TRANSITIONS FROM PAIR-FLOWERED TO NORMAL CYMES IN GESNERIACEAE

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ABSTRACT. In *Chrysothemis friedrichsthaliana*, *Achimenes candida*, and some other taxa in Gesneriaceae, cyme configurations are described which link the pair-flowered to the normal type in that there is slight inhibition to complete suppression of the front-flowers. The findings substantiate the hypothesis that in such gesneriads as *Loxonia hirsuta*, *Stauranthera* cf. *umbrosa*, and *Lenbrassia australiana*, the normal cyme has evolved from the pair-flowered one. Implications relating to the evolution of the cyme in allied families are discussed.

The cymes of Gesneriaceae, and a few genera of Scrophulariaceae, exhibit an unorthodox structure in that each cyme unit seems to end with a flower pair (pair-flowered cyme). This pair is formed by the true terminal flower (T) and an additional flower (front-flower, V, from Vorblüte) arising without a subtending bract in front of the terminal flower and showing the same orientation. Up to now the homology of the front-flower was unclear. Mostly, it was regarded as an accessory (serial) flower with a concaulescent pedicel. However, in a previous paper (Weber 1973) it was demonstrated that the front-flower is a regular branch of the cyme axis, the bract of which is usually aborted. The bract itself is obviously a remnant of a bract-pair located above the prophyll whorl.

The interpretation of the pair-flowered cyme is not only a point of morphological interest, but also has considerable phylogenetical bearing. In the light of the "serial flower-theory" the gesneriaceous cyme appears as a structure derived from the normal type as found widely in Scrophulariaceae (supervention and concrescence of accessory flowers). According to my interpretation, the pair-flowered cyme lies within a reduction series from a paniculate system to the conventional cyme, the latter therefore representing a more derived condition than the pair-flowered cyme (details in Weber 1973). From this point of view, the Gesneriaceae appear to occupy a less advanced status than Scrophulariaceae in respect of inflorescence organization.

This concept will be supported in the following by a new piece of evidence: inflorescences showing direct transitions from pair-flowered to normal cymes.

In the diagram-drawings, fruits and open flowers are marked by large circles, flower buds by smaller circles (size in relation to the developmental stage). Front-flowers are set off by stippling. Rudiments are indicated by black dots.

In the cymes, the prophylls and their axillary branches are often not placed exactly lateral and opposite, but include an obtuse angle on the front-side. For simplification this condition is neglected in the diagrams and all lateral structures occur at right angles.

Diagrams in the text usually refer to open flowers only. The term open flowers includes post-anthetic flowers and fruits.

The letter diagrams in the tables are more detailed and the following are used—capital letters: open flowers; small letters: flower buds; small letters in parenthesis: rudiments and buds at initial developmental stage.

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DEVELOPMENTAL AND REDUCTIONAL SEQUENCE

The development of the flowers in a pair-flowered cyme follows the pattern indicated in fig. 1a (see Goebel 1931: *Ramonda myconi*, *Streptocarpus holstii*; Oehlkers 1962: *Streptocarpus wendlandii*). This pattern is reflected by the sequence of flower opening: in each cyme unit the terminal flower (T) opens first, then the front-flower (V), followed by the lateral flowers.

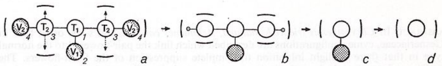

FIG. 1. Main steps of the "standard reduction series" in the pair-flowered cyme. Explanations in the text. In 'a' the figures in italics indicate the sequence of development and opening of the flowers.

The sequence of flower reduction* is exactly opposite to the development and efflorescence mode. This can be observed directly in inflorescences with variable flower number, e.g. in various species of *Chirita*. In *C. hamosa* with its serial axillary inflorescences, different reduction stages can be seen even in one leaf axil (Weber 1973, under *C.* aff. *hamosa*; 1975, fig. 4c). For example, in a six-flowered dichasial system ($\genfrac{}{}{0pt}{}{V_2T_2T_1T_2V_2}{V_1}$) the cyme next becomes four-flowered ($\genfrac{}{}{0pt}{}{T_2T_1T_2}{V_1}$), then two-flowered ($\genfrac{}{}{0pt}{}{T_1}{V_1}$), and finally a solitary flower (T_1). The particular reduction stages can become stabilized and may then provide valuable distinctive characters for the taxonomist. In *C. involucrata* the axillary inflorescences usually contain four open flowers; in *C. elphinstonia*, *C. bimaculata* and *C. micromusa* the "cymes" exclusively consist of two flowers ($\genfrac{}{}{0pt}{}{T_1}{V_1}$, Weber 1975); and in *C. moonii*, *C. hookeri*, and others the inflorescences are represented by solitary flowers (T_1) only. The same reduction series can be found in *Streptocarpus* and *Gesneria* (Skog 1976), and with the exceptions discussed below, all inflorescences examined up to now in this family show this pattern.

