TRANSACTIONS, ILL. STATE ACAD. SCI.
Vol. 67, No. 1 (1974)

POLYCOTYLEDONY AND MORPHOGENESIS OF THE INFLORESCENCE AND FLOWER IN COLLINSIA HETEROPHYLLA

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ABSTRACT. – The polycotyledony and the double (split) leaves in Collinsia heterophylla Buist are considered as precocial manifestations of the action of the Pc-locus, which is assumed to be involved in the formation of the trimerous whorls of the inflorescence. The pentamerous cycles of the inflorescence and flowers appear to be the result of a combination of a bimerous and a trimerous node.

Genetic analysis of Collinsia heterophylla Buist (Scrophulariaceae) conducted by Goršič (1973) revealed that the polycotyledony (schizocotyly) is a simple recessive trait. The polycotyledony is known to occur in more than 30 families of Dicotyledoneae (Compton 1913, Earle 1938, Johnson 1936, Puri 1941, Swamy 1949). The wide-spread occurrence of this trait and the existence of pure-breeding polycotyledonous lines, in the normally dicotyledonous species, suggests the possibility that the gene(s) for polycotyledony (Pc-locus) may be a part of the normal genetic make up (genome) of plants of many, possibly all, families of Dicotyledoneae. If so, then, it is reasonable to assume that the Pc-locus may be involved in a control of some basic pattern of morphogenesis in plants.

Over 2000 plants were grown in the green-house (method for raising plants has been reported by Goršič, 1957). The modifications of leaf development and the number and arrangement of leaves of the polycotyledonous plants were compared with the morphological characteristics and the number and arrangement of bracts in the whorls of the inflorescence. In addition, the sequence of the maturation of flowers in the individual whorls was recorded.

In this article an attempt is made to explore the role the Pc-locus may play in the formation of the inflorescence and in the formation of the pentamerous flowers in C. heterophylla.

OBSERVATIONS AND INTERPRETATIONS

Polycotyledonous seedlings of C. heterophylla (Figs. 1-3) may have one normal and one split (double) cotyledon (1.2), both cotyledons split (2.2), three distinct cotyledons (1.1.1), one normal and one twice (1.3) or three times (1.4) split cotyledon, etc. Plants of this species have a decussate leaf arrangement. One leaf of the pair is usually larger. The leaves of the polycotyledonous plants tend to split - become double - (Figs. 4-6). Tricotyledonous plants commonly produce three leaves per node. Polycotyledonous plants in which the nodes with normal leaves alternated with the nodes having

one leaf split (Fig. 4), and plants in which the nodes with normal leaves alternated with the nodes having both leaves split (Fig. 6) have been observed. Plants having two nodes combined into a tetramerous whorl of four leaves as the result of the inhibition of elongation of the internode have also occurred (Fig. 7). These features of leaf and node configuration appear abnormal but, as will become apparent later, they reflect the normal stages of the development of the inflorescence and flowers.

