A Morphological Observation on the Formation of Abnormal Flowers in Garlic (*Allium sativum* L.)

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Introduction

Garlic is one of the sterile plants. There are a few interpretations referring to the true seed of garlic[16], but it may not be impossible to say that true seed of garlic is unknown, because no author has ever described that viable seed of garlic has been observed[11]. Studies on the sterility of garlic have been done by some workers[9,10,13,17,19], but the causes of the sterility have been left still indistinct.

The pollens of garlic fail to accomplish their development for some unknown reasons, and they degenerate completely at the stage of young microspores.

This investigation has been conducted on the morphological abnormality of garlic flowers which is observed so frequently and seems to be connected with the sterility. Shisa[15] referred to the sterility as being due to morphological abnormality of flowers.

The morphological abnormality in the garlic flowers has been reported by some workers[13,18,19], however, the detail of it has not been investigated.

As all of 46 bolting cultivars grown by the authors had shown morphological abnormality in flowers and sterility, one of them was used in this investigation. The authors observed the materials microscopically, and clarified the parts, the types of abnormalities and their frequency, as compared with those of leek (*A. ampeloprasum* L.) and Welsh onion (*A. fistulosum* L.).

Many clones of garlic do not produce flower stalks, some of other clones may, partially, or not at all, exsert the inflorescences[5], and moreover some of those with flower stalks produce only bulbils in the inflorescence spathes[8]. The clone used for this observation always produces flower stalks and inflorescences bearing more numerous flowers than any other clones grown by the authors, although its flowers are loaded with bulbils in the inflorescence spathes as in case of those of the other clones.

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Material and Method

The observation was made on the cultivar, Shanhai-wase (garlic), American London (leek), and Kujō (Welsh onion). The cloves of garlic and the seeds of the others were planted in fall, 1975, and the flowers were observed in the following spring and summer with the stereoscopic microscope after fixed.

Ten inflorescences were taken from the different plants in each of the three species.

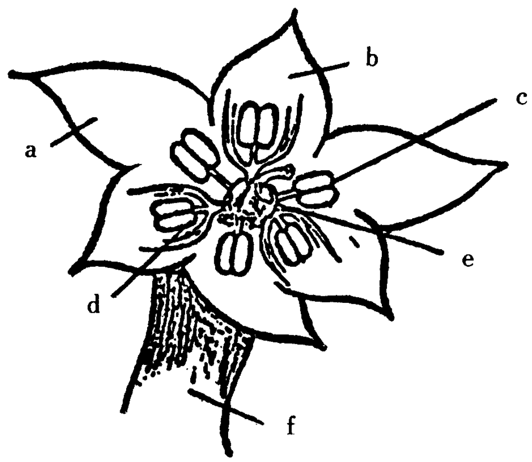
In garlic, all of the flowers in each inflorescence were used as materials. Since leek and Welsh onion had a large number of flowers in an inflorescence, ten flowers, for each inflorescence, were used.

The flower buds, instead of flowers, were observed in garlic, because they do not open usually (Fig. 2).

The flower which showed morphological abnormality, even if in one floral part, was determined as an abnormal flower. The frequency was expressed as a percentage of the number of the abnormal flowers to the number of total flowers in the same inflorescence.

Observation

The flower of garlic is fundamentally a trimerous flower and consists of 5 whorls. Diagram of a normal garlic flower, modified from Shimada and Shozaki[13], was shown in Fig. 1. Six perianth lobes are arranged in the two outer whorls and each whorl contains three perianths. Six stamens are arranged in the next two whorls, three to one whorl, and each of the inner three stamens bears two long teeth. The ovary situated in the most inner whorl is tricarpellary.



a. Outer perianth
b. Inner perianth
c. Outer stamen
d. Inner stamen
e. Pistil
f. Pedicel

Fig. 1. Diagram of a normal garlic flower (Modified from Shimada and Shozaki[13])

Shimada and Shozaki[13] reported that each of the two teeth arranged on both sides of the filament of the inner stamen branched into two at the basal portion of it, and they regarded such teeth as normal (Fig. 1). The authors could not find out any flower which they regarded as normal one. The branched teeth, of course, were often observed, but no flower possessed all of the three stamens bearing long branched teeth. For the above reason, the authors regarded the stamen bearing long teeth, whether branched or not, as normal.