This reveals that in a unit of a pair-flowered cyme the front-flower is more constant than the lateral flowers. The latter are reduced before the front-flower, and for that reason, in this "standard reduction series" a conventional cyme structure, e.g. a simple dichasium (triad) consisting of $T_2T_1T_2$, is never found. This reduction pattern, therefore, is not relevant in the present context and even seems to contradict the idea of a derivation of the normal cyme from the pair-flowered one.

To present evidence for this process, different reduction patterns must be established: patterns in which the front-flowers are inhibited. Various transitional steps from pair-flowered to normal cymes can be conceived by an inhibition range from developmental, and consecutively flowering, delay up to complete abortion of the front-flowers.

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* The term "reduction" is used here predominantly in a formal sense. It does not imply that inflorescences with a low flower number have necessarily originated from high-numbered ones. Nevertheless, two- and one-flowered inflorescences do appear to mark the end of the reduction series phylogenetically as well.

Such a case showing many transitional and reductional stages has been found in the New World gesneriad *Chrysothemis friedrichsthaliana*. It provides a good model for the suggested evolutionary change, and therefore, a detailed description of its inflorescence organisation is given here. A more advanced type is recognised in *Achimenes candida* which has achieved the conventional type almost perfectly. In addition, some further instances will be quoted to show that trends in forming normal cymes can be observed in different and independent groups of Gesneriaceae.

CHRYSOTHEMIS FRIEDRICHSTHALIANA

The neotropical genus *Chrysothemis* Dcne. belongs to tribe *Episcieae* Endl. and includes seven species. Three of them [*C. villosa* (Benth.)Lwbg., *C. friedrichsthaliana* (Hanst.) Moore, and the type species *C. pulchella* (Donn ex Sims) Dcne.] have been investigated either from living plants (cultivated at the Botanical Garden Vienna, seed origin: Utrecht) or from fixed material (*C. pulchella*, received from H. Wiehler, Marie Selby Botanic Gardens, Sarasota; Acc.nr. 1850, Venezuela).

The axillary inflorescences were described by Leeuwenberg (1958, p. 330) as "umbellate or rarely compound umbellate". As expected, however, the analysis of *C. villosa* and *C. pulchella* revealed a pair-flowered-cymose structure absolutely conforming to the standard type in Gesneriaceae. The similarity to umbels is only superficial, due to the condensed hypopodia of the lateral and, if present, subsequent cyme units. *C. villosa* has usually six-flowered inflorescences corresponding to fig. 1a. Reduction of flowers follows the pattern described in the previous section. The inflorescences of *C. pulchella* are more elaborate, bearing cyme units up to 3rd and 4th order.

In contrast, the inflorescences of *C. friedrichsthaliana* deviate remarkably from this standard pattern with the front-flowers being partly inhibited or completely suppressed. During several flowering periods (investigated when the plants were fruiting and flowering was nearly over), c. 60 flowering shoots were checked, i.e. c. 450 inflorescences. In not a single case was a complete pair-flowered cyme detected. All inflorescences were found to represent intermediates between pair-flowered and normal cymes or exactly normal cymes. Before commenting on the particular forms, a short description of the plant follows:

GENERAL SHOOT MORPHOLOGY. *C. friedrichsthaliana* is a geophyte with subterranean tubers which originate from the hypocotyl and later become somewhat flattened. The central parts of the tuber's upper side are densely covered with buds containing tiny, pale cataphylls. From these buds one or several flowering shoots emerge per season. The shoots taper markedly towards the base and emit numerous roots in the underground region. The aerial parts grow to a length of 0·5 m with internodes up to 15 cm long. Phyllotaxis is decussate, the leaves of a pair are equal, ovate to oblong, with serrate leaf-blades decurrent into the petiole, and up to 35 cm long. Above ground level the stem usually bears a cataphyll pair. This is followed by one or two foliage leaf pairs with dormant axillary buds (branching is very rare).

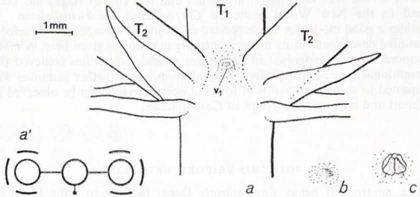

FIG. 2. *Chrysothemis friedrichsthaliana*: a, triad with rudimentary V_1; a', corresponding diagram; b,c, different rudimentary stages of V_1.

