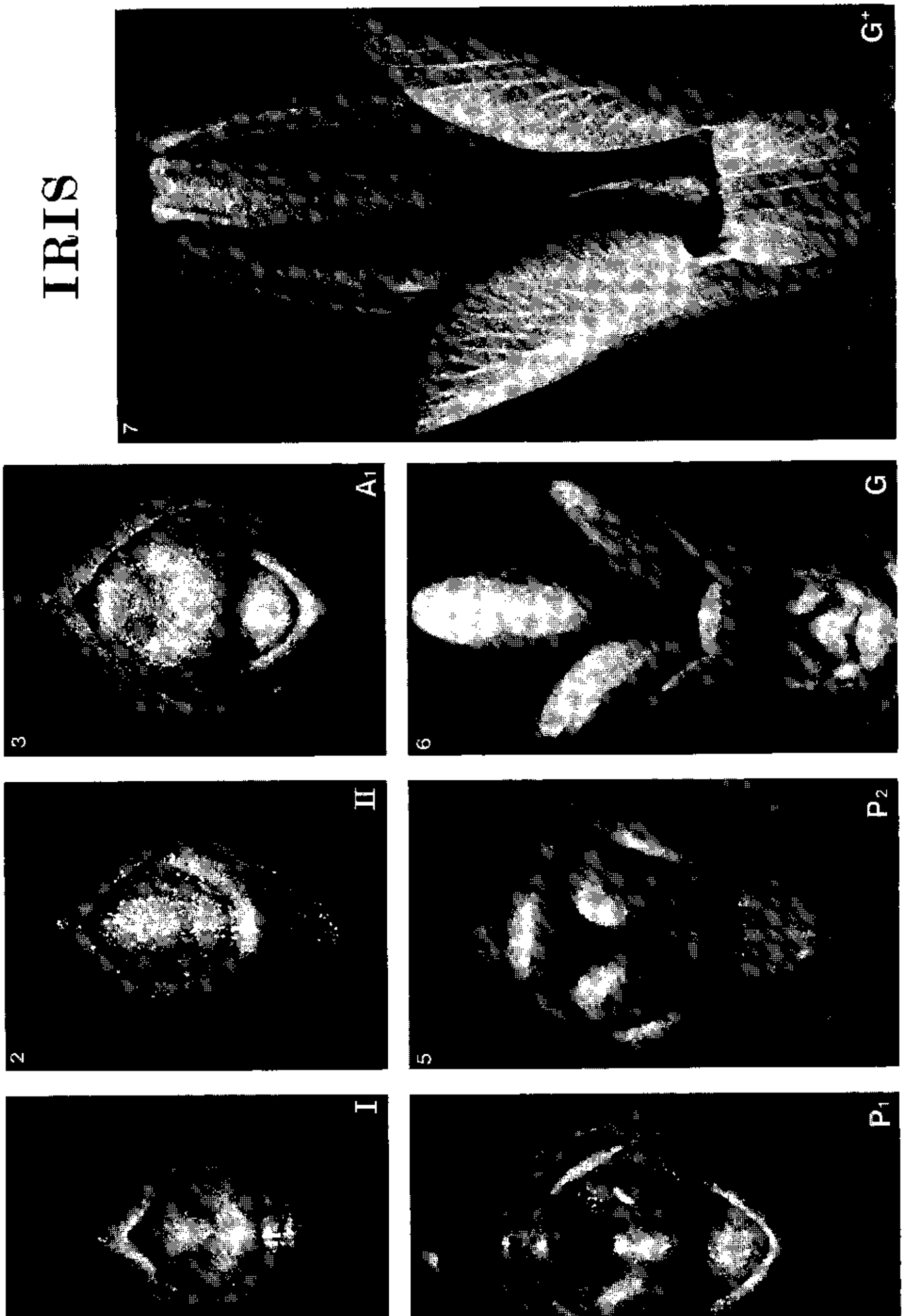
FIG. 8; Stage A2. Six stamen primordia can be observed adaxially to the six organs of the perianth. To make the stamens and apex visible, the tips of the perianth members have been bent outward.

FIG. 9; Stage G. Within the circle of the stamen initials the apex has split off three carpels. As in the preceding Figure, the perianth members are bent outward.

FIG. 10; Stage Pc. After a considerable increase in the size of the primordia after Stage G, the paracorolla (trumpet) will be formed between the young stamens and perianth members (bent downward).

