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Changing Shapes of Inflorescences in Dicotyledons

by

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With 13 Illustrations in the text and 4 in Supplements

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Contents

I. Introduction

There is an extensive literature on the terminology, morphology and phylogeny of the inflorescences, which has also grown considerably in recent times. RICKETT 1944, 1955 deals especially with terminological problems. Of morphological works I mention those of TROLL and his co-workers (HEIDENHAIN 1952, TROLL 1950, 1957, TROLL and HEIDENHAIN 1951, TROLL and WEBER 1955, WEBERLING 1961); I also mention GUSULEAC 1957, HAMANN 1958, 1960 and SCHLITILER 1945. BOLLE 1940 presents the design of a mathematically justified theory of the inflorescences, while SCHÜEPP 1942 a characterization after the temporal course of plant growth and flowering. Following PARKIN 1914, PILGER 1922 and ZIMMERMANN 1935, TAKHTAJAN 1959 has recently expressed himself on the phylogeny of inflorescences.

If, nevertheless, the attempt is made here to communicate some of the morphology of the inflorescences, it is because observations are to be presented, which only partly fit into the conception of the above-mentioned works. This should be illustrated by selected individual examples. From the examples, it is possible to obtain information about possible relationships among the different forms of inflorescence. They also allow us to take a position on the concept of synflorescence represented by TROLL and to provide information on the position of the inflorescences on the vegetative body.

I am indebted to many scholars for this work, especially to Messrs. MARKGRAF, SCHMID, SCHLITTLER, PEISL and GREUTER, whom I am indebted to. As far as the materials used for the investigation were not fresh material, herbarium material from the Botanical Museum of the University of Zurich was available to me. For this, too, I would like to thank the Director, Prof. Dr. F. MARKGRAF. My wife, LISA STAUFFER-IMHOOF, has designed and executed all illustrations under my guidance.

In the morphology of inflorescences, as is generally the case in morphology, most terms are defined and applied differently by different authors. The definitions are also very often insufficient. In order to be able to express clearly in the following, I will first give a brief glossary of the most important terms that will allow me to express myself clearly in what follows. The glossary does not contain any fundamentally new conceptions, but definitions that are as clear as possible, which also include the criterion of flowering sequence.

Glossary

Inflorescence [Blütenstand]: Flower-bearing shoot system, which always carries only additional flower-bearing shoots or flowers as axillary organs, never vegetative shoots. Within the entire system, the flowers open according to the age of their initiation.

Partial Inflorescence, [Teilblütenstand]: Flower-bearing shoot system, which is on the main or on a side axis of any order of an inflorescence.

Paraclade, enrichment axis: (= [Nebenblütenstand] secondary inflorescence BOLLE; [Nebensproß] secondary shoot SCHÜEPP) Axis system with one or more inflorescences which can be reduced to an inflorescence and which develops below an inflorescence in the same growing season but later than this.

Panicle, [Rispe]: Richly branched inflorescence, on which all axes end with terminal flowers and the branching on main and lateral axes decreases continuously to the outside, so that all flowers open more or less simultaneously.

Thyrse: (= cymo-botrys (Eichler), pleiochasium (PARKIN pro parte, BOLLE pro parte, TAKHTAJAN, non EICHLER) Inflorescence of the main axis that has or does not have a terminal flower, bearing dichasia or monochasia, in any number, which towards the apex can be reduced to triads or single flowers. Among the terminal flowers of the lateral axes of the first order, the basal ones open first, after which the next higher ones do.

Dichasium: Partial inflorescence, beginning with a flower with two prophylls which blooms first; from the axils of the two prophylls two flowers provided with prophylls of the second order follow, which bloom secondarily, and from whose prophyll axils four flowers of the third order emerge, etc.

Monochasium: partial inflorescence, beginning with a flower, which is provided with one or two prophylls, which blooms first; from a prophyll axil an analogously built flower of the second order develops, which blooms second, etc.

Triad, [Blütendreier]: (= Dichasium RICKETT, TAKHTAJAN, non BROWN) Partial inflorescence, beginning with a flower with two prophylls, which as a rule blooms first; from the prophyll axils a second-order flower is produced, no further branching occurs, irrespective of whether or not the flowers of the second order have prophylls.

Raceme, [Traube]: inflorescence, the main axis of which ends with or without a terminal flower, with any number of simple, stalked flowers, from which the basal opens first, then the remaining ones ascending.

Umbel, [Dolde]: inflorescences, in which pedunculate flowers, by internode shortening at the end of the main axis, all proceed more or less from the same point.

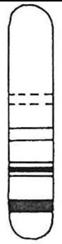
Capitulum, [Köpfehen]: Inflorescence in which the more or less sessile flowers are crowded on the more or less thickened or widened axis terminus.

Racemose panicle, [Traubenrispe]: inflorescence of a racemose branch, but in place of the flowers of the panicle, racemes exist (panicle of racemes). (Likewise, all the other so-called "heterotactic" inflorescences can be designated similarly, for example, umbelliferous panicles, Doldenrispe [panicle of umbels], capitulate panicle, Köpfchenrispe [panicle of heads], thyrse-panicle [panicle of thyrses]; capitate raceme, Köpfchentraube [raceme of heads]; capitate thyrse, Köpfchenthyrsus [thyrse of heads], etc.

Composite racemes, [zusammengesetzte Traube]:

Raceme, which instead of the raceme carrying individual flowers, may or may not be limited in the end portion by a (simple) raceme, whether or not all of these racemes bear terminal flowers. (In the same way: composite umbels, [zusammengesetzte Dolde], composite capitula, [zusammengesetztes Köpfchen]), etc.

Explanation of schematic drawings

Axis normal	▯	
Axis short or young	▮	
Pedicel articulated, or axis on model examples	|	
Leaf or foliar organ	⬭	
Leaf organ bract-like	◞	
Opening state	Single flower	Generalized inflorescence
not specified	○	
in bud	⊕	
half open	⌖	
open	○	
in fruit, young	⊙	
in fruit, ripe	●	

Arabic numerals denote the order of flowering, roman numerals denote parts, e.g., partial inflorescences, in the order of flowering of the respective first flower.

P = Paraclades, Roman index numbers indicate the order of flowering of the first flower.

Ⓐ = Illustration A.

All schemata are shown in the area, but the fine structure of monochasial partial inflorescences were not taken into account.

H. Individual examples

1. *Santalum*

The example deals in particular with the position of the inflorescences on the vegetative body. Fig. 1 A shows a shoot of *Santalum album* L. (DEGENER 27249). The whole flowering shoot system is produced as a unit. It is a partly a leaf-bearing panicle, which still produces numerous flowering accessory shoots, which have been omitted in the illustration for the sake of clarity. The partial inflorescences are panicles, all axes finished with terminal flowers. The partial inflorescences are decussate. The following flowering sequence is not illustrated. The terminal organs are always somewhat ahead of those nearby, however, considered as a whole the lowest partial racemes flower first. The differences in the flowering time are, however, not very large in the whole system depicted.

As a rule, similar inflorescences occur in *S. freycinetianum* GAUDICHAUD as in *S. album*. The partial panicles, however, are never equipped with leafy organs, but always with bracts. FIG. 1B shows an exceptional case of a shoot terminus, as was found once in DEGENER 27261. The axis terminus has returned here to the vegetative phase and has produced a pair of leaves without further developed axillary organs, after the previous whorl had borne bracts.

S. pyrularium A. GRAY is closely related to *S. Freycinetianum*. Here, as shown in Fig. 1C, the return to the vegetative condition of the axis tip is normal. On the shoot apex (depicted in DEGENER 27253) one finds below the vegetative tip only one or two pairs of partial panicles. In this case (similarly to *S. Freycinetianum*) the flowering sequence from whorl to whorl is more delayed than in *S. album*. Thus, in the illustrated specimen, all the flowers were past anthesis in the two lower partial panicles (I), in the two upper (II) all the flowers were open or about to open.

If one considers *S. pyrularium* alone, the partial panicles can be regarded as lateral inflorescences. In fact, they are homologous organs to the partial panicles of *S. album*.

Thus, in this example, it can be seen that an axis which normally ends with terminal panicles and terminal flowers can suddenly revert to vegetative growth, and that such behavior is facultative or obligatory in the case of the most closely related species.

Similar observations are made for other woody plants from different families. The Australian genus *Eucarya*, which is closely related to *Santalum*, can be named; PARKIN 1914 describes a similar transitional series in *Drimys*, another I found in *Calophyllum*. Rubiaceae and Melastomataceae also contain such examples.

2. *Lysimachia*

This example demonstrates a reduction series of inflorescences as well as the delineation of the paraclades.

For the consideration of the inflorescences of the genus *Lysimachia*, we shall proceed from the Myrsinaceae, to which, according to HANDEL-MAZZETTI 1928, there is close affinity. As an example of the Myrsinaceae inflorescence, such as that of *Maesa rufescens* A. DC, Fig. 2 A, drawn according to MEDLEY WOOD 5309, introduces the panicle of racemes for this species. It is possible to see how the terminal raceme is a bit ahead of its surroundings in flowering, and how the lower side racemes bloom before the upper ones. The lowest side axis of the first order carries, for example, a young fruit on the sixth lateral organ from below, the second on the fifth lateral organ, the following on the second, the next three on the lowest, then young fruits are missing on the sides. The racemes as a whole behave in the same way as the individual flowers in a panicle of correspondingly loose structure with regard to the blooming of their respective first flower. The inflorescence is sharply delimited, and bears as leaf organs only bracts. Below each flower are two sterile prophylls, which are omitted from the diagram. Besides, it is to be mentioned that in *Maesa* such inflorescences sometimes occur terminally, sometimes laterally (as in *M. rufescens*), the same is observed in two other genera of Myrsinaceae, *Ardisia* and *Parathesis*.

Let us now compare the inflorescence of *Lysimachia vulgaris* L. with *Maesa*, from which a single case (THULI s.n., 27 August 1912) is taken in Fig. 2B. At first glance they will also be called a panicle of racemes. As with *Maesa*, there is a terminal raceme which is developed in advance of the lateral organs. Under the terminal raceme there are three whorls of simple side racemes, followed by two with branched axis systems, which finishes with racemes. The entire branching system has a decreasing, leafy appearance from the inside to the outside. The unbranched side racemes correspond to *Maesa*'s condition, the lower bloom before the upper ones. The branched systems, which follow the racemes, are different. It is clear that the lower (P_{II}) is less developed than the upper one (P_{I}). The former therefore certainly represents an enrichment axis. This is also illustrated by the lowest pair of leaves which carries small buds in the axils. Is the system P_{I} still to be expected to be an inflorescence or is it also a paraclade? When compared with *Maesa*, it is noticeable that the lowest simple side raceme comes into flower exactly as P_{I}. The 6th organ from below is always the highest open flower, while in the case of *Maesa*, the sixth flower is the uppermost open flower in the lowest simple raceme, but the eighth flower is still open in the following branched system. Since the lowest simple side raceme is higher than P_{I} , so with *Lysimachia* P_{I} is delayed and therefore is also to be regarded as an enrichment axis.

It follows from this that the *Lysimachia vulgaris* inflorescence has an open terminal raceme bounded by a compound raceme from open racemes. The enrichment inflorescences are exactly the same, but they bloom later (in descending order). The lower carries at the base a leaf pair with axillary buds and is thus an example of the positional phenomenon.

Fig. 2C shows the inflorescence of *L. ramosa* WALLICH (according to MERRILL B. S. 822). Upon cursory inspection, the flowering sequence of this species seems quite irregular. From every leaf axil of the main axis, one or two flowers emerge, at the bottom in fruit, then as buds, then again flowering, at the top as buds. A closer analysis shows agreement with the inflorescence of *L. vulgaris*. The strongly reduced side racemes are compressed to small umbels. Again the lowest begins with those flowering, and the others follow. The terminal raceme is developed ahead of its surroundings. The occurrence of sterile leaf organs on the terminal axes suggests a tendency towards percurrent growth.

In the case of *L. thyrsiflora* L., Fig. 3 A (RAU s.n., s.d.), the main axis of the inflorescence has returned to the vegetative condition, without forming the terminal raceme. The lower ones bloom from the side racemes before the upper ones. The lowest are already largely in the state of fruit, the top pair still shows exclusively flower buds. These side racemes are homologous with the simple side racemes of *L. vulgaris*. Enrichment axes do not usually occur in *L. thyrsiflora*.

In very many species of the genus the inflorescence is reduced in such a way that only the terminal raceme is present. Fig. 3 B shows *L. dubia* AIT. as an example. (According to BALANSA s.n., s.d.). The vigorous terminal raceme already bears young fruits around the middle. The lateral shoots P_{I} - P_{V} are immediately recognizable as enrichment axes since they start in descending order with the flowering of their terminal racemes, which are all very late with respect to the inflorescence of the main axis.

Finally, the simple terminal raceme can also be intermixed. This leads to the behavior of *L. Nummularia* L., as shown in Fig. 3C (MUELLER s.n., 24 August 1923) and 3D (FRIES s.n., June 1861). In Fig. 3 D, two pairs of enrichment axes (P_{I}, P_{II}) are formed; in Fig. 3 C, paraclades are missing. Serial accessory flowers can sometimes complicate the situation.