In the adjacent region which includes 3–5(–7) foliage leaf pairs, the axillary inflorescences are borne. The elaboration of this region and to some extent also the elaboration of the inflorescences (see below) evidently depends on nutritive conditions and on the age of the plants. Those flowering for the first time are smaller and more slender than the ones arising from old tubers (see below). On vigorous shoots in the leaf axils there often arise two inflorescences in serial position. In the uppermost part of the shoot the leaves are smaller and the internodes markedly shorter. The inflorescences of these leaves overtop the apex and form a loose terminal cluster. The youngest inflorescences near the shoot apex usually do not flower. As is a regular feature in Gesneriaceae, the shoot apex remains indefinite (=without a terminal flower).

In Troll's terminology (1964), the region bearing the axillary inflorescences (="partial florescences") has to be called a "frondose florescence". Taking into account the absence of lateral branches beneath the florescence ("paracladia" with their "co-florescences"), the whole flower-bearing system of *C. friedrichsthaliana* is represented by the "main florescence" alone.

STRUCTURE OF THE AXILLARY INFLORESCENCES (PARTIAL FLORESCENCES). Many of the observed forms are illustrated (mostly by diagrams) in fig. 3. At the time of analysis fruits, open flowers, flower buds at various developmental stages and obvious flower rudiments were present. The latter always correspond to front-flowers. Rudimentary V_1s are depicted in fig. 2. They are constantly located somewhat above the prophyll level. They may be present as tiny flower buds (fig. 2c), but often they consist of the sepal primordia only (fig. 2a) and even may be reduced to dome-shaped protrusions (fig. 2b). In a few cases, a small, bract-like structure with longitudinal insertion was found on the border of such a protrusion, apparently corresponding to a sepal which had developed to some extent.

As is a regular character of the pair-flowered cyme, the front-flowers lack subtending bracts and prophylls.

Figs 3 a-r cover a representative selection of transitional forms. As has been mentioned already, an entirely complete pair-flowered cyme (with well-developed front-flowers in all cyme units) has never been noticed. The most significant approach to it was that in fig. 3a: V_1 and one V_2 present (=fruiting or flowering), the second V_2 rudimentary, V_3 lacking. From such a structure a practically complete series (fig. 3 b-o) leads to forms with only one rudimentary front-flower in one of the cyme units (fig. 3 p-r).

Inflorescences which exactly conform to the normal cyme plan (absence of front-flowers) are indicated in fig. 3 s-u. The most elaborate type found is a system containing units up to 3rd order (small buds even of 4th order) (fig. 3s). Very frequently there occur simple dichasia (triads, fig. 3u) and from these all possible reductional steps to solitary flowers (fig. 3x) have been observed.

Finally, the total absence of one type must be stressed: $\frac{T_1}{V_1}$. This important link in the several- to one-flowered cyme in the standard reduction series is completely lacking in *C. friedrichsthaliana.* The reduction to solitary flowers always starts from the pure triad.

FREQUENCY AND DISTRIBUTION OF THE PARTICULAR INFLORESCENCE FORMS. The forms just described are not distributed at random on the shoot. There is a clear pattern recognizable from table 1 in which the composition of the flowering region (florescence) of three selected shoots is tabulated. Perhaps more conclusive is table 2 which refers to 16 "old" shoots (=emerged from tubers being some years old) and 16 "first-year" shoots (=developed in the same year as sowing.) It covers the quantitative distribution of Ts and Vs (including buds and rudiments) within the cyme in relation to the position of the cyme.

The following conclusions can be drawn from these tables:

1. The elaboration of the flowering region as well as the cyme complexity depends on the vigour of the shoots. The first-year shoots are more poorly developed than "old" ones.
2. There is a gradient of cyme elaboration (or reduction) within the flowering region. The cymes in the axils of the lower leaves are less complex than the upper ones.
3. The presence of front-flowers is related to the elaboration grade of the cyme and to the position on the shoot, respectively.

As to the individual inflorescence sets (=inflorescence pair of one node):—

In the first-year shoots the cymes of the lowermost leaf-pair of the florescence (=first set) are nearly always reduced to solitary flowers (T_1). In the "old" shoots solitary flowers occur at a ratio of about 50%, the remaining structures are diads (T_1T_2) or triads ($T_2T_1T_2$). Well-developed front-flowers are absolutely lacking. In a single case a rudimentary V_1 was observed, paradoxically on a first-year shoot.

