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SOME RECENT OBSERVATIONS ON  
*DIGITALIS PURPUREA* L.  
f. *HEPTANDRA* DE CHAMISSE

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1. INTRODUCTION

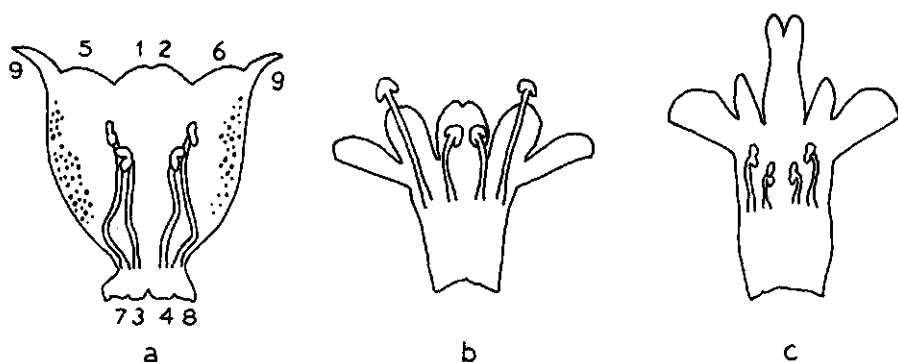
A sudden startling biological experience was for me the finding, in 1964, in our experimental garden, of a plant which later appeared to conform to the one mentioned in the title of this paper (pl. I, photo 1). Since this was the starting point, the composition of this paper differs from the normal habit: I will start with our own observations, and present historical notes further on.

*Digitalis purpurea*, belonging to the Scrophulariaceae (pl. I, photo 2) normally has a sympetal corolla of a trumpet or rather prolonged bell shape on which four stamens, 2 longer ones and 2 shorter ones, are implanted (text figure 1). The corolla can be considered as composed of five leaves, the two dorsal (adaxial) ones still more strongly fused than the other ones, while the (5th) stamen, to be expected between these, normally is lacking.

In the deviating plant from 1964, the corolla consisted of a short proximal rim, from which emerge a bilingual, dorsal, bandshaped petaloid structure and, furthermore, seven stamens, standing free, and protruding outside the flower in all directions (see also plate V, photo 10, representing a similar plant, photographed in 1968, see below).

Seeds of the 1964 plant were collected and descendents were raised in subsequent years. With some ups and downs, we succeeded in propagating the deviation until now, and in 1968 and later some more detailed examinations were made.

The observations, made in 1968 and 1969 will be described here in some detail, followed by some historical notes, and an outlook on further experimental possibilities and problems.



Text figure 1.

a. *Digitalis purpurea* L. Corolla slit open, indicating its composition of five elements (marked 1, 2, 5, 6, and 9), the two short stamens (marked 3 and 4), and the two long stamens (marked 7 and 8). The numbering as indicated is consistent with what has been used in this paper with regard to the *heptandra* form (see below).

b. *Thymus vulgaris* L.

c. *Marrubium vulgare* L.

The figures b and c show increasing split between the elements 1 and 2, as is mostly found in *Digitalis purpurea*, f. *heptandra*. — a, b, and c drawn by Miss M. E. VAN DEN NOORT, after BERG and SCHMIDT (ref. 19).

## 2. DESCRIPTION OF SOME FORMS AROUND *D. PURPUREA* F. *HEPTANDRA*

Plants, fairly identical with the original one, occurred in our cultures in subsequent years, from seeds of the original plant and its descendents in free pollination. However, they were accompanied by forms somewhere intermediate between the real *heptandra* and the normal form, or passing 'beyond' *heptandra* in staminification of the corolla, so that flowers were formed which, in the full possession of the normal calyx and gynoecium, presented nine more or less fully stamiferous elements.

The photographs 3–16 (plates II–VIII) represent plants of the various types (black and white reproductions from color slides, taken in our experimental field in 1968 and '69), showing successive stages of degeneration of the corolla.

Plates IX–XII (photo's 17–24) show a series of isolated spikes, demonstrating the same phenomenon. Plates XIII and XIV (photo 25) show a series of dried flower types, collected in 1968 from various plants. The close sequence of deviations is obvious.

Some discussion on this fact will be presented below.

Plate XV (figures 1–9) shows analytical drawings of flowers with different degrees of staminification of the corolla.

A perusal of the mentioned photographs and figures gives rise to the following remarks.

Normally, in *Digitalis purpurea*, the lower labellum of the corolla is somewhat longer than the upper one. An indication of a tendency towards deviation some-

times is the appearance of a somewhat shorter corolla with a more or less straight circular rim (plate XIII). Also otherwise deformed complete corollae show up, with narrower corollar tubes and more pronounced lobes at the rim, see e.g. plate I, photos 3 and 4; that these types could well belong to the same series of deviations is indicated by some of the flowers, higher up in the spike that show splitting of the corolla and protrusion of some anthers, unfortunately, sufficient attention was not paid to this when the photograph was taken. The next step is the appearance of indications of additional anther formation at the rim of the corolla at the expense of corollar parts (plate XV, fig. 1). A subsequent stage of corollar degeneration shows a more or less broad dorsal corollar element with lateral anthers, whereas the lower lip is represented by a broad filament with corollar appearance, and a large anther at the top (Pl. XV, fig. 2).

Before proceeding with more details, it may be useful to point out that understanding of these deviations will i.a. require an examination of development of organs in the buds for which material has been collected but not yet examined. Until then we will take what we consider as the simplest starting point, and assume that the entire range of forms can be understood by the assumption that there are 5 corollar elements and 4 staminiferous ones, thus together 9, of which the corollar ones are liable to different grades of staminification. It should further be observed that, in the normal form, the dorsal part of the corolla is of rather uniform colour (red, pink or white), while the lateral and lower parts bear round spots, each with a dark centre and a brighter area around it, a pattern which has been interpreted as serving to guide insects towards the nectar (the 'honey-mark').

In the deviation shown Pl. XV, fig. 2, the broad filament of the abaxial stamen still bears the insect guiding design. The next step is formed by types in which the lateral stamens have their filaments detached from the dorsal corollar element (Pl. XV, fig. 3), also these lateral newly formed stamens may bear the insect guiding marks on their filaments. Interestingly, the staminiferous development left and right is not always exactly the same, see e.g. Pl. XV, fig. 4, in which the additional lateral stamen at the right side (no 6) still bears the petaloid marks on its filament, while the left one (no 5) has a 'normal' filament.

We will introduce here a numbering of the elements in a flower of the 'heptandra' type which is to be considered as more or less logical from our preliminary interpretation of the relation between corollar and staminiferous elements indicated above. Thus, we will denote the most persistent dorsal petaloid element as 1, 2 (fused); the stamens 3 and 4 nearest to this are the normal short stamens, the newly formed lateral stamens, just discussed, are 5 and 6, while 7 and 8 are the normal long stamens; the lower (ventral or abaxial) newly formed stamen is element number 9.

In the typical *heptandra*, the elements 5, 6, and 9 are completely staminified and no more distinguishable from the 'real' stamens 3, 4, 7, and 8. Still, also here, types differing in degrees, of dissolution of the corolla are distinguishable. So, e.g., in Pl. XV, fig. 5, the dorsal corollar elements 1 and 2 still are completely fused, while, in fig. 6 (the most typical 'heptandra') the split between elements 1

and 2 is very pronounced. Different degrees of splitting are distinguishable (see the photographs), ultimately leading to fairly complete staminification of the corolla (see, e.g., Pl. XV, figs 8, 9). So far, I have never seen a flower in which complete anthers have developed on the elements 1 and 2; the nearest approach are formations which could be indications of single anthers (Pl. XV, fig. 9), or more or less rudimentary antheric developments which may differ at both sides of the flower (Pl. XV, fig. 8  $\times$ ). An interesting peculiarity shows Pl. XV, fig. 7, in which the dorsal elements has two lateral staminiferous formations (1 and 2), as in Pl. XV, figs 8 and 9, however, with a filamentous element ( $\times$ ) in between. One might speculate that this may be a rudimentary 10th element, or potential 5th stamen, but for a reliable interpretation of these small corollar reminiscences more observations are needed (see also below and section 3). I have, so far, not seen flowers with 10 stamens (those of Pl. XV, figs 7, 8, and 9 may be denoted as types with 9 stamens; 10-staminal flowers have occasionally been mentioned in literature (see section 3).

Small additional corollar elements may be seen at the base of stamens (see, e.g., Pl. XV, fig. 6, in the literature indicated as 'lacinulae corollinae') to which considerable importance has occasionally been attached in literature; in our opinion, however, this will have to await the results of more thorough morphogenetical research.

We conclude our observations with the presentation, in some detail, of a few characteristic flowers.