The frequency of the morphological abnormality in each floral part in garlic is shown in Table 1.

High percentage of abnormality among the flowers in each inflorescence spathe was

Table 1. Frequency of abnormality in each floral parts of garlic flowers (%)

Inflorescence No.	1	2	3	4	5	6	7	8	9	10	Total*[1]
Outer perianths	46	46	73	45	100	78	67	29	14	31	41
Inner perianths	38	31	64	27	50	67	67	31	21	37	30
Outer stamens	77	50	73	55	100	100	67	46	86	77	66
Inner stamens	69	27	73	45	100	78	83	46	36	54	51
Pistil	85	42	91	73	50	89	67	37	29	34	51
Abnormal flowers*[2]	92	65	100	73	100	100	83	69	86	86	81
Number of flowers observed	13	26	11	11	2	9	6	35	14	35	162

*[1]Frequency to total flowers.
*[2]Flowers which show any abnormality in floral parts.

observed, i.e., 69% was the case of the lowest. And furthermore, many of the abnormal flowers possessed two to four abnormal parts in a flower. Frequency of morphological abnormality was the greatest in the outer stamens, it being greater in the stamens and pistils than that in the perianths. It should be noted that abnormality was found in every floral part in all the inflorescences.

Types and frequency of morphological abnormality in each floral part in garlic are shown in Table 2 to 6. Abnormal appearance of flower usually accompanied morphological abnormality in the inner floral parts, for example, anthers, and pistils (Figs. 3, 4).

The morphological abnormality of the outer perianths as shown in Table 2 is summarized as follows;

1. increase or decrease in the number of perianths
2. formation of an 'incomplete' flower in the whorl of the outer perianths ('flower formed in a flower' in Table 2)
3. fusion of perianths
4. abnormality in the shape of the perianths, for example, dwarfness, perianth folded

Table 2. Frequency of various types of abnormal outer perianths in garlic flowers (%)

Inflorescence No.	1	2	3	4	5	6	7	8	9	10	Total*
Lack of two perianths	—	—	36	—	—	11	17	3	—	6	6
Lack of one perianth	38	35	18	9	100	44	33	20	7	23	25
One extra perianth	—	—	—	—	—	—	—	—	—	3	1
Two extra perianths	—	—	—	9	—	—	—	—	—	—	1
Flowers formed in a flower	—	4	—	—	—	—	—	—	—	—	1
Fusion	15	8	—	18	—	11	17	—	—	—	5
Abnormal shape	31	12	27	9	50	67	33	23	7	23	23
Dwarfness or degeneration	—	—	18	—	—	—	—	—	—	—	1
Folded perianth	—	—	9	—	—	—	—	—	—	—	1
Irregular arrangement	—	—	—	—	—	—	—	—	7	—	1

*See table 1.

Table 3. Frequency of various types of abnormal inner perianths in garlic flowers (%)

Inflorescence No.	1	2	3	4	5	6	7	8	9	10	Total*
Lack of three perianths	—	—	—	—	50	22	—	—	—	—	2
Lack of two perianths	—	—	9	—	—	—	—	6	—	11	4
Lack of one perianth	23	19	45	—	—	22	50	17	14	20	20
One extra perianth	8	4	9	—	—	—	—	—	—	3	2
Two extra perianths	8	—	—	—	—	—	—	—	—	—	1
Three extra perianths	—	—	—	9	—	—	—	—	—	—	1
Perianth with hairy appendages	8	—	—	—	—	—	—	—	—	—	1
Fusion	23	8	—	27	—	11	17	—	7	—	7
Abnormal shape	23	8	27	18	—	44	—	9	7	17	15
Dwarfness or degeneration	—	—	—	—	—	—	—	3	—	—	1
Folded perianth	—	—	9	—	—	—	—	3	—	—	1
Irregular arrangement	—	—	—	—	—	—	—	—	7	—	1

*See Table 1.