Second set. Solitary flowers still predominate over diads and triads in the first-year shoots. V_1s occur as buds or rudiments, if at all. Also in the "old" shoots, cymes without any front-flowers are still in the majority. Four cymes with open V_1 have been noticed, one with an open V_2 and several with rudimentary V_1 and/or V_2. In one cyme even a rudimentary V_3 has been observed.

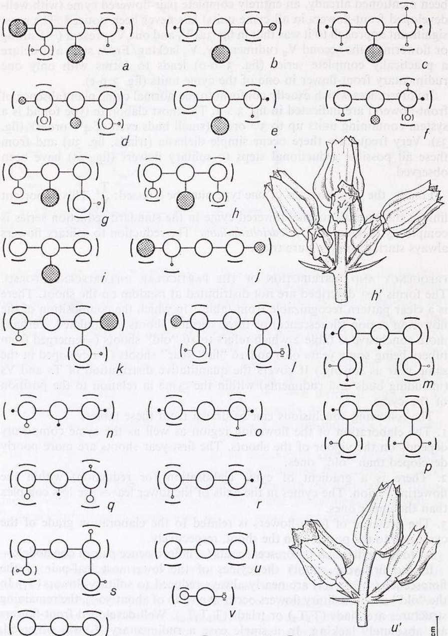

FIG. 3. *Chrysothemis friedrichsthaliana*, diagrams of axillary inflorescences showing various transitional and reductional forms from pair-flowered to normal cymes resp. solitary flowers (for explanation of the signatures see the notes following the introduction); h', u', inflorescences corresponding to the diagrams h and u; in h' corolla of V_1 dry, otherwise corollas already fallen.

TABLE I

Composition of the flowering region (florescence) of 3 selected shoots of *Chrysothemis friedrichsthaliana*. Structure of axillary inflorescences indicated by letter diagrams (for explanation of symbols see introduction).

	first-year shoot no. 2		"old" shoot no. 6		"old" shoot no. 7	
set 6			$t_2T_1T_2$ $V_1(t_3)$	$t_2T_1(t_2)$ v_1		
set 5			(t_3) $(v_2)T_2T_1T_2$ $V_1(t_3)$	(t_3) $(v_2)T_2T_1(t_2)$ V_1	$t_2T_1t_2$ v_1	$t_2T_1t_2$ v_1
set 4	$t_2T_1t_2$ $(t_3)v_1(t_3)$	$t_2T_1t_2$ $(t_3)(v_1)(t_3)$	(t_3) $T_2T_1T_2$ $t_3V_1t_3$	$(v_2)T_2T_1T_2$ $(t_3)V_1t_3$	$t_2T_1T_2(v_2)$ v_1t_3	$T_2T_1t_2$ $(t_3)V_1(t_3)$
set 3	$T_2T_1T_2$ $(t_3)\quad(t_3)$	$t_2T_1T_2$ $(v_1)(t_3)$	$T_2T_1T_2$ $t_3v_1T_3(t_4)$	$T_2T_1T_2(v_2)$ $t_3V_1T_3(t_4)$	$(v_2)T_2T_1T_2$ $t_3V_1t_3$	$T_2T_1T_2V_2$ $t_3(v_1)t_3$
set 2	$t_2T_1T_2$	$T_2T_1t_2$ (t_3)	$T_2T_1T_2$ $(t_3)\quad(t_3)$	$T_2T_1T_2$ $(t_3)\quad t_3$	$T_2T_1T_2$ $(t_4)T_3V_1T_3(t_4)$	$T_2T_1T_2(v_2)$ $(t_3)\quad T_3$
set 1	$(t_2)T_1(t_2)$	$T_1(t_2)$	$T_1(t_2)$	$T_2T_1(t_2)$	$T_2T_1T_2$ (t_3)	$T_2T_1T_2$ (t_3)

Third set. The presence of V_1s increases significantly. In the "old" shoots nearly 50% of the cymes bear an open V_1. Nevertheless, T_2s (of one side) still predominate markedly over V_1s. In this set the number of open V_2s achieves its peak, but is lower than the number of open T_3s.

Fourth set. This is the uppermost one coming into flower in the first-year shoots and usually only T_1 flowers. V_1s are developed very frequently (ca. 85%), but remain in bud stage or are rudimentary. In the cymes of the "old" shoots, V_1 is permanently present, though sometimes as a bud or a rudiment only. Open V_1s approximately have the same steadiness as open T_2s. The most frequent configuration therefore is $\begin{matrix}T_2T_1T_2\\V_1\end{matrix}$. In such cymes the conventional sequence of flower opening (T_1—V_1—T_2 . . .) pertains. V_2s are present sometimes, but usually as rudiments.

