

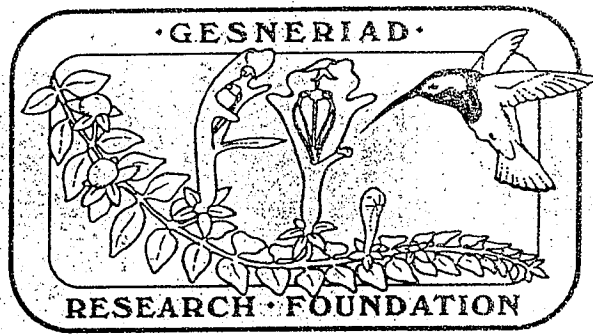
**Developmental aspects of the pair-flowered cyme of  
Gesneriaceae.**

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**Cremosperma, Development, Epithema, Inflorescence, Monophyllaea,  
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## Developmental Aspects of the Pair-flowered Cyme of Gesneriaceae

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**ABSTRACT:** Developmental aspects of the pair-flowered cyme of Gesneriaceae are summarized. As emerges from a study of the cyme development of *Sinningia bulbosa*, the front-flowers are true axillary flowers. The  $\gamma$ -bracteoles are initiated later than the prophylls and the same applies to their axillary structures. Because the primordia of the front-flowers do not produce prophylls and proceed directly to the formation of the floral organs, they are able to develop more rapidly than the lateral flowers and open earlier than these; the acropetal sequence of initiation is thus blurred and appears as a basipetal one (which pattern would contradict a derivation of the pair-flowered cyme from a paniculate branching system). By ontogenetic abbreviation the development of many-flowered cymes (apparently always in the form of ebracteolate cincinni) may switch to a pseudo-monopodial pattern. Examples from paleo- and neotropical Gesneriaceae are cited. Possible developmental mechanisms of bracteole displacement are briefly discussed.

**KEY WORDS:** Gesneriaceae, *Cremosperma*, *Epithema*, *Monophyllaea*, *Saintpaulia*, *Sinningia*, *Streptocarpus*, *Tylopsacas*: inflorescence, development.

Though the occurrence of paired flowers in one or another taxon of Gesneriaceae had been noticed long ago, it only recently became obvious that the inflorescence system of that family is of a very uniform architecture, with the 'pair-flowered cyme' (Fig. 1) being its basic structural component.<sup>1</sup> In this unusual cyme type each cyme unit appears to terminate in a flower pair. The pair is composed of the true terminal flower of the cyme unit and a bractless, median-abaxial flower ('front-flower') showing the same orientation as the terminal flower.

It was suggested by the present author that the front-flower is not an adventitious or accessory flower, but a regular axillary flower, the subtending bract of which is normally suppressed or aborted. In fact, there is a number of taxa in which the front-flowers are associated with bract-like structures, either irregularly or regularly in all cyme units. By strong internode contraction, the front-flower appears to arise  $\pm$  at the same level as the lateral cyme units.

Based on the facts that the front-flower is (a) a regular (and only secondarily bractless) and (b) consistent element of the gesneriaceous cyme, the interpretation was pro-

posed that the front-flowers are r e m n a n t flowers of an originally more complex branching system. The pair-flowered cyme apparently represents an intermediate stage in a reduction series from a paniculate branching system to an ordinary cyme (WEBER 1973).

Due to extensive variation in flower number, in the length of the peduncle, cyme axes and the pedicels, variation in size, shape and coloration of the bracteoles, displacement or complete reduction of bracteoles, etc., a considerable array of forms of the pair-flowered cyme can be found in the family (WEBER 1982). By irregular or (very rarely) regular loss of the front-flowers, cymes of the conventional type did also originate in the family (WEBER 1977, 1978).

In the present paper facts that are noteworthy from a developmental point of view are described and reviewed:

a) Axillary initiation and early development of the front-flower

Evidence that the front-flower is an axillary flower (the bracteole of which is normally lacking) is so far based essentially on the observation that in certain cases a bract-like structure is associated with the front-flower. Developmental evidence appears desirable to confirm the truly axillary origin of the front-flower.

b) Temporal correlation of initiation and development of the front-flower as compared to the lateral flowers

In a panicle or a system derived from a panicle, one would expect that flowers below the terminal flower develop and open in an acropetal succession. However, in pair-flowered cymes the front-flowers, though belonging to a node a b o v e the pro-

1. Early notice of the fruit/flower pairing is reflected in the generic name *Didymocarpus* Wall. and in the sectional name *Didymanthus* C. B. Clarke. HAYEK (1926), FRITSCH (1927, 1931), GOEBEL (1931), IRMSCHER (1959/60), and TROLL (1964) provided more concrete data. GOEBEL (1931) was the first to refer also to the ontogeny. With regards to taxonomy, HILLIARD & BURTT (1971:34) were the first to recognize that "this type of cyme occurs almost throughout the Old World Gesneriaceae." The universal occurrence in the family was pointed out by WEBER (1973, 1982) and WIEHLER (1983). The pair-flowered cyme thus can be considered as a constituent character of the family Gesneriaceae. For the (very few) exceptions see WEBER (1977, 1978).