Table 4. Frequency of various types of abnormal outer stamens in garlic flowers (%)

Inflorescence No.	1	2	3	4	5	6	7	8	9	10	Total*
Lack of three stamens	15	—	9	—	50	11	—	3	—	6	5
Lack of two stamens	—	12	—	18	—	33	—	6	7	6	8
Lack of one stamen	23	38	64	27	50	44	67	17	57	40	37
One extra stamen	—	—	—	—	—	—	—	—	—	3	1
Two extra stamens	—	—	—	9	—	—	—	—	—	—	1
Flowers formed in a flower	8	—	36	—	50	—	—	3	21	14	9
Bulblets formed in a flower	8	—	—	—	—	22	—	—	—	—	2
Fusion	—	—	—	—	—	—	—	—	—	3	1
Abnormal shape	38	8	36	9	—	33	—	14	50	31	23
Dwarfness or degeneration	15	—	—	—	—	—	—	3	—	—	2
Partially leafy and warty anther	31	8	36	9	—	22	—	17	21	31	20
Stamen with hairy appendages	15	—	—	—	—	—	—	20	29	23	13
Petaloidy	15	—	—	—	—	—	—	—	—	—	1

*See table 1.

lengthwise, tube-shaped perianth (Fig. 4), abnormal shape as shown in Fig. 3
5. irregular arrangement of the outer and inner perianths.

Of the abnormality mentioned above, lack of one perianth and abnormal shape were the most common.

The abnormality of inner perianths resembled that of outer ones as shown in Table 3. There were observed some differences between the outer and the inner perianths. The following is abnormality of the inner perianths different from that of the outer ones.

1. conspicuous variability in the number of the perianths
2. formation of hairy appendages instead of an 'incomplete' flower
3. fusion of the inner perianths and the inner stamens.

The abnormality of the outer stamens, as shown in Table 4, is summarized as follows;

1. increase or decrease in the number of stamens (Fig. 6)
2. formation of an 'incomplete' flower in the whorl (Fig. 15)
3. formation of a bulblet in the whorl
4. mutual fusion of stamens
5. abnormality in the shape of the stamens, for example, dwarfness, petaloidy, partially leafy and warty anthers (Fig. 5), hairy appendages (Fig. 5), abnormal shape as shown in Fig. 9.

The most common abnormality was lack of one stamen which was observed not a few times in every inflorescence, and the next common one was abnormal shape as shown in Fig. 9. And the abnormal shape usually accompanied partially leafy anthers. 'Flower formed in a flower' and hairy appendages were found in the limited inflorescences. The latter was occasionally observed in the limited portion of the stamens, particularly all of them in No.8 inflorescence were observed in the same portion of the stamens.

The abnormality of the inner stamens, as shown in Table 5, was almost same as that of the outer stamens, but a little differed in the following;

1. Abnormality was often observed on the teeth of the inner stamens. The most common one was lack of a tooth on one side of the filament, and the next was a formation of extra teeth (Fig. 7).
2. Branching of a filament was rarely observed in the inner stamens, and both of the two branched filaments attached anthers (Fig. 8).

