

## Pair-flowered cymes in the Lamiales: structure, distribution and origin

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- **Background and Aims** In the Lamiales, indeterminate thyrses (made up of axillary cymes) represent a significant inflorescence type. However, it has been largely overlooked that there occur two types of cymes: (1) ordinary cymes, and (2) 'pair-flowered cymes' (PFCs), with a flower pair (terminal and front flower) topping each cyme unit. PFCs are unique to the Lamiales and their distribution, origin and phylogeny are not well understood.
- **Methods** The Lamiales are screened as to the occurrence of PFCs, ordinary cymes and single flowers (constituting racemic inflorescences).
- **Key Results** PFCs are shown to exhibit a considerable morphological and developmental diversity and are documented to occur in four neighbouring taxa of Lamiales: Calceolariaceae, *Sanango*, Gesneriaceae and Plantaginaceae. They are omnipresent in the Calceolariaceae and almost so in the Gesneriaceae. In the Plantaginaceae, PFCs are restricted to the small sister tribes Russelieae and Cheloneae (while the large remainder has single flowers in the leaf/bract axils; ordinary cymes do not occur). Regarding the origin of PFCs, the inflorescences of the genus *Peltanthera* (unplaced as to family; sister to Calceolariaceae, *Sanango* and Gesneriaceae in most molecular phylogenies) support the idea that PFCs have originated from paniculate systems, with the front-flowers representing remnant flowers.
- **Conclusions** From the exclusive occurrence of PFCs in the Lamiales and the proximity of the respective taxa in molecular phylogenies it may be expected that PFCs have originated once, representing a synapomorphy for this group of taxa and fading out within the Plantaginaceae. However, molecular evidence is ambiguous. Depending on the position of *Peltanthera* (depending in turn on the kind and number of genes and taxa analysed) a single, a double (the most probable scenario) or a triple origin appears conceivable.

**Key words:** Inflorescence, thyrse, raceme, cyme, pair-flowered cyme, Lamiales, Calceolariaceae, Gesneriaceae, *Peltanthera*, Plantaginaceae, *Sanango*, Scrophulariaceae, Stilbaceae.

### INTRODUCTION

Some taxa of Lamiales exhibit a special and otherwise unknown type of axillary inflorescences: cymes with flower pairs terminating the cyme units instead of single flowers ('pair-flowered cymes', PFCs). Although already noted by Bravais and Bravais (1837) and Wydler (1851*a, b*), this type of cymes and the 'super-numerary' flowers within these cymes have been, and largely still are, either disregarded (e.g. in virtually all descriptions of *Penstemon* and other genera of Plantaginaceae) or thought to be of rare and/or accidental occurrence and/or have been morphologically misinterpreted.

About 40 years ago, the author directed attention to this special type of cymes and realized its wide distribution in the Gesneriaceae and occurrence in a few genera of Scrophulariaceae (*sensu lato, s.l.*) (Weber, 1972, 1973). Some special aspects, such as particular variations, ontogeny and origin, have been treated in later publications (Weber, 1975, 1978*b*, 1982, 1995). However, as these papers are partly written in German and/or access to some journals is difficult, little notice has been taken of them apart from a small circle of gesneriad specialists. In the meantime, the systematical peripherals have changed considerably: based on the results of molecular analyses, the definition of several families now included in the order Lamiales, particularly Scrophulariaceae, has changed dramatically (for a review

see Tank *et al.*, 2006). In addition, new taxa having PFCs have been detected by me, especially by recent investigation of Plantaginaceae.

The first part of this paper provides an overview of the principal structure, diversity, ontogeny and possible interpretations of the PFC, with a focus on Gesneriaceae. In the subsequent parts the families of Lamiales (in their current circumscription) are surveyed as to the occurrence of PFCs.

With regard to the phylogenetical origin of PFCs, only theoretical speculations have been offered so far. Weber (1973, 1982) hypothesized that the front-flowers within the PFCs are remnant flowers and the PFCs originated from paniculate systems. In the present paper, the inflorescences of *Peltanthera* are described and shown to represent a possibly ancestral type. The genus *Peltanthera* has not satisfactorily been assigned to a family thus far, but has been shown to be related in some way to Calceolariaceae and Gesneriaceae in recent molecular analyses.

Based on the morphological, taxonomic and phytogeographical patterns established, the relationships and phytogeographical origin of the relevant taxa, with a focus on Plantaginaceae, are presented.

The paper is written in a mixed style. In some parts it is a review, but in other parts presents new results. The relevant literature is discussed *ad hoc*. Documentation of some previously published data and the new findings (Plantaginaceae) is

essentially provided in the Supplementary Data (Tables S1–4 and Figs S1–29), which thus forms an integral part of the paper.

## MATERIAL AND METHODS

Analyses of inflorescences from various families of Lamiales have been carried out, based on the following. (1) Living material (plants in flower, in bud and/or in fruiting stage) cultivated at the Botanical Garden of the University of Vienna (HBV) and the Royal Botanic Garden Edinburgh, living plants of *Russelia equisetiformis* (cultivated) and *R. sarmentosa* (encountered in the field) studied in Costa Rica; fresh flowering material of *Peltanthera floribunda* collected in Costa Rica (San Pablo de Pamichal) and studied from pickled material. (2) Herbarium specimens from the herbaria W and WU (a list of representative specimens examined is given in Table S3). (3) Early illustrations in distinguished horticultural magazines such as *Curtis's Botanical Magazine* (1787 onwards), *Edwards's Botanical Register* (1815–1847) or van Houtte's *Flore de Serre* (van Houtte *et al.*, 1845–1888). (4) Photographs on the internet and kindly provided at high resolution by the relevant authors.

Throughout the text and in the supplementary figures the plant names are given without authorities. A list with complete names is given in Table S4.

## INTRODUCTORY NOTES ON THE INFLORESCENCES OF LAMIALES

In the Lamiales, as presently circumscribed (e.g. Olmstead *et al.*, 1993; Bremer *et al.*, 2002; Kadereit, 2004; APG III, 2009), there is considerable variation in inflorescence architecture. In all families of the 'core' Lamiales (*sensu* Olmstead, 2002; e.g. Lamiaceae, Acanthaceae, Bignoniaceae, Orobanchaceae) the inflorescences (= the whole terminal flower-bearing parts of the seasonal shoot system lack a terminal flower: they are 'indeterminate' ('open', 'indefinite'). In the synflorescence concept of Troll (1964) they belong to the 'polytelic' type and represent 'florescences'. The components of these inflorescences ('partial florescences' *sensu* Troll) are either cymes or single flowers. In the former case, the inflorescence can be referred to as an indeterminate thyrsus (thyrsus), and in the latter as an indeterminate raceme (botryum). The cymes and single flowers, respectively, emerge from the axils of subtending leaves and bracts. Depending on the nature of the subtending leaves (foliage leaves, bracts or transitional forms) the so-defined inflorescence can be denoted as frondose, bracteose or frondobracteose (Troll, 1964; Weberling, 1992), and is very different in its outward appearance. As can be seen (rarely) in the Lamiaceae and (more frequently) in the Acanthaceae and Bignoniaceae, thyrses and racemes co-occur in several families and even genera (e.g. *Salvia*). Thyrses and racemes – and thus cymes and single flowers, respectively – can be considered as closely related inflorescence forms, and changes from the former to the latter type, that is by reduction of the cyme to a single flower (= primary cyme unit), have probably occurred often in the evolution of Lamiales. As long as prophylls are present, the converse way is also a possibility.

In the 'basal' Lamiales inflorescence morphology is more varied. Here, we find both 'determinate' ('closed', 'definite',

Troll: 'monotelic') inflorescences, with a terminal flower topping the main inflorescence axis (e.g. Oleaceae, Tetrachondraceae), and 'indeterminate' inflorescences (Calceolariaceae, Gesneriaceae, Plantaginaceae, Scrophulariaceae, Stilbaceae) and the spectrum of forms is wider (a more detailed reference is made in the main body of the text). The presence of determinate inflorescences in the families preceding those with indeterminate inflorescences in all available molecular phylogenies indicates that indeterminate inflorescences have originated from determinate ones in this lineage.

Some families of the 'basal' Lamiales, with indeterminate and mainly thyrse inflorescences, exhibit a peculiarity that is not known from other families in the angiosperms: all units of the cymes seem to end in a flower pair ('PFC', Weber, 1973). Before turning to this special type of cyme in more detail, it seems appropriate to say a few words about the 'ordinary' cyme, its structural elements and its principal branching patterns.

A cyme is a branching system in which equally structured units (modules), each ending in a terminal flower, are concatenated in a sympodial manner. Branching, that is the production of consecutive units, is from the axils of the prophylls (bracteoles = bracts within the cyme). Owing to the essentially decussate leaf arrangement in the Lamiales, the two prophylls ( $\alpha$ ,  $\beta$ ) belong to a single node, stand opposite and no internode (mesopodium) is developed between them. The internode below the flower is the pedicel (epipodium), and the internode below the prophylls is the hypopodium. In the first (primary) cyme unit the hypopodium is commonly referred to as 'peduncle'.

If in each cyme unit both prophylls produce consecutive units from their axils, the resulting cyme is a 'dichasium' (with the 'simple dichasium' or 'triad' consisting of just three cyme units/flowers, and the 'compound dichasium' consisting of several to many units). If only one of the prophylls is 'fertile', the resulting cyme is a 'monochasium'. Principally, there are four types of monochasia, but for the Lamiales only the 'scorpioid' cyme (cincinnus) is of major relevance. This is a monochasium in which the consecutive units develop on alternating sides of each sequential axis. Very often the dichasial and the monochasial patterns are combined, in that the first branching is dichasial, and the following ones are monochasial ('double cyme' or 'double cincinnus').

The 'pair-flowered' cyme must not be confused with the so-called 'geminiflorous' cyme, which is simply a special type of ordinary cyme. Although the literal meaning of 'pair-flowered' and 'geminiflorous' is the same, the underlying structures are completely different. In some cases the term 'geminiflorous' simply means that the inflorescence (e.g. a raceme) is numerically reduced to two flowers (e.g. *Astragalus geminiflorus*, *Cassia geminiflora* – Fabaceae). In other (here more relevant) cases, the term refers to species in which cymes bear flower pairs (e.g. *Dianthus geminiflorus* – Caryophyllaceae, *Dipteracanthus geminiflorus*, *Jussieua geminiflora* – Acanthaceae, *Gomphocarpus geminiflorus* – Apocynaceae). Here the cymose branching pattern is dichasial, but in one of the two lateral leaf/bract axils the axillary shoot is represented by a single flower only. Together with the terminal flower of the cyme unit, this flower forms a pair. In the other leaf/bract axil the cymose branching is continued (Fig. 1B) (for examples see Weberling, 1958; Troll, 1969).

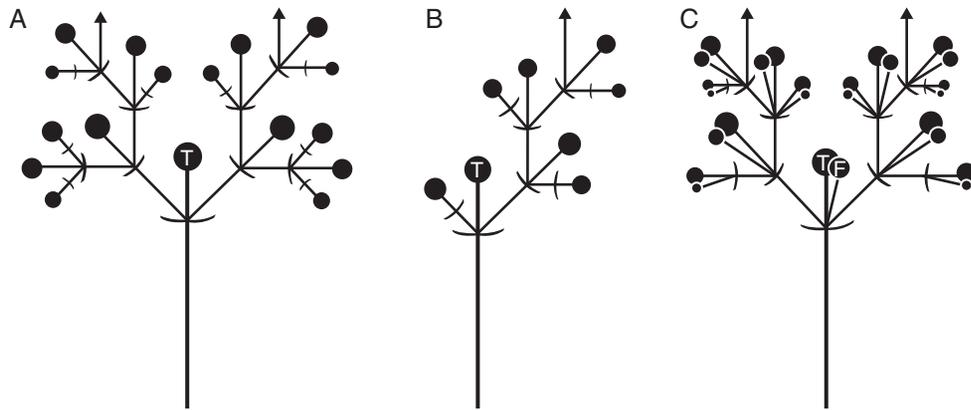


FIG. 1. Principal cyme types. (A) Cyme of the ordinary type, with a single flower terminating each cyme unit. (B) Geminiflorous cyme: special type of ordinary cyme, with one of the two dichasial branches reduced to a single flower. (C) Pair-flowered cyme: each terminal flower of the cyme units accompanied by the ‘front-flower’ in frontal (abaxial-median) position.