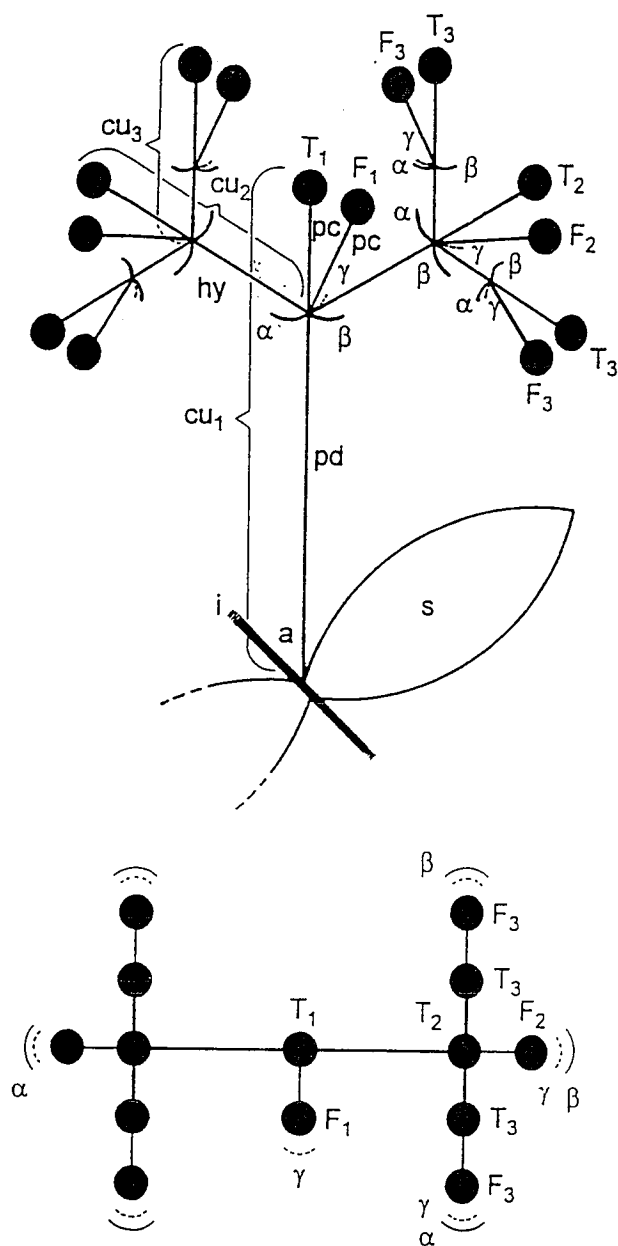


Fig. 1. Diagrams of a pair-flowered cyme (here, a compound dichasium with 7 flower pairs): i: main inflorescence axis, s: subtending leaf or bract of cyme, a: leaf axil, pd: peduncle (= hypopodium of primary cyme unit), pc: pedicel,  $T_1$ - $T_3$ : terminal flowers (of respective cyme units),  $F_1$ - $F_3$ : front-flowers,  $\gamma$ :  $\gamma$ -bracteole,  $\alpha$ ,  $\beta$ : prophylls (bracteoles),  $cu_1$ - $cu_3$ : cyme units.

phyll node, open before the lateral flowers (= terminal flowers of the lateral cyme units). It is, therefore, tempting to conclude that the front-flower is initiated earlier than the lateral flowers. This indeed would be a severe obstacle for the derivation of the pair-flowered cyme from a paniculate branching system. It was already pointed out in WEBER (1982) that precocious development need not reflect precocious initiation. This item is evidenced here in more detail.

c) Progression of the pair-flowered cyme from a cymose to a pseudo-racemose (pseudo-monopodial) pattern of development

Some taxa of Gesneriaceae exhibit a similar inflorescence structure and development pattern as found, for instance, in the Boraginaceae (in which family the term 'boragoid' has been used for the peculiar type of inflorescence).<sup>2</sup> This phenomenon is illustrated and examples are quoted both from paleo- and neotropical Gesneriaceae.

d) Displacement of bracteoles within the cyme

Though no concrete developmental information is presently available, the phenomenon of bracteole displacement is briefly discussed in its developmental aspects.

### Material & Methods

The plants investigated were grown in greenhouses of the Botanical Garden of the University of Vienna (HBV). Young shoots with inflorescences were fixed in 70% ethanol and dissected under a stereo-microscope. The preparations were critical-point-dried, mounted onto aluminum stubs, coated with gold, and viewed and photographed in a JEOL-T300 scanning electron microscope. Clearings of plant parts were produced according to the technique described by RITTERBUSCH (1974). Microtome sections were prepared by the conventional paraffin technique.

### Cyme development in *Sinningia bulbosa*, *S. lineata* and *Saintpaulia ionantha*

#### *Sinningia bulbosa* (Ker-Gawler) Wiehler<sup>3</sup>

This species, belonging to the neotropical subfamily Gesnerioideae (tribe Gloxinieae) is one of the few taxa of Gesneriaceae, in which all units of the cyme (in this species a compound dichasium) have front-flowers regularly associated with bracts or, to say it more cautiously, with bract-like structures (referred to as  $\gamma$ -bracteoles in this study).

Figure 2a shows a cyme unit in a very early stage. Only the primordia of the lateral bracts (prophylls) have been produced, both placed strictly opposite and thus re-

2. Inflorescences that have to be classified as cymes from a comparative point of view, but exhibit a kind of monopodial development, are known in quite a number of families (Boraginaceae, Solanaceae, Apocynaceae, Asclepiadaceae, Hydrocharitaceae, Droseraceae, etc.). For an extensive discussion, with special emphasis on Solanaceae, see HUBER (1980).

3. Synonyms: *Sinningia macrorrhiza* (Dumort.) Wiehler, *Reichsteineria macrorrhiza* (Dumort.) O. Kuntze. The latter was used in WEBER (1973).