Table 5. Frequency of various types of abnormal inner stamens in garlic flowers (%)

Inflorescence No.	1	2	3	4	5	6	7	8	9	10	Total*
Lack of three stamens	—	—	—	—	50	22	—	6	—	3	4
Lack of two stamens	8	—	9	9	—	22	33	6	—	6	7
Lack of one stamen	8	23	55	9	50	22	33	23	29	29	25
One extra stamen	—	—	9	—	—	—	—	—	—	—	1
Three extra stamens	—	—	—	9	—	—	—	—	—	—	1
Flowers formed in a flower	—	—	—	—	—	11	17	—	—	6	2
Bulblets formed in a flower	—	—	—	—	—	22	—	—	—	—	1
Fusion	15	—	—	18	—	11	17	—	7	3	5
Abnormal shape	23	—	36	18	—	33	33	9	21	11	15
Dwarfness or degeneration	15	—	—	—	—	—	—	6	7	3	4
Partially leafy and warty anther	15	—	27	18	—	33	17	9	7	11	12
Abnormal tooth	69	4	9	—	—	11	17	14	—	17	15
Petaloidy	8	—	—	—	—	—	—	—	—	—	1
Branching	—	—	—	—	—	—	—	3	7	—	1

*See Table 1.

Table 6. Frequency of various types of abnormal pistils in garlic flowers (%)

Inflorescence No.	1	2	3	4	5	6	7	8	9	10	Total*
Lack or degeneration of pistil	15	—	—	9	50	22	—	6	—	3	6
Lack or degeneration of style	8	15	36	—	—	11	17	3	—	—	7
Flowers formed in a flower	—	—	—	—	—	—	—	—	—	9	2
Two pistils	—	—	—	9	—	—	—	—	—	—	1
Abnormal shape of ovary	31	23	82	27	—	67	50	14	14	6	25
Split style	—	—	9	—	—	—	—	—	—	—	1
Leafy or flat style	46	15	27	9	—	22	—	—	—	3	10
Slender style	—	—	—	18	—	—	—	17	—	6	6
Bent style	—	—	—	—	—	—	17	—	14	3	2

*See Table 1.

The abnormality of the pistils as shown in Table 6 is summarized as follows;

1. lack or degeneration of a pistil or a style
2. formation of two pistils in a flower (Fig. 13)
3. formation of an 'incomplete' flower instead of a pistil ('flower formed in a flower' in Table 6)
4. deformation of ovary (Fig. 9, 14)
5. deformation of style, for example, leafy or flat (Fig. 11), split, bent (Fig. 12), slender one.

Table 7. Frequency of various types of abnormal leek flowers (%)

Inflorescence No.	1	2	3	4	5	6	7	8	9	10	Total*1
Lack of one perianth	—	—	—	20	20	—	—	—	—	—	4
One extra perianth	—	—	—	—	—	—	20	—	—	—	2
Lack of one stamen	—	—	—	30	—	—	10	—	—	10	5
One extra stamen	—	—	—	10	—	—	10	—	—	—	2
Leafy filament	10	—	—	—	—	—	—	10	—	—	2
Degeneration of anther	—	—	—	—	—	—	—	—	—	10	1
Abnormal shape of anther	—	—	—	10	—	—	—	—	40	—	5
Lack of style	—	—	—	—	—	—	—	—	—	20	2
Abnormal shape of ovary	—	—	—	—	—	—	—	—	—	10	1
Split style	—	—	—	—	—	—	—	30	60	50	14
Slender style	—	—	—	—	—	—	—	—	—	20	2
Bent style	—	—	—	10	—	—	—	—	—	—	1
Abnormal flower*2	10	—	—	40	20	—	20	30	60	90	27

*1,*2See Table 1.

Deformation of ovary was the most common, and the next common one was leafy or flat style, although leafy or flat style was observed in the limited inflorescences. Notice might be paid on the fact that 'flower formed in a flower' was observed only in three of 35 flowers taken from No.10 inflorescence (Table 6).

In addition to the various abnormalities in each floral part, fusion of two pedicels was observed (Fig. 16). All of the flowers on the longer coiled pedicels accompanied abnormality of flower shape as shown in Fig. 3.