In summary, the inflorescences of the woody Myrsinaceae are the richest branched, while in the herbaceous *Lysimachia* species they are reduced by the loss of the basal rich branched section (panicle of racemes - compound raceme - raceme). Percurrent growth occurs in all of these types. It is necessary to distinguish carefully between inflorescence and enrichment axes, which can be used as the most important criterion for the flowering sequence of equivalent organs.

3. *Hebe* and *Veronica*

The third example is a parallel case to the second and again represents a reduction series.

Among the Scrophulariaceae there are only a few arborescent woody plants: the genus *Paulownia* and some representatives of *Hebe*. *Paulovia Paulownia* is sometimes also brought into relationship with Bignoniaceae, with which there is in general a close kinship. This also manifests itself in the inflorescences, which coincide in both families in the basic groundplan. In the woody Bignoniaceae we find panicles or racemes from open thyrses, for example, in the genus *Arrabidaea*. Also *Paulownia* has a raceme (which is often greatly reduced or degenerated from the terminal thyrse) from open thyrses with terminal thyrse. Terminal flowers do not occur in either family. If the prophylls are sterile or are missing, racemes are produced from the thyrse. This is the case with a large number of Scrophulariaceae, as in the genus *Hebe* and *Veronica*, which are to be considered following HAMANN's studies of the inflorescences of these genera. *Hebe* and *Veronica* can not be directly related to each other, but rather one has to consider the two genera as two parallel developmental cohorts of common origin, but they are at present sharply defined, inter alia, by their chromosome conditions.

Let us first consider inflorescences from *Hebe* in Fig. 4. Fig. 4A shows the terminal inflorescence of *H. Hulkeana* (F. MUELL.) COCKAYNE & ALLAN, drawn from PETRIE s.n., d.): a panicle of racemes, the terminal raceme so developed in its vicinity, the lower side axes first and then ascending the following starting with the flowering ones.

In the same way as in *Lysimachia*, either the inflorescence can now proliferate, or be reduced by the fact that the basal, rich, branched parts are eliminated. This reduction can be carried out by means of the compound raceme with terminal racemes (Fig. 4 D: *H. Hastii* [HOOK. F.] COCKAYNE & ALLAN after COCKAYNE s.n., s.d.) to the simple terminal raceme in *H. Hectori* (HOOK F.) COCKAYNE et ALLAN (Fig. 4 E after PETRIE s.n., s.d.) and relatives. There percurrent growth is seen as panicle of racemes, where the lateral organs are racemes of triads (as in *H. Colensoi* [HOOK. F.] COCKAYNE, Fig. 4B according to PETRIE s.n., s.d.), or especially frequently in the compound raceme (here a large number of species, e.g. *H. salicifolia* [FORST F.] PENNELL, Fig. 4 C according to EGLI s.n., s.d.).

The flowering sequence can always be understood from *H. Hulkeana*. In Fig. 4B it is not shown, since only fruitful individuals were present; Nevertheless, it was still possible to see that the lower pair of partial inflorescences was more developed than the upper one. I have not known percurrent growth of the simple terminal racemes for *Hebe*. The foliose percurrent leaves are often quite distinct in contrast to *H. Hulkeana*.

In his assessment of the *Hebe* inflorescence, HAMANN attaches great importance to phyllotaxy, which is mostly dispersed in the racemes, whereas below opposing leaves appear in the vegetative region. In *H. Hulkeana* one can observe how the leaf pairs gradually shift somewhat and finally dispersion occurs (similar to *Lysimachia vulgaris*). However, the leaf position is very variable in the *Hebe* inflorescence area, and there are not a few species in which the flowers in the racemes are also opposed, for example, in the terminal racemes of *H. Hectori*, but also in the axillary racemose partial inflorescences of *H. pimeleoides* HOOK. F. and relatives. To what extent this feature could be used to secure homologies in narrower groups of relatives would have to be clarified by monographic studies throughout the genus, and can not be judged on the basis of a few examples.

The genus *Veronica* can be largely parallelized with *Hebe*. To be sure, no case of a panicle of racemes has become known to me. The basic form for all *Veronica* inflorescences that I have seen are ones with terminal racemes provided with compound racemes, as shown in Fig. 5A (Coquoz sn, 22 June 1928), with deciduous leaf organs. Such inflorescences are found in *V. latifolia* L. em. SCOP. (= *V. urticifolia* JACQ.) under among Swiss herbarium material for about a quarter of all plants. We can see, again, that the terminal raceme somewhat precedes its surroundings, and that for the side racemes the lower ones begin the flowering. In *V. latifolia* the nicely stepwise percurrent growth of the inflorescence can then be observed, as the most common case the axis blindly ends in a raceme pair (Fig. 5B, MEYER s, n., 5. 1883), while in rare cases a return to the vegetative behavior has been recorded by the application through the initiation of one to three leaf pairs at the top (Fig. 5 C and D, according to EGLOFF sn, 8, 1904). The behavior described last is, in many species, e.g. *Chamaedrys* L. completely constant. The side racemes of these species are therefore homologous to the lateral partial inflorescences of the original composite raceme homolog.

In many *Veronica* species, the inflorescence is reduced to the terminal raceme, as is the case with *Hebe*. As an example, I give in Fig. 5 E *V. longifolia* L. (VETTER s.n., 18. d.). The lateral racemes are here not partial inflorescences but enrichment axes P_I - P_{III} , which develop in descending order. They are homologous to the terminal raceme, so not homologous to the lateral racemes of *V. latifolia* and relatives. In the paraclades the increase of the leaf pairs among the terminal racemes from P_I to P_{III} is clearly seen as a positional phenomenon.

One could, by the way, also interpret the circumstances of the illustrated *V. longifolia* differently. There is no definite proof that it is not possible to explain a terminal racemose triad of the inflorescence of this specimen, since the top pairs of racemes could also begin to flourish flower in this view later than the terminal raceme. P_{II} and P_{III} would then be paraclades, which would bloom somewhat impoverished against the inflorescence. At times (not in the case depicted), small side-shoots can be observed in P_{II} and deeper in the following paraclades in the axils of the two uppermost foliage leaves, which could support this view. As there are no equivalent organs, no reliable decision is possible. In many, especially annual *Veronica* species, however, there is certainly only the terminal raceme.

In the genus there are also foliose proliferative leaves, and also the growth of the terminal raceme in *V. filiformis* SM, which may be compared with the details in TROLL, and especially in HAMANN.

Veronica appears as a whole to parallel *Hebe*, but is somewhat more derivative. Again, the phenomena which we already know from *Lysimachia* is shown: reduction of inflorescences by restriction to the apical part, percurrent growth of inflorescences of different branching stages levels.

4. *Helleborus foetidus* L.

This example is used to explain a complicated individual case of inflorescence.

The inflorescences of the genus *Helleborus* have been described and portrayed by PARKIN. This author has also paid attention to the flowering sequence, however, without drawing any conclusions on the nature of these inflorescences.

Fig. 6 shows two cases of inflorescences of *Helleborus foetidus* L. Fig. 6A is conceptualized from a plant that Mrs. W. STAUFFER collected on 22 January 1961 on St. Petersinsel (Bielersee, Switzerland). The terminal inflorescence, which is well delineated on the stem bearing the overwintering foliage leaves, ends with an terminal flower (1), which has been developed before all other flowers. Below can be found on the main axis more or less richly branched dichasia as side organs. In this case, the flowering began somewhat above the middle of the total length with a lateral flower of the first degree (2), and extended from this upwards and downwards to further side flowers of the first degree (3, 4). Within the individual dichasia, the flowering proceeded normally from one axis to the next.

This whole structure could be regarded as a thyrse: an axis which carries numerous partial inflorescences, and ends with a terminal flower. The remarkable flowering sequence, however, suggests that this is a more complex branching system, which is reduced in some way.

The clarification of the conditions is provided by flowering systems, which occasionally occur, of the species shown in Fig. 6B (cultivated Botanical Garden, Zurich, Feb. 1962). Only the side flowers of the first and second order are shown in the drawing; the others are omitted for the sake of simplicity. Likewise, an entry of the flowering condition [phase, state] was omitted.not indicated. Here, at the base, four lateral axes exist which do not represent dichasia, but each bear three lateral axes of the second degree, which then branch out again in dichasia. Thus these four axes are seen as a thyrse. It is now the first dichasium of the thyrse, whose terminal flower (2) opens first after the terminal flower of the main axis (1), followed by other dichasia terminal flowers (3, 4), and the uppermost of the four basal thyrses whose end flower unfolds and only slowly and in descending order follow the other thyrse terminal flowers. From this it is quite clear that under a normal flowering terminal thyrse with a terminal flower four enrichment inflorescences P_I-P_{IV} also stand as thyrse with a terminal flower. It is noteworthy that these enrichment axes are completely integrated with the inflorescence into a single unit and, together with this, stand out from the substructure. As the enrichment thyrses become more reduced, they become dichasia, and on the branch can no longer be distinguished from the partial inflorescences of the terminal thyrse. This is the case in Example Fig. 6A, where only the flowering sequence can create clarity about the nature of the side organs.

Similar to *Helleborus* are the thyrses that are also developed in the genus *Ranunculus*, where, in rich-flowered species, such as *R. lanuginosus* L., the same can be said of a much more relaxed inflorescence, both in structure and in the flowering sequence. There, at the same time, the lower part of the inflorescence, and particularly the section with the enrichment axes, foliar proliferative leaves, and in this respect it transitions into the vegetative substructure.

5. *Hypericum*

This example provides a supplement to the previous one.

In Fig. 7A, a flowering terminal axis of *Hypericum perforatum* L. (FRANKE s.n., June 1881) is reproduced. The opposite leaved main axis finishes with a termnal flower (1), which opens first. The three pairs of lateral organs (III, II, I) following the terminal flower are dichasia with monochasial endings or monochasia. The terminal flowers of the first order of the pair I (2) open first after the terminal flower of the main axis, then follow the pair II (3), then the pair of lateral organs P_I (4) and the pair III (5). The pair P_I does not consist of dichasia, but its axes repeat, if somewhat reduced, the structure of the terminal segment of the axis above. This is, in turn, only partly the result of an inflorescence consisting of a thyrse bounded by terminal flowers and comprising pairs I, II, and III, some of them enrichment axes P_I, P_{II}, etc., which are delayed and clearly show the positional phenomena.

The inflorescence of *Hypericum olympicum* L., which is to be taken as a further example from this genus, shows remarkable variability. This is illustrated in Fig. 7 B (LEUTWEIN s.n., 29 March 1848), Fig. 7 C (CORREVON s.n., 19 June 1923) and Fig. 7 D (LEUTWEIN s.n., April 1849). Enrichment axes have not developed in any case, they are merely marked by buds in the leaf axils. The variation series is derived from a thyrse of reduced pairs of monochasia I and II, which is terminal flowered, through a terminal triad to a terminal single flower. This series can again be deduced by the loss of the basal limbs of the thyrse, so that ultimately only the terminal flower, which terminates the main axis, is present. The flowering sequence coincides with that of the corresponding parts in *H. perforatum* .

For Fig. 7 E, *H. opacum* T. & G. (Biltmore Herb., 3991^{d}), we obtain the best results from Fig. 7C. As is the case, the terminal thyrse is confined limited to the terminal flower and a pair of partial inflorescences, but a (vegetative) pair of paraclades (P_I) follow. The partial inflorescences are well developed dichasia which partly show monochasial endings. In this case, the number of flowers is increased with a reduced number of partial inflorescences by continuous branching from the prophyll. In the case of individual species, this type of increase in the number of flowers goes much further still. For example, in *H. parviflorum* ST. HIL. from the LORENTZ 158 voucher, to nine shoot generations, which would correspond to a total number of flowers of 511 in the case of complete dichasial occupation. In fact, however, many branches had been terminated or developed incompletely, so that a total of about 200 flowers were observed.

Similar design series are also known for other related groups. PARKIN has recorded them for *Helleborus*, and GUSULEAC portrays them, albeit with a totally different interpretation, for the Caryophyllaceae, where there are numerous completely parallel phenomena, such as those described here for *Hypericum*, for example in the genus *Silene*.

6. *Legousia Speculum-Veneris* (L.) F. E. L. FISCHER

This example is closely follows ed by the ones discussed above. It also provides an opportunity to approach the design of the paraclades.

The inflorescence representations of the Campanulaceae are presented by GOEBEL 1931 and HEIDENHAIN. Further remarks can be found in TROLL and WEBER, which differ from the view obtained by HEIDENHAIN. From more extensive investigations in this family, I only extract the example of the Venus' looking-glass, which, on the one hand, can largely illuminate the construction and variability of the flowering section for the whole family, and is, on the other hand, suited to portray the positional phenomenon.