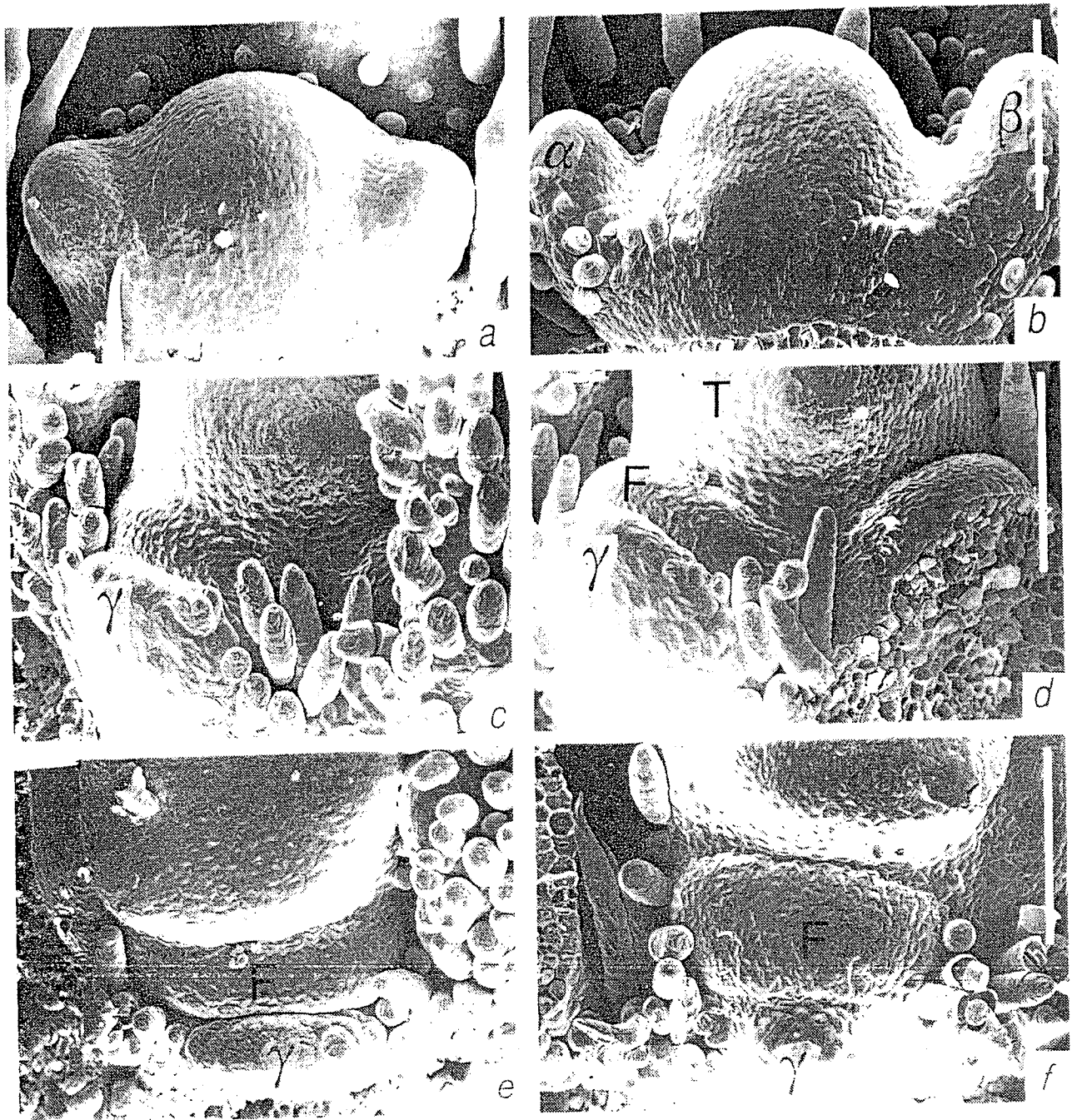


Fig. 2. *Simningia bulbosa*: development of a cyme unit.  $\alpha$ ,  $\beta$ : prophylls,  $\gamma$ :  $\gamma$ -bracteole, = subtending bract of front-flower. T, F: primordia of terminal and front-flower. Bar: 100  $\mu$ m

reflecting the decussate phyllotaxis of the plant. The apical meristem does not exhibit any differentiation yet. In the following stage (Fig. 2b), a bulge becomes visible at the abaxial side. This is the primordium of the  $\gamma$ -bracteole. It arises distinctly above the position of the prophylls. The sequence of initiation and the position thus demonstrate clearly that the  $\gamma$ -bracteole belongs to a node above the prophylls (and is not part of a trimerous prophyll whorl) and that there is an acropetal sequence of bract

initiation. The median bulge then develops into a low bracteole-like structure. Then a swelling becomes visible in its axil (Fig. 2c). The swelling develops into a transverse bulge, the shape and extension of which at first do not resemble a flower primordium. However, as the same photo shows, this also holds true for the axillary meristem of the prophylls (Fig. 2d,  $\gamma$ -prophyll removed). The photo also documents that the axillary bulge of the  $\gamma$ -bracteole is located slightly above the bulge of the pro-