*Pair-flowered cyme* (Fig. 1C). In the PFC each flower is accompanied by a second flower. This flower does not emerge from the axil of one of the prophylls, but is an extra (additional or ‘supernumerary’) flower. Each cyme unit, therefore, seems to end in a flower pair. The following characterization is based largely on the examination of PFCs in the Gesneriaceae, in which family this inflorescence type is not only a characteristic feature, but also reaches its culmination in the range of morphological and ontogenetic diversity.

## STRUCTURE, DIVERSITY, ONTOGENY AND INTERPRETATIONS OF PFCs

### *Position, basic structure and flowering sequence*

*Position.* Like the conventional cymes of the ‘core’ Lamiales the PFCs are always of axillary origin and are never placed in terminal position. The thyrses they build are thus indeterminate. In the Calceolariaceae and most Gesneriaceae the cymes often emerge from the axils of foliage leaves, while bracteose inflorescences are rare. In the Plantaginaceae, they more commonly emerge from the axils of leafy or small bracts, often forming a gradual reduction series within the inflorescence.

*Basic structure.* In the PFC, each terminal flower (T) is associated with a second flower in frontal (abaxial-median = median-phylloscopic) position. This second flower is called the ‘front-flower’ (F). It appears to be inserted at the level of the prophylls ( $\alpha$ ,  $\beta$ ) and consecutive cyme units, respectively, but usually lacks a subtending bracteole. However, in some cases (observed both in Gesneriaceae and in *Penstemon*, Weber, 1973; and frequently found in *Keckiella*, see below) the front-flower is subtended by a distinct bracteole ( $\gamma$ -bracteole) (Fig. S1). As already noted by Bravais and Bravais (1837) and Wydler (1851a, b), the  $\gamma$ -bracteole is probably best perceived as a remnant of a bracteole-pair ( $\gamma$ ,  $\delta$ ) positioned above the prophyll bracteoles ( $\alpha$ ,  $\beta$ ). Owing to the decussate leaf arrangement, with alternation of the bracteole pairs, the orientation of  $\gamma$  and  $\delta$  is median. While the  $\delta$ -bracteole is always suppressed, the  $\gamma$ -bracteole and its axillary product, the front-flower, ‘survived’ in the PFC. In some cases the front-flower bears bracteoles itself and these even

may produce axillary branches (e.g. *Penstemon serrulatus*, Fig. S16).

*Sequence of flower opening.* The first flower to open in the PFC units is the terminal flower ( $T_1$ ). Then the front flower ( $F_1$ ) follows. Finally, the terminal flowers of the subsequent cyme units ( $T_2$ ) open, followed by their front-flowers ( $F_2$ ). The sequence of flower opening is thus descending ( $T_1 \rightarrow F_1 \rightarrow T_2$ ).

### *Morphological diversity*

*Structural diversity.* A considerable diversity of PFC forms is accomplished by simple variation of the length of the internodia within the cyme (peduncle, hypopodia of subsequent cyme units, pedicels). This variation gives rise to long-pedunculate/epedunculate cymes and a lax or congested flower arrangement (Fig. S2). A significant feature is the presence/absence, size, form and coloration of the bracteoles. By displacement of the bracteoles (e.g. *Agalmyla tuberculata*, *Drymonia coccinea* and other species of the genus) a branching pattern is reached as is found in Solanaceae-Solaneae, with two perpendicular bracteoles of unequal size at each node (Weber, 1982; Fig. S3). By the enlargement and fusion of the first bracteole pair a conspicuous cupule embracing the flowers may be formed (e.g. *Cyrtandra cupulata*, *C. burbridgei*).

*Diversity in branching symmetry.* As each cyme unit bears two bracteoles ( $\alpha$ ,  $\beta$ ), and each of them is principally capable of producing a consecutive axillary cyme unit, dichasial branching is the basic pattern of PFC branching. Compound dichasia, such as found in *Sinningia bulbosa* (Weber, 1973; Fig. S1) are rare. Much more common is that the first cyme unit branches dichasially, and the following ones monochasially (pair-flowered ‘double cyme’; common in Gesneriaceae: Fig. S2, or *Penstemon*: Fig. 2). In certain alliances of Gesneriaceae (Epithemateae, *Cremosperma*, *Tylopsacas*, etc.) also the first branching is monochasial, giving rise to pair-flowered ‘unilateral’ cymes. This type of cyme is often associated with the presence of many and small flowers, sometimes also with a reduction of the bracteoles (Epithemateae), and a pseudo-monopodial development.

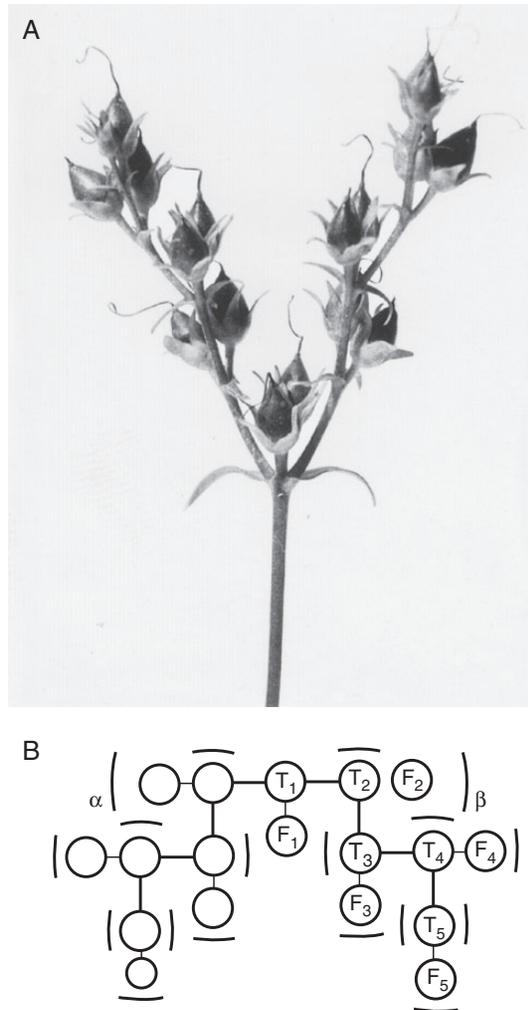


FIG. 2. *Penstemon digitalis*. (A) Pair-flowered cyme in fruiting stage. (B) Corresponding diagram.  $T_1$ – $T_5$ , terminal flowers (fruits) of cyme units 1–5;  $F_1$ – $F_5$ , front-flowers (fruits); only right side of cyme is labelled. Photograph: A. Weber.

**Diversity in cyme elaboration (flower number per PFC).** Flower number per PFC may vary considerably, dependent on the species, the position within the thyrses (usually there is a decrease from the base to the top) and/or the vigour of the individual plant. Conventionally, such a series is referred to as a reduction series (many-flowered  $\rightarrow$  several-flowered  $\rightarrow$  few-flowered  $\rightarrow$  two-flowered  $\rightarrow$  one-flowered with bracteoles  $\rightarrow$  one-flowered without bracteoles, Fig. 3). Phylogenetically, however, the series can be read also in the opposite direction. So it may be better to refer to this series as the ‘standard series’. In this series the front flowers hold a strong position, in that they are more resistant to reduction than the lateral cyme units emerging from the axils of the bracteoles. Notable steps in the series are, therefore, four- and two-flowered cymes. The four-flowered cyme consists of  $T_1$ ,  $F_1$  and  $T_2$  on both sides ( $T_2$ – $T_1F_1$ – $T_2$ ; Fig. 3D). The biflorous cyme produces  $T_1F_1$  only (Fig. 3E). Examples can be found in many taxa (e.g. *Chirita micromusa*, Fig. S8). The

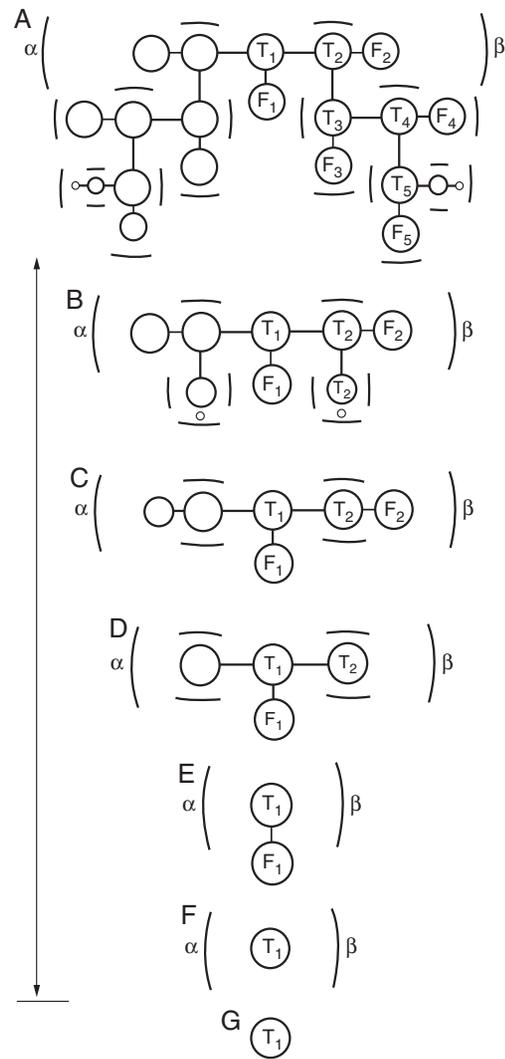


FIG. 3. Diagrams of PFCs illustrating the ‘standard series’. (A) Many-flowered cyme. (B) Several-flowered cyme. (C) Six-flowered cyme. (D) Four-flowered cyme. (E) Two-flowered cyme. (F) Single flower with bracteoles. (G) Single flower without bracteoles.  $T_1$ – $T_n$ , terminal flowers of cyme units;  $F_1$ – $F_n$ , front-flowers;  $\alpha$ ,  $\beta$ , transverse bracteoles.

extreme case is the presence of a single flower (Fig. 3F, G). If it has bracteoles (Fig. 3F), a return to cymose branching seems easy. Complete phylogenetic loss of the bracteoles (Fig. 3G) may mean definite fixation of the single-flowered state.

**Irregular reduction and loss of front-flowers.** Occasional loss of the front-flowers has been documented in several species of Gesneriaceae (Weber, 1978b). The most illustrative example is perhaps *Chrysothemis friedrichsthaliana* (Fig. S4). In this species, the most complete form is a PFC with six flowers, that is consisting of three cyme units each with a flower pair ( $F_2T_2$ – $T_1F_1$ – $T_2F_2$ ). Reduction of flowers does not occur along the standard series, but is irregular (e.g.  $T_2$ – $T_1$ – $T_2F_2$ ). Reduction of the front-flowers may be to a rudiment or may be complete (‘phylogenetic loss’).

Taxa such as *Chrysothemis* show quite plainly how PFCs can progress into a cyme of the ordinary type. Such cases may give some support to the idea that the ordinary cymes of ‘higher’ Lamiales may have originated from PFCs.

### Ontogeny

*Initiation of the front-flowers.* The ontogeny of PFCs was studied by Weber (1995) based on cleared whole mount preparations (according to the technique described by Ritterbusch, 1974) and scanning electron microscopy (Figs S5, 6). Significant is that the ontogenetic sequence of the side flowers of the cyme units (front-flower, lateral flowers) is converse to the sequence of flower opening. The terminal flower is followed by the transverse flowers, and afterwards (!) the primordium of the front-flower is initiated. If a  $\gamma$ -bracteole is present, the primordium of this bracteole emerges later than the transverse bracteoles ( $\alpha$ ,  $\beta$ ). The primordium of the front-flower, however, develops more quickly, gets ahead and opens earlier than the lateral flowers, subsequent to the terminal flower.

