

Fundamental features of modern inflorescence morphology

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ABSTRACT

Great diversity is found in inflorescences of angiosperms. According to Troll this is due to the variation of two types only: the polytelic and the monotelic type.

In the monotelic inflorescence, the apex of the inflorescence axis commonly ends with a terminal flower. This also applies to all the floral branches below the terminal flower. All of these branches, whether branched or not, proved to be homologous elements, and they are all referred to by the term 'paracladia' because these branches repeat the structure of the main axis of the flowering system.

Accordingly, their ramifications are called paracladia of the 2nd to nth order. Since by the presence of the paracladia the number of flowers in the flowering system is increased, they may be called 'enriching branches'. Consequently the whole area which produces the enriching branches may be designated as an 'enriching field'. In the lower part of the flowering shoot this zone is commonly preceded by a 'field of inhibition' within which the development of paracladia is inhibited more or less abruptly. The same zonation can be recognized in the individual paracladia if these are not reduced in any way. In perennials, the axillary buds at the base of the whole stem do not develop within the same season, but will give rise to the innovation shoots at the beginning of the following season. Therefore this area has to be distinguished as a 'field of innovation'.

The polytelic type of inflorescence probably has been derived repeatedly from the monotelic during the evolution of angiosperms by reduction of the terminal flower and specialization of the paracladia of the monotelic system. The distal elements are reduced to single lateral flowers or lateral cymes (partial florescences) which constitute elements of an apical system composed of lateral flowers. Instead of ending in a single flower, the floral axis thus terminates in a multi-flowered so-called polytelic 'florescence'. The lower lateral branches repeat the structure of the main stem by producing (indefinite) florescences themselves and therefore may be termed paracladia (of the polytelic system). As in monotelic inflorescences the area of paracladia — the 'enriching field' — can be preceded by a 'field of inhibition' and, in perennial plants, by a 'field of innovation'.

Though generally we may confirm that the inflorescences of all species investigated (about 20 000 from nearly all angiosperm families) proved to be variations of one of the two fundamental types, it sometimes needs morphological experience to apply Troll's system to woody plants of tropical regions. Difficulties may derive from prolepsis and syllepsis of the innovation shoots, proliferation of the inflorescence axis and, abundantly, by the deficiency of clearly marked limits between sprouts growing in different seasons. In each of such cases, however, the homologous flower-bearing-elements can be identified by comparing their positions within the whole system of ramification.

RÉSUMÉ

ASPECTS FONDAMENTAUX DE LA MORPHOLOGIE MODERNE DE L'INFLORESCENCE

Une grande diversité existe dans les inflorescences des angiospermes. Suivant Troll, on ne le doit qu'à la variation de deux types: le type polytélétique et le type monotélétique.

Dans l'inflorescence monotélétique, le sommet de l'axe de l'inflorescence porte généralement une fleur terminale. Ceci s'applique aussi à toutes les ramifications florales en dessous de la fleur terminale. Toutes ces ramifications, qu'elles soient elles-mêmes ramifiées ou non, s'avèrent être des éléments homologues et on les définit toutes par le terme de 'paracladies' parce que ces ramifications reproduisent la structure de l'axe principal de l'inflorescence.

Par conséquent, leurs ramifications sont appelées paracladies du 2^me au n^me ordre. Comme la présence des paracladies engendre un accroissement du nombre de fleurs dans l'inflorescence, on peut les appeler 'ramifications enrichissantes'. Par conséquent, toute la zone qui produit des ramifications enrichissantes peut être désignée comme 'zone d'enrichissement'. Dans la partie inférieure du rameau floral, cette zone est généralement précédée par une 'zone d'inhibition' dans laquelle le développement des paracladies est plus ou moins brusquement inhibé. La même zonation peut être reconnue dans les paracladies individuelles si celles-ci ne sont réduites d'aucune façon. Chez les plantes vivaces, les bourgeons axillaires à la base de la tige ne se développent pas au cours de la même saison, mais ils donnent naissance à des innovations au début de la saison suivante. Cette zone doit donc être distinguée comme 'zone d'innovations'.

