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## SHOOT AND INFLORESCENCE ARCHITECTURE OF THE NEOTROPICAL GENUS *SINNINGIA* (GESNERIACEAE)

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### Abstract

The neotropical genus *Sinningia*, comprising about 60 species, exhibits a vast diversity with regard to plant size and plant architecture. The size ranges from miniature rosette plants less than 5 cm high to 2–3 m tall shrubs. All species are perennial, the flowering shoots emerge either from an exposed or underground tuber or, less frequently, from a perennial basal shoot portion. Analysis of shoot and inflorescence architecture results in the recognition of c. 20 closely interconnected types which can be roughly categorised into 5 groups (A–E). Caulescent plants with a distinct vegetative region and a frondose, frondo-bracteose or bracteose florescence are considered to represent the central group (A) (e.g., *S. schiffneri*, *S. bulbosa*, *S. cochlearis*). This is also the most prominent one with regard to species number. The frondose type, found in species of forest habitats with high rainfall and showing ± continuous growth throughout the year, is perhaps the phylogenetically most primitive one in the genus. The other groups can be regarded as advanced or terminal points of development. They include rosulate or rosette species (B) (e.g., *S. speciosa*, *S. pusilla*), 'verticillate' plants with an elevated pseudowhorl of foliage leaves and several variants of inflorescence architecture (C) (e.g., *S. douglasii*), 'candle-stick' plants with extensively elongated, spicate florescence (D) (e.g., *S. allagophylla*), unifoliate plants with the shoots separated into bracteose floral shoots and very short vegetative shoots that develop only a single, large leaf (E) (e.g., *S. tuberosa*). Radiation of the partial-florescences (pair-flowered cymes) is considerable, relating to branching pattern, flower number (including frequent reduction to solitary flowers), bracteole presence and texture, presence of [gamma]-bracts, and length of peduncle and pedicels. Loss of front-flowers in the cymes apparently does not occur in the genus. Inflorescence characters are considered significant in ecological respects and form an important part of the pollination syndrome.

### Introduction

*Sinningia* Nees is a genus of neotropical Gesneriaceae (subfam. Gesnerioideae) exhibiting many interesting features: (a) it is one of the few genera of Gesneriaceae in which the perennial habit is dependent on the formation of tubers, (b) the flowers, generally very attractive and spectacular, include a remarkable wide range of pollination syndromes (melittophily [*Euglossine* bees], sphingophily, ornithophily,

psychophily, chiropterophily), (c) the species have a considerable ecological amplitude: they may be saxicolous, terrestrial (with the tuber underground), or epiphytic, (d) there is a remarkably high degree of endemism. The genus is distributed throughout the Neotropics (except the Caribbean area), with the centre of diversity in S.E. Brazil.

Resulting from extensive field work of the first author (leading to the discovery of a number of new species) and many unsolved problems of species delimitation and subdivision of the genus, a taxonomic revision of the genus was undertaken (Chautems, 1990, 1991, 1993, 1995; Wiehler and Chautems, 1995). In the character analysis, the architecture of the shoots (including the inflorescence) has proved of special significance. A joint project, focusing on the habit of the plants and considering the implications for pollination syndrome was initiated. The first results provide important clues for the delimitation of the species and species alliances. They are presented here.

#### A. Previous work

Apart from the diagrams and descriptions of the individual species (with variable degree of accuracy), previous work relating to the shoot and inflorescence morphology of *Sinningia* is rather fragmentary. First, the studies of Troll (1964), which are included in the first volume of his handbook "Die Infloreszenzen" must be mentioned. As the taxonomic concept of *Sinningia* was then different, relevant information is also found under '*Corytholoma*'. Troll (1964) noticed the occurrence of 'Vorderblüten' within the cyme and provided notes and diagrams of the inflorescence morphology of the following species: *Sinningia aggregata* (under '*Corytholoma aggregatum*'), *S. allagophylla* ('*C. allagophyllum*'), *S. cardinalis* ('*C. cardinale*'), *S. macropoda* ('*C. macropodium*'), *S. douglasii* ('*C. maculatum*', '*C. polyanthum*'), *S. pusilla*, *S. speciosa*, *S. tuberosa* ('*C. tuberosum*'), and *S. incarnata* ('*C. warszewiczii*'). Troll (1964) did not fully recognise the special type of cyme characteristic of Gesneriaceae and regarded the additional flowers simply as accessory (serial) flowers. It was then shown by Weber (1973, 1982) that the additional flowers are true axillary flowers (with the subtending bract being reduced), and that the "pair-flowered cyme" is not a secondary elaboration of the conventional type of cyme, but is apparently derived from a paniculate branching system. In some cases Troll's studies were merely based on illustrations published in the literature; it is, therefore, not surprising, that some interpretations (especially in *S. tuberosa*) proved inadequate.

Recently, Boggan (1991) carried out a cladistic analysis of *Sinningia*, based on morphological characters. With regard to the 'axillary inflorescence' (pair-flowered cyme) he referred to five characters (character states in parantheses): (1) 'flower production' ('flowers produced after vegetative growth'/'flowers precocious'), (2) 'hypopodium' (= peduncle of cyme) ('absent'/'present'), (3) 'lateral hypopodia' ('absent'/'present'), (4) 'prophylls' ('absent'/'present'), (5) 'flower number' ('two or more in axil'/'solitary in axil').

#### B. General remarks on the morphology of the genus

The tuber of *Sinningia* is hypocotyledonary in origin (see Weber, 1936 under '*Corytholoma*'). The development of the lateral shoots starts from the axils of the cotyledons. The basal shoot internodia become incorporated into the young tuber and give rise to new axillary shoots in the next season. Over the years, by continuous incorporation of basal shoot internodes, the apex of the tuber grows up and accumulates 'eyes' that give rise to new shoots every year. The tubers (and in a few species perennial basal shoot segments) allow the plants to survive during seasonal

drought or temporary adverse conditions (cold temperatures, fire, epiphytic or marshy habitat). The size of the tuber varies greatly (from a hardly visible underground swelling in species like *S. schiffneri* and *S. barbata*, to huge structures over 30 cm in diameter in *S. sellovii*).

The shoots emerging from the tuber (or in some cases from the perennial basal shoot portion) are herbaceous. They usually come to flower, only late and weak shoots remain in the vegetative state. In two species (*S. tuberosa*, *S. defoliata*), however, the shoots are differentiated into vegetative and floral shoots.

