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Papilionoid inflorescences revisited (Leguminosae-Papilionoideae)

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INTRODUCTION

The form and structure of floral arrangement along a common axis, which is widely referred to as the angiosperm inflorescence, is vital for the reproductive success of flowering plants. Different kinds of inflorescence result in spatiotemporal differences in the presentation of anthetic flowers and their receptive stigmas and/or fertile pollen to suitable pollen vectors (e.g. Wyatt, 1982; Friedman and Harder, 2004; Harder et al., 2004; Iwata et al., 2012). Inflorescence structure is also frequently used as an important systematic character (cf. Briggs and Johnson, 1979; Classen-Bockhoff, 2000; Vrijdaghs et al., 2005).

According to Weberling (1989), the basic branching pattern in legume inflorescences is racemose (Fig. 1A–C), but systems with cymose branching do occur (e.g. Tucker, 1998). Racemes are common in Papilionoideae, which is the largest subfamily of Leguminosae. Among the best known papilionoid examples are cultivated ornamentals such as common laburnum (Laburnum anagyroides), Wisteria spp., black locust (Robinia pseudacacia), lupins (Lupinus spp.; also important crop plants), and the pagoda tree (Styphnolobium japonicum), which flowers late in the year with highly branched multiple racemes. However besides the ‘simple’ raceme there are special cases such as the dorsiventral partial inflorescences in Vicieae, some Trifolieae, Galegae (Naghiloo et al., 2012) and Loteae (Fig. 1D–F; cf. Sokoloff et al., 2007).

Inflorescences with strong reduction tendencies and pseudoracemes are other peculiarities on which the present study focuses. The pseudoraceme was highlighted as a special type of inflorescence in papilionoid legumes (Lackey, 1981; Tucker, 1987a, b, 2003, 2006). Tucker (2003, p. 920) mentioned that ‘pseudoracemes differ from racemes in that two to several flowers are initiated in each bract axil rather than just one as in a raceme’ (see also Tucker, 1987a). This study deals with the following questions. (1) Does distichous phyllotaxis have an impact on inflorescence morphology and symmetry in Swainsona formosa (Galegeae)? (2) How can the unifloral inflorescences in Cicer arietinum (Ciceraceae) be interpreted and is there any evidence for reduction? (3) What is the exact pattern of flower formation in partial inflorescences of Abrus precatorius (Abbreae) and how can this be related to ‘pseudoracemes’ of Hardenbergia violacea and Kennedia nigricans (both Phaseoleae-Kennediae)? (4) Is the papilionoid pseudoraceme just a compound raceme with reduced lateral partial inflorescences?

MATERIALS AND METHODS

Material

Scanning electron microscopy (SEM) micrographs are shown for Abrus precatorius L.: Teppner s.n., cult. Austria, Botanic

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Garden Graz (BGG), Institute of Plant Sciences, Karl-Franzens-University Graz; Adenocarpus decorticans Boiss.: Prenner 783, UK, cult. Royal Botanic Gardens, Kew (K 1995-2238); Cicer arietinum L.: Prenner 443, cult. BGG; Dorycnium germanicum Rouy: Prenner 288, cult. BGG; Ebenus cretica L.: Prenner 440, Greece, Crete, Psiloritis; Hardenbergia violacea (Schneev.) Stearn: Prenner 658, cult. BGG; Kennedia nigricans Lindl.: Prenner 491, cult. BGG; Lotus berthelotii × maculatus Breitfeld: Prenner 404, cult. BGG; Lotus corniculatus L.: Prenner 445, Austria, Graz, Schubertstrasse 21; and Swainsona formos (G.Don) J.Thomson, Prenner 784, Australia, New South Wales, Calder Hwy, N of Mildura. Voucher specimens have been deposited in the herbarium of the Institute of Botany, Karl-Franzens-University Graz (GZU) and/or liquid preserved collections are held by the author. Specimens were determined by the author, except for A. precatorius which was determined by H. Teppner (Institute of Plant Sciences, Karl-Franzens-University Graz, Austria).