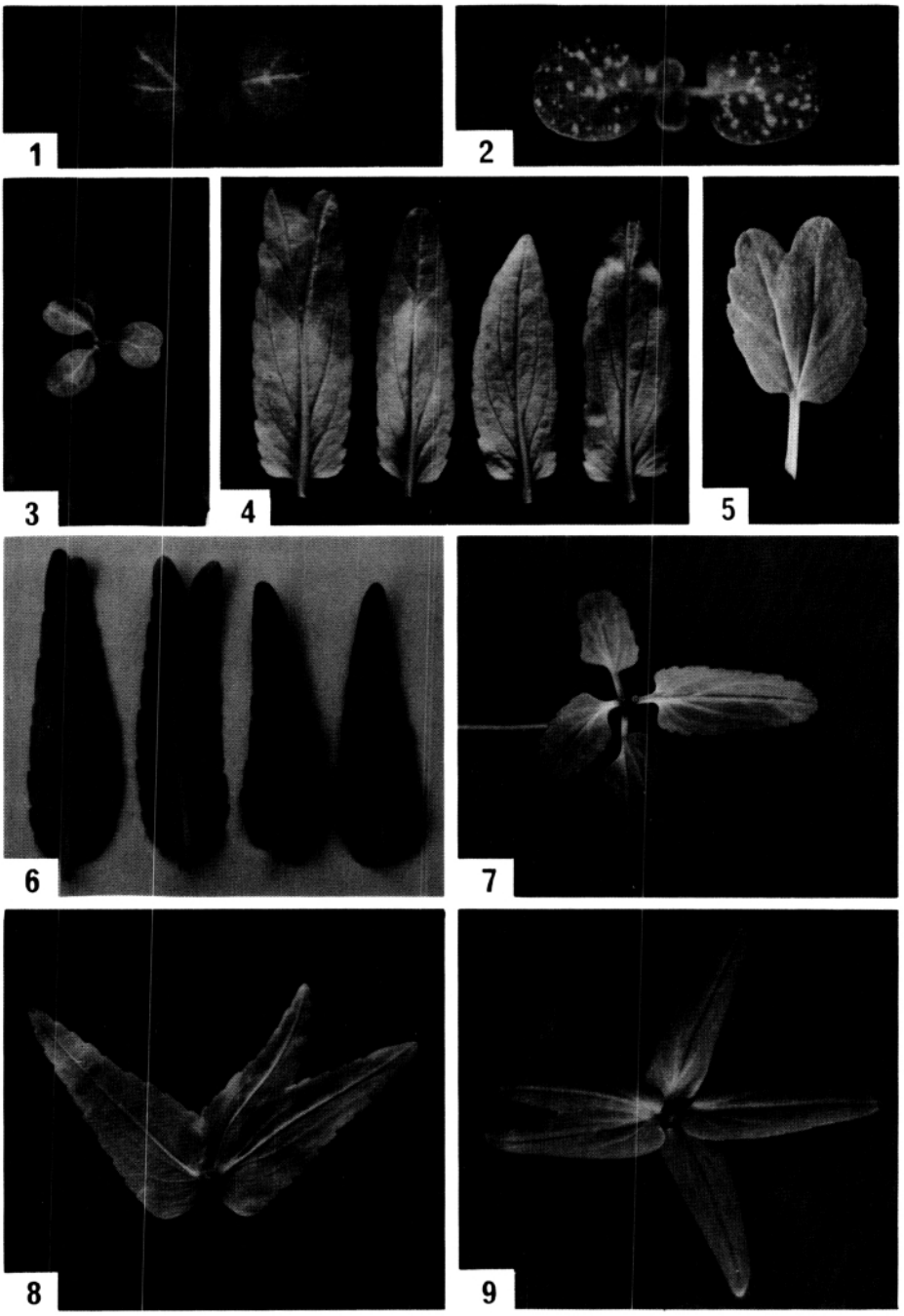
The reproductive growth-pattern in C. heterophylla was usually initiated at the fifth node or higher nodes in plants of certain genotypes and in plants grown in light of low intensity. Leaves at that level of plant development became sessile, the blade widened at the base, one leaf of the pair split, and the result was a trimerous whorl of large bracts (Fig. 8). The first whorl of the inflorescence had either three distinct bracts and 1-3 flowers; or one entire bract with or without an axillary flower, and a split (double) bract with one, two or no axillary flowers (occasionally the entire and double bract became connate, Fig. 8). Rarely the lowermost node of the inflorescence had two leaf-like bracts and one or two flowers. Plants with a four- or five-flowered whorl at the base of the inflorescence occasionally appeared.

These variations in the number of bracts and flowers at the first node of the inflorescence indicate that the transition from the vegetative growth-pattern to the reproductive growth-pattern occurs in some plants more abruptly than in other plants.