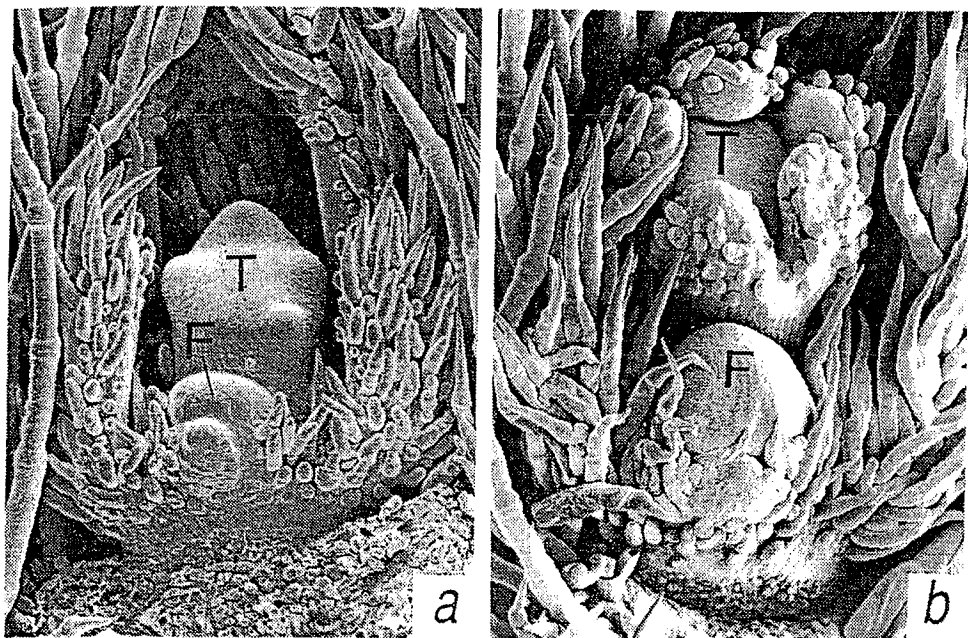
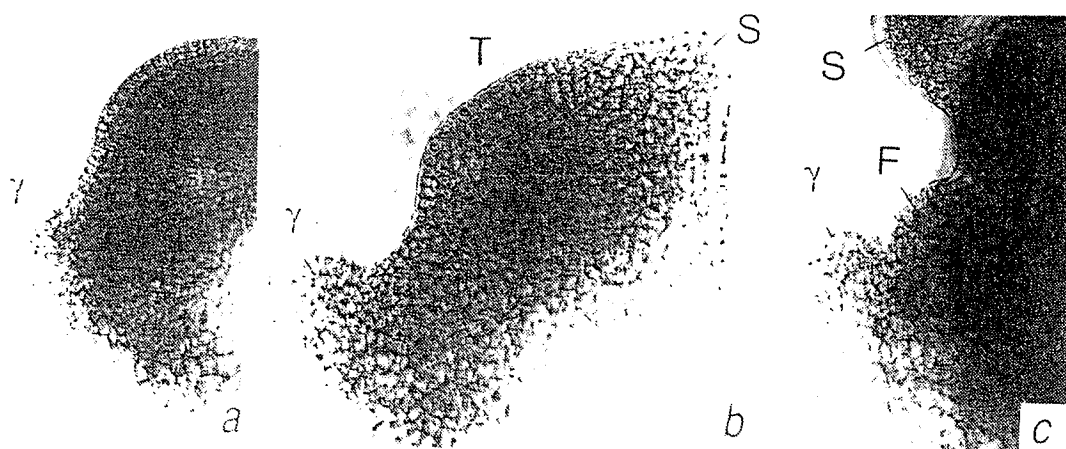


Fig. 3. *Sinningia bulbosa*: development of front-flower and lateral cyme unit. Abbreviations as in Fig. 1. Bar: 100  $\mu$ m.



Fig. 4. *Sinningia bulbosa*: development of  $\gamma$ -bracteole and axillary primordium of front-flower (longitudinal sections, clearings): S: sepal primordium.



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phylls. The latter is also slightly larger (developing from farther below), thus indicating that it was the first to have been developed.

The bulge of the  $\gamma$ -bracteole then becomes broader (Fig. 2e) and is transformed into a globose floral primordium from its original box-shaped form (Fig. 2f; 3a,b).

At the time the primordium of the front-flower flattens (start of sepal initiation), the axillary structure of the prophyll produces the bracteole primordia. Its apex, however, is still undifferentiated.

At this point the front-flower starts to overtake the lateral flower in development. While the axillary product of the lateral bracteoles is occupied with the formation of the prophylls, the primordium of the front-flower proceeds directly to the formation of the first floral organs (sepals). The front-flower, therefore, shows an accelerated development as compared to the lateral flowers and opens earlier than these.

Figure 4 shows the crucial developmental stages in clearings (longitudinal sections): (a) emergence of the  $\gamma$ -bracteole, (b) upgrowth of the  $\gamma$ -bracteole and formation

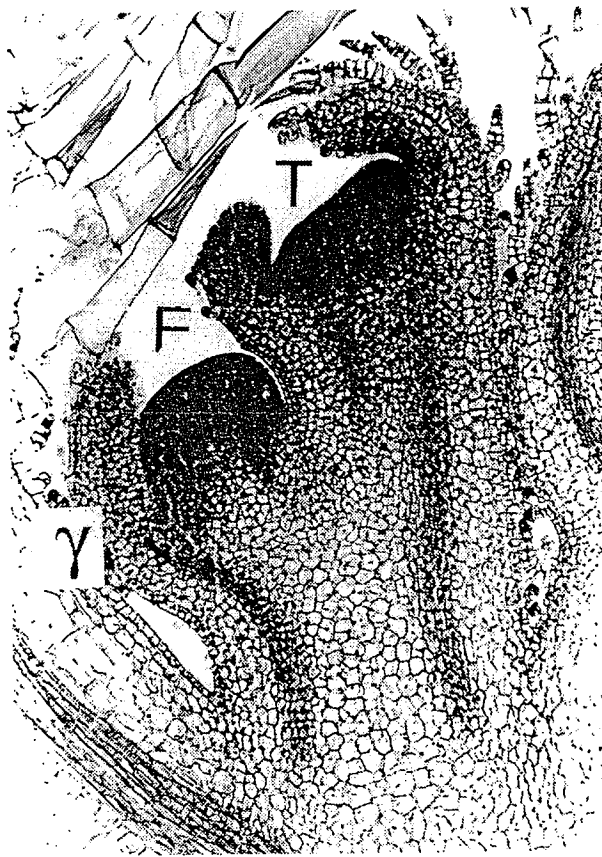


Fig. 5. *Sinningia bulbosa*: longitudinal section through primary cyme unit.

of a proper 'axil', (c) emergence of a meristematic bulge in the axil.

The subsequent stage, the growth of the axillary bulge into a floral primordium, is represented in the microtome section of Fig. 5. This section documents that in the  $\gamma$ -bracteole a vascular strand is differentiated which is connected with the vascular ring in the hypopodium of the cyme unit. This is another indication that the  $\gamma$ -bracteole is a true bract and not an insignificant bract-like emergence that is fortuitously associated with the front-flower.