In varieties that produce a flower cluster, the stages of the individual flowers are identical to those just described. After stage Sp, furthermore, stages Pr and Br can be distinguished by the formation of initials for the individual flowers and bracts, respectively.

IRIS



Iris (Plate III; *Figs. 1–5*: ×45; *Fig.* 6: ×20; *Fig.* 7: ×7.5)

FIG. 1; Stage I. Young leaves are being split off alternately on opposite sides. The apex is small and slightly convex.

FIG. 2; Stage II. The initiation of foliar leaves (and spathe leaves) has come to an end after 6 to 10 leaves have been split off. The apex becomes domed and the diameter is increasing.

FIG. 3; Stage A1. Three stamen primordia can be distinguished, giving the apex a triangular shape. In the axil of the last leafy organ formed (a spathe leaf), the primordium of a second flower develops.

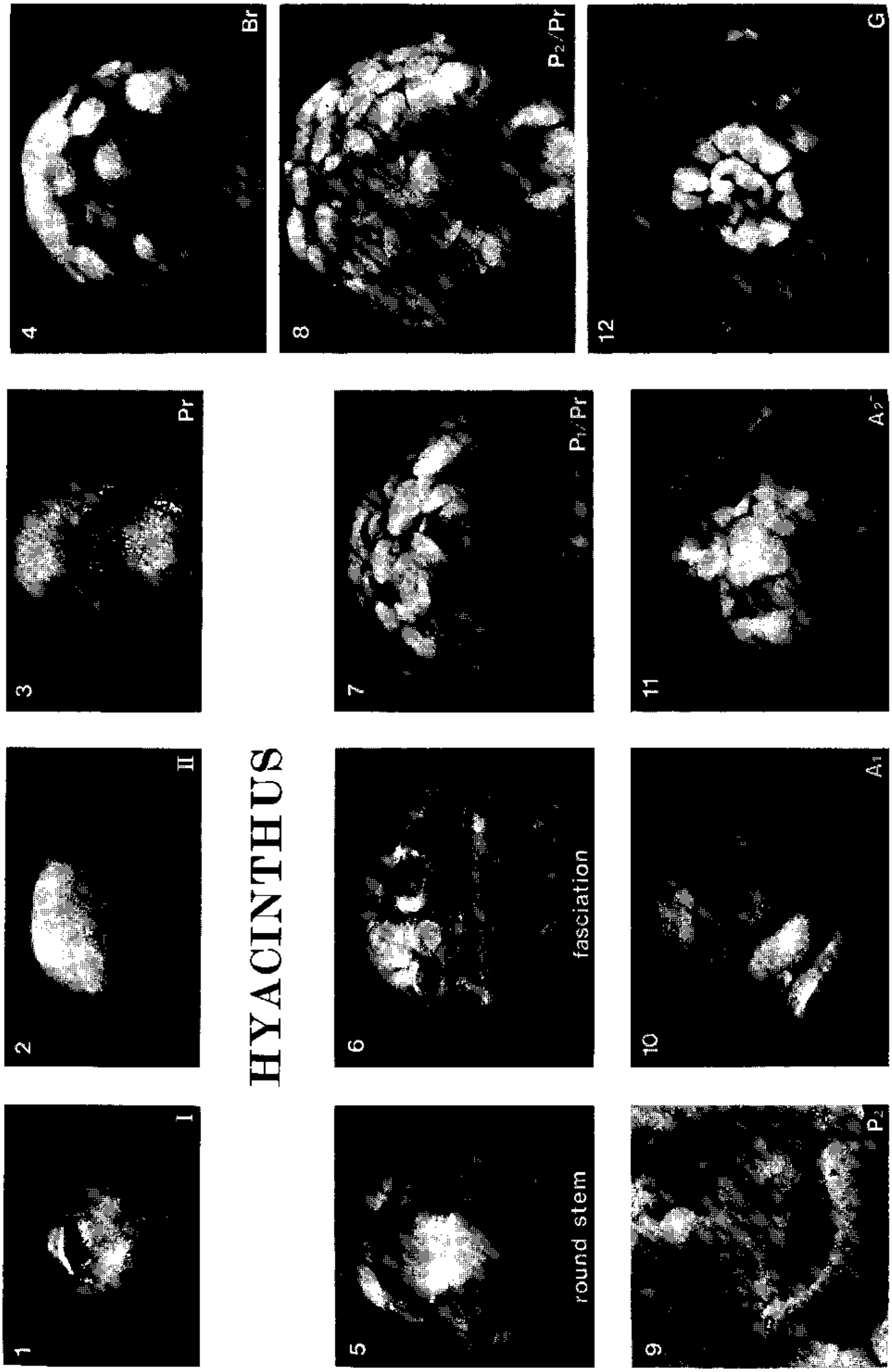
FIG. 4; Stage P1. Abaxially to the three stamen initials, which are now bean-shaped, three perianth members can be distinguished. The centre of the apex has become concave.