Fifth and sixth set. Even in the "old" shoots these sets do not always flower; therefore, the T_1s do not reach the maximum number 32 (cymes completely in bud stage have not been taken into consideration). In respect to the occurrence of V_1s roughly the same holds true as for set four.

CONCLUSIONS. In contrast to other species in the genus, and in such related genera as *Alloplectus*, *Nautilocalyx*, *Paradrymonia*, *Columnea* etc., which are all characterized by typical pair-flowered cymes, in *Chrysothemis friedrichsthaliana* the front-flowers are evidently involved in a specific reduction process (from unknown genetical/physiological and adaptive/evolutionary reasons). Inhibition effecting delay of development and flowering, rudimentation and finally total suppression of the front-flowers becomes progressively prominent towards the base of the flowering region of the shoots. Special

TABLE 2

Structure of the axillary inflorescences in *Chrysothemis friedrichsthaliana*. Analysis based on 16 first-year and 16 "old" shoots. Under set 1–4 the first figure stands for the sum of the indicated flower type (and developmental stage, respectively) on first-year shoots, the second figure as well as those under set 5 and 6 refer to "old" shoots. Only cymes with at least T_1 open have been used for the establishment of the table. Symbols as in Table 1, further explanations and discussions in the text

set 6	V_3	–	T_3	–	V_2	–	T_2	3	T_1	6	V_1	3	T_2	2	V_2	–	T_3	–	V_3	–
	v_3	–	t_3	–	v_2	–	t_2	–			v_1	3	t_2	3	v_2	–	t_3	–	v_3	–
	(v_3)	–	(t_3)	4	(v_2)	–	(t_2)	3			(v_1)	–	(t_2)	2	(v_2)	–	(t_3)	4	(v_3)	–
set 5	V_3	–	T_3	–	V_2	1	T_2	6	T_1	26	V_1	10	T_2	11	V_2	–	T_3	–	V_3	–
	v_3	–	t_3	–	v_2	–	t_2	14			v_1	16	t_2	15	v_2	–	t_3	–	v_3	–
	(v_3)	–	(t_3)	13	(v_2)	6	(t_2)	6			(v_1)	–	(t_2)	–	(v_2)	2	(t_3)	11	(v_3)	–
set 4	V_3	–/–	T_3	–/–	V_2	–/2	T_2	–/21	T_1	19/32	V_1	–/24	T_2	2/24	V_2	–/1	T_3	–/–	V_3	–/–
	v_3	–/–	t_3	–/3	v_2	–/2	t_2	19/9			v_1	13/6	t_2	17/6	v_2	–/–	t_3	–/9	v_3	–/–
	(v_3)	–/–	(t_3)	15/21	(v_2)	2/4	(t_2)	–/2			(v_1)	5/2	(t_2)	–/2	(v_2)	2/13	(t_3)	17/12	(v_3)	–/–
set 3	V_3	–/–	T_3	–/4	V_2	–/3	T_2	10/27	T_1	32/32	V_1	4/14	T_2	14/24	V_2	–/2	T_3	–/3	V_3	–/–
	v_3	–/–	t_3	–/19	v_2	–/2	t_2	22/4			v_1	14/4	t_2	19/6	v_2	–/3	t_3	–/4	v_3	–/–
	(v_3)	–/3	(t_3)	24/4	(v_2)	2/4	(t_2)	–/1			(v_1)	9/8	(t_2)	–/2	(v_2)	2/4	(t_3)	18/8	(v_3)	–/1
set 2	V_3	–/–	T_3	–/6	V_2	–/1	T_2	11/30	T_1	32/32	V_1	–/4	T_2	10/26	V_2	–/–	T_3	–/6	V_3	–/–
	v_3	–/–	t_3	–/8	v_2	–/2	t_2	18/2			v_1	1/2	t_2	16/3	v_2	–/–	t_3	–/6	v_3	–/–
	(v_3)	–/1	(t_3)	21/11	(v_2)	1/2	(t_2)	3/–			(v_1)	3/4	(t_2)	6/3	(v_2)	–/6	(t_3)	16/4	(v_3)	–/2
set 1	V_3	–/–	T_3	–/1	V_2	–/–	T_2	–/14	T_1	32/32	V_1	–/–	T_2	1/16	V_2	–/–	T_3	–/–	V_3	–/–
	v_3	–/–	t_3	–/–	v_2	–/–	t_2	6/6			v_1	–/–	t_2	1/4	v_2	–/–	t_3	–/–	v_3	–/–
	(v_3)	–/–	(t_3)	2/11	(v_2)	–/–	(t_2)	22/6			(v_1)	1/–	(t_2)	28/–	(v_2)	–/–	(t_3)	–/8	(v_3)	–/–

