

Inflorescence development of Whytockia (Epithemateae, Gesneriaceae) and phylogenetic implications within Gesneriaceae.

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Inflorescence development of *Whytockia* (Epithemateae, Gesneriaceae) and phylogenetic implications within Gesneriaceae

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Abstract. The inflorescence development in *Whytockia* has been studied in order to explore the developmental basis for inflorescence architecture. The developmental pattern of the pair-flowered cyme in *Whytockia* basically conforms to that of most members in Gesneriaceae. However, the additional flower beside the terminal one in *Whytockia* is not equivalent to the frontal flower as in other Gesneriaceae because the former is located in the front-lateral position while the latter is in the front-median position. Also, the zigzag monochasial branching system in *Whytockia* represents the consecutive front-lateral branches rather than the lateral branches as in other Gesneriaceae. The inflorescence in *Whytockia* is flowering in a basipetal sequence, and its seemingly acropetal flowering sequence is due to the vigorous development of the consecutive front-lateral branches. In addition, the inflorescence of *Whytockia* does not represent the basic unit of the inflorescence in Epithemateae, and it is derived as compared to that of *Rhynchoglossum*. The development relationships of the inflorescence between *Whytockia* and its allies in Epithemateae are discussed on the basis of developmental and comparative evidence.

Key words: Gesneriaceae, *Whytockia*, development, pair-flowered cyme, inflorescence architecture.

Introduction

The genus *Whytockia* W.W. Smith, endemic to China, has an axillary, simple and ebracteate pair-flowered cyme that is unique to *Whytockia* in the tribe Epithemateae (Fig. 1). This inflorescence is interpreted as the basic unit of the inflorescence evolution in Epithemateae, and the compound and bracteate inflorescence may be derived from that of *Whytockia* (Weber 1976b, 1977, 1978a). Based on this interpretation, *Whytockia* is considered as the most primitive representative of Epithemateae and an ancient relic of the stock from which the other groups of Epithemateae have evolved (Burt 1978; Weber 1982a). Nevertheless, the inflorescence, especially the inflorescence development, has not been studied intensively in the past except for observations of the gross external morphology from dried specimens.

Compared with the conventional cymes in which each unit is terminated by one flower, such as that of *Scrophularia* (Scrophulariaceae) (Weber 1982b, Weberling 1989), the cymes in the Gesneriaceae exhibit an unorthodox structure in which each cyme unit ends with a

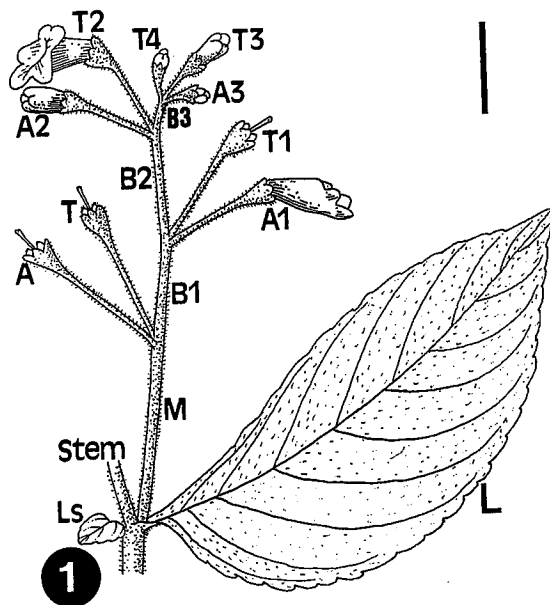


Fig. 1. Drawing of the pair-flowered inflorescence in the axil of the large leaf in *W. hekouensis*, showing flower pairs being born in two rows alternately on the front side of inflorescence axis and no bract subtending the flowers. Note that the inflorescence seems flowering in the sequence from the base to the top, i.e. in an acropetal sequence. Scale bar = 14 mm. **Abbreviation:** A main-axis additional flower (primordium); A1 first-level-branch additional flower (primordium); A2 second-level-branch additional flower (primordium); A3 third-level-branch additional flower (primordium); B1 first-level-branch axis; B2 second-level-branch axis; B3 third-level-branch axis; F two floral primordia below the main-axis terminal flower; I inflorescence primordium; L large leaf (primordium); Ls small leaf (primordium); M main axis of inflorescence; T main-axis terminal flower (primordium); T1 first-level-branch terminal flower (primordium); T2 second-level-branch terminal flower (primordium); T3 third-level-branch terminal flower (primordium); T4 fourth-level-branch terminal flower (primordium); Uc upper calyx lobe