Fig. 8A shows the overall appearance of a richly flowering plant of *Legousia Speculum-Veneris* (L.) F. E. F. FISCHER (STAUFFER s.n., 30 June 1961). The scattered leafy main axis ends with the proteranthous [first blooming] terminal flower (1). Under this (comparable to the conditions in *Helleborus* or *Hypericum*) the first eight lateral organs are formed as monochasia or dichasia, with the terminal flower of the lowest dichasium (2) flowering first, followed by other terminal flowers in ascending order (3, 4, 6). Thus we again recognize a thyrse limited by a terminal flower as the inflorescence. Among these are numerous enrichment axes P_I, P_{II} , etc., which in their construction reflect the end portion of the principal axis, which also carry thyrses with terminal flowers. The enrichment inflorescences unfold in descending order, as the terminal flower of P_I (5) is the fifth in the entire system, those of P_{II} (7) the seventh, and so on. Downward, the paraclades carry more and more leaves.

Poor individuals of the same population show the condition shown in Fig. 8B. There is only the inflorescence of the main axis, paraclades do not develop. Since there is no branching from the prophylls of the respective lateral flowers of the first order, the inflorescence is in the form of a small raceme, bounded by a terminal flower. The flowering coincides exactly with the corresponding section under Fig. 8A, after the terminal flower (1) opens the lowest side flower (2) and then ascending further (3, 4, 5, 6).

Fig. 9 shows two further, highly branched individuals of the same population. The thyrses are as a whole generalized. In Fig. 9A there are relationships in the upper part of the principal axis, which are essentially the same as in Fig. 8A, but indeed the number of paraclades is only four. Under the thyrse of the main axis, whose terminal flower (1) is the first of the whole plant to bloom, there are first two paraclades limited to the inflorescence, then two, which under the thyrse still bear a leaf with axillary buds. In the figure, the leaves are omitted for simplification in all lateral organs, but their axillary products are always drawn in. The paraclades thus repeat the condition of the main axis over the respective points in a somewhat reduced form. The axillary organs of the following three leaves of the main axis remain in the bud state. The basally following side axes are viewed starting from the bottom. No shoots develop from the axils of the cotyledons. The following pair of leaves of the main axis, which shows the transition to spreading, carries in its axils the two strongest lateral shoots of the plant whose terminal flowers (2, 3) open as second and third of the whole system. In construction, these paraclades also repeat the part of the main axis, which is above their point of attachment, in a somewhat reduced form. Upwards along the main axis there follow from four other leaf axils similar shoots, the terminal flowers of which bloom in ascending sequence and which respectively copy the behavior of the main axis above their starting node. An inhibiting zone, which begins between the upper, descending and starting paraclades, begins with the total system. In the paraclades, this zone of inhibition is extended to the entire basal part in the copy of the principal axis, as is often the case on the principal axis with weaker plants.

In the case of Fig. 9B, this inhibition (except in the basal part) now largely appears on the principal axis. Although not all the first-order enrichment axes are present on this plant, the existing ones are distributed more or less over the entire length of the main axis. All paraclades here too, in a somewhat reduced form, repeat the behavior of the main axis above their point of attachment. Again, the terminal flower of the thyrse of the main axis (1) is the first in the whole system, then the terminal flowers of the lower enrichment axes (2, 3, etc.) follow in ascending directions and those of the upper paraclades in descending order until the two flowering zones in the middle collide.Within the paraclades the flowering takes place as shown in Fig. 8 A.

One might imagine a plant in which all the first-order paraclades are formed without inhibition, as are the second-order paraclades, and the third-order basal part of the lower first-order enrichment axes. There would thus be a very complete branching system, which could be designated as a panicle of thyrses bounded with terminal flowers. If we were to suppose further that the terminal flowers of all the thyrses would develop at the same time, the ideal case would have been reached that the whole plant would have become an inflorescence. There would be no leaf axil without a floral axillary branch or partial inflorescence.

It is hard to believe that this borderline case can ever be found in nature. However, in some genera of annual plants, it has been realized, at least with respect to the branching system, with a good approximation, for example, in the individual case of *Veronica arvensis* L., as well as in other *Veronica* species which have become severely degraded in their vegetative structure. The same is found in Cruciferae, Oenotheraceae, Gentianaceae, Rubiaceae, and near *Veronica* also in other Scrophulariaceae.

7. *Bongardia* and *Leontice*

The example is used to reveal connections between seemingly very different inflorescences.

The genera *Bongardia* C. A. MEY. and *Leontice* L. of the Berberidaceae are identical in many traits and so closely related that they are often not separated generically.

The inflorescences (Fig. 10 A of *Bongardia Chrysogonum* [L.] SPACH, V. STERNECK s.n., 8 April 1907, Fig. 10 B of *Leontice Leontopetalum* L., LEUTWEIN s.n., 18 March 1862) seem at first sight very different.

Bongardia has a poor, panicle-like inflorescence, the final-stage thyrses of which are predominant. All axils finish with terminal flowers, which are clearly (pre?)developed in their vicinity; prophylls are only available when they carry axillary organs. The lowest partial inflorescences start to bloom first, the others close in ascending order.

Very different *Leontice*. Here we find a composite raceme, which is finished by a terminal raceme, which previously developed in its vicinity. From the side racemes the lower ones bloom, then the remaining ones in ascending order. (Figure 10B shows, however, that the lowest side-raceme is late developed, and at the same time also poorer in shape. The appearance that one or a few partial elements appear somewhat reduced in the case of a panicle-like or raceme-like whole structure can often be observed. Such somewhat impoverished partial members must not be confused with paraclades.)

How can these two inflorescences in certainly closely related taxa be related? Compare the model Figure 10 C and D, which are suppositional.

Assuming that the initial form for both types would have been a somewhat richer panicle of the *Bongardia* pattern, which is illustrated in Fig. 10C, where here also the strong appearance of the thyrsoid terminal part is presupposed, we first gain an approximation of the *Leontice* inflorescence the inflorescence of *Leontice* is in the first approximation (Fig. 10D) by two assumptions: first, by loss of the terminal flowers of the thyrsoid partial systems (main and lateral axes), secondly by sterility and simultaneous removal of the prophylls. That the assumption of a thyrsoid panicle is justified as a starting form is also confirmed by other genera of the Berberidaceae, where such panicles occur, e.g. in *Nandina domestica* THUNBG. Compare also the inflorescence of *Epimedium* treated in the next example. In the family, too, there are cases in which, with the same species, terminal flowers soon appear, as will be absent under in *Berberis*. Our first requirement view may therefore be accepted as justified. The sterilization and aborting of prophylls can also be observed elsewhere in the family, and we will also meet this again in *Epimedium*.

From Fig. 10D, there is only a comparatively small step to Fig. 10B, which consists of a considerable increase in the number of flowers per axis, which is again to be observed in parallel in *Epimedium*.

So we have here an example of how the panicle and compound raceme can be related. This example gains importance because it occurs in a family that is intermediate between Ranales and Rhoeadales. It is probable that the Rhoeadales inflorescence is similar, and one could, in the same way, proceed from the thyrsoid panicle of the Papaveraceae *Macleaya cordata* (WILLD.) R. BR., and in the same way reach the panicle of racemes of the Cruciferae genus *Crambe*, in which the main mass of the cruciferous plants appears to be reduced in the inflorescence down to the terminal raceme.

8. *Epimedium*

Again a parallel example to the case just treated.

Fig. 11A shows the panicle of *Epimedium pubigerum* MORR. & DCNE. (CZERNIAVSKY s.n., 13 April 1917). In accordance with the inflorescence forms described in the preceding section in Berberidaceae, the panicle is strongly thyrsoid, partly by dichasial partial inflorescences with monochasial origin lateral axes up to fourth order, and the number of dichasial partial inflorescences increases significantly compared to a normal panicle. On the other hand, there can be no mention of a thyrsoid raceme, for, in contrast to the panicoid system, there should be a distinct transition between the terminal thyrse and the uppermost lateral thyrse, which does not occur in *Epimedium*.

The flowering sequence [=efflorescence] of *E. pubigerum* approaches something like simultaneity, especially when flowers of the same axis order are compared. The terminal flowers are somewhat developed in their vicinity, as in *Bongardia*, and the sequence proceeding from the bottom to the top when the flowers of the same axis are blooming can be seen in the diagram, for example, on the side flowers of second and third degrees in the thyroid terminal portion.

Other species of *Epimedium* now show transitions from this panicoid inflorescence to racemes with terminal flowers. For example, *E. Perralderianum* Coss., Fig. 11B, VETTER s.n., 24 May

1887, to *E. pinnatum* FISCH, Fig. 11 C, VETTER, s. n., 15. 5. 1884 Fig. 11 B can be deduced from Fig. 11 A by reduction of the upper part of the panicle, by loss of the axillary organs of the prophylls with shrinkage of the latter, wherein at the base of the terminal raceme in example 11 B still a few prophylls could be observed, as well as by increasing the number of flowers in the racemiform terminal portion. This development of the end region is clearly marked by the panicle through the thyrsoid terminal portion. These tendencies are still advanced in *E. pinnatum*. There is nothing more to be found here than a raceme with a terminal flower and bracteose lateral flowers, the number of which is increased again. Again, it can be seen that the flowering sequence of the terminal flower is somewhat anticipatory of the neighborhood, but that the side flowers also tend strongly to simultaneity, yet the acropetal sequence is still recognizable.

According to BOLLE, rich racemes do not emerge from panicles. *Epimedium*, however, provides a fine example of such a transformation, and others may be called, for example, for *Thalictrum*, the basic inflorescence form of which is a typical panicle. About thyrsoid shaped panicles, for example in *T. isopyroides* C. A. M., one can also observe in this genus a series of forms up to the pure raceme of *T. alpinum* L., which can also carry up to 16 flowers, and the terminal flower, which is always present in the genus, regularly no longer exists.

As a further example of interrelationships between panicles and racemes, the genus *Acer* may be added is still taken. Again, there are typical panicles (for instance, in *A. niveum* BL., *A. tataricum* L.), which in some tribes advance through the thyrsoid terminal portion to the thyrse. From thyrses (example: *A. spicatum* LAM) one reaches racemes with a terminal flower (*A. pennsylvanicum* L., with up to 16 flowers per raceme). Here, too, the racemes efflorescence-wise tend to be strongly simultaneous, likewise with *Thalictrum*, and thus leave the panicle character to somewhat show through.

9. *Thesium*

This example provides further evidence of the fusion of an inflorescence with paraclades.

The inflorescences of the genus *Thesium* are thyrses or racemes with or without a terminal flower. Our indigenous species do not possess any terminal flowers; in the species with a thyrse, the partial inflorescences are rarely more than seven-flowered. In the case of South African species, on the other hand, there are more profusely branched partial inflorescences of dichasial character; compare, for example, the partial inflorescence of *T. triflorum* THUNB, reproduced in Fig. 12.

Furthermore, among our native species it is characteristic that we find enrichment axes below the raceme or thyrse of the main axis, these axes bearing similarly constructed inflorescences and typically developing in basipetal order. Basally, an inhibition zone follows, as is shown in Fig. 12A for *T. alpinum* L. (STAUFFER sn, 6, 1961, from several individuals), where the lower paraclades P_{III} and the following ones are only limited in development. In this species we are concerned with the racemose inflorescence form, since the prophylls remain sterile. For a better understanding of the scheme, it should be added that in the case of *Thesium* the subtending bract and its axillary product are frequently fused in such a way that the subtending bract appears to be raised on the axillary product.

Starting from the conditions just described for *T. alpinum*, a schematic for a species with fertile prophylls and thus a bracteal thyrsoid inflorescence was conceptualized in Fig. 12B. For example, one should expect this in the flowering region of *T. bavarum* SCHRANK (= *T. montanum* EHRH.). In fact, however, a strongly deviant condition is shown in this type, as is shown in a somewhat schematic form for a typical individual case in Fig. 12 C (KEHLHOFER, n., 6, 1908).

Between the thyrse of the principal axis and the enrichment axes P_I, P_{II}, which are more or less impoverished racemes, there appear to be transitional formations (I-IV) between partial inflorescences and thyrses and racemes. These transitional formations alleviate the transitional point and help to combine the inflorescence and the paraclades into a single whole. Morphologically, they consist of impoverished, limited thyrses. I shows a tiny bract at the base of the terminal flower above the two branches of the dichasium, which is to be regarded as a sterile subtending bract of a third lateral flower. II already shows four lateral flowers, the lowest of which is still branched out from a prophyll, but all of them are umbellate, and still largely preserve the character of the dichasium. III is of the same construction as II, but the lowest internode between the lateral flowers is stretched. In IV, there are still four lateral flowers, the lower one of which is branched from a prophyll, but now two internodes are stretched, and as in I, a sterile subtending bract of another lateral flower is found immediately below the terminal flower. The first step is to go to paraclade I, a thyrse almost entirely reduced to a raceme. The formation of the transitional formations in *T. bavarum* is subject to considerable variation; these structures, however, are only rarely absent and are typical for this species.

In terms of flowering sequence, these transitional forms also take an intermediate position. The flowering of the whole plant generally begins here, usually at one of the uppermost transitional inflorescences, in the example of Fig. 12C with the terminal flower as I. Ascending, it continues into the pure thyrse of the principal axis, descending into the paraclades.

