Ontogenetic studies on the determination of the apical meristem in racemose inflorescences

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CONTENTS

SUMMARY OF THE THESIS

This thesis presents a comparative developmental study of inflorescences and focuses on the production of the terminal flower (TF). Morphometric attributes of inflorescence meristems (IM) were obtained throughout the ontogeny of inflorescence buds with the aim of describing possible spatial constraints that could explain the failure in developing the TF. The study exposes the inflorescence ontogeny of 20 species from five families of the Eudicots (Berberidaceae, Papaveraceae-Fumarioideae, Rosaceae, Campanulaceae and Apiaceae) in which 745 buds of open (i.e. without TF) and closed (i.e. with TF) inflorescences were observed under the scanning electron microscope.

The study shows that TFs appear on IMs which are 2,75 (se = 0,38) times larger than the youngest lateral reproductive primordium. The shape of these IMs is characterized by a leaf arc (phyllotactic attribute) of 91,84° (se = 7,32) and a meristematic elevation of 27,93° (se = 5,42). IMs of open inflorescences show a significant lower relative surface, averaging 1,09 (se=0,26) times the youngest primordium size, which suggests their incapacity for producing TFs. The relative lower size of open IMs is either a condition throughout the complete ontogeny ('open I') or a result from the drastic reduction of the meristematic surface after flower segregation ('open II').

It is concluded that a suitable bulge configuration of the IM is a prerequisite for TF formation. Observations in the TF-facultative species Daucus carota support this view, as the absence of the TF in certain umbellets is correlated with a reduction of their IM dimensions. A review of literature regarding histological development of IMs and genetic regulation of inflorescences suggests that in 'open I' inflorescences, the histological composition and molecular activity at the tip of the IM could impede the TF differentiation. On the other side, in 'open II' inflorescences, the small final IM bulge could represent a spatial constraint that hinders the differentiation of the TF. The existence of two distinct kinds of ontogenies of open inflorescences suggests two ways in which the loss of the TF could have occurred in the course of evolution.

ZUSAMMENFASSUNG

Die Dissertation beinhaltet eine vergleichende Studie zur Entwicklung von Blütenständen, wobei der Schwerpunkt auf der Bildung bzw. dem Fehlen von Endblüten (EB) liegt. Morphometrische Veränderungen, die während der Ontogenie der Blütenstandsknospen am Infloreszenzmeristem (IM) auftreten, wurden erstmals ermittelt und quantifiziert, um eventuelle räumliche Zwänge, die das Ausfallen der EB erklären könnten, zu beschreiben. Die Studie umfasst die Infloreszenzontogenie von 20 Arten aus fünf Familien der Eudicotyledonae (Berberidaceae, Papaveraceae-Fumarioideae, Rosaceae, Campanulaceae and Apiaceae) mit offenen (ohne EB) und geschlossenen (mit EB) Blütenständen. Sie basiert auf der Analyse von 745 Infloreszenzknospen unter dem Rasterelektronmikroskop.

Die Ergebnisse zeigen, dass sich Endblüten nur an Infloreszenzmeristemen entwickeln, die 2,75 (se = 0,38) Mal so groß sind wie ihr jüngstes Seitenprimordium. Ihre Form wird weiterhin von einem Primordienansatz von 91,84° (se = 7,32) und einer Wölbung von 27,93° (se = 5,42) bestimmt. Infloreszenzmeristeme offener Blütenständen zeigen dagegen mit nur 1,09-facher (se = 0,26) Größe des jüngsten Seitenprimordiums signifikant kleinere Werte. Dies deutet darauf hin, dass eine bestimmte Gewebemasse für die Endblütenbildung zur Verfügung stehen muss. Die relativ kleineren IMs sind entweder die gesamte Ontogenie hindurch vorhanden (‚open I') oder entstehen erst im Zuge der Blütenausgliederung durch die rasche Abnahme des meristematischen Gewebes (‚open II').

Beobachtungen an *Daucus carota* unterstützen die Annahme, dass eine passende IM-Konfiguration vorliegen muss, bevor eine EB gebildet werden kann. In dieser Art werden fakultativ Endblüten gebildet, wobei das Fehlen der EB immer mit einer Reduktion der IM-Dimensionen einhergeht.

Umfassende Literaturrecherchen weisen darauf hin, dass das Fehlen einer EB in ‚open I' Infloreszenzen auf der noch vegetativ geprägten histologischen Zonierung und genetischen Aktivität an der Spitze des IMs beruhen könnte. Demgegenüber könnten die am Ende der Blütenausgliederung klein gewordenen IMs der ‘open II' Infloreszenzen aufgrund ihrer engen räumlichen Verhältnisse nicht mehr in der Lage sein, eine Endblüte zu produzieren. Der Nachweis von zwei unterschiedlichen Ontogenien in offenen Blütenständen deutet darauf hin, dass auch im Laufe der Evolution die Endblüte durch unterschiedliche Prozesse entstanden bzw. verloren gegangen ist.

1 GENERAL INTRODUCTION

1.1 Historical treatment of the terminal flower production in inflorescences

After the introduction of the term 'inflorescence' by Linnaeus in the XVIII century, Roeper (1826) established the first classification of inflorescences. He distinguished two main types, the `definita´ and the `indefinita´ inflorescences. According to him, the first have a terminal flower (TF) on the main axis and a centrifugal flowering sequence, while the second miss a TF and show a centripetal flowering. This definition provoked the morphologists of the XIX century to pay particular attention to these attributes.

While some botanists as Bravais and Bravais (1837), Wydler (1851) and Hy (1894) accepted the TF as a valuable criterion for inflorescence classification, the majority of the morphologists were skeptical against it since the TF neither represented a stable character within a species nor a clear interdependence with other inflorescence attributes as flowering sequence or ramification mode (e.g. Guillard 1857, Eichler 1875, Čelakovský 1893). The repeated efforts to find a reliable classification for inflorescences is reflected in the diversity of proposals found throughout the XIX century (see Velenovský 1910). They all corresponded in grouping inflorescences according to their ramification pattern resulting in 'racemose' and 'cymose' inflorescences (Velenovský 1910).

This view was maintained throughout the first half of the XX century (Goebel 1931, Zimmermann 1935) and only replaced by the work of Wilhelm Troll (1964). Troll, focusing on herbaceous plants (Troll 1950), distinguished the principal flowering unit from the accessory ones that repeat the principal pattern on subsidiary axes. He used the term 'synflorescence', earlier presented by Goebel (1931) for compound inflorescences, to characterize two types of inflorescences that differed in the nature of their principal flowering unit: the polytelic type, whose principal unit is based on a raceme and called main florescence (Hauptfloreszenz, HF) and the monotelic type, whose principal unit corresponds to a single flower (Troll 1964, Claßen-Bockhoff 2001). This classification implied a grouping of the inflorescences according to the presence or absence of the terminal flower (TF). Referring to

Roeper (1826), Troll simplified the concept of 'determinate' [1] (1964), restraining it to the presence of a TF and excluding complementing attributes as flowering sequence and ramification pattern. Conscious of the fact that TFs and HFs can sometimes fail to be produced (Guillard 1857, Wydler 1860, Eichler 1875, Troll 1964) Troll used the term 'truncation' to denominate the lack of a TF or HF in monotelic and polytelic synflorescences.

A second stream that re-directed attention to the TF in the XX century was the phylogenetic approach to understand inflorescences. It intended to explain the evolutionary origin of inflorescence diversity proposing architectural shifts from putative ancestral inflorescences towards more derivate states. The first phylogeny was presented by Parkin (1914), who postulated that the diversity of inflorescences had arisen from a primitive 'single TF condition'. Variation on this theme followed in the XX century e.g. by Rickett (1944) and Takhtajan (1959). Based on these works, Stebbins (1974) adopted the view that the diversity of inflorescences could be well classified distinguishing between the more primitive 'determinate' inflorescences (with TF) and the more derived 'indeterminate' ones (without TF).

Stebbins' conception, complemented with Trolls ideas that were later expressed in English by his follower Weberling (1989), cemented the modern inflorescence understanding with the presence of the TF as a main issue (Tucker 1999, Claßen-Bockhoff 2000, Prusinkiewicz et al. 2007, Prenner et al. 2009).

1.2 Structural understanding of the TF

Stebbins (1974) also delivered a conceptual framework for understanding the physiology of the presence or absence of terminal flowers in inflorescences. Based on his observations on the variability of TF formation in *Penstemon* and *Pharbitis*, he pointed out, that the 'vigor' of the plant should be related to the TF production in the sense that it hinders the floral hormones to act on the tip of the axis. He complemented this view with the contemporary knowledge of inflorescence histology that classified the inflorescence meristems (IM) as either having a 'central zone' (CZ) or a 'mantle-core' (MC) configuration (Cutter 1965, Gifford

[1] Troll (1964, pp.8) uses the German terms 'begrenzt' and 'determiniert' in direct allusion to the 'definita' category of Roeper (1826).

and Corson 1971). Since terminal flowers were always described in the context of the MC-type, Stebbins (1974) re-proposed the idea formulated almost 20 years before by Plantefol (1957), that the absence of the TF in inflorescences could be related to the existence of the CZ on the IM. This conceptual relation between a histo-physiological quality of the IM and the absence of the TF found spectacular confirmation in the 90's. In this decade, selectively isolated mutants of *Arabidopsis* (Álvarez et al. 1992, Shannon and Meeks-Wagner 1991) and *Antirrhinum* (Bradley et al. 1996) allowed to postulate that the absence of a TF in racemes was related to the action of specific gene products (TFL1 in *Arabidopsis* and CEN in *Antirrhinum*) that impeded the action of floral identity genes to be expressed on the tip of the IM (Coen and Nugent 1994). The present developmental molecular research on inflorescences is significantly based on these facts (Angenent et al. 2005, Benlloch et al. 2007, Wang and Li 2008, Szczęsny et al., 2009). Troll and Weberling (1998) found no biological support in this kind of argumentation, since they did not attribute a 'real' TF status to the described experimental mutants. However, the current hypothesis respecting inflorescence evolution is partly made on this principle (Prusinkiewicz et al. 2007, Castel et al. 2010).

Ontogenetically, the origin of the TF can be traced back to the transformation of the IM into a flower (Troll 1964). This process brings as a consequence that the TF instantaneously adopts a more advanced ontogenetic stage than the subapical flowers. And it disrupts the normal acropetal flowering in an inflorescence axis, since the TF typically is the first to bloom on the inflorescence, or at least, before its adjacent flowers.

1.3 Parallel evolution of the character states referring the TF

Interestingly, open and closed inflorescences are systematically found in diverse lineages of the angiosperms (Troll 1964, Stebbins 1974). Following the inflorescence conception, it is considered that the presence of a TF represents the ancestral state and that the TF has become lost many times in parallel (Stebbins 1974, Sell 1976, Weberling 1989). However, that 'truncation', i.e. loss of the TF, should be the only process in inflorescence evolution has been questioned in the last decades, as cladistic analyses have presented taxa in derived positions showing a reconstitution of the TF (Endress 1978, Sokoloff et al. 2006, Cavalcanti and Rua 2008).

1.4 Matter of the thesis

The repetition of the open and closed phenotype in inflorescences represents the principal subject of the present work. We ask whether the ontogenetic conditions for forming a TF are identical in all closed inflorescences irrespective of the systematic position. At the same time, we question whether the 'openness' of inflorescences can be reduced to a single step of transformation shared in all lineages.

We empirically test these questions studying the ontogeny of open and closed inflorescences within closely and among distantly related taxa. We also test them theoretically by revising the literature of histological and molecular development of inflorescence in the last decades.

Disclosing the ontogeny of the presence and/or absence of the TF allows elucidating the ontogenetic mechanisms for character change. In other words, if all ontogenies of inflorescences without TF share attributes that distinguish them from the ontogenies of closed inflorescences, then potential factors that hinder or promote the TF can be isolated. Such inferences can be lately transformed into experimental working hypotheses.

We specifically focus on the IM, as it is the very source of TF differentiation. We investigate the geometrical characteristics of the IM of different inflorescences and search for attributes that are compatible or incompatible with TF formation. With this data we turn towards the question whether spatial constraints play a role in the formation or failing of the TF.

2 DEVELOPMENTAL CONDITIONS FOR TERMINAL FLOWER PRODUCTION IN APIOID UMBELLETS

2.1 Introduction

The 'terminal flower issue' is as relevant as old in botany, dating from the very beginnings of inflorescence classifications (Roeper 1826) always being dotted of fundamental importance in any morphological treatise (e.g. Čelakovský 1893, Parkin 1914, Zimmerman 1935, Bolle 1940, Troll 1964, Stebbins 1979, Schroeder 1987). This fact situated the terminal flower as an attractive character for developmental genetic studies (Sohn et al. 2007, Wang & Li 2008). *Arabidopsis* / *Antirrhinum* genes *TFL1/CEN* are today considered as the responsible actors in the suppression of the terminal flower production (Shannon & Meeks-Wagner 1991, Alvarez et al. 1992). On the other hand, the production of the terminal flower represents a labile character in some taxa, even within an individual (Troll 1964, Weberling 1989, Bertero et al. 1996, Troll & Weberling 1998, Sedova & Grebennikova 2001, Balthazar & Endress 2002). This shows that the production of a terminal flower can be part of the phenotypic plasticity of a species, extending the ontogenetic causes of the terminal flower production at other levels.

The Apiaceae is a family that shows such an alteration of terminal flower production on their inflorescences (umbellets), a fact that has dared morphologists through decades (Clos 1855, Wydler 1860, Wettstein 1924, Cejp 1926, Froebe 1979). The morphological debate on the family contrasts with the poor attention given to the ontogenetic mechanisms behind the production of a terminal flower on the umbellets. Not that the development of apioid inflorescences has been an unknown matter (Payer 1853, Jochmann 1854, Sieler 1870, Schuchardt 1881, Borthwick et al. 1931, Magin 1959, Erbar & Leins 1985) but the focus on these studies has been situated mainly on phyllotactic arrangement, flower development or mitotic activity, leaving the terminal flower development as an obscure issue for the Apiaceae.

Froebe (1979), following Troll's (1964) typological framework, supposed that the Apiaceae had passed through a process of transformation from the most primitive terminal-flower bearing Hydrcotyloideae and Saniculoideae to the most derived Apioideae. A key

process in this transfer would have been the parallel loss of the terminal flower in different lineages (truncation), resulting in a number of taxa that obligate lack terminal flowers and others that produce them in a facultative way (Wydler 1860, Froebe 1964). *Daucus carota* belongs to the last group and the absence of the terminal flower is reported normally in weaker individuals or smaller umbellets (Reuther 2003). This fact coincides with the hypothesis of Cejp (1926), who proposed that scarcity of resources could account for the disappearance of a terminal flower on an inflorescence.

The fact that umbellets in *Daucus carota* are modified by architectural 'weakening-effects' is well known. For example, umbellets situated near the centre of an umbel (weaker) possess fewer flowers than the peripheral, stronger ones (Troll 1957). Analogously, flowers at the periphery of an umbellet are larger, perfect and usually bear more floral parts than the staminate inner ones (Troll & Heidemann 1951, Troll 1957).

But how can the weakening of an umbellet be ontogenetically related to the disappearance of a terminal flower? Wydler (1860) stated that the absence of terminal flowers in apioid umbellets could be explained by an abortion process. This argumentation could be well suited for *Daucus carota* assuming that the terminal flower primordium wouldn't be successfully nourished in resource-limited plants. However, since the terminal flower seems to originate directly from the apical meristem (Troll 1964), it could also be, that a physical reduction of the umbellet's apical meristem in weak plants would completely eliminate the potential to differentiate a terminal flower. This idea is supported by the fact that geometrical variation in the apical meristem has been shown to correlate with - or even induce - phenotypic variability in the plant body (Snow & Snow 1935, Troll 1937, Hernandez & Palmer 1988, Fleming et al. 1997, Harrison & Aderkas 2004, Kwiatkowska 2008).

In the present paper we test the hypothesis that geometrical modifications of the inflorescence apical meristem explain the loss of the terminal flower in *Daucus carota* umbellets. For this purpose we investigate the ontogeny of open and closed umbellets, setting an emphasis on the size and shape of their inflorescence meristems. Furthermore, we study the development of an obligate open apioid species, *Pastinaca sativa*, and a constitutive closed one, *Chaerophyllum temulum*. We test whether differences in their apical meristem geometry mirror *Daucus carota* open and closed umbellets and thus explain the species-specific lack or presence of a terminal flower in a similar way.

2.2 Materials and Methods

2.2.1 Plant Material

Previous investigations in *Daucus carota* L. (Reuther 2003) illustrate that the production of terminal flowers varies within the plant, tending to disappear towards the centre of an umbel and in umbels of higher order. When the terminal umbel of a plant produces terminal flowers, then the distal first order umbel does so with a likeliness of ca. 60% (Reuther 2003). By absence of terminal flowers in the terminal umbel the entire plant lacks it at all. As the terminal umbels develop earlier than the rest of the umbel-orders we were able to classify individuals after the status of their terminal umbel (terminal flower in the umbellets present or not) and to get still developing young umbellets from the distal first order umbel.

We collected umbels from eight *Daucus carota* terminal flower producing plants and from seven `open´ individuals in June 2008 growing in wild populations on the campus field of Mainz University, Germany. *Pastinaca sativa* L. and *Chaerophyllum temulum* L. were collected unaware from branch order in July 2007 and May 2008 near the university. The plant tissues were conserved in 70% ethanol and then dehydrated in a series of increasing alcohol-acetone series and critical point dried (BAL-TEC CPD030). The umbels were then sputtered with a thin gold film (BAL-TEC SCD005) and analysed under a scanning electron microscope (ESEM XL-30 Philips).

2.2.2 Measurements

Since the meristem changes its shape and size through ontogeny, we were aware to control for the state of development of the observed umbellets. Reuther (2003) showed for *Daucus carota*, that the number of flowers per umbellet didn't differ between the terminal umbel and the distal first order umbel. This way, the average of flowers present in the umbellets of the terminal umbel gave us an estimate of the number of flowers to be produced in the observed outer umbellet. We thus counted the already fractionated flower primordia and assigned a 'state of development' by dividing this number by the total number of flowers expected for that umbellet.

Considering the known morphological variation existing within an umbel, we only investigated outer umbellets. We removed the developing flower primordia to get a clear view of the inflorescence meristem. Suitable material for geometrical measurements comprised 50 umbellets of six closed plants and 17 of two open plants. Their developmental state ranged from 0,25 to 0,91. We also included one plant that presented completely fractionated umbellets. These plant produced exceptionally more flowers in the first order umbel than in the terminal umbel, as the state of development of the umbellet resulted 1,3.

The inflorescence meristem was defined as the dome formed by the tissue present above the youngest primordium (Fig. 2.1A: grey). After standardised side-views of the samples we established the tip of the dome as the intersection of its surface with the longitudinal symmetry axis; its base was defined as the perpendicular to this axis of symmetry passing through the youngest primordium (Fig. 2.1A). We assessed for each sample the meristem height, i.e. the vertical distance from the youngest primordium (p) to the tip of the meristem (t), and the meristem width, i.e. the length of the base of the dome (Fig. 2.1B). From polar views we obtained the average size of a flower primordium defined as the mean length of the insertion lines of the three youngest primordia (Fig. 2.1B).

Material of *Chaerophyllum temulum* L. (23 umbellets) and *Pastinaca sativa* L. (9 umbellets) was qualitatively evaluated.

2.2.3 Statistical Analysis

The height and width of the meristem as well as the floral primordium size of the umbellets were compared between terminal flower-producing and terminal flower-lacking individuals using an ANCOVA analysis. The ‘state of development’ of the umbellets was used as covariate in the analysis. We also regressed these variables with the state of development of the umbellet to find out if any direction of change of the attributes within the ontogeny had statistic support.

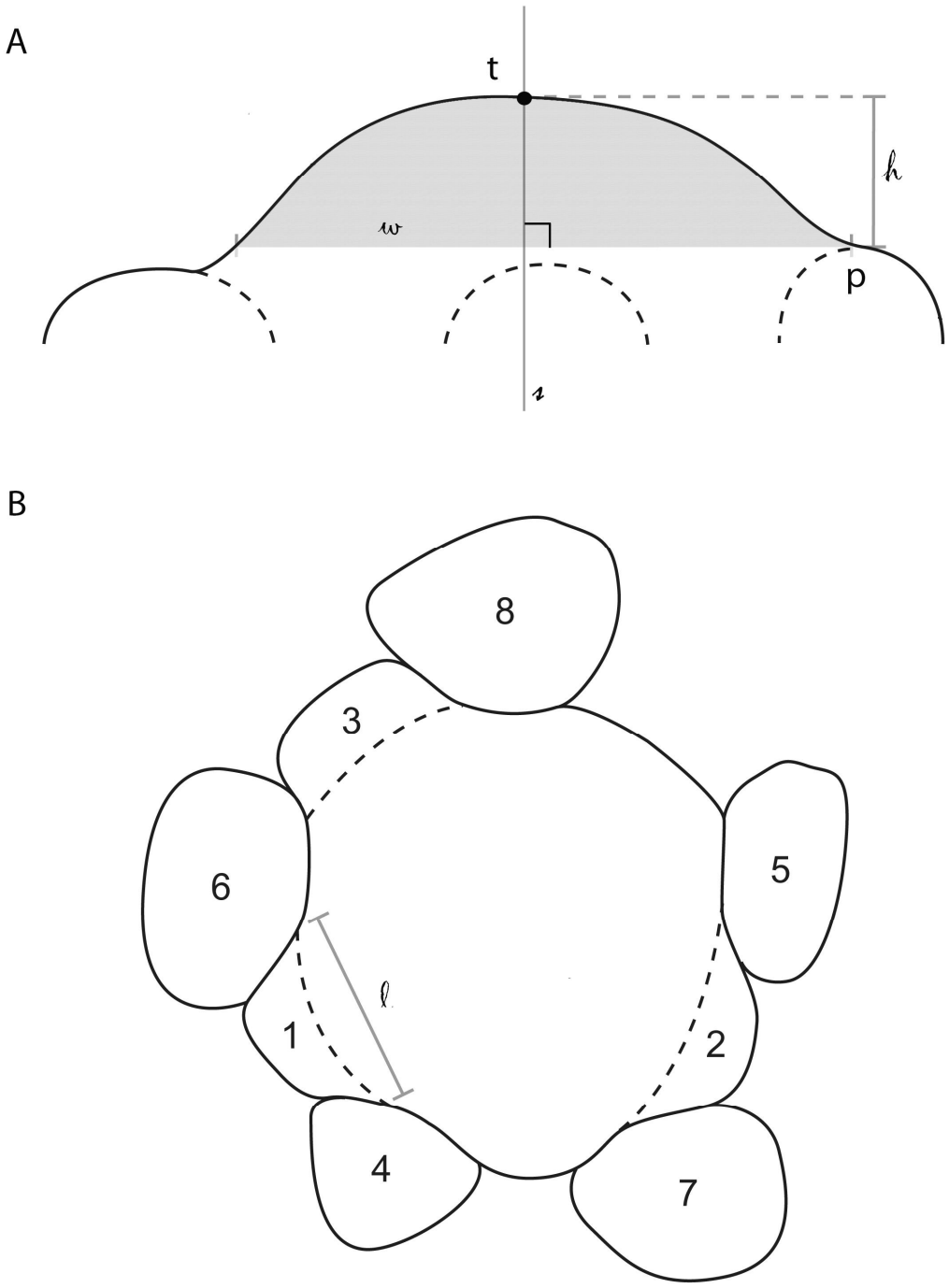


Figure 2.1. Measurements performed on developing umbellets of *Daucus carota*. A. Side view of a developing umbellet. The detached area represents the apical meristem. Note that the base of the dome is perpendicular to the longitudinal symmetry axis. B. Polar view of a developing umbellet. Flower primordia are numbered with increasing age. p = youngest primordium, s = longitudinal symmetry axis, t = tip of the meristem, w = width of the meristem, h = height of the meristem, l = length of the primordium insertion.

2.3 Results

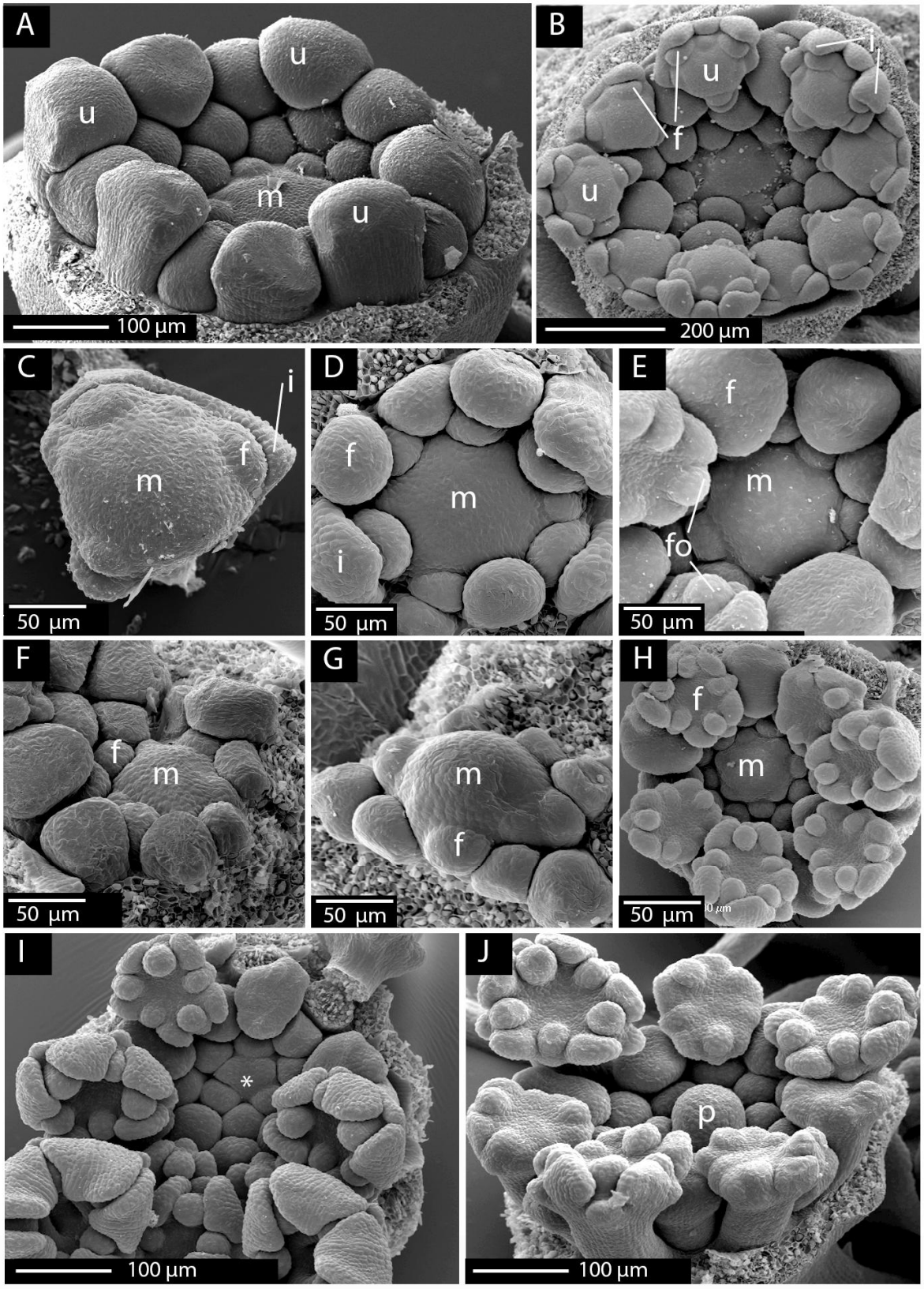
2.3.1 Ontogeny of the umbellets

Umbellets originate from a disc-shaped umbel meristem in an acropetal way (Fig. 2.2A). They then differentiate their involucellum and first flower primordia (Fig. 2.2B, C). Primordia fractionation continues acropetally reducing the remaining area of the umbellet meristem (Fig. 2.2C-E), while the older (outer) flowers already begin to differentiate floral organs (Fig. 2.2E, H). At this time, when about 75% of the flowers have been fractionated, the meristem either shows a flat (Fig. 2.2F) or convex-domed shape (Fig. 2.2G), depending on the 'open' or 'closed' condition of the plant. Umbellets with flat meristems continue to produce flowers until the whole meristematic tissue is used up (Fig. 2.2I). The remaining umbellets intensify the convexity of their meristems. They finally form a central bulge (Fig. 2.2J) which utterly differentiates into the terminal flower that is larger and more advanced in development than their side-flower neighbours (Fig. 2.2K, L).

Umbellet development in *Chaerophyllum temulum* (Figs. 2.2M-O) and *Pastinaca sativa* (Figs. 2.2P-R) share with *Daucus carota* the same developmental sequence. Interestingly, the obligate closed *Chaerophyllum temulum* umbellets (Fig. 2.2N) show a convex dome-shaped meristem like the closed *Daucus carota* umbellets (Fig. 2.2G), while the obligate open *Pastinaca sativa* umbellets present proportionally smaller and flatter meristems when the dimension of its own flower primordium is considered (Fig. 2.2Q).

2.3.2 Measurements

The ANCOVA analysis shows a significant difference between open and closed umbellets in *Daucus carota* with respect to meristem height and width (Table 1.1). Both parameters are larger in closed plants, presenting and average difference of 8,8μm and 15,9μm respectively (Fig. 2.3A, B). The state of development is also found to significantly affect both parameters (Table 1.1). Linear regressions show that the meristem height tends to increase ($R^2 = 0{,}197$; $p < 0{,}001$), and the width to decrease ($R^2 = 0{,}388$; $p = 0{,}003$) through ontogeny (Figs. 2.3A, B). At the end of the development of closed umbellets (developmental state near 1), the meristematic tissue is rough 25μm height and 70μm wide. This height is already achieved


A
u
u
m
u
100 µm
B
u
i
f
u
200 µm
C
i
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m
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D
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i
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f
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fo
50 µm
F
f
m
50 µm
G
m
f
50 µm
H
f
m
50 µm
I
*
100 µm
J
p
100 µm

Figure 2.2.

between the developmental state 0,5 and 0,75, i.e. when flower primordia are still being fractionated. At this time, open plants present a much flatter meristem of ca 10µm. The flower primordium size does not differ between umbellet types. The slight tendency of the primordium to be larger towards the late ontogeny (Fig. 2.3C, $R^2 = 0,139$; $p = 0,002$) is solely explained by the older individual, as the slope isn't distinct from zero when eliminating this individual from the analysis ($p > 0,05$).

Table 2.1. Analysis of covariance for umbellet meristem height and width and floral primordium size between umbellets that produce a terminal flower and those that do not. Note that both the meristem height and width are significantly different between open and closed umbellets, while the primordium size remains equal for both types. The three parameters show also ontogenetic variation as seen by the overall significant effect of the covariate 'state of development'.

Attribute		SS	df	SM	F	p
Height	Terminal flower condition	1045,65	1	1045,65	87,42	<0,001
	State of development	529,60	1	529,60	44,28	<0,001
	Error	657,85	55	11,96		
Width	Terminal flower condition	2748,89	1	2748,89	40,06	<0,001
	State of development	878,88	1	878,88	12,81	0,001
	Error	3773,89	55	68,62		
Flower primordium	Terminal flower condition	12,57	1	12,57	0,80	0,374
	State of development	173,97	1	173,97	11,08	0,001
	Error	1020,37	65	15,70		

Figure 2.2. Inflorescence development. A-L *Daucus carota*. A. Young umbel of *Daucus carota* segregating umbellet primordia (u); note the flat umbel meristem (m). B. Same as in A, but in a later stage, when involllucellum (i) and some flower primordia (f) are evident in the outer umbellets. C. Polar view of a young umbellet showing involllucelar bracts and first flower primordia. D. Same as in C in a later stage with more flower primordia fractionated. E. Same as in D in a later stage when floral organ (fo) differentiation can be seen in older flowers. The umbellet meristem is still active fractionating new flower-primordia. Note that C through E the same magnification is shown. F. Oblique view of a developing umbellet of the 'open type' (state of development = 0,68). Note the rather flat morphology of the meristem. G. Oblique view of a developing umbellet of the 'closed type' (same magnification as in F). In contrast to F, the meristem shows a clear convex-domed shape (state of development = 0,76). H. Polar view of an umbellet, showing the acropetal floral maturation. I. An open umbellet shows its apical meristem absolutely consumed by the flower primordia fractionation (asterisk). J. The central bulge in the umbellet meristem announces the differentiation of the terminal flower.

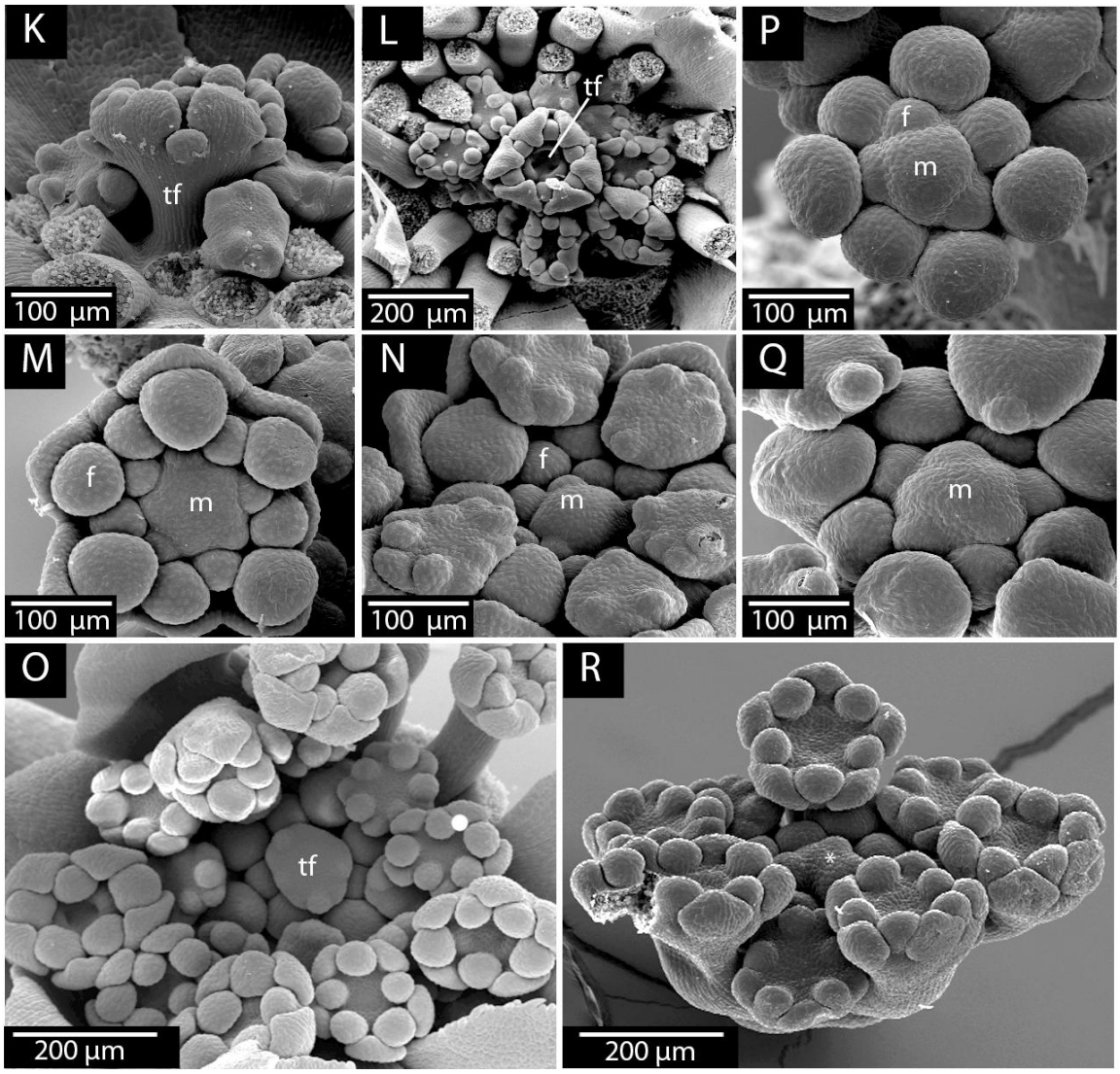


Figure 2.2 (cont.).