The acropetal initiation sequence of the bracteoles ( $\alpha$ ,  $\beta \rightarrow \gamma$ ) and their axillary structures demonstrates that the front-flower and its (usually suppressed) bracteole do not arise from the same node as the lateral bracteoles/branches, but from a distinct node situated above the prophyll node. If a  $\gamma$ -bracteole is present, the primordium of the front-flower originates clearly in the axil of the this bracteole (Figs S5, 6).

*Initiation of the consecutive cyme units.* In general, the consecutive cyme units arise successively, with some time interval between emergence of the primordia. However, especially in small- and many-flowered unilateral cymes development may be accelerated: the primordia of two or several units are already formed in a stage when the mother unit is still in a primordial stage itself. In this case, a kind of ‘false apical meristem’ or ‘pseudoshoot apex’ is present, from which the common primordia of the cyme units appear to be detached successively to the left and the right (pseudomonopodial development, e.g. *Monophyllaea*, *Epithema*, Weber, 1976a, b, 1982, 1988; Fig. S7).

### Interpretations and possible phylogenetic origin

Regarding its phylogenetic origin, at least four interpretations of the PFC appear conceivable (Fig. 4). They can be divided into two groups. (A) The PFC originated from the ordinary cymes. This interpretation implies three possibilities (Aa, Ab, Ac). (B) The PFC originated from an originally more complex, panicle-like branching system.

*Hypothesis Aa: the front-flowers are accessory flowers.* At first sight, this interpretation may appear as the most plausible one and indeed has been applied to the PFCs of Gesneriaceae (in the few cases where noted) and *Calceolaria* (Goebel, 1931; Troll, 1964; Hartl, 1965; Molau, 1978; Weberling and Troll, 1998; Endress, 2010).

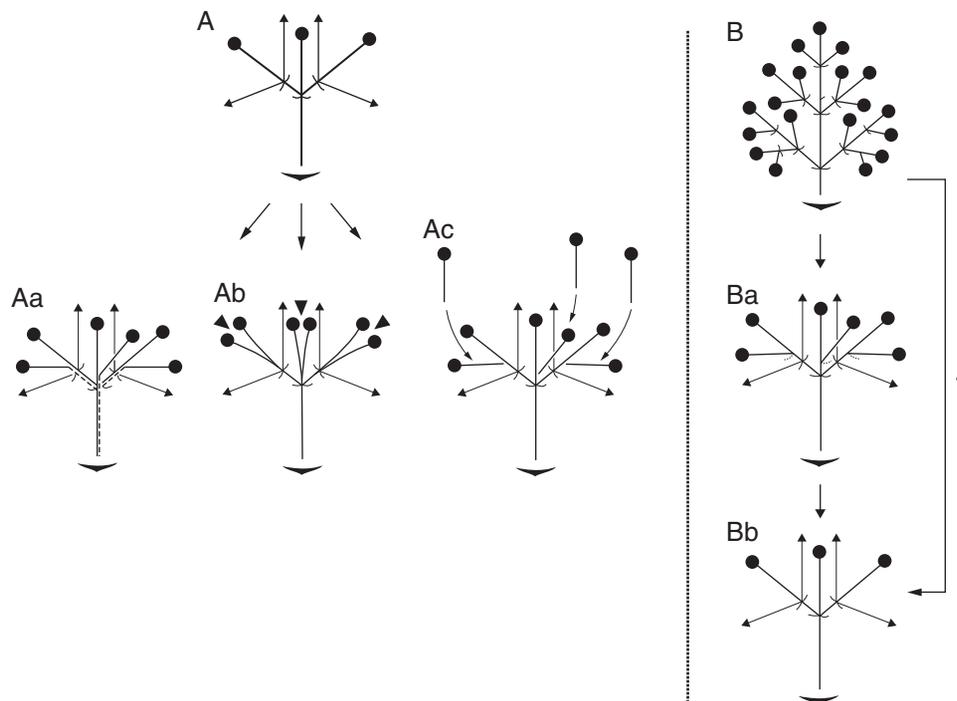


FIG. 4. Conceivable interpretations and hypothetical origin of the PFC. (A) The PFC originated from the ordinary cyme. Hypothesis Aa: the front-flowers are accessory flowers congenitally fused with the axes of the cyme units; both the terminal flowers and the front-flowers originate from the same leaf axil. Hypothesis Ab: the flower pairs originated through splitting of the primordia of the terminal flowers. Hypothesis Ac: the front-flowers are *de novo* acquisitions. (B) The PFC originated from a complex, panicle-like branching system. Ba: pair-flowered cyme (PFC), the front-flowers are remnant flowers. Bb: reduction of the front-flowers gave rise to ordinary cymes. Note: ordinary cymes may also have originated directly from panicle-like branching systems (right arrow).

Note that the term ‘accessory’ has several meanings and can be misleading. Its literal meaning is ‘additional’ or ‘adventitious’ and this evokes the interpretation that an accessory structure is a phylogenetically secondarily acquired structure (in that sense it is also relevant for hypothesis Ac). This is, of course, a possibility, but runs the risk that it blocks alternative interpretations.

In traditional German morphology the term ‘accessory’ means the formation of one or several extra shoots (vegetative shoots/partial inflorescences/flowers) following the ‘legitimate’ first axillary shoot in a leaf/bract axil. Position is usually serial (more rarely biserial or ‘collateral’, see, for example, Troll, 1964: ‘Beispross’, ‘Beiknospe’, ‘Beiblüte’, ‘Vorderblüte’). For developmental aspects see Sandt (1925): the axillary meristem is not fully used up for the production of an axillary shoot or flower. There remains a residual meristem portion, which – after some time of recovery – grows up to form another shoot/flower (in the dicotyledons usually in serial position). The same may happen several times so that a leaf or bract axil may bear several (serial) axillary shoots/flowers. Although emerging in a temporally and spatially consecutive order, they are equivalent as to their origin from the same leaf axil. A review on the occurrence of accessory partial inflorescences/flowers in the Scrophulariaceae, with instructive photos and diagrams, has been given by Weberling and Troll (1998: 368–372). True accessory cymes and flowers occur also in the Calceolariaceae and the Gesneriaceae, for example in the repetitive series of biflorous axillary cymes in many species of the genus *Microchirita* (= traditional *Chirita* sect. *Microchirita*, Wang *et al.*, 2011; Weber *et al.*, 2011; Fig. S8). In other words, accessory shoots/flowers and front-flowers may well occur side by side.

If the front-flowers represent accessory flowers, they should emerge from the same leaf/bract axil as the cyme unit. This is clearly not the case: they emerge at the base of the pedicel of the terminal flower, at or slightly above the prophyll node. To retrieve the interpretation as an accessory shoot, an auxiliary hypothesis would have to be introduced: that the peduncle of the front-flower (and the hypopodia in all following cyme units) is (are) congenitally fused with the peduncle (hypopodium) of the terminal flower (Fig. 4Aa). Curiously, this hypothesis has never been explicitly expressed in words. If it is true one should expect that the peduncles of the PFCs exhibit a ‘double’ or ‘composite’ nature. However, no factual evidence (e.g. externally visible concrescence or internal presence of a double or two-parted vascular ring) is available. The peduncles are simple internodes, in no way different from the peduncles of ordinary cymes.

The strongest counter-argument is that the front-flowers are in some species subtended by a distinct bracteole ( $\gamma$ -bracteole, Weber, 1973; Fig. S1) and that the ontogeny shows that the front-flowers originate like normal axillary flowers. This makes it at once clear that the front-flower is a regular side shoot of the cyme axis, although its subtending bracteole is commonly suppressed.

*Hypothesis Ab: the flower pairs result from primordium splitting.* This hypothesis can be disproved immediately as the ontogeny does not show any kind of primordial splitting: the primordium of the front-flower develops much later than the primordium of the terminal flower, emerging separately as an axillary structure of the  $\gamma$ -bracteole (if present) (Figs S5, S6).

*Hypothesis Ac: the front-flowers are de novo acquisitions.* This means that the front-flowers in the PFCs have originated through a novel evolutionary step. On the one hand, this hypothesis says clearly that the PFC has arisen from the ordinary cyme by a kind of phylogenetic ‘addition’ of the front-flowers, but does not give an explanation for where these flowers come from. It is thus difficult to prove or to disprove this hypothesis from a morphological point of view, but support may come from the systematic side.

*Hypothesis B: the PFC originated from a paniculate branching system.* This interpretation was proposed by Weber (1973, 1982), but no systematic evidence could be provided at that time. It rests on the evidence that the  $\gamma$ -bracteole belongs to a distinct node above the prophyll node. As, moreover, the front-flower sometimes bears bracteoles itself and may even branch (Weber, 1973; Fig. S16), it seems safe to assume that the front-flower is the remnant of a branch.

*Conclusions.* From the four conceivable hypotheses addressed, two (Aa and Ab) can be excluded, as there is no factual evidence. Hypothesis Ac is difficult to prove or disprove, but may become relevant if other interpretations fail. Hypothesis B will be discussed in more detail in the context of *Peltanthera*.

#### OCCURRENCE OF PFCs IN THE CALCEOLARIACEAE, SANANGO, GESNERIACEAE AND PLANTAGINACEAE

The occurrence of PFCs in the Gesneriaceae and some ‘Scrophulariaceae’ (*Calceolaria*, *Tetranema*, *Penstemon*) has been documented by Weber (1972, 1973). However, at that time neither the frequency of occurrence nor the taxonomic bearing was clear. By the wide circumscription of the Scrophulariaceae, the distribution of PFCs in that family seemed totally erratic. By the recent split and reorganization of the Scrophulariaceae (Olmstead and Reeves, 1995; Olmstead *et al.*, 2001; Olmstead, 2002; Oxelman *et al.*, 2005; Albach *et al.*, 2005; APG III, 2009; for details and history see Tank *et al.*, 2006) the situation has changed dramatically. In the following, the distribution of PFCs is reviewed across the new taxonomic entities. Calceolariaceae, *Sanango* and Gesneriaceae are only briefly treated, as little new and original information can be provided. The Plantaginaceae are treated in more detail and evidence is presented that all taxa said to have ‘cymose’ or ‘paniculate’ inflorescences have PFCs. Reports are, however, negative in Scrophulariaceae *sensu stricto* (*s.s.*) and other segregates from the ‘original’ Scrophulariaceae, as well as in all other families of the Lamiales.

The three families with PFCs belong to the ‘basal’ Lamiales in the sense of Olmstead (2002) (for the families included in this group and their rough position see Fig. 7). They are in some way closely related, but there is no general consensus about the details. The various topologies published in the literature will be discussed later, in the context of whether PFCs have originated once or several times.

#### *Calceolariaceae*

Presently, the family includes two genera, *Calceolaria* (approximately 250 spp., Mexico to Patagonia) and *Jovellana*

(4 spp., Chile, New Zealand). The third genus traditionally recognized, *Porodittia* (= *Stemotria*; 1 sp., Chile), has been recently included in *Calceolaria*, but is addressed here as well.

*Calceolaria* (Fig. 5A; Fig. S9). The curious inflorescences, with two flowers between the dichasial cyme branches, have puzzled botanists for a long time, and different interpretations have been proposed (Molau, 1978; Andersson and Molau, 1980; Weberling and Troll, 1998). Clear recognition that the *Calceolaria* inflorescences represent PFCs was given by Weber (1973). More recently, Ehrhart (2000, 2005) has shown that this inflorescence type is omnipresent in the genus. The only exceptions are the species in which the cymes are usually reduced to single flowers (e.g. *C. uniflora*, *C. darwinii*, *C. fothergillii*, *C. tenella*). In *C. biflora* and similar species the PFCs are often (but not consistently) reduced to the primary

flower pair ( $T_1F_1$ ). Between many-flowered cymes and single flowers many transitions are represented and variation is clearly along the standard series. No species has been detected so far, in which occasional or constitutive loss of front-flowers occurs.

*Jovellana* (Fig. 5B; Fig. S10). According to personal observations, all species of the genus (recently reduced to four; Nylander *et al.*, 2012) have several-flowered PFCs.