Transitional formations between partial inflorescences and paraclades have already been described several times. HAMANN mentions them as rare exceptions for *Veronica* species with an open raceme as the inflorescence; TROLL and HEIDENHAIN also portrayed for Cruciferae the inflorescence type of the open raceme. It is remarkable that in the case of *Thesium*, whose underlying inflorescence was originally a closed thyrse, they occur with regularity in individual species. They are also possible in the case of species with open racemes, as shown by the example of *T. pyrenaicum* POURRET (= *T. pratense* EHRH.) where they are also found in most cases. They certainly mean a recourse to the original inflorescence form of the genus.

However, there are also discontinuities in inflorescences, for example, in all racemes from open thyrses with terminal thyrses or in open racemes with terminal racemes. Here, too, we may think of such transitional formations, as well as between inflorescences and paraclades. So far I have found them in a thyrse-raceme of an open thyrse, in the Bignoniaceae *Arrabidaea corymbifera* (VAHL) BUR. from a voucher by HASSLER 12365, where they are similar to *Thesium bavarum*. In the case of compositions made from closed racemes or thyrses, such transitional forms are not recognizable with certainty when placed together with closed racemes or thyrses because structurally they are not distinguishable from partial inflorescences. It is to be expected that they are still to be found in many cases, as long as racemes from open thyrse with terminal thyrses are systematically tested.

On *Thesium* it may be added that with *T. rostratum* M. et K., this genus also has a representative with a percurrent raceme, in which at the same time the prophylls are missing. It is remarkable in this genus that there is also a group of species in which the inflorescences are reduced to the terminal flower, and only that one remains. This is exactly what I have observed earlier (STAUFFER, 1959) within the Tribe Anthoboleae for another group of Santalaceae. This reduction also consists of the loss of the basal part of the original inflorescence.

10. Analogous Examples

For every pursuit of inflorescence morphology, numerous analogies between certainly non-homologous branching systems in the floral region occur, examples of this kind are given by TROLL 1928 among others in connection with the discussion of pseudanthia. In particular, this author compared the various inflorescences of the Compositae with simple inflorescences. There are many parallels that can be worked out. The same applies to the cyathia of *Euphorbia*, whose arrangement is quite analogous to the arrangement of simple flowers. As an example, I would like to refer to Fig. 50 (p. 102), reproduced in TROLL 1928, of three terminal “dichasia”.

Such analogies also particularly concern the inflorescences often referred to as “composite”. An example from the family of Cruciferae is illustrated in Fig. 13A. This figure shows the inflorescence pattern of *Crambe Kralikii* Coss., drawn according to STROHL-MOSER s.n., 1921. The inflorescence is a thyrse of racemes, the partial inflorescences are racemose monochasia. The inflorescence is a complete analogue to a thyrse of monochasia with a terminal flower, also with regard to the flowering sequence, we think of each raceme in *Crambe* replaced by a single flower.

In Fig. 13B, *Crambe* is compared with the example of *Capsella Bursa-pastoris* (L.) MEDICUS, obtained from the analysis of PIPER s.n., 10 June 1904. This comparison has been made only in order to make it clear that *Crambe* is an inflorescence, not a paraclade below a terminal raceme. *Capsella* has a simple terminal raceme, and here we have to deal with paraclades within the branches, which result from the descending flowering sequence, which can be easily seen here from the number of fruits already formed. In *Crambe,* on the other hand, the lowest lateral inflorescence of the first degree begins to flower, as is generally the case, the racemes that finish the inflorescence develop somewhat ahead of their surroundings.

Analogies like those of the racemose thyrse to the thyrse are immensely numerous. Some of them are also found in higher categories, and there are especially well-known examples in the composites. It is only thought of in *Echinops*, whose heads have been correctly interpreted by R. BROWN on the basis of their remarkable flowering, or on species of the genus *Leontopodium*, in which several superimposed heads are again compressed into the aspect of single flower-like structures. Even with other pseudanthia, these condensations of even higher branching categories can be observed.

Essential for our consideration is only one thing from these examples: that in any case it must be examined with great care whether similar organ complexes are really homologous or show only analogies. In the area of inflorescences the structural possibilities are limited. It is always about axes, leaves, ramifications, and axes terminated by flowers or flower-like structures. It must therefore be presupposed that, in the great number of objects, much of the same thing has been achieved by different paths or homologous stages.

III. Discussion

1. On the importance of flowering sequence

In 1857, GUILLARD published an inflorescence classification, which was essentially based on the sequence of flowering, the result of long and very careful observations. BAILLON had already made definite criticism during the first communication: The flowering sequence was not suitable for assessing the inflorescences, and above all not constant. Since GUILLARD also larded his classification with terminological innovations, he consequently did not find any followers either, and EICHLER 1875 remarked:

“It is presently and quite rightly agreed that for the characterization of the forms of inflorescences, the nature of the branching of the hypsophyll [a bracteose or frondose leaf within inflorescence] must be taken into consideration, in the first place, by external appearance, flowering sequence, and the like.”

What EICHLER has predicated here, as a judgement of the inflorescence criteria, has changed little since then. One can find in GOEBEL 1931, for example, there are only more detailed hints to biological questions on flowering sequence (p. 160-162). From a morphological point of view, this author is of the opinion that it is only a question of the placement and not the opening of flowers (p. 85). Further, he says: “In a cymose synflorescence, however, the cymose character is characterized by the descending developmental sequence of the flowers, but this characteristic can not be regarded as an essential difference (which is was barred according to rejected by GOEBEL).”

TROLL 1957, too, gives very little information about the flowering sequence in his extensive overview of the inflorescences, especially in complicated inflorescences. Almost all the examples of panicles that the author gives from the realm of dicotyledons are illustrated with buds stages, from which scarcely any information about the flowering sequence can be obtained. The few text references to the flowering of *Echinops* or *Verbascum,* or the remark on the false umbels (p.389): "At first sight ... one is struck by the basipetal flowering sequence occurs. It is generally observed in false umbels and, so to speak, belongs to its essence" almost emphasizing the fractitious "incidentally (?)" by EICHLER. TROLL makes no attempt at all to use the flowering sequence as planned for the assessment of the inflorescences.

This attempt has recently been undertaken by two authors, who have made a significant contribution to the understanding of the inflorescences because they are thus able to gain more criteria for assessment. Without falling into the error of GUILLARD, only to consider the flowering sequence, these two works have, above all, revealed the connections between branching and flowering. The two studies, almost simultaneously and independent of each other, are from BOLLE 1940 and SCHÜEPP 1942, i.e. particularly from two mathematically interested researchers. Both came to a classification of the inflorescences in three categories: cymose (namely forked), racemose (namely raceme) and paniculate. Both authors can show that, in all of these three main types, branching and flowering sequences are completely linked with each other, by the flowering sequence following the morphological age of the flowers. Both authors have recognized the simultaneity of the termination as the law of the panicle. Both have stated the divergent behavior of the enrichment axes with respect to the placement / flowering sequence which GUILLARD had already known. BOLLES' derivations are largely derived from mathematical considerations, SCHÜEPP relies more on his exact measurements on the living object; there are some divergences between the two authors: BOLLE assumes that the plastochron is constant, SCHÜEPP shows in individual cases that it changes, BOLLE makes assumptions about the placement of the side members, which SCHUEPPS observations do not correspond; nevertheless, all this does not alter the basic consistency and correctness of the two views, but only requires certain modifications. Above all, we are interested in the fact that the two authors agree that the flowering sequence in the inflorescences is strictly regular. lawful.

It has always been emphasized, when it comes to the question of the flowering sequence, that this is often irregular. It is true that there are often cases where the flowering sequence is different from what is to be expected from the scheme, but precisely such cases require a close examination, and especially a comparison with closely related species. The flowering sequence is not accidental, but has become something typical. If it varies within a species, it does so in a manner as limitable as other morphological features, no one expecting them to be without variation. It is, of course, necessary, in the case of more complicated inflorescences, to involve this criterion in the investigation. However, the above-mentioned single examples seem to me to be sufficiently confirmed that this effort is absolutely essential for a better understanding of the inflorescence and especially for the delineation of the inflorescence compared with the paraclades. This will be returned to below.

It is only to be emphasized here that I had not found anything in my investigations which would be quite contrary to BOLLE-SCHÜEPP's conception. For example, all the inflorescences I have found are to be accommodated in the categories set up by BOLLE. Some refinements will, of course, have to be brought to these, where nature simply shows different conditions than the ideal models require. As an example, I would like only to mention p. 231, that the lowest partial inflorescence(s) of panicles, or inflorescences similar to those caused by more or less simultaneous termination, are very often both weaker and time-delayed. BOLLE had such a case with his *Syringa* example, they are quite frequent.

2. Delineation of the inflorescence and the Trollian synflorescence concept

How should the inflorescence be separated from the hypotagma?* It has often been the intention of many to develop standard criteria for leaves for this purpose, and it is thanks to TROLL who showed convincingly that such a delimitation has something very artificial about it. Therefore, something artificial, because again only one criterion for the decision is brought. If, on the other hand, we take into account branching, phyllotaxy, leaf form, and flowering sequence in the delimitation, one will rarely doubt where this has to be done. TROLL has rightly pointed out numerous "axillary single flowers" in herbaceous plants, and especially in annuals, as constituents of inflorescences with foliose hypsophylls, for example, in *Veronica hederifolia* L. In such reduced annuals, where almost the whole plant consists of inflorescence and paraclades, which are also completely reproductive, photosynthesis assimilation can only take place by means of the hypsophyll*, which has a completely different design from that of plants with a rich vegetative hypotagma. One therefore cannot base the delimitation of inflorescence on the design of the leaves.

TROLL 1950 has, starting with hapaxanthic* herbaceous plants of the type of *Lupinus luteus* L., given a delimitation in terminal inflorescences and enrichment shoots. TROLL circumscribes this delimitation protractedly, but does not give any sharp criteria as to how it can be done. For example, pointing to the basal internode (p. 379), "which is often conspicuously prolonged". Of the enrichment shoots he said (p. 379): "They are naturally applied in an acropetal direction. Their unfolding, however, usually takes place in a basipetal direction. Thus, enrichment shoots adjacent to the primary inflorescence reach development before all others."

The examples given by TROLL show as terminal inflorescences exclusively those without a terminal flower, open racemes of Cruciferae, open umbels of Primulaceae and open thyrses of Labiatae. In 1951, TROLL and HEIDENHAIN investigated the length of the basal internode in Cruciferae. This shows, that in many cases it did not indicate a particular length.

In 1952 HEIDENHAIN studied the inflorescences of the Campanulaceae. It now also utilizes the flowering sequence, and in these inflorescences, which are often terminal flowered, leads to a limitation of a thyrse (also known as a panicle) terminal inflorescence and thyrsoid enrichment inflorescences (p.624): "The inflorescence of our plant (*Campanula rapunculus* as an example of this construction plan) shows two sections which are distinguished by the shape of the side branches and can be separated from each other. The lower one corresponds to the enrichment zone, the upper of the terminal inflorescence. This is in harmony with the flowering sequence, which in the upper section is acropetal according to the rule valid for racemose inflorescences, while in the lower section, basipetal, according to the law which is binding for enrichment shoots."

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* Translations of these terms come from Weberling (1992, translation by Pankhurst); they were not in this document by Stauffer but were added for clarification

- The **hypotagma** (Unterbau) is that part of an inflorescence which includes all the nodes of the enrichment zone, the inhibition zone and the innovation zone (Goebel 1931: 3, Troll 1951: 383)
- The **hypsophyll** (Hochblatt) is a bracteose (or sometimes more or less metamorphosed frondose) leaf within the inflorescence [opposite of cataphyll]. Plural Hochblättern.
- A **hapaxanthic** plant is an annual or perennial plant which only flowers once, in contrast to pollacanthic plants, which flower repeatedly.

HEIDENHAIN speaks here of the law, which GUILLARD already knew, and which also was formulated again by BOLLE and SCHÜEPP. Quite differently TROLL 1955 (in TROLL and

WEBER) gives a new representation of his “Synflorescence”. As an “terminal inflorescence,” he mentions the open inflorescences already mentioned in 1950 (p. 38): “The realization that, in many synflorescences, there is a naked flower (terminal flower) instead of the terminal inflorescence is of great importance. The same is then true of enrichment. These, insofar as they are adjacent to the terminal flower, have only the prophylls. On the downstream successive enrichment shoots the number of bracts is increased, to the same degree as the distance from the terminal flower increases.”

Such a system can occur in a panicle-like manner by means of basitonic-mesotonic promotion, but by contrast, by the action of acrotony, either dichasially or monochasially TROLL comes to the conclusion (p. 39) that “the so-called panicles are synflorescences.” Such synflorescences could also take the form of racemes. “From here the difficulties which arose in the treatment of the Campanulaceae inflorescence by HEIDENHAIN, in so far as the separation of the assumed terminal inflorescence from the enrichment zone, has not been successfully achieved. There is no such limit in reality. Rather, a terminal inflorescence is simulated only by the fact that the enrichment shoots at the end portion of the synflorescence, if not to their entire extent, are reduced to their terminal flower.”