K. View of the terminal flower of an umbellet. Note the smaller size and relative retarded development of the immediate neighbours. L. Same as in K from a polar view. In this case, the terminal flower presents more flower parts (hexamerous) than the normal pentamerous lateral-flowers. M-O, *Chaerophyllum temulum.* M. Polar view of a young umbellet. N. Oblique view of an umbellet showing its convex-dome shaped meristem that stands in similarity with the 'closed type' *Daucus* umbellet in G. O. Mature umbellet showing a terminal flower in the middle. P-R, *Pastinaca sativa.* P. Polar view of a young umbellet (same magnification as for *Chaerophyllum* in M). Q. Oblique view of an umbellet whose meristem resembles the flat meristem of the 'open type' *Daucus* in F. Note the proportional smaller meristem considering the dimension of its flower primordia (see *Chaerophyllum* in N, same magnification). R. Mature umbellet with a meristem used-up by flower production. m = meristem, u = umbellet, f = flower primordium, i = involucellum bract, fo = floral organs, p = central protuberance, tf = terminal flower, * = 'open end' of an umbellet that lacks terminal flower.

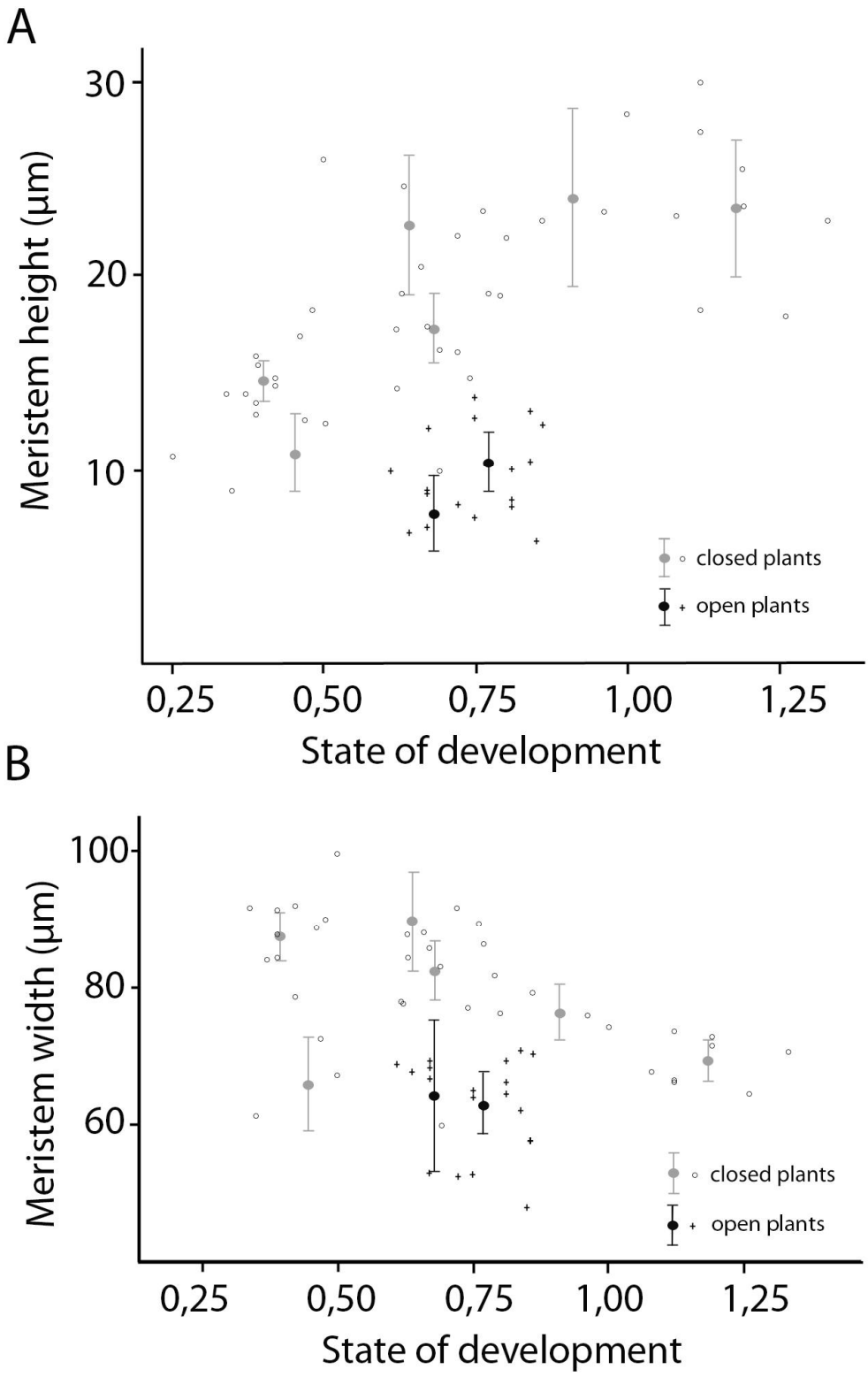


Figure 2.3. Dimensional values of *Daucus carota* umbellets. A. Umbellet-meristem height. Open plants (plus symbol) present a significantly flatter umbellet-meristem than closed plants (circles) at the equivalent developmental state. B. Umbellet-meristem width. Note that the width of the umbellet meristem tends to decrease through the development until it differentiates into a terminal flower in the closed plants. ➔

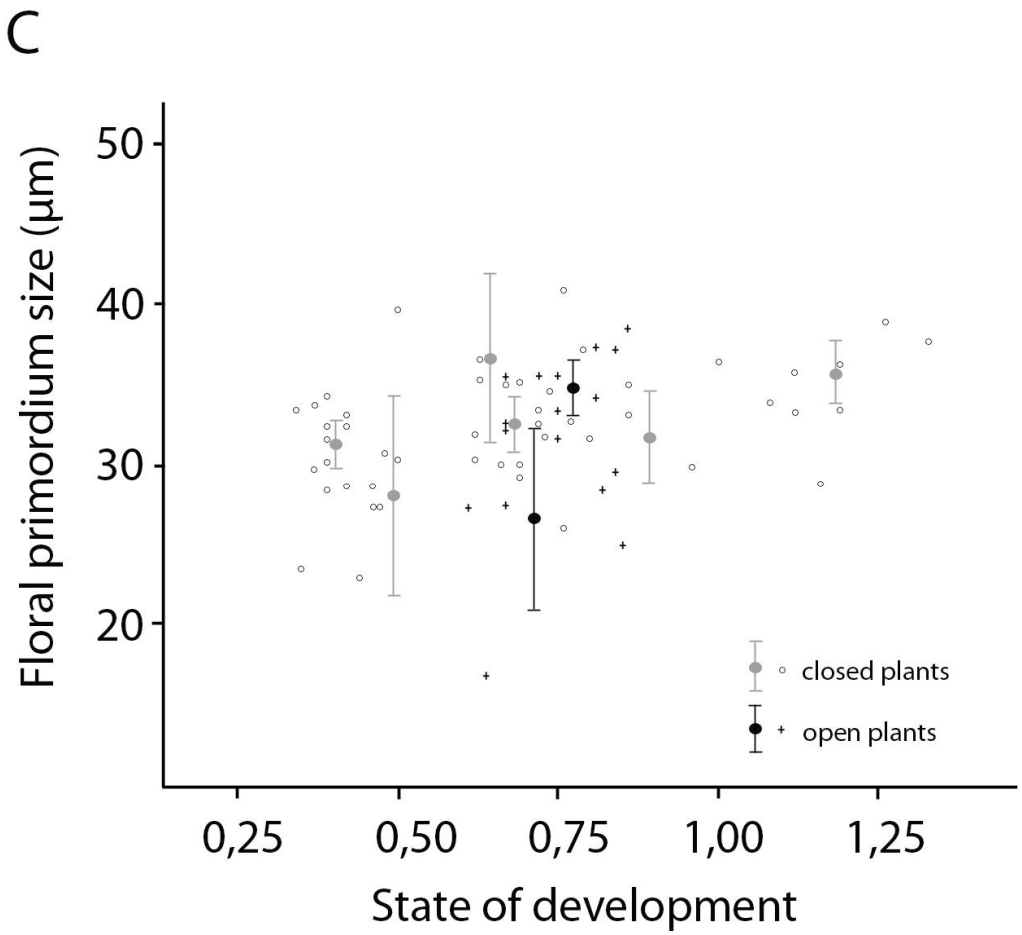


Figure 2.3 (cont.). C. Floral primordium size. The floral primordium size is equivalent between closed and open plants. Bars summarize the data for each individual within the 95% confidence interval and are located at the mean value of the 'state of development' of the respective umbel.

2.4 Discussion

Our data show that the inflorescence meristems of open and closed umbellets in *Daucus carota* have different dimensions, being larger in umbellets that produce a terminal flower. Since the very young umbellet primordia do not differ apparently in size, these distinct dimensions are achieved through the ontogeny. In the second half of the umbellet's flower fractionation process, the height of the apex of the closed type becomes clearly larger than the open type (Fig. 2.4a, c). This growth confers the apex its convex shape that utterly

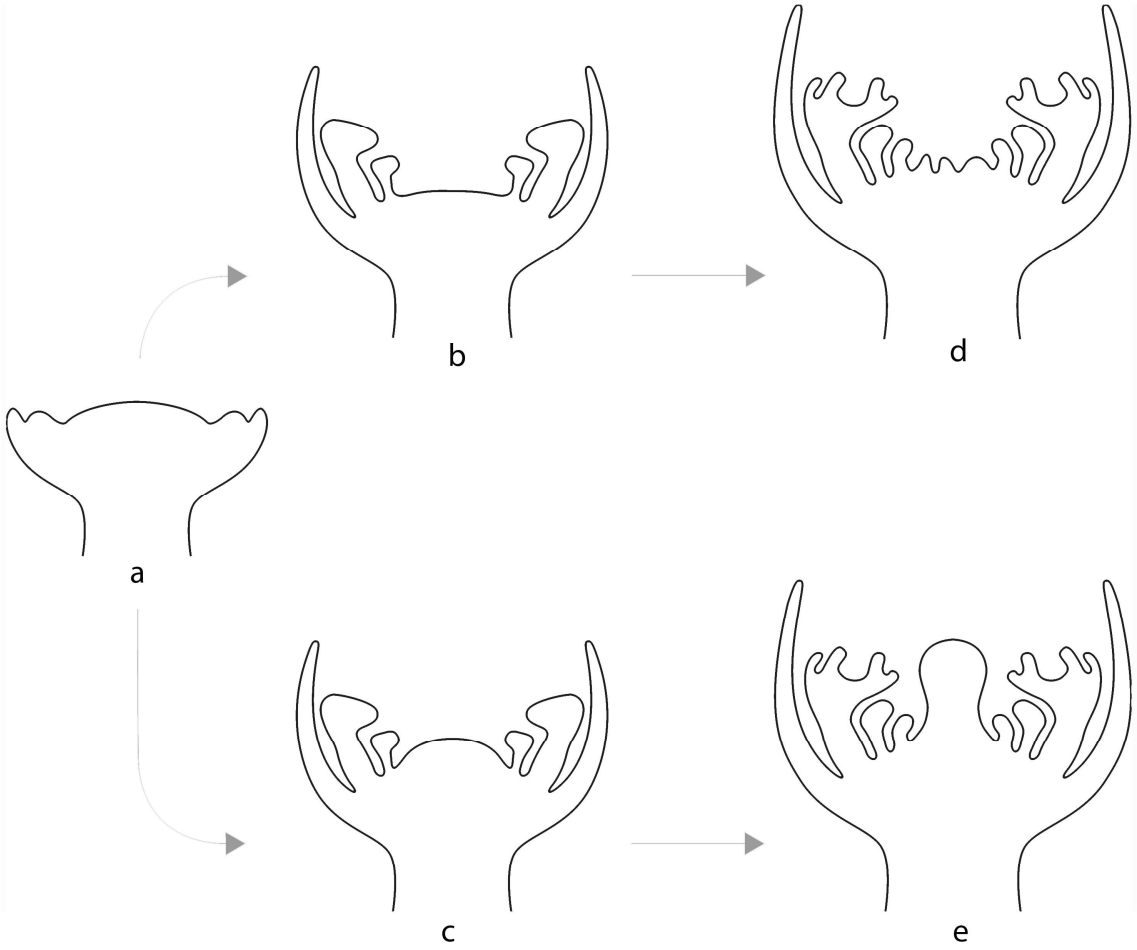


Figure 2.4. Development of open (terminal flower lacking) and closed (terminal flower producing) umbellets in *Daucus carota*, schematically. While the open umbellets maintain a more or less flat apical meristem through ontogeny (a, b), closed umbellets experience an increase in height of their meristems that produces a convex apical-dome (c). This dome utterly differentiates into a bulge that will form the terminal flower (e). The flat meristem of the open umbellet is unable to produce a terminal flower and is used up by the fractionation of side flowers (d).

forms the central bulge (Fig. 2.4e) preceding the differentiation of the terminal flower. This demands a certain volume and / or shape of meristematic tissue available on the young inflorescence.

Daucus carota individuals with obligate open umbellets tend to be smaller and weaker than plants producing terminal flowers (Reuther 2003). The inability of weak plants to differentiate a terminal flower could thus be interconnected with their inability to nurse their apical meristem and to confer it a convex-domed shape (Fig. 2.4a, b) that facilitates the central bulge formation. This behaviour of the inflorescence meristem indicates that the ontogeny between open and closed umbellets differs categorically: the apical meristem differentiates into a terminal flower or completely vanishes by the fractionation of side-

flowers (Fig. 2.4e). This form of terminal flower loss doesn't correspond to the idea of primordium abortion (Wydler 1880), since a terminal flower cannot be preformed at all on flat meristems. Interestingly, the flower-primordium size isn't larger in closed plants, showing that more resources do not induce a homogeneous enlargement of the umbellet parts, but preferentially of the meristem.

The coincident relation found between meristem geometry and presence/absence of a terminal flower in *Pastinaca sativa* and *Chaerophyllum temulum* indicates that our findings may be of general meaning for apioid umbellets. The terminal flower or its absence can thus be seen as a consequence of the ontogenetic processes that a flat or convex inflorescence meristem can trigger. Moreover, this principle seems to be also valid at the higher structural organisation level of the umbel. While Apioideae species normally possess flat umbel meristems (Fig. 2.1a; Sieler 1870, Borthwick et al. 1931, Magin 1959) and lack terminal umbellets (Froebe 1979), *Sanicula europaea* and *Hacquetia epipactis,* members of the sister group Saniculoideae, present both convex umbel meristems and terminal umbellets (Froebe 1964).

Summarising, our data show that the apical meristem growth and shaping can be plastically modified and that this physical variation in the meristem utterly shapes the plant's phenotype. In this sense, more attention should be given to mechanical effects that play a direct role at the AM and determine the plant's morphology (Green 1992, 1999, Dumais 2007).

2.5 Summary

Quantitative ontogenetic studies in *Daucus carota* inflorescences illustrate that terminal flower producing umbellets have larger apical meristems than umbellets that lack terminal flowers. This structural difference is achieved through ontogeny by a different shaping of the apical meristem: in open umbellets it remains flat until it is completely consumed by flower primordia fractionation, while it becomes dome shaped in the closed umbellets. The convex meristem is finally transformed into a terminal flower that is larger than its direct neighbours. Since weaker and smaller individuals use to bear open umbellets, it is assumed that the relative nourishment conditions of the plants have an effect on the apical meristems geometry, that in turn would be capable or not to merge into a terminal flower.

2.6 Appendix

A. Measurements performed in *Daucus carota* closed plants. IND, individual number; FL, mean number of flowers in one umbellet of the terminal umbell; UMBELLETE, umbellete number; FP, number of flower primordia; SD, state of development; l, length of the primordium insertion; h, meristem height; w, meristem width.

IND	FL	UMBELLETE	FP	SD	MEASUREMENTS					
					Top view				Lateral view	
					l 1st	l 2nd	l 3rd	mean	h	w
1	40,9	1	15	0,37	28,52	39,70	32,89	33,70	13,91	84,35
		2	16	0,39	28,19	29,70	44,85	34,25	12,82	84,59
		3	19	0,46	29,93	25,81	26,38	27,37	16,90	88,89
		4	16	0,39	27,11	24,75	33,57	28,48	13,48	87,83
		5	17	0,42	31,04	24,47	44,06	33,19	14,74	92,22
		6	17	0,42	31,17	31,24	34,99	32,47	14,34	78,72
		7	16	0,39	30,88	34,33	29,62	31,61	15,40	88,02
		8	16	0,39	25,80	30,95	33,64	30,13	15,85	91,42
		9	14	0,34	34,12	27,70	38,59	33,47	13,91	91,75
2	31,8	1	22	0,69	33,15	35,37	36,78	35,10	9,96	59,90
		2	16	0,50	36,53	28,78	25,92	30,41	12,38	67,47
		3	15	0,47	30,54	27,02	24,54	27,37	12,61	72,61
		4	8	0,25	24,27	36,74	38,04		10,65	69,38
		5	11	0,35	21,26	20,32	28,83	23,47	8,91	61,31
3	41,8	1	33	0,79	33,70	35,97	41,78	37,15	18,91	81,96
		2	30	0,72	33,86	30,45	33,41	32,57	16,08	74,59
		3	26	0,62	26,33	33,38	31,33	30,35	14,12	77,89
		4	28	0,67	32,02	36,34	36,92	35,09	17,39	85,87
		5	26	0,62	29,32	34,49		31,91	17,17	78,04
		6	20	0,48	29,50	32,02		30,76	18,21	90,42
		7	29	0,69	23,83	25,11	38,72	29,22	16,09	83,26
		8	30	0,72	28,02	35,85	36,24	33,37	21,96	91,96
		9	31	0,74	30,29	38,95		34,62	14,75	77,37
		10	32	0,77	32,47	29,50	36,18	32,72	19,01	86,38
4	31,7	1	24	0,76	36,84	37,50	48,41	40,92	23,26	89,57
		2	21	0,66	31,58	32,47	26,04	30,03	20,43	88,27
		3	16	0,50	27,76	38,32	52,99	39,69	25,87	99,78
		4	20	0,63	31,19	43,69	34,78	36,55	24,56	87,83
		5	20	0,63	35,55	35,11		35,33	19,09	84,68
5	30,1	1	29	0,96	23,15	34,13	32,21	29,83	23,24	76,16
		2	26	0,86	27,98	33,30	38,16	33,15	22,82	79,36
		3	30	1,00	39,23	33,70	36,43	36,45	28,26	74,13
		4	24	0,80	32,81	31,98	30,09	31,63	21,96	76,30
6	28,6	1	32	1,12	32,44	33,07	41,81	35,77	29,92	66,69
		2	31	1,08	33,62	32,60	35,68	33,97	23,06	67,81
		3	32	1,12	33,81	34,72	38,70	35,74	18,23	66,36
		4	36	1,26	36,32	41,17	39,39	38,96	17,85	64,52
		5	34	1,19	33,37	31,08	35,74	33,40	23,47	71,52
		6	34	1,19	37,10	36,68	34,92	36,23	25,44	72,83
		7	32	1,12	33,55	33,55	32,74	33,28	27,39	73,70
		8	38	1,33	37,89	37,06	38,15	37,70	22,75	70,78

Appendix (cont.)

B. Measurements performed in *Daucus carota* open plants.

IND	FL	UMBELLETE	FP	SD	MEASUREMENTS					
					Top view				Lateral view	
					l 1st	l 2nd	l 3rd	mean	h	w
1	35,9	1	27	0,75	28,28	39,88	38,46	35,54	13,70	65,22
		2	30	0,84	32,02	38,58	41,05	37,22	10,43	62,18
		3	29	0,81	31,61	34,92	36,14	34,22	8,04	69,13
		4	31	0,86	36,47	34,12	44,95	38,51	12,28	70,18
		5	29	0,81	34,34	37,81	39,88	37,34	10,00	64,79
		6	27	0,75	30,17	35,91	34,20	33,43	12,69	64,30
		7	27	0,75	31,43	30,98	32,61	31,67	7,53	52,91
		8	29	0,81	31,76	37,08	33,95	34,26	8,47	66,12
		9	30	0,84	28,22	28,86	31,59	29,56	13,04	70,87
		10	24	0,67	28,07	43,06	35,27	35,47	12,17	68,26
		11	26	0,72	35,79	40,18	30,81	35,59	8,17	52,47
		12	24	0,67	30,48	35,09	30,74	32,10	8,91	53,04
2	33,0	1	22	0,67	25,09	27,77	29,42	27,43	8,69	69,36
		2	22	0,67	31,88	32,48	33,43	32,60	6,96	66,96
		3	21	0,64	9,98	17,99	22,75	16,91	6,72	67,75
		4	20	0,61	25,25	27,66	28,93	27,28	9,94	68,83
		5	28	0,85	27,00	18,03	29,89	24,97	6,30	48,06

3 OPEN AND CLOSED INFLORESCENCES: MORE THAN SIMPLE OPPOSITES

3.1 Introduction

One intriguing point in plant morphology is the fact that inflorescences can be topped by a terminal flower or not (Troll 1964, Stebbins 1974, Weberling 1992, Coen and Nugent 1994, Prenner et al. 2009). It is traditionally assumed that the presence of a terminal flower in inflorescences, i.e. 'closed' inflorescences, represents the ancestral state among species, while the loss of the terminal flower through a process known as 'truncation' has occurred many times in parallel among different angiosperm lineages originating the 'open' inflorescences (Troll 1964, Stebbins 1974, Weberling 1992, Coen and Nugent 1994, Prenner et al. 2009). While the directionality in the evolutive change between the closed and the open condition has been newly relativized (Buzgo et al. 2006, Sokoloff et al. 2006, Cavalcanti and Rua 2008), a second implicit assessment has remained untouched until now, which refers to the uniqueness of the mechanisms by which terminal flowers have been lost (or re-gained) through the evolutive history of plants. If the truncation of inflorescences had always a common ontogenetic pathway, then every open inflorescence should share a common structure, particularly respecting the absence of the TF. Are actually all open inflorescences reducible to a common structure? The main purpose of this essay is to shed light on the evidence that convincingly manifest that this is not the case, which automatically broadens the question of terminal flower loss or re-gain to further explanatory fields.

3.2 A determinate inflorescence meristem does not imply a terminal flower

The general developmental sequence of an inflorescence can be divided into two steps: i. the transformation of the vegetative shoot apical meristem (SAM) into an inflorescence meristem (IM) and ii. the transformation of the IM into a flower meristem (FM). When the second step is fulfilled, a terminal flower is formed and the inflorescence axis is considered to be 'determinate' (Troll 1964, Stebbins 1974, Weberling 1992, Coen and Nugent 1994, Tucker 1999, Prenner et al. 2009). In the model plant *Arabidopsis*, that does not form terminal flowers in its wild-type inflorescences, the gene product TFL1 acts as an antagonist

to the FM identity genes at the distal part of the SAM, guaranteeing the maintenance of the IM identity and thus the 'indeterminate' character of the inflorescence axis (Shannon and Meeks-Wagner 1991, Alvarez et al. 1992, Parcy et al. 2002, Bennloch et al. 2007, Sablowski 2007, Argiriou et al. 2008, Wang and Li 2008) (Figs. 3.1B, E). The indeterminate nature of IMs of *Arabidopsis*, and in general of vegetative SAMs, depends on the maintenance of stem cells in the distal part of the SAM, molecularly governed by the CLAVATA-WUSHEL (CLV-WUS) regulative loop (Bäurle and Laux 2003, Carles and Fletcher 2003, Angenent et al. 2005; Sablowski 2007, Wang and Li 2008) (Figs. 3.1A, B). Loss of function of *TERMINAL FLOWER LOCUS 1* (*TFL1*) in *Arabidopsis* allows the floral identity genes in the distal SAM to transform the IM into a FM. When this happens, both decline of the stem cells and floral organ differentiation is promoted (Figs. 3.1C, F). Consequently, in *Arabidopsis* the mutative shift from an indeterminate to a determinate IM implies the appearance of a terminal flower. This model is considered today as one of the benchmarks of inflorescence architectural control (Angenent et al. 2005, Bennloch et al. 2007, Wang and Li 2008, Prenner et al. 2009) and shaping (Prusinkiewicz et al. 2007) whereby the presence or absence of a terminal flower results from the interplay between floral identity genes and an antagonistic molecule (like TFL1) that preserves the indeterminacy on the SAM.

However, this molecular model is not common to all inflorescences as the shift between indeterminate and determinate IMs does not always imply the appearance of a terminal flower. Such a case has been described in *Gerbera*, whose inflorescence posses a quite different pathway of IM termination. Here, a MADS-box FM gene of the E class, *GERBERA REGULATOR OF CAPITULUM DEVELOPMENT 2* (*GRCD2*) acts over the IM playing a role in its determination (Uimari et al. 2004, Teeri et al. 2006). When GRCD2 is down-regulated, indeterminate heads with self-perpetuating IMs are produced. Similar to *Arabidopsis*, the indefinite persistence of an IM in *Gerbera* heads results in the formation of open inflorescences. However, the *wt Gerbera* capitulum, whose IM is completely differentiated and consumed by flower primordia, is an open inflorescence as well (Troll 1964, Stebbins 1974, Weberling 1992, Harris 1995). Thus, the open condition of the *wt Gerbera* inflorescence is not dependent on the indefinite maintenance of the IM as in *Arabidopsis* (Uimari et al. 2004, Teeri et al. 2006) (Figs. 3.1D, G); on the contrary, the open *Gerbera* head arises from a determinate IM (Uimari et al. 2004).

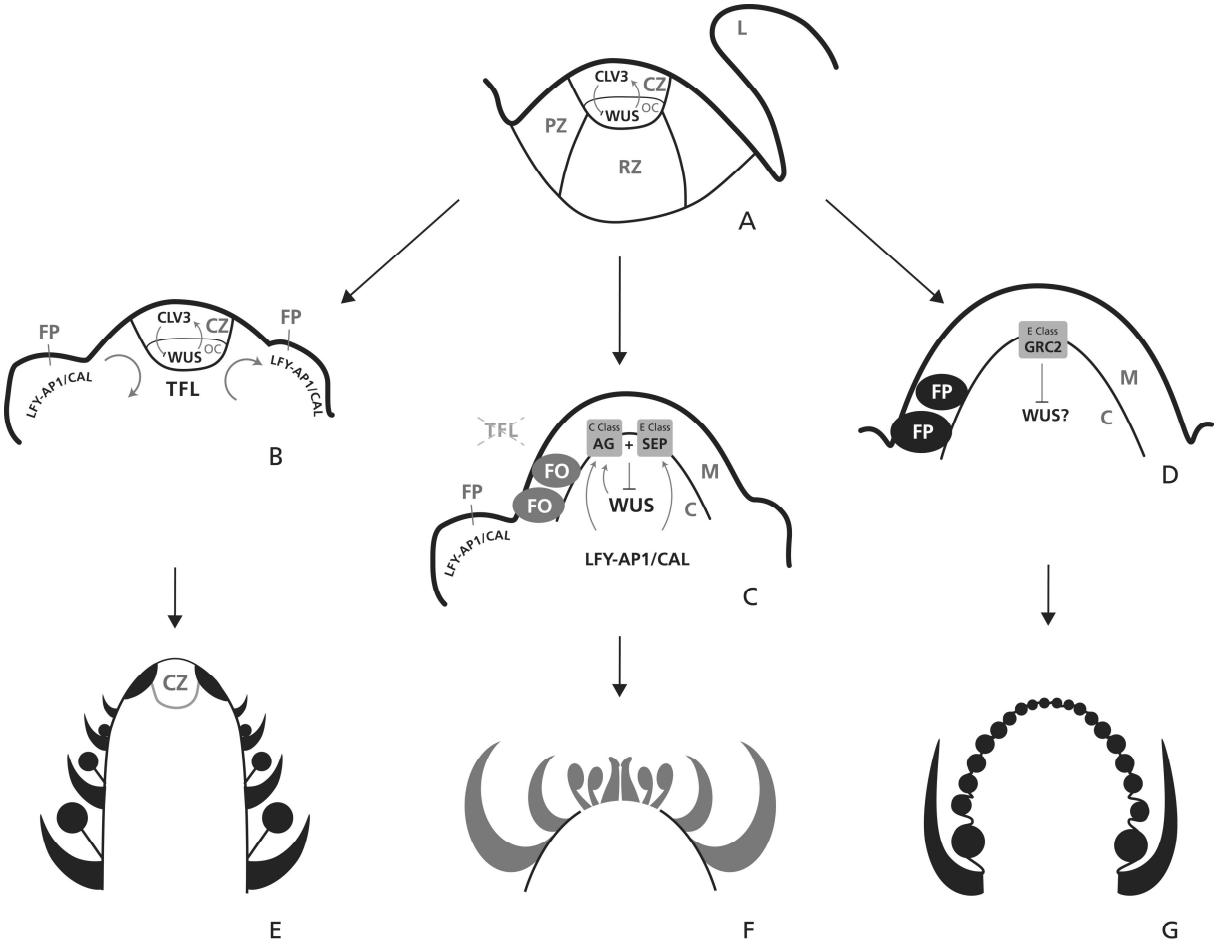


Figure 3.1. Changes in the SAM during the transition from the vegetative to the reproductive stage, based on molecular data known for *Arabidopsis* (A-C; see Shannon and Meeks-Wagner 1991, Alvarez et al. 1992, Parcy et al. 2002, Bäurle and Laux 2003, Carles and Fletcher 2003, Angenent et al. 2005, Bennloch et al. 2007, Sablowski 2007, Argiriou et al. 2008, Wang and Li 2008) and *Gerbera* (D; see Uimari et al. 2004, Teeri et al. 2006), and angiosperm-wide histological evidence (see Tables 3.1, 3.2). (A) Vegetative SAMs generally present a histological zoning composed of three main areas: the central-, peripheral- and rib zones (CZ, PZ, RZ; Sablowski 2007, Wang and Li 2008, Bäurle and Laux 2003, Carles and Fletcher 2003, Kwiatkowska 2004, Reddy et al. 2004, Kwiatkowska 2008). Putative stem cells of the SAM are located in the distal part of the CZ. They have a low mitotic activity and are bigger and more vacuolated than the meristematic active cells (Gifford and Corson 1971, Buvat 1989, Lyndon 1998). The fate of the stem cells is defined by the action of WUSCHEL (WUS) that is expressed in the proximal section of the CZ, the organizing centre (OC). Putative stem cells express *CLAVATA3 (CLV3)* that together with CLV1 and CLV2 have an inhibitory effect on *WUS* expression, thus regulating the extent of the stem cell population (Bäurle and Laux 2003, Carles and Fletcher 2003, Angenent et al. 2005, Sablowski 2007, Kwiatkowska 2008, Wang and Li 2008, Szczesny et al. 2009). (B) IM of the open raceme of *Arabidopsis thaliana* showing the persistence of the CZ due to the action of TFL1, that prevents the expression of the FM identity genes *LEAFY* (*LFY)* and *APETALA1* (*AP1)*/*CAULIFLOWER* (*CAL)* on the distal IM (Parcy et al. 2002, Bennloch et al. 2007, Sablowski →

A comparable case is known from maize. In this species, male flowers are arranged in pairs in structures called spikelets. By their part, spikelets are also organized in groups of two in short branches termed spikelet pair (SP). The SP is a typical feature of the Andropogetonae tribe and is considered to be a phylogenetically derived structure (Bortiri and Hake, 2007). SPs originate from a SP meristem (SPM) placed laterally on the principal inflorescence axis. Despite SPs do not produce a terminal flower on their axes, the SPM is considered to be determinate since it terminates after the production of two spikelets, a process governed by the genes of the ramosa group (Vollbrecht, 2005; Bortiri and Hake, 2007; Barayesh and McSteen, 2008).

The *Gerbera* and *Zea* examples unmask a latent terminological inconsistence: the term 'open inflorescences' is in morphology synonymised with 'indeterminate inflorescences' (Troll, 1964; Stebbins, 1974; Weberling, 1992; Coen and Nugent, 1994; Tucker 1999; Prenner et al*.,* 2009); and, as showed above, indeterminate inflorescences can arise from a developmentally determinate IM. In other words, the concept of 'determinate meristem', that refers to the existence of specific ontogenetic termination pathways (Bäurle and Laux, 2003; Teeri et al*.,* 2006; Sablowski, 2007) and / or to predictable and limited origination of parts (Vollbrecht, 2005; Bortiri and Hake, 2007; Barazesh and McSteen, 2008), is properly applicable to flower meristems (Angenent et al., 2005; Teeri et al*.,* 2006; Sablowski, 2007;

→ 2007, Wang and Li 2008). The floral identity genes can act solely on the flanks producing the floral primordia (FP). (C) Determinate FM with a mantle core (MC) configuration. Genes encoding MADS-domain proteins of the C class *AGAMOUS (AG)* and E class *SEPALLATA (SEP)*, evocated by LFY and WUS, are responsible for the floral meristematic termination through a concertized *WUS* down regulation (Bäurle and Laux 2003, Carles and Fletcher 2003, Angenent et al. 2005, Sablowski 2007). *TFL1* mutation permits the expression of the floral gene-cascade at the distal part of the IM (Shannon and Meeks-Wagner 1991, Alvarez et al. 1992, Parcy et al. 2002, Sablowski 2007), resulting in the formation of flower organs (FO) and consequently, a terminal flower (Fig. 3.1C). (D) IM with a MC configuration. In *Gerbera*, the FM termination is also provided by C and E class MADS-domain proteins: GERBERA-AGAMOUS-LIKE (GAGA) and GERBERA REGULATOR OF CAPITULUM DEVELOPMENT 2 (GRCD2) (Uimari et al. 2004). Interestingly, *GRCD2* is also expressed early in the capitulum bud and regulates the termination of the IM, probably repressing the (still unknown) *Gerbera WUS*-like gene on the IM (Teeri et al. 2006) (D). (E) Mature open inflorescence showing a persisting CZ. F. terminal flower (either solitary or topping a closed inflorescence). (G) open MC inflorescence with a completely used IM.

Kwiatkowska 2008) and analogously, to IMs that are topped by terminal flowers. However, when the terminal flower is absent on an inflorescence, an indeterminate IM is not always the ontogenetic cause for it, as shown in the abovementioned *Gerbera* capitulum and *Zea* SP.

But, beyond this semantic trap, the critical point is that the developmental basis of the 'openness' in inflorescences is clearly not universal: it depends or not on the stem cell-maintenance of the IM. This necessarily implies that the vast parallel loss or re-gain of terminal flowers in the evolution of the angiosperms can not always be traced back to the up- or down regulation of a floral identity gene repressor like *TFL1*, as assumed until now (Coen and Nugent 1994, Prusinkiewicz et al. 2007).

But how common are the '*Gerbera*- or *Zea*- like' open inflorescences? How often do determinate IMs lead to inflorescences without terminal flowers? An angiosperm-wide study of stem-cell-regulation in open inflorescences would be very helpful, but demanding. Fortunately, the expression of regulative stem-cell genes finds a parallel on the histological composition of the shoot apical meristem (Bäurle and Laux 2003, Carles and Fletcher 2003, Sablowski 2007, Kwiatkowska 2008). Basically, the vegetative angiosperm SAM can be differentiated into three cytohistological zones (Fig. 3.1A). Of them, the central zone (CZ) occupies the most distal SAM portion and thus the zone where the stem cells are sheltered (Bäurle and Laux 2003, Carles and Fletcher 2003, Sablowski 2007, Kwiatkowska 2008) (Fig. 3.1A). At this respect, comparing the cytohistological composition of open IMs helps to clarify to which extent the absence of a terminal flower correlates or not with the maintenance of stem cells on the IM.

3.3 Histology of IMs support two kinds of open inflorescences

Current studies in the model plant *Arabidopsis thaliana* have proved the existence of a CZ in the IM (Breuil-Broyer 2004, Kwiatkowska 2004, Reddy 2004), reaffirming the view that stem cells are preserved in the IM and are responsible for the indeterminate nature of its inflorescence. The presence of a CZ in the IM of *Arabidopsis* is well known since the 1950s (Vaughan 1955). Actually, the study of the histology of the SAM, and particularly of its reproductive transition, was principally carried through the 1940-70s (Nougarède 1967, Gifford and Corson 1971, Buvat 1989, Lyndon 1998, Tucker 1999) As in *Arabidopsis*, studies

performed in other members of the Brassicaceae have shown that a CZ is maintained in the IM (Vaughan 1955, Lance-Nougarède 1961, Hagemann 1963, Sadik and Ozbun 1968, Orr 1978) (Table 3.1). Examples of persisting CZs in IMs from other systematic groups are also abundant (Table 3.1). Not surprisingly, all these cases correspond exclusively to open inflorescences, more precisely, to the 'typical' open families (Troll 1964, Stebbins 1974, Weberling 1992) such as Onagraceae (Hagemann 1963, Michaux 1964), Fabaceae (Vescovi 1964), Primulaceae (Vaughan 1955, Hagemann 1959) and Plantaginaceae (Hagemann 1963) (Fig. 3.2A).

Table 3.1. Histological studies in open inflorescences that reveal the persistence of a central zone (CZ) in the IM.