*Porodittia* (= *Stemotria*) (Fig. S11). The only species of the genus, *P. triandra*, has been recently included in *Calceolaria* on molecular grounds (Andersson, 2006; Cosacov *et al.*, 2009). As perfectly shown in the original illustration of Cavanilles (1799, as *Jovellana triandra*, see Mayr and Weber, 2006: Fig. 11), the species has PFCs.



FIG. 5. Examples of PFCs in the families Calceolariaceae, Gesneriaceae and Plantaginaceae. (A) *Calceolaria integrifolia* (Calceolariaceae). (B) *Jovellana sinclairii* (Calceolariaceae). (C) *Streptocarpus dunnii* (Gesneriaceae). (D) *Sinningia macrostachya* (Gesneriaceae). (E) *Tetranema gamboanum* (Plantaginaceae-Russeliaceae). (F) *Penstemon arkansanus* (Plantaginaceae-Cheloneae). (G) *Nothochelone nemorosa* (Plantaginaceae-Cheloneae). (H) *Pennellianthus frutescens* (Plantaginaceae-Cheloneae). (I) *Keckiella breviflora* (Plantaginaceae-Cheloneae). For more details and labelling of the flowers see Figs S9–29.

*Sanango racemosum* (Fig. S12). *Sanango* comprises a single species, *S. racemosum*, distributed in the sub-Andean region of Peru and south-east Ecuador. The genus/species has had a varied taxonomic history, having been assigned to Scrophulariaceae, Loganiaceae and Buddlejaceae. Wiehler was the first to suggest that *Sanango* would belong to Gesneriaceae, in particular to subfam. Gesnerioideae tribe Gesnerieae. The molecular data of Smith *et al.* (1997) seemed in perfect accordance, but proved erroneous (J. F. Smith, Boise State University, ID, USA, pers. comm.). Later molecular work (Oxelman *et al.*, 1999; Perret *et al.*, 2013) revealed that *Sanango* is sister to Gesneriaceae.

At the request of H. Wiehler, I examined the axillary inflorescences. The results, including a drawing of an inflorescence and a diagram, were published by Wiehler (1994). The inflorescences clearly represent cymes of the pair-flowered type, usually comprising around six flowers (F<sub>2</sub>T<sub>2</sub>—T<sub>1</sub>F<sub>1</sub>—T<sub>2</sub>F<sub>2</sub>).

### Gesneriaceae

In the Gesneriaceae (c.150 genera, >3200 spp.), PFCs are almost omnipresent. Exceptions do not occur in the more basal lineages, so that it can be safely stated that PFCs represent the basic type of axillary partial inflorescences in the family. Flower number varies extensively, from numerous (e.g. 40–50 in PFCs of unifoliate *Streptocarpus*) through several, few, two to one (with and without bracteoles) (see Fig. 5C, D and Fig. S12). If reduction of the cymes to solitary flowers is combined with reduction of the subtending leaves to bracts, the flower aggregate forms a distinct phenetic entity: a terminal raceme. Such racemes are constitutive for just a few genera: *Gloxinia* (including *Anodiscus* and *Koellikeria*, Roalson *et al.*, 2005a, b),

*Gloxiniopsis*, *Smithiantha* and *Diastema* (all belonging to the tribe of Gloxinieae). By shortening of the pedicels, the flowers may become sessile and the raceme transgresses into a spike (e.g. *Sinningia allagophylla*, Chautems and Weber, 1999). In the Old World Gesneriaceae, only a single genus has bracteose racemes: *Rhynchoglossum* (tribe Epithemateae) (Weber, 1978a). Taxa with cymes of the ordinary type are extremely rare in the Gesneriaceae. To the best of my knowledge, only two species (both belonging to genera of the morphologically advanced tribe Epithemateae) can be quoted: *Loxonia hirsuta* and *Stauranthera coerulea* (Weber, 1977a, b). *Loxonia* is a genus of three species, two of which have PFCs cymes, and one has ordinary cymes. *Stauranthera* comprises five species (my unpubl. data), and only the one discussed has ordinary cymes. No intermediate forms (occasional loss of front-flowers) between pair-flowered and ordinary cymes have been found in these genera. In these cases there is little doubt that cymes of the conventional type have evolved from PFCs. The two genera can serve as model cases for the evolution of ordinary cymes from PFCs.

### Plantaginaceae

In their new circumscription (Albach *et al.*, 2005; Oxelman *et al.*, 2005), the Plantaginaceae include 12 tribes with around 90 genera and roughly 2000 species. Ten of the 12 tribes can be excluded immediately from further consideration, as these only comprise genera with single axillary flowers and ‘racemose’ inflorescences, respectively.

The two remaining tribes are Russelieae (*Russelia*, *Tetranema*) and Cheloneae (?*Brookea*, *Chelone*, *Chionophila*, *Collinsia*, *Keckiella*, *Nothochelone*, *Pennellianthus*, *Penstemon*,

TABLE 1. Tribes of Plantaginaceae that include genera with pair-flowered cymes (no cymes of the ordinary type are present in the family)

Tribe	Genus	Species number	PFCs present/absent (+/–)	Single, bracteolate flowers present/absent (+/–)	Single, ebracteolate flowers present/absent (+/–)	Distribution
Russelieae	<i>Russelia</i>	~50 (?)	+	–	–	Central and tropical South America
	<i>Tetranema</i>	5	+	–	–	Costa Rica to Mexico
Clade between Russelieae and Cheloneae	<i>Uroskinnera</i>	4	–	–	+	Guatemala to Mexico
Cheloneae	<i>Chelone</i>	4	–	+	–	Eastern half of North America, incl. Florida
	<i>Chionophila</i>	2	–	+	–	Central North America (Montana, Idaho, Wyoming, Colorado)
	<i>Collinsia</i>	~20	–	–	+	North America, many spp. in California
	<i>Keckiella</i>	7	+	+	–	South-western North America (California, Oregon, Nevada, Arizona)
	<i>Nothochelone</i>	1	+	–	–	Western North America (British Columbia to northern California)
	<i>Pennellianthus</i>	1	+	–	–	North-east Eurasia (incl. Kamchatka peninsula), Japan
	<i>Penstemon</i>	~270	+	+	–	Guatemala to Alaska
	<i>Tonella</i>	2	–	–	+	Vancouver Island to central California

*Tonella*, ?*Uroskinnera*) (see Table 1). In the molecular phylogenies of Albach *et al.* (2005) and Oxelman *et al.* (2005) Russelieae and Cheloneae represent sister clades. In the phylogeny of Wolfe *et al.* (2006), relating particularly to *Penstemon* and its allies, Russelieae, *Uroskinnera* (molecular data incomplete) and Cheloneae form successive clades.

#### Plantaginaceae-Russelieae

The tribe Russelieae was for a long time considered monogeneric (Pennell, 1935; Thieret, 1954, 1967), but, based on molecular data, has been recently expanded to include the genus *Tetranema* (Wolfe *et al.*, 2002). *Russelia* and *Tetranema* have, although sharing a similar distribution, morphologically little in common. No morphological characters (synapomorphies) have come to light so far that would show quite plainly their close relationship.

*Russelia* (Fig. S14). In this genus some 50 species have been recognized (Carlson, 1957), ranging from north-east Mexico to Colombia. The species, collectively known as firecracker plants or coralblows, are very similar and often used as ornamentals. The inflorescences emerging from the axils of small, opposite leaves or bracts are known to be cymosely branched (Carlson, 1957; without mention of the pair-flowered condition), with loose or dense clustering of the flowers. As to early illustrations, *Russelia coccinea* (= *R. multiflora*; ? = *R. sarmentosa*) produces many-flowered cymes which together form a dense, elongated, terminal head. *R. sarmentosa* has also dense axillary flower clusters, but these are well separated by long internodia and the subtending phyllomes are leafy [there is, however, some discussion regarding whether *R. coccinea* and *R. sarmentosa* (kept distinct by Carlson, 1957) are conspecific].

The fact that the flowers of '*Russelia juncea*' (= *R. equisetiformis*) are arranged as in *Penstemon* (PFCs) was already briefly mentioned by Wydler (1851a, b) and is confirmed here for that species and *R. sarmentosa*. In *R. sarmentosa* (the type species of *Russelia*), the flowers are arranged in  $\pm$  dense clusters. Branching is 2-3-times dichasial at the base and then monochasial. In contrast, in *R. equisetiformis* flower number is low, with the PFCs often being reduced to the primary flower pair or a single flower. '*Russelia alata*' (Chamisso and Schlechtendal, 1828) has consistently single flowers in the leaf axils. More recently, this species has been accommodated in a genus of its own, *Cubitanthus*, and placed in Gesneriaceae (Barringer, 1984). This placement was doubted by Weber (2004). New molecular data suggest that the genus/species belongs neither to Plantaginaceae nor to Gesneriaceae, but to Linderniaceae (Perret *et al.*, 2013). This taxon is therefore not considered further here.

*Tetranema* (Fig. 5E; Fig. S15). The genus, represented by five species in Central America, has been revised twice in the last two decades (Méndez-Larios and Villaseñor, 1995; Christenhusz, 2010), but in neither was the presence of PFCs mentioned. The habit of the plants is rosette-like (rosulate), with long-scapose axillary inflorescences emerging from the leaf axils and bearing a dense and many-flowered flower cluster at the top. The inflorescences of *T. roseum* have been analysed by Weber (1972; as *T. mexicanum*), with the result that they correspond to the PFCs of Gesneriaceae. The other species

apparently conform to this pattern. An illustration of the recently described *T. gamboanum* (Grayum and Hammel, 1996: fig. 1) shows nicely the pair-flowered structure of the cyme (Fig. S15).

*Conclusions regarding Russelieae.* In view of the substantial morphological differences of *Tetranema* and *Russelia*, the presence of PFCs in the two genera is certainly a welcome common character and it is reasonable to assume that the pair-flowered condition represents a synapomorphy (see Wolfe *et al.*, 2002). However, this interpretation is ambiguous (see below).

#### Plantaginaceae-Cheloneae

In tribe Cheloneae presently 8–10 genera are accepted (Wolfe *et al.*, 2002, 2006): except the doubtful *Brookea*, the alliance is essentially of North American distribution, with one outlier (*Pennellianthus frutescens*) in the far north-east of Eurasia and Japan. A few species of *Penstemon* reach Central America (Mexico) in the south. The position of *Uroskinnera* (Mexico, Guatemala) is still somewhat problematic. Wolfe *et al.* (2006) pleaded for exclusion from Cheloneae, but as it forms the sister genus of Cheloneae, it is at least closely allied. In the following the genera are (formally) grouped as follows: *Penstemon*, *Nothochelone*, *Pennellianthus*, *Keckiella* (all with PFCs), *Chelone*, *Chionophila*, *Collinsia*, *Tonella*, *Uroskinnera* (single axillary flowers with or without bracteoles) and *Brookea* (probably misplaced in Cheloneae and Plantaginaceae, respectively).

*Penstemon* (Fig. 5F; Figs S16, 17). This is by far the largest genus of tribe Cheloneae, comprising >270 species (Lodewick and Lodewick, 1999; Wolfe *et al.*, 2006), from which approx. 75 have been included in the present analysis (Table S3). In the taxonomic literature, the *Penstemon* inflorescence is almost exclusively referred to as a panicle (e.g. Keck, 1932–1940; Pennell, 1935; Keck and Cronquist, 1957; Straw, 1966) and neither the thyrsic nature nor the presence of flower pairs has been noted. Only in two species descriptions (out of approx. 90) in horticultural magazines is the inflorescence designated as 'thyrsoid' (Lindley, 1842; van Houtte *et al.*, 1845–1883). Only Lindley (1842: t.3884) made explicit reference to the flower pairs in the axillary inflorescences: 'Gradually, towards the upper part of the stem, the leaves become smaller, and, in proportion, broader, till at length they constitute ovate bracteas; from the axils of these leaves the bracteated peduncles arise, each generally with two branches, and two rather large, handsome flowers, which are subsecund.' More frequently, the pair-flowered condition can be seen in illustrations (e.g. *Penstemon palmeri*, Fig. S16). For simple descriptive purposes the reference as 'panicle' may be sufficient, but it is not acceptable for morpho-phylogenetic analyses. The *Penstemon* inflorescence must be classified as an indeterminate thyrses, which is consistently made up of PFCs. In principle, this was already recognized by early morphologists such as Bravais and Bravais (1837) and Wydler (1851a, b), but was largely overlooked and/or ignored in taxonomy. Wettstein (1891: fig. 19) even presented an inflorescence diagram of *P. digitalis* in which he completely dismissed the pair-flowered condition and showed a cyme of the ordinary type.