The shoots can be roughly categorised into three groups: (a) the stem has rather short internodes throughout, bearing the leaves in a basal rosette or loose tuft ('rosulate habit'), (b) the stem has an elongated basal internode, by which the rosette pseudowhorl of leaves is elevated ('verticillate' habit), (c) all internodes are  $\pm$  elongated ('caulescent habit'). In the bulk of species phyllotaxis is decussate, in some whorled (usually whorls of three, rarely of four). The most variable and morphologically/taxonomically informative portion of the shoot is the inflorescence. The core of the present analysis, therefore, relates to this topic.

#### C. Inflorescence terminology

As the term 'inflorescence' is ambiguous, a more specialised terminology is used here for designating the particular structures and substructures of the reproductive region, following essentially Troll (1964).

(a) '**Partial florescence**'. This term relates to the lateral = axillary inflorescences, either subtended by foliage leaves, bracts or transitional forms. In Gesneriaceae, including *Sinningia*, the partial florescences are of a special nature. They represent cymes, in which each of the cyme units seems to end with a flower pair ('pair-flowered cyme'). Each of the 'true' terminal flowers of the cyme units is accompanied by a subsidiary flower in frontal position ('front-flower'). The stalk (hypopodium) of the primary flower pair is the 'peduncle', the stalk supporting the flower is the pedicel, the bracts occurring within the cymes (= subtending bracts of subsequent cyme units) are the 'bracteoles'.

For brevity, the partial florescences are usually referred to as cymes. If not stated otherwise, this always means pair-flowered cymes.

(b) '**Florescence**'. This is the region made up of the partial inflorescences including their subtending leaves. The size and texture of the latter allow the following distinction: (b1) '**Frondose florescence**': subtending leaves of cymes (or solitary flowers) of foliar nature (not or scarcely distinct from the leaves of the vegetative region). (b2) '**Frondo(-bracteo)se florescence**': subtending leaves becoming gradually reduced in size, within the florescence, at least in the lower part of  $\pm$  foliar nature. (b3) '**Frondo(-) bracteo)se florescence**': subtending leaves becoming reduced to bracts in the lower or middle part of the florescence. (b4) '**Bracteo)se florescence**': all subtending leaves reduced to small ( $\pm$  scaly) bracts (abrupt discontinuity between the vegetative and reproductive region).

In the cases of (b3) and (b4) the whole florescence appears as a phenetical unit, for which traditionally the term 'terminal inflorescence' has been used. It must be borne in mind that, when contrasting it with 'axillary inflorescence', one refers to structures of different homology.

(c) '**Paracladia**' or '**enriching branches**': lateral (axillary) branches produced  $\pm$  immediately below the main florescence; they copy the main shoot in structure, ending again in a florescence ('co-florescence'). Main florescence + paracladia form the 'synflorescence'.

**Material and Methods**

Living material was collected by the first author in the field, during several collecting trips to Brazil. Numerous species were studied from cultivated material, grown in the greenhouses of the Conservatoire Botanique de Genève (Switzerland), Mauro Peixoto's private greenhouse (São Paulo, Brazil), the Gesneriad Research Foundation (Sarasota, Florida, USA), and the Botanical Garden of the University of Vienna (Austria). The investigations were complemented through the study of herbarium material from B, CEPEC, F, FCQ, G, GUA, HBR, HCMT, ICN, K, MBM, MBML, MO, NY, P, PACA, PY, R, PY, R, RB, SEL, SP, SPF, UEC, UFSE, US, W, WU. For documentation, a large collection of photographic transparencies was established by the first author. Drawings (based on material preserved in ethanol) and diagrams were produced by Ms. Dagmar Hadl and Mag. Andrea Lindenhofer.

**Results and Discussion**

The c. 60 species known for the genus *Sinningia* exhibit a surprisingly wide range of shoot architecture. In the present investigation 56 species have been analyzed, based on observation of wild or cultivated material as well as herbarium collections (the few remaining species are poorly known, that is only from a single or few herbarium specimens).

**A. Shoot and florescence architecture**

The present analysis resulted in the recognition of 20 types that can be categorised into 5 groups (Table 1). Examples of types (represented by diagrams) belonging to the 5 groups are shown in Figs. 2-5, illustrating some possible transitions between them. Figs. 6-15 show photographic illustrations (taken in the wild or from cultivated material) of species characterising some morphological types or groups.

Most types are closely interconnected, so that practically a continuum exists. Based on successive reduction of basal stem, vegetative internodes, florescence condensation and overall size reduction, the suggested arrangement for the 5 groups and most of the types is shown in Fig. 1.

B4		C4								
B3		C3								
B2		C2								
B1		C1				D				
↑		↑				↑				
A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	
						↓				
						E				

FIG. 1. Arrangement of the 5 groups and most of the types based on successive reduction of basal stem, vegetative internodes, florescence condensation and overall size reduction.

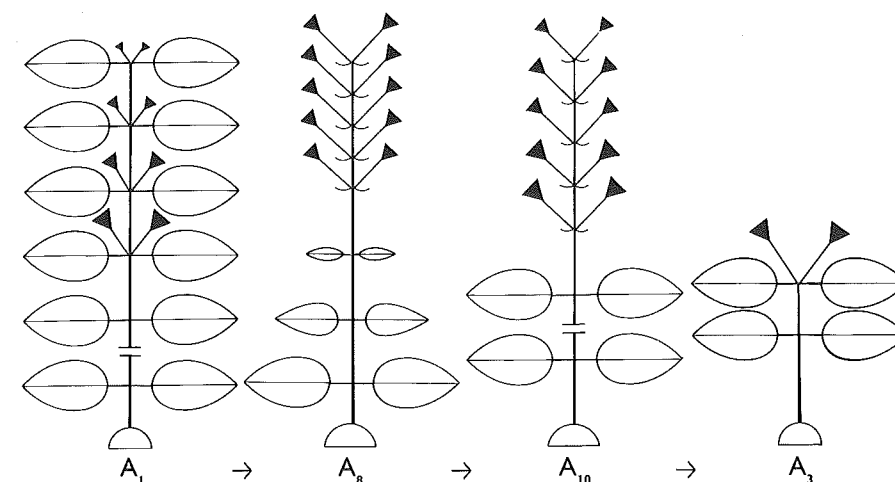


FIG. 2. Possible transitions (arrows) between types in group A (caulescent species). Triangles symbolise cymes

It must be noted, that the arrows in Fig. 1 primarily indicate a formal connection between the particular types and do not necessarily link the respective species in a phylogenetical sense. However, particularly at the 'periphery' (terminal lineages) the probability of direct phylogenetical connections greatly increases. The species exhibiting a highly advanced type of shoot (inflorescence) architecture are often closely related (e.g. D - *S. allagophylla*/*S. curtiflora*; E - *S. tuberosa*/*S. defoliata*) and/or can easily be linked phylogenetically to their formal precursors (C1/C3 e.g. *S. canescens*/*S. leucotricha*).