TROLL does not mention the flowering sequence. Only in the synflorescence schemata accompanying the demonstration of basi-mesotony and acrotony, which are, by the way, developed in the style of GOEBEL 1931 Fig. 72, it can be seen in the paniculate form of the first order terminal flowers of the lateral axes flower in descending order, and also in the area which is still racemose.

In the following years, TROLL has provided further, mainly terminological contributions to his synflorescence concept, which were summarized by WEBERLING in 1961 (p. 247 ff.). Here, the above-mentioned scheme with descending flowering from the terminal flowers is reproduced unchanged. A distinction is now made between “monotelic” and “polytelic” synflorescences. Furthermore, the terms “pseudoflorescence”, “segregation internodes” and “open synflorescence” are explained, what one might read at the relevant place. The Trollian view has essentially remained unchanged since 1955. It is important to note that all paraclades are expressly declared to be homologous to each other, and WEBERLING (p. 247) now says: “According to TROLL, we are almost always concerned with synflorescences in inflorescences.”

Let us return to our examples after this necessary excursion! Consider *Helleborus*, *Legousia* and *Hypericum*, or other genera not treated here, such as *Rubus*, *Saxifraga*, *Ranunculus*, *Symphytum*. We shall always find a thyrse with a terminal flower at the terminal portion of the axis, the partial inflorescences of which begin with the flowering sequence from below upward, while the underlying lateral organs, which more or less completely repeat the structure of the terminal thyrse, open in descending order. Here, a morphological boundary, both with regard to branching mode and with respect to flowering, can be clearly seen. If, as TROLL maintains, in *Legousia*, leaf number increases as much as the distance from the terminal flower increases, how would it be understood then that, for example in the example of Fig. 8A, eight lateral organs with constant two leaves follow, and then suddenly those with four, five, and six leaves?

According to TROLL, an extended internode (“segregationinternodium”) can sometimes occur at this point, but this is of only descriptive importance since it does not constitute a limitation by which morphologically distinct sections are separated from each other.

There are, of course, also flowering branching systems which exactly correspond to the synflorescence schematics designed by TROLL, in which the inflorescence is reduced to the terminal flower, or even to this and one or two partial inflorescences of dichasial or monochasial character, and enrichment axes continue to flower; such as the Polemoniaceae (see WEBERLING

1957) or Solanaceae. In these families, such a reduced inflorescence has been largely constant, and the modification takes place in other features.

The Trollian schemes have arisen on the basis of a generalization of the relations between the Polemoniaceae. The long discussions that WEBERLING 1961 had to make for the Valerianaceae show the difficulties that arise with their application to other families. It is precisely in this family that it is questionable to postulate a fundamental difference between a thyrse without a terminal flower and one with terminal flower, in such a way that the one is composed of partial inflorescences, the other by paraclades, because a "fork" occurs here instead of the terminal flower, while related families have a terminal flower. It is not easy for WEBERLING to blur the morphological boundary between the terminal thyrse and the paraclades – which despite the almost consistent neglect of the flowering sequence phenomena – has become visible to him from the branching of many species, so that it can be dismissed as insignificant, and the Valerianaceae can be inducted into the Polemoniaceae scheme of the "monotelic synflorescence". It is even acknowledged (p. 255) that "TROLL has succeeded in finding transitions between the two types of synflorescence types, even within some other families," so that WEBERLING is no longer hesitant to consider the inflorescences of the Valerianaceae as transitional forms between monotelic and polytelic synflorescences. How, however, the transition from partial inflorescences to paraclades can be conceived is not explained.

We do not overlook the fact that many flowering branch systems are composed of a terminal inflorescence and flowering paraclades. This has been known since GUILLARD and has also been highlighted by BOLLE and SCHÜEPP. The term "synflorescence" can be applied to such a system. So far we are able to follow TROLL. However, we would like to restrict this term largely to herbaceous plants, and above all, do not use it where flowering systems are structurally unfolding one season apart, as in the case of many woody plants under temperate climates. Even in the case of flowering branching systems of tropical trees, which originate in a thrust, it is not easy to parallelize the "synflorescence" of an herbaceous plant.

We can not follow TROLL in the pronounced division of the synflorescences into monotelic and polytelic, and in the delimitation of the (terminal) inflorescence for the polytelic synflorescence as a terminal single flower. For us, there is no fundamental difference between a thyrse with or without a terminal flower, for example, in the Campanulaceae or *Thesium,* in closely related units, just as the raceme with or without the terminal flower in Berberidaceae or Ranunculaceae. Thyrses with and without a terminal flower have, in our opinion, homologous sections with partial inflorescences, which are serially homologous among themselves, as well as in a raceme or a panicle.

Accordingly, all possible closed or open flower branching systems of a simple or complicated nature can occur as (terminal) inflorescence, but enrichment or absence of enrichment may occur below. It is quite often the case that inflorescences and flowering paraclades are fused together again, either by the paraclades of the branches approaching the partial inflorescences (*Helleborus*) or by the formation of transitional forms (*Thesium*). The flowering sequence is often more conservative than certain branching features, which are especially blurred in panicles and thyrses. From this fusion of the synflorescences, which is analogous to the phenomenon of pseudanthia, comes the difficulty elucidating the Campanulaceae inflorescences.

3. On the positional phenomenon

Under the positional phenomenon, we mean the fact that the separation of lateral organs (partial inflorescences or paraclades) with regard to the number of leaves present on it is closely linked with their position on the relative principal axis. This well-known fact, of which SCHÜEPP 1942 has mainly been concerned with in his investigations, and he gives an excellent account of this. He also quotes A. BRAUN 1851, p. 31, who says “that the individual shoots, and indeed the leading shoots as the side shoots, in the majority of cases do not present themselves at all stages of plant metamorphosis which are ascribed to the shoot as a whole .... The formation, with which a shoot is raised, is usually related to the region of the mother shoot, from which it originates. Thus, we often see an order of shoots from the successive regions of the main shoot spring from this sequence, for example, starting with the prophyllar region, leaves beginning with foliage leaves from the foliage leaf region, bracts beginning from the bract [Hochblatt] region … But it is also possible to reverse the shoot to a lower formation as well as to anticipate a higher formation”.

Our example of *Legousia*, cited above, can be taken as a model for the case where the paraclade copies the behavior of the subtending axil above its starting point. It is also similar in *Lysimachia vulgaris*. The diagram of *Capsella* given in Fig. 13B would be an example of a retrogressive design of the enrichment axes, another one is *Lysimachia dubia*. In this case, however, more leaves are separated from the lower paraclades in relation to the position of the paraclades on the main axis than on the uppermost ones. In the limiting case, all lateral organs may show the same number of leaves over longer axis sections, as can be seen in the paraclades of *Helleborus foetidus* in Fig. 6A. I have never found any lower paraclades than a higher one. Very often, however, an inhibition takes place in such a way that deeper lower organs do not grow completely.

For the three main types of inflorescences SCHÜEPP describes the alternating condition with regard to the anticipation or falling back of the lateral axes. The limit of the same number of leaves over longer periods is realized in the raceme or thyrse. For the inflorescences, too, I have only been able to find, as a special exception, that lower-lying organs of the organs form a smaller number of leaves than those above them. One such exception is the somewhat reduced branches at the base of panicles, as already described.

It would be attractive to look more closely at the genetic and physiological side of this positional phenomenon. The fact that the branching form can be based on gene action is shown, for example, in the crossing experiments which HAERLE 1932 carried out on *Veronica* Sect. *Pseudolysimachia*. In these species, even after the identification of our Fig. 5E, only a few paraclades are developed at the shoot tip, followed by a longer inhibition zone. In a cross from such parents, a complete removal of the inhibition resulted, which HAERLE’s Fig. 45 shows very nicely. This behavior can certainly be considered as a genetic condition.

It is also reminiscent of the reciprocal inhibition of the seasonally dimorphous species, in which very similar branching types appear to be fixed, as we find them alternately changing in a population in *Legousia*. A certain genetic fixation of the branching condition is also found in a race of *Arabidopsis Thaliana* (L.) HEYNHOLD studied by NAPP-ZINN 1957. It is probable that the gene effects are from growth substance distribution.

It remains unclear whether a rich spectrum of alleles is evident in labile populations such as *Legousia*, or whether this is an environment related manifoldness resulting from changing nutritional possibilities. Only experiments could decide that.

A particularly fine example of the positional phenomenon is given by WEBERLING in 1961 in Fig. 37 for *Valeriana urticaefolia* HBK. The normal plant depicted in I has seven vegetative leaf pairs, and an terminal thyrse with five pairs of partial inflorescences. In II the main axis was somehow disturbed in its growth and produced only four leaf pairs. In the three lower axes, axes with terminal thyrses are present, and from the uppermost leaf pair there arises partial inflorescences. In III, the axis has already stopped its growth after three pairs of leaves, and the branches of the uppermost pair of leaves show only the side branches, which, as they are, correspond to their position as poor thyrses without sterile leaf organs formed at the base. IV finally shows that a partial inflorescence and an enrichment axis can originate at the transitional point from a pair of leaves (it is not clear from the figure whether the third or fourth pair of leaves are from below). Such irregularities and discontinuities occur more often. TROLL and HEIDENHAIN 1951 provide the example of cruciferous racemes (Fig. 62), even single flowers among paraclades, HAMANN reports similar cases for *Veronica*. In such examples, however, it must not be overlooked that the leaf spirals present do not have to agree with one another with respect to their axis organs, which can be seen particularly well in *Veronica*, and HAMANN reports this in detail.

From the juxtaposition of a partial inflorescence and an enrichment axis in the same whorl, to infer the homology of these two structures, as WEBERLING does and as TROLL and HEIDENHAIN imply, I would not dare.

4. Something on the phylogeny of the inflorescences

Already in the introduction we have referred to studies dealing with the phylogeny of inflorescences. A distinction must be made between mainly deductive-theoretic treatises, such as those of NAEGELI 1884, CELAKOVSKY 1893, ZIMMERMANN 1935 and TAKHTAJAN 1959, and empirical investigations of living plants, under which PARKIN 1914, in particular, used the transformations of the inflorescences in related orders, whereas PILGER 1922 investigated the position of the inflorescences on the vegetative body of woody plants. The work of SCHLITTLER 1945 on the inflorescences of the Anthericumtypus is also to be mentioned here. It provides a monographic treatment of the inflorescences from a restricted range of relatives, combined with general discussions on the inflorescences. Moreover, in very many monographs of narrower circles of relatives, there is valuable information on the changes of inflorescence.

With PILGER, we agree that phylogenetic considerations about inflorescence are essentially hypothetical in the context of angiosperms generally. The organ complex of the inflorescence is extremely plastic, in addition to which are analogies and to which homologies is are often difficult to separate.

However, this is different in the case of narrower affinities, where the inflorescence morphology can contribute substantially to the clarification of the affinities, which, as TROLL and WEBERLING emphasize, are still far too little evaluated.

In addition, it seems possible to make some statements about the transformation processes occurring in the inflorescences. From these, a certain idea of the course of phylogeny at large can be obtained, but such general ideas can not be illustrated with examples of recent plants.

These conversion operations can be counted as follows:

1. The transformation of the terminal axis: occurrence of a far-ahead terminal flower - terminal flower still present, but not further developed - terminal flower disappears - percurrence of axis terminus. (The parallel can also occur with a terminal inflorescence section to a larger extent.)
2. The restriction of the branching from the floral prophylls: prophylls fertile - prophylls sterile.
3. The gradual elimination of basal inflorescence sections.
4. Increase or decrease the number of branches [limbs]
5. Reconstruction of covering bracts [Deckblätter]: Leafy bracts - bracteose condition - bracts absent. (Secondary return of bracts to foliose bracts is probable in some herbs.)
6. Stretching and compression of internodes, associated changes in the phyllotaxy and displacements in the over-topping of the main and lateral axes.
7. Curvatures and twists of axes and leaves.
8. Fusions of axes and leaves or mutual axes or mutual leaves.
9. Occurrence of accessory shoots.

The most important processes are those mentioned in the first to fourth cases.

To 1: The terminal flower may be considered as the original characteristic for the dicotyledons. PARKIN has described the process of its diminution to the point of complete abortion. However, with the fading disappearance of the terminal flower, the end of this developmental tendency has not yet been found, which is expressed by the vegetative growth of the inflorescence or a basal inflorescence section. Although PARKIN was aware of such a processes, it was a separate category of intercalary inflorescence without any connection with the terminal inflorescences. It was not concealed from him that transitions occur, but he thought they had to be connected to the intercalary as pseudo-terminal inflorescences and not to be able to relate them to the terminal ones. The examples given above for these transformations are sufficient to show that intercalary inflorescences can also be derived from terminal ones.

To 2: The branching from the prophylls may also be regarded as something primary. This is in addition to the fact that a differentiation in the axillary organs and missing leaves is already a specialization, especially the fact that dichasial and monochasial terminal branches occur in the inflorescences of the dicotyledons in the majority of cases. Incidently, this led RICKETT to consider the dichasium and/or the dichasium impoverished to the triad as the original inflorescence. He did not notice that these structures occur regularly only as parts of larger compositions and are individually rare.