The second and higher nodes of the inflorescence had typically 3-5 flowers; the whorls with five flowers were prevalent. Two types of pentamerous whorls were observed: (a) in some, three flowers subtended by larger bracts matured ahead of the remaining two flowers subtended by smaller bracts (Fig. 10); (b) in other whorls two flowers were ahead in the development and three lagged behind (Fig. 11). In tetramerous whorls carrying five flowers one bract was always split (Figs. 9, 12). The typical tetramerous whorls were also of two types: (a) in some, two adjacent flowers matured slightly ahead of the remaining two; (b) in others, opposite flowers opened in succession with a 2-3 days interval (Fig. 13).

Thus, the formation of the inflorescence of C. heterophylla may be outlined as follows. The splitting of one of the two bract primordia at a node results in a trimerous whorl. Normally, the splitting of a bract occurs at every second node, but it may occur at adjacent nodes, or it may be skipped. The inhibition of elongation of alternate internodes results in a combination of nodes of the peduncle in a two by two pattern. The combination of a bimerous plus bimerous node results in a tetramerous whorl (another type of the

PLATE 1. Collinsia heterophylla. FIGURE 1. Semitricotyledonous (1.2). FIGURE 2. Semitetracotyledonous (2.2). FIGURE 3. Tricotyledonous (1.1.1). FIGURE 4. A double (split) and a normal leaf of the sixth (left) and seventh (right) node. FIGURE 5. Split leaf of the second node. FIGURE 6. Two split leaves of the fifth node (left) and two normal leaves of the sixth node (right). FIGURE 7. A whorl of four leaves. FIGURE 8. A trimerous (1.2) whorl of the inflorescence. FIGURE 9. A tetramerous whorl of the inflorescence with a double bract.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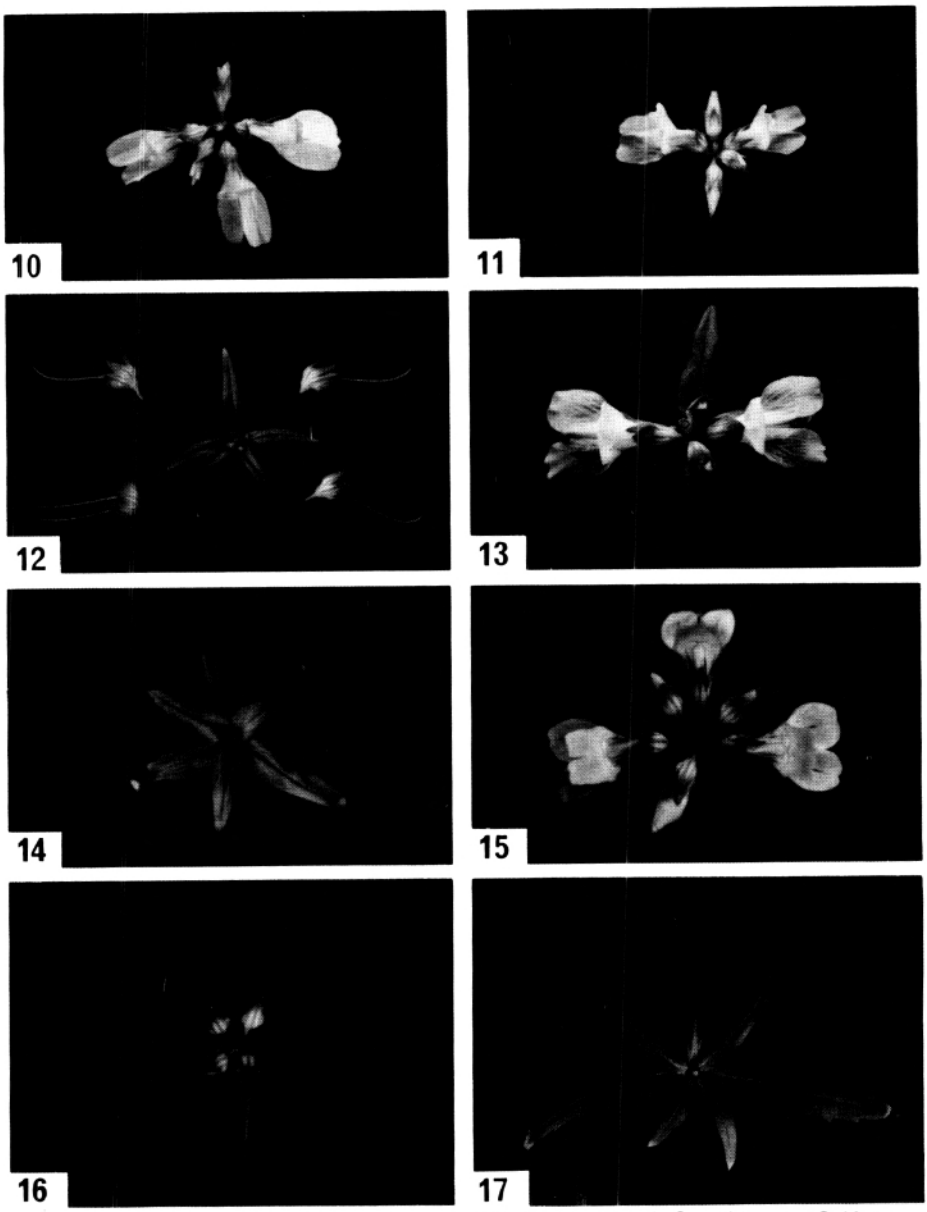