While it is relatively easy to recognise the specialised and advanced types, it is more difficult to designate the most primitive type. Certainly a type has to be envisaged in which distinct vegetative region and a florescence with pair-flowered cymes (not solitary flowers) can be recognised. It is difficult, however, to decide whether a frondose, frondo-bracteose, or bracteose florescence should be considered as the original condition.

With respect to species number, the (frondo)-bracteose type (A6, A7, A8, A9) is the most prominent one. However, the species are closely related, thus indicating that diversification was a rather recent event.

In contrast, the frondose and frondo-bracteose types (A1, A2, A3, A4) include different alliances of species and are more heterogeneous. This may be taken as an argument that the frondose condition is the ancestral one. In the closely related genera *Pahavania* and *Vanhouttea*, most species have frondose cymes. These taxa differ from *Sinningia* mainly by the absence of a tuber, a shrubby habit and a nectary formed by five small glands. As such characters can be viewed as more primitive, this provides additional evidence to the hypothesis.

**B. Structure and variation of the partial florescence**

The pair-flowered cyme of *Sinningia* shows various kinds of elaboration and reduction:

*Branching pattern.* The usual pattern found in the genus is dichasial branching of the first, and monochasial branching of the subsequent cyme units ('double-cincinnus'). An exception was found only in *S. bulbosa*, where several or all cyme units branch dichasially ('compound dichasium').

TABLE 1. *Sinningia* species arranged into the 5 main groups (A - E) and 20 types based on shoot and inflorescence morphology. For each species, the author, pollination syndrome (CHIR: chiropterophilous; MEL: melittophilous; ORN: ornithophilous; PSY: psychophilous; SPHI: sphingophilous) and range (vl: very local range, up to 100 km; l: local range, from 100 - 500 km; w: wide range, from 500 - 2000 km; vw: very wide range, more than 2000 km; ?: no data available on wild collection).

## A. Caulescent species

A1. Caulescent species with frondose florescence (typical form)			
<i>S. schiffneri</i> Fritsch	MEL	1	
A2. Caulescent species with frondose florescence (special forms)			
<i>S. amambayensis</i> Chautems	ORN	vl	
<i>S. mauroana</i> Chautems	ORN	1	
<i>S. reitzii</i> (Hoehne) L.Skog	ORN	1	
<i>S. villosa</i> Lindl.	MEL	1	
A3. Caulescent species with shoots reduced to frondose florescence			
<i>S. lineata</i> (Hjelm.) Chautems (2-3 leaf pairs) (Figs. 6-7)	ORN	vl	
<i>S. macropoda</i> (Sprague) H.E.Moore (1 leaf pair) (Fig. 9)	ORN	w	
A4. Caulescent species with frondo(-bracteose) florescence with cymes			
<i>S. carangolensis</i> Chautems	ORN	vl	
A5. Caulescent species with frondo(-bracteose) florescence with solitary flowers			
<i>S. glazioviana</i> (Fritsch) Chautems	ORN	vl	
<i>S. harleyi</i> Wiehler & Chautems	ORN	vl	
<i>S. helleri</i> Nees	MEL	vl	
<i>S. lindleyi</i> Schauer (Fig. 10)	MEL	vl	
<i>S. guttata</i> Lindl.	MEL	vl	
A6. Caulescent species with (frondo-)bracteose florescence with cymes (variation may include occasional reduction to solitary flowers)			
<i>S. aggregata</i> (Ker Gawl.) Wiehler	ORN	w	
<i>S. bulbosa</i> (Ker Gawl.) Wiehler	ORN	1	
<i>S. cardinalis</i> (Lehm.) H.E.Moore (wild form)	ORN	vl	
<i>S. elatior</i> (Kunth) Chautems	ORN	vw	
<i>S. incarnata</i> (Aubl.) D. Denham	ORN	vw	
<i>S. lateritia</i> (Lindl.) Chautems	ORN	1	
<i>S. magnifica</i> (Otto & A.Dietr.) Wiehler	ORN	w	
<i>S. macrostachya</i> (Lindl.) Chautems	ORN	w	
<i>S. striata</i> (Fritsch) Chautems	ORN	vl	
<i>S. sulcata</i> (Rusby) Wiehler	ORN	w	
<i>S. valsuganensis</i> Chautems	ORN	1	
A7. Caulescent species with (frondo-)bracteose florescence with solitary flowers			
<i>S. brasiliensis</i> (Regel & Schmidt) Wiehler & Chautems	CHIR	w	
<i>S. sceptrum</i> (Mart.) Wiehler	ORN	w	
<i>S. tubiflora</i> (Hook.) Fritsch	SPHI	1	
A8. Caulescent species with (frondo-)bracteose, down-curved florescence (with cymes)			
<i>S. cooperi</i> (Paxt.) Wiehler	ORN	w	
A9. Caulescent species with (frondo-)bracteose florescence (with cymes) and flowering side branches (paracladia)			
<i>S. sellovii</i> (Mart.) H.E.Moore	ORN	w	
<i>S. warmingii</i> (Hiern) Chautems (Fig. 8)	ORN	vw	
A10. Caulescent species with strictly bracteose florescence (with cymes)			
<i>S. cochlearis</i> (Hook.) Chautems	ORN	vl	
<i>S. gigantifolia</i> Chautems	ORN	1	

TABLE 1 continued

## Group B. Rosette species

B1. Species with rosulate-caulescent habit			
<i>S. barbata</i> (Nees & Mart.) G.Nicholson	MEL	w	
<i>S. conspicua</i> (Seem.) G.Nicholson	MEL	1	
B2. Species with prostrate-rosulate habit			
<i>S. kautskyi</i> Chautems	MEL	vl	
B3. Species with rosulate or rosette habit (typical form)			
<i>S. eumorpha</i> H.E.Moore (Fig. 11)	MEL	1	
<i>S. richii</i> Clayberg	MEL	vl	
<i>S. speciosa</i> (Lodd.) Hiern	MEL	w	
<i>S. hirsuta</i> (Lindl.) G.Nicholson	MEL	vl	
B4. Species with miniature rosette habit			
<i>S. pusilla</i> (Mart.) Baill. (Fig. 14)	PSY	1	
<i>S. concinna</i> (Hook.f.) Hanst.	PSY	?	