flower pair, which is termed as pair-flowered cyme (Weber 1978b, 1982b). The pair-flowered cyme is the basic type of the inflorescences in the Gesneriaceae. According to Weber (1978b), this flower pair consists of a true terminal flower and an additional flower, also called frontal flower, for it is located in the axil of the front-median bract. The tribe Epithe-

mateae has been traditionally placed in the subfamily Cyrtandroideae. However, the inflorescences in Epithemateae are diverse with racemose, paniculate and capitate-cincinnal cymose, one-flowered or pair-flowered (Burt 1977; Weber 1978b, 1982b; Wang et al. 1997) types. Moreover, the inflorescences in case of the pair-flowered cyme in Epithemateae, especially that of *Whytockia*, seem racemose (Burt 1977, see also Fig. 1), and each flower pair is located on the front-lateral (alternate right and left) side without subtending bract (Fig. 1), rather than in the front-median position with subtending bract. This branching system is morphologically distinctive from that of other Gesneriaceae, especially Cyrtandroideae. It is unknown whether the pair-flowered inflorescence in Epithemateae is homologous with that of other Gesneriaceae or not. In addition, even though traditional classification schemes have placed the tribe Epithemateae in the subfamily Cyrtandroideae, it is sharply distinctive from the rest of Cyrtandroideae in a lot of morphological characters (Burt 1977, Wang et al. 1997, Wang and Pan 1998). The cladistic analyses based on both morphological data and *ndhF* sequence data consistently support the tribe Epithemateae as a separate monophyletic subfamily within the Gesneriaceae (Smith 1996, Smith et al. 1997). A precise morphological understanding of the pair-flowered cymes in *Whytockia* is not only a point of morphological interest, but also has considerable phylogenetical bearings.

Frequently, homology is difficult to interpret and to determine on a morphological basis without developmental evidence. Developmental data are valuable to decide whether taxonomically important structures of flower and inflorescence are strictly homologous or convergent, and offer insights into the origins of particular structures (Crisci and Stuessy 1980, Kampny and Canne-Hilliker 1988). Therefore, the information on the inflorescence development of *Whytockia* is necessary to elucidate the phylogenetic relationship of taxa within Epithemateae and between Epithemateae and other Gesneriaceae, especially Cyrtandroideae.

The goal of this research is at first to explore the developmental basis for the inflorescence architecture of *Whytockia*, a key genus in the phylogeny of the tribe Epithemateae. Considering the above interpretations, this research also aims to gain an understanding of the homology in the inflorescence evolution through a comparative analysis of the early developmental stages of *Whytockia*, as a representative of Epithemateae, and other Gesneriaceae, especially Cyrtandroideae. The developmental relationships of inflorescences between *Whytockia* and its allies within the tribe Epithemateae are also discussed, taking into account other comparative and developmental evidence.

Materials and methods

Material of two species in *Whytockia*, *W. hekouensis* Y. Z. Wang and *W. bijieensis* Y. Z. Wang was collected from Yunnan and Guizhou (China). Young shoots and inflorescences at different developmental stages were fixed in formalin-acetic acid-alcohol (FAA). Voucher specimens (Wang, 93019, 95001) are deposited in the Herbarium (PE), Institute of Botany, the Chinese Academy of Sciences. Material used for SEM was dehydrated in 100% ethanol, 100% ethanol + amylacetate (1:1) and amylacetate, then critical point dried with a Hitachi HCP-2 Critical Point Dryer and Au/Pd Sputter coated with a SPI-MODULE sputter Coater. The prepared samples were examined with a Hitachi S-800 Scanning Electron Microscope (SEM) and photographed on Shanghai Panchromatic film.

Results

Organography. The aerial part of *Whytockia* bears several unequal opposite leaves, i.e. the large leaves and small leaves (Fig. 1). Ebracteate inflorescences are unbranched, emerging from the axils of the large leaves in the upper part of the stem (Fig. 1). Several flower pairs are born in two rows alternately along the front side of the inflorescence axis (Fig. 1). The inflorescence seems flowering in the sequence from the base to the top, i.e. in an acropetal sequence (Fig. 1). Therefore, the inflorescence

in *Whytockia* has been considered as racemose cyme or pseudo-raceme (Burt 1977).