Family	Species	References
Brassicaceae	*Alyssum maritimum*	Lance-Nougarède 1961
	Arabidopsis thaliana	Vaughan 1955, Breuil-Broyer et al. 2004, Kwiatkowska 2004, Reddy et al. 2004
	Brassica campestris	Orr 1978
	Brassica oleracea	Sadik and Ozbun 1978
	Capsella bursa-pastoris	Vaughan 1955
	Cheiranthus cheirii	Hagemann 1963
	Hesperis matronallis	Hagemann 1963
Capparaceae	*Cleome spinosa*	Hadj-Moustapha 1957
Crassulaceae	*Kalanchoe* sp.	Stein and Stein 1960
Fabaceae	*Spartium junceum*	Vescovi 1964
	Lathyrus aphaca	Vescovi 1964
Onagraceae	*Oenothera biennis*	Hagemann 1963, Bersillon 1957
	Jussieua grandiflora	Michaux 1964
Primulaceae	*Anagallis arvensis*	Vaughan 1955
	Cyclamen persicum	Hagemann 1959
Plantaginaceae	*Digitalis purpurea*	Hagemann 1963

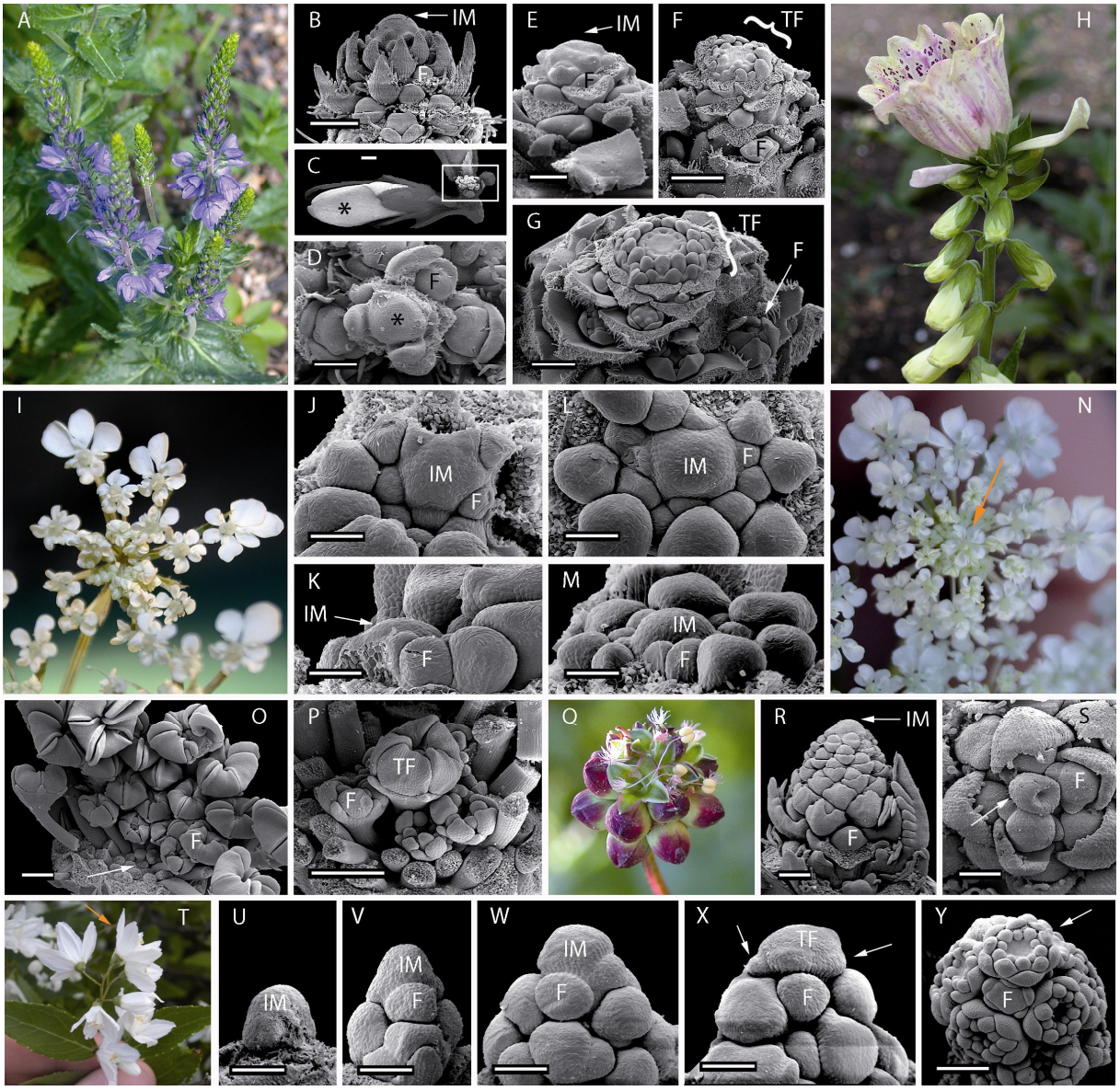


Figure 3.2. Development of open and closed inflorescences of polytelic Plantaginaceae (A-H) and monotelic Apiaceae, Rosaceae and Hydrangeaceae (I-Y). (A) Mature individual of *Veronica teucrium* showing their open racemes that are characteristic for the genera. (B-D) Development of the raceme of *V. longifolia*. (B) An inflorescence meristem (IM) segregates lateral flower primordia (F). (C) Tip of a mature raceme showing the last blooming flower (asterisk) and the rest of the axis containing several flower buds that will not bloom (demarked by the white box). (D) Magnification of the white box in (C), showing the arrested lateral flower buds and a parenchymatized IM (asterisk). (E-H) Peloric individuals of *Digitalis purpurea*. (E) Developing inflorescence showing an active IM after forming the first flower primordia (F). (F) The IM of the peloric individuals suddenly transforms into a terminal flower (TF) of aberrant shape; note the larger bud size of the TF in comparison to lateral flower primordia (F). (G) A more advanced developmental state of the inflorescence showing the ring of stamina and carpels of the TF; the size of TF corresponds roughly five times to the size of a lateral flower in a similar developmental state (F). (H) A peloric *D. purpurea* individual at blooming; note the radial symmetry and larger size of the TF and its early blooming on the plant. ➔

On the contrary, the CZ invariably disappears when a terminal flower is formed. This notion was introduced in the seminal work of Gregoire (1938), who stressed that the reproductive transition produced an enlargement of the SAM going along with the appearance of an homogenized deep-staining meristematic coat ('manchon meristematique') that provides a 'mantle-core' (MC) configuration to the meristem (Nougarède 1967, Gifford and Corson 1971, Buvat 1989, Tucker 1999, Kwiatkowska 2008). Examples of histological transitions that endorse this proposition have been repeatedly described, particularly on closed inflorescences belonging to Rosaceae (Grégoire 1938, Rauh and Reznik 1951, Phelouzat 1963), Papaveraceae (Bersillon 1955), and Ranunculaceae (Grégoire 1938). Plantefol (1957) and Stebbins (1974) noted that the retention of a CZ in the IM seemed to be a reasonable ontogenetic explanation for the absence of a terminal flower in inflorescences, a view that

←(I-P) *Daucus carota* (Apiaceae). *D. carota* has a composed inflorescence termed umbel that is composed by many umbellets (Weberling, 1992). This species produces terminal flowers in a facultative way on the top of the umbellets. (I) 'Open' umbellet (without terminal flower). (J) Polar view of a developing open umbellet at the time when 30 flower primordia (F) have been produced, being 36 expected (see for details Bull-Hereñu and Claßen-Bockhoff 2010). (K) Side view of (J) showing the flat IM. (L) Polar view of a developing 'closed' umbellet that will produce a terminal flower; at that time, there have been produced 26 flower primordia (F) of 30 expected for that umbellet (see Bull-Hereñu and Claßen-Bockhoff 2010). (M) Side view of (L). Note the convex IM shape in comparison to the flat IM of the open umbellet in (K). (N) Mature closed umbellet. The arrow denotes the terminal flower that blooms before the immediate flower- neighbours. (O) An open umbellet after complete fractionation of the IM. The arrow signals to the centre of the umbellet where no rest of meristematic tissue can be found, in contrast to *Veronica* (D). The scars of the removed flowers fill the space. (P) Complete developed closed umbellet showing the larger terminal flower (TF) at the middle surrounded by smaller lateral flowers (F). (Q-R) Open head of *Sanguisorba minor* (Rosaceae). (Q) Note the basipetal sequence of blooming. (R) Lateral view of a young head developing in acropetal sense. (S) Polar view of a complete developed head after the whole meristematic tissue has been used up, similar as in *Daucus* (O). The arrow signals a tubular structure that probably appears as a consequence of the insufficient space required for a last lateral flower (Sokoloff et al. 2006). (T-Y) Development of the closed thyrse of *Deutzia gracilis* (Hydrangeaceae). (T) Blooming inflorescence; arrow signals the terminal flower. (U) Young inflorescence bud showing a bulged IM. (V) Young developing inflorescence after segregation of some flower primordia (F). (W) Inflorescence shortly before terminal flower differentiation; the IM covers the space where the TF will differentiate. Note that this space is present from the beginning on (U,V). (X) Beginning of floral organ differentiation of the TF; arrows indicate incipient sepals. (Y) Complete segregated inflorescence; arrow denotes the terminal flower, which is larger and developmentally advanced in comparison to its direct neighbours (F). Scale bars: C,F,G = 500µm; B,E,O,P,R,Y = 200µm; D,S,U-X = 100µm; J-M = 50µm.

was later confirmed by the molecular and cytohistological studies conducted in *Arabidopsis* (Vaughan 1955, Shannon and Meeks-Wagner 1991, Alvarez et al. 1992, Parcy et al. 2002, Sablowski 2007, Breuil-Broyer et al. 2004, Reddy et al. 2004). However, this observation can not be generalized, as evidence coming from the 'non-typical' open families as Rosaceae, Ranunculaceae or Campanulaceae shows that open inflorescences can also be derived from MC-IMs (Table 3.2).

The ontogeny of these open inflorescences differs from the ontogeny of the 'typical' open families and resembles more the development of solitary flowers (Figs. 3.1C, D, F, G): the reproductive transition is firstly marked by a tissue homogenization, i.e. a loss of the CZ, followed by a considerable enlargement of the meristematic cone and the concomitant rapid segregation of densely packed flower primordia that entirely use the IM. This kind of ontogeny results often in inflorescences with a head-like appearance as in Asteraceae, Dipsacaceae, Campanulaceae or Rosaceae (Figs. 3.1G, 3.2Q-S).

Considering the above exposed evidence and the today-known distinct molecular pathways for IM termination, it arises as evident that the structural basis of open inflorescence differs among families and that this diversity can be reduced to two basic types: i. open inflorescences with persisting CZ, in which stem cells are preserved and prevent the formation of a terminal flower and ii. open inflorescences derived from a MC-IM, in which vegetative stem cells merge into the meristematic coat producing lateral flowers until it gets exhausted.

3.4 What represses terminal flower formation in MC inflorescences?

As seen above, closed and open-MC inflorescences correspond in their development and histology. If the stem-cell maintenance is already broken in the open MC inflorescences, the reason behind the lack of a terminal flower will not be found in the action of a given FM-antagonist like *TFL1*. What else determines the presence or absence of a terminal flower in these cases? Proper material to test this question will be found in angiosperm taxa with both open and closed inflorescences based on a MC-IM. Ideal study cases are represented by species where the production of terminal flowers is even plastically performed. *Daucus carota* (Apiaceae) represents such a case with open and closed inflorescences, termed 'umbellets', on a single individual (Figs. 3.2I,N). A recent study in this species has shown that

Table 3.2. Histological studies in open inflorescences that reveal a shift to a mantle/core (MC) configuration in the IM.

Family	Species	References
Butomaceae	*Butomus umbellatus*	Grégoire 1938
Apiaceae	*Daucus carota*	Magin 1959
	Myrrhis odorata	Grégoire 1938
Asteraceae	*Arnoseris minima*	Lawalrée 1949
	Bellis perennis	Lawalrée 1949, Phillipson 1946
	Chrysanthemum segetum	Nougarède et al. 1987
	Dahlia gracilis	Philipson 1948
	Galinsoga parviflora	Lawalrée 1949
	Helianthus annuus	Palmer and Palmer 1982
	Hieracium boreale	Philipson 1948
Campanulaceae	*Jasione* sp.	Rauh and Reznik 1951
Dipsacaceae	*Dipsacus fullonum*	Philipson 1947a
	Scabiosa sp.	Lance 1956
	Succisa pratensis	Philipson 1947a
Moraceae	*Ficus carica*	Rauh and Reznik 1951
Ranunculaceae	*Aconitum napellus*	Grégoire 1938
	Delphinium ajacis	Grégoire 1938
Rosaceae	*Sanguisorba minor*	Phelouzat 1963
	Spiraea ulmaria	Grégoire 1938
Saururaceae	*Anemopsis californica*	Tucker 1985
	Houttuynia cordata	Tucker 1981
	Saururus cernuus	Tucker 1979
Valerianaceae	*Valeriana officinalis*	Philipson 1947b

umbellet meristems that produce terminal flowers are bigger and more convex than the umbellet-meristems that do not form a terminal flower (Figs. 3.2J-M, O, P). The latter are rather flat and form lateral floral primordia until the IM gets exhausted (Fig. 3.2O) - comparable to the ontogeny seen in Asteraceae heads (Harris 1995, Bull-Hereñu and Claßen-Bockhoff 2010). Apparently, the form and size of the apical meristem is critical at the time of deciding if a terminal flower will appear on the top of the *D. carota* IM or not. A similar hypothesis was proposed by Sokoloff et al. (2006) who postulated that the presence of a

terminal flower or terminal flower-like structures in *Potamogeton natans* would respond to the space remaining by chance on the tip of the developing spadix at the time after the lateral floral whorls were segregated.

In this sense, the key developmental processes in clades with MC-IMs determining if a terminal flower will be formed or not seem to be closely related with the availability of space and suitability of the form of the IM at the time prior to terminal flower differentiation. This view has been reinforced by a study concerning different angiosperm families that shows that at the time of a terminal flower differentiation, IMs form a bulge of a particular form, phyllotaxis and relative size (Figs. 3.2T-Y; Bull-Hereñu and Claßen-Bockhoff, unpublished). The size and morphology of plant meristems have already been shown before to be critical in some shaping processes. For example, the cotyledon number in *Larix* is linearly related to the diameter of the apical surface of the embryo (Harrison and Aderkas 2004). In Alismatales, restricted space availability in the distal portion of the spicate inflorescence seems to explain the adaxial reduction of flower organs as in *Triglochin* (Buzgo et al. 2006) and *Acorus* (Buzgo and Endress 2000). On the other hand, canalization of the geometrical conditions of the IM could lead to lineages with stable open- or closed inflorescences. In this sense, genetic control of the terminal flower production among clades with MC-IMs should be searched among candidate genes that regulate size and shape of the IM.

The conception that a terminal flower is a plastic possibility of an IM with a MC structure also explains why angiosperm families with closed inflorescences often include members that have lost their terminal flowers (Table 3.2). This fact was noticed by Troll (1964), who introduced the typological framework of inflorescence classification, distinguishing between open or 'polytelic' and closed or 'monotelic' inflorescences. He remarked that the species facultatively producing terminal flowers actually facultatively *lacked* a terminal flower, since they always belonged to the monotelic families ('Rumpfsynfloreszenzen'). Troll did not perform histological studies, but it is noteworthy that the examples of open MC inflorescence here given almost completely correspond to his monotelic families. The solely exception is given by the Asteraceae (Table 3.2), that he classified into his polytelic type, but that according to our interpretation, would have the potential of forming terminal flowers when the geometric relations on the IM were met. In fact, some Asteraceae produce inflorescence structures that appear to be topped by terminal flowers. These structures are found in aggregated heads of second order termed 'syncephalia' (Weberling 1992). For

example, *Gundelia* (Claßen-Bockhoff et al. 1989) and *Lagascea* (Kunze 1969, Harris 1994) produce syncephalia that are composed of tiny partial inflorescences of 3-10 flowers each. These subunits are topped by larger terminal flowers (or, alternatively, by 'single flowered capitula') that are the first to develop inside the subunit. Consequently, these structures can be actually understood as closed inflorescences and have been elsewhere interpreted as partial inflorescences with secondary monotelic nature (Claßen-Bockhoff et al. 1989). After our view, the production of densely packed syncephalia probably implies a readjustment of IM sizes that could simply lead to the geometrical conditions of IMs that allow terminal flower formation. Experimental manipulation of head meristem shapes and sizes would permit to test this hypothesis.

As long as the CZ is maintained in the IM, the shape of the IM is irrelevant with respect to the terminal flower question, since the stem cells in the distal IM hinder any floral differentiation at the top (Figs. 3.2B-D). Assuming the retention of the CZ in the IM as a systematic attribute would explain why there are clades that exclusively produce open inflorescences constituting the 'typical' open families.

Indeed, among the families that show CZ in their IMs (Table 3.1), occurrence of facultative terminal flowers are actually very rare (Troll, 1964). Such cases are represented principally by mutants, such as the *Arabidopsis tfl1* in Brassicaceae (Shannon and Meeks-Wagner 1991, Alvarez et al. 1992, Parcy et al. 2002, Sablowski 2007), the *Pisum det veg* in Fabaceae (Singer et al. 1999) and the *Antirrhinum cen* in Plantaginaceae (Bradley et al. 1996). The mentioned cases are characterized by a variable number and arrangement of floral organs in the terminal structure. Moreover, in *Antirrhinum* the contrast between the monosymmetric lateral flowers and the radial terminal flower arises as an additional feature (Bradley et al. 1996). A very close natural phenomenon is found in another species of the family, *Digitalis purpurea*, in which the terminal structure is considered to be a peloria (Rudall and Bateman, 2003) (Figs. 3.2E-H). In fact, it has been suggested for these families that the terminal flower re-appearance is generally related to peloria formation (Weberling and Troll 1998), what we assume to be developmentally related to a 'forced' loss of the CZ via mutation or exceptional environmental conditions. By mutants (of the '*tfl1* – kind'), these forced changes are related to a shortening of the ontogeny (Argiriou 2008). Interestingly, the loss of a CZ through exceptional environmental conditions is contemporarily performed to induce an early flowering in *Pharbitis nil* (Convolvulaceae), whose resulting phenotype include the formation

of an otherwise absent terminal flower (Marushige 1965, Herbert et al. 1992, Zheng et al. 2009).

Summarising, the production of a terminal flower apparently includes at least two developmental conditions to be met on an IM: a first histological one that refers to the dilution of the stem cells in the CZ of the IM; and a second physical one that demands a given shape and space availability on the IM at the time of terminal flower differentiation.

3.5 Concluding remarks

From the beginnings of morphological classification, inflorescences have been grouped according to their architecture and branching pattern. The presence / absence of a terminal flower as a predominant classificatory criterion has indirectly suggested a common nature of open inflorescence constructions such as racemes, spikes, spadices, heads and umbels (Roeper 1836, Troll 1964, Stebbins 1974, Weberling 1992, Prenner et al. 2009). This has founded the expectation that the evolutionary loss of terminal flower in inflorescences could be explained by one common mechanism (Coen and Nugent 1994, Prusinkiewicz et al. 2007). As hither discussed, the available evidence points out that open inflorescences can not be structurally grouped under one class.

Rather than re-defining what should be called indeterminate inflorescences or not, it arises as necessary to uncouple this term from the concept of indeterminate IM, and visualize the different mechanisms behind the evolutionary loss or re-gain of the terminal flower.

3.6 Summary

Absence of a terminal flower in inflorescences (’open inflorescences’) is presently explained by the maintenance of putative stem-cells in the central zone (CZ) of the inflorescence meristem (IM) governed by the *CLAVATA – WUSCHEL* regulatory loop. Disruption of this regulative pathway, as in *Arabidopsis TERMINAL FLOWER LOCUS 1* mutants, leads to terminal flower production. However, recent studies in other taxa reveal novel mechanisms of inflorescence termination, as the SEPALLATA-like MADS-box floral identity gene *GERBERA REGULATOR OF CAPITULUM DEVELOPMENT 2* in *Gerbera*, which excludes the retention of a CZ as an ontogenetic cause for the openness of these inflorescences. Moreover, comparative

histological studies show that the retention of a CZ in the IM is present in some, but absent in many other open inflorescences of diverse systematic groups. This evidence points out that the multiple loss and re-gain of the terminal flower in angiosperms is necessarily based on more than one ontogenetic pathway and opens the questions about the role that play spatial and geometrical attributes of the IM by the production of terminal flowers.

4 ONTOGENETIC COURSE AND SPATIAL CONSTRAINTS IN THE APPEARANCE AND DISAPPEARANCE OF THE TERMINAL FLOWER IN INFLORESCENCES

4.1 Introduction

The diversity of inflorescences is divided into two main groups concerning the presence or absence of a terminal flower (TF). The acknowledgement of these two groups, namely the closed inflorescences (i.e. with a TF) and the open ones (i.e. TF lacking) was already stated in the very first inflorescence treatise (Roeper 1826), whose vision was trespassed by influential botanists of the XX century (Parkin 1914; Troll 1964; Stebbins 1974; Weberling 1992) and remained valid until now (Prenner et al. 2009). From an evolutive point of view, the presence of a terminal flower (TF) on inflorescences represents an intriguing character of the plant architecture. It is striking to see that the condition of closed and open inflorescences has evolved repeatedly and independently in many systematic groups among angiosperms (Weberling 1992). Disclosing the developmental basis of terminal flower inception is thus fundamental for understanding its appearance and disappearance in the course of evolution, particularly as a mean for understanding the intriguing tendency to parallelism in plants (Yoon and Baum 2004).

Today, TF production is discussed in terms of molecular development. Departing from the seminal contributions of Shannon and Meeks-Wagner (1991) and Alvarez et al. (1992) for *Arabidopsis* and Bradley et al. (1996) for *Antirrhinum*, a consensus has been established that the production of the TF depends on the down regulation of the *TFL1/ CEN* genes, which is the actual working hypothesis in plant molecular research (Benlloch et al. 2007, Wang and Li 2008, Szczęsny et al. 2009, Rijpkema et al. 2010) and inflorescence modelling (Prusinkiewicz et al. 2007, Castel et al. 2010). Nevertheless, knowledge about genetic regulation or hormone balance does not exclude the possibility that factors of other nature are co-determining the plants phenotype, such as mechanical and physical constraints (Dumais 2007, Uyttewaal et al. 2010). Actually, physical input and genetic control are intimately related as the mechanotransductional processes have shown (Vogel and Sheetz 2006, Orr et al. 2006, Koizumi et al. 2009). Known physical constraints on plant shaping operate

fundamentally on the meristematic tissues, as they are the place of organ determination. For example, the size of meristematic tissues can have an effect on the number of organs to be produced on certain structures [cotyledons number in *Larix* (Harrison and Aderkas 2004), number of floral organs in *Ranalisma* (Charlton 1991)], external pressure can shape the organs either naturally [adaxial reduction of floral organs (Buzgo and Endress 2000, Buzgo et al. 2006), kind of aestivation of sepals (Ronse De Craene and Stuppy 2010)] or experimentally [phyllotaxis (Hernández and Green 1993)]; similarly, invasive wounding can elicit specific organogenesis (Hernández and Palmer 1988).

In this sense, the question of the production of a TF can be addressed in terms of physical constraints and shaping of the inflorescence meristem (IM). Bertero et al. (1996) showed that the presence of a TF in an inflorescence is related to specific geometries of the IM. More recently, Sokoloff et al. (2006), referring to natural variation of TF production in Alismatales, argued that the production of the TF can be related to availability of space on the IM. Bull-Hereñu and Claßen-Bockhoff (2010a) showed that in *Daucus carota* (Apiaceae), another facultative species for the TF production, the size of the IM is larger and more convex in the umbellets that produce the TF than in the ones that lack it.

But how general are these statements? Many basic questions regarding the TF production have remained unsolved or even unasked. Does the terminal flower arise as a consequence of space availability and geometric suitability of the IM? Is the required configuration of the IM related to any dynamic of the inflorescence ontogeny? Is the absence of a TF in different taxonomic groups reducible to similar ontogenetic pathways?

For answering these questions it arises as necessary to comparatively study the ontogenies of both open and closed inflorescences, the wider the focus, the general the conclusions. Studies on inflorescence development are not scarce in the last decade. However, when the production of a terminal flower is involved (Doust 2001, Balthazar and Endress 2002, Poole et al. 2002, Chen et al. 2003, Foster et al. 2003, Ronse De Craene 2004, Evans and Dickinson 2005, Buzgo et al. 2006, Sokoloff et al. 2006, Tian et al. 2006, Uemachi et al. 2006, Prenner and Rudall 2007, Gouvêa et al. 2008, González and Bello 2009) it is hard to look for answers to the abovementioned questions, since the rapidity of terminal flower production makes it very difficult to catch the time shortly before its inception. This is particularly difficult when studying species that do not grow under controlled conditions.

Here we present a comparative-quantitative ontogenetic study of inflorescences including 19 species of 4 families of the Eudicots. These families include both open and closed inflorescences in diverse shapes, architectures and sizes and simultaneously offer an attractive study field of relatively closely related species that vary in their TF aspect.

The aims of this work are to know i. whether the production of terminal flowers is given by certain characteristics of the IM, such as a minimum space availability or specific geometry, ii. whether the ontogenies of closed inflorescences share characteristics among species of different systematic positions, iii. whether the absence of the terminal flower is correlated with the failing of certain attributes of the IM, and iv. whether the open species share a common ontogeny independent of their taxonomic placements.

4.2 Materials and Methods

4.2.1 Plant material

Plant material was collected at the botanic garden of the Johannes Gutenberg-Universität in Mainz, Germany, between 2006 – 2009 (Table 4.1). Nineteen woody and herbal species from four families were included in the study: Berberidaceae (4ssp), Papaveraceae-Fumarioideae (4ssp), Rosaceae (5ssp) and Campanulaceae. Their inflorescences are open and closed racemes and thyrses of different shapes (Table 4.1; Fig. 4.1). Vouchers of the species are deposited at MJG (Table 4.1).

The inflorescences of each species were characterized counting the total number of lateral units (LU). In racemes the lateral units correspond to flowers, in thyrses to cymes (Fig. 4.2). Few- and many-flowered inflorescences were represented in the material, ranging on average from 5 to 105 LUs (Table 4.1). In order to reduce the typical variability among inflorescences of a same species, we just collected terminal inflorescence-buds, i.e. we avoided to collect basipetal repetition units that usually appear later in the season.

Plant tissues were conserved in 70% ethanol and then dehydrated in a series of increasing alcohol-acetone series (1 hour steps through EtOH 80%, 90%, 96%, acetone; then 12 hours acetone) and critically point dried (BAL-TEC CPD030). The developing inflorescences were then sputtered with a thin gold film (BAL-TEC SCD005) and analysed under a scanning electron microscope (ESEM XL-30 Philips). All techniques were made following manufacturers protocols.

Table 4.1. Species studied including collection time (CT), plant's growth form (GF), inflorescence type (IT), inflorescence shape (IS), average number of lateral units (LU) in mature inflorescences, method of age estimation (AE), the total number of inflorescence buds observed (N) and the number of inflorescence buds used in the numerical analysis (n). LU was estimated after counting 30 individuals, with exception of *C. sempervirens* (n=23), *S. minor* (n=28), *C. thyrsoides* (n=6) and *A. eupatoria* (n=6). Roman numbers represent months and years are abbreviated in two digits. W = woody, A = annual, P = perennial herb, B = biennial; Ra = raceme, cRa = closed raceme, T = closed thyrse, M = multiple raceme; E = elongated, Co = condensed, G = globose, U = umbellate, C = corymbose, D = disc-shaped; LP = number of lateral primordia, BL = sum of the length of the three youngest bracts. * the low number of sample didn't allow the numerical analysis.** *Jasione* doesn't produce floral bracts in the inflorescences, so no AE could be performed.*** LU could not be estimated as the meristem used to fasciate.

Family	Species	Voucher	CT	GF	IT	IS	LU	St. dev.	AE	N	n
Berberidaceae	*Berberis aristata* DC.	Bullher 1 MJG	IX 07	W	cRa	E	16,2	1,8	LP	39	11
	Berberis darwinii HOOK.	Bullher 2 MJG	X 07	W	Ra	E	13,2	1,6	LP	72	19
	Mahoberberis x aquisargentii Jensen	Bullher 3 MJG	III 07	W	cRa	E	12,2	2	LP	60	12
	Mahonia aquifolium (PURSH) NUTT.	Bullher 4 MJG	X 07	W	Ra	E	33,7	4	LP	42	26
Papaveraceae-Fumarioideae	*Capnoides sempervirens* (L.) BORKH.	Bullher 5 MJG	V,VI 08	A	T	E	5,5	0,6	LP	27	12
	Corydalis elata BUREAU et FRANCH.	Bullher 6,7 MJG	IV 09	P	Ra	E	31,1	5	BL	34	24
	Dicentra eximia (KER-GAWL.) TORR.	Bullher 8 MJG	II 08	P	T	E	5,1	0,6	LP	22	9
	Lamprocapnos spectabilis (L.) T. Fukuhara	Bullher 9,10 MJG	II 09	P	Ra	E	11,5	3,3	LP	28	14
Rosaceae	*Agrimonia eupatoria* L. *var 'Alba'*	Bullher 11 MJG	IV,V 09	P	cRa	E	105	25,7	BL	38	22
	Neviusia alabamensis A.GRAY	Bullher 12,13 MJG	VIII 07	W	cRa	Co	5,1	0,7	LP	26	5
	Sanguisorba minor SCOP.	Bullher 14,15 MJG	II 08	P	Ra	G	43,2	6,5	BL	23	10
	Spiraea chamaedryfolia L.	Bullher 16,17 MJG	IX,X 07	W	Ra	U	27,6	6,5	BL	25	14
	Spiraea japonica L.f.	Bullher 18,19 MJG	V 06, IV 08	W	M	C	5	0,7	LP	37	12
Campanulaceae	*Asyneuma canescens* (WALDST. et KIT.) GRISEB. et SCHENK	Bullher 20 MJG	V-VI 06, IV 08	P	T	E	30,9	9,4	*	25	3
	Campanula thyrsoides L.	Bullher 21 MJG	V,VI 09	B	T	E	94,3	25,8	BL	41	16
	Edraianthus tenuifolius (WALDST. et KIT.) A.DC.	Bullher 21,22 MJG	IV 08, IV 09	P	cRa	D	10,8	1,7	LP	35	7
	Jasione montana L.	Bullher 23 MJG	VI 06, VI 08	A	Ra	D	62,8	7,6	**	32	9
	Lobelia cardinalis L.	Bullher 24 MJG	VI 06	B	Ra	E	***	-	BL	20	8
	Phyteuma orbiculare L.	Bullher 25 MJG	III-V 08	P	Ra	G	38,8	6	BL	20	11
									Total	**646**	**244**

Figure 4.1. Plant species studied and inflorescences types and shapes (in parenthesis). A-D, Berberidaceae. E-H, Papaveraceae-Fumarioideae. I-M, Rosaceae. N-S, Campanulaceae. A, *Berberis aristata* – closed raceme. B, *Berberis darwinii* – raceme. C, *Mahoberberis* x *aquisargentii* – closed raceme. D, *Mahonia aquifolium* – raceme. E, *Capnoides sempervirens* – closed thyrse. F, *Dicentra eximia* – closed thyrse. G, *Lamprocapnos spectabilis* – raceme. H, *Corydalis elata* – raceme. I, *Agrimonia eupatoria* var 'Alba'- closed raceme. J, *Sanguisorba minor* – raceme (globose). K, *Spiraea chamaedryfolia* – raceme (umbellate).L, *Neviusia alabamensis* – closed raceme. M, *Spiraea japonica* – multiple raceme (corymbose). N, *Campanula thyrsoides* – closed thyrse. O, *Asyneuma canescens* – closed thyrse. P, *Edraianthus tenuifolius* – closed raceme (disc-shaped). Q, *Jasione montana* – raceme (disc-shaped). R, *Phyteuma orbiculare* – raceme (globose). S, *Lobelia cardinalis* – raceme.

A total of 646 inflorescence buds were observed (Table 4.1, N). For the quantitative study of the meristematic dimensions of the IMs we excluded material that was too young (i.e. in vegetative or transitional meristems) or too old (i.e. with evident terminal flowers formed or degenerating IMs) leaving 244 IMs for the measurement (Table 4.1, n).

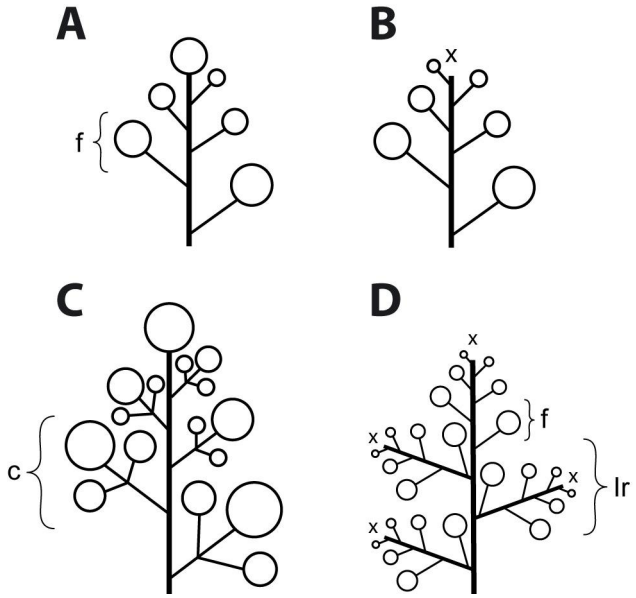


Figure 4.2. Schematic diagram of the inflorescences studied. A, closed raceme. B, raceme. C, closed thyrse. D, multiple raceme. tf, terminal flower, f, flower, c, cyme, lr, lateral raceme. Closed racemes and closed thyrses posses a terminal flower, while the raceme and the multiple raceme have an 'open end' (marked by the cross).

4.2.2 Measurements

The number of the developing LUs, termed 'lateral primordia' (LP) was counted in each inflorescence bud. From top views of the IM, the youngest LP with developing reproductive product was identified (Fig. 4.3A). Taking the youngest LP as reference, frontal (Fig. 4.3B) and

lateral (Fig. 4.3C) views of the IM were obtained. With the aid of the software Image Access, measurements were performed on the images taken (Fig. 4.3A-C).

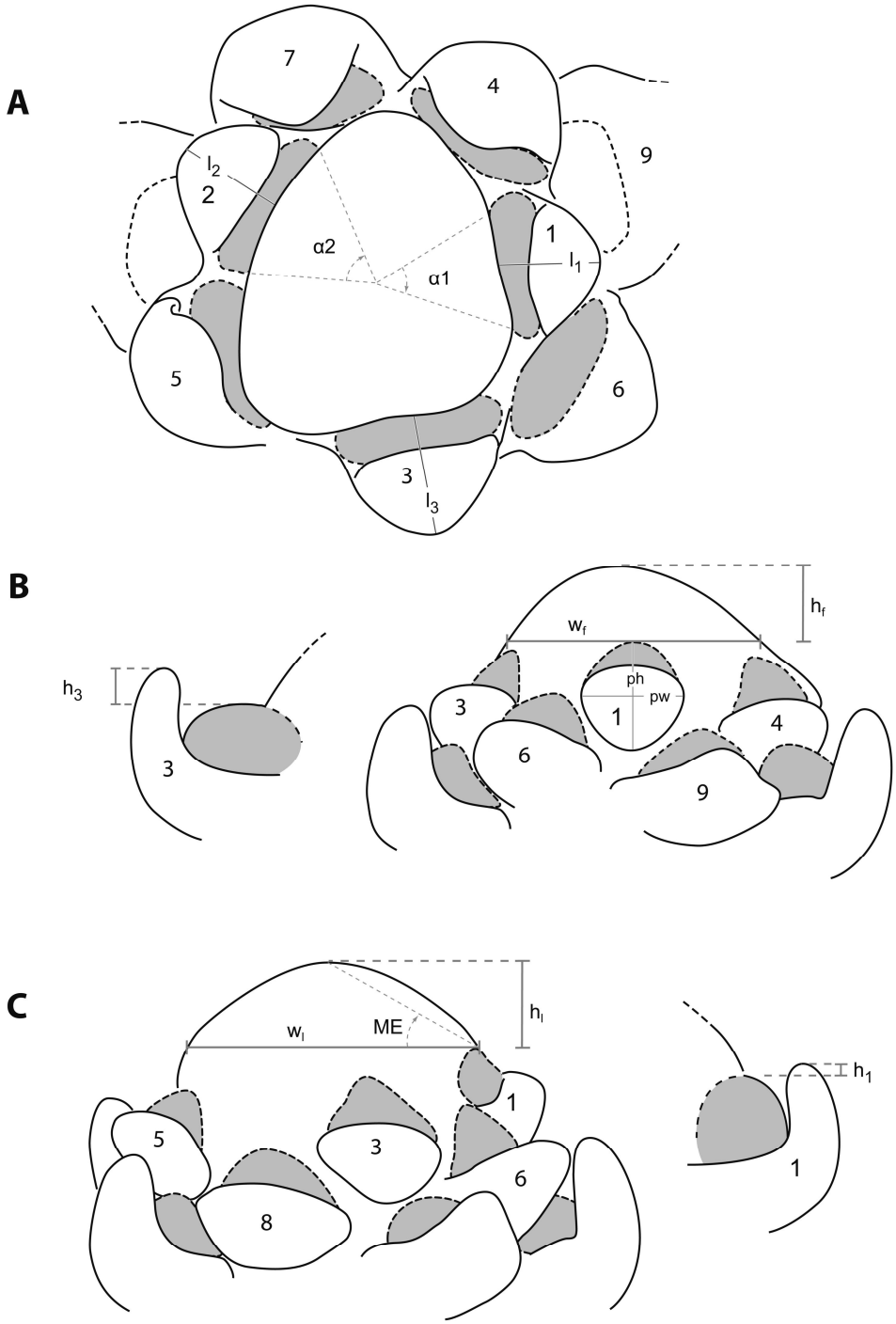


Figure 4.3. Measurements performed on the developing inflorescences. Lateral primordia numbered according to their age, the youngest being the first. A, Top view. α, angle formed by the primordium insertion line and the centre of the meristem; l_1, l_2, l_3, length of the three youngest primordia. B, Frontal view. h_f, frontal height of the meristem; w_f, frontal width of the meristem; ph, height of the youngest primordium; pw, width of the youngest primordium; h_3, protrusion height of the third youngest bract. C, Lateral view. h_1, lateral height of the meristem w_l, lateral width of the meristem; h_1, protrusion height of the youngest bracts; ME, elevation of the meristem; note that this parameter was not measured directly from the pictures, but calculated from the meristematic height and width averages. See text for details.