attention must be attached to the rudiments, because they definitely stipulate the evolutionary direction of pair-flowered to normal cyme, and not vice versa. Total suppression of the front-flowers gives rise to the formation of conventional cymes (usually in the appearance of triads) in the lower leaf axils. Further reduction to solitary flowers always starts from that cyme type. The total lack of a $\frac{T_1}{V_1}$-configuration which links the several- to the one-flowered cyme in the standard reduction series underlines the force of the inhibition.

Thus *C. friedrichsthaliana* gives substance to the hypothesis that normal cymes may have evolved from pair-flowered ones. The significance as well as the limitations of this concept will be discussed later.

ACHIMENES CANDIDA

The likewise neotropical genus *Achimenes* comprises, as delimited by Wiehler (1976), 21 species, nearly half of which were available for investigation from cultivated material.

The axillary inflorescences are mostly reduced to solitary flowers, reduction extending sometimes to the prophylls (*A. misera* Lindl., *A. patens* Benth.). A number of species are noteworthy in possessing three "prophylls", all with tiny flower buds in their axils [e.g. *A. erecta* (Lam.) Fuchs, *A. grandiflora* (Schiede)DC.]. The bract additional to the true prophylls is the subtending bract of V_1 (γ_1). These species are of special interest because they show the axillary origin of the commonly bract-less front-flowers (Weber 1973).

In *A. candida* Lindl. there is a slight gradient within the flowering region (florescence) in relation to the axillary structures (± parallel with reduction of size of the subtending leaves). In the upper portion they are restricted to one flower (with 3 bracts on the pedicel), in the lower portion they are two-

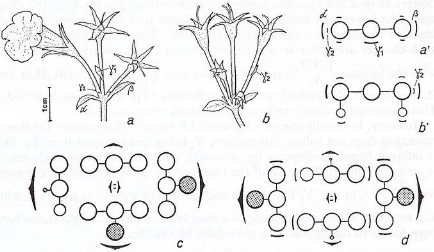

FIG. 4. a,b, *Achimenes candida*, axillary inflorescences: a',b', corresponding diagrams. c, diagram of the terminal inflorescence cluster of *Aeschynanthus evrardii* (Edinb. *C.* 2002), d, *Aeschynanthus* x *splendidus* (Edinb. *C.* 2850).

or three-flowered (fig. 4a). Not infrequently two further flowers develop into considerable buds, but do not seem to come into flower (fig. 4b). As shown in the corresponding diagram (fig. 4b′), the flower arrangement strictly conforms to the normal cyme type. Front-flowers or corresponding buds or rudiments are always absent. Nevertheless, these inflorescences are not called typical cymes because of the abundant occurrence of bracts homologous to subtending bracts of front-flowers. The most prominent bract is γ_1, occasionally being nearly as large as a prophyll. In contrast to the species mentioned above, this bract is not located closely above the prophylls, but has moved up the pedicel to a distance of up to 10 mm. Also on one or both T_2 a γ-bract may be present (fig. 4a) and the reverse condition (γ_1 lacking, both γ_2 present) is sometimes observable as well. Often the γ-bracts are reduced to tiny pads densely covered with hairs. Total lack of all γ-bracts is rare. As is implicit above, these bracts never produce axillary structures.

A. candida, therefore, appears to have achieved a more advanced position on the way from the pair-flowered to normal cyme than *Chrysothemis friedrichsthaliana*. Moreover, the change is apparently perfect in *A. flava* Morton: in the few diads and triads found (the inflorescences are nearly always reduced to T_1), γ-bracts, naturally as well as front-flowers, have not been observed.

SOME FURTHER EXAMPLES

AESCHYNANTHUS. The investigation of the inflorescence structure of a number of species recently introduced into cultivation was carried out during a visit to the Royal Botanic Garden, Edinburgh, in 1975. A collection of a few common horticultural species is also in Vienna.