## Group C. Verticillate species

C1. Species with caulescent-subverticillate vegetative region and compact (condensed flowers)			
<i>S. canescens</i> (Mart.) Wiehler	ORN	1	
<i>S. cardinalis</i> (cultivated strains)	ORN	-	
C2. Species with verticillate leaves (pseudowhorl) and elevated, capitate florescence			
<i>S. douglasii</i> (Lindl.) Chautems (Fig. 12)	ORN	w	
<i>S. iarae</i> Chautems	ORN	vl	
<i>S. insularis</i> (Hoehne) Chautems	ORN	vl	
<i>S. micans</i> (Fritsch) Chautems + <i>arenicola</i>	ORN	vl	
<i>S. nivalis</i> Chautems	ORN	1	
<i>S. rupicola</i> (Mart.) Wiehler	ORN	vl	
C3. Species with verticillate leaves with axillary cymes			
<i>S. calcaria</i> (Malme) Chautems	ORN	vl	
<i>S. leopoldii</i> (Planch.) Chautems	ORN	vl	
<i>S. leucotricha</i> (Hoehne) H.E.Moore	ORN	vl	
C4. Species with verticillate leaves and a single, ± erect long-pedunculate cyme			
<i>S. aghensis</i> Chautems	MEL	vl	

## Group D. Spicate species

Caulescent species with bracteose, elongated, spicate florescence			
<i>S. allagophylla</i> (Mart.) Wiehler (Fig. 13)	ORN/PSY?	w	
<i>S. curtiflora</i> (Malme) Chautems	ORN	1	

## Group E. Unifoliate species

<i>S. tuberosa</i> (Mart.) H.E.Moore (Fig. 15)	ORN	1	
<i>S. defoliata</i> (Malme) Chautems	ORN	1	

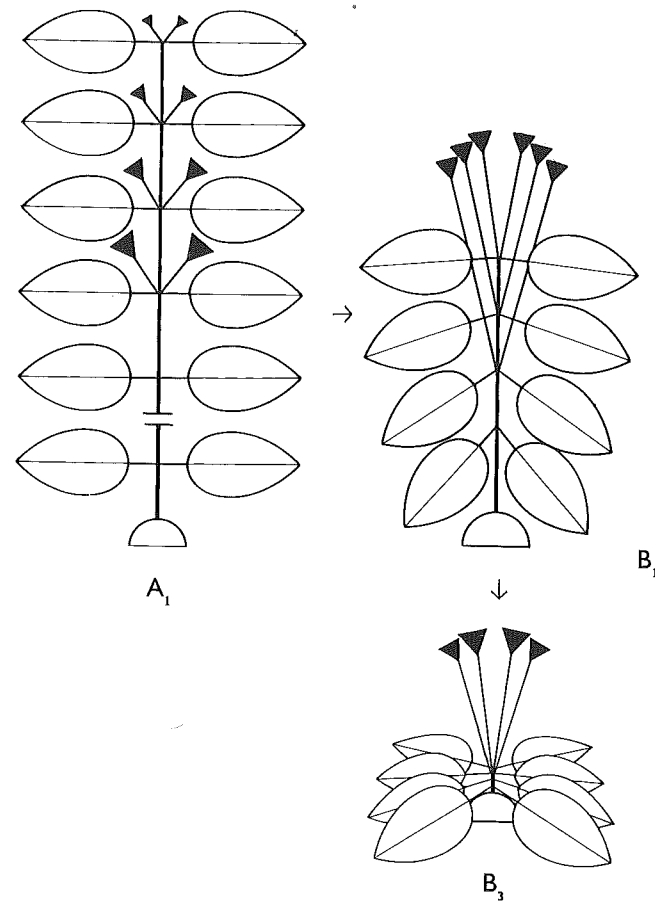


FIG. 3. Possible transitions (arrows) from group A (caulescent species) to types in group B (rosette species).

*Number of flowers.* Flower (pair) number is subject to considerable variation, not only from species to species, but also in the specimens of a single species (mainly due to growing conditions) as well as within a single plant (e.g., gradual reduction towards the florescence apex). In most species, the range of variation can be defined. In *S. aggregata*, however, a variation range from 1-24 flowers has been found, allowing practically no specification.

*Reduction of cymes to solitary flowers* (= terminal flowers of primary cyme units). Single flowers in the leaf/bract axils are often within the variation range of few-flowered inflorescences. However, there occur also obligatory solitary flowers (the pair-flowered thyrses thus changing to a raceme). When prophylls are present, these are usually placed at the base of the stalk supporting the flowers, thus demonstrating that the stalk corresponds to the pedicel.

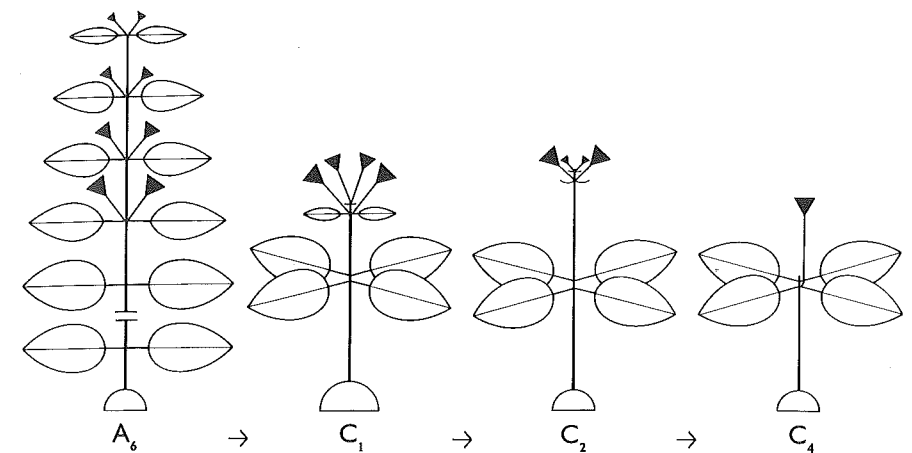


FIG. 4. Possible transitions (arrows) from group A (caulescent species) to types in group C (verticillate species).

*Reduction of front-flower.* Apart from the obligatory reduction of the cyme to a single flower, reduction (loss) of front-flowers, either irregular or regular (see Weber, 1978), has not been observed. It often occurs, however, that the latest units of a cyme are incompletely developed and the front-flowers are arrested in early development.

*Bracteole presence and texture.* Bracteoles are usually present in the form of scale-like, oblong or lanceolate bracts. Only in *S. reitzii* it was observed that the primary bracteoles (prophylls) were enlarged and differentiated into a short petiole and a small lamina. Bracteole reduction occurs in a number of species and to a different degree. In *S. macropoda*, for instance the bracteoles are reduced to a hump or slight swelling located below the lateral cyme branches. In *S. lineata* such a swelling is scarcely recognisable, but can be still seen in the early stages of cyme development (Weber, 1995).