FIG. 5; Stage P2. Another whorl of three perianth members has split off. The newly formed organs can be observed between the stamen-perianth units of the first whorl. The apex of the second flower has reached stage A1; a bract is developing between the two flower primordia.

FIG. 6; Stage G. After a considerable increase in the size of perianth and stamen initials, among which the stamen opposite the last-formed leaf often dominates, the three carpels are split off adaxially at the bases of the stamens. The carpels can be observed after bending of the stamens. The primordium of the second flower has reached stage P2; the bract between the two flowers is enlarging.

FIG. 7; Stage G^+. This picture shows the development of the styles after the G stage has been reached. The dominant position of the three stamens is illustrated. A perianth member of the second whorl has been bent downward and fixed in a substrate of plasticine.

PLATE IV


HYACINTHUS
1
I
2
II
3
Pr
4
Br
5
round stem
6
fasciation
7
P_1/Pr
8
P_2/Pr
9
P_2
10
A_1
11
12
G

Hyacinth (Plate IV; Figs. 1–8: ×17; Figs. 9–12: × 34)

The flower formation of hyacinths and lilies is more complicated than in the foregoing genera, because more flowers are formed, arranged in a cluster. This made it necessary to distinguish three additional stages, Pr, Br, and Bo, after stage II, with respect to cluster formation. Furthermore, the indication of stages P1, P2, A1, and A2 and G refers to a single flower primordium only. To indicate the developmental stage of the cluster, we therefore prefer the indication of the developmental stages of the lowermost and uppermost individual flower. Usually, the lower flowers develop faster than those at the tip.

FIG. 1; Stage I. A small, slightly convex apex, which will produce foliar primordia, can be seen.

FIG. 2; Stage II. The apex bulges, grows upward and becomes more and more convex.

FIG. 3; Stage Pr. Individual swellings on the apical dome indicate the formation of flower primordia.

FIG. 4; Stage Br. At the base of the apical dome several primordia showing a bract primordium at the base can be distinguished. At the tip of the apex new flower primordia are still being formed. At this stage it can already be seen whether the cluster will have a round or a flat stem (fasciation), Fig. 5 illustrates a round stem, Fig. 6 a flat stem seen from above.

FIG. 7; Stage P1/Pr. The lowermost flower primordium of the young cluster has produced three perianth members (Stage P1); at the tip of the cluster newly formed primordia (Stage Pr) can be distinguished.

FIG. 8; Stage P2/Pr. The lowermost flower primordium of the cluster has produced a second whorl of perianth members, which can be observed as small triangular organs alternating with the enlarged perianth members of the first whorl. The size of the abaxial bracts at the base of the flower primordia is increasing. At the tip of the cluster new primordia are still being formed.