PLATE 2. Collinsia heterophylla. FIGURE 10. The 3-2 pattern of the maturation of flowers in a pentamerous whorl. FIGURE 11. The 2-3 pattern of maturation of flowers in a pentamerous whorl. FIGURE 12. A tetramerous whorl with a double bract having two fused flowers in its axil. FIGURE 13. The opposite (2-2) pattern of the maturation of flowers in a tetramerous whorl.

tetramerous whorl is produced when both primordia at a node split). The combination of a bimerous plus trimerous node results in a whorl of five bracts. The combination of a bimerous plus semitrimerous (1.2) node results in a whorl of five bracts two of which are connate (Figs. 9, 12). The combination of a trimerous plus trimerous node (Figs. 14-15) or a semitrimerous plus semitrimerous node (Fig. 16) results in a whorl of six bracts. Another hexamerous whorl is produced by the combination of a tetramerous plus bimerous node. The combination of a trimerous plus tetramerous node results in a whorl of seven bracts (Figs. 17-18). Splitting of both primordia at two adjacent nodes and the subsequent joining of the two resulting tetramerous nodes is one of the possible methods that yields a whorl of eight bracts (Fig. 19).

The 7-12-bracteate whorls were regularly produced by the mutant, terminal rosette (beaked) bk (Fig. 20). In this mutant the high incidence of splitting of bract primordia and/or the inhibition of elongation of two or more successive internodes resulted in whorls with exceptionally high numbers of bracts.

The flowers in the individual whorls of the inflorescence matured as follows (Table 1). At the nodes with two flowers, the flower in the axil of the larger bract opened slightly ahead of the other flower. In the trimerous whorls two flowers opened slightly ahead of the third, or one opened slightly ahead of the remaining two. In all compound whorls (made up of two or more nodes) the flowers of the lower (older) node matured 2-3 days ahead of the flowers of the upper (younger) node. Thus, in the tetramerous whorls opposite flowers matured in succession with a 2-3 days interval (2-2 pattern, Fig. 13). In the pentamerous whorls three flowers opened 2-3 days ahead of the remaining two (3-2 pattern, Fig. 10), or two flowers opened 2-3 days ahead of the remaining three (2-3 pattern, Fig. 11). Two of the three flowers that matured in unison were adjacently located. It is assumed that in the first case (3-2 pattern) the split of one bract primordium occurred at the lower node of the whorl, and in the latter case (2-3 pattern) one bract primordium of the upper node had split. Whorls with the 3-2 and 2-3 pattern of the maturation of flowers occurred interchangeably in the same inflorescence. The tendency to adhere to the 3-2 or 2-3 pattern was noticed in some plants. In the hexamerous whorls the alternate (3-3) pattern of the maturation of flowers was prevalent (Fig. 15); less common were 4-2 (four older, two younger opposite flowers) and 2-4 patterns. Flowers of the heptamerous whorls matured in a 3-4 or 4-3 (four older, three younger flowers) pattern in such a way that two of the four flowers that matured in unison were adjacently located, and the remaining five flowers of the whorl alternated as to their age (Fig. 18). In the whorls with eight or higher number of bracts, the flowers were usually of three categories. A nine-flowered whorl exhibited clearly a 4-2-3 pattern (four oldest flowers alternated with two younger opposite flowers, and three youngest flowers, two of them adjacently located).