#### *Sinningia lineata* (Hjelmqvist) Chautems

This species was chosen for comparison because in its cymes the front-flowers are not subtended by a bracteole. Also the ordinary bracteoles (prophylls) are small and show various stages of reduction. The cymes branch in the common manner of double-cincinni. Examination was by SEM and clearings, the latter giving better results, because indistinct outgrowths ( $\gamma$ -bracteoles) can be clearly observed in longitudinal sections (Fig. 6).

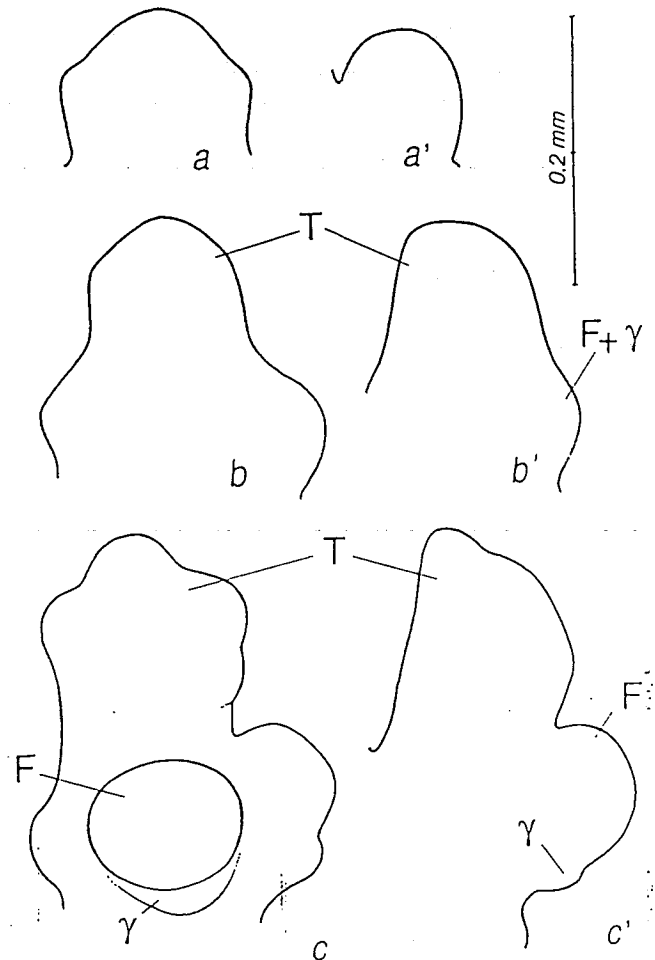


Fig. 6. *Sinningia lineata*: development of a cyme unit (drawn from clearings; each stage is shown in front-view and in longitudinal section).



The young cyme units resemble those of *S. bulbosa*, but there is a marked difference: in place of the prophylls there arise large, dome-shaped bulges. The bulges (in Fig. 6b only the right one, due to the monochasial branching in cyme units of higher order) differentiate secondarily into two structures (Fig. 6c): the primordium of the consecutive cyme unit and its subtending bract ( $\gamma$ -prophyll). Thus a change in the developmental chronology can be observed: prophylls and their axillary structures do not develop successively, but emerge together as a unitary 'common primordium.' The same holds true for the front-flower and its subtending bract: distinctly after the emergence of the lateral primordium a low dome-shaped bulge is produced on the abaxial side. It does not simply grow into the primordium of the front-flower, but differentiates into a floral primordium and a low bulge below that. The latter obviously is a vestige of the  $\gamma$ -bracteole subtending the front-flower.

As was said above, the  $\gamma$ -bracteole is no longer recognizable in the mature inflorescence. Reduction is not only in size, but is also expressed in the delayed development, differentiating secondarily from a common primordium.

#### *Saintpaulia ionantha* Wendl.

GOEBEL (1931) was the first to study the ontogeny of the cyme in this species. He did not observe a bract subtending the front-flower and interpreted the latter as a primarily bractless *Vorderblüte*.

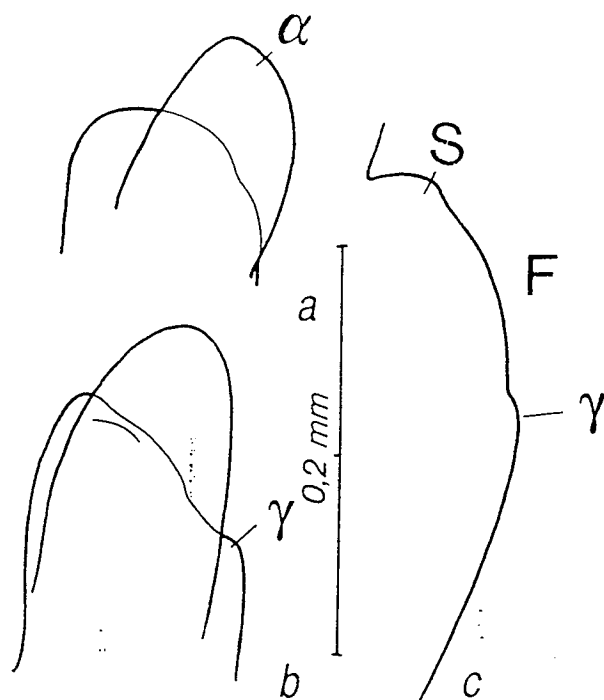


Fig. 7. *Saintpaulia ionantha*: development of a cyme unit (longitudinal sections, clearings).

The early development is similar to *Sinningia*. Longitudinal sections (clearings, Fig. 7) show that a wide 'axil' is formed between the primordium of the terminal flower and a low abaxial swelling. The primordium of the front-flower arises in this 'axil' - not as a narrow bulge, but as a flat dome that produces the posterior sepals very early. There is hardly any other option than to interpret the abaxial swelling as the vestige of a  $\gamma$ -bracteole.