- From the polar view (Fig. 4.3A):
    - the angle α formed by the line of insertion of a lateral primordium (LP) and the meristem centre. This parameter, also known as 'leaf arc', represents a phyllotactic indication of the IM (Snow & Snow 1962, Rutishauser 1998). This angle was obtained for the two youngest LP (α_1, α_2).
    - the length of the of the three youngest LP (l_1, l_2, l_3)
- From the frontal view (Fig. 4.3B):
    - the meristem width (w_f)
    - the meristem height I (h_f)
    - the youngest LP height (p_h)
    - the youngest LP width (p_w)

In case of flat meristems (*Lobelia* and *Edraianthus*), these entries were obtained from top views.

- From the lateral view (Fig. 4.3C):
    - the meristem width (w_l)
    - the meristem height (h_l)

In case that some of the subtending bracts of the three youngest LP overgrew their axillary product, we used both frontal and lateral views to measure the height of their protrusion (h_1,h_2, h_3; Fig. 4.3B, C)

4.2.3 Parameter calculation

Based on the measurements obtained, we calculated following parameters of the IM.

- The meristematic width (W) was defined as the diameter of the circle encompassing the transversal section area of the meristem. As normally w_f was different from w_l, the section area of the meristem was rather represented by an ellipse. Thus we obtained W calculating the geometrical mean of both width entries:

$$W = \sqrt{w_f \times w_l}$$

- The height of the meristem (H) was calculated as the arithmetic mean of both height values h_f and h_l:

$$H = \frac{h_f + h_l}{2}$$

- The total surface of the meristem (MS) was idealized as the surface of a rotation paraboloid of height H and ratio $W/2$, given by the geometric equation:

$$MS = \frac{\pi \times W/2}{6H^2} \times \left[\left(\left(W/2 \right)^2 + 4H^2 \right)^{3/2} - \left(W/2 \right)^3 \right]$$

In the cases where the IM was evidently plane (*Lobelia*, *Edraianthus*), the MS was idealized as the transversal section area of an ellipse with semi axes $w_I/2$ and $w_{II}/2$:

$$MS_{Lobelia, Edraianthus} = \left(\frac{W}{2} \right) \times \pi$$

- The area of insertion of the youngest primordium (YPA) was calculated as the surface of an ellipse with semi axes $pw_I/2$ and $pw_{II}/2$:

$$YPA = \frac{p_h}{2} \times \frac{p_w}{2} \times \pi$$

- The areal ratio of the IM (AR) represented the relation between MS and the area of insertion of the youngest primordium (YPA)

$$AR = \frac{MS}{YPA}$$

- The angular insertion of the primordia on the IM, the leaf arc (LA), was calculated as

$$LA = \frac{\alpha_1 + \alpha_2}{2}$$

- The meristematic elevation (ME) represented the angle formed between the top of the IM and the width line (Fig. 4.3C). This was calculated assuming this angle inside a rectangle triangle with an opposite cathetus of value H and an adjacent cathetus equal $W/2$:

$$ME = \operatorname{Arc\,tan}\left(\frac{H}{W/2} \right)$$

4.2.4 Inflorescence bud age

For the analysis it was essential to attain a developmental state of each inflorescence bud, to be able to regress the parameters against age. In species whose total number of LUs in the mature inflorescences didn't vary strongly among individuals, the inflorescence bud age could be estimated counting the number of LPs produced at that time. For example, if an

inflorescence bud of *Lamprocapnos spectabilis* had formed 6 flower primordia at the time of harvesting, we could assume that it was roughly in the middle of its development, since *L. spectabilis* produces an average of 12 LUs ± 3,3 (Table 4.1). The use of LP number as age indicator was not suitable when individuals of a given species showed a higher LU variability. For example, an *Agrimonia eupatoria* inflorescence with 60 flower primordia, could be either in the middle or near the end of development, since the closed raceme of this species bears on average 105 ± 25 LUs (Table 4.1). Based on our data we defined a maximal variability acceptable in the total number of LUs as st. dev. < 5 to consider the number of LP as a good age estimate. Ten species fulfilled this criterion and not surprisingly corresponded to the species with lower amount of flowers in the inflorescences, roughly up to 30 LUs (Table 4.2). For the remaining species we had to search an alternative method of age estimation. For this purpose, we performed an explorative analysis with the ten abovementioned inflorescences looking for an alternative structural property of the inflorescence bud that helped to predict its age. We noticed in eight of the ten species that the size of the youngest bracts in the inflorescence bud, measured as:

BL = $l_1 + l_2 + l_3 + h_1 + h_2 + h_3$ (Fig. 4.3A-C)

augmented exponentially with increasing number of LPs (mean R^2 for exponential regressions = 0,66). Biologically this means that the youngest primordia tend to grow and differentiate faster in older inflorescence buds. Conversely seen, in these inflorescences the number of lateral primordia could be predicted by using the logarithmic function of BL. Assuming that this relation was also true for larger inflorescences, we took the BL as an age estimate for the nine species whose inflorescences presented a st. dev. of LU > 5 (Table 4.2). For *Jasione montana* no age could be estimated, since no subtending bracts are produced; it was therefore left out of the analysis.

4.2.5 Statistical analysis

-Regression Analysis: The calculated parameters width (W), height (H), meristematic surface (MS), youngest primordium area (YPA), areal ratio (AR), leaf arc (LA) and meristematic elevation (ME) were regressed against the age of the inflorescence bud. Significant regressions ($p < 0,05$) indicated that the parameter increased or decreased during ontogeny. If the regression was not significant, the parameter was considered to be 'stable'. From the

regression curve we defined an initial and final state of the parameters at the youngest and oldest age-states found in the respective sample. In the case of non significant regressions, the initial and final states were assumed to be equal and were estimated with the mean of the data pool. The number of suitable buds of *Asyneuma* (n=3) was not enough to perform the regression analysis, which left 17 species on the analysis.

-T test: The initial and final states of the abovementioned parameters were compared by means of a T test between the open and closed species.

-Correlation analysis: We calculated table of correlations for the parameters LA, ME, AR and LU inside the closed and open species, to see whether there were syndromes in the shape of the IM.

All analyses were performed with the SPSS package. *Lobelia* was excluded from the T test and correlation analyses since its values severely outranged the pool of data.

4.3 Results

4.3.1 Inflorescence ontogeny by systematic groups

4.3.1.1 Berberidaceae

Berberis open and closed racemes (Fig. 4.1K, L) begin their ontogeny on a dome-shaped meristem (Fig. 4.4A5, B1) that expands from a relatively smaller vegetative meristem (Fig. 4.4A1, B4). Both cones diminish in their width (Fig. 4.4A2-4, B5-7; Table 4.3) and height (Fig. 4.4A5-7, 4B1-3; Table 4.3) while giving rise to lateral flowers. However, they differ in the decrease of their height, which is more marked in the open *B. darwinii* than in the closed *B. aristata* (-4,26 µm/LP; se=0,67 against -1,62 µm/LP, se=0,48; Table 4.3; Fig. 4.5A,B). The over 30° meristem elevation in *B. aristata* permits a bulge at the end of the ontogeny that utterly differentiates into a terminal flower (Fig. 4.4A7, A8). In contrast, the meristem in *B. darwinii*

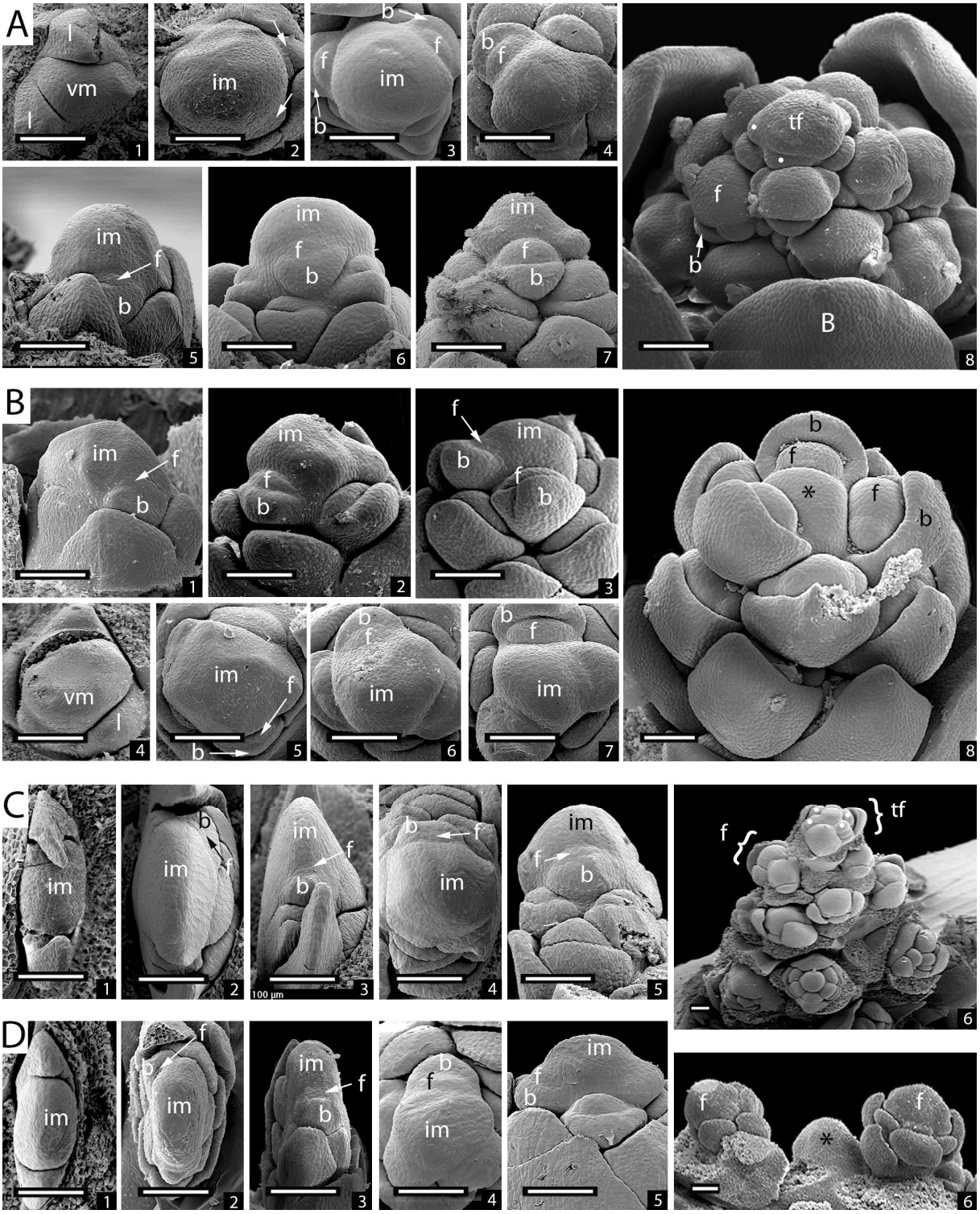


Figure 4.4. Development of Berberidaceae inflorescences. A, *Berberis aristata*. B, *Berberis darwinii*. C, *Mahoberberis* x *aquisargentii.* D, *Mahonia aquifolium.* All bars: 100µm.

A1-4, Top views of the developmental sequence of *B. aristata*. A1, Vegetative state showing leaf buds (l) surrounding a vegetative meristem (vm). A2, Reproductive state with four lateral flower primordia (arrows). The flower primordia are markedly smaller than the inflorescence meristem (im), which in turn is larger than the vegetative meristem. A3, Individual with six lateral primordia; note the larger →

→ size of flower (f) and bract (b) primordia in comparison to the previous state. A4, Individual with 16 flower primordia showing a slight decay of the diameter of the inflorescence meristem. **A5-8**, Lateral views of *B. aristata.* A5, Same individual as in A2 revealing the conic elevation of the inflorescence meristem; note the relatively larger size of the bract primordium compared with the flower bud. A6, Same individual as in A3. The size of the flower/bract primordium is larger than in the previous state, while the elevation of the meristem has decayed. A7, Individual with 16 flower buds, which are clearly in a more advanced state than in the previous state. At this state the inflorescence meristem represents the bulge from which the terminal flower will develop. A8, Completely developed closed raceme of *B. aristata*. The terminal flower bud (tf) shows sepals differentiating (dots). The developmental state of the terminal flower bud is clearly more advanced than that of the distal lateral flower buds. Parts of four bud-protective bracts (B) are also visible. **B1-3**, Lateral views of the developing raceme of *B. darwinii.* B1, Individual with four flower primordia; note the similarity to the young inflorescence of *B. aristata* in A5. B2, Individual with five primordia. The larger size of the lateral primordia in relation to *B. aristata* is evident (A6). A marked reduction of the in volume is also expressive. B3, Individual with 12 flower primordia, whose inflorescence meristem has lost any convexity (almost flat), contrary to the remaining bulge in *B. aristata* (A7). **B4-7**, Top views of developing *B. darwinii* inflorescences. B4, Vegetative state. B5, Same individual as in B1 showing the enlargement of the meristem when converting to the reproductive state. B6, Same individual as in B2. B7, same individual as in B3. The size of the youngest primordium tends to become bigger through development (B5-7). **B8**, Completely developed *B. darwinii* raceme, showing floral primordia enclosed by bracts and a flat meristematic rest at the top (star). **C1**, Top view of *Mahoberberis* inflorescence prior to flower segregation. **C2**, An early developmental stage of the closed raceme having formed nine flower primordia at an enlarged inflorescence meristem. The oval form of the inflorescence is probably due to the tight junction of the bracts that enclose the bud. **C3**, Side view of C2 showing the prominent elevation of the inflorescence meristem. **C4**, Top view of an inflorescence with 14 flower bud. By this time the meristem has adopted a more rounded shape. **C5**, Side view of C4 showing the meristematic bulge (im) that is close to differentiate into a terminal flower. **C6**, Completely developed closed raceme of *M. x aquisargentii* showing the terminal flower (tf) in a developmental state similar to a proximal lateral flower. Stamen primordia are not present in the higher lateral flowers, but in the terminal one (dots). **D1**, Top view of *Mahonia* inflorescence prior to flower segregation. Note the similar dimensions to the respective *Mahoberberis* meristem in C1. **D2**, Top view of a raceme with 12 flowers. The inflorescence meristem has a similar size as in the vegetative state (D1), contrasting with the situation in *Mahoberberis* (C2, C4). **D3**, Side view of D2. The vertical dimension of the inflorescence meristem is also markedly lower than in *Mahoberberis* (C3). **D4**, Top view of a raceme in a later state with 17 flower primordia. Compared with *Mahoberberis* (C4), the inflorescence meristem is smaller which has the consequence that the lateral primordia have a higher leaf arc. **D5**, Side view of the individual in D4. The lower elevation of the meristem has persisted from D3 and is clearly smaller than in C5. **D6**, View of the tip of a *Mahonia* raceme at a mature state showing the two youngest (sub apical) lateral flowers. Between them a conic rest can be seen (star). b= subtending bract; f = lateral flower primordium; im, inflorescence meristem; l, leaf bud; tf = terminal flower; vm, vegetative meristem.

remains flat after the fragmentation of the last flower primordia (Figs. 4B3, 8, 6A) and presents an areal ratio that is much smaller than that of the closed one (Fig. 4.5A, B).

Mahonia aquifolium and *Mahoberberis x aquisargentii* inflorescences (Fig. 4.1M, N) originate in tight groups around the vegetative axis (Fig. 4.1D). The lateral pressure of the bud scales forces the inflorescence meristems to develop in an elliptic form (Fig. 4.4C1, D1). In contrast to the *Berberis* species, whose meristems are used up, *Mahonia* and *Mahoberberis* exhibit stable meristematic sizes during ontogeny (Table 4.3; Fig. 4.5C, D). These two species clearly differ in their meristematic dimensions. Due to a marked enlargement of the vegetative meristem, *Mahoberberis* attains an inflorescence meristem that exceeds the width and even doubles the height of the one in *Mahonia* (Table 4.2; Fig. 4.4C2, C3, 4D1-3). Consequently, the ME and AR of *Mahoberberis* are also higher than in *Mahonia* (Figs. 4C5, D5, 5C, D). The LA is stable in both species but lower in *Mahoberberis* (Figs. 4.4C4, D4, 5C, D). The 40° meristematic bulge that is present in the final state of *Mahoberberis* (Figs. 4.4C5, 4.6A) differentiates into a terminal flower (Fig. 4.4C6); in contrast, the tip in *Mahonia* merges into an undifferentiated meristematic rest (Fig. 4.5A). This remaining tip is not as flat as that in *B. darwinii* (Fig. 4.4B8) and experiences a posterior longitudinal extension (Fig. 4.4D6) that makes it even macroscopically visible at the adult state.

The four species of the Berberidaceae correspond in their final leaf arc (LA) ranging between 80-110°. Interestingly, the two closed species show a bulge that is more elevated than in the two open species (Fig. 4.5A).

4.3.1.2 Papaveraceae-Fumarioideae

The ontogeny of the two closed thyrses in the Fumarioideae (*Dicentra eximia, Capnoides sempervirens*; Fig. 4.1A, B) is very similar (Fig. 4.7A1-9, 4.7B1-9) and characterised by stable meristematic dimensions and forms during the short development (Fig. 4.8A, C; Table 4.3). After the enlargement of the vegetative meristem (Fig. 4.7A1, A2, A5, A6, B1, B2, B5, B6), both inflorescences share a meristem height of ca. 35 µm (Table 4.2). However, due to its higher meristematic width and primordial size *Dicentra eximia* (Table 4.2) has larger general

Table 4.2. Initial (i) and final (f) values of the geometrical parameters of the inflorescence meristems and youngest primordium obtained from the regression curve (see Material and Methods). In case of no significant regression, the mean of the data pool was taken for both initial and final state (see Figs. 4.5, 4.8, 4.10, 4.12). *Edraianthus* and *Lobelia* present no values for H (height) and ME (meristematic elevation) as they possess flat inflorescence meristems. Families demarked by lines. S = initial or final state, W = meristem width, H = meristem height, MS = meristematic surface, YPA = youngest primordium area, AR = areal ratio, LA = leaf arc, ME = meristematic elevation, c.i = 95% confidence interval.

	S	W (µm)	c.i.	H (µm)	c.i.	MS (µm²)	c.i.	YPA (µm²)	c.i.	AR	c.i.	LA (°)	c.i.	ME (°)	c.i.
B. aristata	i	170,27	24,83	57,34	9,01	31059	7490	7376	927	4,45	1,02	78,50	11,31	32,95	1,33
	f	120,86	19,07	37,95	6,92	16798	5109	7376	927	2,00	0,78	96,02	8,69	32,95	1,33
B.darwinii	i	178,28	12,56	62,22	6,55	33563	4107	6388	1913	4,81	0,85	67,99	9,95	35,99	3,14
	f	117,04	18,29	19,64	9,55	11548	5982	12018	2786	,79	1,24	106,07	14,49	20,30	4,57
M. x aquisargentii	i	135,05	12,76	71,65	8,63	28983	3219	10082	3652	4,16	0,88	80,75	13,73	49,12	5,92
	f	157,59	9,43	71,65	8,63	28983	3219	6133	2700	4,16	0,88	80,75	13,73	40,00	4,37
M. aquifolium	i	125,87	7,07	36,24	2,96	16252	1771	7340	642	2,29	0,25	94,42	4,79	29,83	1,79
	f	125,87	7,07	36,24	2,96	16252	1771	7340	642	2,29	0,25	94,42	4,79	29,83	1,79
C. sempervirens	i	101,50	7,98	36,23	6,20	11632	2189	4258	562	2,75	0,45	108,58	6,58	34,83	3,07
	f	101,50	7,98	36,23	6,20	11632	2189	4258	562	2,75	0,45	108,58	6,58	34,83	3,07
C. elata	i	225,05	18,13	75,74	9,26	48118	6498	7728	452	6,28	0,78	46,32	7,45	38,05	3,25
	f	97,80	21,47	15,01	10,96	8602	7698	7728	452	1,07	0,90	105,24	8,83	16,42	3,86
D. eximia	i	135,81	12,00	34,91	5,94	16964	3805	11007	1386	1,52	0,20	106,06	10,13	26,97	1,99
	f	135,81	12,00	34,91	5,94	16964	3805	11007	1386	1,52	0,20	106,06	10,13	26,97	1,99
L. spectabilis	i	159,25	23,30	37,81	4,70	19393	3837	13173	1663	1,94	0,44	109,92	7,87	28,69	2,69
	f	116,27	24,14	37,81	4,70	19393	3837	13173	1663	1,04	0,45	109,92	7,87	28,69	2,69
A. eupatoria	i	275,46	39,77	74,66	8,81	76503	20321	9575	989	8,32	2,30	39,95	14,23	30,06	3,04
	f	118,62	67,58	74,66	8,81	17581	34526	9575	989	1,57	3,89	110,67	24,17	42,23	5,17
N. alabamensis	i	91,08	9,37	35,40	8,77	10245	3071	3140	1563	3,60	1,58	85,85	15,70	37,58	5,72
	f	91,08	9,37	35,40	8,77	10245	3071	3140	1563	3,60	1,58	107,15	9,74	37,58	5,72
S. minor	i	285,65	65,71	99,48	23,69	90542	37408	6473	1198	15,35	5,37	29,35	7,30	36,20	2,72
	f	146,45	88,72	22,80	31,99	11052	50510	6473	1198	,85	7,24	68,23	9,86	20,35	3,68
S. chamaedryfolia	i	159,53	24,76	43,84	7,99	21795	5282	3282	309	7,73	2,24	62,16	15,84	30,24	4,88
	f	56,04	28,33	6,23	9,14	-188	7192	3282	309	,03	2,16	95,59	18,12	17,23	5,58
S. japonica	i	100,80	17,17	23,84	3,79	9880	2749	4754	889	2,07	0,40	104,06	5,58	28,86	2,38
	f	75,69	12,71	23,84	3,79	6032	2035	3091	658	2,07	0,40	104,06	5,58	28,86	2,38
C. thyrsoides	i	258,50	16,44	20,93	4,36	53315	11000	7515	2216	8,09	2,11	52,25	7,95	9,11	1,68
	f	258,50	16,44	20,93	4,36	53315	11000	13553	3359	2,28	3,59	68,96	12,05	9,11	1,68
E. tenuifolius	i	178,04	23,88	0	-	25334	6505	17944	4967	,79	2,14	56,33	6,26	0	-
	f	178,04	23,88	0	-	25334	6505	5298	3755	4,08	1,61	56,33	6,26	0	-
L. cardinalis	i	631,61	100,45	0	-	323082	96091	7013	1498	50,53	21,24	16,53	4,56	0	-
	f	631,61	100,45	0	-	323082	96091	7013	1498	50,53	21,24	16,53	4,56	0	-
P. orbiculare	i	186,64	23,24	20,47	5,15	28792	6731	4541	599	6,53	1,66	39,60	5,59	11,36	1,80
	f	77,08	41,23	5,61	9,15	2170	11943	4541	599	,60	2,94	72,74	9,92	11,36	1,80
Closed species	i	168,26	56,73	41,38	21,31	31754	18967	8862	3832	4,21	2,31	76,02	20,83	27,58	13,23
	f	165,01	57,73	39,00	20,65	22607	11632	7542	2989	2,75	0,90	91,84	17,31	27,93	12,82
Open species	i	177,70	48,23	49,81	22,70	33542	21619	6710	2521	5,88	3,71	69,22	25,58	29,90	7,00
	f	101,50	25,21	21,00	10,06	9358	5566	7206	3144	1,09	0,63	94,55	13,17	21,47	5,77

Table 4.3. Change of geometrical parameters during development. Given are the slope (s) and goodness of fit (R^2) of the regression curves for each measured parameter. In case of non significant regression the parameters are thought not to change during ontogeny (no value given). * p < 0,05. ** p < 0,01. *** p < 0,001.

	W		**H**		**MS**		**YPA**		**AR**		**LA**		**ME**	
	s	R^2	s	R^2	s	R^2	s	R^2	s	R^2	s	R^2	s	R^2
B. aristata	-4,12	0,52*	-1,62	0,56**	-1296	0,54*			-0,20	0,61**	1,46	0,40*		
B.darwinii	-6,12	0,57***	-4,26	0,70***	-2201	0,60***	563	0,33*	-0,40	0,56***	3,81	0,45**	-1,57	0,59***
M. x aquisargentii	1,50	0,42*											-0,61	0,35*
M. aquifolium														
C. sempervirens														
C. elata	-90,89	0,72***	-43,38	0,69***	-28225	0,66***			-3,72	0,71***	42,09	0,77***	-15,45	0,70***
D. eximia														
L. spectabilis	-3,58	0,31*							-0,74	0,34*				
A. eupatoria	-157	0,36**			-58922	0,24*			-6,74	0,24*	71	0,48**	12	0,37**
N. alabamensis											10,65	0,80*		
S. minor	-126,54	0,42*	-69,71	0,63**	-72263	0,42*			-13,18	0,54*	35,35	0,82***	-14,42	0,85***
S. chamaedryfolia	-103,49	0,66***	-37,61	0,71***	-24426	0,62**			-7,35	0,63**	0,33	0,33*	-13,00	0,44*
S. japonica	-5,02	0,35*			-769	0,34*	-332	0,47*						
C. thyrsoides							6038	0,36*	-5,28	0,32*	16,71	0,25*		
E. tenuifolius									0,47	0,57*				
L. cardinalis							15797	0,54*						
P. orbiculare	-156,52	0,70**	-21,23	0,47*	-38031	0,63**			-8,48	0,58**	47,35	0,79***		

dimensions, a flatter curvature and a smaller areal ratio than *Capnoides sempervirens* (Table 4.2; Fig. 4.5B). Before forming the terminal flower, both inflorescences develop a meristematic bulge at which the TF differentiates (Fig. 4.7A3, A4, A7-9, B3, B4, B7-9).

The development of the open *Lamprocapnos spectabilis* raceme (Fig. 4.1C) shows higher meristematic dimensions throughout (Fig. 4.7C1-7; Table 4.2). The inflorescence meristem does not enlarge significantly when merging from the vegetative into the reproductive state (Fig. 4.7C1, C2). As in the open *Berberis* ssp, the meristematic width of *L. spectabilis* diminishes while the lateral primordium size (YPA) grows (Table 4.3), what provokes an AR fall from 1,94 to1,04 (Fig. 4.8D; Table 4.2). This lies beyond the data of both closed thyrses. The primordium size is the highest of the Fumarioideae investigated,(Fig. 4.6B). Despite this transformation, *L. spectabilis* presents a stable phyllotaxis (LA) and ME (Fig. 4.8D).

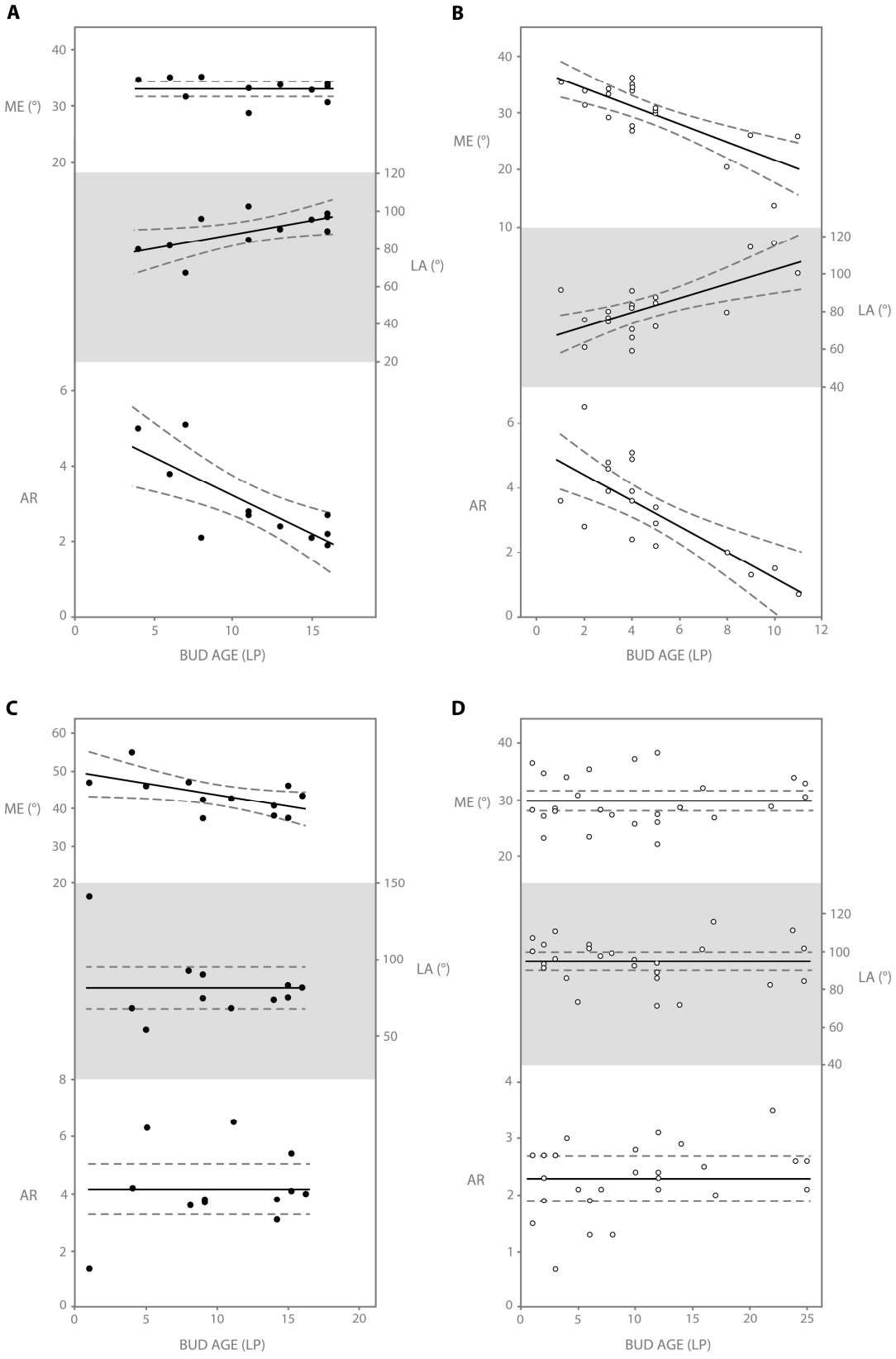


Figure 4.5. Development of the areal ratio (AR), leaf arc (LA), and meristematic elevation (ME) with increasing age in Berberidaceae inflorescences. A, *Berberis aristata*. B, *Berberis darwinii*. C, *Mahoberberis x aquisargentii*. D, *Mahonia aquifolium*. Black circles represent closed species and empty circles open species.

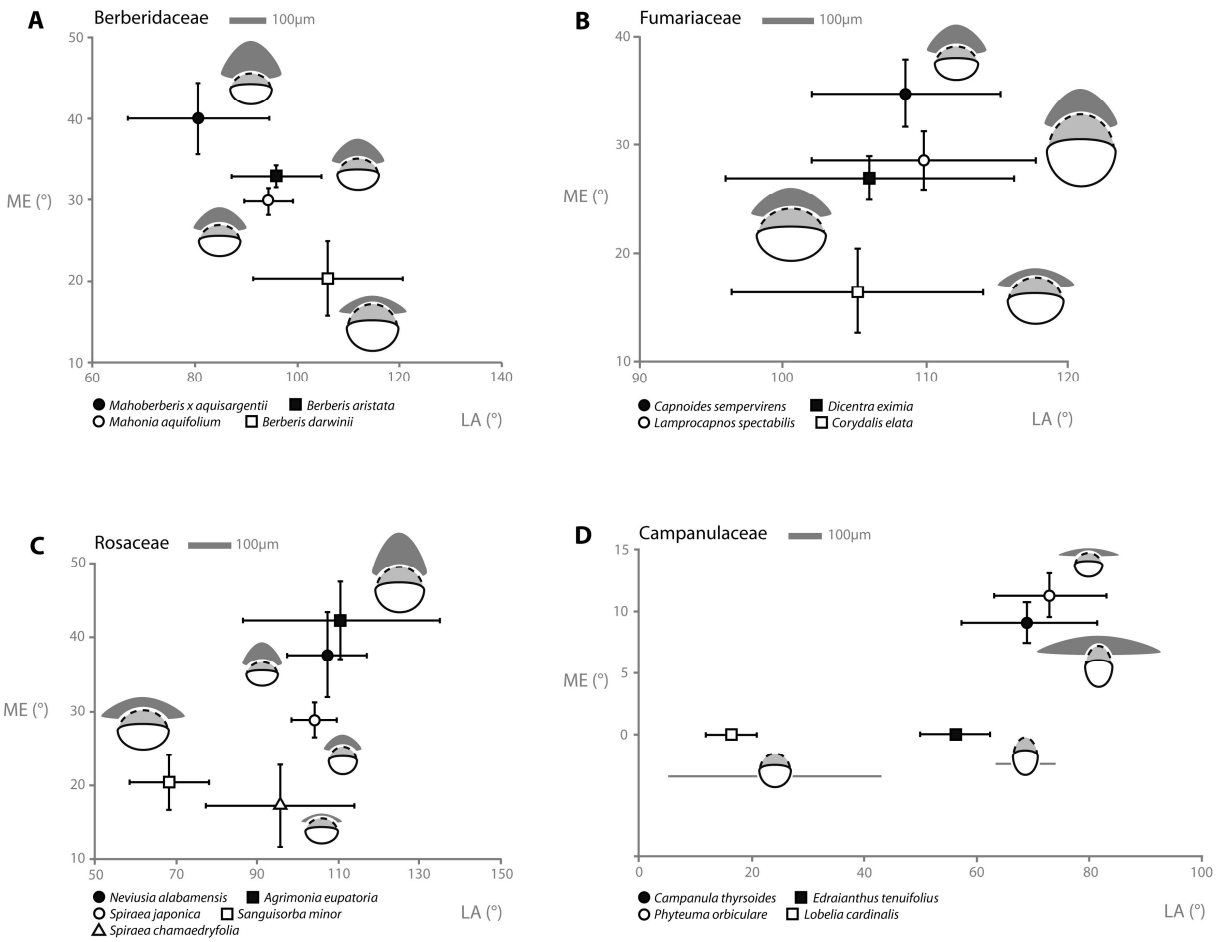


Figure 4.6. Final leaf arc (LA) and meristematic elevation (ME) of the inflorescence meristems in the species studied. Shown are the mean values (filled symbols: closed species; empty symbols: open species) with the 95% confidence intervals inferred from the regression analyses (see Table 4.2 and Figs. 4.5, 4.8, 4.10, 4.12). Sketches depict the frontal view of the inflorescence meristems idealized as a parable (dark grey) with its youngest primordium idealized as an ellipse (light grey: axillar reproductive product; white: subtending bract). The sketches were drawn after the dimensions estimated for each species (Table 4.2).