The pattern of the development of the inflorescence seems to be adhered to in the morphogenesis of the flower. The typical pentamerous whorl of the

PLATE 2 (continued). FIGURE 14. A hexamerous whorl (1.1.1 + 1.1.1). FIGURE 15. The alternate (3-3) pattern of the maturation of flowers in a hexamerous whorl. FIGURE 16. A hexamerous whorl (1.2 + 1.2); two bracts, one of each node, have fused. FIGURE 17. A heptamerous whorl.

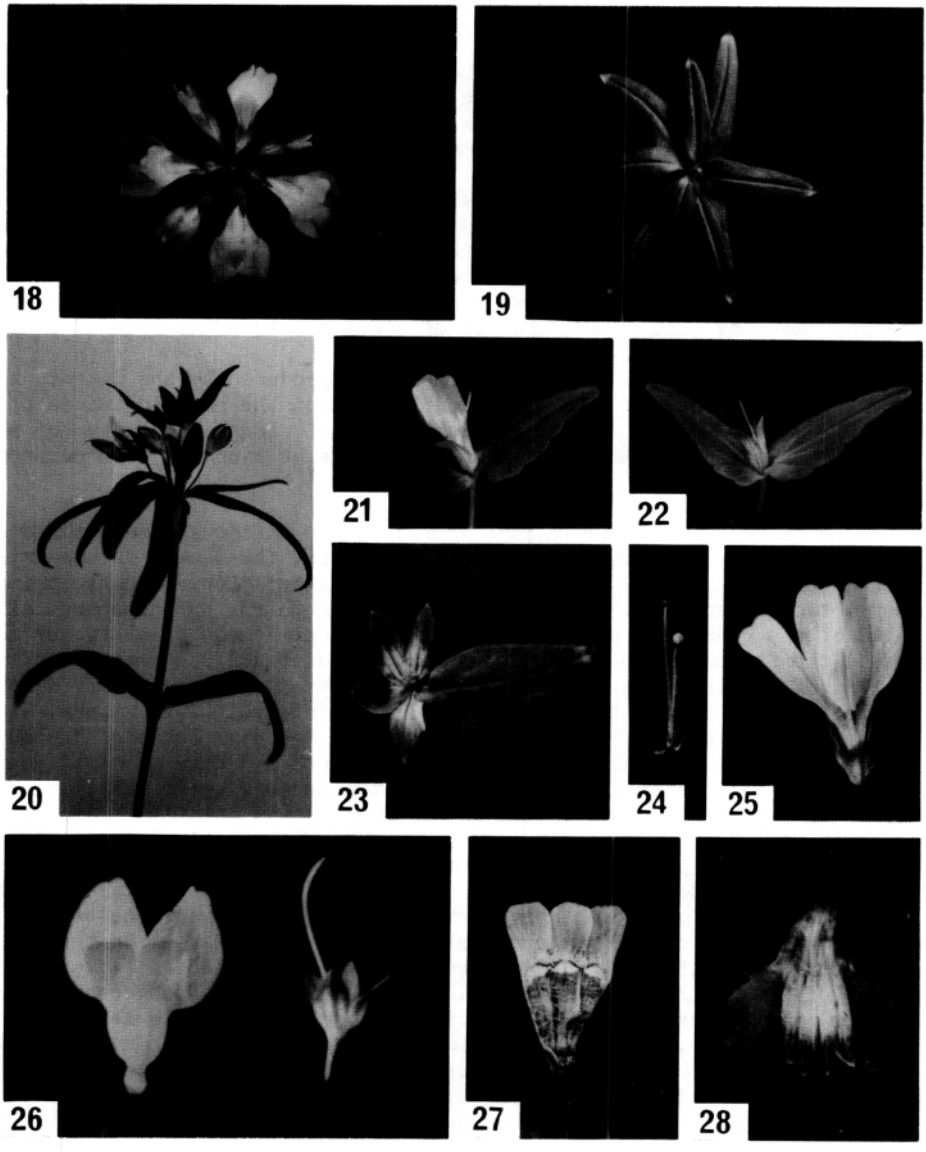

PLATE 3. Collinsia heterophylla. FIGURE 18. The 4-3 pattern of the maturation of flowers in a heptamerous whorl. FIGURE 19. An octamerous whorl. FIGURE 20. The terminal rosette phenotype with seven flowers at the first node of the inflorescence. FIGURE 21. The terminal flower. FIGURES 22-23. Incompletely developed calyces of terminal flowers. FIGURE 24. Adjacently positioned stamens of flowers with a tetramerous corolla and a pentamerous androecium. FIGURE 25. Sporadic polypetaly - the lower lip of the corolla with a double side lobe. FIGURE 26. A tetramerous flower.

inflorescence is reflected in the pentamerous cycles of the floral parts.

The flower of C. heterophylla has a five-lobed calyx, and a zygomorphic corolla composed of five united petals. The corolla has a two-lobed upper lip and a three-lobed lower lip (having two side lobes and a folded middle lobe

TABLE 1.– Patterns of flower maturation in the individual whorls of the inflorescence in Collinsia heterophylla