Plates XVI–XVIII (photo 26, a–l) present dried flowers. Photo's 26a–d represent flowers, all grown on the same plant; photographs of the same flowers in fresh state are shown on Pl. XIX, photos 27–30; analytical drawings of the same flowers are presented on Pl. XX, figs 10–13. This set of illustrations shows the considerable variation that may occur on one plant. Photo 26d (cf. Pl. XIX, photo 30, Pl. XX, fig. 13) presents a practically normal flower, probably, the lower lip is somewhat more dissected than normally, and between the lower lobe of the labellum and the side lobes something that possibly represents initials of anther formation, is visible. Photo 26c (cf. Pl. XIX, photos 29a and b, Pl. XX, fig. 12) shows an unusual but interesting and beautiful aberration. The abaxial part of the flowers has split into 2 more or less equal and symmetrical lobes, deeply separated from the dorsal (adaxial) fused lobes. The unusual of this flower is that the element 9 appears split into two, half of each belongs to each of the two abaxial lobes; anther development was not observed on this element. The two mentioned lobes are somewhat twisted, and partly turned inside out (see Pl. XX, fig. 12), the anthers of stamen no 6 also appear separated, those of stamen 5 are near together at the left side lobe (see Pl. XX, fig. 12).

The figures Pl. XX, 11 and 10 represent flowers developed further towards the *heptandra* type, no 10 is a more or less typical *heptandra*, however, with the filament of stamen 6 still attached to the corollar part 1–2, and stamen 9 with corollar marks on the filament. No 11 can be seen as a more 'normal' intermediate type than no 12; it is about intermediate between figures 1 and 2 on Plate XV.

Plate XVII, photos 26e and f show two flowers, artificially slit open; the analytical drawings of these flowers, both in natural state and slit open, are presented Plate XX, figs 14a, 14b and 15a, 15b respectively, the flower of Pl. XX, fig. 14 is photographed in fresh state on Plate XXI, photo 31. These two flowers (from the same plant) represent a type with only moderate corollar deformation but well-developed additional anther formation (cf. the cited analytical figures).

Three more flowers, from different plants, are presented as dried flowers (Plate XII, photo 26g, slit open; photo 26h, and Plate XVIII photo 26i). The corresponding analytical drawings are shown Plate XX, fig. 16a, b (normal and artificially slit open respectively), fig. 17 and fig. 18. Photographs of the fresh flowers are shown Plate XXI, photos 32, 33, 34 respectively. They are selected for showing the gradual increase towards *heptandra* formation (most typical in Pl. XXI, photo 33), and beyond (Pl. XXI, photo 34). Together with what has already been said above, the possibility for detailed comparison of dried flowers, analytical figures, and enlarged photographs seems to make further comments superfluous.

Plate XXII shows a final set of three flowers (photos 35–37) corresponding to the dried flowers Plate XVIII, photo 26 j–l (from different plants). No analytical drawings have been made of these flowers. Pl. XXII, photo 35 is a rather typical *heptandra*; photo 37 shows an intermediate type with stamen 5 (cf. the numbering in the previous analytical drawings) and 6 still largely attached to the corollar part 1–2; like in stamen no. 9 their filaments are corollarily developed. The large, spadeshaped anthers of stamens 5 and 6 (and sometimes of stamen 9) in this type of flower, show up clearly. Flower Pl. XXII, photo 36 is somewhat more difficult to understand. The downward pointing stamen probably is no 8 (the normal long stamen at the right side), stamen no 6 is seen attached to the corollar element 1–2 which, at the left side shows a broad element which probably contains stamen 5 and stamen 9, still mutually fused and connected with elements 1, 2.

The foregoing presentation was mainly meant to present a survey of types surrounding the typical *heptandra*, in analytical drawings and photographs, as clear as possible. The existence of this large variation of flower forms seems to render the idea of one single gene difference, as advocated in older literature (see below) rather unlikely, at least in its most simple form.

### 3. HISTORICAL NOTES

Nowadays, biology appears not so much inclined to study aberrations of plants incidentally observed in nature or in culture. Big problems of biochemistry, genetics, taxonomy, physiology and ecology take up the main streams of interest. Having talked about our observations in four or five different botanically interested circles here and in England, I found that nobody in the audience had ever seen this plant. It would, however, probably be premature to conclude that the aberration is very rare (see also section 4).

Especially in earlier literature, before 1914, a number of more or less extensive reports are found, and, in plant collections in the Netherlands, specimens collected more recently occur in small numbers (see below). The earlier literature can relatively easily be traced in consulting PENZIG's admirable compilation (1). Some of the figures published by earlier authors are compiled on Plates XXIII to XXVII and numbered figures 1–7. Plate XXIII (fig. 1) shows the oldest document, accompanying what is known as the first description of the plant by DE CHAMISSO in 1826 (2). A glance at DE CHAMISSO's figures may convince the reader that the deviations described in the present paper closely agree with DE CHAMISSO's findings, and also that the same pluriformity in details, indicating differences in the completeness of the transformation, existed in DE CHAMISSO's material.

The next record seems to be the one founded upon a plant supplied by W. EARLEY (3) (Plate XXIII, fig. 2). It represents a type with a fairly broad dorsal corollar lobe, and 7 stamens, the numbers 5 and 6 appear fused with the corollar lobe (numbers in the figure: our interpretation<sup>1</sup>). The position of stamens 3 and 4 (the short ones which should be nearest to the (broad) corollar lobe is not clear, and neither is that of the long stamens 7 and 8, and 9. That also the latter is fully staminiferously developed is clear from the presence of 5 pairs of normally developed anthers on normally formed filaments. Of interest are the clearly visible 'lacinulae corollinae'. Recently collected evidence in our group which will be discussed in a subsequent paper suggests that these are normally situated between the bases of stamens 7 and 8, and stamen 9.

After a preliminary note in 1881 (4), G. HENSLOW a year later presented a figure of a 'monstrous foxglove' (5), reproduced Plate XXIII, fig. 3. The stem top reveals a normal *heptandra* with a rather narrow corollar lobe, representing the 'upper lip'. The detailed figures (nos 2–6) do not much contribute to further clarification of the picture; the best one is no 2 in which stamen 9 is in the characteristic position, accompanied by the 'lacinulae corollinae', etc. (numbers: our interpretation<sup>1</sup>). It seems that stamen 5 has already developed anthers, while element 6 still may be represented as a corollar side lobe.

Ref. (6) contains a very short note of 1902, without a figure, on a demonstration of a 'malformed' *Digitalis*, by HOLMES, which was mentioned to be similar to the one described by HENSLOW (5).

A little later we again find a demonstration, with a clear figure, by SMITH (7) (see Plate XXIII, fig. 4) showing a fairly broad, spoonshaped corollar lobe with the elements 5 and 6 in full staminiferous development, and element 9 as a stamen with a broad filament, and the two lacinulae corollinae aside. The following may be quoted from the (adequate) description:

'The tube of the corolla is normal, and so are the two petals constituting the upper lip, but the three lower ones, save only the basal tubular portion, are quite absent. Whilst there is this defect in the corolla, the number of stamens is increased from four to seven, all of them springing from the tube of the corolla...'

Observations made in 1970 and '71 in our group (to be discussed elsewhere)

<sup>1</sup> For this numbering consult plate XV and text figure 1,a (p. 2).

confirm the view that the additional stamens 5, 6, and 9, represent the three ventral petals. Since all stamens, also according to SMITH's observations, are implanted on the corollar tube, it is not quite clear why, in the accompanying flower diagram, the stamens 7 and 8 are sort of referred to the two lower sepals. Similarly, the other normal stamens 3 and 4 might then be referred to the two upper side sepals, instead of to the upper corollar lobe (representing elements 1 and 2).

The most outstanding article, in the earlier literature is that by SAUNDERS (8, 1911) from which Plate XXIII, fig. 5, and Plate XXIV, fig. 1 are taken. The author observed that the degree of staminody shows a definite sequence along the spike, proceeding from further to less reduction of the corolla, moving upwards (Plate XXIII, fig. 5). She also noticed that, sometimes, after a certain point, a reverse reaction sets in, leading to flowers at the top with, again, a more reduced corolla. Plate XXIV, shows a range of deviations. The figures, marked 1, 2, and 6 to 11 by the author are very similar to those described in the first part of our paper as observed in our experimental field. Together with the 2 dorsal petaloid elements, the total number of petaloid and staminodial elements is 9, as was in general so in the plants we observed. Reduction of petaloid elements, without development in staminodial direction is shown in SAUNDERS' figures 3, 4, and 5 (cf. Plate XXIV, fig. 1 in the present paper). In these cases, the flower shows only 7 stamens, without or with only very small reminiscences of the elements 1 and 2. Up to now, this type was not observed in our cultures. SAUNDERS also observed the lacinulae corollinae in some cases. Besides making these morphological observations, SAUNDERS carried out an extensive genetical analysis. When cross-fertilization with normal individuals was prevented, only *heptandra* forms were obtained from *heptandra* individuals. The degree to which the deviation developed, seemed to depend on external conditions, notably on the amounts of light and moisture, though the results varied (even in opposite directions) between various 'families'.

It became further evident that the *heptandra* form was related to the type as recessive to dominant. 'Plants derived from the original *heptandra* parent but resembling the type – hence evidently crossbreds – invariably gave a mixed offspring, the numbers approximating to the ratio 3 Type: 1 *Heptandra*, or 1 Type: 1 *Heptandra*, according as they were fertilized with their own or sister-pollen, or were crossed back with the *heptandra* form' (l.c.p. 58).

It was already mentioned that SAUNDERS observed different flower types along one spike. She distinguishes three main types which we will mention here since they bear a relation to our own observations (this paper) and new ones made in our group (to be published at a later stage), viz.,

'1° Extreme *heptandra* form. Plants in which all, or almost all, the flowers are without petal-like structures.