The important point is that in *Penstemon* PFCs do not only occur here and there, but seem to be a characteristic feature of the whole genus. In the present analysis no species was detected

in which the cymes were of the ordinary type. Due to the poor sampling their occasional occurrence cannot be excluded, but there is little doubt that PFCs are the typical and original form in the genus.

As in panicles, the degree of elaboration of the partial inflorescences decreases from the base to the top, so that the outward form of the *Penstemon* inflorescence is usually a pyramid or slender cone. According to the average flower number, the *Penstemon* cymes fall roughly into four groups (see Fig. S17): (1) cymes (including the uppermost ones) many- and usually dense-flowered (e.g. *P. cyananthus*, *P. procerus*); (2) cymes several-flowered, becoming few- to one-flowered towards the top of the inflorescence (bulk of species); (3) cymes two- (rarely three- or four-)flowered (the two flowers representing T<sub>1</sub>F<sub>1</sub>, the occasional third and fourth flower are the lateral flowers T<sub>2</sub>; e.g. *P. barbatus*, *P. centranthifolius*, *P. gentianoides*, *P. richardsonii*, *P. wrightii*); (4) cymes consistently reduced to single flowers (e.g. *P. angustifolius*, *P. azureus*, *P. fruticosus*, *P. humilis*, *P. menziesii*). No species with ebracteolate single flowers has been found.

*Nothochelone* (Fig. 5G; Fig. S18). This genus is monotypic with *N. nemorosa*. Common names such as woodland beardtongue or woodland penstemon indicate that the species is very similar to *Penstemon*, in which genus it has been originally described (Straw, 1966, 1967). The axillary inflorescences are made up of two to several flowers. In several-flowered cymes the presence of front-flowers can be well observed and the cymes have the typical appearance of a *Penstemon* PFC.

*Pennellianthus* (Fig. 5H; Fig. S19). This is another segregate of *Penstemon*, comprising a single species, *P. frutescens* (Crosswhite and Kawano, 1970), with distribution in north-east Eurasia including Japan. The inflorescences are rather dense-flowered heads, held tightly above the foliage, with the flowers much like in *Penstemon* with insect-pollinated flowers. The partial inflorescences emerging from the bract axils are one- to four-flowered, with a front-flower placed beneath the terminal flower of the cyme.

*Keckiella* (Fig. 5I; Figs S20–24). This is a genus of seven woody, sometimes squarrosely branched shrubs, with main distribution in California. The genus has been separated from *Penstemon* by Straw (1966, 1967). The species can be roughly referred to two groups, one with yellow, cream or whitish, short-tubed and strongly bilabiate flowers (apparently bee-pollinated: *K. antirrhinoides*, *K. breviflora*, *K. lemmonii*, *K. rothrockii*) and another with brilliant red, long-tubed and galeate flowers (obviously hummingbird-pollinated: *K. cordifolia*, *K. corymbosa*, *K. ternata*). In the first group the inflorescences are rather lax, in the second group sometimes dense- and multi-flowered (but variation is considerable, even between the individual plants of a given species). Freeman *et al.* (2003) showed that the relationships do not conform to these anthecological groups.

With the exception of *K. rothrockii*, the inflorescence of all species represents a pyramidal or elongate thyrses. The cymes represent PFCs, with flower number decreasing towards the apex. They are special in that the front-flowers are usually (always?) subtended by a distinct bracteole ( $\gamma$ -bracteole) and bear bracteoles themselves. In other words, the front-flowers seem to be 'replaced' by (poorly developed) cyme branches.

In *Keckiella antirrhinoides*, *K. breviflora* and *K. lemmonii* the inflorescence organization is very similar (Figs S20, 21). The terminal inflorescence is an indeterminate, rather lax thyrses with pedunculate cymes. The cymes are few-, often four- and rarely up to six-flowered. In general, only one or two flowers seem to open in a cyme, while the others remain in bud stage (at least for a long time). In the upper part of the inflorescence only single, bracteolate flowers are produced (characteristic of *K. antirrhinoides*). Analysis of four-flowered cymes shows that below the terminal flower (T<sub>1</sub>) there is a front-flower in median-abaxial position (F<sub>1</sub>) and two lateral flowers (T<sub>2</sub>) emerging from the axils of the bracteoles ( $\alpha, \beta$ ). Remarkably, the front-flower has (always?, occasionally?) a subtending bract and frequently bears bracteoles itself. This is a condition sometimes found in *Penstemon* (Weber, 1973; Fig. S16) which provides evidence that the front-flower is a reductional form of a branch and the PFC a reduced form of an originally more complex branching system.

*K. rothrockii* (Fig. S22) has similar flowers as the previous species, but the inflorescence is different: the flowers emerge singly from the bract axils, they are sessile and bear two bracteoles below the calyx. The inflorescence looks like a simple (occasionally basally branched) spike. Freeman *et al.* (2003) concluded from molecular data that *K. rothrockii* would be the 'most basal species' of the genus *Keckiella*, while it appears as a derived form with respect to inflorescence morphology.

The terminal inflorescences of *K. cordifolia*, *K. corymbosa* and *K. ternata* (Figs S23, S24) are lax or dense pyramidal thyrses in downcurved position (*K. cordifolia*) or many-flowered 'clusters' in suberect (*K. corymbosa*) or erect position (*K. ternata*). For *K. cordifolia* and *K. ternata* it can be demonstrated clearly that front-flowers are present and the cymes thus represent PFCs. Analysis of the dense and many-flowered cymes of *K. corymbosa* proved difficult, but the presence of front-flowers could be confirmed by examination of soaked samples of herbarium specimens.

*Chelone* (Fig. S25). This genus, comprising four species (Nelson and Elisens, 1999) is uniform with respect to the inflorescences and flowers. The inflorescences are dense, cone-like terminal aggregates. From the axils of the opposite bracts there emerge single sessile, bracteolate flowers, which form together four tight longitudinal rows. No flower pairs and front-flowers, respectively, are present.

*Chionophila* (Fig. S26). This genus comprises two species, *C. jamesii* and *C. tweedyi*. The first has inflorescences (and flowers) very similar to *Chelone*, but, due to sectorial anisoclady, only two of the four rows of bracts bear axillary flowers, so that the spike is secund and bears two adjacent rows of flowers only. According to the original description of Bentham (1846: 325) the flowers bear two bracteoles ('Pedunculi brevissime bibracteati'). *C. tweedyi* has elongate, lax inflorescences with shortly stalked flowers. Again only two rows of flowers are present, in that in every bract pair only one bract bears an axillary flower. No flower pairs and front-flowers, respectively, are present.

*Collinsia* (Fig. S27). This is a genus of about 20 annual species with main distribution in California. The inflorescences roughly fall into two groups that have been referred to as 'pedicel-

flowered' and 'sessile-flowered' (Gray, 1880, 1886; Newsom, 1929). Recently, Baldwin *et al.* (2011) showed that this grouping has little taxonomic relevance. In the 'pedicel-flowered' group the flowers are not only long-stalked, but emerge singly in the axils of opposite bracts (e.g. *C. parviflora*, *C. violacea*), while in the 'sessile-flowered' group the pedicels are short, and the large flowers form conspicuous circles around the stem (e.g. *C. heterophylla*, *C. tinctoria*). As the flowers open almost synchronously, the latter type results in a pagoda-like appearance of the inflorescences (therefore the common name 'Chinese houses'). *C. verna* occupies a transitional position, in that the circles are formed by long-stalked flowers. The reason for the ring-like arrangement of the flowers is that the decussate leaf arrangement in the vegetative region switches to the formation of 6–8-merous pseudowhorls. The bracts are inserted at almost the same levels and the pseudowhorls are separated by elongated internodes (compare with Kwiatkowska, 2012). The stalks of the axillary flowers, regardless of being long or short, lack bracteoles, so that the formation of cymes is impossible. Also, no front-flowers have been observed.

*Tonella* (Fig. S28). This is the putative sister genus of *Collinsia* (Baldwin *et al.*, 2011), comprising two delicate, annual species (*T. floribunda*, *T. tenella*). The inflorescence organization is very similar to *Collinsia*. In *T. tenella*, a single flower emerges per leaf axil, comparable to *C. parviflora*. In *T. floribunda* circles of flowers are formed, each flower being stalked. These inflorescences correspond to *C. verna*. Again, no PFCs are present.

*Uroskinnera* (Fig. S29). This is a little known genus of four species native to southern Mexico and Guatemala (Schultes, 1941; Daniel and Breedlove, 1992). As can be concluded from the drawings and photos shown in Fig. S27, the inflorescences are short or long, many- and dense-flowered terminal racemes, with the single, short and apparently ebracteolate flowers emerging from small, opposite (*U. almedae*) or alternately arranged bracts (*U. hirtiflora*). There is no indication of the presence of front-flowers or PFCs, respectively.

*Brookea*. This is a genus of four species from Borneo, representing shrubs or small trees. It was originally placed in Scrophulariaceae (Bentham, 1876b), but transferred to Gesneriaceae by Hallier (1903). Burt (1965) and Thieret (1967) considered a position in the Scrophulariaceae-Cheloneae. Fischer (2004) placed the genus in Scrophulariaceae-'Stilbaceae', a position which, however, does not fit with the mainly South African distribution of Stilbaceae. The inflorescences are said to be racemose and this has been observed in an unidentified species on Borneo by me. With regard to both morphology and phytogeography (molecular data are lacking), *Brookea* is completely alien to the Cheloneae and does not have PFCs.

*Conclusions regarding Cheloneae.* Of the eight (to ten) genera presently accepted in the tribe Cheloneae, four have PFCs (*Keckiella*, *Nothochelone*, *Pennellianthus*, *Penstemon*) and four (to six) have single flowers building up terminal racemes or spikes (*Chelone*, *Chionophila*, *Collinsia*, *Tonella*; the inclusion of *Uroskinnera* and *Brookea* in Cheloneae is doubtful, see Wolfe *et al.*, 2006). *Nothochelone* and *Pennellianthus* have been originally described in *Penstemon* and segregated by Straw (1966, 1967) and Crosswhite and Kawano (1970). In the

molecular phylogenies of Cheloneae (Wolfe *et al.*, 2002, 2006) the three genera appear at different places: *Pennellianthus* is sister to the rest of Cheloneae, *Nothochelone* appears within a clade comprising also *Chionophila* and *Chelone*, and *Penstemon* forms the crown group. *Keckiella* occupies a sister position to the clade made up of *Penstemon* + the clade comprising *Chionophila*, *Nothochelone* and *Chelone*. This topology gives support to the idea that PFCs represent the original condition in the Cheloneae. They apparently have given rise to single flowers in several alliances, but have been retained in *Nothochelone* and *Penstemon* as an ancestral condition. The opposite interpretation, namely that the pair-flowered condition evolved several times independently, appears less probable.

*Collinsia* and *Tonella*, genera included in the Cheloneae only recently for molecular reasons (Wolfe *et al.*, 2002), appear morphologically somewhat out of place in the Cheloneae. Their species never produce cymes and the single flowers are always ebracteolate. Moreover, the increase and whorled arrangement of bracts in some species has no parallel in other members of Cheloneae. Their divergent morphology, however, may be seen in context with their progression to an annual habit.

Although the outer appearance of the inflorescences is very different, *Chelone* and *Chionophila* fit much better to *Penstemon*, *Nothochelone* and *Pennellianthus*. The flower form is similar (except to bird-pollinated species of *Penstemon*) and the single flowers can be explained as reduced forms of cymes.