The restriction of the branching from the preceding pages has also been precisely grasped by PARKIN.

To 3: The process of the gradual elimination of basal inflorescence sections has hitherto never been described as a major factor for the conversion of inflorescences. Although we have discussed extensively on acrotony and basitony, especially in NAEGELI, GOEBEL and TROLL, we have also mentioned the limitation of the lower (better: inner) inflorescence range. According to SCHLITTLER 1945, the branching in each inflorescence can be distributed to a lower (inner) racemous and an upper (outer) cymous. (The latter is identical with the branching from the preceding pages, already discussed.) In the limiting case, the inner branch can be broken down to two leaf axils (“terminal dichasium”) or one leaf axils (“terminal monochasium”). Is this the result of acrotony? It would then be necessary, as GOEBEL in his schema, 1931, p. 88, Fig. 72 II, under such a terminal dichasium or monochasium, there are leaf axils with undeveloped systems of partial inflorescences.

Let us, however, compare our *Hypericum* example, in which such a terminal dichasium is associated with a thyrse*. In Fig. 7 E, there is nothing to be seen under the terminal dichasium of a reduced partial inflorescence, but the first node under the inflorescence carries paraclades. The same can be observed in *Silene* and other Caryophyllaceae. This means, however, that the inflorescence is not promoted acrotonically, but is reduced to its uppermost end (the next step being the reduction to the mere terminal flower, which also occurs in *Hypericum* and *Silene* as in many other genera). In such inflorescences, an increase in the number of flowers can only be obtained by a repeated branching out from the prophylls, since, according to positional phenomena, the number of leaves on the lateral axis of the first order is limited to two (the prophylls).

It is therefore much more correct to speak of a loss of basal inflorescence than of acrotonic stimulation. This loss can also be observed in the case of our *Hebe* example, where, in several stages, from the rich panicle of racemes to the compound raceme, only a small terminal raceme remains, and under it nothing is found which might be regarded as the remainder of the lower inflorescence part, but enrichments which precisely copy the structure of the restricted terminal inflorescence.

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* In GOEBEL's scheme, derived from the Campanulaceae, it is associated with a panicle which, besides thyrse, occurs in that family. Since, however, panicles have a thyrsoid terminal-section, it is not possible to determine whether a thyrse or a panicle is the basis of a terminal dichasium or monochasium. In other words, the scheme can equally well be applied to a thyrse bounded with terminal flowers.

One could put the described process in analogy to what happens in the transition from the tree with its powerful branching system to the herb with its limited branching possibilities above the cotyledonary node. For this purpose it is quite well that especially richly branched inflorescences occur predominantly in woody plants, where panicles or compound panicles of thyrsoid or racemoid partial inflorescences are particularly frequent in the tropics, while in our herbs the thyrse and its modifications are particularly frequently found.

In the case of the herbaceous plants, a richly structured synflorescence frequently replaces the (reduced) inflorescence. Like the inflorescences, the branching systems of the paraclades can be made bifid, racemose or paniculate. In an extreme case, the inflorescence can disappear completely, and only the paraclades can assume the reproductive function, for which *Euphorbia* of Sect. *Anisophyllum* can serve as an example. The analogy to this would be an herb whose hypocotyl falls disappears completely over above the roots and which develops vegetatively from the roots.

To 4: In addition to the appearance phenomenon of the elimination of the basal inflorescence parts there are probably just as often reduced numbers of branches. For this PARKIN and more recently TROLL 1957 have given splendid examples: uniflorous racemes, umbels and heads as extreme.

The general impoverishment of richly branched inflorescences may also occur; SCHLITTLER 1945, gives examples of the monocotyledons, but in the dicotyledons they are certainly absent to this extent. BOLLE mentions *Chamaemeles* in such a context.

The conditions resulting from the increase of the number of terms need no further discussion.

To 5: Again, there is little to say. With regard to the secondary return to foliar construction development, I think of types such as *Veronica hederifolia* L., *Lysimachia nummularia* and the like. The step is not great and should be possible in leaps and bounds, if one remembers the frequent defaults in deviating leaf development in the floral area.

To 6-9: These ratios need not be discussed further. BOLLE has delivered provided good comments about these variations. They represent the accessory structure, which is important for the individual case.

5. Summary and Concluding Remarks

Plants flower and in so doing stand in relation to needs of pollination and seed dispersal. They evolved structures that we call “inflorescences”. Nature does not know this term. Hence our difficulties arise in creating a definition, and particularly in drawing up a general theory of inflorescence on a deductive basis.

In our view, the more criteria we use for analysis, the more we approach nature. If, when a new criterion is introduced, differences arise with an existing theory, the new criterion must not be rejected, but the theory must be checked. We must start from go out of nature and not from preconceived opinions.

The purpose of this study should be to demonstrate by empirical observations certain weaknesses of existing theories. No new and comprehensive theory of inflorescence could be presented here. It was, however, possible to formulate certain tendencies in the alteration of the inflorescences in general, and it was also possible to separate clear series of progress within groups of relatives, since here the homologies can be recognized with sufficient certainty.

It seems, however, very risky to build up a general theory from such examples by incorporating such progressive series as binding parts into a general scheme, as PARKIN and TAKHTAJAN have attempted. For if, for example, a relationship can be proved, that a raceme is a reduced form of a thyrse, this does not yet prove that all racemes should be derived in this way. In the series of progressions, too, it is often necessary to remain open to which direction they are to be read.

If, however, I have been induced here and there to generalize from my own, limited observations, I am aware that such generalizations must be corrected by new empirical observations. What our knowledge in this field promotes in the long run are observations on the objects, which have been gained from theoretical ideas.

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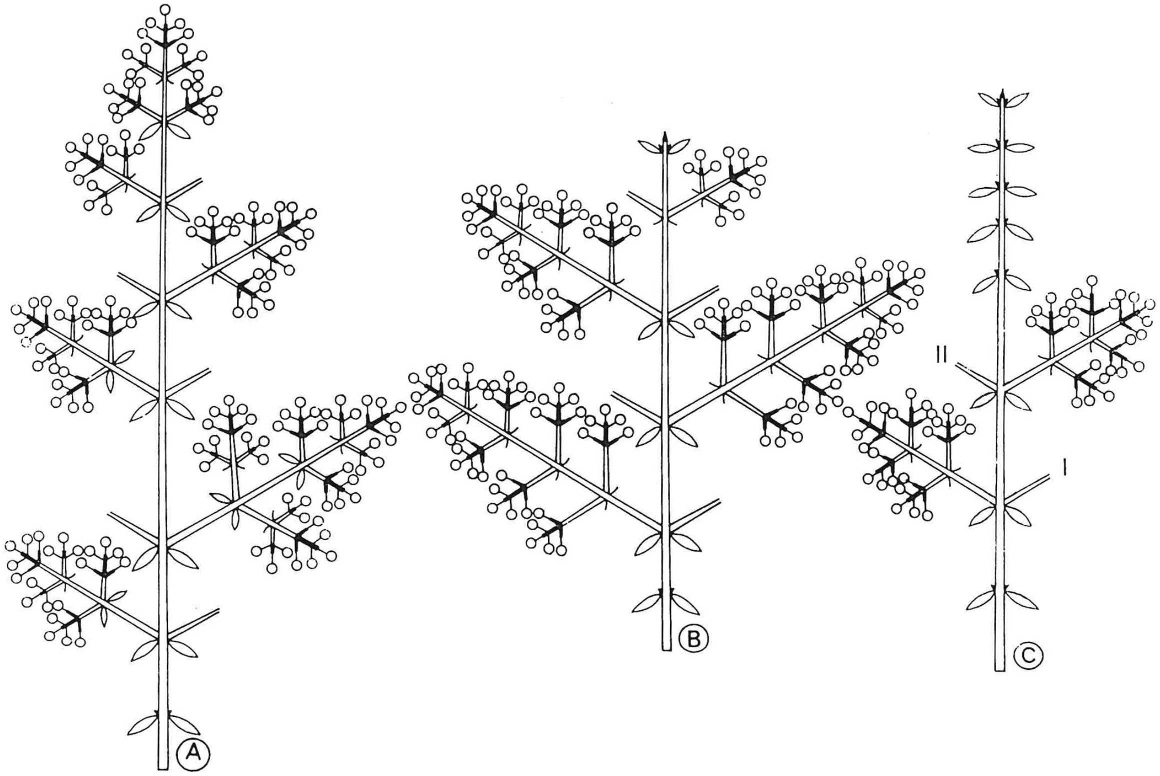