In this ornithophilous Old World genus, the inflorescences either arise from the axils of the foliage leaves (and are sometimes reduced to solitary flowers as in *A. pachyanthus* Schltr.) or emerge from 2–4 bracts at the shoot apex (the lower pair usually being transitional to foliage leaves) and then together forming a ± dense terminal cluster. The partial inflorescences of such clusters are either several-(pair-)flowered cymes (widely four-flowered with the formula $\genfrac{}{}{0pt}{}{T_2T_1T_2}{V_1}$), or flower pairs with $\genfrac{}{}{0pt}{}{T_1}{V_1}$ [*A. pulcher* (Bl.)Don and *A. boscheanus* De Vriese], or solitary flowers (T_1; *A. musaensis* Woods). This enumeration clearly reflects the standard reduction series.

However, in certain species with several-flowered inflorescences the flower reduction does not follow this pattern, V_1 being less constant than T_2. This is inferred from the diagram fig. 4a which refers to the terminal cluster of *A. evrardii* Pellegr. Only two of the four axillary inflorescences are complete with $\genfrac{}{}{0pt}{}{T_2T_1T_2}{V_1}$, in one V_1 is obsolete and in the last one V_1 is totally lacking and thus this inflorescence becomes a pure triad. Similar configurations have been found in the hybrid *A.* x *splendidus* Moore (fig. 4d).

RAMONDA, HABERLEA and JANKAEA. The inflorescences of these European members of the family have already been accurately described by Fritsch (1927) and Hayek (1926). According to Fritsch's (and my own) observations

Ramonda myconi (L.)Schltz. has axillary inflorescences with a maximum of six flowers and then representing typical pair-flowered dichasia ($\underset{V_1}{V_2T_2T_1T_2V_2}$). Usually only four flowers are present ($\underset{V_1}{T_2T_1T_2}$) and further reduction leads through $\underset{V_1}{T_1T_2}$ and $\underset{V_1}{T_1}$ to solitary flowers (T_1).

However, and this is relevant here, Fritsch (l.c., fig. 1/5) reported a 5-flowered inflorescence with V_1 lacking ($V_2T_2T_1T_2V_2$) and a four-flowered one with developmental delay of V_1. The same holds true for *Haberlea rhodopensis* Friv. and *Jankaea heldreichii* Boiss. Here the inflorescences are usually four-flowered, but occasionally three-flowered through loss of V_1 (Hayek l.c., fig. a,b,g). For my part I have observed several inflorescences in *Haberlea* being more elaborate (T_3 present), but V_2 obsolete or absent.

CHIRITA LAVANDULACEA. Besides four-flowered cymes ($\underset{V_1}{T_2T_1T_2}$), pure triads have also been noticed among various reduction forms in *C. lavandulacea* Stapf.

INDICATIONS FROM LITERATURE. In taxonomic literature several gesneriads are depicted as having normal cymes. An example is the Australian monotypic genus *Lenbrassia*, recently established and illustrated by Gillett (1974), which appears to bear simple triads ($T_2T_1T_2$). After checking some fine herbarium specimens (*Gillett* 2606, K; *Schodde* 4151, *Cook* 10099, L), this taxon indeed seems to produce this type exclusively and is therefore an additional example of a gesneriad with "non-gesneriaceous" (normal) cymes (cf. discussion). In general, however, illustrations give no reliable proof and, unfortunately, confirmation from herbarium material is often difficult, because it is insufficient in most cases for a thorough inflorescence analysis. Also, little information can be traced from the species descriptions: most taxonomists have not been aware of the pair-flowered condition of the gesneriaceous cyme and their reference to the inflorescence structure is often superficial and merely descriptive. An exception is Burtt, who, for instance (in Humbert et al. 1971), mentions explicitly the irregular occurrence of the front-flowers in *Colpogyne betsiliensis* (Humb.)Burtt ["inflorescentia . . . floribus saepe singulis (nec regulariter per paria orientibus)"].

Discussion

As pointed out at the start of this paper, the front-flowers are generally very stable elements within the gesneriaceous cyme. Their integration is marked by development and efflorescence prior to the lateral branches and equivalent reduction stability. Therefore, evolution of the normal from the pair-flowered cyme may appear difficult to conceive at first sight. However, the foregoing instances demonstrate very clearly that the fixation of the front-flowers is not irrevocable: In different taxonomic groups of the family, trends of "relaxation" can be traced which are manifest in developmental delay through to total abortion, thus giving rise to transitional cyme forms and eventually pure conventional cymes. This proof has particular bearing on two points:

1. *Evolution of the normal cyme within Gesneriaceae.* According to present, and still very defective, knowledge and apart from the relevant examples described above (*Achimenes*, *Lenbrassia*), there are two genera in the family which include species with normal cymes (even with high flower number!): *Loxonia* and *Stauranthera* (Weber 1977a,b), both members of the tribe *Klugieae* (incl. *Loxonieae*). As to the first, two of the three species (*L. discolor* Jack, *L. burttiana* Weber) have pair-flowered cymes, the third (*L. hirsuta* Jack) is characterised by normal ones. In the poorly known *Stauranthera* at least the type species, *S. grandiflora* Benth., belongs to the pair-flowered, and at least one species (probably *S. umbrosa* Clarke) to the conventional type. The contrast within one genus in respect of the inflorescence structure is mitigated considerably by the present record of transitional forms, and the evolutionary change from the one type to the other is easier to understand.