*Presence of O-bract.* Normally, the front flowers are not subtended by a bract and, therefore, have been regarded as accessory (adventive) flowers by Troll (1964) and earlier authors. *S. bulbosa* is one of the few exceptions (both with regard to the other species of *Sinningia* and to the family), in which the front-flowers exhibit their axillary nature by the presence of a subtending bract (Weber, 1973, 1982, under *Reichsteimeria macrorhiza* and *Sinningia macrorhiza*, names recently were put into synonymy by Chautems, 1990). It has recently been shown in a developmental study that the association of the bract with the front-flower is not a superficial and accidental positional relationship (Weber, 1995).

*Peduncle.* The length of peduncle is subject to considerable specific (and, to a lesser degree, individual) variation. In its ecological significance it has to be seen in connection with the length of the pedicels. Short peduncles are usually correlated with (at least somewhat) elongated pedicels (and vice versa), particularly in ornithophilous species.

The complete suppression ('absence') of the peduncle in the *S. speciosa*-alliance is remarkable. If more than one flower is present, they all seem to emerge from a single point at the petiole, without the intercalation of a peduncle. The obscured existence of a peduncle is sometimes indicated by the presence of basally inserted prophylls. Subsequent cyme axes (hypopodia). These are usually short and never extensively elongated. By progressive shortening the flowers appear crowded, with the pedicels finally seeming to emerge from a single point.

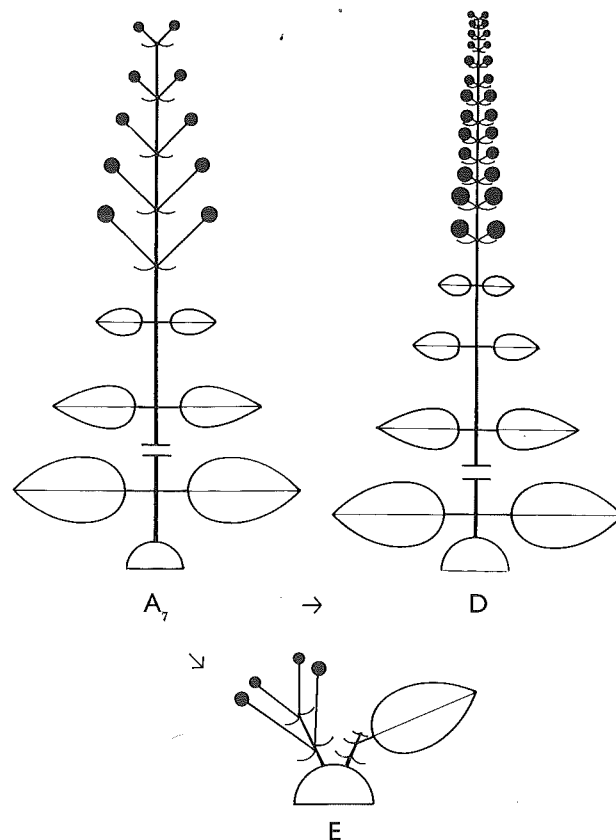


FIG. 5. Possible transitions (arrows) between types in group A (caulescent species), D (spicate species), E (unifoliate species). Circles symbolise solitary flowers.

*Pedicels.* The pedicels are usually of medium length to distinctly elongated, rarely shortened or lacking (*S. allagophylla*, *S. curtiflora*). As mentioned before, pedicel length must be seen in relation to peduncle length. Orientation (position in space) is a significant part of the pollination syndrome. Spreading to (sub)erect position usually serves to expose the flowers above the foliage (e.g., *S. speciosa*, *S. reitzii*). Flower exposed by pendent pedicels are found in *S. sellovii* and *S. sulcata*. Remarkable are the pedicels of the ornithophilous *S. carangolensis*, which curve at the base and then spread roughly horizontally below the leaf. In the epiphytic *S. cooperi*, with downcurving florescences and thus 'wrongly positioned' cymes, the pedicels twist in order to bring the flower into the correct functional position.

*Serial cymes* (flowers). In *Sinningia* usually a single cyme (or solitary flower) is produced in a leaf axil. An accessory bud is often present, but normally does not develop to a cyme or flower. The only exception found was *S. barbata*. Here the solitary flower is occasionally followed by another one in serial position. The first impression is that a cyme reduced to a single flower pair (terminal + front flower) is present. However, the presence of lateral bracts on the second flower demonstrates, that it is an extra, accessory flower, corresponding to a reduced cyme.

### C. Pollination, habitat and distribution patterns

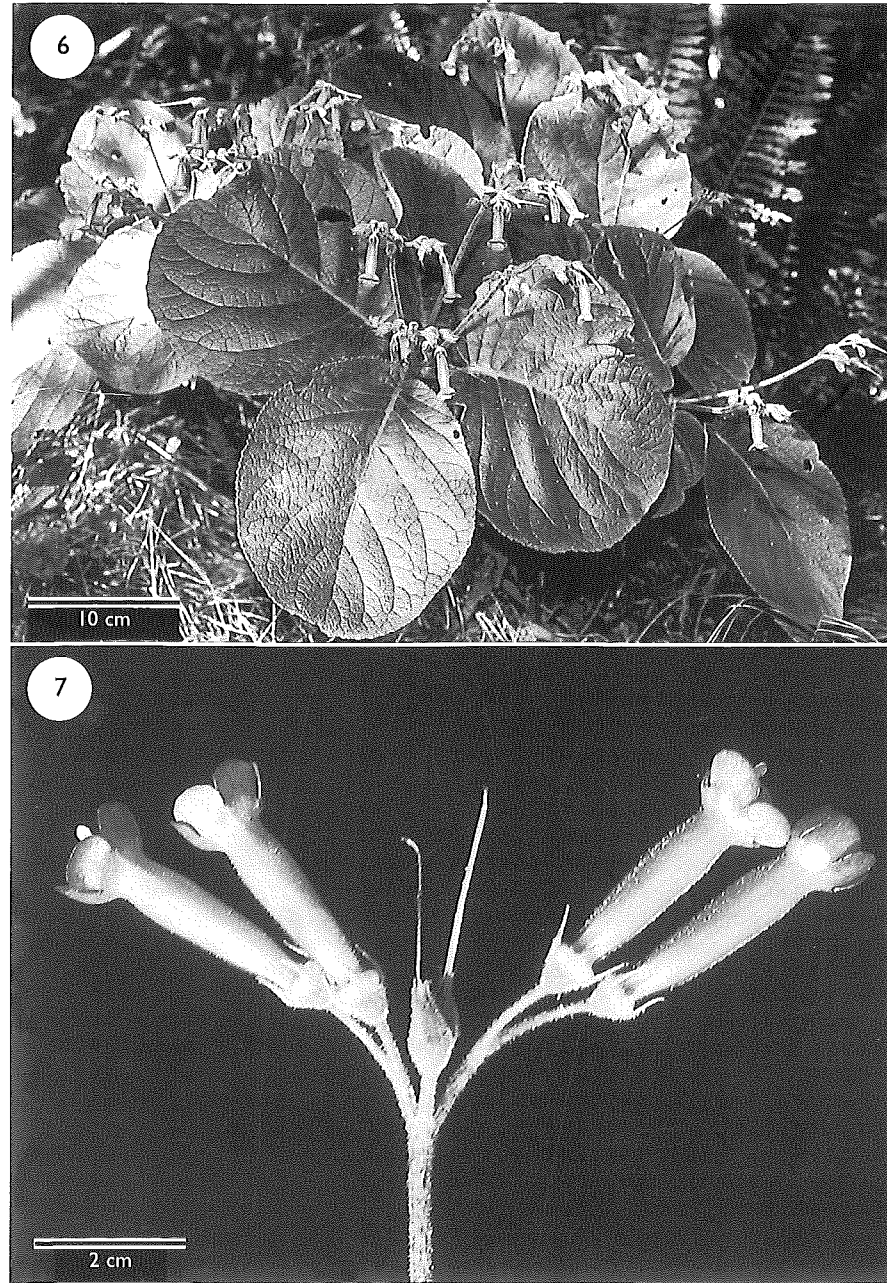
The genus *Sinningia* displays such a wide range of morphological and biological variation, that it is not easy to identify and understand the responsible factors. Some interesting correlations can be noted between pollination biology and forms of shoot/florescences observed. Habitat adaptations and distribution patterns also deserve a few comments.