2° *Heptandra* form proper' (see the figure reproduced Plate XXIII fig. 5). 'Plants in which only the flowers in the lower region of the spike and those at the extreme tip appear to have no corolla. In the intervening region the upper lip appears as a conspicuous petaloid structure which is usually deeply bifid. By far

the larger number of *heptandra* plants belong to this group.

3° Intermediate *heptandra* form. Plants in which all, or nearly all, the flowers are more or less petaloid. The lowest flowers, in which an upper lip is often already well-developed, are succeeded by others in which a lower lip also gradually makes its appearance, and finally tubular or even quite normal flowers may be found towards the top'. (l.c., p. 55).

Another paper is rather comparable to that of SAUNDERS, viz. the one by SHULL (9, 1911/12) appearing only little later, and giving full acknowledgement to SAUNDERS' results which were very much the same as those of SHULL himself. Plate XXV, (fig. 2) and Plate XXVI, fig. 3 reproduce SHULL's illustrations. His figures A and B (Plate XXV) are reproductions from DE CHAMISSO's figures 2 and 3 (see Plate XXIII, fig. 1). Again, the forms observed are quite similar to those of the previous records. SHULL started from seeds asked and obtained from Mr. T. SMITH, which were offsprings of the plant pictured in (7), and reproduced Plate XXIII, fig. 4 (I feel some uncertainty regarding Mr. SMITH's initials, T being mentioned by SHULL, while the figure appears monogrammed W. G. S. Drawer and sender, however, may not be the same person. In the text of (7), no initials are mentioned).

SHULL made morphological observations, and also carried out crossing experiments, arriving at the same conclusion as SAUNDERS, viz. that *heptandra* differs from the normal one by one recessive characteristic. Attack by thrips greatly damaged the cultures and affected the results. In general, SHULL's observations fully confirm those by SAUNDERS, both as to the variability and the heredity of the *heptandra* form. He, too, noted that 'offspring of *heptandra* parents all show dialysis and staminody of the corolla, but the extent to which these malformations are exhibited varies not only in different individuals, but in different flowers on the same individual'.

None, however, was found with 10 stamens, as reported by SAUNDERS, nor was any observed with complete absence of petaloid structures; even if there were 9 stamens there appeared two 'linear-subulate petal-like phyllodes subtending the lower pair of normal stamens' (i.e. in most of the figures on Plate XXV). In these respects, our own observations agree more closely with SHULL's ones than with those of SAUNDERS. SHULL considers the mentioned structures (conforming to DE CHAMISSO's 'lacinulae corollinae') together with the larger dorsal petaloid structures, characteristic for most of the *heptandra* types, as an 'accessory corolla'. He also mentions that there often is (in the more extreme *heptandra*'s) an unpaired small median dorsal lobe between the 2 major ones (also observed in our group in some cases). SHULL thus considers the two major and the small unpaired dorsal lobes as the three dorsal parts, and the two lacinulae adjacent to the two lower normal stamens as the two ventral parts of the accessory corolla, and points out that they alternate with the normal corolla which has two dorsal and three ventral lobes.

This interpretation to me does not appear very plausible. Certainly, more observations are required regarding the genesis of the various parts of the corolla and the stamens of the *heptandra* forms. The existence, however, of the 'inter-



mediate *heptandra* forms' (SAUNDERS, see p.8) strongly suggests that hardly anything happens to the normal stamens (3, 4, 7, 8) and that the basis of the malformations is the normal corolla only, in which staminification starts in the three lobes of the lower lip (yielding the stamens 5, 6, and 9, which may still bear the 'honey marks', cf. section 2 of this paper), and in a further stage proceeds with the upper lip (parts 1 and 2), which may yield two additional stamens, mostly each with only one anther. Recent additional observations in our group on different flowers of one spike, by Miss VAN DEN NOORT and the author, to be presented in detail elsewhere, suggest the continuity of the sequence between fairly normal flowers to the extreme *heptandra*'s. This includes also more detailed observations regarding the (lower) lacinulae corollinae.

SHULL, additionally, also states that the genesis of the accessory corolla is still unclear. An interesting introductory remark is that, in the family of the *Scrophulariaceae* there is a strong tendency to a reduction of the number of stamens, viz. 5 in *Verbascum*, the 5th replaced by a staminode in other genera; in *Ilysanthes* and some species of *Gratiola* there are 2 functional stamens and 2 staminodes, and in *Veronica* and its relatives and in some *Gratiola* species there are only 2 stamens without a trace of the other three (l.c., p. 257). Therefore, the staminiferous tendency displayed in *Digitalis purpurea heptandra* seems all the more remarkable.

It has already been mentioned that, in a few breeding experiments, SHULL has confirmed SAUNDERS' finding that *heptandra* differs from the normal form in one Mendelian character which is recessive in *heptandra*. Interestingly, SHULL mentions that Dr. Tine TAMMES from the Groningen University in the Netherlands, in 1903, found a single individual of *heptandra* in the Botanical Garden of the University, also conducted crossing experiments and arrived at the same conclusion regarding its Mendelian behaviour. SHULL mentions that TAMMES had not yet published her results when SAUNDERS' paper appeared, and would not publish them anymore. Meanwhile, she obviously sent a photograph of one of her plants to SHULL, reproduced from SHULL on our Plate XXVI, fig. 3c. Fig. 3a and b show a normal *Digitalis purpurea* L., and the more common form of *Digitalis purpurea heptandra* DE CHAMISSE from SHULL's cultures, respectively. TAMMES' figure is, as far as I know, the earliest published document of the occurrence of this plant in The Netherlands (for more recent findings, and documentation by herbarium material, see below). TAMMES' plant shows the extreme *heptandra* form.

It has already been mentioned that literature, later than PENZIG, is very difficult to find. Up to now, I have been able to find only very few papers which deal with the *heptandra* form. It should be stressed, however, that I do not consider our research as completed in this respect, so that the possibility remains that additional data are found, and I would be very much indebted to readers, mentioning them to me.

Two papers that appeared after PENZIG's review should be mentioned in any case. The first, by COSTERUS (10) appeared in 1925 and discussed some plants found in the Netherlands, respectively at Bussum, Wageningen, and Utrecht.

The accompanying plate clearly shows that the flowers at least considerably resemble those described elsewhere as *heptandra*. COSTERUS' interpretation is that *heptandra* constitutes a very important atavism in that it represents a diplostemonous form whereas the normal *purpurea* is haplostemonous. For the present we will not enter into this discussion, much depends also upon the interpretation of the lacinulae corollinae etc. However, we should like to remark that an unbiased look at the series of flowers as present in our material does not suggest the interference of any elements not normally present in a *Digitalis* flower; all can be understood rather simply by a more or less extensive replacement of corollar elements by staminodial ones.

It should be remarked that COSTERUS does not refer to any previous observation of *heptandra*, nor to any preceding literature.

Some of COSTERUS' figures have been presented in Plate XXVI under number 4.

An important, more recent paper is that by WEILING (11) which may be indicated as the most comprehensive paper in recent literature, as such following the papers by SAUNDERS (8) and SHULL (9). The author refers to SAUNDERS' distinction of 'extreme', 'proper' and 'intermediate' *heptandra* forms, and proposes other denominations, viz., *heterandra* for the entire complex of deviations, and, for the various distinguishable forms: *enneandra* (9 stamens), *heptandra*, and *intermedia* (for intermediates between *heptandra* and the normal flower type). So far, in our opinion, this change does not immediately seem advisable, since a fairly complete range of intermediates can be observed between the normal flower and the most extreme (9-stamen) *heptandra* types (see, e.g., our figure 25 and a subsequent paper (12). As already remarked, we will refrain from a detailed morphological interpretation of our observations made so far, WEILING (l.c.) presents an interpretation which reminds of the one presented by COSTERUS (10) (not quoted by WEILING) in which the author also operates with an accessory corolla represented by the 'lacinulae corollinae' and, in his material as well as in that of SHULL also by fairly conspicuous petaloid elements. Our experience in this field is rather limited, but in some cases, to be discussed elsewhere, we also have observed additional petaloid elements (as well as various other corollar deformations) which, however, so far seem to us to belong to the normal corollar elements (e.g., split off from their margins in relation to their deformation to stamens, etc.), and we see, so far, no definite reasons to interpret them as signs of atavism in the direction of pentacyclic flowers belonging to ancestors of the Scrophulariaceae. Also in this respect ontogenetical observations may be helpful.

We agree with WEILING's statement that the great variability of flower types suggests that more than one gene is in play, in which probably one determines the appearance of the *heptandra*-complex as such, and others determine the degree of deformation.

It should also be observed that the variation of flowers within one flower stalk (observed variously in literature and for which more material will be presented in a subsequent paper) suggests the interference of non-genetical factors, probably related e.g. to nutritional or positional effects.

Some of WEILING's figures are reproduced on Plate XXVII, under number 5.

Some attention has been paid in recent years to malformations in *Digitalis purpurea*, without *heptandra* having been mentioned.