Fig. 1. A. *Santalum album*. B. *S. freycinetianum*. C. *S. pyrularium*

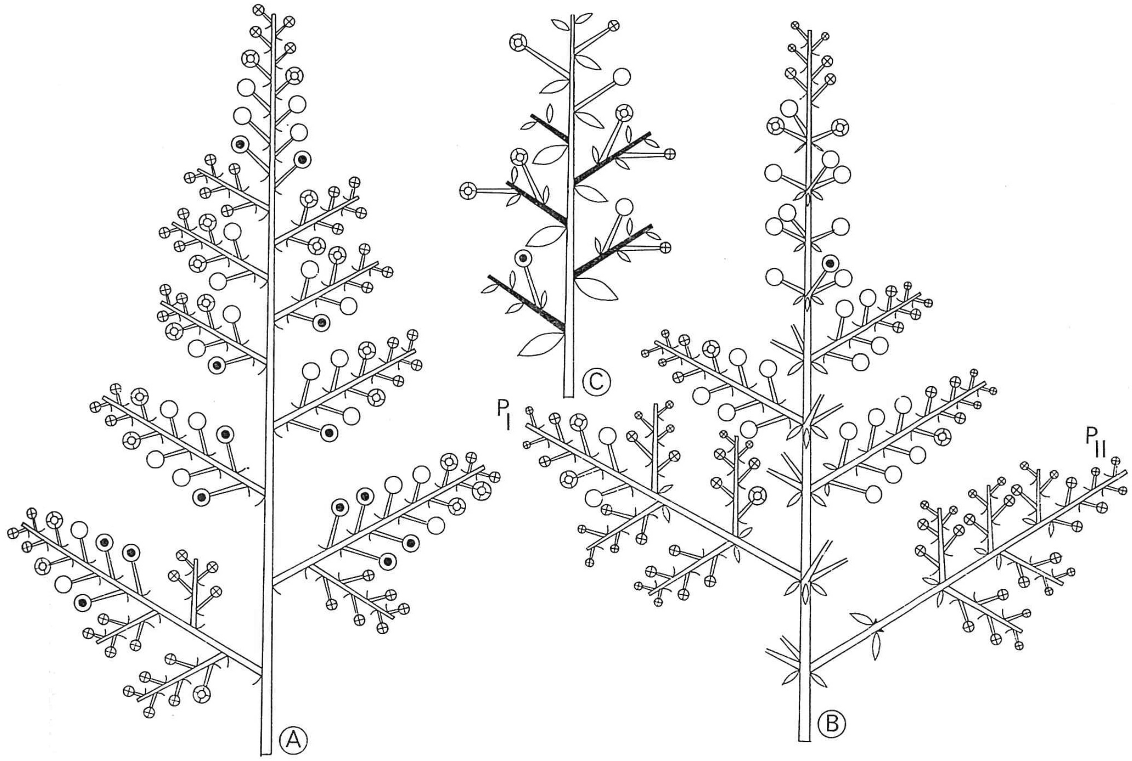

Fig. 2. A. *Maesa rufescens*. B. *Lysimachia vulgaris*. C. *L. ramosa*

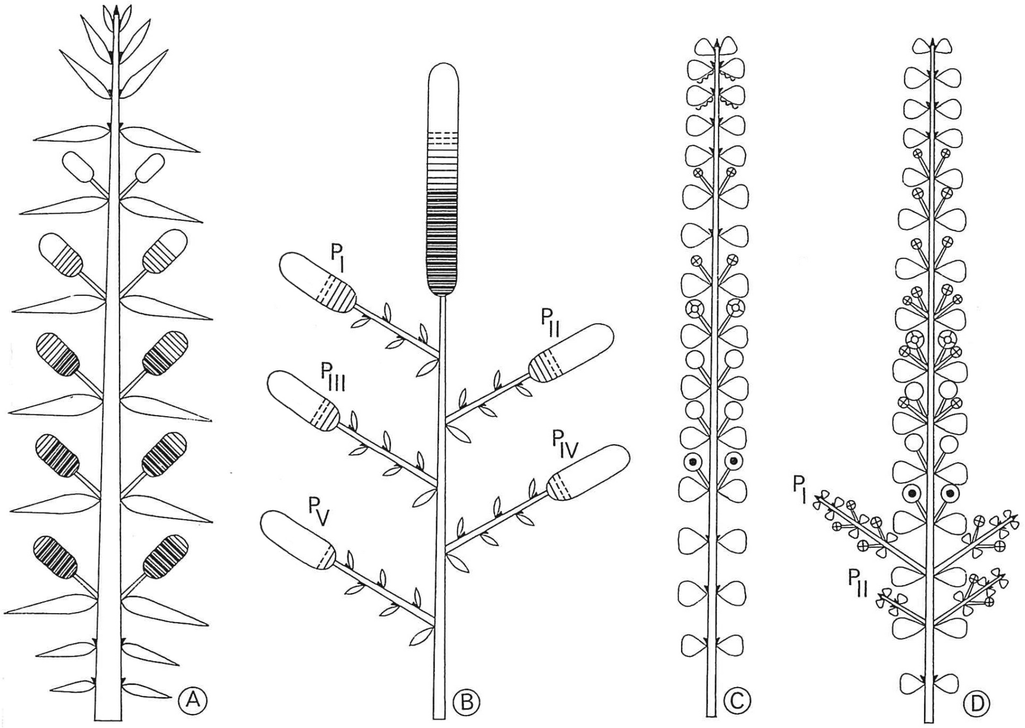

Fig. 3. A. *Lysimachia thyrsifolia*. B. *L. dubia*. C & D. *L. nummularia*

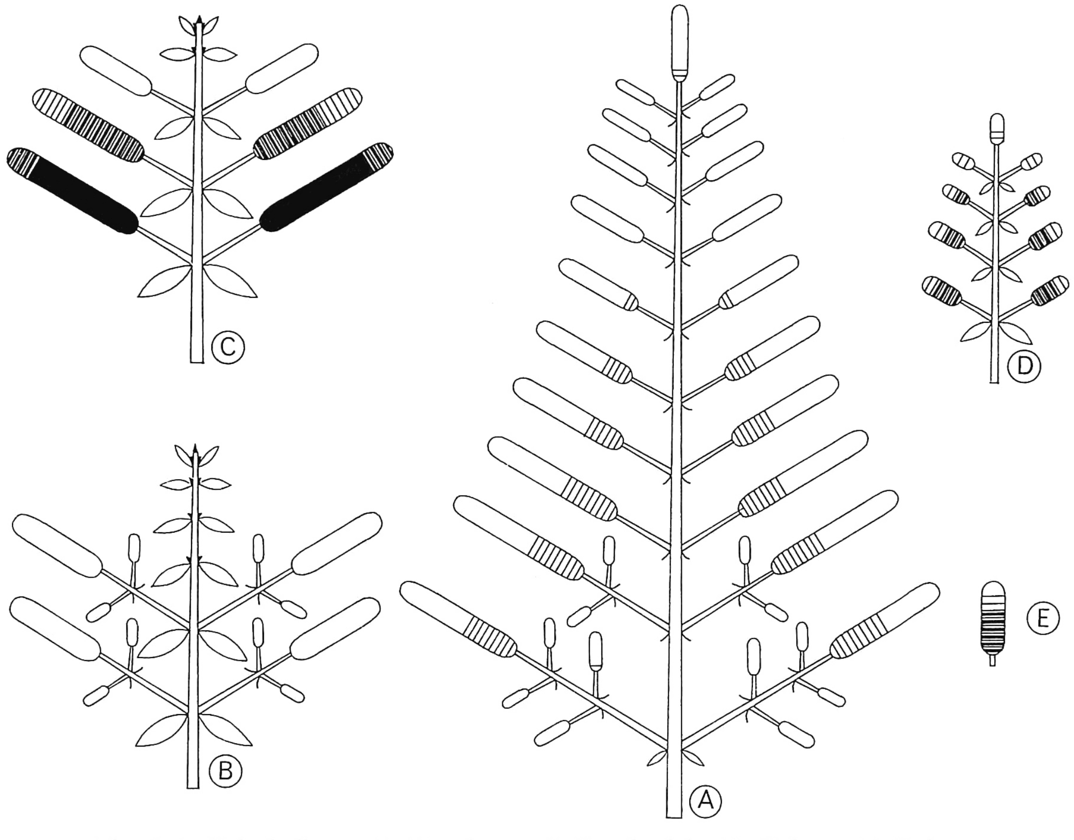

Fig. 4. A. *Hebe hulkeana*. B. *H. colensoi*. C. *H. salicifolia*. D. *H. hastii*. E. *H. hectori*