No. of bracts (flowers) per whorl	No. of bracts at the nodes making up the whorl 1-st 2-nd 3-rd	Pattern of maturation of flowers* 1-0	1-1	1-2	2-2°	2-2ª	2-3	3-2
2	1.1 --- ---	+	+	-	-	-	-	-
3	1.2 --- ---	-	-	+	-	-	-	-
4	1.1 1.1 ---	-	-	-	+	-	-	-
	2.2 --- ---	-	-	-	-	+	-	-
5	1.1 1.2 ---	-	-	-	-	-	+	-
	1.2 1.1 ---	-	-	-	-	-	-	+

No. of bracts (flowers) per whorl	No. of bracts at the nodes making up the whorl 1-st 2-nd 3-rd	3-3al	2-4	4-2	4-3	3-4	4-4	4-2-3
6	1.2 1.2 ---	+	-	-	-	-	-	-
	1.1 2.2 ---	-	+	-	-	-	-	-
	2.2 1.1 ---	-	-	+	-	-	-	-
7	2.2 1.2 ---	-	-	-	+	-	-	-
	1.2 2.2 ---	-	-	-	-	+	-	-
8	2.2 2.2 ---	-	-	-	-	-	+	-
9	2.2 1.1 1.2	-	-	-	-	-	-	+

* ◯ ○ - Flowers of the 1-st node (older)
○ - Flowers of the 2-nd node (younger)
• - Flowers of the 3-rd node (youngest)
ⓒ - Peduncle
ª adjacent al alternate ° opposite

called keel). Attached to the basal part of the corolla tube, in alternate arrangement with the petals, are five stamens (the stamen located between the lobes of the upper lip is reduced to a staminodium; the filaments of the upper two stamens are hairy and spurred). The pistil is composed of two united carpels. The ovary is superior, two-locular, and contains about 18 ovules.

Flowers of the polycotyledonous plants and flowers of the wild-type plants were morphologically identical (pentamerous).

PLATE 3 (continued). FIGURE 27. Polypetaly - three-lobed upper lip of the corolla. FIGURE 28. Polypetaly - the lower lip of the corolla with two side lobes and four keels.