In 1960, a short note appeared by HERMAN, GUSULEAC and BALOESCU (13), dealing with the appearance of large, campanulate, more or less actinomorphic end flowers (commonly known as peloria). They conclude that the phenomenon is accompanied by shortening of the upper part of the floral axis, and clustering of bracts with aborted flowers in the axillae. Fourteen to 25 sepals and 12–18 stamens belong to the abnormal flower, leading to the assumption that the phenomenon results from the concrescence of 3 to 5 flowers. Exceptional is the large number of carpellae, viz. up to 50. *Peloria* were also (in small number) among our seedlings from the mixed normal/*heptandra* populations we have grown so far.

A new line of research is recently developing by studies in experimental teratology, attempting to induce deviation by treatment with certain chemicals. At Nantes, DEBRAUX, ASTIÉ, and their associates (14, 15, 16) carry out an extensive programme, studying especially floral abnormalities in several plant species after application of 2–4D (2, 4 dichlorophenoxyacetic acid). These studies also include *Digitalis purpurea*. Among other abnormalities, as a trimerous flower (with 6 stamens) and flowers with the 5th stamen developed, reduction in number of stamens often occurred, so that completely female flowers may be formed. A 'fasciation biflore' is described, having 7 stamens, a 7-element corolla and 7 carpelles; this deviation seems to be quite different from *heptandra*. From the viewpoint of the present paper, the most interesting effect probably is the dialysis of the corolla, observed in some cases (see (16), fig. 3). The flower no. 2 in this figure resembles very much certain *heptandra*-types, except that no additional anther formation is apparent (see our Plate XXVI, fig. 6).

ANGULO-CARPIO and REAL (17, 18) studied the effect of colchicin on the induction of floral variations in *Digitalis thapsi* L. The reports are of some interest in relation to our subject, since they produced a type named 'retracted corolla', viz. with a short, tubular corolla with stamens protruding towards all sides, like in *D. purpurea heptandra*. The number of stamens may also be increased; however, as far as I could ascertain, to not more than 5 (see Plates XXVI and XXVII, under no 7. Crossing experiments were made, indicating that 'retracted corolla' behaved, towards the normal form as differing in one, recessive, Mendelian character (thus, the same as was previously concluded for *D. purpurea heptandra*).

#### 4. OCCURRENCE OF *D. PURPUREA HEPTANDRA* IN THE NETHERLANDS

The earliest evidence that could be traced is SHULL's mentioning of TAMMES' results, and publishing of a figure (see Plate XXVI, fig. 3c). Questioning of the Herbaria at Leiden, Groningen, Utrecht, and Wageningen yielded 2 plants in the Rijksherbarium (Leiden), collected at Doesburg (1940), and Epe (1955). I

am very much indebted to Dr. S. J. VAN OOSTSTROOM, Rijksherbarium, Leiden, for sending these plants. They will be examined and the floral situation described elsewhere. Dr. VAN OOSTSTROOM also mentioned two water colours in the collection of the Rijksherbarium from a *heptandra* plant collected at Voorschoten, near Leiden, and three specimens in ethanol, collected: 1927 presumably at Amsterdam; in a garden, 1928 at Oegstgeest; 1955 at Voorhout. Further, it should be mentioned that COSTERUS (10) refers to three plants collected probably at Bussum, Wageningen, and Utrecht, in 1924. Together with the occurrence at Groningen, the available evidence indicates that *heptandra* has been incidentally observed at widely divergent spots in The Netherlands. The exact spots, probably reflect more the geographic distribution of the observers than that of the plant variety.

This situation suggests that *heptandra* findings may be expected all over The Netherlands and that more reports will follow if one cares to look for these plants. The distribution of *Digitalis purpurea* is 'atlantic' as is well-known. It, therefore, probably is not very surprising that reports of *heptandra* findings so far appear mainly restricted to Great Britain and The Netherlands. The only exceptions so far are DE CHAMISSO's finding (locality not indicated, however), and WEILING's plants at Bonn (1951) which came forth from an 'Inzuchtgeneration eines Digitalisstammes'. It is also remarkable that PENZIG, a German author, does not mention a single report from European countries other than Britain and the Netherlands (e.g. France, Belgium, West Germany, Denmark). In this respect it is of interest to quote a remark by SHULL (l.c.) who stated that the deviation is worthless in a horticultural respect, and will be discarded in commercial and decorative gardens, but, owing to its recessive character, is able to hide in phenotypically normal plants for several generations, until, from time to time, it will find a 'refuge' in the experimental gardens of geneticists (and, we may add, of morphogenetically interested plant physiologists). The circumstances under which WEILING (11) found his first plant seem almost exactly to fit SHULL's supposition!

## 5. OUTLOOK ON FURTHER RESEARCH

As, we hope, will have eloped from the preceding discussion, there are a number of interesting things about *Digitalis purpurea* f. *heptandra* DE CHAMISSO both for the morphogenecist and the geneticist.

The first point seems to be that the aberration, ontogenetically, appears of very little consequence, changing initials for petals into stamens, and a first object for further investigation may be to see at what stage in the flower bud development the difference in development becomes apparent. Spikes have been preserved for this purpose. Morphogenetically, the difference seems to be a minor one, elements of one range of initials assuming properties of the one next to it. Intermediate forms between petals and stamens are not unknown; they occur in 'double' flowers e.g. of Rosaceae and Ranunculaceae, but in those cases

the development is in the reverse direction, viz. from stamens to petals. Moreover, it seems more 'acceptable' that this should occur in flowers of more primitive families, like those mentioned with a rather indefinite number of stamens. These types are quite different from *Digitalis* and other Scrophulariaceae in which the flower would seem to have a much more rigid pattern in which, moreover, a tendency to reduce the number of stamens, rather than increasing it, seems to prevail (cf. SHULL, l.c.). Furthermore, the existence of different degrees of heptandry, as exposed above, probably will offer an opportunity to follow the genesis of the deviation in more detail, as some preliminary evidence, collected in our group in the 1970 and '71 seasons, seems to suggest.

The second line of research would seem to be a cytogenetic approach to the subject. Crossing experiments, combined with studies of nuclear and chromosomal behaviour – of the latter no evidence exists in earlier literature – appear to be of importance. In section 3 it has been exposed that the earlier authors who carried out crossing experiments, agreed in their conclusion that a monofactorial, recessive characteristic distinguishes *heptandra* from the normal form. The evidence for this conclusion seems well founded in their experimental results. Nevertheless, it appears remarkable that so many types of *heptandra* – almost a continuous series from the most extreme forms with 9 stamens and hardly any corollar elements to forms with supplementary anther development on a tubular corolla – arise side by side in an experimental field under fairly the same conditions, as well as the fact that a range of flower types usually is found in each spike (8, 9). This seems compatible only with the genetic results, if the monofactorial difference only decides over increased anther formation while other, may be metabolic, effects determine the ultimate realisation of the deviation. It still remains remarkable, then, that in the normal form, metabolic effects do not seem to have any conspicuous effects on the shape of the flower. It thus seems that the genetic difference of *heptandra*, apart of promoting staminody, renders its flower structure more labile throughout.

For the sake of tackling the indicated problems, preliminary contacts have been laid with Professor J. H. VAN DER VEEN. Genetics Laboratory of this University.

As a third point of further research, chemogenetic studies appear indicated. This, probably, will constitute a difficult and time consuming subject, but one might ask, how possible deviations in the DNA pattern affect RNA production and the enzyme apparatus of the plant. Since the deviation occurs only in a late, and very distinct stage, one might hope to have some chance to localize an effect. A practical approach to this line of work has not yet been made; contacts with a chemogeneticist are indispensable herefor.

As a fourth, promising and relatively easier line of work, we may indicate physiological studies on the effects of environmental factors on the developing degree of 'heptandry'. Since deviating plants, so far, are not well distinguishable from normal ones at an early stage, this work can only be initiated if predictable populations (e.g. from *heptandra*  $\times$  *heptandra* crosses) are available. It will take some years of careful and successful crossings to establish populations of suffi-

cient numbers of genetically identical plants (as far as the *heptandra* factor is concerned). In view of the preliminary data available in literature, it seems especially indicated to study the effects of light intensity, light quality, temperature, and certain formatively active chemicals (auxins, gibberellins, and others, probably also colchicin). Effects of chemicals on the development of single flowers on the spike or on nutrient media, may also be tried.

During the development of a programme, new problems will arise, and may be worth further pursuit.

## 6. SUMMARY

The finding of a plant with the characteristics of *Digitalis purpurea* f. *heptandra* DE CHAMISSO, in the garden of our laboratory, in 1964, and its subcultivation in free pollination in subsequent years has been reported. The present paper deals with a description of flower types observed (section 2) and in this respect mainly confirms earlier literature. The material is presented in analytical drawings, and, extensively, in photographs of single spikes and separate flowers (Plates I–XXII). In this respect it might be the most extensive documentation available up to now. The description and documentation of our material is supplemented with some historical notes (section 3), and a small collection of historical illustrative documents (Plates XXIII–XXVII). Reports of findings from the Netherlands are discussed (section 4). The paper is concluded with an outlook on further research. In this respect some remarks on problems in the fields of ontogeny, cytogenetics, chemogenetics, and physiology of the deviation have been made (section 5).