Le type d'inflorescence polytélétique a probablement dérivé par paliers successifs du type monotélétique durant l'évolution des angiospermes par réduction de la fleur terminale et spécialisation des paracladies du système monotélétique. Les éléments distaux sont réduits à de simples fleurs latérales ou à des cymes latérales (florences partielles) qui constituent les éléments d'un système apical composé de fleurs latérales. Au lieu de se terminer par une seule fleur, l'axe floral se termine donc en une 'florences' multiflore appelée polytélétique. Les ramifications latérales inférieures reproduisent la structure de la tige principale en produisant elles-mêmes des florences (indéfinies) et on peut donc les appeler paracladies (du système polytélétique). Comme dans les inflorescences monotéliques, la zone des paracladies — 'zone d'enrichissement' — peut être précédée par une 'zone d'inhibition' et, chez les plantes vivaces, par une 'zone d'innovations'.

Bien que généralement nous pouvons confirmer que les inflorescences de toutes les espèces examinées (environ 20 000 appartenant à presque toutes les familles d'angiospermes) se sont avérées être des variations de l'un des deux types fondamentaux, il est parfois nécessaire d'avoir une certaine expérience en morphologie pour appliquer le système de Troll aux plantes ligneuses des régions tropicales. Des difficultés peuvent provenir du développement prématuré ou non des innovations, de la prolifération de l'axe de l'inflorescence et, bien souvent, par le manque de limites bien définies entre les pousses croissant en différentes saisons. Dans chacun de ces cas cependant, on peut identifier les éléments florifères homologues en comparant leurs positions au sein de l'entière du système de ramification.

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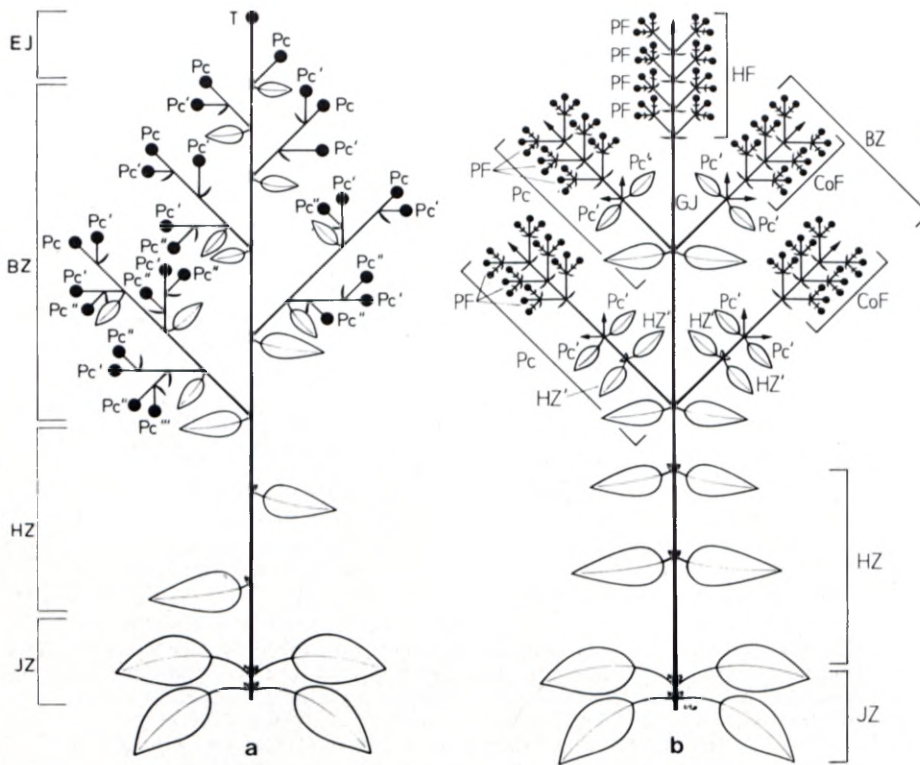


FIG. 1.—Diagrams of (a) a monotelic and (b) a polytelic inflorescence. T, terminal flower; Pc, paracladium; Pc', Pc'', paracladia of 2nd and 3rd order; HF, main-florescence ('Hauptfloreszenz'); CoF, co-florescence; PF, partial florescence; GJ, basal internode ('Grundinternodium'); EJ, final internode ('Endinternodium'); BZ, field of enrichment ('Bereicherungszone'); HZ, field of inhibition ('Hemmungszone'); JZ, field of innovation ('Innovationszone').