The raceme of *Corydalis elata* (Fig. 4.1D) develops in a quite different way as the volume of its meristem considerably increases at the beginning of the ontogeny (Fig. 4.7D3-5). In an initial state, the meristematic ratio corresponds to the six fold area of the lateral primordium, promoting a relative low LA value of 46,3° (Fig. 4.8B; Table 4.2). However, this areal dominance is almost completely lost towards the end of the ontogeny when the width and height of the meristem significantly decrease due to the lateral flower production (Table 4.3; Fig. 4.7D2, D6, 8B). This change goes along with an augmentation of the LAs (Fig. 4.8B)

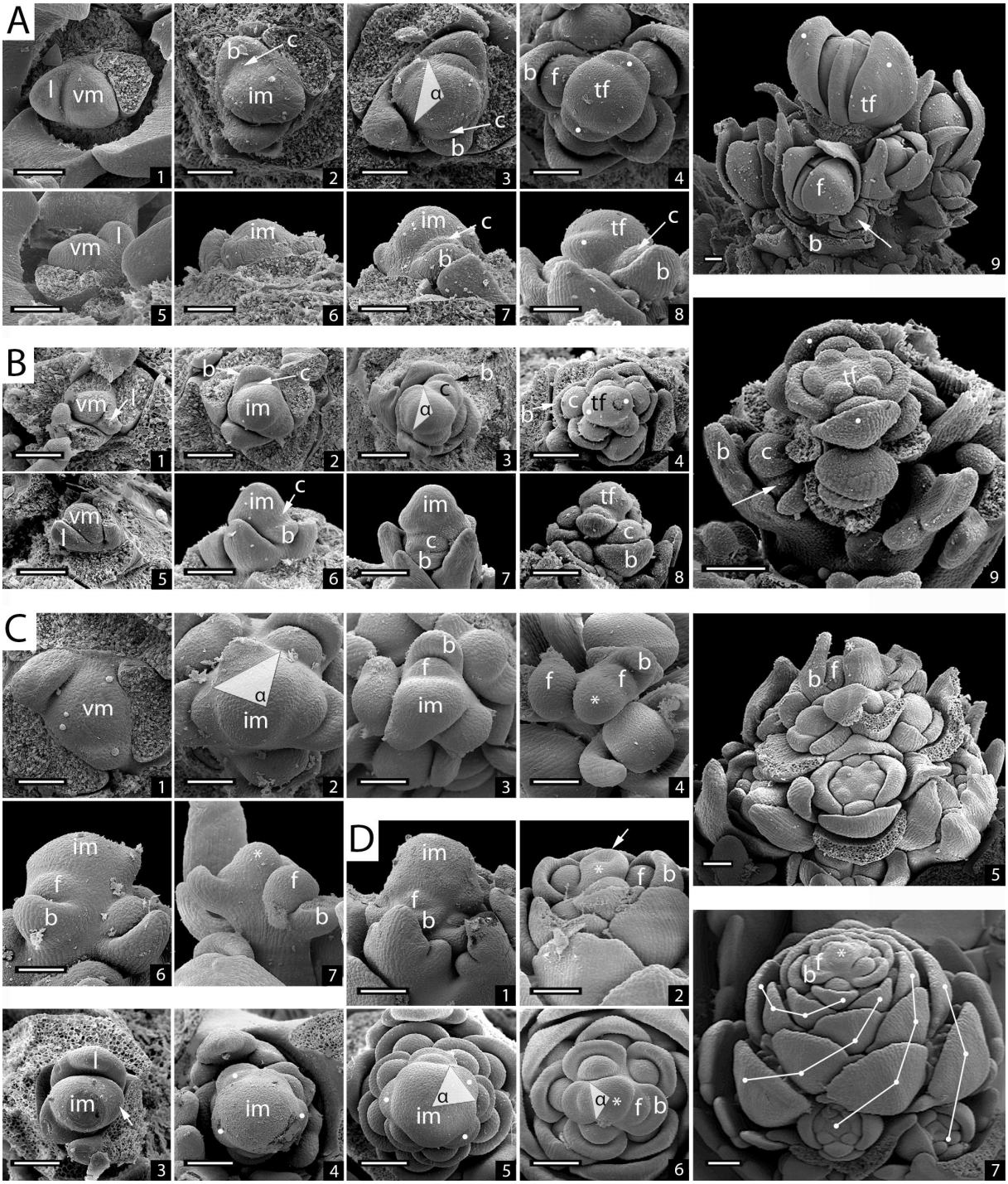


Figure 4.7. Development of Papaveraceae-Fumarioideae inflorescences. A, *Dicentra eximia*. B, *Capnoides sempervirens*. C, *Lamprocapnos spectabilis*. D, *Corydalis elata*. All bars:100µm.

A1-4. Top views of the developmental sequence in *D. eximia*. A1, Meristem in the vegetative state. A2, Early reproductive state presenting the first cyme primordium (c). A3, A more advanced reproductive state showing three cyme buds and a leaf arc (LA) of ca 90° (α angle). A4, Closed thyrse, whose terminal flower (tf) has already begun to differentiate two sepals (white dots). **A5-8**, Lateral views Same individuals as in A1-4. A9, Completely developed closed thyrse; note the higher size ➔

to similar values as in the other Fumarioideae (Fig. 4.7A3, C4, B3) and with a loss in the ME from 38° to 16° (Table 4.2; Figs. 4.7D2, 4.8B). The ontogeny of the raceme ceases and leaves an open tip on its top (star in Fig. 4.7D2, D6, D7). The arrangement of the flowers buds in spiral parastichies (Fig. 4.7D7) reveals the higher phyllotaxis of *Corydalis* compared to *Lamprocapnos* (Fig. 4.7C5).

← of the disymmetric terminal flower compared to the first flowers of the lateral cymes. White dots indicate the sepals of the terminal flower and the arrow a secondary flower bud of a lateral cyme. **B1-8**, Top view of the developmental sequence of *C. sempervirens*. B1, Vegetative state. B2, Reproductive state showing three cyme primordia (c). B3, Advanced reproductive state with five cyme primordial; note the similar phyllotaxis (LA, α angle) as the one found in *Dicentra* at a similar stage (A3). B4, Almost completely developed thyrse, with its terminal flower beginning to differentiate sepals (white dots). **B5-8**, Lateral views of *C. sempervirens.* B5, Vegetative state. B6-8 same individuals as in B2-4; note the similar aspect, but the smaller absolute size of the developing inflorescence compared to *D. eximia* (A5-8). B9, Completely developed thyrse of *C. sempervirens*, showing the disymmetric terminal flower enclosed by two sepals (white dots; the terminal flower develops a monosymmetric symmetry in the adult state, see Fig. 4.1A); note the evidently retarded developmental state of the lateral cymes (c), whose secondary flowers are just appearing (arrow). **C1-4**, Top view of the developmental sequence of *L. spectabilis.* C1, Vegetative state. C2, More advanced reproductive state with six flower primordia (f); note the similar phyllotaxis (LA, α angle) as the ones found in *Dicentra* and *Capnoides* (A3, B3, respectively).C3, Advanced reproductive state with 11 flower buds. C4, An already mature inflorescence bud showing the meristematic rest at the top (star). **C5-7**, Lateral views. C5, Mature raceme showing the acropetal developmental sequence of the lateral flowers and the meristematic rest at the top (star). C6, 7 Same individuals as in C2, 4 respectively; note the generally larger size of meristems and primordia as compared with *Dicentra* and *Capnoides*. **D1, 2** Lateral views of *Corydalis* inflorescence. D1, Young inflorescence bud; note the distinct relative size of the inflorescence meristem (im) and lateral primordium (f + b) in comparison with *Lamprocapnos* (C6, 7). D2, The almost completely used up meristem of a *Corydalis* inflorescence (little rest marked by the star), with a sub apical sterile bract (arrow). **D3-6**, Top views of the developmental sequence of *C. elata*. D3, Very early reproductive state showing the first lateral floral primordium (arrow). D4, A more advanced stadium with seven flower primordia (three youngest demarked by white dots). D5, Same individual as in D1 showing 15 floral primordia (three youngest marked by white dots). Note the lower leaf arc of *Corydalis* (α angle of ca. 60°, higher phyllotaxis) in comparison to the rest of the Fumarioideae (A3, B3, C2). D6, Raceme completing its development; note the much reduced meristem (star) and its reduced final phyllotaxis (higher leaf arc, α angle of ca. 90°) in comparison to the former state. **D7**, Lateral view of a mature raceme of *C. elata* showing already mature flowers arranged in spiral parastichies (4 parastichies demarked) and a small meristematic rest on its top (star). b, subtending bract; c, cyme primordium; f, lateral flower primordium; im, inflorescence meristem; l, leaf bud; tf, terminal flower; vm, vegetative meristem

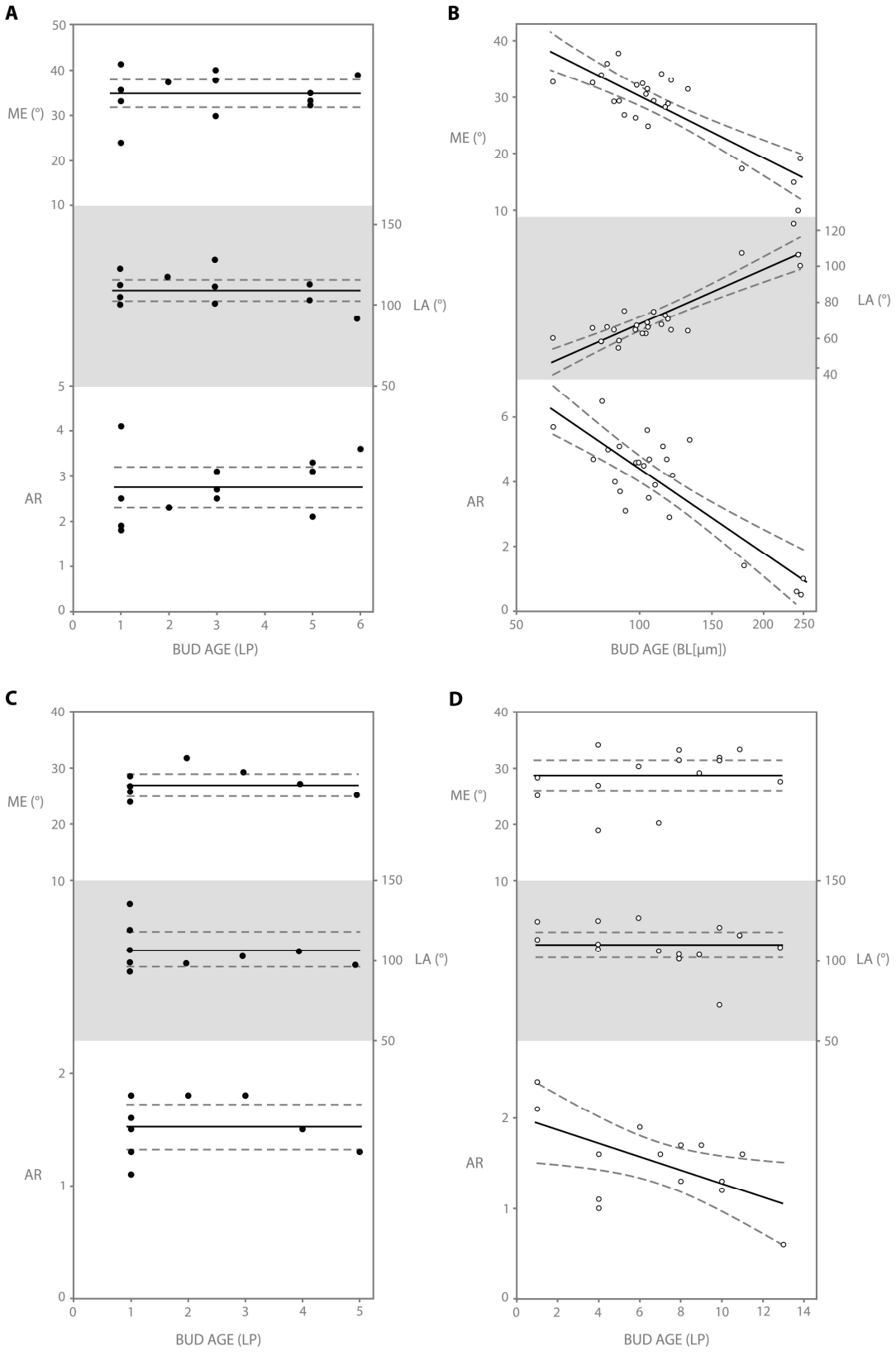


Figure 4.8. Development of the areal ratio (AR), leaf arc (LA), and meristematic elevation (ME) with increasing age in Papaveraceae-Fumarioideae inflorescences. A, *Capnoides sempervirens*. B, *Corydalis elata*. C, *Dicentra eximia*. D, *Lamprocapnos spectabilis*. Black circles represent closed species and empty circles open species.

The four Fumarioideae species share a similar LA (100-120°) at the final state of their inflorescence development (Fig. 4.5B). Notably, both open species present smaller areal relation (Figs. 4.6B, 4.8A-D) than the closed ones.

4.3.1.3 Rosaceae

The small closed raceme of *Neviusia alabamensis* (Fig. 4.1R) shows stable dimensions whilst its ontogeny (Table 4.3; Fig. 4.10B). This begins with a considerable enlargement of the vegetative meristem (Fig. 4.9A1, A2, A5, A6) that acquires and maintains an elevation of 38° until the terminal flower formation (Figs. 4.6C, 4.9A6-9, 4.10B). Relatively high LA values are evident (over 80°, Fig. 4.10B) which even increase in the late ontogeny (Figs. 4.9A2-4, 4.10B). *Spiraea japonica*, though forming a many-flowered inflorescence (Fig. 4.1S), is comparable to *N. alabamensis* as it forms a short raceme of ca. five flowers on its top (Fig. 4.9B9; Table 4.1). Its phyllotaxis (LA) is comparable to that of *Neviusia* (Table 4.2; Figs. 4.9B3, B4, 4.10E), while its ME is lower (Table 4.2; Figs. 4.9B7, B8, 4.10E). Similar to the open inflorescences in *Mahonia* (Fig. 4.3D1, D2) and *Lamprocapnos* (Fig. 4.5C1, C2), the enlargement of the vegetative meristem is low (Fig. 4.9B1, B2, B5, B6). A further reduction of meristem width and primordium size with age can be seen (Table 4.3; Fig. 4.9B2-4, B6-8), but it doesn't significantly affect the form and areal ratio of the meristem which both remain constant during ontogeny (Fig. 4.10E). The mature *S. japonica* inflorescence shows a reduced meristem (Fig. 4.5C) that just arrests its activity and remains present on the top of the open inflorescence (star on Fig. 4.9B9).

The open head of *Sanguisorba minor* and the umbellate raceme of *Spiraea chamaedryfolia* (Fig. 4.1P, Q) share similar ontogenies and resemble the one seen in *Corydalis*. In both cases, a relatively small vegetative meristem enlarges (Fig. 4.9C1-3, D1-3) to form an inflorescence meristem with a relatively low LA and high AR (Table 4.2; Fig. 4.10C, D). The development proceeds with the production of the lateral flower buds and the parallel reduction of meristematic width (Fig. 4.9C3-5, 4.9D3-5; Table 4.3) and height (Fig. 4.9C6-9, 4.9D6-9; Table 4.3). As a consequence of this process, the values of the AR and ME decrease (Table 4.3; Fig. 4.10C, D), and the LA increases (Table 4.3; Figs. 4.9C5, D5, 4.10C, D). The final LA values (Table 2; Fig. 4.5C) lay in the same range as those in *S. japonica* and *Neviusia* (Table 4.2; Figs. 4.9A3, B4, 4.6C).

The raceme of *Agrimonia eupatoria*, topped by a terminal flower (Fig. 4.9E7), bears more than 100 flowers in average (Figs. 4.1O, 4.9E6; Table 4.1). The huge size of the inflorescence contrasts with the relatively small inflorescence meristem that originates it (Fig. 4.9E1-6).

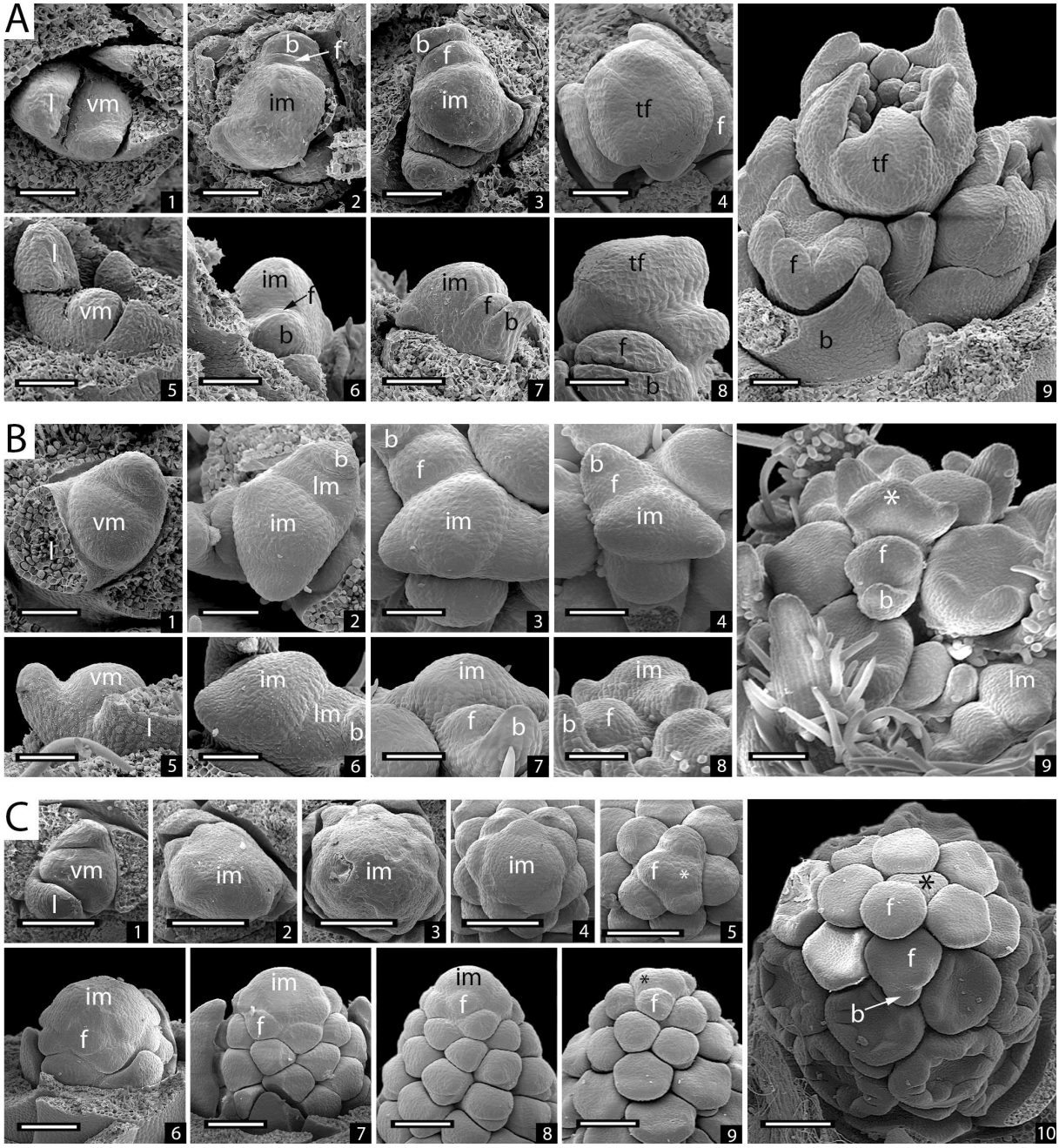
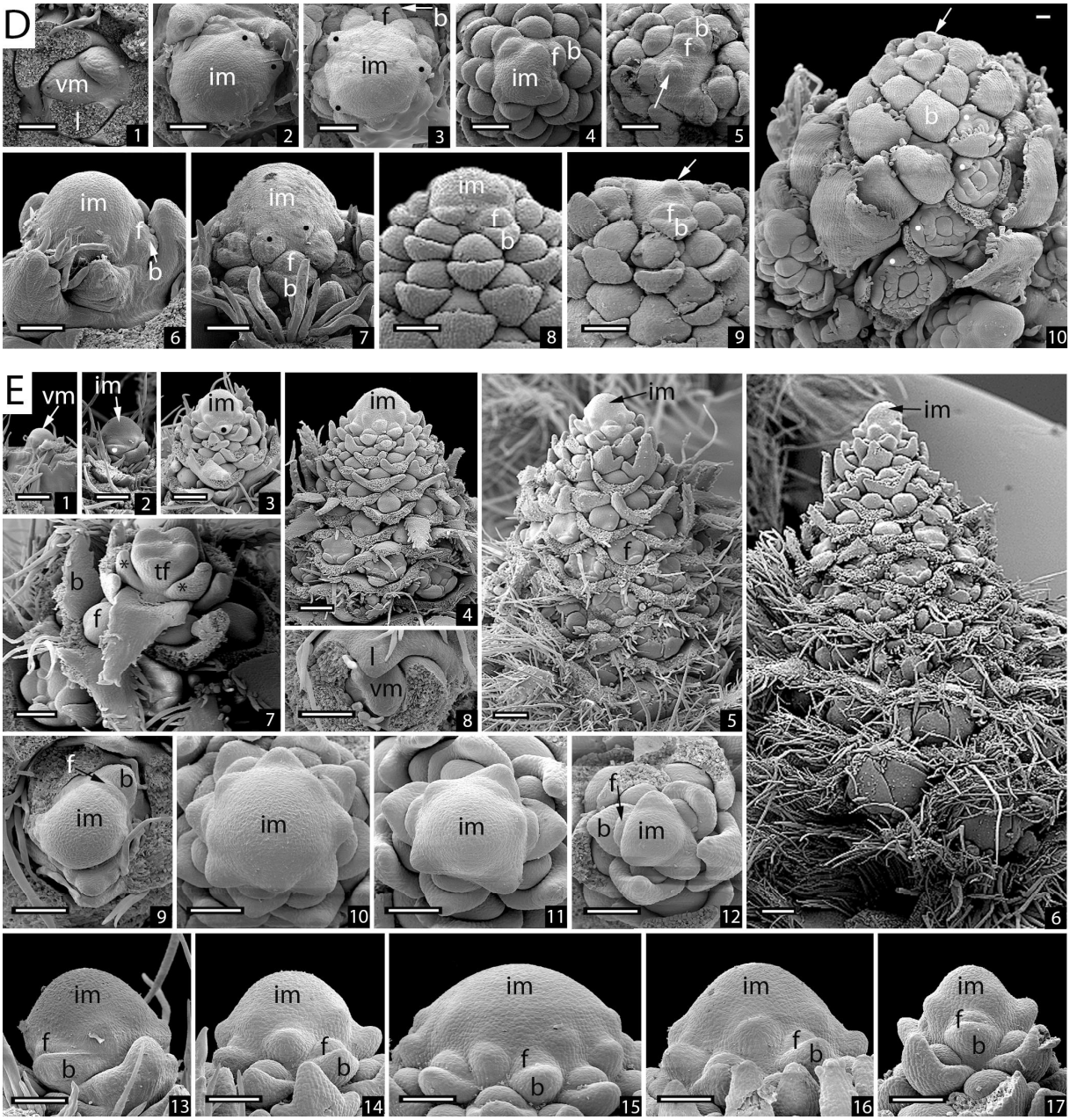


Figure 4.9. Development of Rosaceae inflorescences. A, *Neviusia alabamensis*. B, *Spiraea japonica*. C, *Sanguisorba minor*.D, *Spiraea chamaedryfolia*.E, *Agrimonia eupatoria*.

Bars in A,B: 50µm, in C, D, E7-17: 100µm, in E1-6: 200µm.

A1-4,Top view of the developmental sequence of *Neviusia alabamensis.* A1, Vegetative state. A2, Reproductive state with two flower primordia (f). A3, Developing inflorescence with three flower primordia. A4, Advanced developmental state with the terminal flower (tf) beginning its differentiation on an enlarged bulge. **A5-8**, Lateral views, same individuals as in A1-4**A9**, Completely developed closed raceme with a predominant terminal flower. **B1-4**, Top views of the developmental sequence of *S. japonica*. B1, Vegetative state. B2, Reproductive state with the first three lateral racemes (lm). ➔



→ B3, Inflorescence with eight lateral primordia, of which the two youngest probably correspond to flower buds. B4, Inflorescence in an advanced development, having already formed five flower primordia (f) of the terminal raceme. **B5-8**, Lateral views of *S. japonica*, same individuals in B1-4; note the lower curvature of the open *S. japonica* meristem in comparison to the closed *Neviusia* one (A6, 7). B9, Lateral view of a completely developed compound raceme of *S. japonica*. Lateral raceme meristems (lm), lateral flowers (f) and the arrested inflorescence meristem (im) can be seen. C**1-5**, Top view of the developmental sequence of *Spiraea chamaedryfolia.* C1, Vegetative meristem. C2, Transitional state towards the reproductive state after having formed seven flower buds. C3, Developing raceme with 12 flower buds. C4. Advanced developmental state with 44 flower-buds. C5, Raceme at its final state of development with 44 flower buds. The almost complete extinction of →

At the beginning of the ontogeny, the vegetative meristem enlarges (Fig. 4.9E8-10). The decrease of the meristem width and increase of the LA with flower production (Figs. 4.9E10-12, 10A; Table 4.3) is shared with the open inflorescences in *S. minor* and *A. chamaedryfolia.* However, in contrast to them, the height of the meristem remains stable during ontogeny showing a mean of 75 μm (Fig. 4.9E13-17; Tables 4.2, 4.3).

→ the inflorescence meristem (star) is evident. **C6-9**, Lateral views of *S. chamaedryfolia*. C6, Same individual as in C3. C7, Individual with 30 flower buds. C8, 9, Same individuals as in C4, 5; note the extremely reduced size of the subtending bracts in comparison to the flower buds and the decrease of the meristematic surface in C3-5 and C6-9. **C10**, Completely developed raceme of *S. chamaedryfolia* showing the acropetal progression of the lateral flowers, arrested bract development (arrow) and the sterile rest on its top (star). **D1-5**, Top view of the developmental sequence of *Sanguisorba minor.* D1, Vegetative state. D2, Individual with eight flower primordia (youngest marked by the black dot). D3, More advanced developmental state with 20 flowers buds (three youngest indicated by the black dots). D4, Advanced developmental state with 52 floral buds. D5, Final developmental state with no further meristematic activity; note the protrusion differentiating on the resting inflorescence meristem (arrow, probably leading to a tubular structure as seen in D10) and the decreasing meristematic size in D2-5. **D6-9,** Lateral views, same individuals as in D2-5. **D10**, Side view of an open head showing developing flowers and a tubular undefined organ on the top (arrow); note the acropetal development of the flower organs in the uncovered flower primordia (white dots) that are arranged in one parastichy. **E1-6**, Lateral view of the developmental sequence of the inflorescence of *A. eupatoria*. Youngest lateral primordia marked by dots; note how a very long inflorescence is formed by a relative small meristematic tissue (im). E7, View of the top of a mature closed raceme showing the terminal flower (tf), surrounded by sterile bracts (stars) and small lateral flower primordia (f) subtended by bracts. **E8-12** Top views of the developmental sequence of the inflorescence meristems. E8, Vegetative state. E9, Transition to the reproductive state, after forming the first floral bud (f). E10, Enlarged inflorescence meristem of an inflorescence carrying 29 flower buds, same individual as in E3. E11, A more advanced stage showing the decrease in the meristematic width; note the larger size of the flower bracts compared to the earlier stages (E10). E12, State of development close to the production of the terminal flower after having formed 96 flower primordia: note the relative small diameter of the meristem, the high leaf arcs and larger size of floral subtending bracts (b). **E13-17**, Lateral view of the inflorescence meristem. E13, A young reproductive meristem with four flower buds. E14, Same individual as in E3,10. E15, A much enlarged inflorescence meristem on an inflorescence bud with 70 flower primordia. E16, A less enlarged meristem, topping a 73 flowered inflorescence. E17, Individual carrying 117 flower buds and a convex inflorescence meristem; note the quite similar height of the meristem through the development (E13-E17), in contrast to the variable width (E9-E12). b, subtending bract; f , lateral flower primordium; im, inflorescence meristem; l, leaf bud; lm, lateral raceme meristem; tf, terminal flower; vm, vegetative meristem.

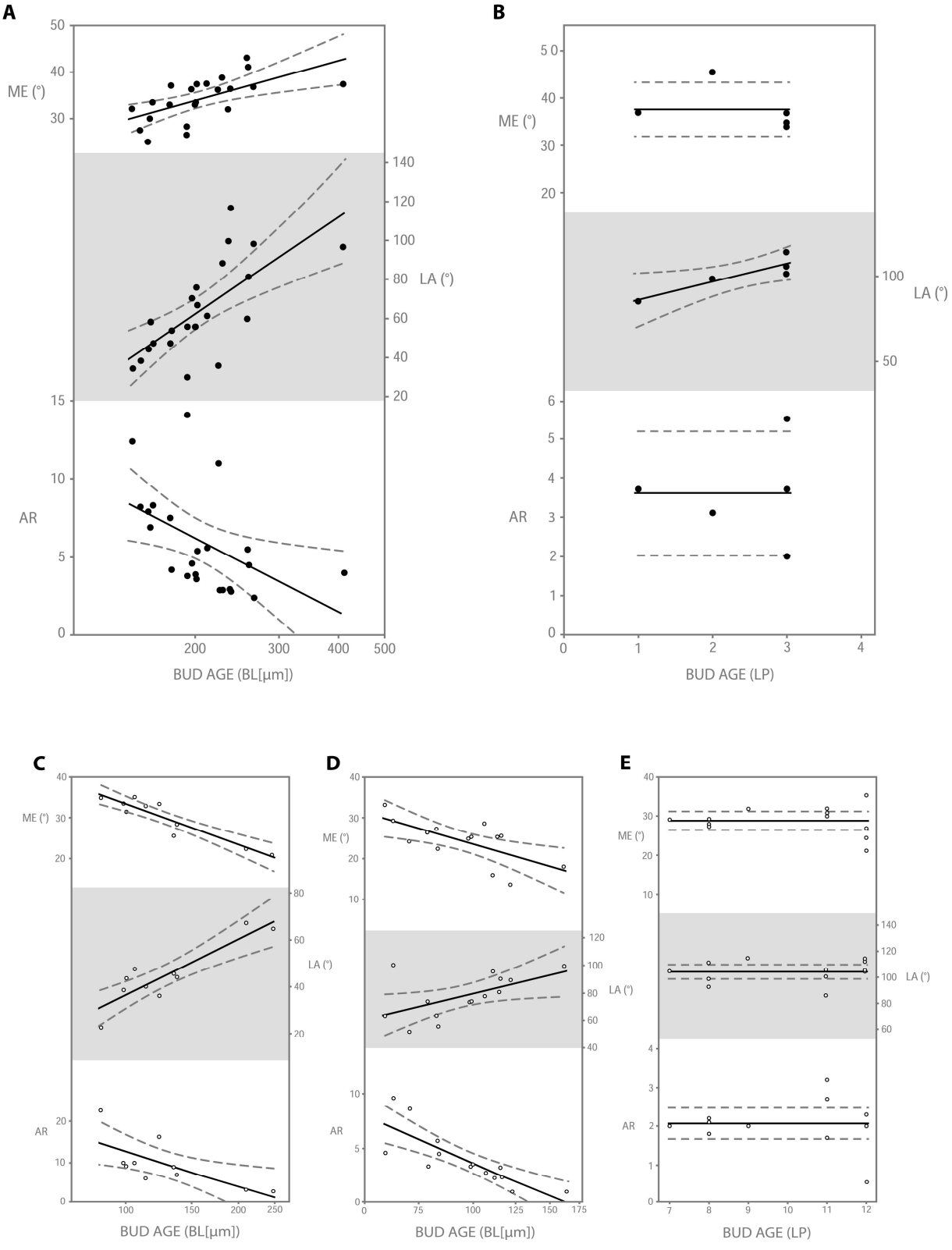


Figure 4.10. Development of the areal ratio (AR), leaf arc (LA), and meristematic elevation (ME) with increasing age in Rosaceae inflorescences. A, *Agrimonia eupatoria*. B, *Neviusia alabamensis*. C, *Sanguisorba minor*. D, *Spiraea chamaedryfolia*. E, *Spiraea japonica*. Black circles represent closed species and empty circles open species.

As a consequence, the meristem elevation increases with age (Fig. 4.10A, Table 4.3), allowing a remaining bulge that, similar to *Neviusia*, differentiates into the terminal flower (Figs. 4.6C, 4.9E17).

Comparing the final developmental states of the Rosaceae inflorescence meristems, the higher areal ratio and meristem elevation of the closed *Neviusia* and *Agrimonia* are evident (Fig. 4.10C; Table 4.2). However, except *S. minor*, the final LA is similar among all species (Fig. 4.10C; Table 4.2).

4.3.1.4 Campanulaceae

The open head of *Jasione montana* (Fig. 4.1H) begins its development with the enlargement of the vegetative meristem (Fig. 4.11A1, A2). Then, the segregation of ebracteate flower primordia starts in a centripetal direction on the disc-shaped meristem (Fig. 4.11A3). The inflorescence meristem remains active generating new tissue while more and more flower primordia are produced above the first ones already differentiating flower organs (Fig. 4.9A4). At an advanced time, the inflorescence meristem ceases its growth and the tissue is used up by the distal flowers (Fig. 4.11A5). The whole construction acquires a slightly concave form, while a small and flat meristematic rest is left in the centre (arrows Figs. 4.11A5, A6).

The open globose head of *Phyteuma orbiculare* (Fig. 4.1H) begins its development in a similar way as the vegetative meristem enlarges and forms a circular platform that is much larger than the flower primordia (Figs. 4.9B2, 4.11B1). This results in a LA value of round 40° and an areal ratio higher than six (Table 4.2; Fig. 4.12B). The bracteates flower primordia originate from the meristematic platform and, similar to *Jasione*, the diameter of the meristem is reduced (Table 4.3; Fig. 4.11B3) until the last floral primordia can be seen on the top (Fig. 4.11B4). Consequently, the LA value increases with age (Fig. 4.12B; Table 4.3). The meristem elevation of *Phyteuma* remains stable (Figs. 4.6D, 4.12B), because the height of the meristem also decreases from 20 down to 6 µm (Table 4.3; Fig. 4.11B5-7). Similar to *Jasione*, a rather flat meristematic rest on the top of the open head remains at the end (Fig. 4.11B7, B8).