## 7. ACKNOWLEDGEMENTS

The author is indebted to Miss N. BOK and Miss M. E. VAN DEN NOORT for intelligent and devoted cooperation throughout the work, to Mr. D. STEDELAAR for taking practically all the photographs, and converting several from colour slides to black and white copies for publication, to Miss M. E. VAN DEN NOORT for adapting the author's original analytical drawings of separate flowers for publication, and to Professor J. H. VAN DER VEEN for his interest in the genetic and cytogenetic aspects of the problem. And, last but not least, to Dr. S. J. VAN OOSTSTROOM (Leiden) for information about plants preserved in the Rijksherbarium, and for references to more recent literature.

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## 9. SURVEY OF LEGENDS OF THE PLATES

### PLATE I

*Photo 1.* The original plant of *Digitalis purpurea* f. *heptandra* found in 1964 in the laboratory garden.

*Photo 2.* A spike of the normal *Digitalis purpurea*.

### PLATES II–VIII

*Photos 3–16.* Spikes photographed in 1968 and 1969 in our experimental fields of descendants of the 1964 plant (photo 1) obtained through free pollination, showing various stages of deformation of the corolla. They are arranged so as to suggest successive replacement of corollar elements by stamiferous ones.

### PLATES IX–XII

*Photos 17–24.* Isolated spikes from the above plant material arranged for photographing in the laboratory against a black background. The arrangement again shows successive types of replacement of corollar elements by stamiferous ones.

### PLATES XIII–XIV

*Photo 25.* A large range of successive stages shown in dried flowers, collected from various plants in our fields in 1968. The 3<sup>rd</sup> to 6<sup>th</sup> flowers in the top row show a rather characteristic feature, viz, a fairly 'normal' flower with a slightly abbreviated lower lip, representing the first stage towards staminification of corollar elements. These flowers still have the normal stamiferous pattern (2 long stamens and 2 short ones). The 7<sup>th</sup> to 9<sup>th</sup> flowers in the top row show this type with additional anther formation along the rims. Cf. also plate XV, fig. 1, and compare text. The utmost right figure in the lower row is the flower photographed without calyx.

### PLATE XV

Analytical drawings of flowers with different degrees of staminification of the corolla. From different plants in our experimental fields. Mostly taken in 1968.

### PLATE XVI

*Photos 26a–d.* Dried flowers, showing the considerable variation that may occur between flowers of the same plant, from practically normal (photo 26d) to strongly staminified (photo 26a).

### PLATE XVII

*Photos 26e–f.* Two dried flowers of one plant, artificially slit open.

*Photos 26g–h.* Two dried flowers from different plants (26g: artificially slit open).

### PLATE XVIII

*Photos 26i–l.* Four dried flowers from different plants (26l: calyx and fruit with pistil shown separately).

For pictures of the fresh flowers, cf plates XIX, XXI and XXII, for analytical drawings, cf plate XX.

### PLATE XIX

*Photos 27–30.* The same flowers as shown in photos 26a–d, in fresh state.

### PLATE XX

Analytical drawings of flowers shown dried on plates XVI to XVIII and in fresh form on plates XIX and XXI.

Fig. 10, 11, 12 and 13 corresponding to plate XVI, photos 26a–d, and plate XIX, photos 27–30. Figs. 14a–b, 15a–b corresponding to plate XVII, photos 26e–f which represent these



flowers slit open and dried (cf. figs 14b and 15b respectively); figs 14a and 15a show these flowers in their original state; fig. 14a corresponds to the fresh flower photo 31 on plate XXI. Figs. 16b–18 corresponding to photos 26g–i respectively (plates XVII and XVIII); fig. 16a represents the same flower before having been artificially slit open. Photos 32–34 (plate XXI) show the same flowers in fresh state.

#### PLATE XXI

*Photos 31–34.* The flowers shown dried on plates XVII and XVIII, photos 26e, g–i respectively, in fresh state. Showing some stages from relatively modest corollar reduction to 'heptandra' and beyond.

Photo 31 with additional anther formation, stamen N° 9 already fully separate, anthers 5 and 6 clearly visible and attached to lateral parts of the 'corolla'. Photos 32 to 34 show further stages of corollar reduction; photo 33 is a fairly typical heptandra, photo 34 shows a further stage in anther development on elements Nos 1 and 2 (for the numbering of the elements, cf text and plate XV). Flowers photos 31 and 32 photographed without calyx, from the ventral (abaxial) side; photos 33 and 34 show intact flowers from the dorsal (adaxial) side.

#### PLATE XXII

*Photos 35–37.* Photo 35: a more or less typical heptandra.

Photo 37: an intermediate form with the stamens 5 and 6 still largely attached to the corollar lobe (to somewhat different degrees left and right) and their filaments still with a corollar pattern, the same holds (very clearly to be seen) for stamen 9.

Photo 36: a flower with stamen 9 probably still attached to stamen 5 and together (left) at the corollar lobe (elements 1 and 2). See also text.

#### PLATES XXIII to XXVII

Historical documents regarding *D. purpurea* f. *heptandra*, cf. also the comments in the text.

#### PLATE XXIII,

*Fig. 1.* The earliest document, DE CHAMISSE's drawings (1826). In its briefness a very complete survey of forms. Cf. e.g. picture labeled 'fig. 4', with different degrees of freedom of stamens 5 and 6 (labeled h by DE CHAMISSE) and the indication of corollar spots on the filament of stamen 9 (labeled g by DE CHAMISSE), features also encountered by us (cf. text, section 2).

*Fig. 2.* A flower supplied by W. EARLEY (1874), showing a type with anthers 5 and 6 connected sidewise to the (broad) corollar lobe, and clearly visible 'lacinulae corollinae'.

*Fig. 3.* A 'monstrous foxglove' presented by G. HENSLOW (1882). See also text.

*Fig. 4.* A figure presented by SMITH (1904) with a diagram of a flower much resembling that of plate XXIII, figure 2. See also text.

*Fig. 5.* A spike presented by SAUNDERS (1911), showing more or less typical *heptandra* flowers at the top, and further reduction of the corolla in the lower flowers. See also plate XXIV, figure 1.

#### PLATES XXIV–XXVII

Some more pictures from literature (marked 1–7).

#### PLATE XXIV

*Fig. 1.* A range of deviations as pictured by SAUNDERS (1911). See, e.g., the lower stamen showing corollary spots in the figures numbered 9–11.

#### PLATE XXV

*Fig. 2.* A set of deviations similar to those of plate XXIV, as presented by SHULL (1911–12). (Figures A and B, presented by SHULL as reproductions from DE CHAMISSE).

PLATE XXVI

Fig. 3a. A normal *D. purpurea* from SHULL's cultures.

Fig. 3b. A spike of *heptandra* from SHULL's cultures.

Fig. 3c. An extreme *heptandra*, published by SHULL, and provided by Miss T. TAMMES, representing the earliest published document of *heptandra* found in The Netherlands. See also text.

Fig. 4. Another picture of *heptandra* flowers found in The Netherlands (COSTERUS, 1925).

PLATE XXVII

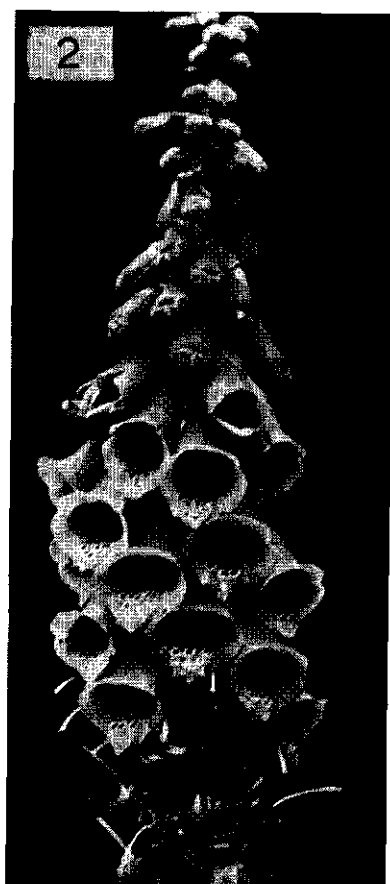
Fig. 5. Some pictures of spikes and flowers of *heptandra* from an extensive article of WEILING (1955).