## THE INFLORESCENCES OF THE REMAINING LAMIALES

'Core' Lamiales (sensu Olmstead, 2002). In this large series of families PFCs are not found (Table 2). Cymose branching of the axillary inflorescences (and thus thyrsc structure of the inflorescence) is most common in the Lamiaceae, Acanthaceae and (to a lesser degree) Bignoniaceae. In the families Byblidaceae, Lentibulariaceae, Linderniaceae, Phrymaceae-Mazoideae (sometimes considered as a family of its own: Mazaceae) and Orobanchaceae cymes are not found. The only exceptions of taxa having cymes in the 'upper' clades are the Phrymaceae (with *Leucocarpus* and *Hemichaena* having cymes, while the remaining genera, e.g. *Mimulus*, have single axillary flowers) and the small and monogeneric family Paulowniaceae. The overall impression is that racemic inflorescences have evolved many times in parallel from thyrsc ones and that the switch from the one type to the other (by reduction of the cyme to its primary cyme unit) is an 'easy' evolutionary process. It would be worthwhile to perform an ancestral state reconstruction analysis to confirm/reject this view and to get more detailed information on the evolutionary patterns.

'Basal' Lamiales. Although comprising fewer families, the 'basal' Lamiales are more varied in their inflorescence organization. The inflorescences are either determinate or indeterminate, and the form spectrum includes panicles, thyrses (both with ordinary and PFCs) and racemes. There is essential agreement in all available molecular phylogenies that the families preceding the Calceolariaceae, Gesneriaceae and Plantaginaceae form a grade of clades comprising (from bottom to top) Plocospermataceae,

TABLE 2. The families of Lamiales (+ unplaced genera) and their basic types of inflorescences

Name of family or genus	No. of genera	No. of species	Inflorescence determinate (+)/indeterminate (-)	Thyrse with PFCs	Thyrse with ordinary cymes	Raceme ( <i>s.l.</i> ), flowers singly in leaf/bract axils
Plocospermataceae	1	1	-?		?	
Carlemanniaceae	2	5	+?		?	
Oleaceae	~25	~600	+		+	+
Tetrachondraceae	2	3	+			+
<i>Peltanthera</i>		1	+			
Calceolariaceae	2	~270	-	+++		
<i>Sanango</i>		1	-	+++		
Gesneriaceae	>150	~3300	-	++ (+)		(+)
Plantaginaceae (incl. Callitrichaceae, Hippuridaceae, Globulariaceae)	~90	~2000	-	+		++
Scrophulariaceae (incl. Myoporaceae, Buddlejaceae, Selaginaceae)	~60	~1700	-		++	+
Stilbaceae (incl. Retziaceae)	~10	~40	-		++	+
Linderniaceae	~13	~195	-			+++
Byblidaceae	1	6	-			+++
Martyniaceae	5	~15	-			+++
Pedaliaceae	~15	60–85	-		(+)	++
Schlegeliaceae	4	25–30	-		++	(+)
Bignoniaceae	>100	~850	-		++	+
Acanthaceae (incl. Avicenniaceae)	~250	~2500	-		++	+
Lentibulariaceae	3 (-5)	~350	-			+++
Thomandersiaceae	1	6	-			+++
Verbenaceae	~35	~1200	-		+	++
Lamiaceae (incl. Symphoremataceae)	~235	~7000	-		++	+ (e.g. <i>Holmskioldia</i> , <i>Scutellaria</i> , <i>Tinnea</i> , <i>Teucrium</i> p.p.), ++
Phrymaceae	11	~160	-		+ ( <i>Leucocarpus</i> , <i>Hemichaena</i> ) +++	++
Paulowniaceae	1	~7	-			
<i>Rehmannia-Triaenophora</i> – clade (Xia <i>et al.</i> , 2009)	2	9	-			+++
Orobanchaceae (incl. Cyclocheilaceae)	~90	>2000	-			+++

Arrangement is roughly according to presumed phylogeny (based on Olmstead *et al.*, 2001; Schäferhoff *et al.*, 2010; and N. Refulio and R. G. Olmstead, pers. comm.). Data regarding the number of genera and species are according to the family treatments in Kadereit (2004) and current online information. Rough assessment of the frequency of the occurrence of cyme types and single flowers is according to the author's experience; +++ all genera, ++ predominance, + rare, (+)/(-) very rare.

Oleaceae + Carlemanniaceae, and Tetrachondraceae. Unfortunately, the inflorescences of most are still insufficiently known. The monotypic Plocospermataceae are said to have 'inflorescences subtended by two leaves, axillary, in 1–7 congested racemes or dichasia, often reduced to only 1–2 flowers' (Struwe and Jensen, 2004: 330). It is not clear what this means. The Carlemanniaceae (two genera, five species) are said to have 'axillary or terminal cymes' (Thiv, 2004). Also this reference is ambiguous. The same holds true for the brief descriptions of Solereder (1897: *Plocosperma*, under Loganiaceae) and Schumann (1897: *Carlemannia*, under Rubiaceae). The Tetrachondraceae (two genera, three species) have been analysed by E. M. Sehr and A. Weber (unpubl. data). Here, terminal flowers are present, each preceded by two pairs of small bracts. Branching is cymose. The inflorescences of Oleaceae are variable and still incompletely known. Terminal flowers are said to be always present (Knoblauch, 1895), so that the inflorescences can be classified as determinate ('monotelic', Troll, 1964: 177). Branching of the inflorescences is said to be racemose, paniculate or cymose, but statements such as 'a simple cyme . . . is rare, but more commonly the cyme is thyrseid and more or less paniculate' (Green, 2004: 297) are of little help to get a clear picture of the inflorescence organization of Oleaceae. The only inflorescences of the family that

have experienced a proper analysis are those of *Forsythia* and *Abeliophyllum* (Troll, 1969: 529 ff.). Their partial inflorescences are reduced to single flowers and these constitute rich-flowered spikes.

Detailed studies in the 'balsalmost' families are badly needed to elucidate the morphological and phylogenetic basement of the Lamiales. Regardless, it can be said that racemic inflorescences do not play a major role. The picture changes in the families following the Calceolariaceae–*Sanango*–Gesneriaceae clade(s). The first family in the succession is the Plantaginaceae, in which, apart from the two genera of Russeliaceae and four genera of Cheloneae, all (around 90) genera have racemic inflorescences. The two successive families, Scrophulariaceae and Stilbaceae, are the first ones having indeterminate inflorescences with ordinary cymes. Both include also racemic inflorescences. In the Scrophulariaceae thyrses/cymes of the ordinary type are represented in the majority of tribes. In the Aptosimeae, Buddlejaceae, Freyliniaceae, Scrophulariaceae and Teediaceae all or the majority of genera have cymes (see Table S1). In the Stilbaceae only one of the three tribes includes genera with cymes (Bowkeriaceae, with two genera having cymes and one having single flowers in the leaf axils; see Table S2), while the rest (ten genera) have racemic inflorescences.

What is important here is that none of the families mentioned so far seems to have inflorescences that could be regarded as particularly close to PFCs. However, there is one taxon which is, according to recent molecular data, in some way related to the families with PFCs: the (as to family unplaced) genus *Peltanthera*. Its phylogenetic position and its inflorescence structure will be addressed in the following section.

#### THE GENUS *PELTANTHERA* AND THE ORIGIN OF THE PFC

##### *Peltanthera* and its position within the Lamiales

The genus *Peltanthera* was previously placed in Loganiaceae and Buddlejaceae (e.g. Bentham, 1876a; Leeuwenberg and Leenhouts, 1980; Norman, 2000). Its only species, *P. floribunda*, is represented by small trees occurring in Central and northern South America and having small, actinomorphic flowers. Oxelman *et al.* (1999) were the first to recognize that *Peltanthera* belongs to the Lamiales and suggested a position sister to *Sanango* + Gesneriaceae (represented by a single species of *Streptocarpus* and *Nematanthus*). Since then *Peltanthera* has been included in several molecular analyses. Its position varies as to the particular studies. This will be addressed in more detail in the section ‘Phylogenetic scenarios’. In any topology *Peltanthera* diverges earlier than Gesneriaceae and *Sanango*, sometimes ‘earlier’ and sometimes ‘later’ than Calceolariaceae. The genus is possibly the last remnant of a once larger group which evolved from oleaceous-like ancestors (with tree-like, woody habit!) and which gave rise to the remaining Lamiales with generally zygomorphic flowers. If the axillary partial inflorescences are cymes of the ordinary type, it would be almost inevitable to assume that the PFCs have originated from

ordinary cymes by elaboration, that is by *de novo* acquisition of the front-flowers (hypothesis Ac above). If they represent elaborate branching systems (more elaborate than PFCs, panicles in the widest sense) it would seem likely that the PFCs originated by reduction, with the front-flowers being remnant flowers (hypothesis B above).

##### The inflorescences of *Peltanthera*

The most detailed reference to the inflorescences was by Norman (2000, under Buddlejaceae), who described the inflorescences as many- and small-flowered panicles and referred to their position as terminal and axillary. The somewhat close relationship of *Peltanthera* to Gesneriaceae (and Calceolariaceae) gives some general support to the idea that the PFCs of these families have originated from panicle-like branching systems as represented in *Peltanthera*. The two opposite basal branches of the panicle are strong (Fig. 6C) and it is easy to imagine that they would ‘survive’ in case of reduction of the panicle to a few-flowered system.

The author’s investigations in Costa Rica (unpubl. data) revealed that *Peltanthera floribunda* is a small tree (Fig. 6A) with the branches showing monopodial (but seasonally interrupted) growth. The most interesting point is that at the end of the panicle branches usually (but not always) four-flowered aggregates are present that consist of a terminal flower, a second flower in frontal (median-abaxial) position, and two lateral flowers emerging from a node below the frontal flower (Fig. 6D, E). The terminal and the frontal flower show some precocious development, opening before the lateral flowers and most other flowers of the panicle branch. Remarkably, neither the lateral flowers nor the frontal flower are subtended by bracteoles, while the more basal branches of the partial inflorescence are.

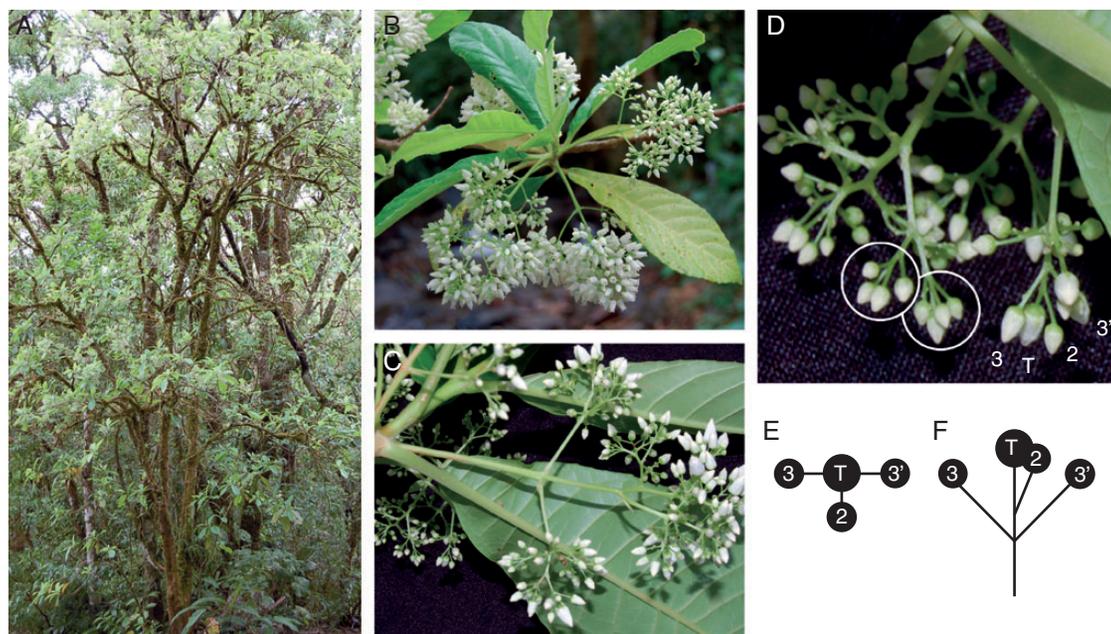


FIG. 6. *Peltanthera floribunda*. (A) Tree habit. (B) Branchlet of tree with inflorescences. (C) Inflorescence; note position in axil of foliage leaf and paniculate structure, with two vigorous side branches at base. (D) Detail of (C); note four-flowered aggregates on top of panicle branches. (E, F) Corresponding diagrams. Photographs: A. Weber.