Correct interpretation of the morphology of inflorescences which reflects natural relationships must try to ascertain the flower-bearing elements which may legitimately be compared as identical structures. This, however, is connected with the elucidation of the structural plans of flowering plants. According to Troll (1955, 1964, 1969), the great diversity of inflorescences is due to the variation of two types only: the polytelic and the monotelic types.

In the *monotelic* inflorescence (Fig. 1a) the apex of the inflorescence axis commonly ends with a terminal flower. This also applies to all the floral branches below the terminal flower. All of these branches, whether branched or not, proved to be homologous elements, and they are all referred to by the term 'paracladia', because these branches repeat the structure of the main axis of the flowering system.* Accordingly, their ramifications are called paracladia of the 2nd to nth order. Since, by the presence of the paracladia, the number of flowers in the flowering systems is increased, they may be called 'enriching branches'. Consequently, the whole area which produces the enriching branches may be designated as an 'enriching field'. In the lower part of the flowering shoot this zone is commonly preceded by a 'field of inhibition' within which the development of paracladia is inhibited more or less abruptly. The same zonation can be recognized in the individual paracladia if these are not reduced in any way. In perennials the axillary

buds at the base of the whole stem do not develop within the same season, but will give rise to innovation shoots at the beginning of the following season. Therefore, this area has to be distinguished as a 'field of innovation'.

In the *polytelic* type of inflorescence, which is no less frequent in angiosperms, there is no terminal flower at the summit of the primary axis. The shoot apex remains indefinite after developing a smaller or greater number of lateral flowers, the last of which often do not complete their development but atrophy in the same way as the end of the axis. This apical flowering system, which is composed of lateral flowers only, is a constant feature of this type of inflorescence and is now referred to by the special term 'florescence'. Instead of ending in a single flower, as in the monotelic inflorescence, the floral axis here terminates in a multiflowered so-called polytelic florescence.

If the lateral flowers composing the florescences are provided with prophylls, these may produce secondary flowers or sympodial flowering systems from their axils. When this is so, the florescence consists of cymose 'partial florescences' as for example in the inflorescences of most Scrophulariaceae and Labiatae (Fig. 1b). Within both families, this derivation is verified by many transitional forms.

Below the florescence terminating the main axis, there may be some branches which repeat the structure of the main stem by producing florescences themselves and which are therefore called 'paracladia' again. Their florescences are termed co-florescences, in order to distinguish them from the main florescence of the main axis. The apices of the co-florescences remain indefinite like those of the main-florescence.

* The choice of the word paracladium (pl. paracladia) points to the fact, that the structure of inflorescences implies a regular repetition of equivalent elements according to a certain order. To this extent, the structure of inflorescences is a matter of symmetry and accessibility to mathematical methods (Frijters, 1976; Lindenmayer, 1977).

Within these polytelic synflorescences**, the same zonation can be observed as in monotelic flowering systems: a paracladial zone: 'enriching field' which precedes the main florescence, a 'field of inhibition' and, in perennials, a 'field of innovation'. The florescence is separated from the enriching field by a 'basal internode' ('Grundinternodium', Troll), which may be of remarkable length.

In both the monotelic and the polytelic types, the different elements may vary in many different quantitative respects according to the principle of variable proportions: in polytelic synflorescences, the main florescence may be extended, the number of its flowers may be increased in many different ways or, in other taxa, the main florescence may be reduced or even be missing altogether (truncate polytelic synflorescences). The paracladia, or any other part, may be well developed or reduced, their number may be increased, they may be missing or modified in different ways. The development of paracladia may be basitonic or acrotonic. Variations also exist in the diversity of phyllotaxis and foliation, shortening or lengthening of the internodes in different parts of the plant, different intensity and different modes of ramification and so on.

All species investigated to date (about 20 000 from nearly all angiosperm families) fit into the typological concept elaborated by Troll. Some problems, however, must still be investigated in more detail and some terminological questions must be discussed.