Methods

Material was collected and immediately fixed in FAA (90 parts 70 % ethanol, 5 parts 100 % acetic acid, 5 parts formalin) and stored in 70 % ethanol. The specimens were critical point dried in an Autosamdri-815B critical-point dryer at the Royal Botanic Gardens (RBG), Kew (UK) or in a Polaron 7010 CPD at the Institute of Plant Sciences, Karl-Franzens-University Graz (Austria). Dried material was mounted onto specimen stubs using clear nail polish and coated with platinum using an Emitech K550 sputter coater at RBG, Kew or coated with gold using an Agar sputter coater in Graz. SEM studies were made with a Hitachi cold field emission SEM S-4700-II at RBG, Kew or a Philips XL 30 ESEM at the Institute of Plant Science in Graz (Austria). Between two and ten inflorescences were studied from each examined species, and between 40 and 140 SEM images were analysed per species.

RESULTS

Swainsona formosa (Galegeae; Fig. 2A–G)

In S. formosa, racemose inflorescences are formed in a distichous phyllotaxis in the axil of frondose leaves, each with two large stipules at the base (Fig. 2A, B). The position of the subtending leaf changes at each node (pendulum symmetry; Fig. 2A–F). During the earliest developmental stages, the subtending leaf points towards one side of the subtended inflorescence meristem. Depending on the position of the subtending leaf, the inflorescence meristem shows a characteristic asymmetric shape and is broader either to its left or to its right side (Fig. 2C, E). Flower formation always starts in the position furthest away from the subtending leaf (Fig. 2B, C, F). Flowers are formed in an acropetal spiral, in either an anticlockwise (Fig. 2B) or a clockwise direction (Fig. 2C, G).
The inflorescence axis does not elongate significantly and the inflorescence stays flat and dense, resulting in a five- to eight-flowered umbel. The inflorescence is open and terminates with a prominent vegetative tip in its centre (Fig. 2G).

Cicer arietinum (Cicerae; Fig. 3A–D)

In *C. arietinum*, inflorescences are reduced to a single flower which is formed in the axil of a frondose leaf (Fig. 3A). The leaf which subtends the reduced inflorescence is pinnate and early forms two stipules at its base. The inflorescence meristem is positioned between the leaf and the stipule. Later in development, the inflorescence meristem forms a single floral primordium which is subtended by an abaxial bract and preceded by two bracteoles (Fig. 3A–C). When the flower is still at the primordial stage, a meristematic bulge becomes visible in the adaxial position opposite the subtending bract. This can be interpreted as the sterile ending of the reduced inflorescence (Fig. 3A, B, D). At maturity, this sterile ending is still visible as an approx. 1 mm long appendix opposite the bract (not shown).
Abrus precatorius (Abreae; Fig. 4A–F)

In *A. precatorius*, partial inflorescences are formed in acropetal direction along a common inflorescence axis (not shown). The axis of each partial inflorescence is nodose, and the inflorescence meristem (orange dot in Fig. 4A–F) is positioned off-centre, towards the main inflorescence axis (asterisk in Fig. 4A–E). Individual flowers are formed acropetally (Fig. 4A–E) and in a characteristic pendulum pattern, switching between right (blue arrows in Fig. 4F) and left (red arrows in Fig. 4F). Each flower is subtended by an abaxial bract and preceded by two bracteoles (Fig. 4C, E). Within each partial inflorescence, a complete ontogenetic series from fully developed flowers (e.g. flower number 1 in Fig. 4D) to floral primordia (e.g. 15 in Fig. 4C, E) can be found.

Hardenbergia violacea (Phaseoleae-Kennediinae; Fig. 5A–C)

In *H. violacea*, three-flowered partial inflorescences are formed in an acropetal spiral (Fig. 5D). Within each partial inflorescence, flowers are formed simultaneously (Fig. 5E) and their further development is also simultaneous (Fig. 5F). The meristem of the partial inflorescence is used up gradually in the course of flower formation. While there is a small residuum of the meristem visible in early ontogeny (Fig. 5E, F) there is no remnant left in later stages (not shown). Each flower is subtended by an abaxial bract and preceded by two bracteoles which stop growing early and deteriorate subsequently (i.e. initiated but reduced bracteoles; Fig. 5F).

Kennedia nigricans (Phaseoleae-Kennediinae; Fig. 5D–F)

In *K. nigricans*, two-flowered partial inflorescences are initiated in an acropetal spiral (Fig. 5D). Within each partial inflorescence, flowers are formed simultaneously (Fig. 5E) and their further development is also simultaneous (Fig. 5F). The meristem of the partial inflorescence is used up gradually in the course of flower formation. While there is a small residuum of the meristem visible in early ontogeny (Fig. 5E, F) there is no remnant left in later stages (not shown). Each flower is subtended by an abaxial bract and preceded by two bracteoles which stop growing early and deteriorate subsequently (i.e. initiated but reduced bracteoles; Fig. 5F).