It may be that the terminal flower pair corresponds to the flower pair at the end of the cyme units of Calceolariaceae, Gesneriaceae and Plantaginaceae. The PFC now can be (formally) derived from the *Peltanthera* inflorescence by assuming the following steps: (1) genetic fixation of the frontal flower, (2) successive reduction of the nodes between the basal = prophyll node and the node of the frontal flower (that is including the node of the two lateral flowers in the four-flowered aggregates of *Peltanthera*), (3) increasing morphological homogenization of the branching units and (4) progression to a sympodial branching pattern (successive branching from the axils of the prophylls, perhaps in compensation for the loss of nodes and their flowers).

### Conclusions

The truly paniculate structure of the inflorescences of *Peltanthera* favours an origin of PFCs through reduction. Nonetheless, it must be clear that the inflorescence of *Peltanthera* is not immediately ancestral to the PFC of Calceolariaceae and Gesneriaceae (and perhaps Plantaginaceae). At the moment no taxa are known which could serve to bridge the morphological gap between the two types.

### PHYLOGENETIC SCENARIOS OF PFC ORIGIN

At first sight, the phylogenetic interpretation of the distribution of PFCs in the Lamiales seems easy. As they are found in three families that form two or three successive clades in molecular phylogenies, it seems likely that PFCs have originated once, that is in the ancestors of Calceolariaceae and Gesneriaceae, and have been inherited to the Plantaginaceae (Fig. 7). In the Plantaginaceae they have survived in the clade Russelieae + Cheloneae, but became extinct in the large remainder of the family in that the PFC was reduced to a single flower and the thyrses progressed to a raceme. Extinction was apparently forever: PFCs do not turn up in any of the subsequent families of 'basal' Lamiales and in the 'core' Lamiales. If this scenario is true, the ordinary cymes found in these families may have evolved from PFCs by reduction of the front-flowers in the cymes, as was noted above for two species in the Gesneriaceae.

Remarkably, the situation is not as simple as that. Molecular phylogenies are partly, but not unambiguously, in agreement. While the 'basement' of the Lamiales seems to be rather stable in the molecular phylogenies, the topologies of Calceolariaceae, Gesneriaceae and Plantaginaceae vary. The statement by Oxelman *et al.* (2005: 414) that: 'There is emerging support that the bulk of "core" Lamiales does not include Calceolariaceae, Gesneriaceae, *Sanango*, and *Peltanthera*. The relationships among these are, however, contradictory' is still valid. Moreover, so far no major attempts have been made to correlate the molecular phylogenies with the distribution and evolution of morphological characters. Apart from inflorescence morphology, the present alliance is of particular interest as to floral symmetry. The Plocospermataceae, Carlemanniaceae, Oleaceae and Tetrachondraceae have radially symmetric and (except Plocospermataceae) usually tetramerous flowers. Bilateral symmetry or slight zygomorphy is reached in the Carlemanniaceae and Oleaceae by reduction of the four stamens to two. The Calceolariaceae and the Gesneriaceae are the first diverging families in which the flowers are strongly zygomorphic. There seems

to be a strong correlation between pronounced floral zygomorphy and the lack (phylogenetic loss) of a terminal flower in the inflorescences. In the families under consideration and their ancestors, respectively, the switch from determinate to indeterminate inflorescences and radial to zygomorphic flowers seems to go hand in hand, but may have not been reached in one step. This is the possible reason that phylogenetic reconstruction is rather difficult. Apparently there is a deep gap (resulting from almost complete extinction of linking lineages) between the 'basalmost' (Plocospermataceae to Oleaceae) and the 'higher' families of the 'basal' Lamiales. *Peltanthera* could be the last survivor of an alliance that once gave rise to the evolution of families with PFCs and zygomorphic flowers.

There are two critical points to be discussed in detail: (1) the position of *Peltanthera*, and (2) the relationships within Plantaginaceae.

### Position of *Peltanthera*

Conflicting phylogenies have been published as to the position of *Peltanthera*, which also concern the phylogenetic relationship between Calceolariaceae and Gesneriaceae. As compared with *Peltanthera*, the position of *Sanango* is much more stable. This genus appears always in closer vicinity of Gesneriaceae than *Peltanthera* and holds a sister position to that family in all molecular studies where *Sanango* has been included. From the different positions of *Peltanthera*, a single, a double and a triple origin of the PFCs can be inferred.

*Scenario 1: PFCs originated once* (Fig. 8A). From all available molecular phylogenies only Qiu *et al.* (2010) support this scenario to some extent. This phylogeny is interesting as it is the only one based on (four) mitochondrial genes. Support for the Lamiales, Oleaceae (*Syringa*) and *Peltanthera* is moderate [bootstrap support (BS) values between 75 and 80] and high for the sister clades branching off from the node following

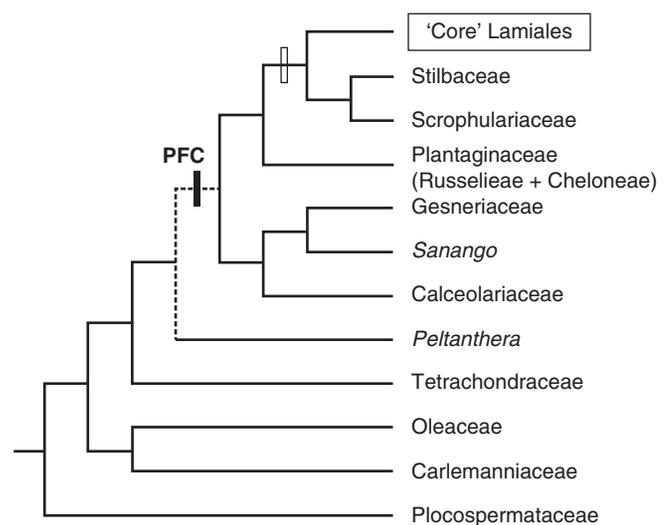


FIG. 7. Phylogeny of the 'basal' Lamiales (*sensu* Olmstead, 2002) under the assumption that PFCs have originated once, have survived in the sister clades Russelieae and Cheloneae of Plantaginaceae, and became extinct in the common ancestor of Scrophulariaceae, Stilbaceae and 'core' Lamiales (C). Note, however, that the position of *Peltanthera* is uncertain (dotted line).

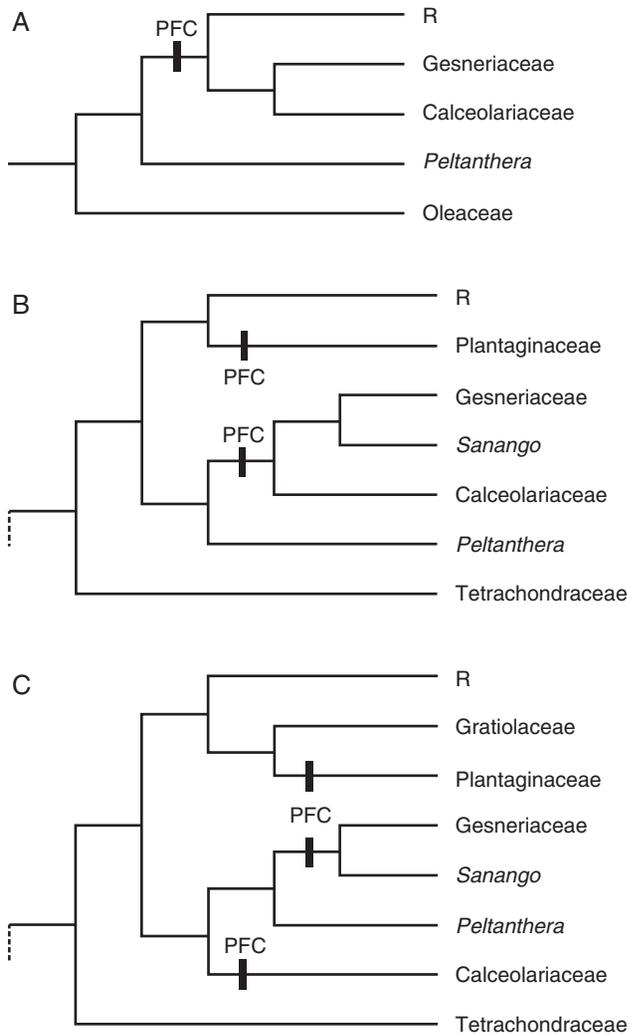


FIG. 8. Phylogenetic scenarios regarding the origin of PFCs in the 'basal' Lamiales as emanating from different molecular phylogenies. (A) Single origin (Qiu *et al.*, 2010: extract of fig. 2/6 relating to the Lamiales); weakly supported internal topology of R (= remainder of Lamiales, including Plantaginaceae) not shown. (B) Double origin (Olmstead, 2002; N. Refulio and R. G. Olmstead, pers. comm.). (C) Triple origin (Wang *et al.*, 2004; Perret *et al.*, 2013); Plocospermataceae and Carlemanniaceae + Oleaceae not shown. Black bar: origin of PFCs in the common ancestor. For simplicity, the (groups of) generic names are replaced by family names.

*Peltanthera*: one clade comprises Calceolariaceae + Gesneriaceae (BS 96) (*Sanango* was not included in the study), and the other clade (BS 92) comprises a grade of the 'higher' Lamiales (nine families, including Plantaginaceae). Support for the particular families within the grade is low (BS between 20 and 40).

On the one hand, the position of *Peltanthera* supports well the idea that PFCs have originated once in the 'basal' Lamiales. On the other hand, the tree does not show where they became extinct. The Plantaginaceae (and Scrophulariaceae) turn up at the top of the 'core' Lamiales. However, in view of the generally low support values in the grade this position should not be weighed too strongly.

**Scenario 2: PFCs originated twice (Fig. 8B).** This is the scenario suggested by Olmstead (2002), Soltis *et al.* (2011), and N. Refulio and R. G. Olmstead (unpubl. data). In these phylogenetic trees *Peltanthera*, Calceolariaceae, *Sanango* and Gesneriaceae are on a clade which is sister to a grade of Plantaginaceae, Scrophulariaceae, Stilbaceae and the 'core' Lamiales. According to this topology, the assumption of a double origin of the PFC is almost inevitable: PFCs have developed in the ancestors of Calceolariaceae and Gesneriaceae, from which group *Peltanthera* is perhaps the last survivor, and independently in the Plantaginaceae (more precisely: in the common ancestors of Russelieae and Cheloneae). The question remains: from which type of inflorescences did the PFCs of Russelieae and Cheloneae evolve?

**Scenario 3: PFCs originated triply (Fig. 8C).** A triple origin of the PFC (and zygomorphic flowers) is suggested by the phylogenies of Wang *et al.* (2004), Oxelman *et al.* (2005) and Perret *et al.* (2013). The content of the clade with Gesneriaceae is the same as in the trees of scenario 2, but the succession of the taxa is different: Calceolariaceae branch off earlier than *Peltanthera*, *Sanango* and the Gesneriaceae.

Another remarkable difference is that the clade sister to the Gesneriaceae contains a (topologically) basal clade of Gratiolaceae + Plantaginaceae, while in the trees of scenario 2 the *Gratiola*-alliance is an ingroup of Plantaginaceae. Gratiolaceae (like Linderniaceae) were at first recognized as a distinct family by Rahmanzadeh *et al.* (2005) but (unlike Linderniaceae) this family has not been generally accepted (APG III, 2009).

Again the question remains open: from which inflorescence type did the PFCs of Calceolariaceae and Plantaginaceae evolve?

#### Relationships and distribution of PFCs within the Plantaginaceae

The family Plantaginaceae has been essentially shaped by Olmstead *et al.* (2001), Oxelman *et al.* (2005) and Albach *et al.* (2005). These studies and in more detail those of Wolfe *et al.* (2002, 2006) show (1) that *Russelia* and *Tetranema* are sister genera, constituting the tribe Russelieae, and (2) that the Russelieae and Cheloneae are sister groups, forming (together with *Uroskinnera*) a clade.