An essential difference between the types seems to be that in the inflorescences of the polytelic type the shoot apex of the inflorescence axis remains indeterminate. This, however, also occurs in some monotelic inflorescences in which the terminal flower aborts. In such truncate, monotelic synflorescences, however, the paracladia usually end in terminal flowers, thus revealing the monotelic character of the whole system.

The terminal flower of a monotelic system may be stunted or altogether missing, because the primordia of the uppermost paracladia 'comprise the whole of the apex, leaving no residuum to continue the growth of the axis'. This statement is made by Philipson (1947) for *Valeriana officinalis*, where the terminal flowers are missing in all paracladia of thyrsoid structure. As another example, *Linanthus liniflorus*, belonging to the Polemoniaceae, may be mentioned here. In this case, the terminal flowers are often more or less rudimentary.

In other examples, such as *Campanula rapunculoides* (Troll, 1969, p.286) or *Agrimonia eupatoria*, the development of the vigorous distal part of the inflorescence often takes a very long time and frequently remains incomplete, thus the terminal flower fails to develop on the main axis of the inflorescence. Terminal flowers, however, are produced in the paracladia, which are less vigorous. Examples like these command our attention, when we consider the aspect of inflorescence-evolution.

In many lianas and rosette geophytes, the growth of the main axis is indefinite. Therefore the main axis, though it may produce lateral flower bearing branches, never ends in a terminal flower. This may be demonstrated here by two closely related Rubiaceae, *Sabicea laxothyrsos* and *Bertiera le-touzeyi*. The latter is a liana and, unlike *Sabicea*, it does not produce a terminal flower. Rosette geophytes with indefinite main axes are represented by many species of *Plantago*, by *Pleio craterium plantaginifolium* (Rubiaceae) and the species of the genus *Phyllactis* (Valerianaceae). Here, the apex of the rosette changes periodically from the formation of absolutely sterile zones to the formation of fertile regions, in which thyrsoid 'partial inflorescences' originate from the axils of the rosette leaves. Later we shall return to this mode of growth commonly called 'proliferation'.

Comparing the two types of inflorescences, we conclude that the polytelic type is more highly evolved than the monotelic. There is much evidence that the polytelic type is derived from the monotelic by two steps of evolution:

1. reduction of the terminal flower and
2. specialization of the lateral branches, some of which are reduced to single lateral flowers or lateral cymes which constitute elements of the florescences, whereas the other branches are differentiated as paracladia (of the polytelic type!) which themselves form florescences.

This evolution has taken place in different taxa of the angiosperms, sometimes even in several groups of the same family, for example Rubiaceae (Weberling, 1977). Though both steps — reduction of the terminal flower and specialization of the lateral branches — may occur independently from each other, the pathway of evolution, usually indicated by transitional forms, is that of 'homogenization,' mostly combined with 'racemization' (Maresquelle, 1970; Sell, 1969, 1976) and then, 'truncation' or the reduction of the terminal flower.

The process of *homogenization* produces an increasing uniformity of the lateral branches within the distal parts of the flowering system which constitute the florescences in the polytelic synflorescences. Whereas, in monotelic synflorescences, the terminal flower usually blooms before the neighbouring laterals, now the sequence of flowering within the distal flower bearing parts is reversed. Finally, the efflorescence within the presumptive florescences follows the way of the initiation of the flowers, advancing from base to apex. The result of this process of *racemization* is that the last flowers often do not develop and at least the terminal flower is reduced. This is referred to as 'truncation' (Sell, 1969, 1976; see also Weberling, 1961, 1965; Troll & Weberling, 1966).

Following this argument, one can assume that the starting point of inflorescence-evolution must have been the (monotelic) panicle. By studying the primitive families of the Magnoliales (and Dilleniaceae), however, one finds only poor evidence for this assumption. The inflorescences of most taxa within these families are relatively highly derived by specialization into longshoots and flower bearing

** synflorescence: a system of florescences or a system of a terminal flower and monotelic paracladia.

shortshoots or by proliferation. The polytelic type of inflorescence is not rare in these families. Therefore, it seems to be more advisable to accept the panicle as the 'central type' only, from which all the other forms of inflorescences can be derived. This does not necessarily imply a phylogenetical interpretation. Some previous authors, as Parkin (1914, p.559), pointed out that 'it seems highly probable that flowers were originally borne on the plant singly, each terminal to a leafy shoot.' We find such flowers in *Liriodendron*, many *Magnolia*, *Calycanthus* and others. These could as well represent a state close to the starting point of inflorescence-evolution (though we have to pay attention to the fact, that single flowers also 'may have arisen through the reduction of an inflorescence').