Initiation and development. Each inflorescence is initiated in the axil of the third large leaf from the top of the vegetative shoot (Fig. 2). In an oblique polar view, the inflorescence primordium is tangentially oblong. It averages 130 μm in tangential diameter, 70 μm in radial diameter (Fig. 2). While growing upward, the inflorescence primordium gradually becomes ascendantly flattened (Fig. 3), and then develops into a single flower (Figs. 4, 5). This is the true terminal flower of the main axis of the inflorescence. When the upper calyx lobe of this terminal flower expands forward, two floral primordia almost simultaneously become visible on the front side below it (Fig. 4). The two floral primordia enlarge and become transversely circular in shape as five calyx lobes enclose the floral apex in the terminal flower (Fig. 5). Next, they elongate and become ascendantly flattened as the differentiation between the two floral primordia is manifested (Fig. 6). The left floral primordium becomes flattened earlier than the right floral primordium while the right elongates more than the left (Fig. 6). The left will develop into an additional flower of the main axis beside the terminal one, and there is no further branching below it, while the right will function as the first-level-branch terminal flower due to further development and branching taking place below it (Fig. 7). It is chance whether the right or the left develops into the main-axis additional flower or the first-level-branch terminal flower. Below the first-level-branch terminal flower (the right), the primordium of the first-level-branch additional flower appears on the front-right side, followed by the second-level-branch terminal flower on the front-left side (Fig. 7). Two tiny protuberances emerge on the front side below the main-axis additional flower (the left) (Fig. 7), but become suppressed after a very primary growth (Fig. 8). At the same time, an intercalary growth becomes active below the node bearing the first-level branch and results in a primary elongation of the main axis of the inflorescence (Fig. 7). Meanwhile, the

intercalary growth below the node bearing the second-level-branch terminal flower gives rise to a primary elongation of the first branch terminal flower is pushed up through the elongation of the first-level-branch axis (Figs. 7, 8). Thus, the first-level-branch terminal flower is pushed up through the elongation of the first-level-branch axis, while the main-axis additional flower stays beside the main-axis terminal flower (Figs. 7–10). When the floral apices of the main-axis additional flower and the first-level-branch terminal flower are enclosed by five calyx lobes, the upper and lateral calyx lobes gradually become visible in the first-level-branch additional flower and the second-level-branch terminal flowers, respectively (Fig. 8). The second-level-branch additional flower is initiated on the front-left side below the second-level-branch terminal flower,

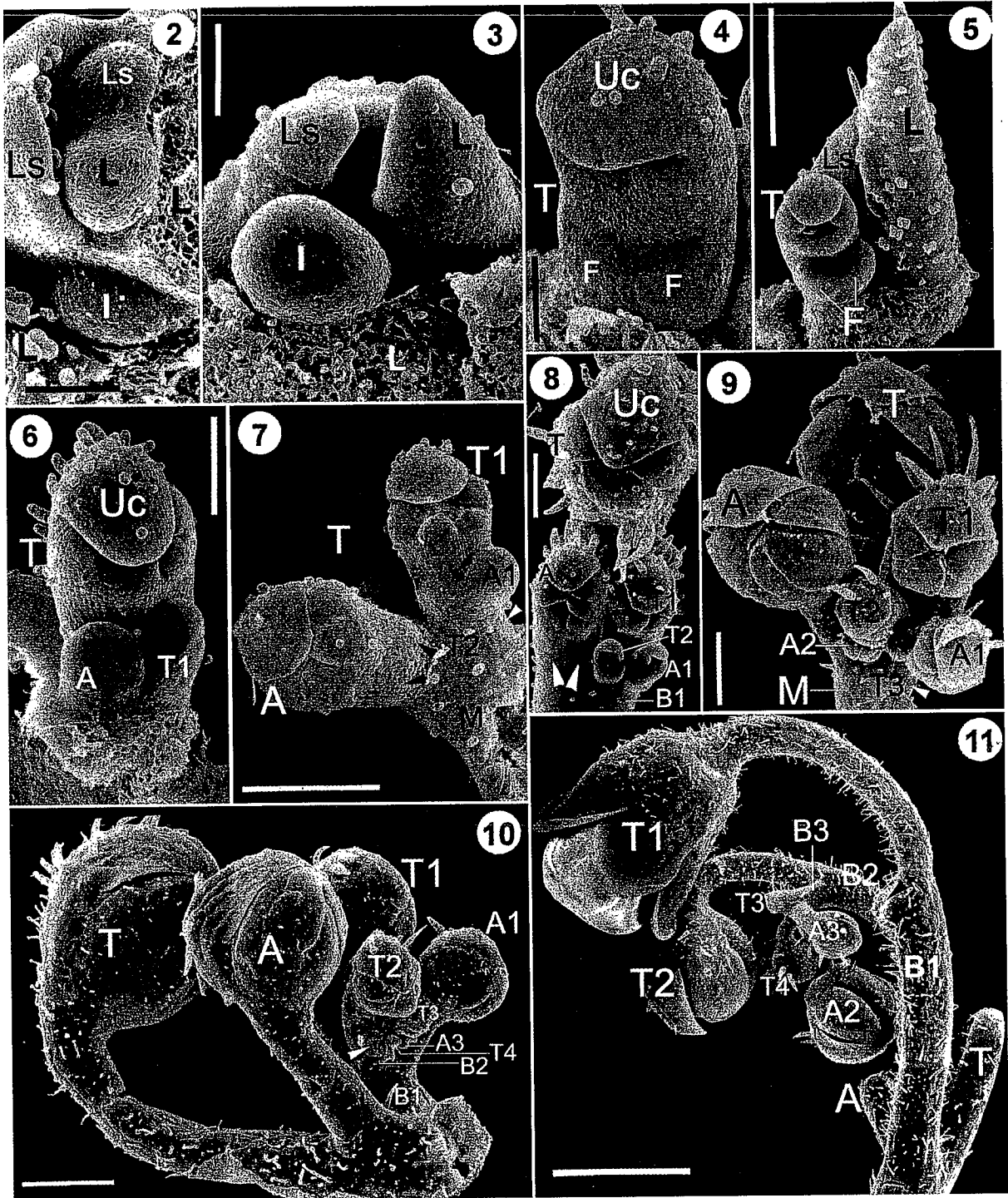
followed by the third-level-branch terminal flower on the front-right side (Fig. 9). Meanwhile, a primary elongation of the second-level-branch axis is led by the intercalary growth below the node bearing the third-level-branch terminal flower while the first-level-branch axis is further elongated (Fig. 10). Next, below the third-level-branch terminal flower, the primordium of the third-level-branch additional flower arises on the front-right side slightly earlier than the fourth-level-branch terminal flower on the front-left side (Fig. 10). The third-level-branch axis is formed by the intercalary growth below the node bearing the fourth-level-branch terminal flower while the first and second level branch axes are further more elongated (Fig. 11). The inflorescences are usually helicoid downward on the front side at the early development (Figs. 10, 11). During maturation,