The tetramerous flowers with four sepals, four petals, and four stamens have been observed (Fig. 26). Some plants developed terminal flowers at the first node of their uppermost branches (Fig. 21). The calyces of these flowers were incompletely developed; three sepals were associated with two vegetative leaves (Fig. 22), or four sepals were associated with one vegetative leaf (Fig. 23). In the terminal flowers having a tetramerous corolla and a pentamerous androecium two stamens were adjacently positioned (Fig. 24). – This observation supports the hypothesis of the autonomy of cycles in floral morphogenesis. – The pistils of the terminal flowers were normal. Similar heteromerous flowers (partly tetramerous partly pentamerous) were observed among the flowers of normal inflorescences.

This inconsistency in the number of floral parts indicates that here too, as in the morphogenesis of the inflorescence, the splitting of a primordium of a floral organ may not occur, and the result is a tetramerous cycle. On the other hand, the sporadic occurrence of polysepalous, polypetalous (Fig. 25), polystaminous and polycarpellate flowers in the inflorescences with normal flowers indicates that a primordium of any floral organ may split repeatedly, or that two or more primordia of an organ may split.

Two types of polypetalous flowers were observed in this study (Figs. 27--28). In the polypetalous-1 type the increase in the number of petals of the upper and/or the lower lip of the corolla was associated with a comparable increase in the number of the stamens. The supernumerary lobes of the corolla of these flowers were of two types: (a) major lobes with a true midvein, and (b) minor lobes with a midvein derived from the lateral vein of the adjacent petal (petals and sepals of normal flowers have a midvein and two lateral veins).

Corolla of the polypetalous-2 flowers had 1-3 additional major lobes in the lower lip, and, rarely, an extra stamen associated with the lower lip. The upper lip of the corolla of the polypetalous-2 flowers was not affected. Pistils of the polypetalous-2 and polypetalous-1 flowers were normal.

DISCUSSION

The arrangement of bracts of the unequal size in the whorls and the pattern of the maturation of flowers in the individual whorls of the inflorescence, as well as the configuration of the incompletely developed calyces of the terminal flowers, corroborate the hypothesis that the pentamerous whorls are the result of the combination of a bimerous and a trimerous node.

The phrase "splitting of primordia", used throughout this article, stands for the "initiation of new growth centers". The increase of the number of organs per node is the characteristic of the reproductive growth-pattern. A double bract (Figs. 8, 9, 12, 16) may develop when two growth centers are initiated in the area where one bract primordium normally occurs. At a later stage two such closely positioned primordia may fuse, but retain two growth centers, and develop into a double bract with two flowers in the axil (Fig. 12). A double bract carrying one flower in the axil (Fig. 16) would develop when two growth centers are initiated in that part of the apical meristem which has already been induced to develop into a bract primordium; such double bract is functionally one bract and can truly be referred to as being split.

Morphogenetically of great interest is the formation of the minor lobes in the polypetalous-1 flowers. The minor lobes are produced as the side lobes of the petals. At the site where the adnate filament of the stamen becomes detached from the tube of the corolla, the lateral vein of the adjacent petal enlarges and assumes the role of the midvein of the minor lobe. When, during the early stage of the flower development, the filament of the stamen does not attach itself properly along the line of connation of two petals but slightly to one side, then the lateral vein of the petal and the vascular bundle of the stamen are brought into a close proximity or become superimposed. Under these conditions, it appears, the regulatory influence of the growth center of the stamen is transferred to the adjacent petal's lateral vein enabling it to function as a midvein, and the result is the formation of a minor lobe. In contrast, the major lobes (having a true midvein) of the polypetalous-1 and polypetalous-2 flowers develop upon the initiation of new growth centers at the level of inception of the petal primordia.

The tendency to increase the number of primordia - that is, to initiate new growth centers - of the organs with the determinate growth (cotyledons, leaves, bracts, floral organs) of C. heterophylla presents itself as a continuum, which, in the wild-type plants, appears to be repressed during the vegetative stage, but in the polycotyledonous plants the repression mechanism seems to be broken down.

ACKNOWLEDGMENT

The author is indebted to Miss Huguette Theodore for reading the manuscript.

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