DISCUSSION

Inflorescence ontogeny in *Swainsona formosa* shows a rare form of pendulum symmetry

The consecutively formed inflorescences in *Swainsona formosa* show a pronounced pendulum symmetry which

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**Fig. 3.** Inflorescence development in *Cicer arietinum* (SEM). (A) A reduced inflorescence is formed in the axil of a pinnate leaf (L) with basal stipules (Si). Flower (F) subtended by a bract (B) and preceded by bracteoles, of which only the left one is visible (arrow). In the adaxial position, the inflorescence meristem is found (IM). In the background, a second inflorescence meristem (IM’) associated with a young leaf (L’) can be seen. To the right of this complex, the shoot apical meristem (SAM) can be found. (B) Side view of (A). The bracteole of the first formed flower and the bract which subtends the flower are visible. Another undifferentiated inflorescence meristem is formed to the left in the axil of a leaf, with a stipule forming at its base. (C) Abaxial view of a flower primordium subtended by a bract. The flower (i.e. reduced inflorescence) sits between the subtending leaf and its stipule. (D) Young flower with the formation of the abaxial sepal immediately followed by the two lateral sepals (unidirectional sepal formation). The inflorescence meristem which does not produce any more flowers can be seen in the upper/adaxial position (arrow). Abbreviations: B, bract; Bl, bracteole; F, flower; IM, IM’, inflorescence meristem; L, L’, frondose leaf; s1, s2, sepals; Si, Si’, stipule. Scale bars=50 μm throughout.
FIG. 4. Inflorescence in *Abrus precatorius* (SEM). (A) Young partial inflorescences with initiation of three flowers (1–3) and three flower subtending bracts (4–6). No flowers or bracts are formed in an adaxial position (asterisk); inflorescence meristem is highlighted with an orange dot. (B) Partial inflorescence with nodose axis and acropetal formation of individual flowers (1–15). The partial inflorescence meristem (highlighted with an orange dot) is located off-centre close to the main inflorescence axis (asterisk). (C) Detail of (B). Complete numbering of flowers (4–10), flower primordia (11–15) and flower subtending bracts (16–21). Flowers and flower primordia are highlighted in red. No flowers are formed in an adaxial position (asterisk). (D) Partial inflorescence with a nodose axis and acropetal formation of individual flowers (1–18). The partial inflorescence meristem (highlighted with an orange dot) is located off-centre close to the main inflorescence axis (asterisk). (E) Detail of (D). Complete numbering of flowers (7–10), flower primordia (11–15) and flower subtending bracts (16–21). Flowers and flower primordia are highlighted in red. No flowers are formed in the adaxial position (asterisk); partial inflorescence meristem highlighted with an orange dot. (F) Same as (D). The pendulum direction of flower formation is highlighted with blue (to the right) and red (to the left) arrows. Scale bars: (A) = 100 μm; (C) = 200 μm; (E) = 300 μm; (B, D, F) = 500 μm.
seems to be influenced by the position of the subtending leaf. The following morphological characters can be determined in relation to the position of the subtending leaf: (1) the asymmetric shape of the early inflorescence meristem; (2) the position of the first formed flower, always furthest away from the subtending leaf; and (3) a switch between clockwise (with the subtending leaf pointing to the right) and anticlockwise (with the subtending leaf pointing to the left) formation of flowers in consecutive inflorescences (Fig. 6A).

The term Pendelsymmetrie, or pendulum symmetry, was coined by Goebel (1928) for left/right oscillation of symmetry in plants. Pendulum symmetry is more often studied and apparently more common in vegetative shoots (see Charlton, 1998). In Ulmus, distichous pendulum symmetry of the leaves was studied in detail by Charlton (1993, 1998), who found that leaf primordia are asymmetrical from their inception.