Pilger (1922, p.21) said: 'Die primitive Form des Blütenstandes der Angiospermen ist die 'beblätterte' Rispe; erst die Trennung von Laub- und Blütenzweigen resp. von solchen Jahresabschnitten führt zu einer schärferen Begrenzung der Blütenstände'. Translated, this means: The most primitive form of the inflorescence in angiosperms is the leafy panicle; only the separation of leafy and flowering branches respectively, of such seasonal shoots, leads to a more distinct delimitation of inflorescences.

This statement refers especially to woody plants. We must emphasize, however, that the zonation of a flowering system which has been described here for the inflorescences of both types applies equally to herbaceous and to woody plants. Nevertheless, in woody plants of tropical regions the delimitation of an inflorescence and consequently the identification of homologous elements may be difficult. This is largely due to the fact, that, in contrast to woody plants of the temperate and subtropical zones which develop distinct renewal shoots from the axils of the leaves below the terminal inflorescence, the synchronous (sylleptic) development and flowering of branches met with in many tropical trees and shrubs, sometimes leaves hardly any indication permitting determination of the position of a flower bearing system equivalent to that of other taxa.

The development of seasonal shoots, so characteristic for woody plants of the temperate zones, is often combined with a specialization between vegetative and flower producing shoots. This division of labour can also be observed in tropical woody plants and in some herbaceous plants (*Tussilago*, *Petasites*). In woody plants we often find a differentiation of the shoot system into long shoots and short shoots. Here, the production of flowers is limited to the short shoots situated in the axils of the long shoots, whereas the long shoots by their 'proliferating' growth contribute to the expansion of the whole branching system. In the temperate regions particularly, but not limited to them, the short shoots commonly develop and flower in the year that follows the development of the long shoot. Therefore, except in evergreen plants, at flowering time of the whole branch, the long shoot has already lost its leaves.

The problem of delimitation of comparable flower bearing parts may be explained by two examples, *Weigela* and *Symphoricarpos*. At first

glance, a flowering branch of *Weigela* (Fig. 2a) might look like a polytelic synflorescence with an apical main florescence and lateral paracladia ending in co-florescences. We must, however, note that the foliation of the flower bearing branches as well as of the apical flowering system is preceded by a series of bud scales. On the other hand, the main branch of the whole flowering system has already lost its leaves. Our interpretation is, that we have to deal here with flower-bearing short shoots situated in terminal and lateral positions on a last year's long shoot. Each short shoot has to be regarded as a flowering system by itself. Results of comparative studies suggest that their inflorescences can be interpreted as much reduced, truncate, monotelic synflorescences with originally thyrsoid ramification.

In contrast, on a flowering branch of *Symphoricarpos rivularis* (Fig. 2b) we observe a leafy foliation throughout the whole branching system with the exception of the distal parts. Since all the flower-bearing branches are indefinite, the whole flowering system could be interpreted as a polytelic synflorescence with spike-like florescences (representing reduced thyrses). The lateral flowering systems, however, though blooming synchronously with the terminal inflorescence, are provided with one or several pairs of scale-like leaves at their bases, which actually function as bud scales for a short time. Therefore, we may assume that the lateral flower bearing shoots are short shoots which develop and flower without a preceding period of rest. This would not permit regarding them as paracladia of the same flowering system. The scale-like leaves, however, though temporarily functioning as bud scales, may also bear flowers in their axils. All this seems to indicate that we have to do with intermediate forms between a sylleptic branching system flowering more or less synchronously, and the differentiation into long shoots and (cataleptic) short shoots. Such transitional forms were found throughout the whole genus *Symphoricarpos*.