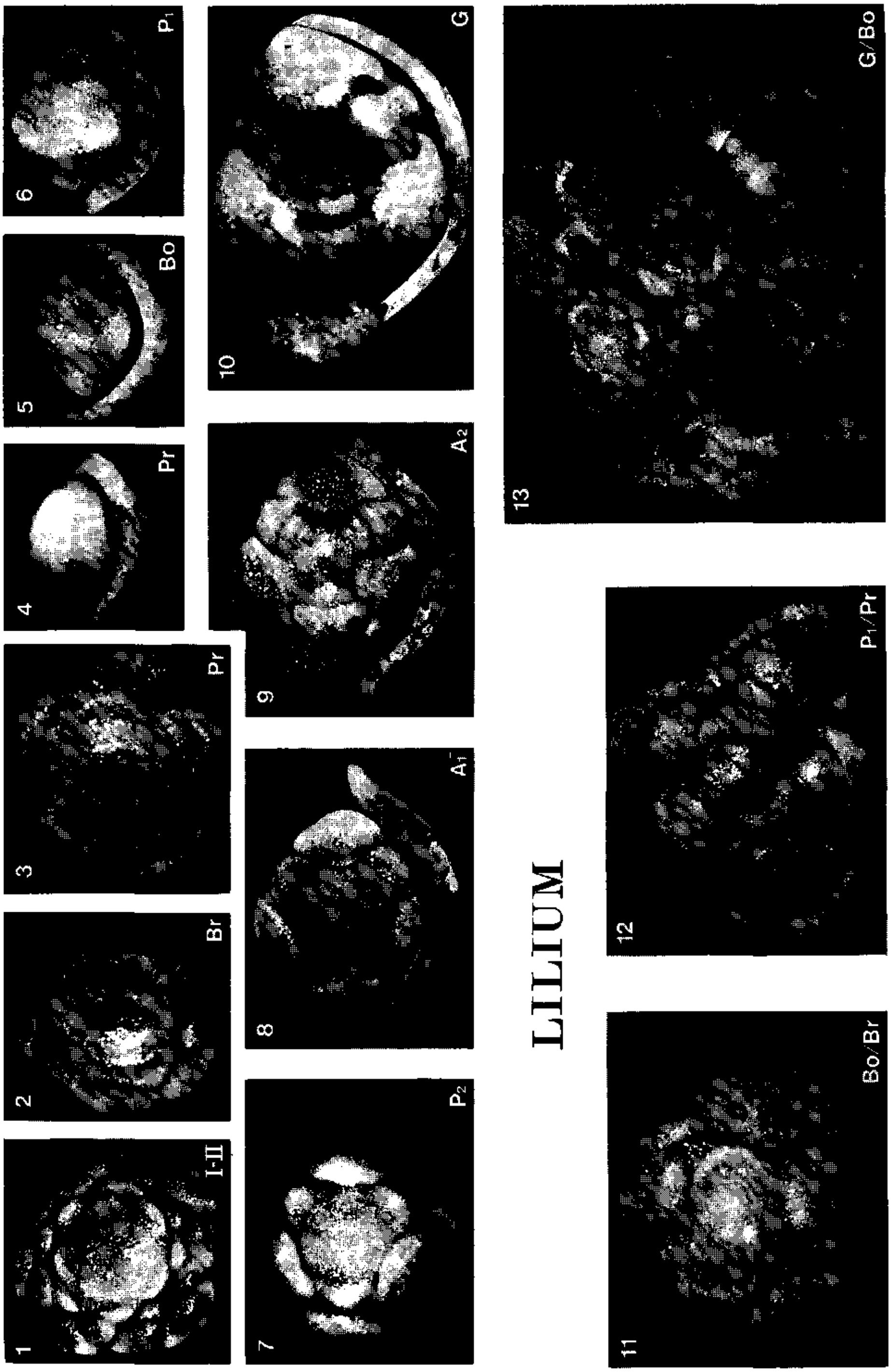
FIG. 9; Close-up of a single flower primordium in stage P2. The three perianth organs of the first whorl are dissected, making the three newly formed perianth organs of the second whorl clearly visible.

FIG. 10; Stage A1. Adaxially to the perianth members of the first whorl (dissected) three newly formed stamen primordia can be observed alternating with the three perianth organs of the second whorl.

FIG. 11; Stage A2. Six stamen primordia are now present. To show these organs, the darker perianth members of the first whorl have been bent outward. The centrally positioned apex is triangular in outline.

FIG. 12; Stage G. Flower formation has been completed with the initiation of the three carpels in the centre. The stamen primordia show the formation of lobes for the anther development. The perianth organs have been bent outward again.

PLATE V


LILIUM
1 I-II
2 Br
3 Pr
4 Pr
5 Bo
6 P1
7 P2
8 A1
9 A2
10 G
11 Bo/Br
12 P1/Pr
13 G/Bo

Lily (Plate V; Figs. 1–3: ×30; Figs. 4–10: ×35; Figs. 11 and 12: ×25; Fig. 13: ×20)

FIG. 1; Stage I to II. The apex is slightly convex and is splitting off foliar leaves. The total number of leaves can vary from 80 to 120. During the process of foliar formation a stem primordium has been formed such that the apex can rise some centimeters above the disc tissue.

FIG. 2; Stage Br. The bracts corresponding with the first flower primordia to be formed have split off. The primordia of the bracts can be distinguished from leaf primordia by their broader base and the coincidence of changes in the shape of the apical dome as described for stage II. Fig. 2 shows three bract primordia.