Pendulum symmetry is also found in flowers of Centranthus (Valerianaceae), where the chirality changes in a regular pattern in the monochasial partial inflorescence, or in flower pairs of Marantaceae (Kirchoff, 1983; Endress, 1999). In flowers of Oxalis (Oxalidaceae) and Malvaceae, the direction of petal contortion changes with every node in monochasial partial inflorescences (Endress, 1999, 2001). In Leguminosae,
The genus *Cicer* comprises 44 species which were recently reclassified by Davies et al. (2007). Its flowers are either solitary or organized in two- to five-flowered axillary racemes (van der Maesen, 1972). In *C. arietinum*, which has unifloral inflorescences, very early in ontogeny a sterile tip is evident on the adaxial side of the flower. This can be interpreted as a sterile opening of the open and unifloral inflorescence which is most probably derived via reduction from an ancestor with more than one flower per raceme (Fig. 6B–D). Note that Weberling (1989) treated unifloral units of *C. arietinum* as ‘coflorescences’ of a more complex ‘synflorescence’ (see also Weberling and Troll, 1998). However, this does not affect the above interpretation significantly.

Besides this, an abaxial bract and two bracteoles can be found at the base of the young flower. This observation is in contrast to those of Hutchinson (1964, p. 452) who quoted the absence of bracteoles in *Cicer*, and Tucker (1987a) who cited Cicereae as having bracteoles converted to spines. It seems more likely that the spines occurring in some species of *Cicer* are the sterile endings of reduced inflorescences, rather than converted bracteoles (cf. Wydler, 1860).

**A new interpretation of the papilionoid pseudoraceme**

The present study provides strong evidence that in partial inflorescences of *Abrus*, flower initiation follows a very consistent pendulum pattern. A single flower is formed per node and the inflorescence axis is strongly condensed to a nodose structure. All flowers are formed in a continuous ontogenetic series as found in ‘normal’ papilionoid racemes (cf. Fig. 1A–C) and no evidence was found for a temporary suppression of flowers as mentioned by Tucker (1987b). Therefore, the inflorescence of *Abrus* can be interpreted as a compound raceme (*sensu* Prenner et al., 2009) with condensed partial inflorescences (Fig. 7A, B). In the course of this condensation, the meristem of partial inflorescences was relocated towards the main inflorescence axis. The reason for this relocation might be an inhibitory field acting from the inflorescence...
which prevents flower formation on the adaxial side of the partial inflorescence. The relocation of the meristem might in turn disturb spiral flower formation; instead, flower formation oscillates in a pendulum pattern around the inflorescence axis. It is important to highlight that this pattern is not related to the pendulum symmetry of *Swainsona* because the direction of flower formation among individual partial inflorescences appears not to follow a fixed pattern, which would be expected for pendulum symmetry.

‘Pseudoracemes’ are found in Abraees (this study; Tucker, 1987b), Desmodieae (Prenner, 2004a), Millettieae (Teixeira et al., 2009), Psoraleeae and Phaseoleae (cf. Lackey, 1981; Tucker, 2006). The phylogenetic position of the tribe Abraees is rather isolated at the base of the ‘core Millettioids’ sensu Hu et al. (2000), and various elements which were excluded from Phaseoleae sensu lato (see also Wojciechowski et al., 2004; Lewis et al., 2005). Taking this into account, one scenario is that more reduced inflorescence types could have evolved from an inflorescence similar to that of *Abrus*. The three-flowered partial inflorescences of *H. violacea* may have evolved via a reduction of the number of flowers per partial inflorescence and a synchronization of the flower initiation within partial inflorescences (Fig. 7C, D). Moreover, the two-flowered partial inflorescences in *K. nigricans* can be derived from a *Hardenbergia*-like inflorescence via further reduction in flower number (Fig. 7D, E). Other types such as those found in *Apios*, *Vigna*, *Erithrina*, *Desmodium*, *Dioclea* and *Pongamia* (all depicted by Tucker 1987b, fig. 60, p. 200) can be deduced accordingly. However, the phylogenetic relationships among these taxa are not fully resolved and understood (see Wojciechowski et al., 2004; Lewis et al., 2005) and, therefore, it is not possible to draw final conclusions. Based on the available phylogenetic data, it seems most probable that a condensation of partial inflorescences took place independently several times. An alternative hypothesis for the evolution of compound racemes with condensed lateral inflorescences is via the reduction of ‘normal’ radially symmetric partial inflorescences. *Butea monosperma* could provide evidence for such a scenario. According to Tucker (1987b), in this species, a triad of flowers is formed first, subsequently followed by helical formation of flowers.