Abnormality in leek (*A. ampeloprasum* L.) and Welsh onion (*A. fistulosum* L.) differed from that in garlic (*A. sativum* L.). None of the flowers belonging to Welsh onion showed abnormality, namely even only one floral part of it did not.

Leek showed an intermediate result between garlic and Welsh onion. Various types of abnormality and their frequencies in leek are summarized in Table 7. Three of ten inflorescences of leek did not present any abnormality. The frequency of abnormality in leek was far lower than that in garlic, and the abnormality in leek was not observed in every part as in garlic. Most of abnormality in leek was restricted to lack of one floral part, abnormal shape of anther and split style. The abnormality in leek, then, was not so various as that in garlic.

Discussion

There is a little trouble in determining a flower to be abnormal one in garlic, because strict criterion for abnormality has not been stipulated and the decision of abnormality is usually entrusted to individual worker's judgment.

A normal flower in garlic had been reported by Shimada and Shozaki[13], and Yamada[18,19]. They regarded the flower bearing long branched teeth on both sides of the filament as normal. As mentioned in 'Observation', the authors could not find out any flower such as Shimada and Shozaki[13], and Yamada[18,19] regarded as normal. The branched teeth, of course, were observed here, but no flower possessed three stamens bearing long branched teeth. For that reason, the authors regarded the stamens bearing long teeth as normal, whether the teeth were branched or not.

A large number of abnormal flowers in garlic, cultivar Shanhai-wase, were observed here, and also all of 46 bolting cultivars were observed, previously. Abnormal flowers in garlic have been observed in various cultivars, Saga-ooninniku by Shimada and Shozaki[13], Saga-ooninniku and Iki-wase by Yamada[18,19]. In India, early degeneration of garlic flowers and formation of morphologically normal flowers were reported by Khoshoo *et al.*[6] and Koul and Gohil[9] respectively. Koul and Gohil[9] mentioned about the formation of complete and regular flowers and the complete degeneration of microspores in three cultivated populations in Kashmir, India. However, there is a little problem in their reference on the formation of complete and regular flowers in shape, because they did not report concrete and detailed descriptions on the flowers. Hence, it is probable that most of garlic flowers show morphological abnormality as is shown in this investigation.

Garlic is a sterile plant and most of garlic flowers seem to show various morphological abnormalities. It is possible to assume that both of the sterility and the morphological abnormality in garlic flower are related with each other. Provided both of them are related with each other, it would be considered what is the cause of the sterility accompanied by morphological abnormality.

Gates and Goodspeed[2] classified the causes of pollen sterility as follows;

"1. crossing of sufficiently distinct species,
2. a condition of variability or mutability in the species,
3. the substitution of vegetative for sexual reproduction,
4. unknown physiological causes."

Takenaka[17] reported that the irregular behaviour of the chromosomes at meiotic mitosis in garlic seemed to be caused by hybridity. In addition to his suggestion, there is the fact that the wild species and the native land of garlic are unknown. From those facts it may be possible to assume that garlic is derived from the crossing of two species. However, in many experiments it was scarcely observed that the sterility caused by hybridity was connected with the morphological abnormality of flowers.

The sterility which results from variability or mutability is sometimes accompanied by malformation of flowers. For example, the sterility caused by petaloidy[14,20] and the sterility caused by 'warty anther' in maize[1] are known. Nevertheless, the sterility which results from variability or mutability in garlic is less probable, because garlic is propagated vegetatively and all of them in the world are regarded as sterile[4].