The closed thyrse of *Asyneuma canescens* (Fig. 4.1F) begins its ontogeny with a considerable increase of the vegetative meristem (Fig. 4.11C1, C2). The inflorescence meristem gets partly reduced by the cyme formation (Fig. 4.11C3) and finally differentiates a terminal flower (Fig. 4.11C4). The elevation of the inflorescence meristem is higher than in the two open heads (Fig. 11C7). It results from the flat vegetative meristem after enlargement (Fig. 4.11C5, C6)

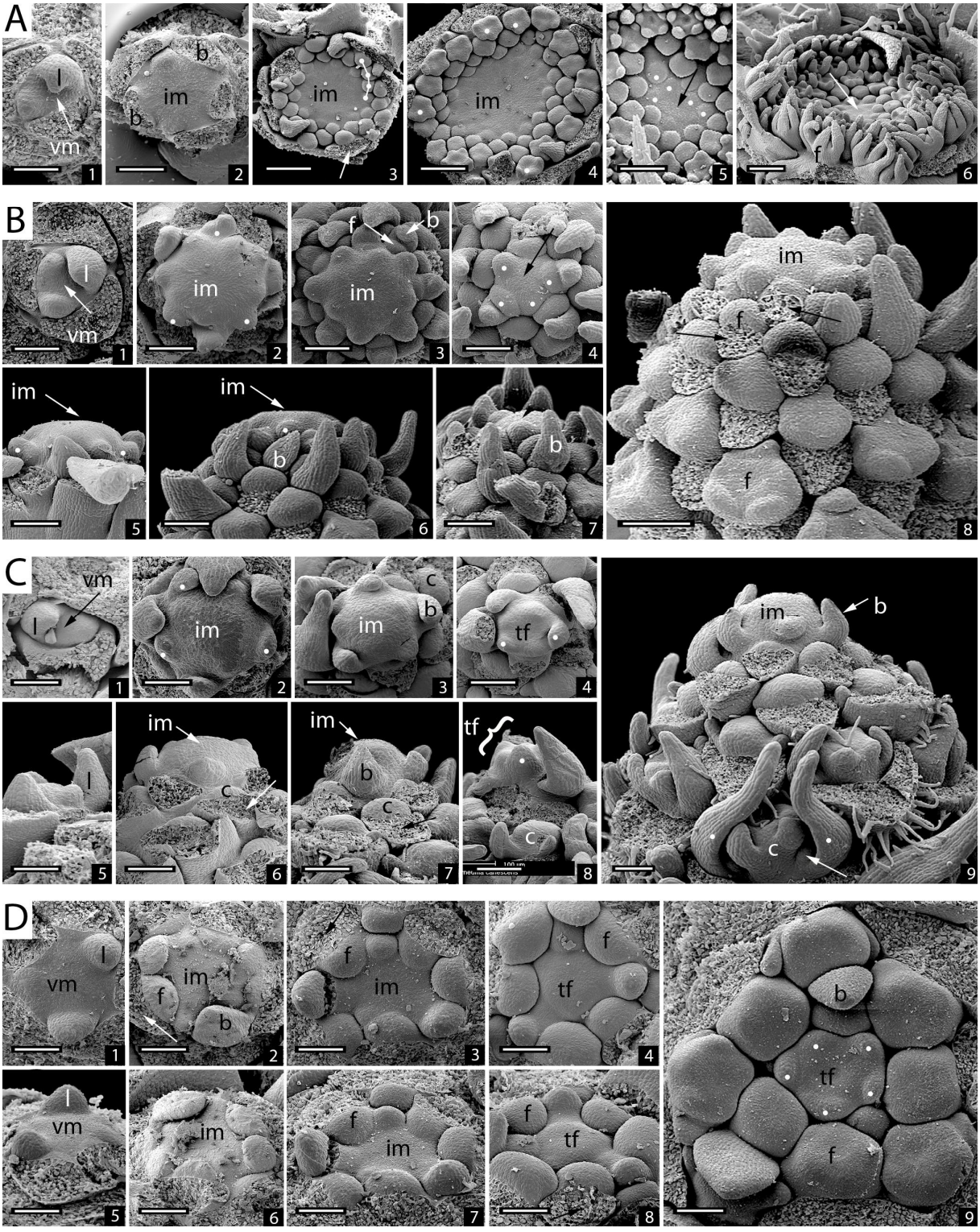
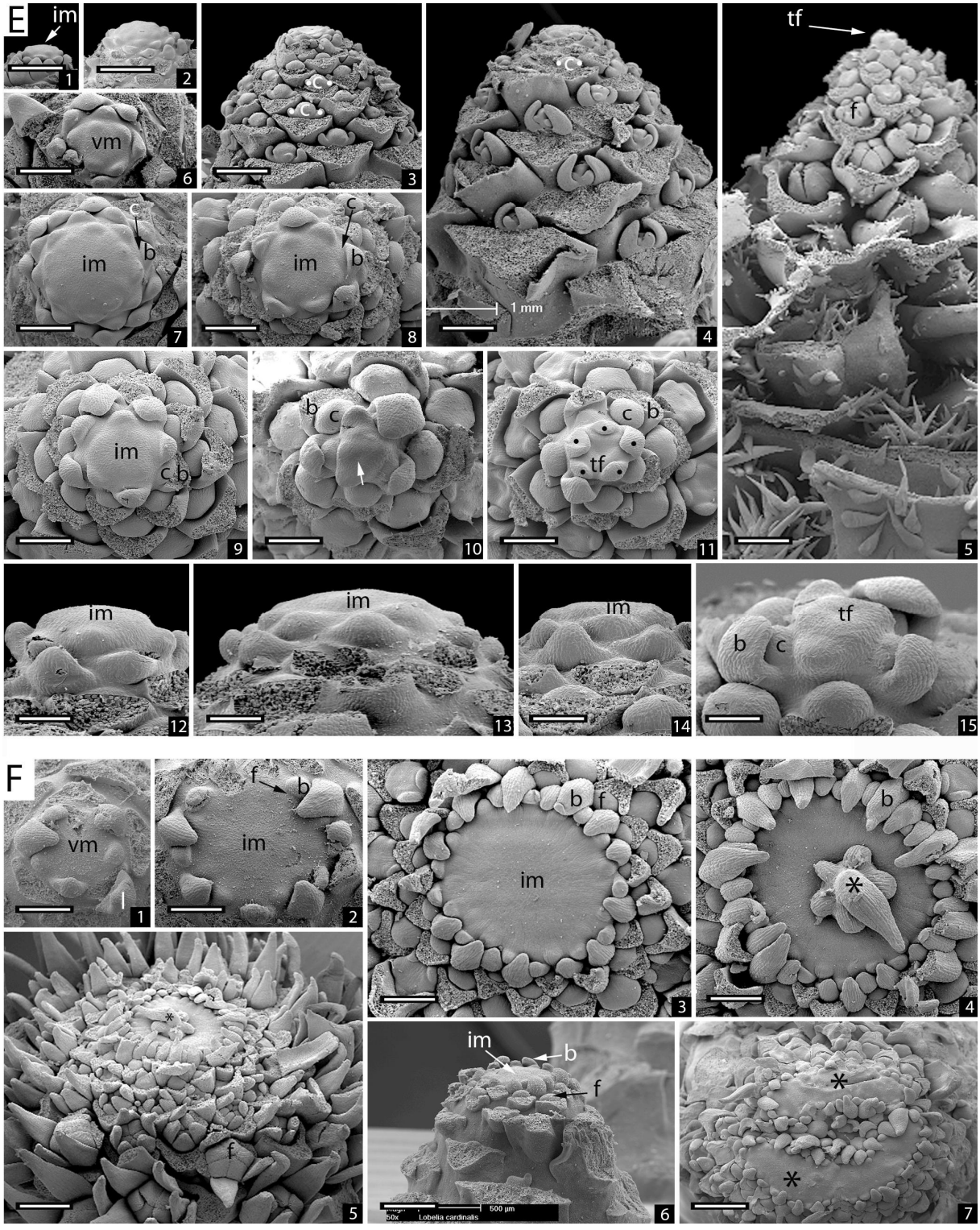


Figure 4.11. Development of Campanulaceae inflorescences. A, *Jasione montana*. B, *Phyteuma orbiculare*. C, *Asyneuma canescens*. D, *Edraianthus tenuifolius*. E, *Campanula thyrsoides*. F, *Lobelia cardinalis*. Bars in A1, A2, B, C, D, E12-15: 100µm, in A3-6, E6-11, F1-4, F6, F7: 200µm, in E1-5, F5: 400µm. **A1-7**, Top view of the developmental sequence of *J. montana.* A1, Vegetative meristem. A2, Meristem enlargement before the formation of the first flowers. A3, Young inflorescence meristem showing a ring of ebracteate flower primordia arranged in spiral parastichies (one parastichy demarked) and a relatively large inflorescence meristem (im). A4, An older inflorescence showing ➔



→ more flower buds and a still active meristematic zone; the older flowers begin sepal differentiation (marked by white dots). A5, Central part of an older inflorescence showing the notable diminution of the meristematic area (arrow); youngest floral primordia marked by white dots. A6, Oblique view of an inflorescence bud showing its concave form and centripetal bud progression (arrow). **B1-4**, Top view of the developmental sequence of *Phyteuma orbiculare*. B1,Vegetative meristem. B2, An enlarging inflorescence meristem with the first three floral primordia (white dots). B3, Inflorescence bud with →

➔ 47 flower primordia. B4, Inflorescence at the end of the development with 40 flower buds. Note the larger size of the subtending bracts of the youngest primordia (marked by white dots) compared to B2. **B5-7**, Lateral views of *P. orbiculare,* same individuals as in B2-4. B8, View of a mature inflorescence; note the flat meristematic rest at the top (im). **C1-4**. Top view of the developmental sequence of *Asyneuma canescens*. C1, Vegetative meristem. C2, An enlarged meristem at the beginning of the reproductive phase showing three young primordia (white dots). C3, A more advanced inflorescence meristem carrying 24 lateral cymes (c). C4, A terminal flower can be seen differentiating on the top of the inflorescence, whose calyx becomes progressively evident (white dots). **C5-9**, Lateral views, same individuals as in C1-4. C8, Mature inflorescence showing the sepal differentiation (s) of the terminal flower. The terminal flower is clearly larger than the first flower of the older lateral cyme (c). C9, An almost completely developed *Asyneuma* closed thyrse showing the meristematic bulge (im) prior to the terminal-flower formation. The oldest cyme on the picture (c) shows its already differentiated terminal flower, while its secondary flowers are in bud stage (arrow) and enclosed by the prophylls (white dots). **D1-4**, Top view of the developmental sequence of *Edraianthus tenuifolius.* D1*,* An enlarged vegetative meristem prior to flower bud segregation. D2, A young inflorescence bud showing four flower primordia (f). D3, Advanced inflorescence development with eight flower-primordia. D4, An almost completely differentiated inflorescence, showing the initial differentiation of the terminal flower (tf). **D5-8**, Oblique view of *E. tenuifolius* inflorescences, same individuals D1-4; note the internal ring elevation that will differentiate into the terminal flower perianth (tf). **D9**, Completely developed *Edraianthus* disc-shaped raceme with a prominent terminal flower (tf), whose calyx is being differentiated (white dots). **E1-5**, Lateral view of the developing *C. thyrsoides* inflorescence; note how a very large inflorescence bud is formed by a relatively small inflorescence meristem (im). Lateral cymes (c) evidence prophylls production (white dots). **E6-11**, Top view of the developmental sequence of *C. thyrsoides.* E6, Vegetative meristem. E7, Enlarged apical meristem beginning the reproductive state. E8. Inflorescence with 72 lateral cymes. E9. A quite more advanced inflorescence with 86 lateral cymes; note the generally larger size of the cyme primordia and subtending bracts than in younger states (E7). E10. Terminal flower beginning its differentiation; note the central cavity (arrow) that delimits a rig-like protuberance, similar as in *Asyneuma* (Fig. 4.9C4) and *Edraianthus* (9D4), that subsequently differentiates into the perianth of the terminal flower. Note the larger size of the lateral cyme primordia and subtending bracts (c + b) compared with the immediately previous states (E7-9). E11, Mature inflorescence showing a terminal flower with sepals already differentiated (black dots). **E12-15**, Lateral view of the *Campanula* inflorescence meristem. E12, Young inflorescence meristem E13, An inflorescence meristem attaining its maximum enlargement (same individual as in E2). E14, An advanced inflorescence meristem after the production of 57 cymes. E15. Terminal flower differentiation at the top of the inflorescence (same individual as in E10). **F1-4**, Top view of the developmental sequence of *L.. cardinalis*. F1, Vegetative meristem. F2, An enlarged young inflorescence meristem just before flower differentiation begins. F3, A developing inflorescence showing the large meristematic area in comparison to the floral primordia. F4, A mature inflorescence showing an exhausted meristem that is comparable in size to the individual in F3, but with larger bracts and an irregular protuberance in the centre of the meristematic tissue (star). **F5**, Oblique view of the inflorescence of the individual in F4, showing the high number of flowers already differentiated in

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and forms the meristematic bulge from which the terminal flower differentiates (Fig. 4.11C4, C7, C8, 4.11C7). It results from the flat vegetative meristem after enlargement (Fig. 4.11C5, C6) and forms the meristematic bulge from which the terminal flower differentiates (Fig. 4.11C4, C7, C8).

The head in *Edraianthus tenuifolius* (Fig. 4.1I) differs from that in *Jasione* in the lower number of flowers (ca. 10 against 60 in average, see Table 4.1) and in the terminal flower production. Both inflorescences share a rather flat meristem that originates from an enlarged vegetative meristem (Fig. 4.11D1, D5). The size of the enlarged inflorescence meristem in *E. tenuifolius* is maintained until the ca. ten lateral flowers (Fig. 4.11D2, D3, D6, D7; Table 4.3), and the terminal flower are formed (Fig. 4.11D4, D8). While the IM dimensions remain stable (Table 4.3), the primordium size decreases (Fig. 4.11D) resulting in an increase of the areal ratio (Fig. 4.12C; Table 4.3). The final value of the AR approximates four (Table 4.2; Fig. 4.12C) and indicates begin of the terminal flower differentiation (Figs. 4.6D, 4.11D9).

The many-flowered closed thyrse of *Campanula thyrsoides* (Fig. 4.1E) is the result of the long-lasting activity of an inflorescence meristem that is much smaller compared with the large final size of the inflorescence (Fig. 4.11E1-5). After the vegetative meristem has enlarged (Fig. 4.11E6, E7), the segregation of lateral primordia begins. During cyme production, the meristem width decreases (Fig. 4.11E8, E9), though this is not statistically supported (Tables 4.2, 4.3). The primordium area (YPA) gets larger (Tables 4.2, 4.3), resulting in a significant increase of the LA towards the end of the development (Figs. 4.11E10, 4.12A; Table 4.3), when the differentiation of the terminal flower takes place (Fig. 4.11E11). The elevation of the meristem is rather low, but stable throughout the ontogeny (Fig. 4.12A). This is given by the constant height of the IM from the first vegetative enlargement (ca. 20 µm, Table 4.2) to the terminal flower differentiation (Fig. 4.5D, 11E12-15).

Lobelia cardinalis presents the largest inflorescence meristem of all the species investigated (width > 600µm, AR >50, LA < 17°, Table 4.2). The meristem of the open raceme originates from the enlargement of the vegetative meristem (Fig. 4.11F1-3). It exhibits an evident flat

→ centripetal direction. **F6**, Side view of a young inflorescence with just a few flower primordia showing the flat form of the meristem. **F7**, Top view of a *Lobelia* raceme showing fasciation, which divides the meristem into two elongated parts (stars). b, subtending bract; c, cyme primordium; f, lateral flower primordium; im, inflorescence meristem; l, leaf bud; lm, lateral raceme meristem; tf, terminal flower; vm, vegetative meristem.

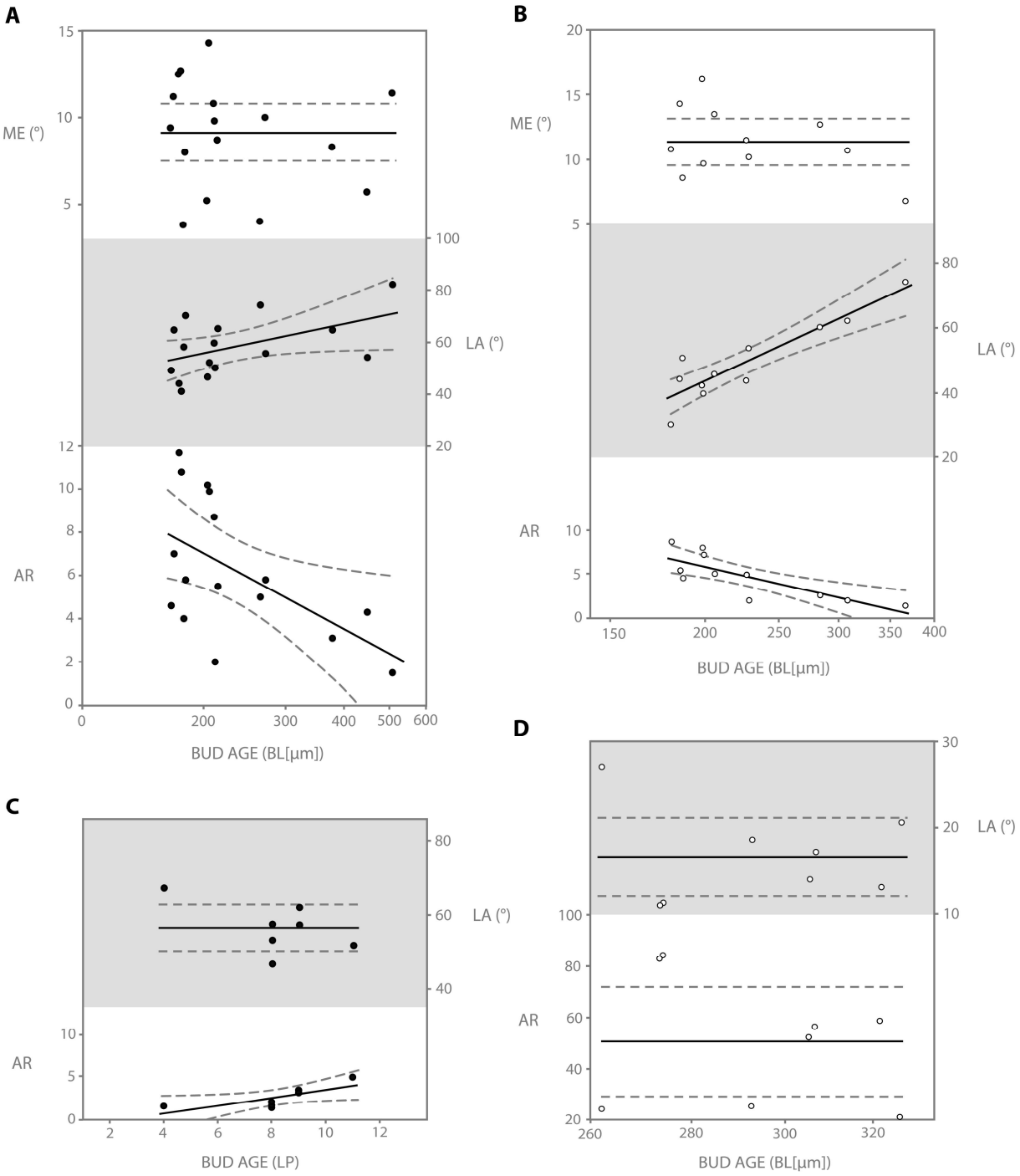

Figure 4.12. Development of the areal ratio (AR), leaf arc (LA), and meristematic elevation (ME) with increasing age in Campanulaceae inflorescences. A, *Campanula thyrsoides*. B, *Phyteuma orbiculare* C, *Edraianthus tenuifolius*. D, *Lobelia cardinalis*. Black circles represent closed species and empty circles open species.

form (Fig. 4.11F6) throughout the development and maintains its high phyllotaxis (low LA) and high AR (Fig. 4.12D). The huge meristem (Fig. 4.5D) is not used up but instead produces irregular protuberances (Fig. 4.11F4, F5) or shows fasciatiation (Fig. 4.11F7).

In general, Campanulaceae are characterized by low to rather flat apical vegetative and reproductive meristems. If *Lobelia* is not considered, the terminal flower producing species maintain a higher areal ratio towards the end of ontogeny than the open species (Table 4.2).

4.3.2 Comparison between closed and open inflorescences

4.3.2.1 T test for the initial and final states of the meristems

All inflorescence meristems, whether they from a terminal flower or not, correspond in the parameters estimated for their initial states. They also show no differences in the size of the youngest primordium.

However, the T-test shows that the AR at the final state of development differs significantly between open and closed inflorescences. Terminal flower producing species have a final inflorescence meristem (shortly before the terminal flower differentiation) with a mean LA of 91,84° (se = 7,32) and mean ME of 27,93° (se = 5,42) corresponding to an areal ratio (AR) of 2,75 (se = 0,38; Table 4.2). The latter significantly differs from the value found in the open species (mean AR of 1,09;se=0,26; T=3,56; p = 0,003). The higher AR value in the closed species is explained by the significantly higher width dimensions of their IMs (165,00 µm; se=24,41 compared to 101,50µm; se = 10,66; T=2,38; p =0,32), while the height values are not statistically different.

4.3.2.2 Correlation analysis

The correlation analyses show that the initial configuration adopted by the IM of closed inflorescences depends on the size of the mature inflorescence. This is seen in the significant correlation found between LU and initial AR (Table 4.4A) indicating that larger inflorescences start with a higher initial enlargement of their meristems than smaller ones (Fig. 4.13). This enlargement involves lower initial LA values (higher phyllotaxis: growth in

the horizontal plane, Table 4.4A), but no higher elevation values of the initial IM (initial ME v/s LU not significant, Table 4.4A). The relation between initial enlargement (AR) and size of the inflorescence can be visualized by a regression curve (Fig. 4.13). Open inflorescences do not show a statistically supported correlation between LU and AR (Table 4.4B).

Contrary to the initial state, the final form of the IM in closed inflorescences is independent from the size of the inflorescence (Table 4.4A). This is shown by the non-significant correlation among the final AR, LA and ME values (Table 4.4A). Nevertheless, the final phyllotaxis (LA) shows a positive interdependence with the final ME, which can be visualized by a regression curve between both parameters (Fig. 4.14). This means that flat meristems that produce TF possess comparatively lower LA values (higher phyllotaxis, Fig. 4.14) at the final state than bulged ones. This relation between final LA and ME is not seen in open inflorescences (Table 4.4B) whose parameters fall in part outside the mentioned regression curve (Fig. 4.14).

Table 4.4. Tables of correlation of the geometrical parameters in the initial and final states. A. Species with terminal flower (n=8). B. Species without terminal flower (n=8). Given are the Pearson's coefficients (R^2) of the correlations. n.s. = not significant, * $p < 0,05$, ** $p < 0,01$, *** $p < 0,001$.

A.

INITIAL / FINAL	**log(LU)**	**AR**	**LA**	**ME**
log(LU)	-	0,89**	-0,86**	n.s.
AR	n.s.	-	n.s.	n.s.
LA	n.s.	n.s.	-	n.s.
ME	n.s.	n.s.	0,82*	-

B.

INITIAL / FINAL	**log(LU)**	**AR**	**LA**	**ME**
log(LU)	-	n.s.	-0,74*	n.s.
AR	n.s.	-	-0,84**	n.s.
LA	n.s.	n.s.	-	n.s.
ME	n.s.	0,76*	n.s.	-

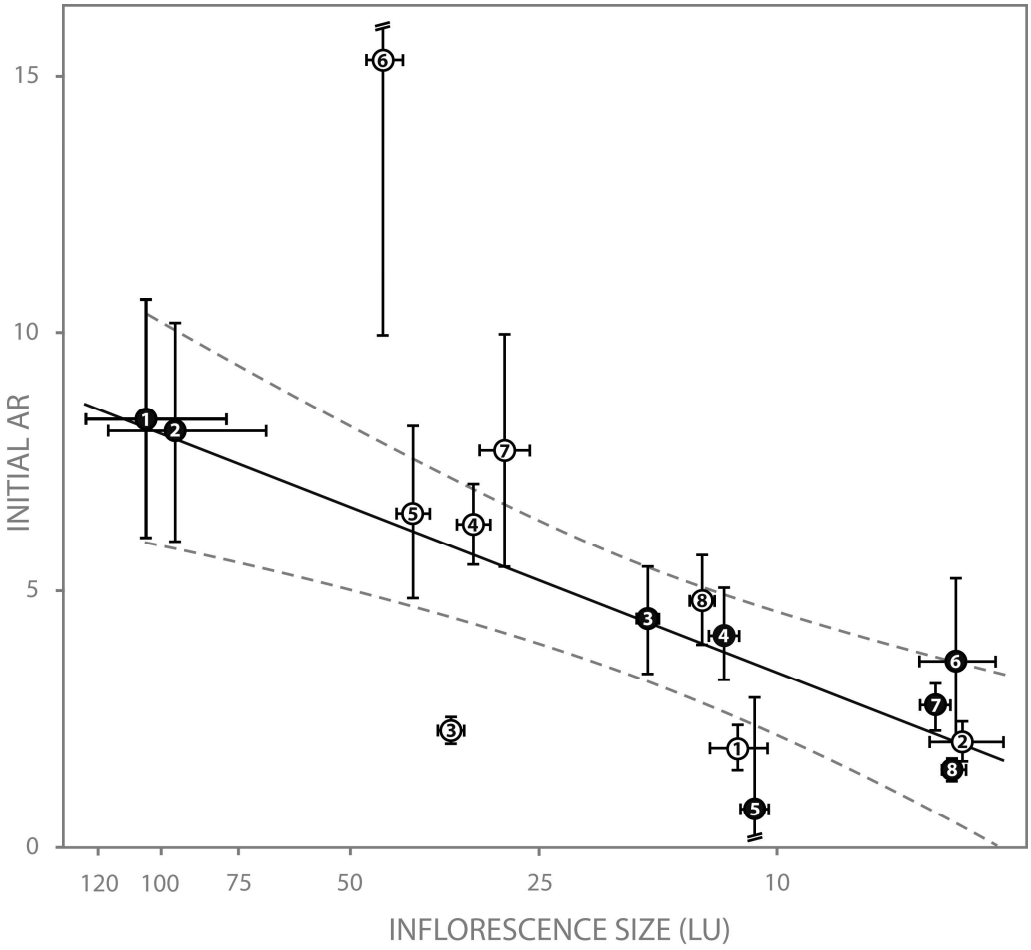

Figure 4.13. Relationship between the size of the mature inflorescence (LU, Table 4.1) and the initial relative enlargement of the inflorescence meristem (AR, Table 4.2). Closed species (black circles) show a positive correlation between these parameters (Table 4.4A), which is illustrated by linear regression curve ($p < 0,01$; $R^2 = 0,81$). Larger closed inflorescences (e.g. 1, 2) adopt a significantly higher AR than smaller ones (e.g. 7, 8). Open inflorescences (white circles) do not present a significant correlation between these two variables (Table 4.4B). Some open species (6, 7) show a marked initial enlargement (above the curve, see Table 4.5) indirectly suggesting inflorescence meristems that will not present renewal activity towards the later ontogeny (as the tissue needed for flower production is already present, see Fig. 4.15C). Other open inflorescence (1, 3) show a weak initial enlargement (underneath the curve, see Table 4.5) implying that these inflorescence meristems must show renewal activity towards the forthcoming ontogeny in order to construct the flower buds. Open species inside the curve (4, 5, 8) are distinguished from the closed species, as their IM show decaying meristematic height through ontogeny (Table 4.3). White numbers in black-filled circles indicate closed species: 1, *A. eupatoria*, 2, *C. thyrsoides*, 3, *B. aristata*, 4, *M. x aquisargentii*, 5, *E. tenuifolius*, 6, *N. alabamensis*, 7, *C. sempervirens*, 8, *D. eximia*. Black numbers in empty circles denote open species: 1, *L. spectabilis*, 2, *S. japonica*, 3, *M. aquifolium*, 4, *C. elata*, 5, *P. orbiculare*, 6, *S. minor*, 7, *S. chamaedryfolia,* 8, *B. darwinii.*

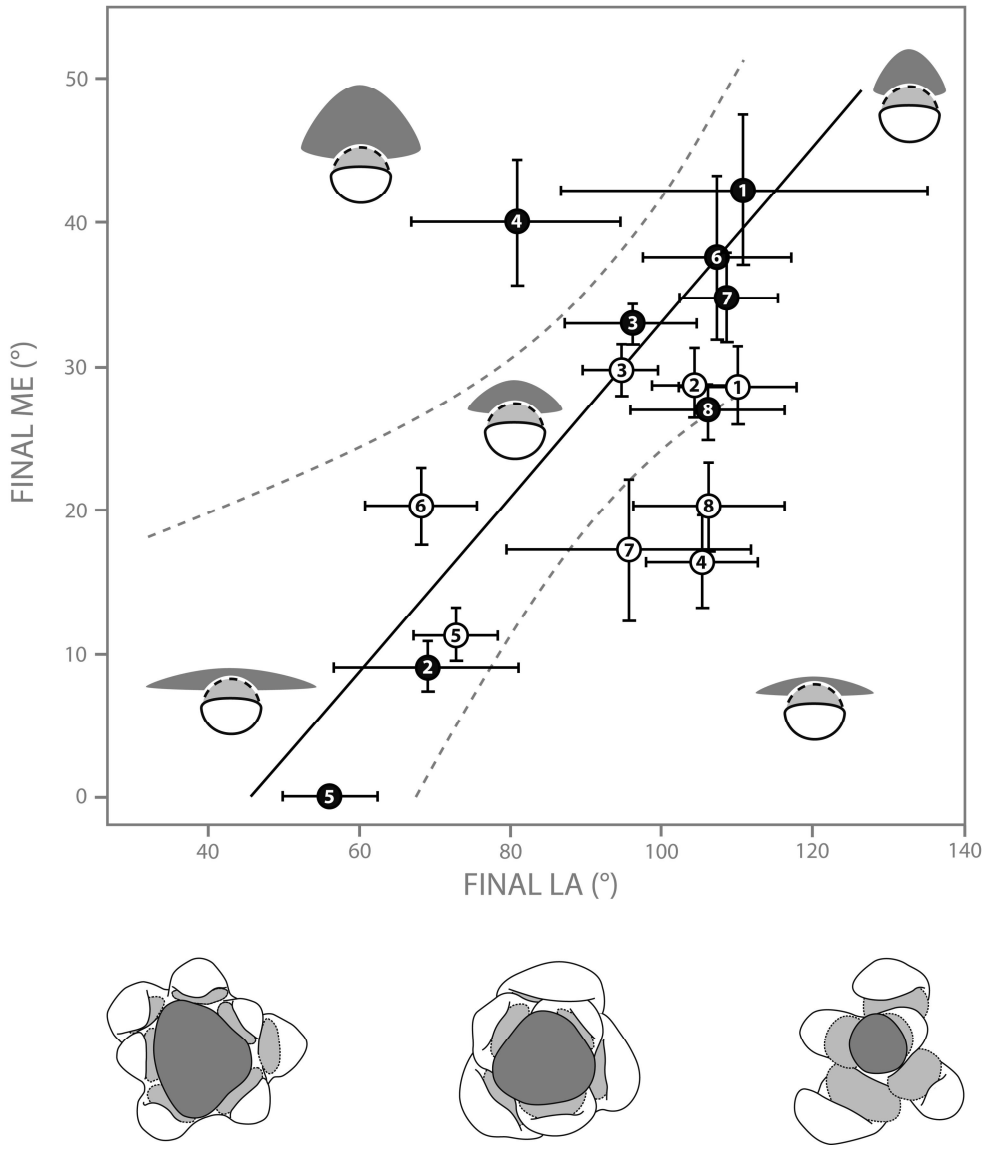

Figure 4.14. Form of the inflorescence meristem in its final state expressed as the final leaf arc (LA) and meristematic elevation (ME); values obtained after the regression analyses (Table 4.2). Sketches depict the frontal view of inflorescence meristems and youngest primordium combining LA and ME values in the space. The figures represent an idealized inflorescence meristem (IM) as a parable (dark grey) with its youngest primordium idealized as an ellipse (light grey: axillary reproductive product; white: subtending bract). Under the x axis are depicted top views of inflorescence buds, representing the increasing LA values in the x axis (decreasing phyllotaxis, same shading as in the sketches inside the graphic).

Closed species (black circles) present a positive correlation between LA and ME (Table 4.4A) as the regression curve also shows ($p < 0,05$; $R^2=0,68$). The relation between LA and ME represents a syndrome in the geometry of the IM that is capable of differentiating into a terminal flower. Open inflorescences do not present a significant correlation between LA and ME (Table 4.4B). Although the majority of the closed IMs are in the upper right sector of the diagram, (LA ~ 110° , ME ~ 35°), flatter ➔

4.4 Discussion

4.4.1 Spatial and shape requisites of the inflorescence meristem (IM) for terminal flower (TF) production

The present study shows that the production of a terminal flower (TF) occurs on an inflorescence meristem (IM) with a meristematic tissue corresponding to a surface area of 2,75 (SE = 0,38) times the size of the youngest lateral primordium. Notably, this areal ratio (AR) is either existent from the beginning of the ontogeny (in small inflorescences) or is achieved by reduction of a higher initial AR (in larger inflorescences). In any case, the production of a terminal flower occurs on a meristematic tissue that is already present and does not arise as a response to the TF induction.

Irrespective of the taxonomic relationship, meristematic bulges producing a terminal flower always follow the same particular syndrome. It does not describe a certain phyllotaxis (LA) or meristematic elevation (ME), but a specific interdependence of these two parameters (Fig. 4.14). Terminal flowers are either produced at convex IMs (> 25°; Fig. 4.14: species no.1,3,4,6,7,8 in) with high LA values (> 80; Fig. 4.14) or, more rarely, at flat IMs (Fig. 4.14: species no. 5 and 2) with low LA values (< 80).

Interestingly, this syndrome can take place at different absolute sizes as shown by the similar shapes but different sizes of the meristematic bulges in *Dicentra eximia* (Fig. 4.7A1-9) and *Capnoides sempervirens* (Fig. 7B1-9) . The finding that relatively smaller IMs get more

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→ IMs also produce TFs, but present instead lower LA values (higher phyllotaxis). This relationship suggests that the minimal area required for TF formation can be distributed both in the vertical (conical) and / or horizontal (phyllotaxis) dimension. Some of the open species also fall inside the syndrome-curve (1, 2 ,3 ,5 , 6) suggesting that the form of the IM alone offers no predictive power with respect to the production of a terminal flower or not. Anyway, these open species possess lower AR values than the closed species, because they posses relatively larger lateral primordia (YPA, Table 4.2). Species falling underneath the curve (4, 7, 8) can be directly recognized as open species, since an IM shape given by a low ME and a high LA (low phyllotaxis) implies a small areal ratio (AR, Table 4.2). White numbers in black-filled circles indicate closed species: 1, *A. eupatoria*, 2, *C. thyrsoides*, 3, *B. aristata*, 4, *M. x aquisargentii*, 5, *E. tenuifolius*, 6, *N. alabamensis*, 7, *C. sempervirens*, 8, *D. eximia*. Black numbers in empty circles indicate open species: 1, *L. spectabilis*, 2, *S. japonica*, 3, *M. aquifolium*, 4, *C. elata*, 5, *P. orbiculare*, 6, *S. minor*, 7, *S. chamaedryfolia,* 8, *B. darwinii.*

convex - and *vice-versa* - is probably a consequence of the providing of meristematic space in the vertical (ME) and horizontal (LA) dimension. The combination of a LA and ME lying beneath the 'final IM shape' regression curve (Fig. 4.14) would probably result in a meristematic tissue insufficient for a TF formation (sketches bottom right, Fig. 4.14).

The form and relative size of the bulge that produces a TF is by no means influenced by the size of the inflorescence (total number of LUs; see Table 4.4A). This means, that both large and small inflorescences with terminal flowers tend to converge in their late IM aspects, supporting a common TF-meristematic bulge for all closed species., The correlation analysis furthermore shows that the size of an inflorescence is related to the IM size at the beginning of the ontogeny (Table 4.4A). This is for example illustrated by the large closed inflorescence of *A. eupatoria* (Fig. 4.9E10) that shows a considerably higher initial meristem enlargement than the smaller closed inflorescence of *M.x aquisargentii* (Fig. 4.4C2).Within open species this correlation is not significant, partly seen in the fact that large open inflorescences as e.g. *M. aquifolium* (Fig. 4.4D2) can also derive from less enlarged IMs.

Though the adoption of a meristematic bulge (inside the area of the curve, Fig. 4.14) is typical for terminal flower producing species, it is not a synonym to TF induction. Some open species also produce a bulge, but in these cases, the IM merges into a sterile rest (Fig. 4.14).

4.4.2 One common ontogeny for closed inflorescence and at least two ontogenies in open inflorescences

The interplay between the initial IM enlargement, the developmental dynamic of the IM and its final shape allows distinguishing three main groups of inflorescences (Table 4.5, Fig. 4.15). The first group represents ontogenies characterized by a weak enlargement of the vegetative meristem in the shift to the reproductive phase corresponding to open species ('open I', Table 4.5, Fig. 4.15A). Examples are *M. aquifolium* (Fig. 4.3D1,D2), *L. spectabilis* (Fig. 4.5C1, C2) and *S. japonica* (Fig. 4.9B1, B2). The production of flower buds involves a reduction of the meristematic tissue (Kwiatkowska 2008). As the IMs in these species are relatively small, their meristematic tissue must be constantly renewed in order to restore the gap left by the excised flower-buds and continue with the floral production. The relative

weak enlargement of such IMs can be graphically recognized as the values of their initial AR lie below the ones of closed inflorescences (nos. 1 and 3 in Fig. 4.13).

Table 4.5. Attributes of the ontogeny of inflorescences that suggest the distinction of three main groups: 'open I', 'closed' and 'open II'. Initial AR refers to the initial enlargement of the inflorescence meristem (Fig 13). IM height dynamic refers to the slope of the regression analyses between the meristematic height (H) and inflorescence bud (Table 4.3). Final AR corresponds to the mean of the final areal ratio (AR) considering the species within each group. Final shape refers to the final leaf arc (LA) and final meristematic elevation (ME) of the inflorescence bud in relation to the regression curve in Fig 14. The meristematic rest was qualitatively evaluated according the SEM micrographs (Figs 4.4, 4.7, 4.9, 4.11). The terms 'proportional' and 'syndrome' indicate that the respective value is found inside the area comprised by the regression curve and the 95% confidence interval brackets; 'weak': underneath the areal of the curve; 'high': above the areal of the curve; 'renewal': positive slope or slope non significantly distinct form zero; 'decaying': negative slope.