It is important to highlight that compound racemes are also sometimes referred to as ‘panicles’ (e.g. Lackey, 1981; Tucker, 1987b) which might be one of the reasons why the pseudoraceme was long considered as a special type of inflorescence. However, from recent attempts to clarify conflicting definitions, it is clear that the panicle is a special case and not to be confused with compound (double or triple) racemes (cf. Prenner et al., 2009; Endress, 2010). It is therefore timely to emphasize that in legumes we frequently find compound racemes (sensu fig. 1b in Prenner et al., 2009; fig. 3 in Endress, 2010), but there is currently no solid proof for the existence of true panicles in the group.

The situation found in *Abrus* demonstrates the need for careful (re-)investigation of flowers in groups or ‘fascicles’ across angiosperms. Flower fascicles can result either from the condensation of racemose systems as shown in the present study or via condensation of cymose systems. These two scenarios represent two significantly different evolutionary histories. The euphorb cyathium is a classic example of such a condensed cymose system (cf. Prenner and Rudall, 2007; Prenner et al., 2008; Horn et al., 2012).

**The role of bracts and bracteoles as key markers in inflorescence architecture**

Bracts and bracteoles are key markers of inflorescence architecture (Prenner et al., 2009). Therefore, it is important that these structures are characterized correctly by carefully investigating their (relative) position and presence or absence. In the present study, I have shown that bracts or pherophylls are also involved in the symmetry of inflorescences in *S. formosa*, and that in *C. arietinum* a sterile protrusion opposite the flower subtending bract represents the sterile ending of the inflorescence axis and therefore should not be confused with a bract.

As shown earlier (Prenner, 2004b), bracteoles may also be discernible only at the earliest developmental stages. They stop growing at a primordial stage and are considered to be lost or resorbed in the anthetic flower. According to Lackey (1981), bracteoles are missing in Phaseoleae subtribe Kennediniinae which includes the genera *Hardenbergia*, *Kennedia* and *Vandasina*. However, Prenner (2004b) found initiated but reduced bracteoles in *K. nigricans*, and further
evidence for this was shown in the present study. Initiated but reduced bracteoles are also found in Kennedia beckxiana F. Muell. and K. rubicunda Vent. (G. Prenner, unpubl. res.). Furthermore, the present study shows that bracteoles are also formed in *H. violacea* (Fig. 5C). This character was not mentioned by Tucker (2006) who labelled similar structures as pedicels (cf. fig. 2J in Tucker, 2006). It remains to be studied whether initiated but early resorbed bracteoles also occur in *Vandasina* and whether this character is a synapomorphy for the subtribe Kennediinae.

A plea for detailed ontogenetic studies and uniform usage of terminology

Detailed ontogenetic studies are vital for the evaluation of complex and/or highly reduced morphological structures such as found in some inflorescences. Such studies are also invaluable in the context of determining characters and character states and/or in the context of further homology assessments. To avoid misinterpretations and to obtain a conclusive result, it is particularly important to generate and compare as many developmental stages as possible. This can be achieved by collecting plant material over a longer period of time and/or by dissecting samples of various developmental stages from single collections.

Another important aspect is the uniform usage of terminology, and a major objective for the future should be to find a broad consensus on a widely accepted terminology of inflorescences (see recent attempts by Prenner et al., 2009; Endress 2010; Bull-Herenu and Classen-Bockhoff, 2011). This is especially critical at the interface of ‘classical’ plant morphology and more recent scientific fields such as developmental genetics or plant modelling where often different terms are used for the same structure, or the same terms are used for different structures, which are prone to create confusion.

Conclusions

It seems likely that in *S. formosa*, distichous phyllotaxis has an impact on the morphology and symmetry of inflorescences. It will be interesting to study other taxa with distichous phyllotaxis and to test the hypothesis that spatial constraints via developing inflorescences act on the morphology and symmetry of the SAM (and in this way induce pendulum symmetry). The results found in *C. arrietinum* lead on to the question of how often and where in the phylogeny of the genus inflorescences were reduced and if the ontogenetic pathways are the same within the genus. Clarification of the genetic background of this reduction could prove important for the cultivation of multiflowered taxa with a potential increased crop yield. The redefinition of the pseudoraceme as a compound raceme with condensed partial inflorescences is a good starting point for a re-investigation of the evolution of such inflorescences among papilionoid legumes. It is most probable that such reductions have taken place several times independently. The advantages or disadvantages of inflorescences with condensed lateral inflorescences await further investigation.

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LITERATURE CITED