With regard to the typology of inflorescences which was explained before, we may confirm that the species of *Symphoricarpos* represent a state of transition between the monotelic and the polytelic type. These statements may be unsatisfactory for people who expect a definite assignment of all forms of inflorescences. We need to remember that the aim of comparative morphology is to elucidate relationships of forms and not to serve as pigeon-holes in which each organic form has its definite place.

In this sense, the application of the typological concept of Troll has already proved to be useful for the elucidation of morphological relationships and, hence, for the elucidation of systematic problems. This also applies to the inflorescences of the Caprifoliaceae which, at first, seem to be fundamentally different (Troll & Weberling, 1966).

Some confusion in the evaluation of flowering systems may also result from the proliferation of certain inflorescences. This peculiarity has been mentioned already in connection with the fact that the inflorescence axis may remain indefinite.

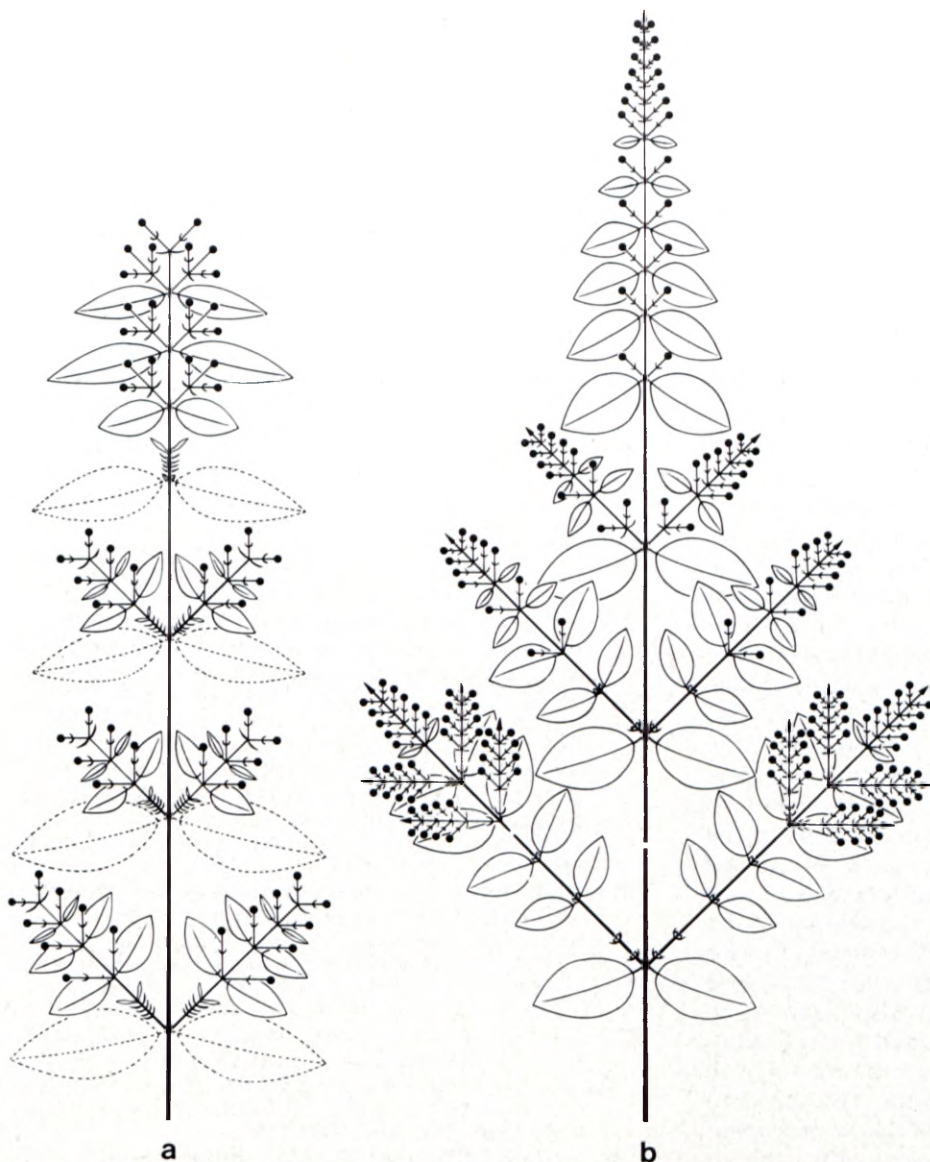


FIG. 2.—Diagrams of flowering branches of (a) *Weigela floribunda* (Sieb. & Zucc.) K. Koch and (b) *Symphoricarpos rivularis* Suksd.