Ontogeny	Species	Initial AR	IM height dynamic	Final AR (mean ± se)	Final shape	Meristematic rest
Open I	*M. aquifolium*	weak	renewal	1,80 ± 0,39	syndrome	conspicuous
	L. spectabilis	weak	renewal		syndrome	conspicuous
	S. japonica	proportional	renewal		syndrome	conspicuous
Closed	*B. aristata*	proportional	decaying	2,75 ± 0,38	syndrome	absent
	M. x aquisargentii	proportional	renewal		high	absent
	C. sempervirens	proportional	renewal		syndrome	absent
	D. eximia	proportional	renewal		syndrome	absent
	A. eupatoria	proportional	renewal		syndrome	absent
	N. alabamensis	proportional	renewal		syndrome	absent
	C. thyrsoides	proportional	renewal		syndrome	absent
	E. tenuifolius	weak	-		syndrome	absent
Open II	*B.darwinii*	proportional	decaying	0,67 ± 0,18	weak	conspicuous
	C. elata	proportional	decaying		weak	apparent
	P. orbiculare	proportional	decaying		syndrome	absent
	S. minor	high	decaying		syndrome	absent
	S. chamaedryfolia	high	decaying		weak	apparent

In opposition to the first group, the next two represent ontogenies characterized by a significant enlargement of the meristematic tissue on the shift from the vegetative to the reproductive phase (Table 4.5; Fig. 4.15B,C). As an initial IM enlargement provides new meristematic tissue, the flower-bud segregation can proceed without the necessity of a great posterior renewal of the IM. This implies that the meristematic dimensions will decrease from the early to the late ontogeny. Particularly, when the meristematic height (H)

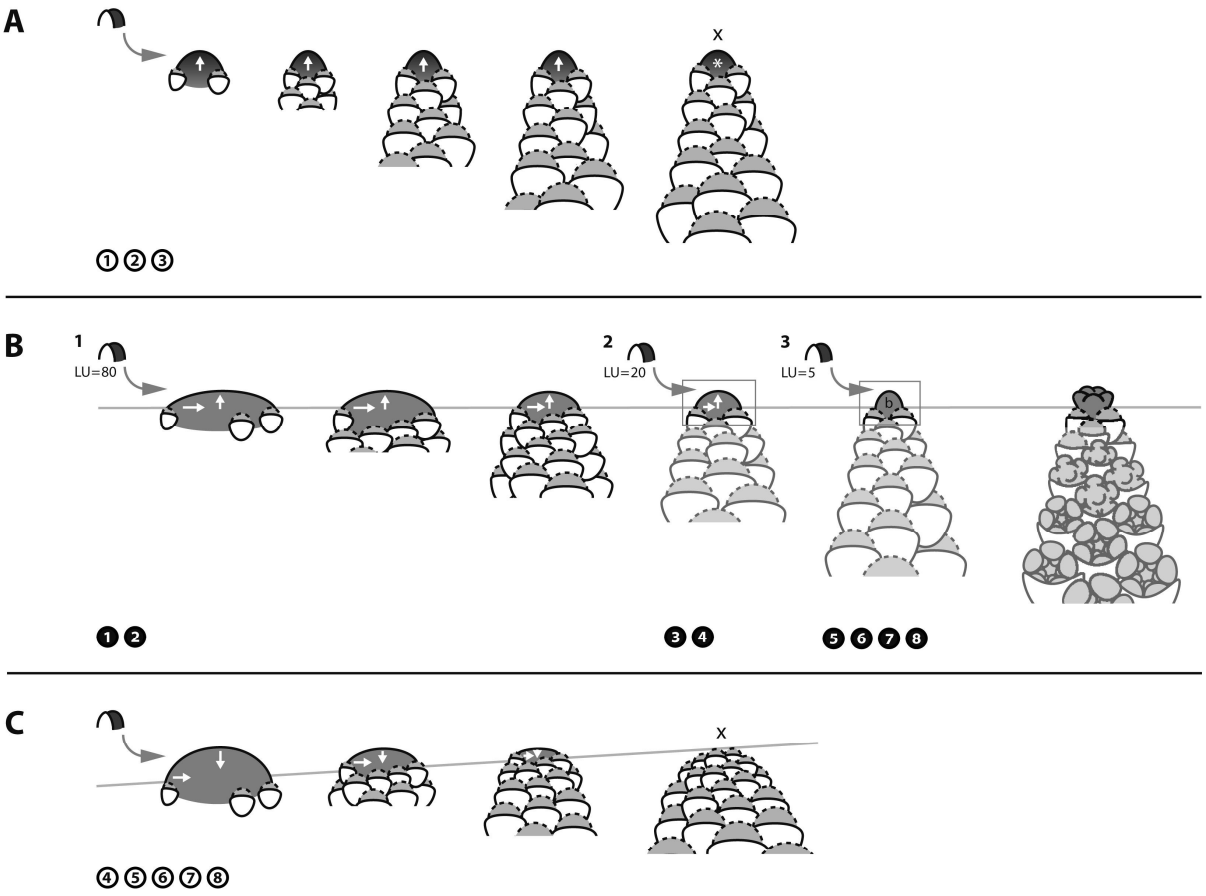

Figure 4.15. Schematic representation of the ontogenetic sequence of open (A, C) and terminal flower producing inflorescences (B). Sketches depict lateral views of inflorescence buds whose inflorescence meristems (im) are idealized as a parable (dark grey) and the lateral primordia are composed of a subtending bract (white) and an axillary product (light grey). Sketches of vegetative meristems (marked by their darker shading of the meristematic cone) can be seen preceding each ontogenetic sequence. A, Typical ontogeny of an open inflorescence derived from a weakly enlarged vegetative meristem as e.g. in *L. spectabilis* (1), *S. japonica* (2) and *M. aquifolium* (3). The IMs show a rather invariable aspect during their ontogeny while giving rise to the flower buds. This implies a constant renewal activity of the meristematic tissue (arrow) in order to produce the forthcoming flowers. At the end of the ontogeny these inflorescences evidence a meristematic rest on the top (star), remaining the inflorescence open (symbolized by the cross). The retention of vegetative attributes in the IM is insinuated by its darker colour towards the tip.

B, Typical ontogeny of an inflorescence that develops a terminal flower. The initial enlargement of the IM during the reproductive transition corresponds to the size of the inflorescence (LU, Fig 13, Table 4.1). B1, Large inflorescences (>80 LU) are characterized by a marked initial enlargement of the IM as shown by *A. eupatoria* (1) and *C. thyrsoides* (2). The high dimensioned IM tends to get reduced through the sequence until the terminal flower bulge is formed (b).B2, Medium-sized inflorescences (50>LU>10) show a moderate initial IM enlargement. The inception of this ontogeny can be →

gets diminished, i.e. 'decaying IM', the final IM-bulge adopts a minute size and the resulting inflorescence is open again ('open II', Table 4.5; Fig. 4.15C).

The ontogeny of closed inflorescences represents an intermediate pathway as their IMs present an initial enlargement and an additional renewal activity guaranteeing stable height (H) values through development (Fig. 4.15B; Table 4.5).

The initial enlargement in closed inflorescences is proportional to the number of LUs in the mature state (Tables 4.4, 4.5; following the regression curve in Fig. 4.3). Consequently, the largest closed inflorescences *A. eupatoria* (Fig. 4.9E10) and *C. thyrsoides* (Figs. 4.11E7, 4.15B1) show the highest initial enlargement; moderate-sized inflorescences as *M. x aquisargentii* (Fig. 4.4C2), *B. aristata* (Fig. 4.4A2) and *A. canescens* (Figs. 4.11C2, 4.15B2) show moderate enlargement; and small closed inflorescences as *E. tenuifolius* (Fig. 4.11D2), *N. alabamensis* (Fig. 4.9A2), *C. sempervirens* (Fig. 4.7B2) and *D. eximia* (Figs. 4.7A2, 4.15B3) present an even more limited initial enlargement.

A major enlargement of the IM is a precedent for a forthcoming decaying IM dynamic and, as mentioned above, decaying IMs result in open inflorescences (Table 4.5). The major

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→ compared with a direct entering into an advanced ontogenetic state of a large inflorescence (box detailing an excerpt of the respective sketch). This means that the initial relative size of the IM is dependent on the number of flowers that are still to be formed (see Fig 14). Such an ontogeny can be seen in *B. aristata* (3), *M. x aquisargentii* (4) and *A. canescens* (see Fig. 4.11C6). B3, Small inflorescences (LU<10) form almost directly the bulge (b) required for the terminal flower formation, as seen in *E. tenuifolius* (5), *N. alabamensis* (6), *C. sempervirens* (7) and *D. eximia* (8). Note that the aspect of the IM in the advanced ontogeny is irrespective of the final size of the inflorescence, suggesting that all closed inflorescence flow into a similar development. The steepness of the bulge that will form the terminal flower can vary in relation to the phyllotaxis present in the inflorescence (LA, Fig. 4.14). Notably a constant height (H) of the meristem is seen through the whole ontogeny (see horizontal reference line), which implies that the IM shows a 'vertical' renewal activity (Table 4.3, 4.5, vertical arrow), while the width (W) gets diminished (Table 4.3, horizontal arrow).

C, Typical ontogeny of an open inflorescence derived from a markedly enlarged meristem. The IM firstly expands and is consecutively used up by lateral flower production (see the oblique reference line) and remains open (symbolized by the cross). This suggests a weak renewal activity of the meristem as the width (W) and height (H) decay through development (see Table 4.3, 4.5, arrows). Such an ontogeny is seen in *P. orbiculare* (5), *S. minor* (6) and *J. montana* (see Fig. 4.11A6). A meristematic rest is also apparent in some open inflorescences, e.g. in *C. elata* (4, Fig. 4.7D2, 6, 7), *S. chamaedryfolia* (7, Fig. 4.9C5,9,10) and *B. darwinii* (8, Fig. 4.4B8).

enlargements can be recognized as the values lying above the 'initial AR' regression curve (nos. 6 and 7 in Fig. 4.13), as seen in the open *Sanguisorba minor* (Table 4.5; Fig. 4.9D2) and *Spiraea chamaedryfolia* (Table 4.5; Fig. 4.9C2). The incapacity of decaying IMs for differentiating a TF can also be acknowledged in their resulting final form, usually not-coincident with the TF bulge-syndrome (see nos. 4,7,8 in Fig. 4.14; Table 4.5). This is observed in the decaying IMs of *C. elata* (Fig. 4.7D2), *S. chamaedryfolia* (Fig. 4.9C9) and *B. darwinii* (Fig. 4.4B3). Also appears to be related to an 'open II' ontogeny a tight packing of reproductive primordia and a small size or even absence of subtending bracts, as in *S. minor* (Fig. 4.9D8, D9), *S. chamaedryfolia* (Fig. 4.9C8, C9) and *J. montana* (Fig. 4.11A3-6).

The continuous IM activity of closed species implies that these inflorescence buds naturally adopt a more or less pyramidal form (see Figs. 4.9E6, 4.11C9, E5). Contrary, the lack of renewal activity of 'open II' IMs is manifested in their typical spherical form, partly caused by the strong initial enlargement (see Figs. 4.7D1, 4.9C6, D6). Interestingly, this difference in the inflorescence bud shape can be sometimes also observed in the adult form. For example, within the genus *Phyteuma*, the species that produce a TF as *P. nigrum* and *P. spicata* show a pyramidal inflorescence (Weberling and Troll 1998), while the open *P. orbiculare* presents a rather spherical form (Fig. 4.1H).

4.4.3 Histophysiological correlates

The three groups of ontogenies appear to elucidate two categories of IMs. The 'open I' group (Fig. 4.15A) represents IMs that probably conserve some vegetative characteristics in the shift from vegetative to the reproductive stage because i. they do not show much morphological difference through this transition, and ii. the generative tissue must be constantly renewed to allow further flower segregation, a feature that is typical to vegetative meristems. Bull-Hereñu and Claßen-Bockhoff (2010b) recently proposed that inflorescences that conserve a cytohistological zone termed 'central zone' (CZ, Kwiatkowski 2008) are forced to produce open inflorescences, as the tissue encompassed in this CZ can not differentiate into a flower at all. The species belonging to the 'open I' group are probably inflorescences that maintain a CZ in their IM, an idea that is reinforced by the presence of conspicuous remnants at the tip of their inflorescences. Such 'remaining tips' could represent the parenchymatized cone that earlier sheltered the CZ (Table 4.5), as seen in the

'open I' species *M. aquifolium* (Fig. 4.4D6), *L. spectabilis* (Fig. 4.7C5) and *S. japonica* (Fig. 4.9B9). Interestingly, the open inflorescences species that have been subjected to genetic studies as *Arabidopsis thaliana* (Brassicaceae, Shannon and Meeks-Wagner 1991) and *Pisum sativa* (Fabaceae, Singer et al., 1999) also show a meristematic rest at the end of the ontogeny. Further studies also demonstrate the presence of such meristematic remnants, e.g. in *Veronica* (Plantaginaceae, Bull-Hereñu and Claßen-Bockhoff 2010b), *Glycine* (Fabaceae, Washburn and Thomas 2000), *Securidaca* (Polygalaceae, Krüger and Robbertse 1988), *Brassica* (Brassicaceae, Kieffer et al., 1998) and Cyperoideae (Cyperaceae, Vrijdaghs et al. 2010). An interesting fact is that these species all belong to the 'typical' open families (Troll 1964, Stebbins 1974, Weberling 1992, Weberling and Troll 1998, Bull-Hereñu and Claßen-Bockhoff 2010b). This evidence supports the assumption that the maintenance of the CZ in an inflorescence meristem could be a character of systematic importance explaining the existence of 'classical' open families (Bull-Hereñu and Claßen-Bockhoff 2010b).

The second category of IM is given by the closed and 'open II' groups (Fig. 4.15B, C; Table 4.5). These ontogenies correspond to IMs whose tissue is completely differentiated into flower buds, independent of the formation of a terminal flower. IMs that are completely differentiated are histological related to the disappearance of the CZ in the reproductive transition and the establishment of a 'mantle-core' (MC) organization (Kwiatkowska 2008, Bull-Hereñu and Claßen-Bockhoff 2010b). As seen above, in this case it is the IM shape and dynamic of its ontogeny that determines whether a TF will be produced at the end or not: either the IM bulge meets the geometrical conditions and is transformed into a TF or it gets extremely reduced due to the using-up of the IM, as in *S. minor* (Fig. 4.9D10)*, P. orbiculare* (Fig. 4.11B4) and *J. montana* (Fig. 4.11A5). Open inflorescences that possess IMs with an early sudden enlargement followed by a rapid segmentation of tight packed flower primordia include Asteraceae (Claßen-Bockhoff 1992b, Harris 1995, Lacroix 2007, Thomas et al. 2009), Araceae (Barabé 1994, Buzgo 2001, Barabé and Lacroix 2008), Acoraceae (Buzgo and Endress 2000[2]), Betulaceae (Zhu and Lu 2008) and recently described Balanophoraceae (Eberwein et al. 2009).

Considering these two IM-histological categories, it is probable that the described low-space availability of open IMs (T-test, 'final AR' in Table 4.5) can be traced back to two different

[2] Note the similarity of the tubular organ seen in *S. minor* Fig (9D10) compared with the one seen in *Acorus calamus* in this reference (Fig 13d).

phenomena: in ‘open I’ to the remaining meristematic areal that eventually sheltered the CZ, and in ‘open II’ to the remaining reproductive tissue that is too small to permit terminal or lateral flower origination. Both a decaying-dynamic (‘open II’) and retention of a CZ (‘open I’) could also be possible (Table 4.5; see the apparent meristematic rests of *C. elata* in Fig. 4.7D1, D2; *S. chamaedryfolia* in Fig. 4.9C6-9; and *B. darwinii* in Fig. 4.4B1-3, B8). Clearing the nature of corresponding meristematic rests by means of histological studies would be very helpful to shed light into these hypotheses.

L. cardinalis did not match our grouping, as it presented a huge meristematic rest at its final state (Fig. 4.11F4). The appearance of such a meristem reminds the typical condition seen in cultivars that use to show big naked meristematic rests or even singular appendages on the summits of the inflorescences (Retallack and Willson 1990, Gerber et al. 2001, Bertero et al. 1996, Cook-off et al. 2006). Such a phenomenon, also known as fasciation, is probably due to overgrowth of the IM caused by overfeeding conditions under culture, and has as such, no possibility of TF formation.

4.4.4 Concluding remarks

The contribution of our work to the understanding of terminal flower formation in angiosperms can be summarized in four statements:

i. a TF is only produced on an IM that provides sufficient space (already present).

ii. the space from which the TF differentiates represents a meristematic bulge whose shape results from a special interrelation between phyllotaxis and cone elevation.

iii. ontogenies leading to TF formation demand an initial enlargement of the IM at the transition from the vegetative to the reproductive phase proportional to the final size of the inflorescence.

iv. IMs leading to terminal flower formation show a renewal capacity and maintain stable vertical dimensions.

Simultaneously, these observations indicate that

i. no terminal flower will be produced if the early enlargement of the IM is either too low (‘open I’) or too pronounced (‘open II’) (Table 4.5, Fig. 4.13).

ii. the form of the IM alone is no criterion for predicting the presence of a TF.

iii. the production of a TF can be discarded when the relative area of the IM is too small (Table 4.5) or when the IM shows a very large rounded naked area. In the last case, the IM would be prone to decay in the later ontogeny, and as such, be unable to form the TF-bulge. Our work shows that the ontogenies of closed inflorescences are alike as they present IMs with renewal capacity and that adopt a given geometry prior to the terminal flower differentiation. Contrarily, open inflorescences can develop in at least two distinct ways, distinguishing between active ('open I') or decaying ('open II') IMs whose final sizes are smaller than those of closed inflorescences. As the diversity of open inflorescences is based on distinct ontogenetic natures, the evolutive shift from closed to open inflorescences (or vice-versa) must have occurred involving distinct ontogenetic shifts.

4.5 Summary

We carried out a quantitative study of inflorescence development aiming to know how far developmental constraints determine the production of a terminal flower (TF). We observed a total of 646 inflorescence buds of 19 species in four families of the Eudicots (Berberidaceae, Papaveraceae-Fumarioideae, Rosaceae, Campanulaceae) including both closed (i.e. with terminal flower, TF) and open (i.e. without terminal flower) species. We quantified their inflorescence meristem (IM) dimensions throughout the development measuring their relative area (AR), phyllotaxis (LA) and elevation (ME). Our study shows that TFs appear on IMs that show an average AR of 2,75 (se = 0,38) and a shape characterized by a LA of 91,84° (se = 7,32) and a ME of 27,93° (se = 5,42). All ontogenies begin with an enlargement of the IM. This is proportional to the final size of the mature inflorescence in the closed type but not in the open one. TFs are normally formed on convex-shaped IMs, but they also occur on more flat-shaped IMs that show higher phyllotaxis. IMs of open inflorescences show significant lower relative surface at their final state than the closed ones (AR = 1,09 ± 0,26), illustrating their unsuitability for producing TFs. The relative lower AR found in open IM is either existent during the whole ontogeny ('open I') or is the consequence of a drastic reduction of the meristematic area after flower fractionation ('open II'). We conclude that the TF can be understood as a consequence of the adoption of a suitable bulge by the IM, which in turn depends on the dynamic of the ontogeny. The

existence of two kinds of ontogenies of open inflorescences suggests two natures of open IMs, and therefore, two ways in which the loss of the TF could have occurred in the course of evolution.

4.6 Appendix

A. Measurements and calculations in species with convex inflorescence meristems. For abbreviation explanations see Material and Methods.

IND	LP	MEASUREMENTS														CALCULATIONS							
		Top view					Frontal view				Lateral view												
		α_1 (°)	α_2 (°)	l_1 (µm)	l_2 (µm)	l_3 (µm)	w_f (µm)	h_f (µm)	ph (µm)	pw (µm)	w_l (µm)	h_l (µm)	h_1 (µm)	h_2 (µm)	h_3 (µm)	BL (µm)	W (µm)	H (µm)	MS (μm^2)	YPA (μm^2)	LA (°)	ME (°)	AR
Berberis aristata																							
1	4	74	85	21,36	26,08	40,47	186,11	66,67	80,73	102,79	174,31	57,64	-	-	-	87,91	180,11	62,16	32359	6514	79,50	34,62	4,97
2	6	76	87	25,26	41,85	54,09	190,45	60,50	95,76	119,93	173,76	66,65	-	-	-	121,20	181,91	63,58	34529	9015	81,50	34,96	3,83
3	7	62	72	34,06	25,57	41,61	146,49	42,98	73,80	97,38	166,34	52,97	-	-	-	101,24	156,10	47,98	28987	5642	67,00	31,58	5,14
4	8	89	102	64,85	70,86	56,58	121,05	44,30	80,69	107,61	115,87	39,00	-	-	-	192,29	118,43	41,65	14413	6816	95,50	35,13	2,11
5	11	80	89	44,74	49,69	67,88	152,55	40,10	90,31	122,95	156,06	44,50	-	-	-	162,31	154,30	42,30	24405	8716	84,50	28,74	2,80
6	11	91	113	55,27	70,22	67,09	114,37	34,11	72,94	108,95	124,96	43,69	-	-	-	192,58	119,55	38,90	17060	6238	102,00	33,06	2,73
7	13	79	101	43,62	56,17	67,27	140,35	46,49	100,89	126,33	149,14	50,00	-	-	-	167,06	144,68	48,25	23835	10005	90,00	33,71	2,38
8	15	105	85	53,40	79,79	85,70	118,86	37,11	83,70	110,65	118,89	39,46	-	-	-	218,89	118,87	38,29	15078	7270	95,00	32,79	2,07
9	16	94	102	59,09	58,54	66,72	122,37	35,09	78,78	114,31	123,96	37,63	-	-	-	184,35	123,16	36,36	15780	7069	98,32	30,57	2,23
10	16	83	95	45,65	67,14	72,89	138,16	47,37	91,73	109,22	141,62	46,64	-	-	-	185,68	139,88	47,01	21321	7865	89,00	33,91	2,71
11	16	89	104	52,49	64,51	73,96	117,54	39,47	77,76	97,97	104,34	33,61	-	-	-	190,96	110,74	36,54	11462	5980	96,50	33,43	1,92
Berberis darwinii																							
1	1	70	113	35,36	45,16	48,53	173,86	60,45	92,21	109,67	149,50	54,46	-	-	-	129,05	161,22	57,46	28657	7938	91,50	35,49	3,61
2	2	50	72	48,75	37,67	28,29	147,76	47,83	69,59	86,84	203,27	58,19	-	-	-	114,71	173,31	53,01	30940	4744	61,00	31,46	6,52
3	2	65	86	43,01	42,55	33,75	144,01	46,44	107,34	118,45	180,70	62,28	-	-	-	119,31	161,32	54,36	27950	9981	75,50	33,98	2,80
4	3	60	100	34,06	39,56	33,49	144,78	47,35	72,53	98,78	175,44	57,89	-	-	-	107,11	159,37	52,62	27033	5624	80,00	33,44	4,81
5	3	69	84	33,40	23,62	58,46	165,79	55,26	75,18	128,95	181,84	42,05	-	-	-	115,48	173,63	48,66	30014	7610	76,50	29,27	3,94
6	3	83	66	38,54	38,64	38,83	198,25	67,54	85,20	118,50	171,19	58,22	-	-	-	116,01	184,22	62,88	36666	7926	74,50	34,33	4,63
7	4	76	65	64,04	44,39	59,14	148,26	57,01	120,50	111,49	157,90	47,37	-	-	-	167,57	153,00	52,19	25284	10546	70,50	34,31	2,40
8	4	64	68	33,21	54,09	29,94	150,01	50,87	87,72	114,04	177,46	59,54	-	-	-	117,24	163,16	55,21	28646	7853	66,00	34,09	3,65
9	4	74	91	32,93	59,75	49,64	212,20	64,65	98,48	122,38	159,12	64,55	-	-	-	142,32	183,75	64,60	36986	9461	82,50	35,12	3,91
10	4	36	82	32,46	34,61	52,55	186,84	66,67	87,76	95,61	153,51	57,89	-	-	-	119,62	169,36	62,28	32111	6587	59,00	36,34	4,88

A. Measurements and calculations in species with convex inflorescence meristems (cont.)

IND	LP	MEASUREMENTS														CALCULATIONS							
		Top view					Frontal view				Lateral view												
		α_1 (°)	α_2 (°)	l_1 (µm)	l_2 (µm)	l_3 (µm)	w_f (µm)	h_f (µm)	ph (µm)	pw (µm)	w_l (µm)	h_l (µm)	h_1 (µm)	h_2 (µm)	h_3 (µm)	BL(µm)	W(µm)	H(µm)	MS (µm^2)	YPA (µm^2)	LA (°)	ME (°)	AR
11	4	91	91	44,87	62,14	52,16	142,92	42,59	99,85	114,37	152,14	34,62	-	-	-	159,17	147,46	38,61	21132	8965	91,00	27,64	2,36
12	4	80	86	25,54	27,19	41,40	149,19	37,26	82,68	73,70	170,60	44,39	-	-	-	94,13	159,54	40,83	24547	4783	83,00	27,11	5,13
13	5	75	100	55,44	59,88	59,78	176,32	56,58	107,63	129,43	133,34	34,21	-	-	-	175,10	153,33	45,40	23903	10935	87,50	30,64	2,19
14	5	61	83	38,73	47,44	43,55	182,46	53,51	95,28	121,28	167,00	50,77	-	-	-	129,72	174,56	52,14	31089	9071	72,00	30,86	3,43
15	5	84	85	14,14	33,88	18,94	124,19	41,21	87,81	100,44	161,42	41,23	-	-	-	66,96	141,59	41,22	20248	6923	84,50	30,22	2,92
16	8	77	82	54,05	71,94	56,48	90,81	13,59	65,29	128,07	165,79	32,46	-	-	-	182,47	122,70	23,03	13357	6564	79,50	20,58	2,03
17	9	94	135	117,27	99,25	82,33	61,59	13,55	93,13	112,43	175,81	37,62	-	-	-	298,85	104,06	25,59	10310	8219	114,50	26,19	1,25
18	10	130	103	82,68	84,43	122,13	165,15	21,04	116,64	132,13	135,47	15,66	-	-	-	289,24	149,58	18,35	18587	12098	116,50	13,79	1,54
19	11	102	99	81,07	92,11	82,38	88,77	23,96	146,87	139,52	139,05	30,26	-	-	-	255,56	111,10	27,11	11725	16086	100,50	26,02	0,73
Mahoberberis x aquisargentii																							
1	1	141		45,11			196,50	78,06	103,51	191,26	78,25	54,21	-	-	-	45,11	124,00	66,14	21364	15541	141,00	46,86	1,37
2	4	53	82	23,60	14,14	15,54	141,24	106,12	89,46	123,52	150,94	101,69	-	-	-	53,28	146,01	103,91	36450	8674	67,50	54,92	4,20
3	5	43	64	17,11	37,73	31,19	160,89	87,59	97,39	71,58	157,03	77,19	-	-	-	86,03	158,95	82,39	34451	5472	53,50	46,04	6,30
4	8	85	99	37,27	34,74	25,62	126,75	81,58	86,29	105,79	145,18	64,04	-	-	-	97,63	135,65	72,81	25675	7166	92,00	47,04	3,58
5	9	77	71	27,92	29,82	36,98	128,56	66,63	76,75	107,90	153,47	61,80	-	-	-	94,72	140,46	64,22	24876	6501	74,00	42,45	3,83
6	9	85	94	41,85	9,04	43,42	165,98	62,23	78,16	116,67	141,75	54,90	-	-	13,69	108,00	153,39	58,57	26843	7158	89,50	37,37	3,75
7	11	49	86	37,73	18,44	28,07	99,13	71,48	82,16	65,85	219,78	64,84	-	-	-	84,24	147,60	68,16	27635	4247	67,50	42,73	6,51
8	14	59	87	21,72	31,44	24,09	119,94	61,73	86,27	107,02	187,86	68,00	-	-	-	77,25	150,11	64,87	27491	7248	73,00	40,84	3,79
9	14	67	79	40,01	37,24	26,72	163,18	62,26	86,91	127,39	141,83	56,84	-	-	-	103,97	152,13	59,55	26749	8691	73,00	38,06	3,08
10	15	72	77	27,74	47,16	16,32	118,79	51,95	71,95	110,00	186,86	62,28	-	-	-	91,22	148,99	57,12	25378	6213	74,50	37,48	4,08
11	15	78	87	29,88	48,28	55,82	177,20	78,94	73,27	115,26	148,99	89,80	-	-	-	133,98	162,48	84,37	36042	6629	82,50	46,09	5,44
12	16	73	89	23,70	22,09	40,04	192,98	83,33	85,13	130,85	140,45	72,13	-	-	-	85,83	164,63	77,73	34845	8744	81,00	43,37	3,98
Mahonia aquifolium																							
1	1	100		31,89			31,13	109,69	67,16	99,61	114,47	51,75	-	-	-	31,89	112,05	41,44	14097	5251	100,00	36,49	2,68
2	1	107		34,91			26,09	104,34	83,09	114,66	111,42	31,82	-	-	-	34,91	107,82	28,96	11398	7479	107,00	28,25	1,52
3	2	99	108	53,36	22,09		26,30	120,23	90,46	135,24	186,87	50,43	-	-	-	75,45	149,89	38,37	21671	9604	103,50	27,11	2,26
4	2	81	106	53,36	54,81		28,06	117,60	74,56	110,54	113,16	21,49	-	-	-	108,17	115,36	24,78	12189	6470	93,50	23,25	1,88
5	2	75	109	56,88	43,58		35,95	131,23	73,27	120,31	128,64	53,94	-	-	-	100,46	129,93	44,95	18352	6920	92,00	34,68	2,65

A. Measurements and calculations in species with convex inflorescence meristems (cont.)

IND	LP	MEASUREMENTS														CALCULATIONS							
		Top view					Frontal view				Lateral view												
		α_1 (°)	α_2 (°)	l_1 (µm)	l_2 (µm)	l_3 (µm)	w_f (µm)	h_f (µm)	ph (µm)	pw (µm)	w_l (µm)	h_l (µm)	h_1 (µm)	h_2 (µm)	h_3 (µm)	BL(µm)	W(µm)	H(µm)	MS (μm^2)	YPA (μm^2)	LA (°)	ME (°)	AR
6	3	110	111	40,55	31,31	33,40	30,70	87,72	103,52	135,98	96,53	18,42	-	-	-	105,26	92,02	24,56	8284	11050	110,50	28,10	0,75
7	3	75	117	24,81	60,79	21,53	49,10	142,20	96,35	107,02	158,45	31,69	-	-	-	107,13	150,11	40,40	22107	8094	96,00	28,30	2,73
8	4	81	90	37,88	47,82	52,79	32,46	121,05	74,06	100,75	134,42	53,52	-	-	-	138,49	127,56	42,99	17478	5857	85,50	33,99	2,98
9	5	59	87	31,98	31,58	36,41	35,77	119,57	83,39	113,46	125,76	37,45	-	-	-	99,97	122,63	36,61	15339	7427	73,00	30,85	2,07
10	6	100	107	16,55	30,25	40,96	48,25	147,81	92,37	145,85	87,64	32,67	-	-	-	87,76	113,82	40,46	14265	10576	103,50	35,42	1,35
11	6	95	108	48,31	46,54	103,81	21,49	90,36	71,93	98,70	124,53	24,48	-	-	-	198,66	106,08	22,99	10331	5573	101,50	23,43	1,85
12	7	103	92	31,79	66,35	27,19	29,36	113,67	76,82	118,19	132,47	36,40	-	-	49,44	174,77	122,71	32,88	14752	7127	97,50	28,19	2,07
13	8	88	110	40,85	58,01	79,03	32,45	124,57	100,81	113,20	95,18	23,68	-	-	-	177,89	108,89	28,07	11463	8958	99,00	27,28	1,28
14	10	89	102	39,42	60,48	43,56	49,91	152,31	82,43	119,56	123,28	53,93	-	-	-	143,46	137,03	51,92	21339	7736	95,50	37,16	2,76
15	10	75	109	48,40	42,55	68,27	35,51	148,75	92,98	120,15	147,02	35,50	-	-	-	159,22	147,88	35,51	20670	8770	92,00	25,65	2,36
16	12	76	95	49,88	57,04	49,15	31,13	120,63	78,82	123,84	140,39	32,45	-	-	-	156,07	130,14	31,79	16092	7662	85,50	26,04	2,10
17	12	86	91	63,71	58,77	20,18	33,33	149,12	72,83	109,65	136,15	40,59	-	-	-	142,66	142,49	36,96	19670	6269	88,50	27,42	3,14
18	12	91	96	36,87	68,04	50,51	26,31	121,09	69,50	103,26	118,45	22,36	-	-	-	155,42	119,76	24,34	12957	5634	93,50	22,12	2,30
19	12	52	90	28,64	32,83	15,89	34,58	62,84	80,86	76,75	158,82	44,28	-	-	-	77,36	99,90	39,43	11585	4872	71,00	38,29	2,38
20	14	71	72	41,11	47,44	43,15	40,09	141,12	93,29	120,80	183,81	47,80	-	-	-	131,70	161,06	43,95	25576	8847	71,50	28,63	2,89
21	16	80	122	59,92	49,32	55,21	41,67	138,60	90,09	107,95	133,78	43,86	-	-	50,88	215,33	136,17	42,77	19311	7634	101,00	32,14	2,53
22	17	89	142	36,88	36,32	34,92	40,76	140,87	83,81	117,98	115,08	23,65	-	-	28,14	136,26	127,32	32,21	15576	7762	115,50	26,84	2,01
23	22	78	86	49,95	60,45	66,41	44,28	162,37	74,15	111,71	142,15	39,09	-	-	-	176,81	151,92	41,69	22803	6502	82,00	28,76	3,51
24	24	107	115	32,12	36,14	71,01	35,82	114,92	64,78	109,58	116,81	42,02	-	-	-	139,27	115,86	38,92	14398	5572	111,00	33,90	2,58
25	25	87	116	55,95	67,14	72,19	36,21	113,90	81,63	104,60	117,33	38,61	-	-	28,73	224,01	115,60	37,41	14098	6703	101,50	32,92	2,10
26	25	78	90	57,98	36,05	58,97	39,00	125,13	73,56	112,60	132,02	36,84	-	-	-	153,00	128,53	37,92	16773	6502	84,00	30,55	2,58
Capnoides sempervirens																							
1	1	105		33,57			68,87	15,35	47,10	67,20	71,89	15,84	-	-	-	33,57	70,36	15,60	4573	2485	104,54	23,73	1,84
2	1	122		42,49			98,13	31,92	73,77	92,58	100,01	32,64	-	-	-	42,49	99,07	32,28	10384	5361	122,00	33,95	1,94
3	1	100		33,78			102,19	35,09	62,77	89,91	100,01	37,27	-	-	-	33,78	101,09	36,18	11291	4430	99,85	34,20	2,55
4	1	112		43,16			128,22	59,41	77,27	78,23	122,22	50,69	-	-	-	43,16	125,18	55,05	19313	4745	112,00	40,18	4,07
5	2	103	131	23,26	38,37		92,55	35,52	67,31	85,10	97,97	37,02	-	-	-	61,63	95,22	36,27	10332	4497	117,00	36,46	2,30
6	3	114	141	22,87	42,28	47,00	109,69	44,28	69,36	93,98	100,49	36,83	-	-	-	112,15	104,99	40,56	12652	5117	127,50	36,48	2,47