FIGS. 3 and 4; Stage Pr. The meristematic lobes for the formation of individual flowers can be distinguished in the axils of the bracts. Fig. 3 shows an apex with six bract primordia, three of which are accompanied by clearly visible flower primordia. Fig. 4 shows an isolated flower primordium with the corresponding bract.

Before the development of the flower cluster as a whole is described further, the development of the individual flower will be considered.

FIG. 5; Stage Bo. A primordium for the little bract is split off laterally by the flower primordium; the tip of the bract (in all Figures underneath the flower primordium) has been cut off because it covered the organs formed later.

FIG. 6; Stage P1. The apex has lost its spherical shape and become triangular in outline. Perianth members of the first whorl have split off. The bracteole to the left of the flower is becoming larger.

FIG. 7; Stage P2. Two whorls of three perianth members can be distinguished.

FIG. 8; Stage $A1^-$. Adaxially to the perianth members of the first whorl (the largest organs), stamen primordia can be distinguished.

FIG. 9; Stage A2. Six stamen primordia are present adaxial to the six perianth members. A lateral expansion of the three perianth members of the first (outer) whorl is clearly evident.

FIG. 10; Stage G. Three carpels have been formed within the ring of the six stamen primordia, in which differentiation of the anthers has started (bean-like shapes).

The development of the cluster, indicated by the symbols of the most advanced and the least developed flower, can be seen in the following pictures:

FIG. 11; Stage Bo/Br. The flower primordia at the circumference of the apical dome has reached stage Bo, while in the centre bracts have just been split off for more flower primordia.

FIG. 12; Stage P1/Pr. The furthest-developed flower primordia (left and right on the circumference of the apex) have reached stage P1; the flower primordia in the centre are still undifferentiated (Stage Pr).

FIG. 13; Stage G/Bo. The furthest-developed flowers (on the left and right) have reached stage G; the least-developed primordium (in the centre of the cluster) is still in stage Bo. Intermediate stages can be observed; stage A2 in the middle or the lower part of the picture; A1 upper left; P2 in the middle.