Certainly, it does not seem advisable to refer the term 'proliferation' to the unlimited growth of any shoot bearing leafy branches which may, after further ramifications, finally produce flower-bearing elements. In the sense used by Troll (1959, p.116), it means a return of the inflorescence apex to vegetative growth. In *polytelic synflorescences* this may happen early, before the initiation of the main florescence: proliferation of the paracladial zone ('Frühprolifikation', Troll). As an example, *Lysimachia thyrsoiflora*, may be mentioned here. Proliferation may also take place later when the apex of the main florescence reverts to vegetative growth: proliferation of the florescence ('Spätprolifikation', Troll). This applies, for instance, to *L. punctata* and *L. nummularia*, to *Eucomis punctata* and other monocotyledons. Proliferation may also occur in monotelic synflorescences (some species of *Campanula* and some Boraginaceae and Myrtaceae).

Parkin (1914, p.556) regarded proliferating inflorescences as a separate type of inflorescences, which he called *intercalary inflorescences*, because 'the flower-bearing part of the axis is . . . intercalated between two foliage-bearing portions'.

We must emphasize, however, that there are many taxa, *Veronica* and *Lysimachia* among others, which comprise both species with terminal bracteose and terminal foliose inflorescences and species with proliferating leafy inflorescences. Often these forms are connected by a continuous series of intermediate forms. At least, in these cases, we must regard these proliferating inflorescences as highly derived from terminal ones. This, in my opinion, also applies to woody plants.

Another problem is that of perennial inflorescences which we find, for example, in *Mitrophyllum grande* (Mesembryanthemaceae). The species, indeed the whole genus, is characterized by its heterophyllous, dimorphic or rather trimorphic foliation. Within each season the vegetative shoot develops only two pairs of leaves. The leaves of the primary pair are spreading, slightly flattened and have a short gamophyllous base. The leaves of the second pair, the 'mitre-leaves', are connate for the greater part of their length forming a double-pointed tube. The inflorescences, which are developed after many years of vegetative growth, are very simple. They only develop two prolonged internodes with

one pair of bracts and end in a terminal flower. From the axils of the bracts secondary flowers may arise. They are provided with one pair of bracts. Their anthesis, however, is delayed until the next season. The same is repeated by the paracladia of the next order, which arise from the bracts of the preceding paracladia. They flower one after another with an interval of one season. Therefore, following Troll's interpretation, we have here a plurannual inflorescence. Troll regards this peculiarity as the antithesis of the successional innovation of certain plants (species of *Juncus*, *Asparagus* and *Canna indica*), in which several renewal shoots develop in a sympodial order within the same season.

According to Poppendieck (1976), in his monograph of the genus *Mitrophyllum*, the inflorescence is uniflorous. In his opinion, the secondary flowers which develop from the axils of the bracts are renewal shoots. He reports that species like *Mitrophyllum roseum*, the consecutive flowers are separated by vegetative parts with mitre-leaves (functioning as 'resting leaves', 'Ruheblattpaar'). In other species seasonal vegetative parts may be intercalated within the flower-bearing system. The question arises, however, as to whether the interpretation of these parts as renewal shoots is correct, considering the fact that the innovation of the vegetative parts proceeds from the axils of the basal, flattened leaves and consists of shoots producing flattened leaves and mitre-leaves in turn during a longer period. However, the solution of the question remains controversial. Plurannual inflorescences have not only been reported for Aizoaceae (Troll & Weberling, 1981), but also from some palms (Müller-Doblies, unpubl.) and some Chenopodiaceae (Urmi-König, unpubl.) and probably will be reported from other families too. We need to study them in more detail. Though the controversies mentioned here and other questions still open to discussion do not principally affect the typological concept elaborated by Troll, there still remains much research to be done.

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