A. Measurements and calculations in species with convex inflorescence meristems (cont.)

IND	LP	MEASUREMENTS														CALCULATIONS							
		Top view					Frontal view				Lateral view												
		α_1 (°)	α_2 (°)	l_1 (µm)	l_2 (µm)	l_3 (µm)	w_f (µm)	h_f (µm)	ph (µm)	pw (µm)	w_l (µm)	h_l (µm)	h_1 (µm)	h_2 (µm)	h_3 (µm)	BL (µm)	W (µm)	H (µm)	MS (µm^2)	YPA (µm^2)	LA (°)	ME (°)	AR
7	3	96	126	15,97	45,90	51,82	112,76	47,35	71,50	85,60	109,77	45,93	-	-	-	113,69	111,25	46,64	14846	4805	111,00	38,82	3,09
8	3	88	113	16,23	31,73	47,97	113,27	*	62,67	79,43	91,45	29,16	-	-	-	95,93	101,78	29,16	10399	3908	100,50	34,31	2,66
9	5	87	118	40,08	45,12	35,57	98,71	31,47	55,28	70,69	97,39	30,25	-	-	-	120,77	98,05	30,86	10021	3068	102,59	31,70	3,27
10	5	102	103	29,18	29,47	49,47	99,14	32,45	74,56	87,74	100,89	32,89	-	-	-	108,12	100,01	32,67	10595	5135	102,50	31,85	2,06
11	5	102	123	36,64	56,95	68,11	116,74	37,11	59,96	84,81	98,36	37,67	-	-	-	161,70	107,16	37,39	12533	3992	112,38	36,58	3,14
12	6	85	97	36,73	51,11	54,32	103,98	34,64	58,70	77,00	103,52	49,11	-	-	-	142,16	103,75	41,88	12645	3548	91,08	38,01	3,56
Corydalis elata																							
1	16	52	68	21,79	22,00	17,76	204,54	68,38	81,96	113,43	193,87	59,65	-	-	-	61,55	199,13	64,02	41712	7298	60,00	34,50	5,72
2	14	59	72	21,79	37,24	18,08	179,08	55,23	84,66	103,36	173,76	56,99	-	-	-	77,11	176,40	56,11	32583	6869	65,50	32,88	4,74
3	22	63	53	26,68	35,10	19,26	202,39	67,94	104,17	86,81	211,40	71,05	-	-	-	81,04	206,85	69,50	45892	7099	58,00	32,62	6,46
4	7	64	68	24,37	24,62	34,79	192,86	65,68	90,44	118,00	196,18	74,96	-	-	-	83,78	194,51	70,32	42005	8377	66,00	34,29	5,01
5	19	63	66	23,60	31,69	31,79	186,07	49,97	97,38	114,20	187,30	54,25	-	-	-	87,08	186,68	52,11	34647	8730	64,50	28,48	3,97
6	15	57	52	27,74	28,19	33,34	204,86	76,68	91,44	120,20	188,20	75,00	-	-	-	89,27	196,35	75,84	44251	8628	54,50	36,34	5,13
7	15	59	58	25,45	26,68	37,50	179,43	52,62	92,17	121,72	180,71	48,56	-	-	-	89,63	180,07	50,59	32313	8807	58,50	28,19	3,67
8	10	78	72	26,17	24,09	42,11	160,54	42,98	84,23	111,53	150,49	35,52	-	-	-	92,37	155,43	39,25	23200	7374	75,00	26,61	3,15
9	13	63	66	36,74	28,07	33,62	185,71	49,52	84,46	99,45	171,16	38,57	-	-	-	98,43	178,29	44,05	30310	6594	64,50	26,06	4,60
10	18	72	62	39,26	23,53	36,25	179,02	55,23	95,00	115,48	214,34	67,41	-	-	-	99,04	195,89	61,32	39908	8612	67,00	30,30	4,63
11	19	66	59	36,06	28,57	37,73	203,63	65,74	104,42	113,16	196,52	61,39	-	-	-	102,36	200,04	63,57	41884	9276	62,50	31,72	4,52
12	21	61	64	28,41	37,02	38,93	229,83	69,30	98,25	104,42	192,20	54,36	-	-	-	104,36	210,17	61,83	44799	8054	62,50	30,15	5,56
13	12	60	77	38,69	40,01	26,52	160,09	50,00	81,64	105,30	143,85	42,75	-	-	-	105,22	151,75	46,38	23714	6748	68,50	29,97	3,51
14	22	60	72	26,32	33,34	45,92	182,71	45,55	80,78	99,22	173,13	36,77	-	-	-	105,58	177,86	41,16	29574	6292	66,00	25,01	4,70
15	17	69	80	31,01	33,59	44,47	155,29	47,36	86,39	99,18	170,32	43,82	-	-	-	109,07	162,63	45,59	26336	6726	74,50	28,85	3,92
16	13	65	70	30,60	33,34	50,01	188,60	65,78	90,36	109,71	195,46	64,37	-	-	-	113,95	192,00	65,08	39699	7782	67,50	33,26	5,10
17	18	74	71	33,44	35,05	47,92	169,30	46,49	75,95	106,50	180,70	47,37	-	-	-	116,41	174,91	46,93	29985	6350	72,50	27,67	4,72
18	15	72	69	22,64	43,02	52,47	153,51	45,82	92,49	117,26	164,58	41,67	-	-	-	118,13	158,95	43,75	24988	8514	70,50	28,75	2,94
19	18	61	68	38,48	37,76	44,05	172,15	59,60	93,58	102,84	175,47	53,06	-	-	-	120,29	173,80	56,33	31887	7555	64,50	31,58	4,22
20	22	60	68	35,10	50,70	46,52	214,34	65,70	91,38	116,65	200,02	60,51	-	-	-	132,32	207,06	63,11	44098	8368	64,00	30,33	5,27
21	33	95	119	48,27	66,69	64,34	95,18	14,91	72,84	103,51	104,50	16,21	-	-	-	179,30	99,73	15,56	8528	5919	107,00	16,94	1,44

A. Measurements and calculations in species with convex inflorescence meristems (cont.)

IND	LP	MEASUREMENTS														CALCULATIONS							
		Top view					Frontal view				Lateral view												
		α_1 (°)	α_2 (°)	l_1 (µm)	l_2 (µm)	l_3 (µm)	w_f (µm)	h_f (µm)	ph (µm)	pw (µm)	w_l (µm)	h_l (µm)	h_1 (µm)	h_2 (µm)	h_3 (µm)	BL(µm)	W(µm)	H(µm)	MS (µm^2)	YPA (µm^2)	LA (°)	ME (°)	AR
22	29	97	150	65,76	82,94	91,58	78,51	9,65	104,82	119,35	93,09	13,15	-	-	-	240,28	85,49	11,40	6130	9821	123,50	13,80	0,62
23	31	105	107	75,18	83,63	87,51	102,83	10,18	94,45	134,03	56,59	3,07	-	-	-	246,32	76,28	6,63	4705	9937	106,00	0,00	0,47
24	28	90	110	76,92	84,23	88,10	102,20	18,42	86,19	117,62	93,11	15,33	-	-	-	249,25	97,55	16,88	8306	7958	100,00	17,83	1,04
Dicentra eximia																							
1	1	135		81,61			144,74	37,28	83,35	147,60	124,20	27,62	-	-	-	81,61	134,08	32,45	14261	9657	135,00	25,83	1,48
2	1	106		85,74			133,36	30,70	100,50	134,33	114,04	24,12	-	-	-	85,74	123,32	27,41	11865	10598	106,33	23,97	1,12
3	1	93		72,60			133,75	31,49	89,78	142,84	128,40	34,76	-	-	-	72,60	131,05	33,13	16210	10067	92,89	26,82	1,61
4	1	119		63,24			140,38	39,46	102,17	132,78	121,06	31,58	-	-	-	63,24	130,36	35,52	14226	10649	118,79	28,59	1,34
5	1	98		94,57			143,93	33,32	92,44	139,00	139,81	29,74	-	-	-	94,57	141,86	31,53	17860	10087	98,47	23,97	1,77
6	2	93	103	41,89	95,81		178,08	55,26	122,31	159,69	163,75	50,77	-	-	-	137,70	170,76	53,02	27776	15332	98,00	31,84	1,81
7	3	93	112	36,09	66,46	87,88	142,14	37,27	109,24	143,49	146,06	43,72	-	-	-	190,43	144,09	40,50	21785	12305	102,50	29,35	1,77
8	4	95	116	65,46	69,48	119,41	112,77	26,08	102,11	121,30	120,21	33,82	-	-	-	254,35	116,43	29,95	14408	9723	105,50	27,23	1,48
9	5	91	103	33,16	73,63	107,87	139,04	44,30	113,21	119,78	122,04	30,68	-	-	-	214,66	130,26	30,68	14282	10645	97,00	25,23	1,34
Lamprocapnos spectabilis																							
1	1	113		72,74			154,55	35,05	88,70	137,32	155,57	37,50	-	-	-	72,74	155,06	36,28	22550	9562	113,13	25,08	2,36
2	1	124		104,40			189,51	46,48	112,05	175,70	176,78	52,18	-	-	-	104,40	183,03	49,33	32888	15454	124,32	28,33	2,13
3	4	94	122	73,77			146,49	51,32	126,68	120,27	119,44	38,19	-	-	-	73,77	132,28	44,76	18828	11960	108,05	34,09	1,57
4	4	104	146	65,88	53,40	91,58	127,64	18,86	111,45	139,91	120,49	23,61	-	-	-	210,86	124,01	21,24	13398	12240	124,79	18,91	1,09
5	4	105	114	75,76	75,44	110,44	122,86	32,44	127,21	143,20	122,82	29,82	-	-	-	261,64	122,84	31,13	14507	14300	109,33	26,88	1,01
6	6	90	163	55,95	70,84	127,87	174,84	49,49	131,37	152,74	173,61	52,38	-	-	-	254,66	174,22	50,94	30709	15751	126,59	30,32	1,95
7	7	119	94	77,72	139,95	115,81	185,19	39,45	133,62	167,59	170,14	32,67	-	-	-	333,48	177,51	32,67	27840	17579	106,14	20,21	1,58
8	8	109	94	82,50	138,62	138,62	118,42	33,33	123,69	125,52	131,63	42,96	-	-	-	359,74	124,85	38,15	16050	12188	101,74	31,43	1,32
9	8	97	111	89,05	85,03	142,62	126,68	40,24	120,72	113,43	133,38	44,72	-	-	30,60	347,30	129,99	42,48	17901	10749	103,79	33,18	1,67
10	9	98	110	80,42	130,12	130,91	124,56	37,28	108,48	99,24	116,67	29,82	-	-	30,18	371,63	120,55	33,55	14432	8451	103,71	29,11	1,71
11	10	136	73	144,60	126,22	165,87	136,08	26,73	127,09	136,28	117,36	50,69	13,19	74,49	202,61	726,98	126,37	38,71	16461	13596	72,74	31,50	1,21
12	10	102	139	59,66	108,80	153,28	117,98	33,64	126,83	121,15	124,56	41,23	-	-	29,82	351,56	121,23	37,44	15198	12062	120,57	31,71	1,26
13	11	121	111	66,44	101,09	152,11	138,61	36,40	120,75	127,09	128,95	43,86	-	21,93	45,61	387,18	133,69	43,86	18969	12047	115,81	33,28	1,57
14	13	115	102	98,26	165,98	157,87	106,26	30,56	169,47	138,89	114,06	27,05	-	-	134,97	557,08	110,09	28,81	11777	18477	108,26	27,63	0,64

A. Measurements and calculations in species with convex inflorescence meristems (cont.)

IND	LP	MEASUREMENTS														CALCULATIONS							
		Top view					Frontal view				Lateral view												
		α_1 (°)	α_2 (°)	l_1 (µm)	l_2 (µm)	l_3 (µm)	w_f (µm)	h_f (µm)	ph (µm)	pw (µm)	w_l (µm)	h_l (µm)	h_1 (µm)	h_2 (µm)	h_3 (µm)	BL (µm)	W (µm)	H (µm)	MS (µm^2)	YPA (µm^2)	LA (°)	ME (°)	AR
Agrimonia eupatoria																							
1	35	30	38	42,11	56,04	49,20	328,95	108,77	91,18	113,32	294,74	86,84	-	-	-	147,35	311,38	97,81	100982	8111	34,00	32,14	12,45
2	83	43	33	52,81	49,51	50,92	305,39	78,04	110,33	117,07	282,12	74,43	-	-	-	153,24	293,52	76,24	83507	10139	38,00	27,45	8,24
3	53	40	48	56,26	52,99	49,95	270,29	64,89	93,91	111,43	256,26	57,86	-	-	-	159,20	263,18	61,38	64902	8215	44,00	25,01	7,90
4	42	53	63	45,75	54,60	60,42	231,58	67,54	104,83	112,40	272,07	77,13	-	-	-	160,77	251,01	72,34	63391	9250	58,00	29,96	6,85
5	29	42	52	51,78	49,19	61,93	242,98	81,58	92,11	104,48	242,18	78,92	-	-	-	162,90	242,58	80,25	62682	7555	47,00	33,50	8,30
6	73	52	42	55,96	52,63	68,44	276,32	84,21	121,10	102,77	249,94	86,56	-	-	-	177,03	262,80	85,39	72983	9770	47,00	33,02	7,47
7	96	52	55	54,62	52,24	71,36	190,35	72,81	117,81	121,93	216,67	80,70	-	-	-	178,22	203,08	76,76	46812	11276	53,50	37,09	4,15
8	70	25	34	57,29	68,33	66,67	333,41	78,93	87,83	100,06	305,28	79,82	-	-	-	192,29	319,04	79,38	97275	6899	29,50	26,46	14,10
9	111	51	60	56,39	68,17	67,86	271,33	65,71	152,69	113,61	192,11	57,02	-	-	-	192,42	228,31	61,37	51121	13617	55,50	28,27	3,75
10	78	68	72	54,96	57,93	83,86	199,12	74,56	106,23	121,94	208,77	75,44	-	-	-	196,75	203,89	75,00	46546	10169	70,00	36,35	4,58
11	138	59	52	69,51	58,00	72,70	192,11	72,81	117,60	137,74	245,61	68,42	-	-	-	200,21	217,22	70,62	49874	12716	55,50	33,04	3,92
12	120	70	81	61,21	61,56	78,31	175,44	57,02	100,03	120,18	179,82	60,53	-	-	-	201,08	177,62	58,78	33609	9437	75,50	33,50	3,56
13	*	66	67	64,52	56,69	80,80	219,30	84,21	103,60	114,92	200,88	76,30	-	-	-	202,01	209,89	80,26	50299	9346	66,50	37,41	5,38
14	*	56	66	58,83	79,59	73,44	200,00	72,81	114,37	118,43	260,56	102,62	-	-	-	211,86	228,28	87,72	59651	10633	61,00	37,55	5,61
15	79	36	35	70,14	73,44	80,20	331,58	133,33	113,17	128,96	340,51	112,24	-	-	-	223,78	336,02	122,79	126008	11457	35,50	36,17	11,00
16	64	74	102	60,04	72,26	82,01	150,07	54,27	101,35	121,63	162,32	71,03	-	-	14,03	228,34	156,07	62,65	28532	9677	88,00	38,77	2,95
17	*	92	106	57,42	59,51	64,61	135,53	37,28	74,25	90,90	108,77	38,60	-	31,58	21,93	235,05	121,41	37,94	15320	5298	99,42	32,01	2,89
18	96	97	136	60,79	74,81	83,52	160,53	55,26	84,37	123,06	125,00	49,31	-	-	18,64	237,76	141,66	52,29	22506	8150	116,50	36,44	2,76
19	*	61	58	76,63	80,76	100,25	238,60	107,89	135,10	133,34	257,02	123,68	-	-	-	257,64	247,64	115,79	78372	14141	59,50	43,09	5,54
20	117	77	85	67,75	76,36	95,15	178,07	76,32	91,23	117,66	173,69	77,19	-	-	20,00	259,26	175,87	76,76	37951	8426	81,00	41,12	4,50
21	70	90	106	58,56	86,22	89,48	155,30	53,50	103,51	125,67	138,64	56,12	-	-	31,58	265,84	146,73	54,81	24293	10211	98,00	36,77	2,38
22	*	88	105	65,81	65,75	75,18	170,14	47,22	68,76	113,90	126,32	64,91	28,95	75,44	100,00	411,13	146,60	56,07	24541	6148	96,43	37,42	3,99
Neviusia alabamensis																							
1	1	85		31,80			89,05	36,39	47,50	66,67	92,11	31,58	-	-	-	31,80	90,57	33,99	9185	2486	85,00	36,89	3,69
2	2	88	108	30,95	46,32		87,28	46,05	62,76	85,97	99,51	48,91	-	-	-	77,27	93,19	47,48	13051	4235	98,24	45,55	3,08
3	3	98	130	27,97	36,18	13,51	79,39	28,07	69,57	86,84	89,96	35,07	-	-	-	77,66	84,51	31,57	9333	4743	114,00	36,77	1,97
4	3	76	127	27,54	32,75	37,32	100,00	29,82	43,44	67,11	105,45	39,11	-	-	-	97,61	102,69	34,47	12502	2288	101,12	33,88	5,46

A. Measurements and calculations in species with convex inflorescence meristems (cont.)

IND	LP	MEASUREMENTS														CALCULATIONS							
		Top view					Frontal view				Lateral view												
		α_1 (°)	α_2 (°)	l_1 (µm)	l_2 (µm)	l_3 (µm)	w_f (µm)	h_f (µm)	ph (µm)	pw (µm)	w_l (µm)	h_l (µm)	h_1 (µm)	h_2 (µm)	h_3 (µm)	BL(µm)	W(µm)	H(µm)	MS (μm^2)	YPA (μm^2)	LA (°)	ME (°)	AR
5	3	88	123	27,97	35,11	39,93	83,33	35,96	45,28	54,83	85,54	22,80	-	-	-	103,01	84,43	29,38	7155	1949	105,50	34,84	3,67
Sanguisorba minor																							
1	23	20	25	30,72	26,69	28,15	378,95	124,56	100,38	82,75	356,87	132,05	-	-	-	85,56	367,74	128,31	147606	6521	22,50	34,91	22,64
2	31	32	45	29,80	38,13	30,45	220,18	72,80	82,26	79,84	216,71	71,92	-	-	-	98,38	218,44	72,36	50856	5156	38,50	33,53	9,86
3	40	31	56	24,81	31,15	44,15	158,86	49,11	65,88	62,28	178,47	54,17	-	-	-	100,11	168,38	51,64	29237	3221	43,50	31,53	9,08
4	8	45	50	44,05	26,39	34,93	260,62	92,95	101,26	97,47	268,07	93,04	-	-	-	105,37	264,32	93,00	76557	7748	47,50	35,14	9,88
5	28	35	45	30,00	30,40	52,46	209,65	72,81	102,60	87,88	194,74	57,89	-	-	-	112,86	202,06	65,35	43058	7078	40,00	32,90	6,08
6	20	33	39	38,60	42,25	41,82	279,83	89,47	81,58	72,57	252,88	85,77	-	-	-	122,67	266,01	87,62	75231	4647	36,00	33,38	16,19
7	46	43	48	46,23	38,84	49,04	279,83	78,95	92,17	92,11	225,48	41,22	-	-	-	134,11	251,19	60,09	59570	6664	45,50	25,57	8,94
8	24	45	43	42,25	49,25	45,28	236,84	60,53	97,37	115,82	266,70	75,42	-	-	-	136,78	251,33	67,98	62085	8853	44,00	28,42	7,01
9	47	57	77	58,40	67,95	83,02	152,63	26,32	86,95	105,28	161,86	38,60	-	-	-	209,37	157,18	32,46	22405	7186	67,00	22,45	3,12
10	52	64	65	70,75	88,07	89,29	178,09	31,58	77,76	125,45	131,58	26,75	-	-	-	248,11	153,08	29,17	20858	7658	64,50	20,86	2,72
Spiraea japonica																							
1	7	91	118	64,47	79,53	94,40	109,21	29,39	64,92	94,88	88,60	25,44	-	27,08	47,44	312,92	98,37	27,42	9614	4835	104,57	29,14	1,99
2	8	88	97	45,59	78,85	88,32	92,54	24,56	59,22	78,38	84,65	21,05	-	25,34	56,61	294,71	88,51	22,81	7572	3644	92,41	27,27	2,08
3	8	98	124	55,47	85,74	106,75	96,05	23,68	68,00	82,02	99,12	31,14	-	34,62	50,10	332,68	97,57	27,41	9487	4378	111,04	29,33	2,17
4	8	92	105	67,41	89,08	97,02	99,56	24,56	72,02	89,47	95,18	27,19	-	39,06	60,90	353,47	97,35	25,88	9258	5058	98,63	28,00	1,83
5	9	102	127	65,20	80,63	103,42	92,98	28,07	66,76	80,72	87,28	28,07	-	42,11	80,64	372,00	90,08	28,07	8424	4230	114,62	31,94	1,99
6	11	79	121	48,98	64,11	103,78	93,86	30,26	60,57	75,00	98,28	29,82	-	-	38,66	255,53	96,04	30,04	9591	3566	100,39	32,03	2,69
7	11	69	103	47,15	66,06	102,32	94,74	26,32	56,66	69,74	103,51	32,89	-	-	49,38	264,91	99,03	29,61	10009	3102	85,75	30,88	3,23
8	11	109	103	50,88	68,25	97,47	84,22	20,18	59,24	75,44	70,18	24,12	-	-	50,03	266,63	76,88	22,15	5946	3508	105,55	29,96	1,69
9	12	110	100	34,39	69,23	92,11	62,29	20,17	50,05	59,24	67,20	25,85	-	30,40	33,82	259,95	64,70	23,01	4611	2327	105,28	35,43	1,98
10	12	114	89	68,48	77,38	96,63	68,87	17,11	44,76	55,73	70,18	14,47	-	11,40	30,65	284,54	69,52	15,79	4495	1958	114,25	24,43	2,30
11	12	81	143	62,78	65,18	98,52	100,88	22,37	60,60	80,72	91,24	26,31	-	15,97	56,00	298,45	95,94	24,34	8852	3840	111,99	26,91	2,31
12	12	98	111	55,27	82,61	134,44	52,64	10,52	79,34	68,91	47,38	8,77	36,05	48,77	64,82	421,96	49,94	9,65	2227	4292	104,15	21,12	0,52
Spiraea chamaedryfolia																							
1	12	65	61	23,46	18,51	20,91	112,72	44,74	59,75	75,00	136,21	36,22	-	-	-	62,88	123,91	40,48	16264	3518	63,00	32,01	4,62
2	32	54	56	28,29	32,79	22,43	124,13	25,87	55,31	86,85	151,38	30,69	-	-	-	83,51	137,08	28,28	17037	3771	55,00	21,45	4,52

A. Measurements and calculations in species with convex inflorescence meristems (cont.)

IND	LP	MEASUREMENTS														CALCULATIONS							
		Top view					Frontal view				Lateral view												
		α_1 (°)	α_2 (°)	l_1 (µm)	l_2 (µm)	l_3 (µm)	w_f (µm)	h_f (µm)	ph (µm)	pw (µm)	w_l (µm)	h_l (µm)	h_1 (µm)	h_2 (µm)	h_3 (µm)	BL(µm)	W(µm)	H(µm)	MS (μm^2)	YPA (μm^2)	LA (°)	ME (°)	AR
3	20	47	56	27,23	21,65	22,76	166,68	38,16	50,02	70,92	155,95	34,15	-	-	-	71,64	161,23	36,16	24087	2785	51,50	23,47	8,65
4	12	97	103	23,79	18,76	23,16	198,26	53,50	52,89	82,25	166,03	48,46	-	-	-	65,71	181,43	50,98	32805	3415	100,00	28,85	9,61
5	44	70	77	23,94	30,05	24,95	108,48	28,12	54,24	69,28	95,61	22,37	-	-	-	78,94	101,84	25,25	9901	2950	73,50	25,36	3,36
6	39	62	64	26,37	30,12	26,41	159,70	41,65	53,73	88,52	138,06	35,01	-	-	-	82,90	148,49	38,33	21326	3734	63,00	26,52	5,71
7	33	68	78	31,01	35,10	32,60	99,12	23,68	45,43	71,06	93,07	21,03	-	-	-	98,71	96,05	22,36	8639	2534	73,00	24,89	3,41
8	25	71	84	32,26	41,30	33,57	125,00	35,96	57,19	85,10	87,76	21,04	-	-	-	107,13	104,74	28,50	10806	3820	77,50	26,78	2,83
9	48	63	84	29,48	35,10	35,36	114,91	27,19	49,17	76,35	98,69	23,25	-	-	-	99,94	106,49	25,22	10675	2947	73,50	25,02	3,62
10	44	87	104	37,45	35,89	38,62	101,32	16,23	45,28	60,97	58,33	5,70	-	-	-	111,96	76,88	10,97	5000	2167	95,50	14,18	2,31
11	24	81	80	39,31	36,05	40,17	117,54	26,75	55,12	72,58	94,31	23,24	-	-	-	115,53	105,29	25,00	10442	3140	80,50	24,60	3,32
12	44	89	89	50,82	30,95	41,34	69,30		65,40	71,05	61,49	7,92	-	-	-	123,11	65,28	7,92	3536	3648	89,16		0,97
13	16	85	95	31,14	34,18	51,19	89,47	17,54	63,63	73,26	102,65	28,07	-	-	-	116,51	95,83	22,81	8657	3659	90,00	24,12	2,37
14	32	93	105	54,63	53,24	55,62	57,90	8,77	59,65	82,65	76,74	12,84	-	-	-	163,49	66,66	10,81	3833	3870	99,00	19,90	0,99
Campanula thyrsoides																							
1	**	50	48	52,81	60,32	57,13	261,44	21,93	72,12	157,03	225,44	18,42	-	-	-	170,26	242,77	20,18	40956	8890	49,00	9,44	4,61
2	**	72	57	51,78	54,05	66,87	264,91	21,93	61,43	162,37	257,20	29,80	-	-	-	172,70	261,03	25,87	54642	7830	64,50	11,21	6,98
3	**	46	42	55,92	54,67	66,46	298,25	31,58	60,55	150,90	319,36	36,84	-	-	-	177,05	308,62	34,21	84211	7173	44,00	12,50	11,74
4	**	47	35	61,93	51,95	65,20	200,88	20,18	64,76	143,48	309,18	36,10	-	-	-	179,08	249,21	28,14	79019	7294	41,00	12,73	10,83
5	**	58	58	64,06	61,93	55,27	305,26	12,28	61,76	146,75	189,49	3,51	-	-	-	181,26	240,51	7,90	28234	7115	58,00	3,76	3,97
6	53	67	73	61,93	57,63	63,31	239,50	19,30	64,04	153,55	236,88	14,03	-	-	-	182,87	238,19	16,67	44675	7719	70,00	7,97	5,79
7	**	43	50	67,19	71,67	64,91	305,26	12,28	64,34	170,62	333,39	16,66	-	-	-	203,77	319,02	14,47	88146	8617	46,50	5,18	10,23
8	**	49	55	76,17	61,10	68,43	257,05	31,57	72,94	141,27	308,92	40,33	-	-	-	205,70	281,79	35,95	79835	8089	52,00	14,32	9,87
9	**	56	63	69,14	70,20	71,24	318,42	33,33	43,06	215,09	279,82	23,68	-	-	-	210,58	298,50	28,51	63213	7270	59,50	10,81	8,69
10	**	49	51	73,69	66,20	71,70	268,44	28,07	127,22	180,81	210,67	13,15	-	-	-	211,59	237,81	20,61	35388	18057	50,00	9,84	1,96
11	**	63	67	63,65	73,31	77,54	263,16	21,93	67,55	158,19	240,35	16,67	-	-	-	214,50	251,50	19,30	46224	8388	65,00	8,73	5,51
12	**	70	78	57,12	79,67	68,23	258,91	11,88	59,90	141,14	204,39	4,39	-	37,72	21,93	264,67	230,04	8,14	32864	6637	74,00	4,05	4,95
13	62	56	55	80,53	86,50	95,79	259,66	21,05	75,44	155,30	255,28	24,56	-	-	8,77	271,59	257,46	22,81	53023	9197	55,50	10,05	5,77
14	86	71	58	114,04	110,54	99,77	274,58	13,16	120,19	164,04	243,02	24,56	-	23,68	31,79	377,82	258,32	18,86	48222	15477	64,50	8,31	3,12
15	72	50	58	114,62	111,93	112,46	263,21	22,80	94,12	168,48	262,28	3,51	26,32	31,80	51,60	448,73	262,74	13,16	54057	12448	54,00	5,72	4,34

A. Measurements and calculations in species with convex inflorescence meristems (cont.)

IND	LP	MEASUREMENTS														CALCULATIONS							
		Top view					Frontal view				Lateral view												
		α_1 (°)	α_2 (°)	l_1 (µm)	l_2 (µm)	l_3 (µm)	w_f (µm)	h_f (µm)	ph (µm)	pw (µm)	w_l (µm)	h_l (µm)	h_1 (µm)	h_2 (µm)	h_3 (µm)	$BL_{(\mu m)}$	$W_{(\mu m)}$	$H_{(\mu m)}$	MS (μm^2)	YPA (μm^2)	LA (°)	ME (°)	AR
16	*	76	88	125,08	135,25	145,83	249,16	25,43	114,94	153,52	158,33	14,58	-	34,74	67,07	507,97	198,62	20,01	20338	13852	82,00	11,39	1,47
Phyteuma orbiculare																							
1	32	30	30	43,86	64,65	72,20	197,92	15,97	74,51	75,21	240,35	25,44	-	-	-	180,71	218,11	20,71	38670	4399	30,00	10,75	8,79
2	9	47	41	60,19	60,73	64,70	204,86	27,78	79,97	92,87	186,81	22,22	-	-	-	185,62	195,63	25,00	31936	5830	44,00	14,34	5,48
3	48	47	54	59,33	60,98	66,85	154,39	10,53	53,19	92,11	142,11	11,84	-	-	-	187,16	148,12	11,19	17616	3846	50,50	8,59	4,58
4	28	44	40	63,99	69,16	65,37	207,89	32,46	64,04	79,84	185,09	24,56	-	-	-	198,52	196,16	28,51	32640	4014	42,00	16,21	8,13
5	47	39	40	66,17	64,94	68,23	172,89	13,15	59,71	76,64	186,84	17,54	-	-	-	199,34	179,73	15,35	26092	3592	39,50	9,69	7,26
6	36	47	44	64,66	68,39	72,99	183,81	22,80	82,46	85,09	185,42	21,53	-	-	-	206,04	184,61	22,17	28251	5508	45,50	13,50	5,13
7	44	41	46	74,34	69,79	82,79	128,26	13,85	60,40	67,83	154,96	14,85	-	-	-	226,92	140,98	14,35	16237	3216	43,50	11,51	5,05
8	30	63	44	61,76	85,88	80,94	99,81	11,81	75,64	96,40	138,12	9,41	-	-	-	228,58	117,41	10,61	11172	5724	53,50	10,25	1,95
9	30	62	58	89,33	83,83	96,89	107,45	13,36	63,64	82,68	120,83	12,37	-	-	13,36	283,41	113,94	12,87	10698	4130	60,00	12,73	2,59
10	31	53	71	81,45	95,37	100,42	101,09	7,44	67,54	86,08	109,50	12,36	12,36	-	18,32	307,92	105,21	9,90	8993	4564	62,00	10,66	1,97
11	40	65	83	97,57	96,96	91,24	102,25	5,26	71,83	90,90	85,15	5,94	30,20	27,92	22,89	366,78	93,31	5,60	6934	5126	74,00	6,85	1,35

* Material damaged.

** Lack of differentiation in lateral primordia made any counting difficult.

B. Measurements and calculations in species with flat inflorescence meristems.

IND	LP	MEASUREMENTS												CALCULATIONS							
		Top view																			
		α_1 (°)	α_2 (°)	l_1 (µm)	l_2 (µm)	l_3 (µm)	ph (µm)	pw (µm)	w_l (µm)	w_f (µm)	h_1 (µm)	h_2 (µm)	h_3 (µm)	BL (µm)	W (µm)	H (µm)	MS (µm²)	YPA (µm²)	LA (°)	ME (°)	AR
Edraianthus tenuifolius																					
1	4	77	57	134,37	149,49	145,96	127,12	176,14	213,32	181,64	-	-	-	429,82	196,84	-	30417	17577	67,00	-	1,73
2	8	49	44	123,71	159,84	165,95	126,18	106,11	169,52	117,73	-	-	-	449,50	141,27	-	15667	10510	46,50	-	1,49
3	8	51	55	123,73	163,87	174,66	126,43	100,97	156,14	146,49	-	-	-	462,26	151,24	-	17955	10021	53,00	-	1,79
4	8	64	51	141,05	152,29	187,13	141,05	127,95	216,57	186,32	-	-	-	480,47	200,88	-	31676	14167	57,29	-	2,24
5	9	59	56	119,12	158,34	167,48	120,97	59,47	171,26	152,64	-	-	-	444,94	161,68	-	20521	5647	57,13	-	3,63
6	9	67	57	116,86	128,54	158,23	116,86	105,09	210,77	194,43	-	-	-	403,63	202,44	-	32169	9640	61,75	-	3,34
7	11	46	57	79,26	96,89	159,66	79,26	90,86	197,44	186,68	-	-	-	335,81	191,98	-	28934	5653	51,58	-	5,12
Lobelia cardinalis																					
1	73	22	32	88,30	81,78	92,10	84,23	96,51	538,40	367,14	-	-	-	262,18	444,60	-	155170	6381	27,00	-	24,32
2	>120	12	10	85,67	91,05	96,86	85,67	68,05	747,82	646,15	-	-	-	273,58	695,13	-	379315	4576	10,85	-	82,88
3	>120	12	11	98,88	81,17	94,18	98,88	69,33	828,83	696,04	-	-	-	274,23	759,54	-	452866	5381	11,20	-	84,15
4	77	19	18	100,37	93,45	98,80	98,17	114,16	578,75	492,47	-	-	-	292,62	533,87	-	223738	8798	18,50	-	25,43
5	100	13	15	96,27	104,55	104,37	109,93	72,00	678,19	609,29	-	-	-	305,19	642,82	-	324373	6213	14,00	-	52,21
6	>120	19	15	90,08	107,56	108,89	90,08	109,32	799,79	693,74	-	-	-	306,53	744,88	-	435554	7730	17,06	-	56,34
7	117	13	13	107,73	106,50	107,30	106,16	83,88	796,01	655,88	-	-	-	321,53	722,56	-	409838	6990	13,00	-	58,63
8	22	21	20	115,84	107,12	103,33	100,31	127,46	536,22	484,17	-	-	-	326,29	509,53	-	203803	10037	20,50	-	20,31

5 GENERAL CONCLUSIONS

From the beginning of modern inflorescence research, the terminal flower (TF) on inflorescences has received particular attention, starting with its use as a morphological classification criterion up to the study of its genetic regulation pathways.

The present work shows that the TF arises from an inflorescence meristem (IM) that possesses a syndrome of geometrical characteristics. It includes both the relative sizes and given shapes. In small closed inflorescences, the adoption of this syndrome occurs almost directly during the transition from the vegetative to the reproductive state, while in larger ones, the IM is initially enlarged to relatively bigger dimensions that are gradually reduced throughout the ontogeny until the syndrome is acquired at the end. These observations allow the conclusions i) that the space from which the TF differentiates is already present at the beginning of the ontogeny and not originated *de novo* by the induction of the TF, and ii) that space availability on the IM is a prerequisite for the TF production.

In contrast, open inflorescences exhibit at the end of the ontogeny an IM that is smaller than the ones documented for closed inflorescences. This brings out the incapacity of the IM of open inflorescences to differentiate a TF. Our empirical evidence allows classifying open inflorescences in two groups, depending on the time at which the IM exhibits its smaller size. 'Open I' inflorescences show a relative lower size from the beginning of their ontogeny, while the 'open II' inflorescences suffer a reduction of their meristematic dimensions after flower segregation.

The failure of the TF in an open inflorescence is thus presumably related to two different structural causes or constraints. Following the known molecular and histological research on IM development, it arises as possible that the 'open I' IMs posses physiological characteristics incompatible with the formation of a TF. It is probable that these IMs posses a 'central zone' (CZ) histology with the action of IM identity genes repressing the floral identity genes on the tip of the meristematic cone. This view is confirmed by the fact that these inflorescence buds show a conspicuous meristematic rest at the end of the ontogeny that could represent the area of the CZ.

In 'open II' inflorescences, the space necessary for TF formation is already present in the beginning of the ontogeny. It is based on the marked initial enlargement of these IMs during the transition from the vegetative to the reproductive state. However, in the course of lateral primordia segregation the IM gets smaller and smaller in both horizontal and vertical

planes. This dynamics results in an IM bulge that is smaller than the one observed in closed inflorescences. 'Open II' inflorescences suffer from spatial constraints inhibiting the formation of the TF.

The absence of a TF in *Daucus carota* umbellets whose IM size is below a critical value corroborates the assumption that scarcity of space impedes TF differentiation. This inference can be empirically tested by inducing physical modifications on typical closed IMs attempting to produce an experimental suppression of TF-formation.

The small final size of the IMs in 'open II' inflorescences is caused by the decaying dynamic of the IMs. This is the main difference compared to closed inflorescences. Closed inflorescences show stable vertical dimensions in their IMs throughout ontogeny, implying a permanent tissue renewal. In 'open II' inflorescences the production of meristematic tissue occurs preferentially in the beginning of the ontogeny. The marked initial enlargement observed in some 'open II' announces that these IMs will be used up in the ongoing ontogeny and fail in forming the TF.

Throughout the history of inflorescence morphology the use of the terminal flower as a classificatory criterion has maintained the implicit assumption that open inflorescences such as racemes, spikes, spadices, heads and umbels are members of the same basic structure (Roeper 1836, Troll 1964, Stebbins 1974, Weberling 1992, Prenner et al. 2009). This has founded the expectation that the evolutionary 'loss' (i.e. 'truncation') of the terminal flower in inflorescences could be explained by one common mechanism (Coen and Nugent 1994, Prusinkiewicz et al. 2007). However, the diversity of open inflorescences disclosed in this work indicates that the assumed truncation may not be explained solely by one ontogenetic shift in the different plant lineages. More precisely this means that the appearance and disappearance of the TF could be explained in some taxa by shifts in the histological composition/molecular regulation of the IM, and in other taxa, by shifts on IM size regulation. Thus, research on the genetic control of the TF could be complemented by focusing on the regulative pathway affecting IM size and segregation dynamics.

Our work shows that comparative ontogenetic studies allow testing identity-assumptions of the phenotype of organisms. This is particularly relevant in the plant kingdom, where the parallelism of forms is widespread. Correspondence in the ontogeny of similar phenotypes that have evolved independently could reflect the restricted developmental possibilities that arise in nature. This knowledge is of principal importance for our understanding how the plant shapes arise and evolve.

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Hiermit versichere ich, dass ich die vorliegende Arbeit selbstständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.