#### Conclusions

As *Sinningia bulbosa* clearly shows, the sequence of initiation: (1) prophylls, (2)  $\gamma$ -bracteole, (3) lateral cyme units, (4) front-flower, is a c r o p e t a l, as should be expected in a paniculate system. Because the front-flower does not form prophylls, it directly proceeds to the development of floral organs and thus is able to overtake the lateral flowers in development. *Sinningia lineata* and *Saintpaulia ionantha* mark the step in which the  $\gamma$ -bracteole is reduced to a tiny rudiment (not visible in the mature inflorescence). This is paralleled by delayed initiation.

#### Pair-flowered cymes with pseudo-racemose development

##### *Monophyllaea* R. Brown and *Epithema* Blume

GOEBEL (1931) was first to notice a 'monopodial' development of a gesneriaceous inflorescence (*Monophyllaea horsfieldii* R. Brown, Fig. 11a, page 25). Based on the observation that the flowers are grouped in pairs, GOEBEL recognized the similarity with the cyme of *Saintpaulia* and interpreted the inflorescence of *Monophyllaea* as a cincinnus with 'monopodial' development. GOEBEL's observations were confirmed by the present author (WEBER 1976a). In Fig. 8 the apex of the cyme of *M. horsfieldii* is shown. Indeed, there is a large 'apical' meristem present - much larger than the primordium of a single consecutive cyme unit could ever be. This meristem seems continuously to produce meristem portions in an alternate sequence which then differentiate into flower pairs.

In the genus *Monophyllaea* only part of the more than thirty species (BURTT 1978) are expected to show a pseudo-monopodial inflorescence development. These are the species with  $\pm$  densely crowded flowers and a prominent, continuous cyme axis (*M. horsfieldii*, *M. glauca* C. B. Clarke, *M. tetrasepala* B. L. Burtt, *M. merrilliana* Kraenzlin, *M. insignis* B. L. Burtt, etc.). In the other species (e.g., *M. hirticalyx* Franch., *M. longipes* Kraenzlin, *M. elongata* B. L. Burtt, etc.), the cyme has a thin,  $\pm$  flexuous axis with loosely arranged flower pairs. A study of *M. hirticalyx* shows that the youngest flower pair is apically followed by a relatively small meristematic body (Fig. 9), which apparently corresponds to the primordium of a single consecutive cyme unit. The chronology of unit formation and



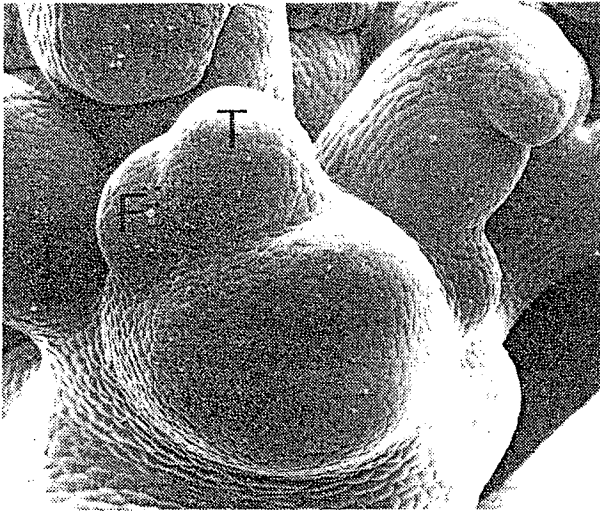


Fig. 8. *Monophyllaea horsfieldii*: apex of pair-flowered cyme.

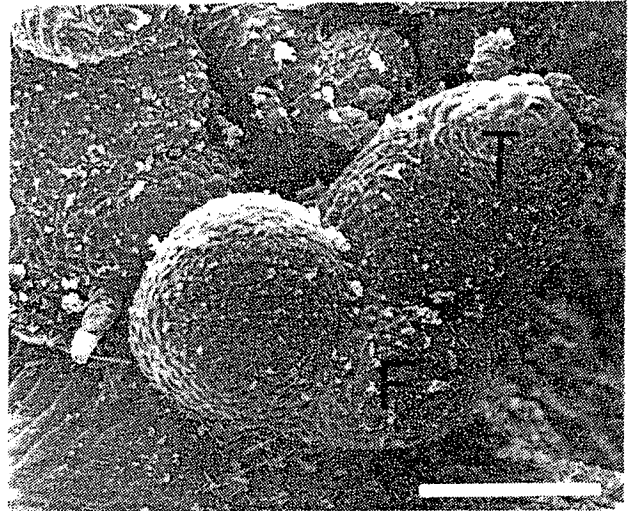
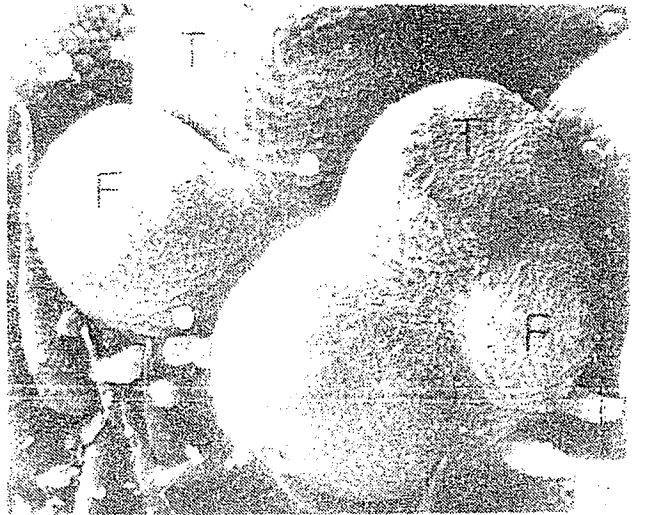
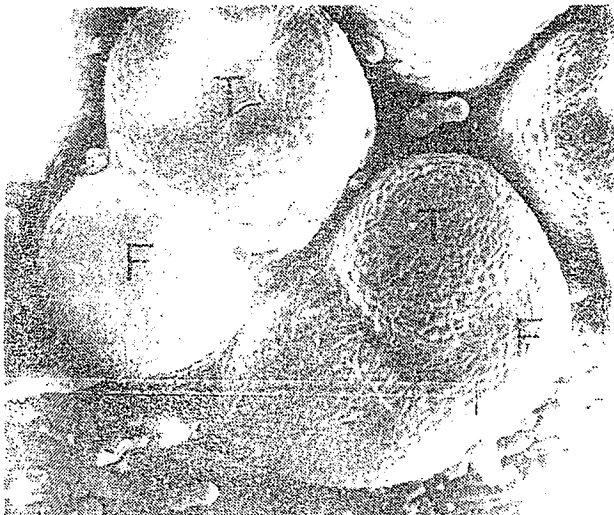
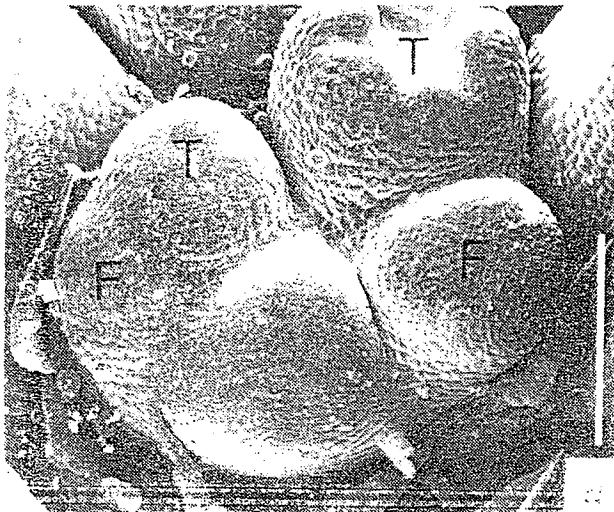