PLATE XXVI

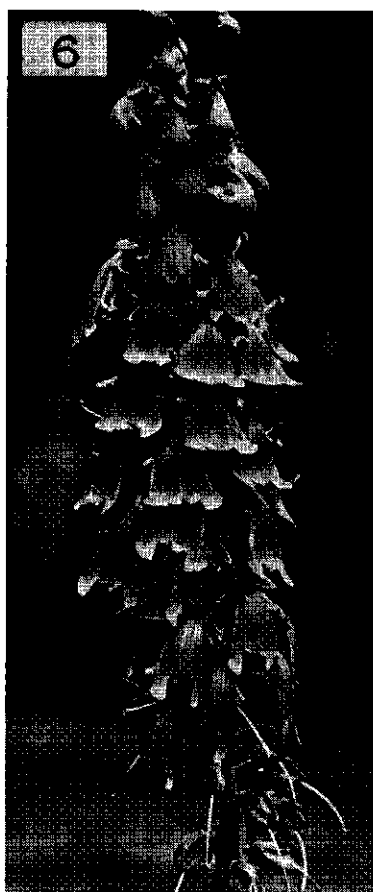
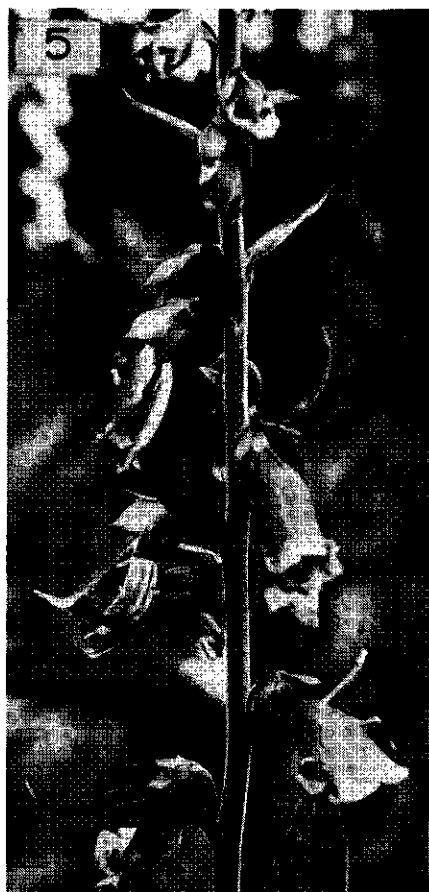
Fig. 6. Experimentally produced dialysis of the corolla in *D. purpurea* (from LECOCQ, 1963) reminding of *heptandra* forms, however without additional anthesis.

PLATES XXVI and XXVII

Fig. 7. Experimentally produced variations in *D. thapsi* L., reminding of some '*heptandra*' variations ('retracted corolla' with protruding stamens). From ANGULO-CARPIO and REAL (1960), see also text.







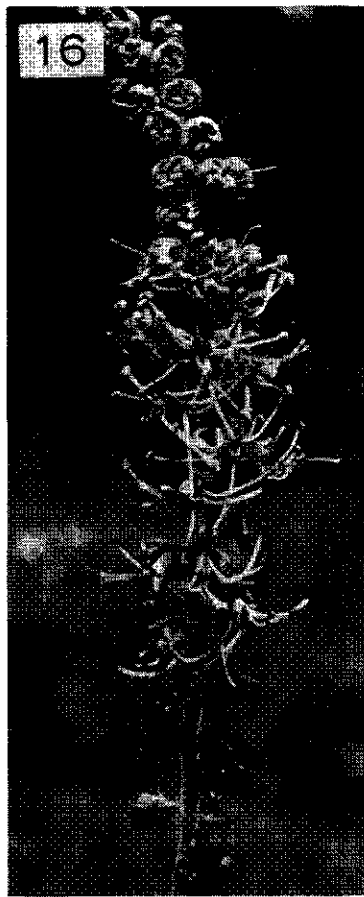
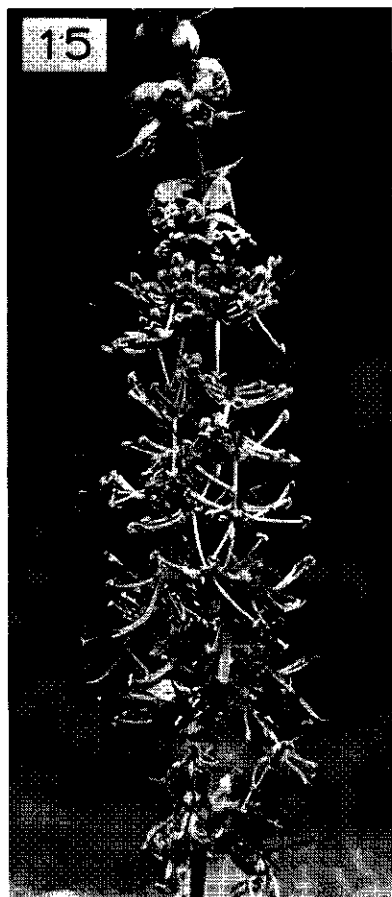


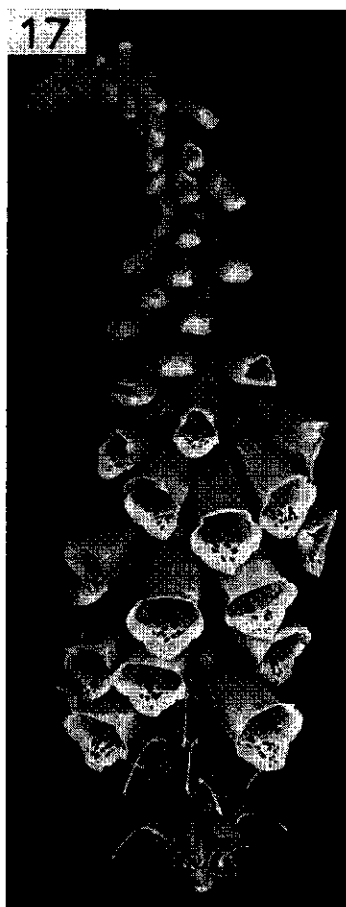




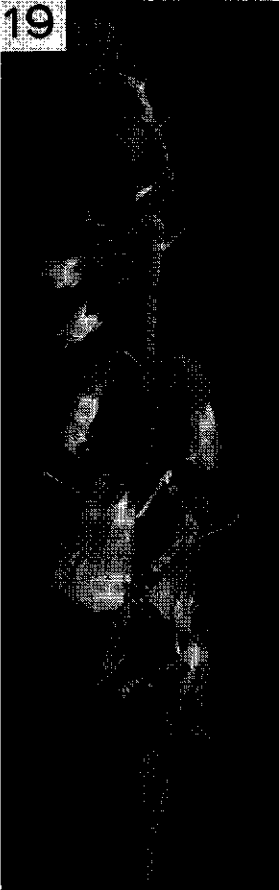




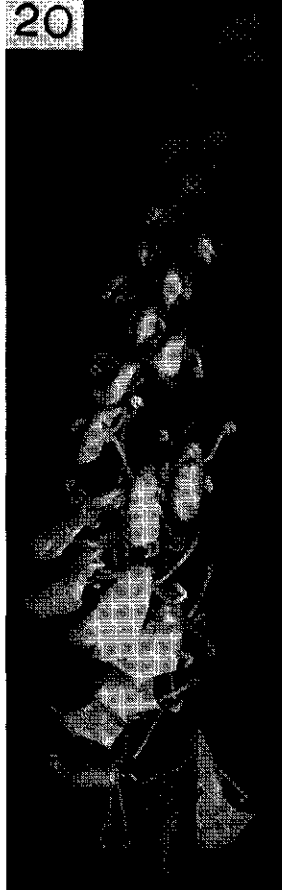




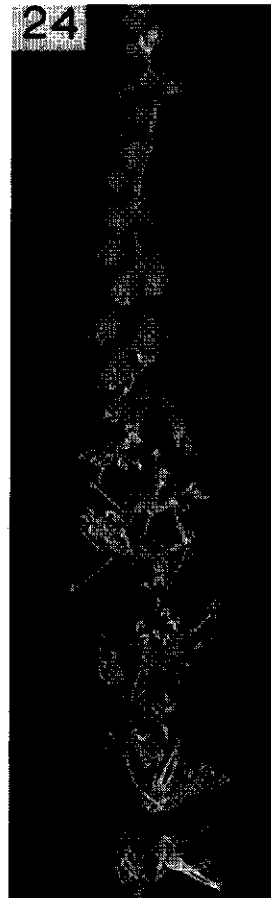
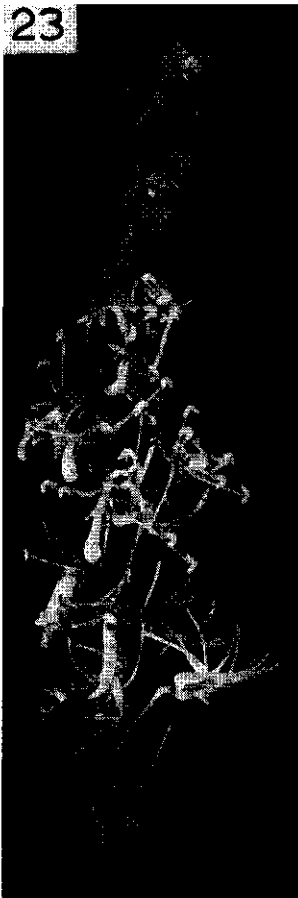
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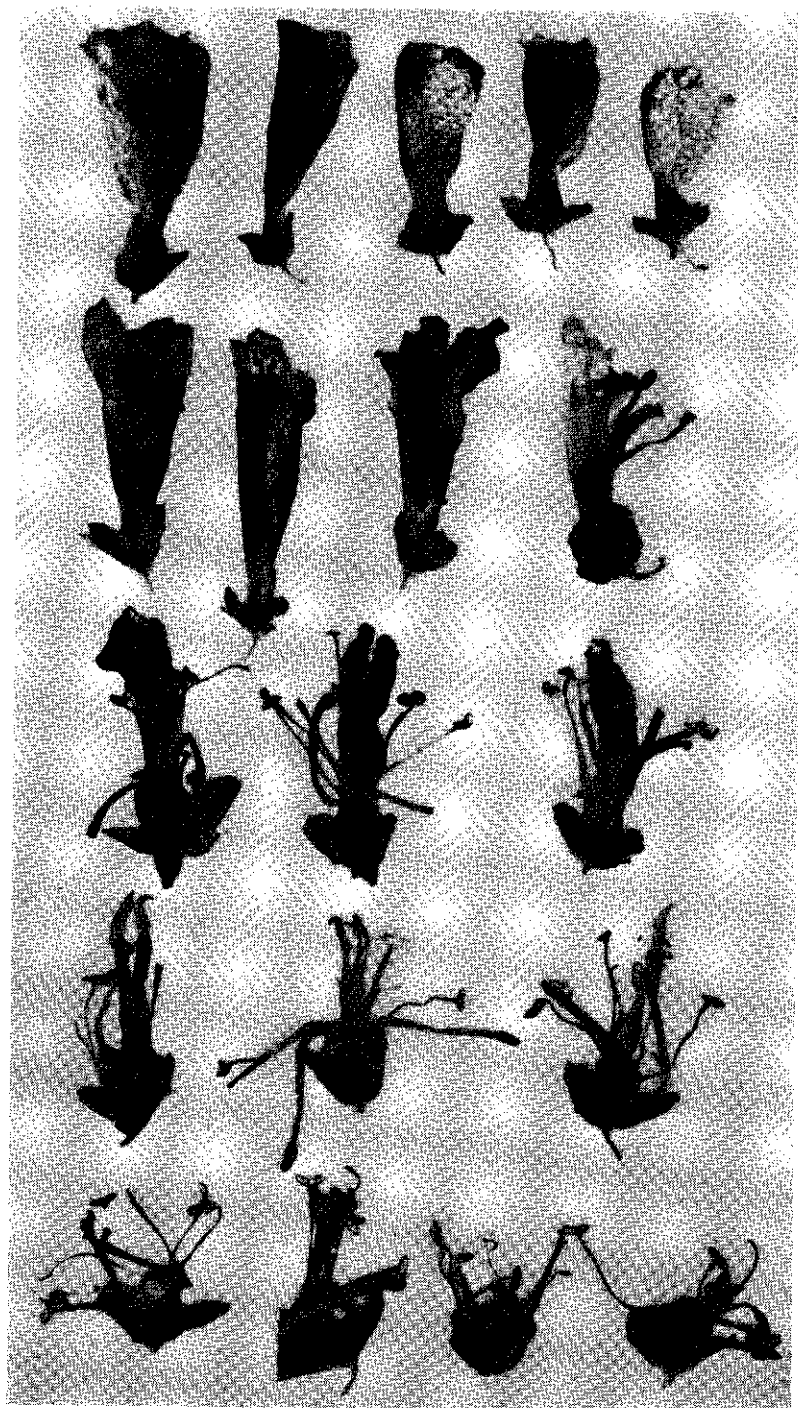