Among the 5 pollination syndromes noted (Table 1), ornithophily plays a dominant role in 66% of the species. Melittophily comes second and is observed in about 20% of the species. Psychophily and sphingophily concern only 2 species each, while chiropterophily is restricted to only 1. The rosette habit (cf. group B) seems especially well correlated with bee (probably *Euglossine*) visits. Hummingbirds would probably have difficulty in reaching flowers very low on the ground. Group A includes species belonging to 4 different pollination syndromes, re-inforcing its placement at a less specialised phylogenetic level. From our present knowledge, it is highly speculative to say that melittophily is a more primitive stage from which the other syndromes are derived. Several fertile interspecific hybrids between species belonging to different syndromes have been produced (recapitulated in Boggan, 1991). These hybridisation experiments also indicate that similar floral morphology is not always a good indication of narrow phylogenetic relationships. Shoot and florescence morphology in hybrids of different groups are fully intermediate between the 2 parent species. This suggests again the close relation between the taxa. The significance of the morphological groups and types, therefore, must not be over-emphasised with respect to a phylogenetic arrangement of the genus.

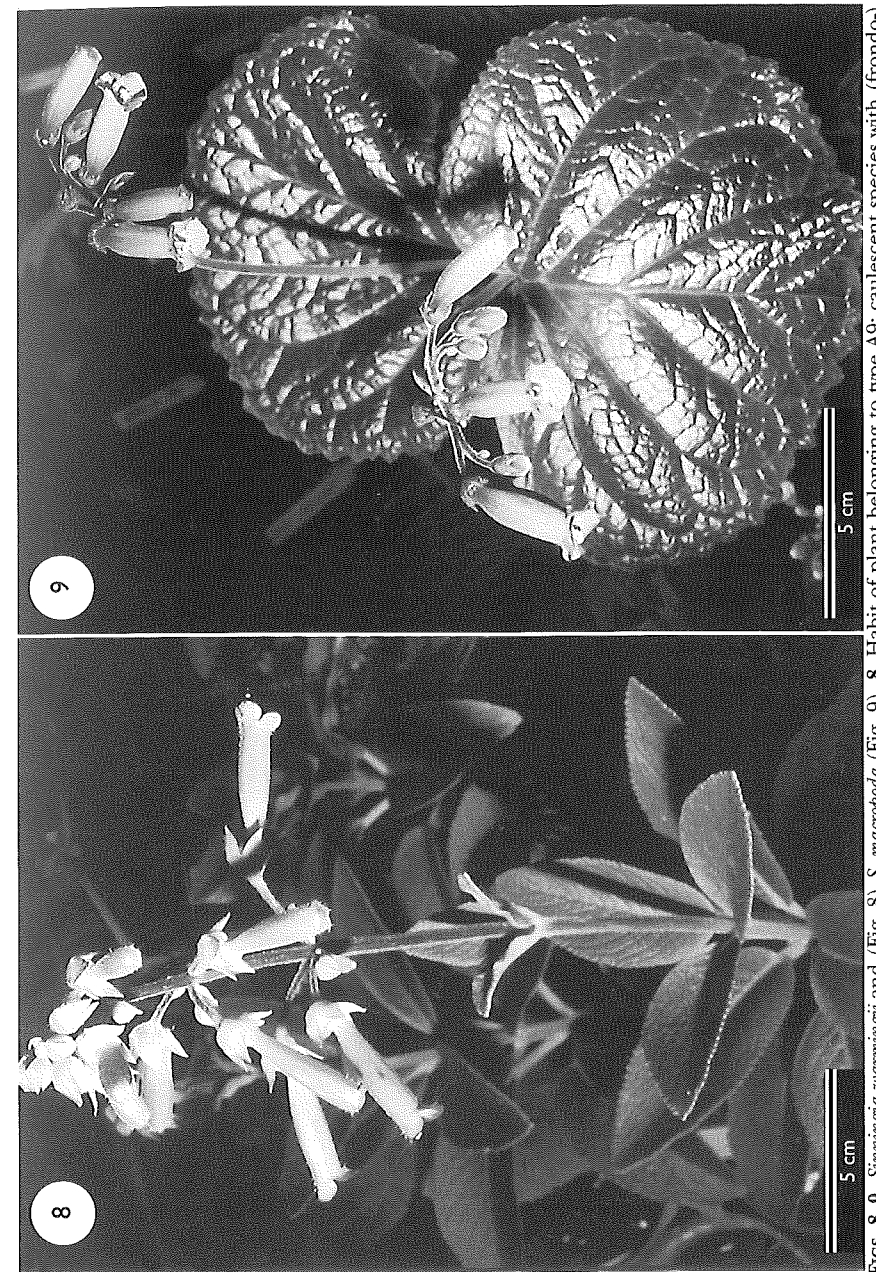
Among the 5 groups distinguished in our study, some habitat adaptations become apparent. Group A (caulescent plants) again is more heterogenous and does not show specific habitat preferences: it is composed of a wide array of types with tuber sometimes lacking or  $\pm$  developed in accordance with adaptation to forest, semi-open or open habitat. Group B (rosette plants) thrives usually in dense forests with accumulation of organic matter on a  $\pm$  rocky substrate. Group C (verticillate plants) usually prefers open rocks or even grow as epiphytes (*S. douglasii*). Group D (spicate plants) is found in campos or forest edges with underground tubers. Group D (unifoliate plants) is highly specialised and restricted to shady and humid rocks.