Fig. 9. *Monophyllaea hirticalyx*: apex of pair-flowered cyme. Bar: 100  $\mu$ m.



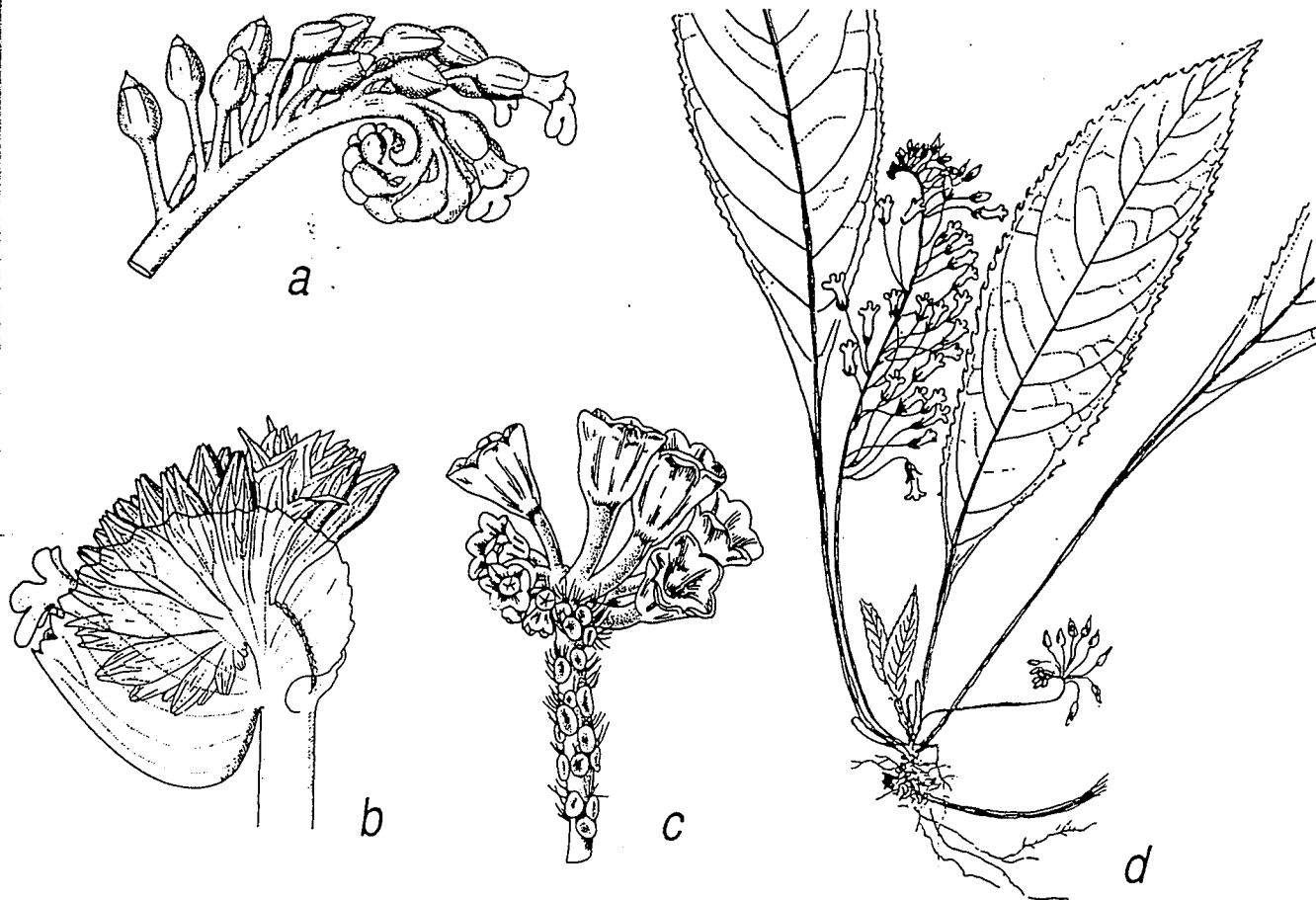


Fig. 11. Pair-flowered cymes with character syndrome of pseudo-monopodial development. a: *Monophyllaea horsfieldii*, b: *Epithema saxatile*, c: *Cremosperma reldioides* (from KVIST & SKOG, 1988), d: *Tylopsacas cuneatum* (from LEEUWENBERG, 1958).

differentiation into a flower pair is in full congruence with the cymose structure of the inflorescence.