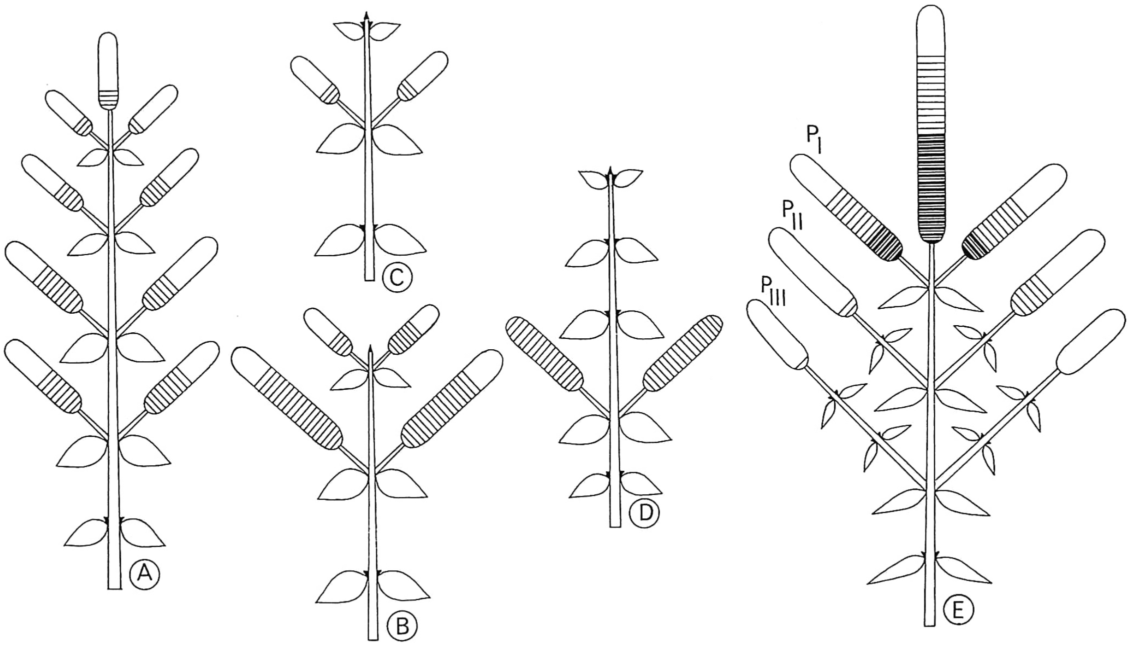

Fig. 5. A-D. *Veronica latifolia*. E. *V. longifolia*

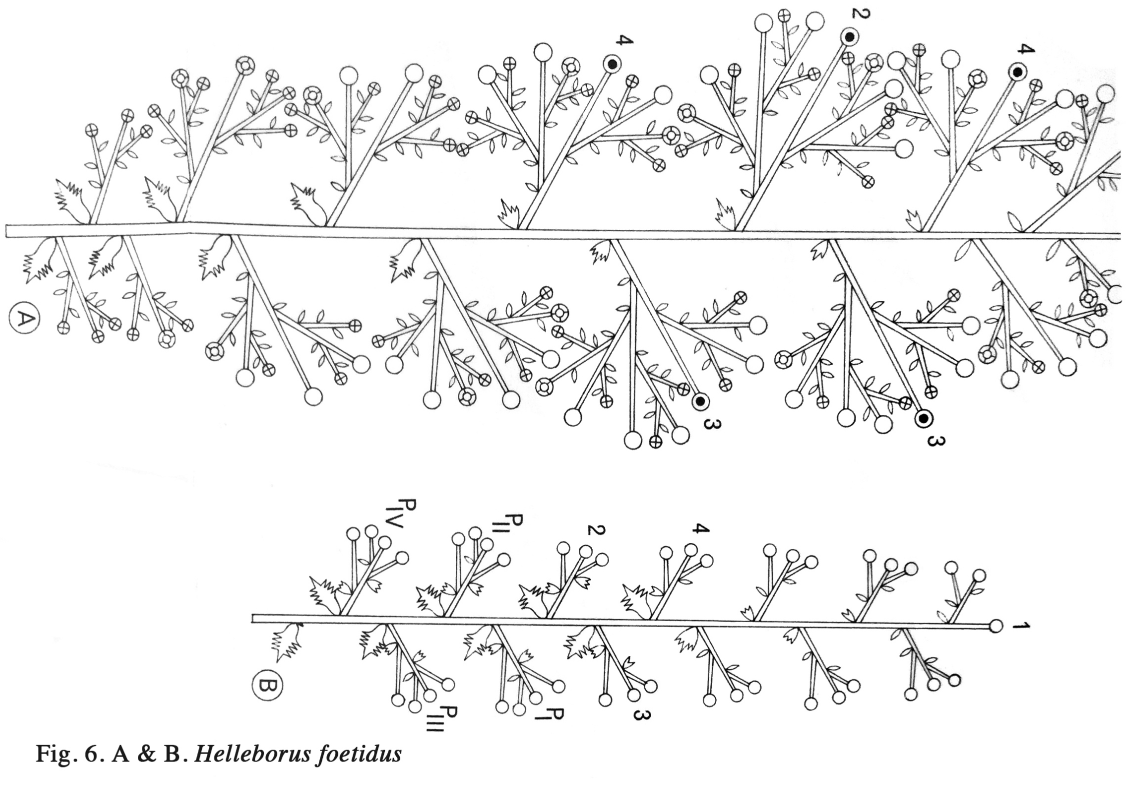

Fig. 6. A & B. *Helleborus foetidus*

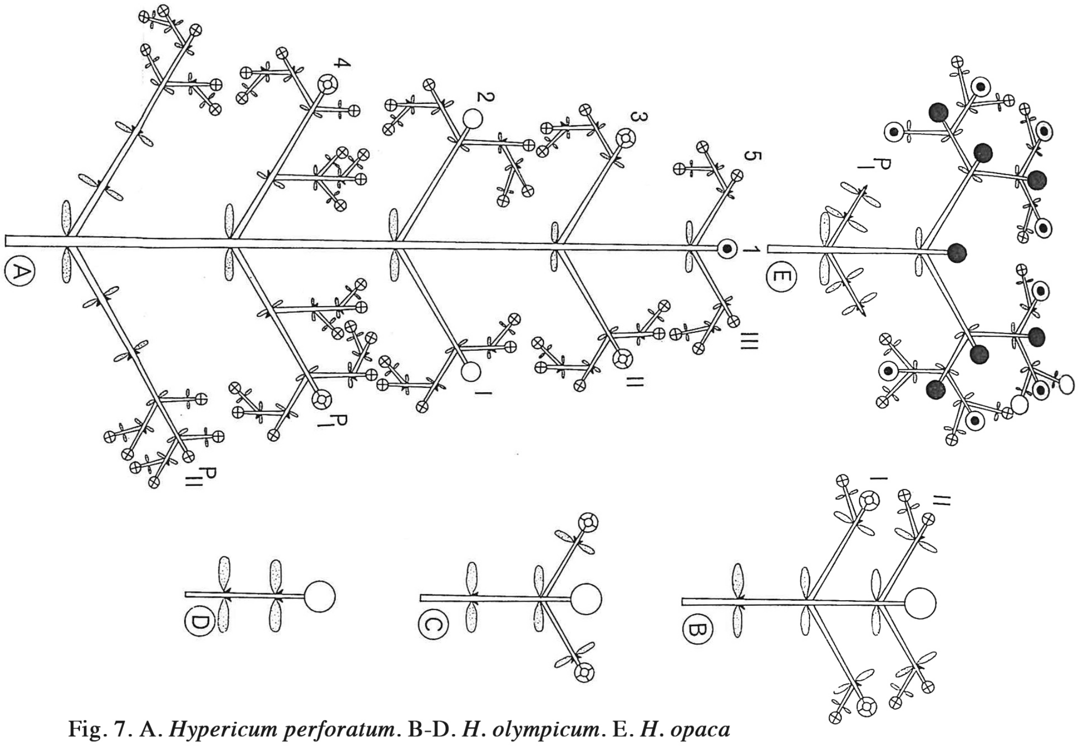

Fig. 7. A. *Hypericum perforatum*. B-D. *H. olympicum*. E. *H. opaca*

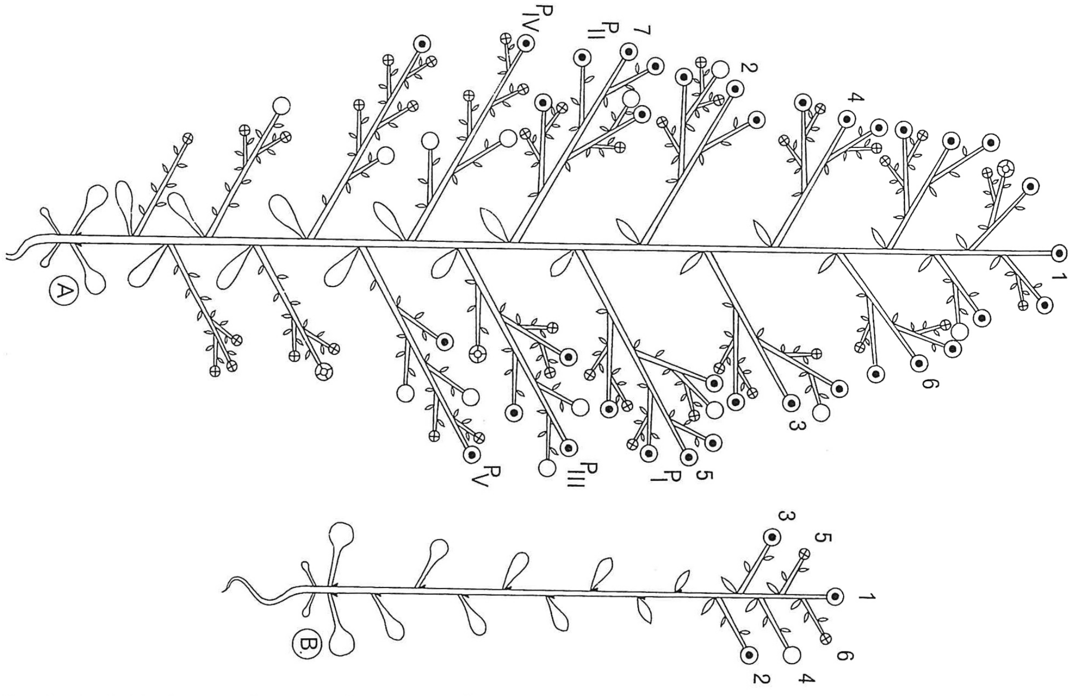

Fig. 8. A & B. *Legousia speculum-veneris*

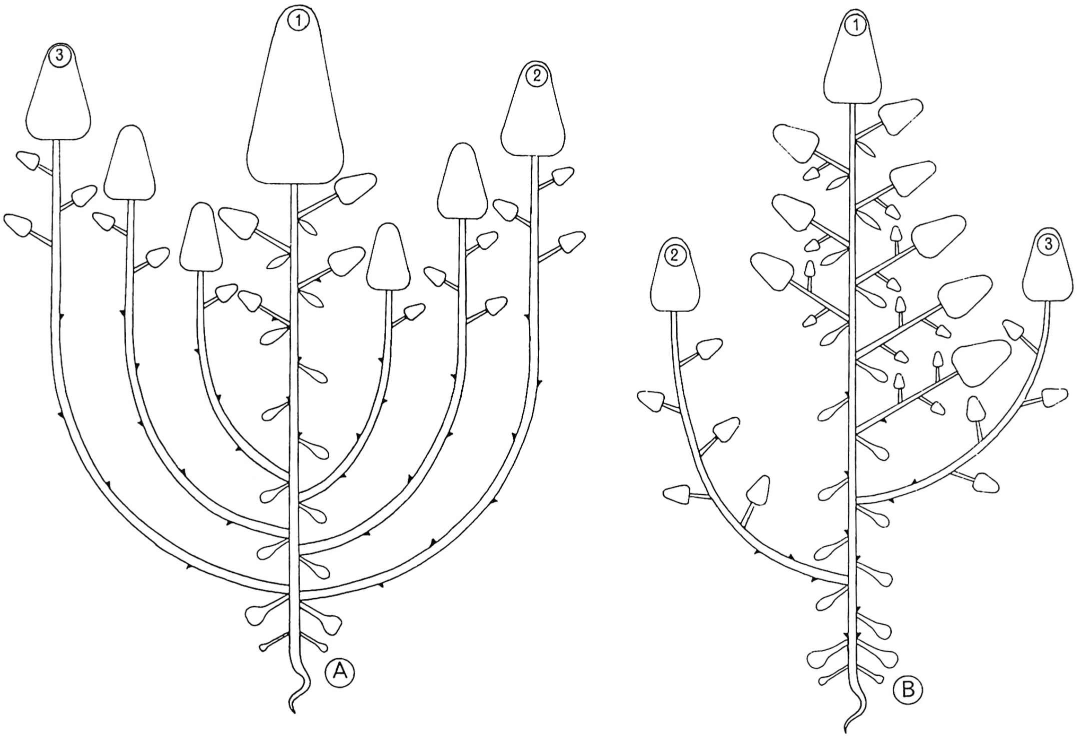

Fig. 9. A & B. *Legousia speculum-veneris*

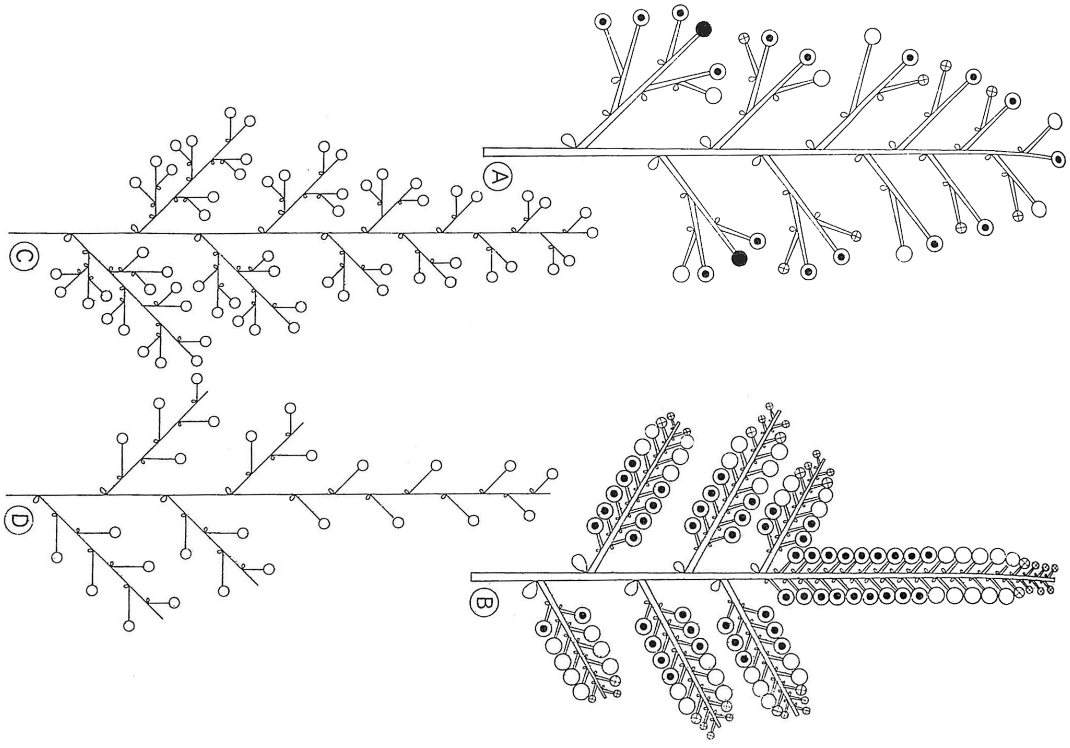

Fig. 10. A & C. *Bongardia chrysogonum*. B & D. *Leontice leontopetalum*

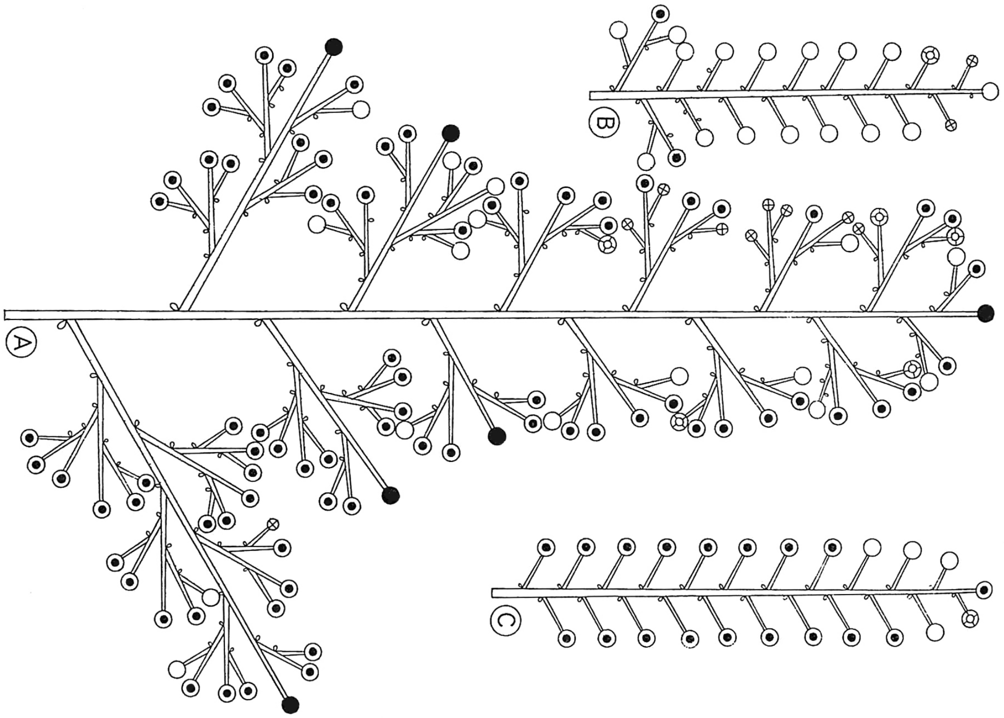

Fig. 11. A. *Epimedium pubigerum*. B. *E. perralderianum*. C. *E. pinnatum*

Fig. 12. A. *Thesium alpinum*. B & C. *T. bavarum*

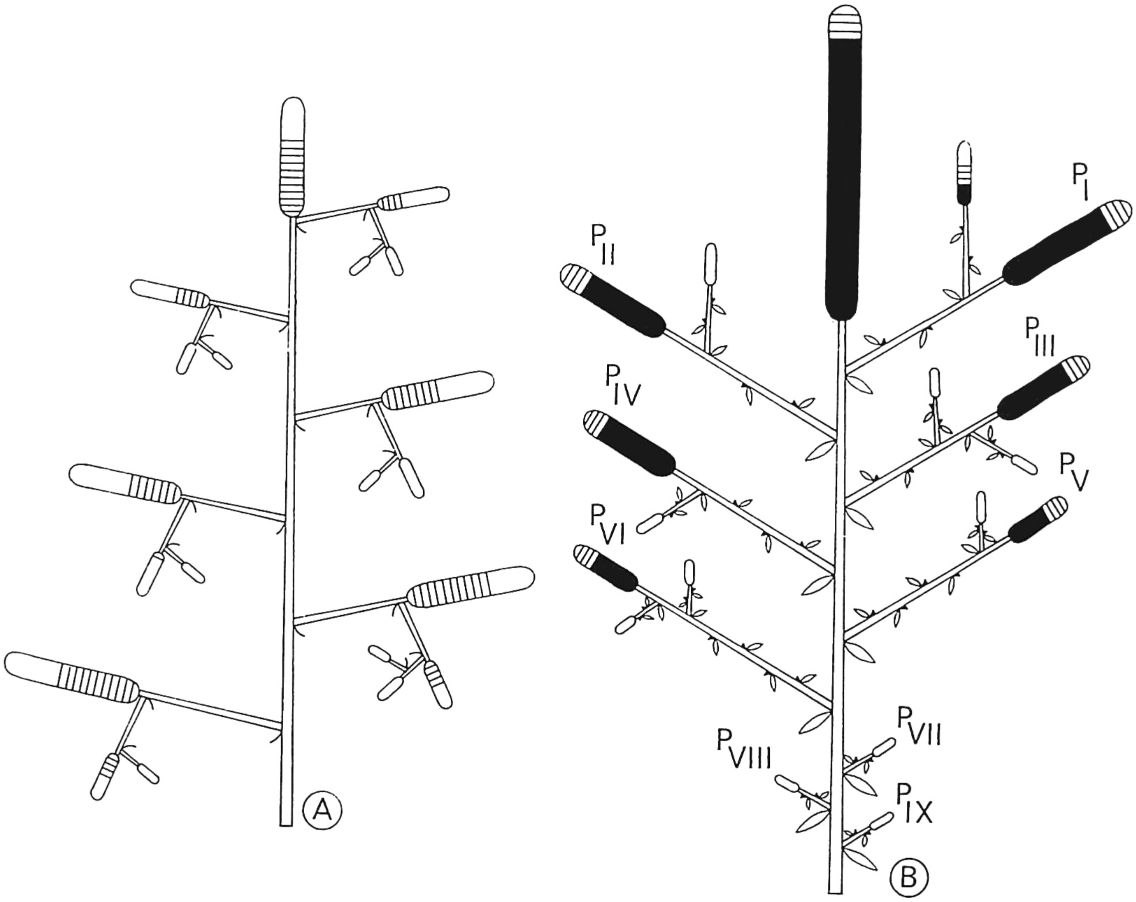

Fig. 13. A. *Crambe kralikii*. B. *Capsella bursa-pastoris*