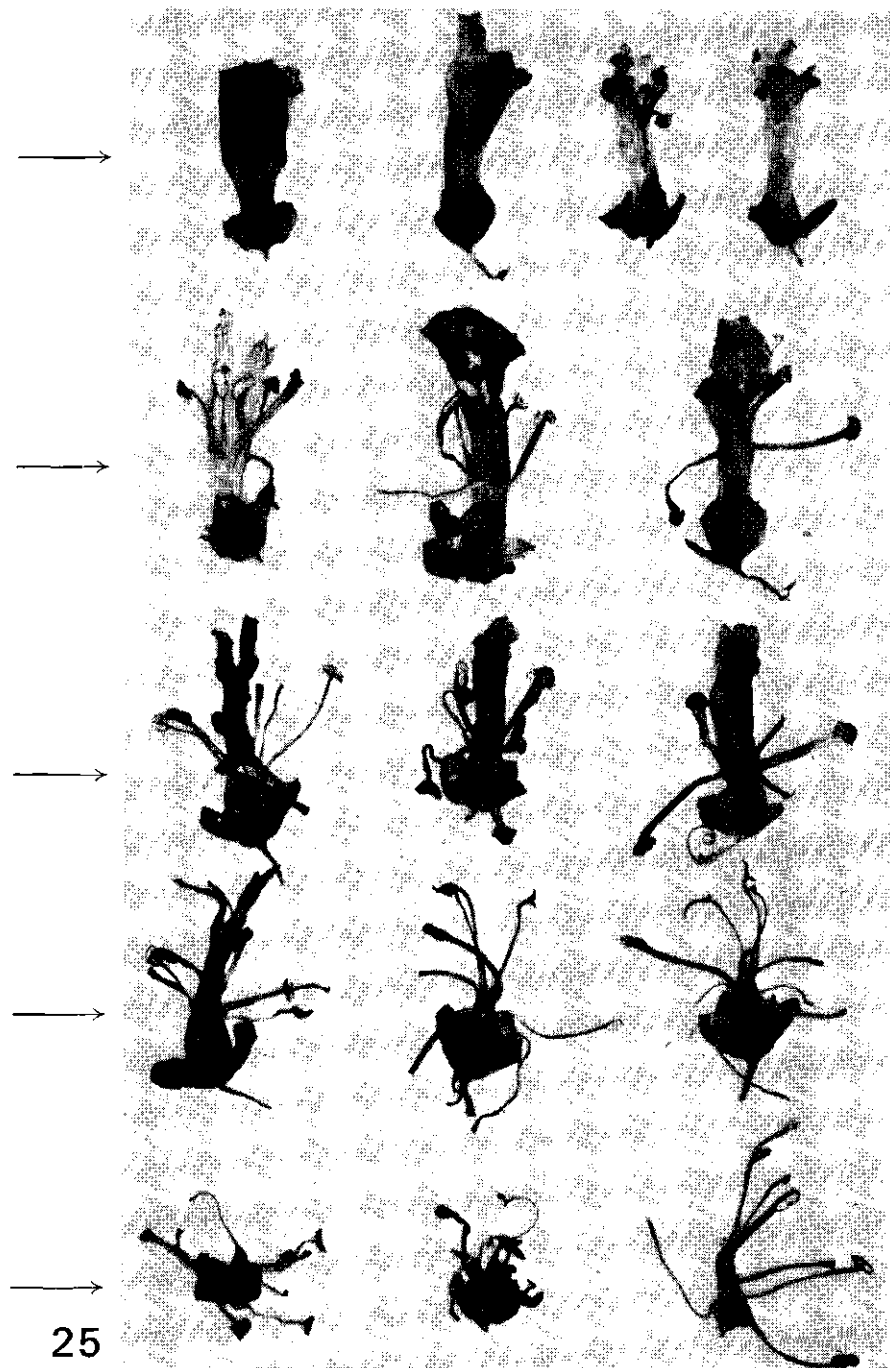
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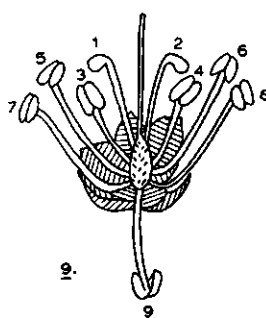
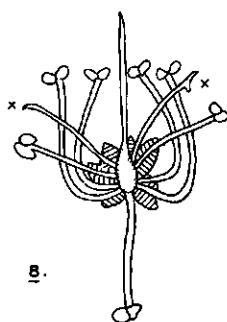
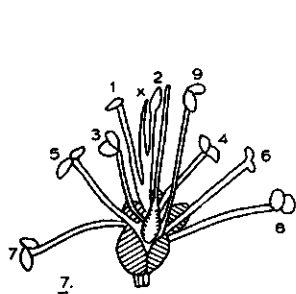
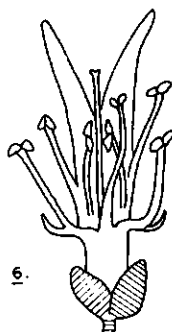
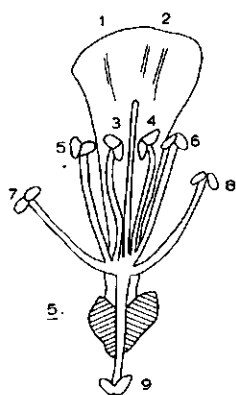
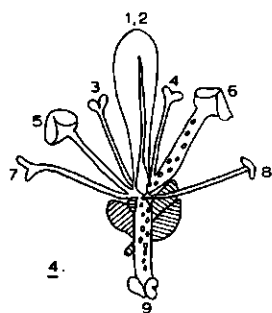
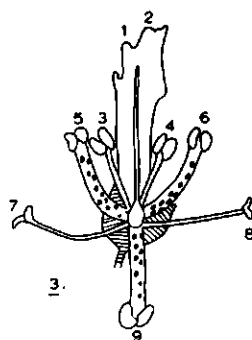
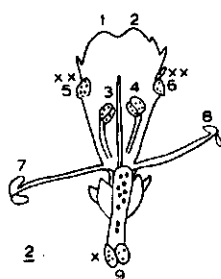
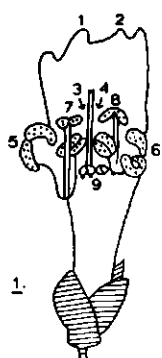