Another striking example was found in *Epithema* (WEBER 1977, 1988; Fig. 11b), a genus (characterized by capitate, dense-flowered inflorescences) in which probably all species exhibit a pseudo-racemose inflorescence development. The photo series of Fig. 10 shows a full cycle of formation and early modelling of a new cyme unit (flower pair) in *Epithema saxatile* Blume. At first, the apex appears completely undivided and the external shape is that of a slightly asymmetrical, triangular pillow. Then a first division becomes visible, with a shallow furrow separating a small apical portion from a much larger proximal portion. The latter corresponds to a whole, completely undifferentiated cyme unit. Subsequently, the cyme unit divides into two portions. They represent the primordial terminal flower unit and its front-flower. In this stage the apical portion has almost recovered its original size. In Fig. 11d the terminal flower of the cyme unit appears flattened at the top. This stage marks the start of development of the floral organs (sepal

initiation). The front-flower is still undifferentiated. The apex exhibits the first sign of fractionation. This time the prospective cyme unit falls to the left side.

The observed mode of development can be described in principle as a monopodial pattern: an apical meristem is permanently present, which produces unit primordia in an alternate (zig-zag-like) manner, each subsequently differentiating into two flower primordia.

The interpretation, however, has to read quite opposite. Evidently due to strong ontogenetic abbreviation, the (at least) two youngest consecutive cyme units are merged together to form a unitary apical meristematic body. The production of a new cyme unit takes place before the preceding one becomes recognizable as a distinct unit primordium; it takes place at the level of undifferentiated meristems. The external shaping of distinct primordia is postponed. A change in the chronology of primordium initiation and primordium differentiation is, therefore, responsible for the pseudo-monopodial development (heterochrony).



Fig. 12. Pair-flowered cymes with displaced bracteoles. a, b: *Drymonia coccinea*. c: explanatory diagram. d: *Agalmyla tuberculata*.

#### Character syndrome

As can be inferred from the inflorescences of (some species of) *Monophyllaea* and (probably all species of) *Epithema*, a special character syndrome is apparently associated with - or is perhaps the prerequisite of - a pseudo-monopodial inflorescence development:

- a) high number of flowers (flower pairs);
- b) small flower size;
- c) shortening of the cyme internodes between the flower pairs (peduncle and pedicels are not necessarily involved);
- d) flower pairs arranged in a cincinnus (scorpioid cyme),

eventually with a single dichasial branching at the base (never in a compound dichasium);  
e) absence of bracteoles.

Small flower size and shortness of cyme axes certainly can be seen in direct connection with a rapid production of a high flower number. The loss of bracteoles is specially remarkable. This feature seems to be characteristic of the gesneriaceous 'monopodial' cyme (but is not found, for instance, in Boraginaceae or Solanaceae).

### Survey of taxa

So far, only species of *Monophyllaea* and *Epithema*, are definitely known to exhibit a 'monopodial' cyme development. However, judging from the character syndrome, further taxa can be expected to have this pattern.

In Old World Gesneriaceae, species of *Streptocarpus* Lindl. with 'capitate' inflorescences (*S. glabrifolius* H. Humbert, probably also *S. hilsenbergii* R. Brown, both from Madagascar) may exhibit this pattern.

In New World Gesneriaceae the whole tribe Beslerieae is characterized by the lack of bracteoles within the pair-flowered cymes and thus appears promising. Indeed, in this tribe there are at least two genera which fully exhibit the above character syndrome: *Tylopsacas* Leeuwenbg. [*T. cuneatum* (Gleason) Leeuwenbg., Fig. 11d] and *Cremosperma* Benth. The latter genus comprises around 25 species, most of them having strongly congested cymes, often with numerous flowers. As can be deduced from the illustrations of KVIST & SKOG (1988), the flower 'heads' could well represent scorpioid cymes. This is definitely so in *C. reldioides* Kvist & Skog, in which the floral arrangement appears to resemble that of *Epithema* (Fig. 11c). No indication of 'monopodial cymes' has been found in other genera and tribes.

### Conclusions

In Gesneriaceae with about 150 genera and over 3700 species, pair-flowered cymes with monopodial development are very rare and have originated independently in different taxa. The underlying mechanism is ontogenic abbreviation in connection with the production of a great number of flowers in a relatively short time.

### Bracteole displacement

Within the pair-flowered cyme the bracteoles are normally placed  $\pm$  strictly opposite. Slight displacement (recaulescence) occurs, for instance, in species of *Streptocarpus*. More striking examples have been found in *Agalmyla tuberculata* Hook. f. and *Drymonia coccinea* (Aubl.) Wiehler, in which taxa the displacement of the bracteoles extends over the whole hypopodia (Fig. 12).

Unfortunately, no developmental information is available so far, and, due to lack of appropriate material, no studies could be carried out. Two developmental patterns are conceivable:

(a) Heterochrony is not involved. The bracteoles emerge first, then the primordia of the subsequent cyme units develop in their axils. Since the growth of the new

cyme units is predominantly from the common base of the unit primordium and the bracteole, the latter is lifted up.

(b) Heterochrony is involved. The 'axillary' primordium emerges before its subtending bracteoles. The latter emerges when the unit primordium has already developed to some extent. The delay of initiation results in an uplifted position.

Future investigations have to show which of the two possibilities is characteristic of Gesneriaceae.

### ACKNOWLEDGMENTS

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