The sterility caused by the substitution of vegetative for sexual reproduction is probable in the case of garlic. It is well known that vegetative reproduction of the plants causes the transmission of virus to their progeny. Occasionally, morphological abnormality resulting from the infection of virus has been observed in various plants. The morphological abnormality caused by virus might be transmitted to the progeny in the plant propagated vegetatively. Flowers infected by virus show various symptoms, though their aspects depend on the kind of the virus or the plant. Important symptoms in the infected plants are as follows[3]; dwarfness of flower (chrysanthemum flower distortion disease), fusion of enlarged sepals (tomato big bud), cessation of blossoming (pigeon-pea sterility disease), narrow and distorted petals (prune dwarf), 'apiculated' petals (white necrosis), bending of flower stalks (onion yellow dwarf), distorted and twisted calyx (sour cherry necrotic ringspot), failure of pollen cells and egg cells to function (tomato aspermy disease), abortive pollen grains (tobacco ringspot), transformation of ovules to leaflets (Koksaghyz yellows), aborting of flowers (cowpea mosaic), aborted pistils (prune dwarf), and so on.

No one stated about the flower symptoms of garlic infected by virus[12], because garlic is usually harvested before flowering and the flower of virus-free garlic has never been seen. However, the morphological abnormality of garlic flower is supposed to resemble some symptoms of flower infected by virus as mentioned above. Actually the sterility caused by infection of virus was reported[7]. The authors are trying to clarify the effect of virus on the formation and development of flower in garlic by means of the production of virus-free plants.

It is probable that some of sterility accompanied with malformed flowers in garlic results from some physiological causes.

Koul and Gohil[9] attributed the cause of the sterility in garlic to the food competition between the developing flowers and bulbils in the inflorescence. However, Shimada and Shozaki[13] mentioned that the flowers of garlic failed to seed, even if the bulbils were removed from the inflorescence in the early stage of their development. Most of abnormal flowers showed lack of each floral part and abnormal shape of it, which means that the development of flower is not disturbed only by the deficiency of nutrition. It seems to be suggested that the competition between flowers and bulbils for nutrition in garlic is not the only one cause of sterility.

It may be possible to suppose that the complete and regular flower in shape, though failure of microspores to differentiate into pollen grains, as is reported by Koul and Gohil[9], is formed under the cool weather at high altitudes in Kashmir. They pointed out that high altitudes might favour differentiation beyond sporogenous stage, as compared with the report by Khoshoo *et al.*[6] Khoshoo *et al.*[6] investigated on the north west Indian garlics, and attributed the failure of sexual reproduction to the degeneration of sporogenous tissues both within anther and ovule. However, the abnormality in garlic flowers seems to suggest that it results not from physiological causes but from constitutional. The following three are the reasons why the abnormality in garlic flowers is not supposed to be due to physiological causes;

1. A few characteristic abnormalities were observed in the limited inflorescences as mentioned in 'Observation'.
2. Various abnormalities in garlic, for example, lack of floral parts, seemed to show that the flowers were not affected physiologically at the late stage of growth. The flowers seemed to be affected at or before the differentiating stage.
3. The types and their frequency in abnormality of garlic flower differed in accordance with the inflorescences.

The complete and regular flowers in shape were always observed in Welsh onion, and the abnormal flowers in shape were occasionally observed in leek. Most cultivars of leek commonly yield about half or less seeds per acre than those of Welsh onion[5]. It may be suggested that the two facts, morphological abnormality of leek flower occasionally observed here and poor yield in seed production of leek, are related one another. The frequency of abnormal flowers should be investigated in more cultivars of leek.

Summary

The types and their frequency of the morphologically abnormal flowers appearing in 162 flowers taken from ten inflorescences of garlic *(Allium sativum* L.*)* were clarified on each of their floral parts. Those on 100 flowers from each of leek *(A. ampeloprasum* L.*)* and Welsh onion *(A. fistulosum* L.*)* were clarified, too. Morphological abnormality was observed in 81% of flowers in garlic, while 27% in leek and none in Welsh onion.

The types of morphological abnormality in garlic flowers mainly observed were as follows; increase or decrease in the number of each floral part, formation of flowers or bulblets in a flower, fusion of floral parts, abnormal shape of floral parts including dwarfness, partially leafy and warty anther, and branching of a filament. The most common ones were lack of one floral part and abnormality in the shape of each floral part.