In an attempt to correlate shoot and inflorescence morphology with distribution, we divided the species into four range classes (Table 1). A general look at the distribution patterns shows that a vast majority of species occupies a small range, 22 are very local and 16 local. Only 12 colonise a wide range and 3 reach a "continental" distribution.

Considering the morphological groups, we found again more heterogeneity in group A, which contains taxa with a very local to a very wide range. Among those species with a very wide range, 2 species (*S. elatior* and *S. warmingii*) extend their distribution from northern Argentina through to Venezuela and Peru respectively, establishing a connection through the Andes; *S. incarnata* is found from the eastern coast in Brazil to southern Mexico, following the Atlantic coast all through to the Guianas and Central America. None of the species in B, C, D and E has a very wide range. From a geographical point of view, the vast majority of the species grows in southeastern Brazil, with a center of diversity located between the states of Minas Gerais, Rio de Janeiro and São Paulo. This fact might suggest that this area, known to have kept rather stable climatic conditions throughout the past, is a center of origin for the genus. There is nevertheless a puzzling situation with *S. richii*. This species found only in Mexico, stands completely isolated from the rest of the species and its nearest morphological "relative" is *S. eumorpha* from São Paulo/Paraná in Brazil. This case could be considered a striking example of homoplasy in the genus, unless one imagines extinct ancestors as a former link.



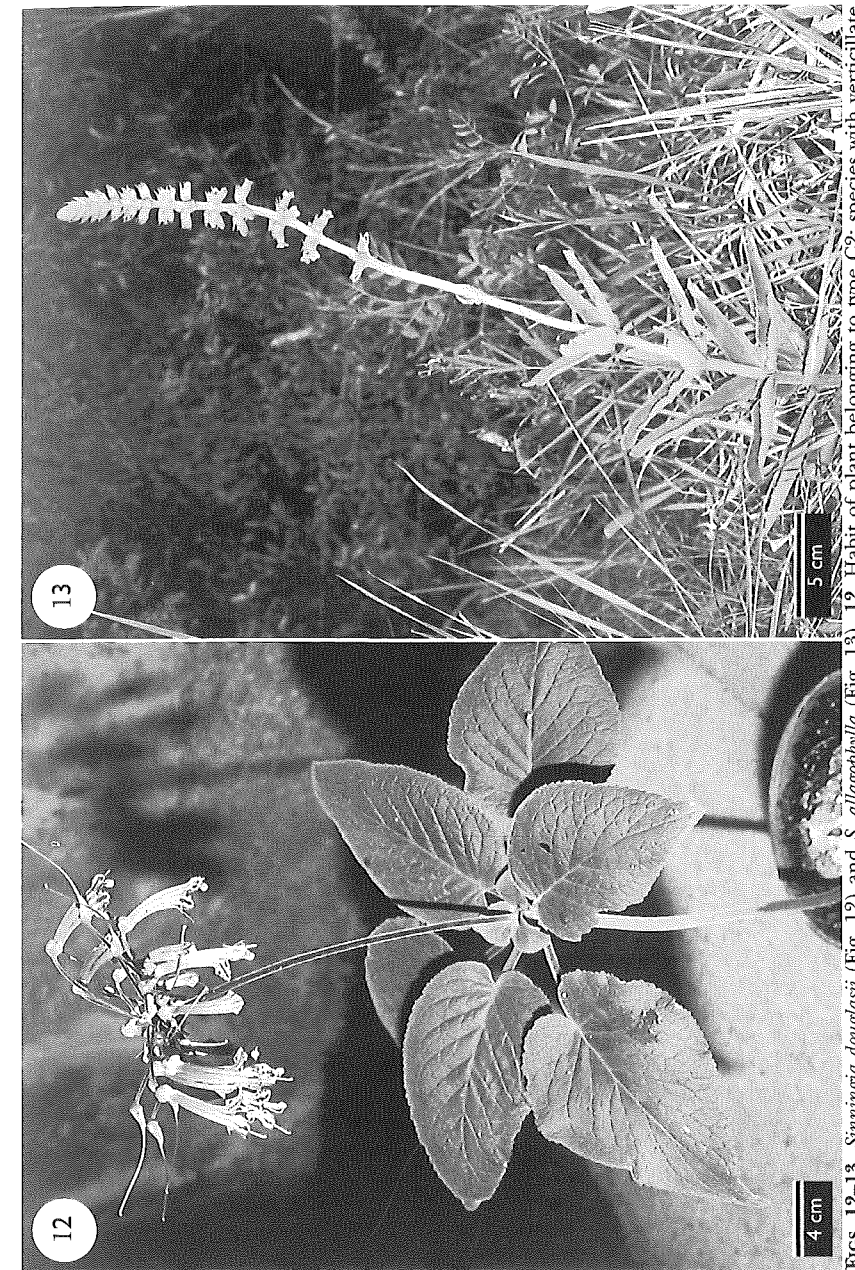
FIGS. 6-7. *Sinningia lineata*. 6. habit of plant belonging to type A3: caulescent species with shoot reduced to frondose florescence. 7. detail of partial florescence with 'pair-flowered cymes'.



FIGS. 8-9. *Sinningia uanmingii* and (Fig. 8) *S. macropoda* (Fig. 9). 8. Habit of plant belonging to type A9: caulescent species with (frondo-) bracteose florescence with cymes and flowering side branches. 9. Another example of type A3 with leaves reduced to one leaf pair.