There is slight uncertainty about the position of *Collinsia*: in some topologies it branches off earlier than the remainder of Cheloneae (Oxelman *et al.*, 2005), while in the targeted studies on Cheloneae (Wolfe *et al.*, 2002, 2006) *Collinsia* appears as an ingroup of Cheloneae, branching off at the node following *Pennellianthus*.

**Racemes in the Cheloneae.** Within Cheloneae, the genera that have racemic inflorescences do not form a coherent group, but appear scattered over the tribe. If, as some studies suggest, Russelieae and Cheloneae are sister groups, and given the scattered distribution of taxa with racemic inflorescences within Cheloneae, then the most parsimonious hypothesis is that the ancestor of both tribes had PFCs and that racemic inflorescences evolved at least twice independently in Cheloneae. From its position sister to Cheloneae, the racemic inflorescence of *Uroskinnera* apparently evolved from PFCs too.

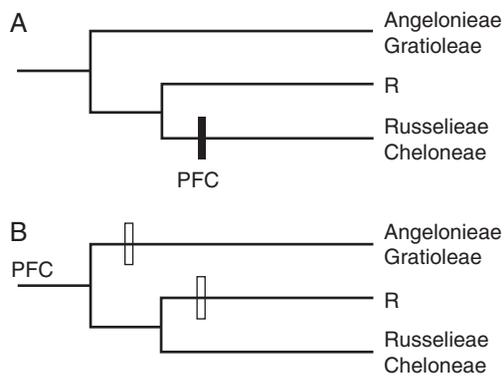


FIG. 9. Contrasting interpretations regarding the occurrence of PFCs in the Plantaginaceae. (A) Interpretation 1: PFCs have originated *de novo* in the ancestors of Russelieae and Cheloneae. (B) PFCs have been inherited from an ancestor with PFCs; loss (reduction of PFCs to single flowers) was in two lineages and successive steps: Angelonieae + Gratioleae and the remainder of Plantaginaceae (R). Topology according to Olmstead *et al.* (2001) and Oxelman *et al.* (2005), genera subsumed under tribal names.

*Presence of PFCs: a synapomorphy or a symplesiomorphy?* There is reasonable consensus about the internal structure of the family, at least with respect to the nodes relevant here (Fig. 9). Similar topologies, but usually with fewer genera, are seen in Olmstead *et al.* (2001: figs 1, 2), Schäferhoff *et al.* (2010: figs 2, 3) and in the ten-gene analysis of N. Refulio and R. G. Olmstead (unpubl. data; R. G. Olmstead, pers. comm.): the clade of Russelieae and Cheloneae does not branch off from the first node, but from a second one.

*Interpretation 1: PFCs are synapomorphic of the Russelieae-Cheloneae clade (Fig. 9A).* In view of the fact that in the Plantaginaceae the bulk of the genera have racemic inflorescences it appears reasonable to interpret the occurrence of the discordant inflorescence type as a synapomorphy. Indeed, Wolfe *et al.* (2002, 2006) explicitly argue that the ‘cymose’ inflorescences of Russelieae-Cheloneae would represent a synapomorphy of the two clades. In view of the fact that (ordinary) cymes are common in the Lamiales (especially the ‘core’ Lamiales), this interpretation is indeed most plausible, at least as long as the Plantaginaceae are seen in isolation.

*Interpretation 2. PFCs are plesiomorphic in the Russelieae-Cheloneae clade (Fig. 9B).* This interpretation assumes that the PFCs have been inherited from (gesnerioid-like?) ancestors. This would mean that PFCs were lost in two successive steps: (1) in the Angelonieae + Gratioleae clade, and (2) in the clade sister to Russelieae + Cheloneae, comprising the whole remainder of Plantaginaceae (R).

Other topologies do exist, but are of little relevance. In the *rps16* tree of Albach *et al.* (2005) the backbone branching is similar, but Gratioleae appear as the sister group of Russelieae + Cheloneae and the remainder includes the Angelonieae. The two above interpretations apply in the same way as discussed. In the phylogeny of Perret *et al.* (2013; including five genera of Plantaginaceae) *Tetranema* (the only member of Russelieae-Cheloneae included in the analysis) appears as the topologically lowermost clade in Plantaginaceae. At first sight, this appears to be in agreement with the idea that the Russelieae-Cheloneae are the most primitive alliance in the Plantaginaceae.

However, the family is topologically preceded by the Linderiaceae and Gratiolaceae, both with racemic inflorescences.

*Conclusions.* The many scenarios emanating from the molecular-phylogenetic studies clearly illustrate the difficulties of interpreting the phylogenetic origin and inheritance of PFCs in the given alliance. It is clear that the scenarios are not equivalent (being based on different numbers and kinds of genes and taxa) and are not all equally well supported. It is impossible to discuss and to evaluate the studies mentioned above in detail. The most authoritative studies suggest a combination of scenario 2 (double origin of PFCs) and interpretation 1 (PFCs are synapomorphic to Russelieae and Cheloneae), meaning that PFCs originated twice: in the common ancestors of Calceolariaceae and Gesneriaceae and, within Plantaginaceae, in the common ancestors of Russelieae and Cheloneae.

If PFCs represent characters such as an inferior ovary, indehiscent fruit or racemic inflorescence, in other words characters that are known to have originated many times in angiosperm evolution, there would be no reason for considering seriously alternative interpretations. PFCs, however, are special in several respects: (1) they are not known from families outside the Lamiales, (2) within the Lamiales they are only known from three major families (+ *Sanango*) that turn up in close proximity in all recent molecular phylogenies, (3) they are almost omnipresent in the Calceolariaceae and Gesneriaceae, representing here surely the original condition of inflorescence organization, and (4) appear to ‘fade out’ in the clade following these families (Plantaginaceae). Therefore, the combination of scenario 1 (single origin of PFCs) and interpretation 2 (PFCs are plesiomorphic in the Russelieae and Cheloneae) should not be dismissed completely, although molecular support is not optimal.

The main problem is the position of *Peltanthera*. From a morphological point of view (as to both the presence of PFCs and zygomorphic flowers) the most logical position is ‘ahead’ of all taxa mentioned, as shown in the ‘combined tree’ of Fig. 7. The only molecular support for this position so far is the study of Qiu *et al.* (2010). Less problematic is the occurrence of PFCs in the Plantaginaceae. The idea that PFCs were inherited from the common ancestors of Calceolariaceae and (*Sanango*+) Gesneriaceae and conserved in the Russelieae and Cheloneae, but were lost (by reduction to single flowers) in two successive steps in the remaining Plantaginaceae, is probably an reasonable option, although it is not the most parsimonious one. If it is true that *Peltanthera* is a relict of a once larger group (see above), the Russelieae (and successively the Cheloneae) may have evolved from a different (perhaps northern Meso-American) section of this group, which possibly had similar inflorescences as *Peltanthera*. A double origin of PFCs then would be no longer a great surprise.

## CONCLUDING REMARKS

PFCs are shown to represent a morphological character that has been largely overlooked or ignored by plant systematists so far. Their occurrence in four, in some way coherent taxa seems easy to explain: they have originated in the ancestors of Calceolariaceae, *Sanango* and Gesneriaceae and inherited to the Russelieae-Cheloneae alliance in the Plantaginaceae. In the remainder of that family and in the ancestors of the subsequent

families of Lamiales they became extinct, by reduction either to ordinary cymes or to single flowers, giving rise to conventional thyrses and racemes, respectively. The available molecular phylogenies are, however, ambiguous and alternative interpretations, suggesting a double (or even triple) origin of PFCs, have to be taken into consideration. Virtually nothing is known about the ecological significance of PFCs. Generally speaking, this applies also to the ordinary cymes and racemes in the Lamiales. Presently, we have at best a rough picture of the occurrence of various ‘inflorescence types’ in the Lamiales (and even that is very fragmentary in the basalmost families), but our phylogenetic and ecological understanding is very poor. Questions such as ‘why did thyrse inflorescences proceed to racemic ones (and vice versa)?’ and ‘what is the correlation of inflorescence structure with the habitat, with the ecophysiology, with the flower structure, with the pollinators etc.?’ have been little addressed so far. One of the few studies in which inflorescence structure, plant habit and habitat are seen in a context is that of Chautems and Weber (1999), relating to the species of *Sinningia* (Gesneriaceae).

Today, molecular studies provide an increasingly reliable basis for recognizing and understanding morphological changes and progressions. Traditional inflorescence morphology, especially the ‘typology’ of Wilhelm Troll and collaborators (Troll, 1964, 1969; Troll and Weberling, 1989; Weberling and Troll, 1998; Weberling, 1992), is a rather static approach, attempting to establish a solid classification throughout the angiosperms and to develop an adequate terminology. With regard to phylogenetic inferences, readers are largely left to their own devices. The Lamiales, in particular the large series of families with indeterminate inflorescences, could serve as a model system to address various phylogenetic and ecological questions. A prerequisite is an increasing solidity of phylogenetic reconstructions, that is analysis of more taxa and more genes. Understandably, in available multigene analyses such as the 17-gene analysis of Soltis *et al.* (2011) many families are represented by a single species only. A forthcoming paper by Refulio and R. G. Olmstead, dealing specifically with the Lamiales, and based on ten genes (R. G. Olmstead, pers. comm.), will provide a better basis. However, for understanding variations and progressions in inflorescence morphology and the driving forces behind them, molecular phylogenies at the generic and specific level will be needed. The application of modern methods (such as ancestral state reconstruction methods) and conceptual frameworks (such as the ontogenetic approach of Classen-Bockhoff and Bull-Hereñu, 2013) must and will play a significant role in future concepts and understanding of inflorescence morphology.

#### SUPPLEMENTARY DATA

Supplementary data are available online at [www.aob.oxfordjournals.org/](http://www.aob.oxfordjournals.org/) and consist of the following. Table S1: inflorescences of Scrophulariaceae (*s.s.*). Table S2: inflorescences of Stilbaceae. Table S3: representative herbarium specimens of Plantaginaceae with PFCs (W, WU). Table S4: full scientific names of all genera and species referred to in the paper. Figs S1–4: structure and variation of PFCs. (S1) Presence of  $\gamma$ -bracteoles and axillary position of front-flowers. (S2) Variation of PFCs as to length of internodia and branching symmetry. (S3) Displacement of bracteoles. (S4) Irregular reduction

and loss of front-flowers. Figs S5–7: ontogeny of PFCs. (S5) Ontogeny of PFC, documentation by cleared whole mounts. (S6) Ontogeny of PFCs, SEM documentation. (S7) Homaxonic (scorpioid) cymes showing pseudo-monopodial development. Fig. S8: front-flowers and accessory cymes in Gesneriaceae. Figs S9–29: presence of PFCs in Calceolariaceae, *Sanango*, Gesneriaceae and Plantaginaceae (where appropriate, showing variation along the standard series). Figs S9–11: Calceolariaceae. (S9) *Calceolaria*, (S10) *Jovellana*, (S11) ‘*Porodittia*’ (= ‘*Stemotria*’). Figs S12, 13: *Sanango* (S12) and Gesneriaceae (S13). Figs S14, 15: Plantaginaceae–Russellieae: (S14) *Russelia*, (S15) *Tetranema*. Figs S16–19: Plantaginaceae–Cheloneae, genera with PFCs (1): (S16, S17) *Penstemon*, (S18) *Nothochelone*, (S19) *Pennellianthus*. Figs S20–24: Plantaginaceae–Cheloneae, genera with PFCs (2): (S20) *Keckiella antirrhinoïdes*, (S21) *K. breviflora* and *K. lemmonii*, (S22) *K. rothrockii*, (S23) *K. cordifolia* and *K. corymbosa*, (S24) *K. ternata*. Figs S25–27: Plantaginaceae–Cheloneae, genera with single axillary flowers (1): (S25) *Chelone*, (S26) *Chionophila*. Figs S27–29. Plantaginaceae–Cheloneae, genera with single axillary flowers (2): (S27) *Collinsia*, (S28) *Tonella*, (S29) *Uroskinnera*.

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