The causes of formation of morphologically abnormal flowers in garlic were discussed with relation to its sterility.

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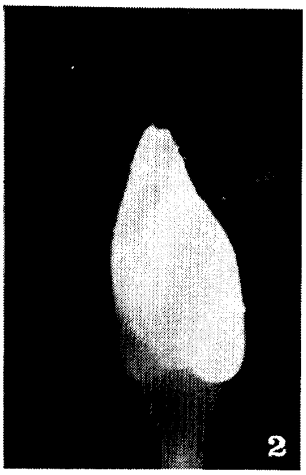
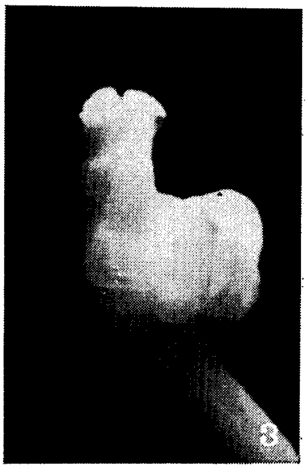
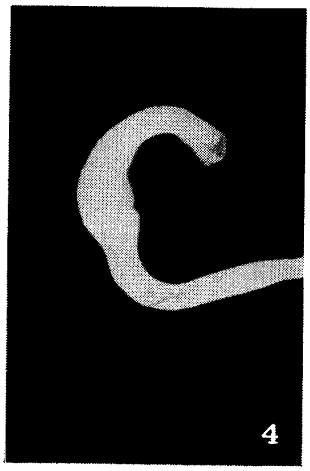
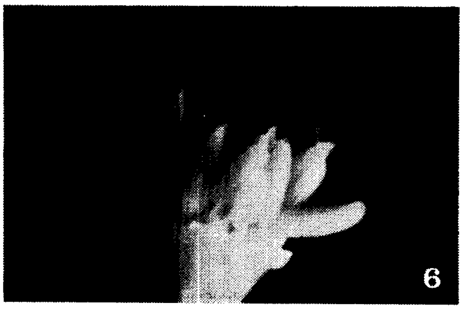
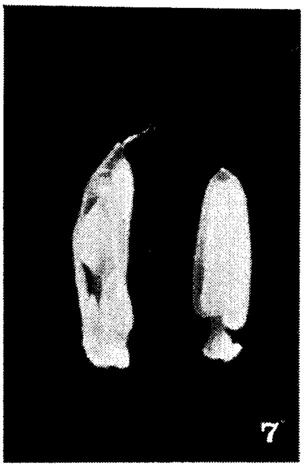
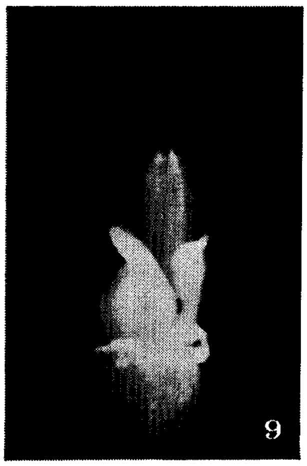