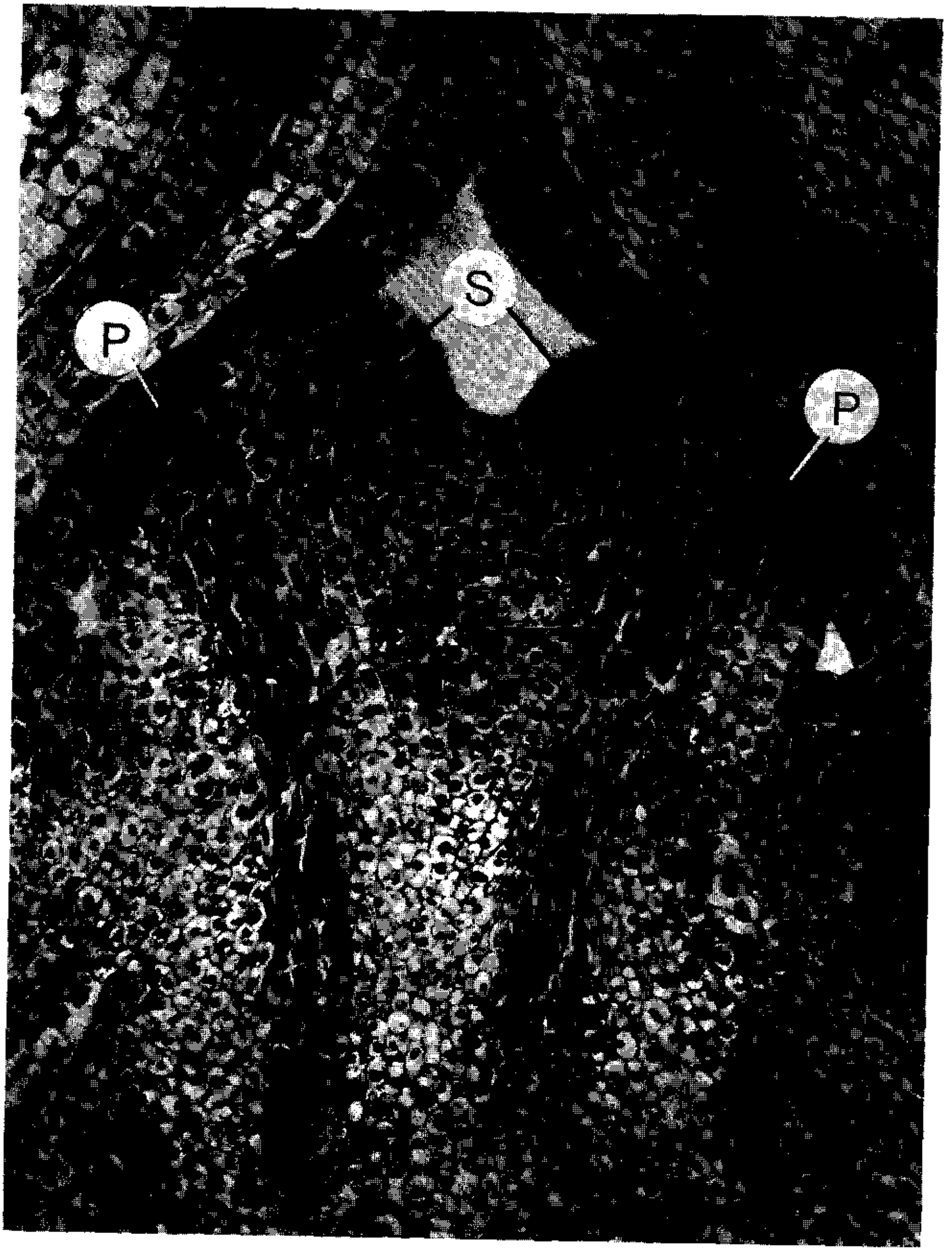


PLATE VI. Longitudinal section (thickness: 8 μ) through iris apex at stage A1, showing procambium strains leading to the perianth initials (P) and staminal primordia (S) adaxial to the perianth initials.

Sequence of developmental stages

Comparison of the stages of the tulip, hyacinth, lily, and narcissus shows a close resemblance with respect to the sequence of the developmental processes. In lilies, however, stage Br precedes stage Pr in contrast to hyacinths, in which Br follows Pr. In iris stage A1 precedes stage P1 reversing the sequence in the other described genera, where A1 follows P1. This aberrant sequence and the absence of stage A2 have also been described for other *Iridaceae*, i.e. the gladiolus and crocus (HARTSEMA, 1937; BEIJER, 1942). A histological analysis of the apex of iris in stages II and A1 shows the presence of small perianth primordia abaxial to the stamen initials (plate VI). Because these primordia are accompanied by pro-cambium strains and the stamen initials are not, it may be suggested that the same sequence as in the other genera once occurred in iris, but that the stamens became dominant very early in its evolution.

DISCUSSION

During the investigation we observed some aberrant flowers, which were put aside for further analysis. In the tulip both an increase and a decrease of the number of flower organs was found. BLAAUW *et al.* (1932) assigned importance to the influence of the storage temperature on flower formation: at a low temperature (9 °C) the total number of floral organs was generally lower than at a high temperature (28 °C), but wide variation was found at both temperatures.

In irises aberrations can occur when the duration of storage at 30 °C (which inhibits development almost completely) is longer than 9 to 10 months. If the bulbs are stored at lower temperatures (25 °C) at which some development takes place, aberrations can occur even after shorter storage periods. Moreover, aberrant flowers can also originate if the temperature drops below zero at the onset of the flower initiating process after planting (de MUNK, unpublished).

In hyacinths the so-called flat stems (fasciations) occur (Plate IV, Fig. 6). This aberration will be often wanted for practical purposes, because of the associated increase in the number of individual flowers, which makes the clusters denser (BEIJER, 1936).

In lilies it has been observed that the sequence of flower-primordia form a spiral on the apical dome, that can turn clockwise or counterclockwise at random (GRELLER, 1969). For the sake of uniformity in the series of photographs, we have presented only clusters turning clockwise.

For the so-called double varieties, the designations P1, P2, A1, and A2 cannot be used in the sense of the formation of a whorl comprising three organs. In this case P1, A1, and P2, A2 can be used to indicate the onset or the end of the process of perianth and stamen formation, respectively.

Possibilities for practical application of the findings on the origin and development of the flowers have been published by BLAAUW (1921), BLAAUW and VERSLUYS (1925), BEIJER (1952a), HARTSEMA (1961), RÜNGER (1971), REES (1972), and HOOGETERP (1973).

ACKNOWLEDGEMENTS

The authors are greatly indebted to Mrs. J. MENS-KROES, who photographed the stages of Narcissus and Hyacinth some years ago, and to Mr. D. TIMMERMAN and Mr. H. INGENHOES for their accurate technical assistance.

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