It does not appear as mere accident that the perfect change has just been achieved in *Loxonia* and *Stauranthera*. Both exhibit an extraordinary complexity of morphological organization and undoubtedly are highly evolved taxa in the family (Weber 1977b). It is therefore not very surprising that at species level too the cyme structure has been involved in evolutionary progress. At any rate, a counter-current view regarding the normal cyme in these genera as an original condition and representative of a relic scrophulariaceous-like pre-gesneriad stock (a view which eventually could be favoured by the "serial flower-theory") is hardly acceptable. Even without knowledge of the present results it appears most improbable to meet features of an ancestral stock of the family at species level in such highly advanced genera. Moreover, this concept would imply that the pair-flowered cyme in the indicated species has originated by parallel evolution without any genetical connexion to the other members of the family.

2. *Evolution of the cymes in related families, particularly in Scrophulariaceae.* Hitherto, no clear idea exists as to how the inflorescence in the Scrophulariales (Scrophulariaceae, Acanthaceae, Bignoniaceae, Gesneriaceae, etc.) has evolved. The indeterminate character of the main axis is generally considered to be a derived feature and this certainly holds true for these families. However, the question of the origin of the axillary cymes is still open.

With special reference to Gesneriaceae and Scrophulariaceae the following working hypothesis, which links the pair-flowered and the normal cyme, was proposed by Weber (1973). Both kinds are derived from a paniculate axillary system. By progressive loss of the distal branches and the proximal (=prophyll-) branches becoming gradually capable of continued branching, stages preparatory to cymes are achieved. The pair-flowered cyme becomes established by the fixation of a median branch above the prophyll-branches, its reduction to a single flower (front-flower), and the accurate repetition of this pattern in the consecutive branches.

Formally, the typical cyme now follows by reduction of the front-flowers. As discussed above, such a reduction does indeed appear to have taken place in Gesneriaceae. But this, and the fact that there are about half a dozen scrophulariaceous genera with pair-flowered cymes (e.g. *Penstemon*, *Calceolaria*), need not and must not lead to the conclusion that in Scrophulariaceae the normal cyme has generally originated from the pair-flowered one. However, from the currently presented model case pointing this way in Gesneriaceae, the inference appears at least plausible that in Scrophulariaceae and related families the cyme is also derived from a more complex ramification system. Evolution may have started here from the same paniculate ancestral type and proceeded to normal cymes directly, that is without passing a stage of strong fixation of distal branches or front-flowers.

With regard to the evolutionary position of the normal cyme in the present concept, it makes no difference whether it has originated from a pair-flowered cyme or from a yet more panicle-like system: by the stronger reduction grade it appears more advanced than the pair-flowered cyme.

This idea has particular bearing on the status of certain genera and groups within Scrophulariaceae and on the relationship of Gesneriaceae and Scrophulariaceae. However, at present it is too early to draw concrete conclusions. Nevertheless, one glimpse may be pointed out. From the concept put forward, Gesneriaceae as a whole (the vast majority with pair-flowered cymes, very few with normal ones, and a fair number—mainly neotropical members—with solitary flowers in leaf or bract axils) appear not to have achieved the grade of inflorescence reduction as in Scrophulariaceae (few genera with pair-flowered cymes, plenty with typical ones, and the vast majority—including all hemi- and holo-parasitic representatives—with solitary flowers). This pattern is apparently paralleled by the geographical distribution: Gesneriaceae nearly exclusively inhabit tropical and subtropical climates and have obviously persisted in the area of origin. In contrast, Scrophulariaceae, presumably of tropical origin as well, are distributed from the tropics up to the arctic circle, displaying the greatest species richness in temperate regions. These pointers might indicate a stronger evolutionary "activity" in the latter family—a supposition which, of course, does not overlook the fact that certain taxa in the Gesneriaceae have achieved an evolutionary height which has no parallel in Scrophulariaceae.

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