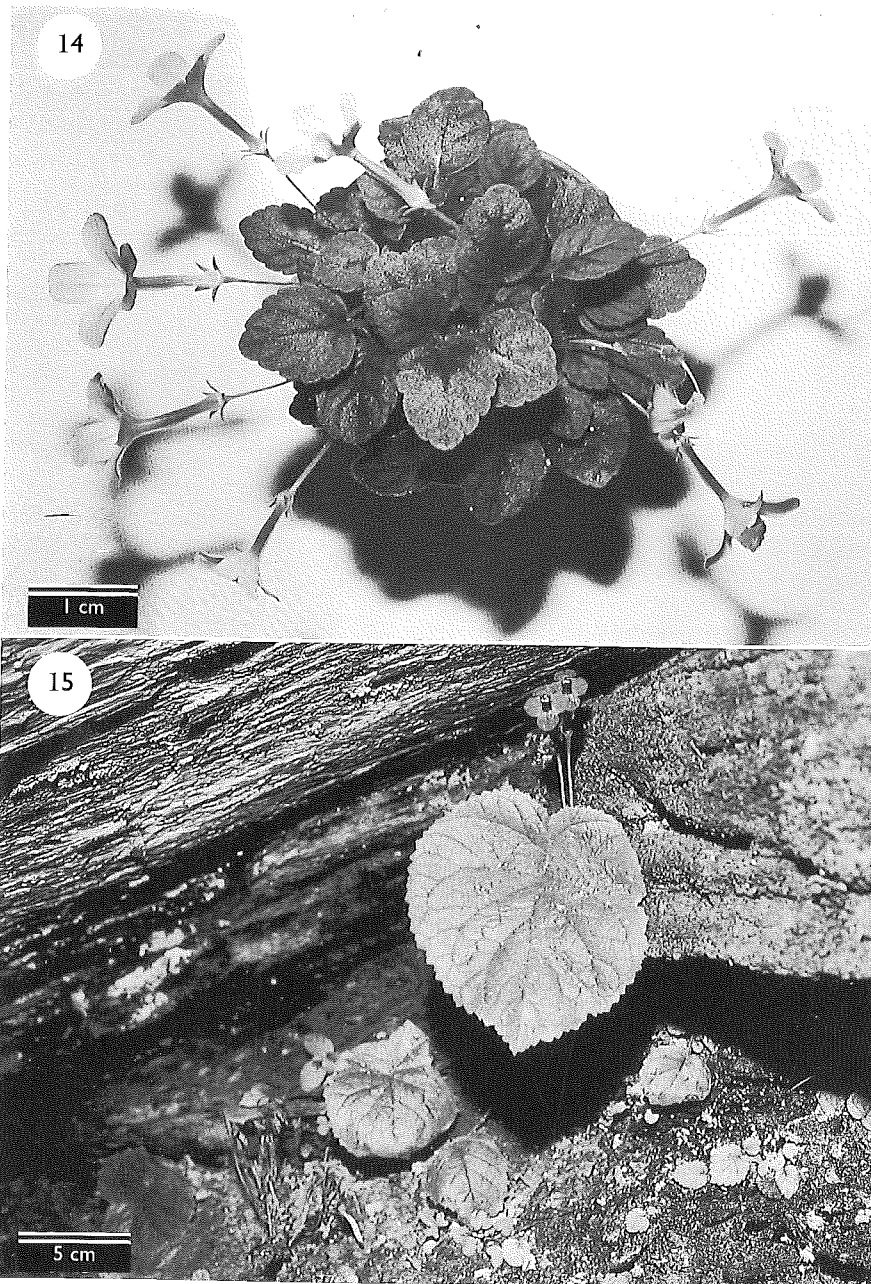


FIGS. 10–11. *Sinningia lindleyi* (Fig. 10) and *S. eumorpha* (Fig. 11). 10. Habit of plant belonging to type A5: caulescent species with frondo (-bracteose) florescence with solitary flowers. 11. Habit of plant belonging to type B3: species with rosulate or rosette habit (typical form).



FIGS. 12–13. *Sinningia douglasii* (Fig. 12) and *S. allagophylla* (Fig. 13). 12. Habit of plant belonging to type C2: species with verticillate leaves (pseudowhorl) and elevated, capitate florescence. 13. Habit of plant belonging to group D: caulescent species with bracteose, elongated, spicate florescence.





FIGS. 14–15. *Sinningia pusilla* (Fig. 14) and *S. tuberosa* (Fig. 15). 14. Habit of plant belonging to type B4: species with miniature rosette habit. 15. Habit of plant belonging to type E: unifoliate species.

#### D. Conclusions

The discussion on the shoot and florescence morphology of *Sinningia* shows that a well established phylogenetic classification of the genus is not easy to reach. The genus still lacks a reliable infrageneric classification. All the treatments published previously were chiefly based on corolla shape and nectary glands. Such features, however, only reflect pollination adaptations and are of very limited taxonomic value. The arrangement into types and groups proposed here is a first attempt, which needs further discussion and testing with information from other fields such as analysis of artificial hybridisation, as initiated by Clayberg (1968, 1970). New techniques of molecular biology would probably help in establishing a firmer phylogeny for *Sinningia*. For these reasons it is too early to propose a new systematic arrangement for the genus. Nonetheless the groups and types suggested here form a convenient configuration and open the way to future studies.

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## ALLOCATION OF REPRODUCTIVE RESOURCES WITHIN INFLORESCENCES OF *ANTHYLLIS VULNERARIA* SUBSP. *VULGARIS* (FABACEAE)

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### Abstract

The grouping of flowers in inflorescences is a common characteristic of plants and has important implications for resource distribution. It was investigated whether the position of inflorescences on plants of *Anthyllis vulneraria* subsp. *vulgaris* affects fruit set, seed weight, and/or fruit weight. *Anthyllis vulneraria* subsp. *vulgaris* is a perennial herb. Each plant comprises several independently arising flowering shoots. Each shoot bears several inflorescences which flower acropetally. The results indicate that fruit set, seed weight and fruit weight all vary significantly ( $p < 0.05$ ) among inflorescences within shoots, and are in all cases higher for early-flowering than for later-flowering inflorescences of a shoot. This ranking order is not an artifact due to among-inflorescence differences in phenology, since neither fruit set, seed weight nor fruit weight differed significantly between inflorescences of the early and late subperiods of the population flowering period. These results suggest that shoots of *Anthyllis vulneraria* subsp. *vulgaris* function as semi-autonomous units in regard to resource utilization.

### Introduction

Architectural effects could be responsible for fruit and seed development patterns (Diggle, 1995). In this sense, the role played by a flower in the plant's overall reproductive strategy may differ according to the position of that flower within the inflorescence, and flowers within the same inflorescence may have different reproductive "values" (Stephenson, 1981; Lee, 1988). In many species, early-opening flowers or inflorescences have a higher probability of setting fruit than late-opening flowers or inflorescences. This may for example be due to allocation of more resources during the early stages of the flowering period (see Ashman and Baker, 1992 and references therein). In addition to such temporal advantages, spatial advantages may also be relevant. In some species, proximal flowers have a higher probability of setting fruit and tend to produce heavier seeds, than more distal flowers. This may be related to preferential access to nutrients. Spatial and temporal advantages of this type may be relevant among flowers in the same inflorescence or among inflorescences (Lee, 1988; Solomon, 1988; Devlin, 1989; Herrera, 1991; Stephenson, 1992; Ehrlen, 1993; Guitián, 1993; Vaughton, 1993).

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