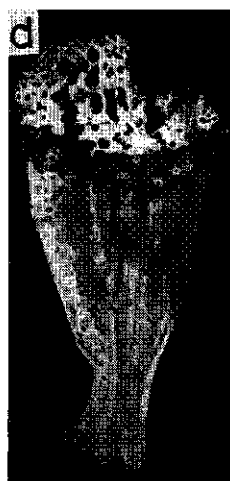
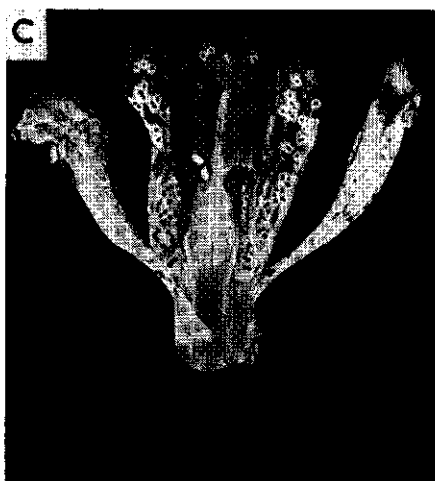
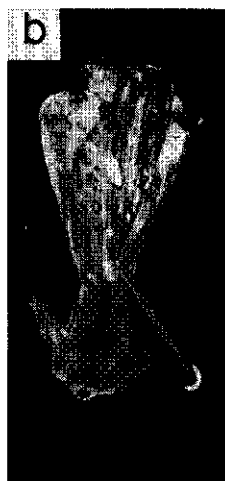


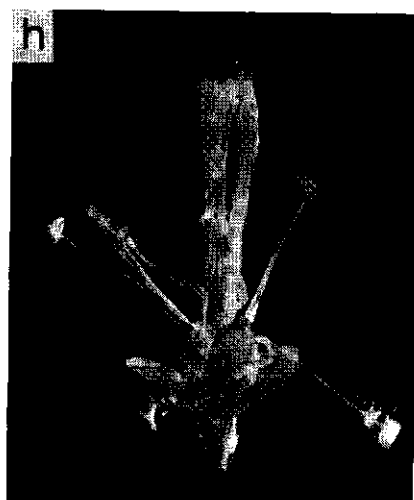
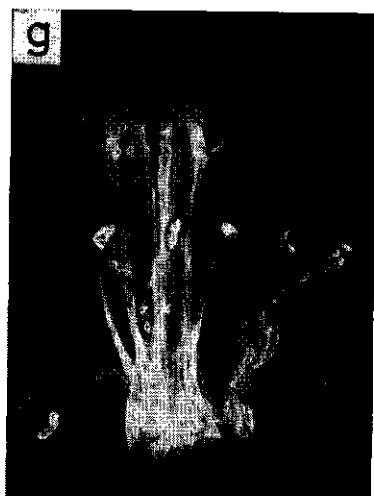
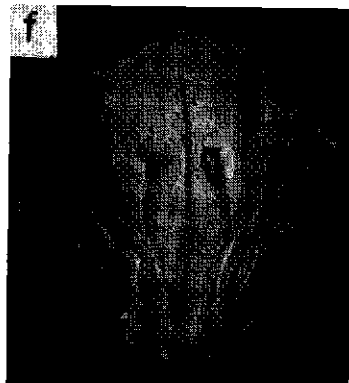
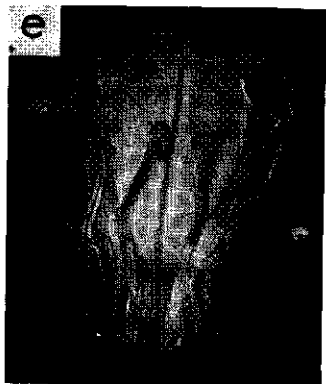


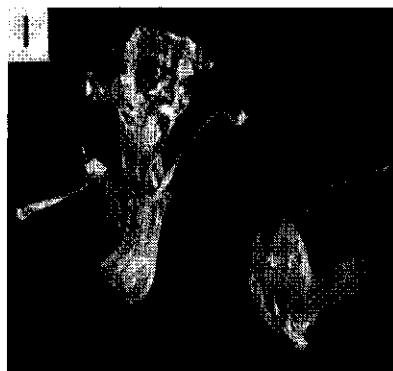
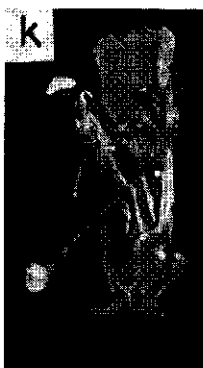












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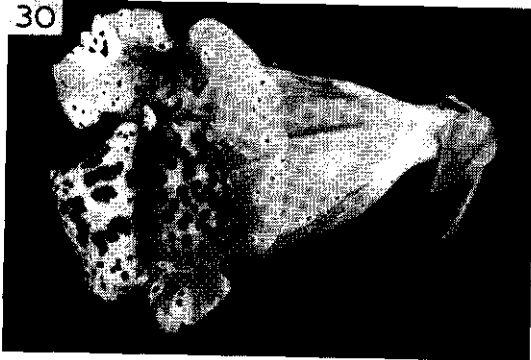
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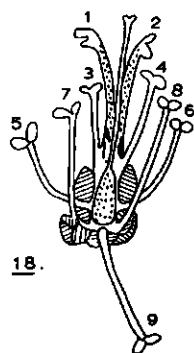
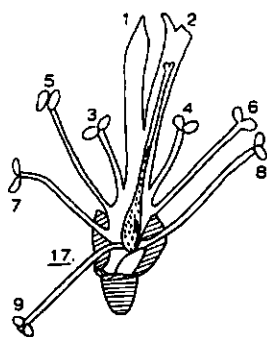
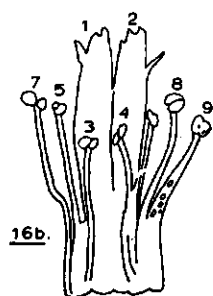
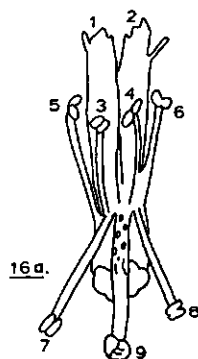
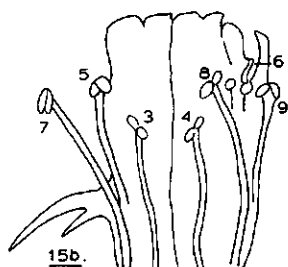
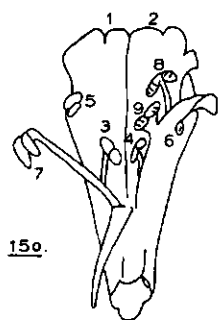
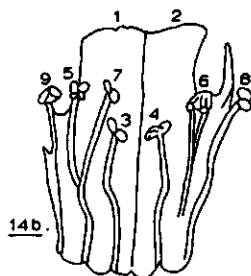
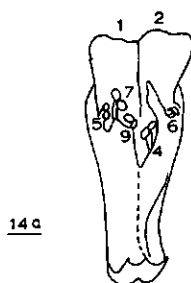
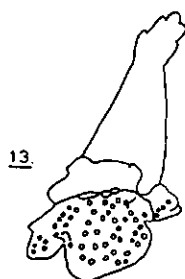
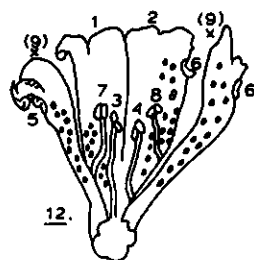
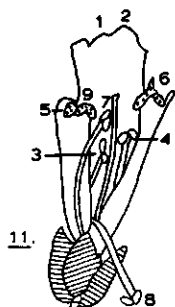
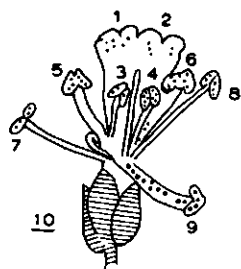


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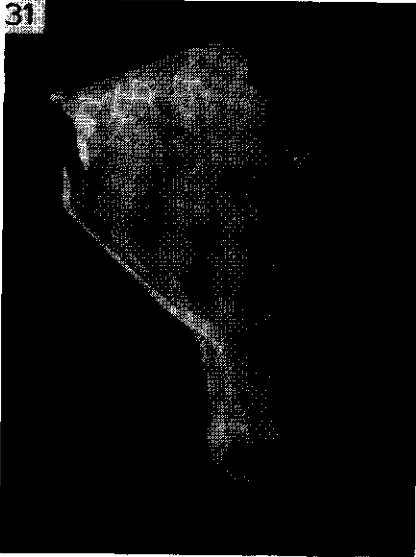


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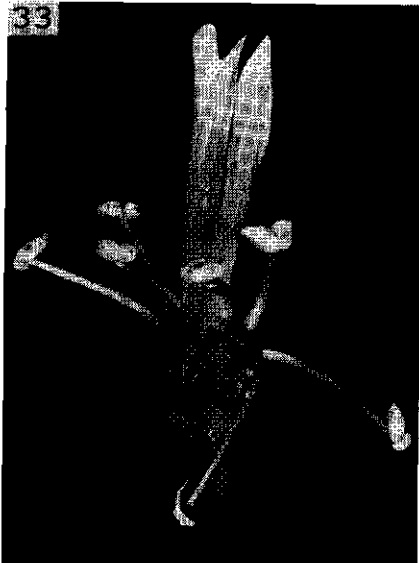
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