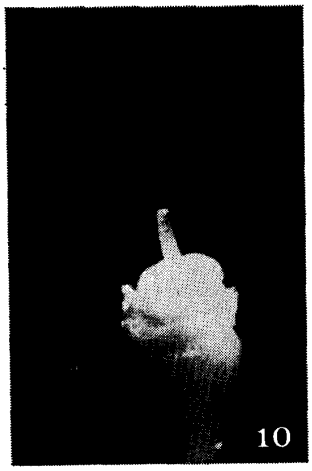
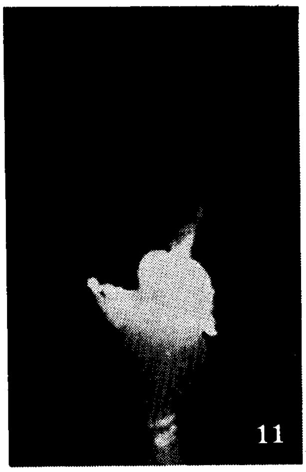
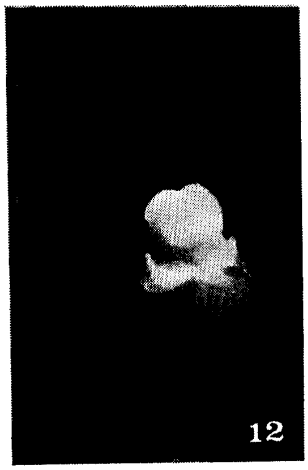
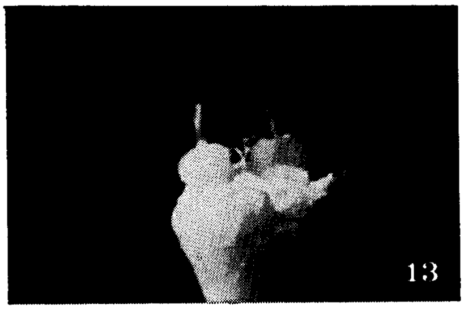
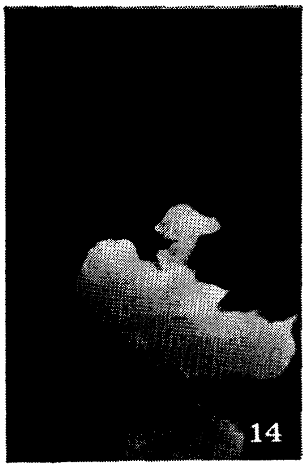
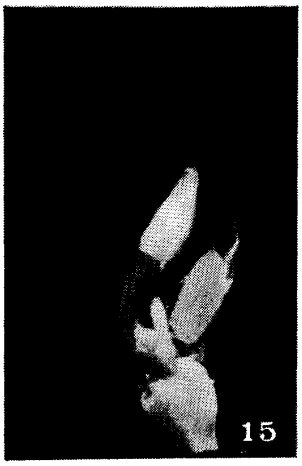
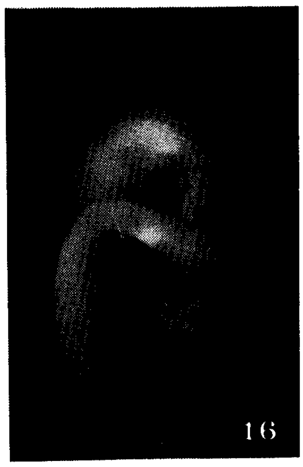






Explanation of figures

Fig. 2. A normal flower bud (× ca. 7.2)
Fig. 3. A flower with deformed perianths (× ca. 7.2)
Fig. 4. A flower with a tube-shaped perianth (× ca. 3)
Fig. 5. A normal anther (left) and a leafy anther with hairy appendages (right) (× ca. 8.7)
Fig. 6. Eleven anthers in a flower (Perianths are removed.) (× ca. 7.2)
Fig. 7. A warty anther with an extra tooth (left) and a normal one (right) (× ca. 11.1)
Fig. 8. A branching filament (× ca. 11.1)
Fig. 9. A deformed pistil (front left) and a deformed anther (front right) (× ca. 13.4)

Explanation of figures

Fig. 10. A normal pistil (× ca. 11.1)
Fig. 11. A leafty style (× ca. 11.1)
Fig. 12. A bent style (× ca. 11.1)
Fig. 13. Two pistils in a flower (× ca. 11.1)
Fig. 14. A deformed pistil (× ca. 11,1)
Fig. 15. A flower formed in a flower (× ca. 7.2)
Fig. 16. Two flowers fused at their pedicels (× ca. 3)