Figs. 2–11. Initiation and development of inflorescence. *W. hekouensis* in Figs. 3, 5–11, *W. bijieensis* in Figs. 2, 4. **Fig. 2.** Oblique polar view, showing inflorescence primordium (I) and top of the vegetative shoot. Scale bar = 120 μm . **Fig. 3.** Oblique view of the ascendantly flattened inflorescence primordium. Scale bar = 118 μm . **Fig. 4.** Lateral view of the main-axis terminal flower (T), showing that when its upper calyx lobe (Uc) expands forward, two floral primordia (F) become visible below it. Scale bar = 112 μm . **Fig. 5.** Lateral view, showing that five calyx lobes of the main-axis terminal flower overarch to the floral apex while the two floral primordia (F) below it become transversely circular in shape. Scale bar = 446 μm . **Fig. 6.** Lateral view, showing that the floral apex is enclosed by five overlapped calyx lobes of the main-axis terminal flower and that the two elongated and ascendantly flattened floral primordia differentiate respectively into the main-axis additional flower (A) and the first-level-branch terminal flower (T1). Scale bar = 197 μm . **Fig. 7.** Oblique view showing early development of the calyx in the main-axis additional flower (A) and the first-level-branch terminal flower (T1), the initial primordium of the first-level-branch additional flower (A1) initiated earlier than that of the second-level-branch terminal flower (T2), a primary elongation of the main axis (M) and the first-level-branch axis (white arrowhead) of inflorescence, and two tiny protuberances (black arrowhead) emerging below the main-axis additional flower. Note that the main-axis terminal flower has been removed (T). Scale bar = 310 μm . **Fig. 8.** Stage slightly later than Fig. 7, showing the elongation of the first-level-branch axis (B1) of inflorescence, upper and lateral calyx lobes becoming visible in the first-level-branch additional flower (A1) and the second-level-branch terminal flower (T2), and two tiny protuberances (arrowhead) becoming suppressed after a very primary growth. Scale bar = 335 μm . **Fig. 9.** Inflorescence with seven initial flowers. Note early development of the second-level-branch additional flower (A2), the third-level-branch terminal flower (T3), and elongation of the main axis (M) and first-level-branch axis (arrowhead) of the inflorescence. Scale bar = 669 μm . **Fig. 10.** Lateral view of inflorescence with nine flowers initiated. Note the primordial initiation of the third-level-branch additional flower (A3) and the fourth-level-branch terminal flower (T4) (the second-level-branch additional flower at arrowhead has been removed), and primary elongation of the second-level-branch axis (B2) and further elongation of the first-level-branch axis (B1). Scale bar = 1184 μm . **Fig. 11.** Young inflorescence at the developmental stage containing nine flowers with further more elongation of branch axes, showing the inflorescence being helicoid downward on the front side. Note that the main-axis terminal (T) and additional (A) flower, the first-level-branch additional flower (arrowhead) and the third-level-branch terminal flower (T3) have been removed. Scale bar = 3184 μm

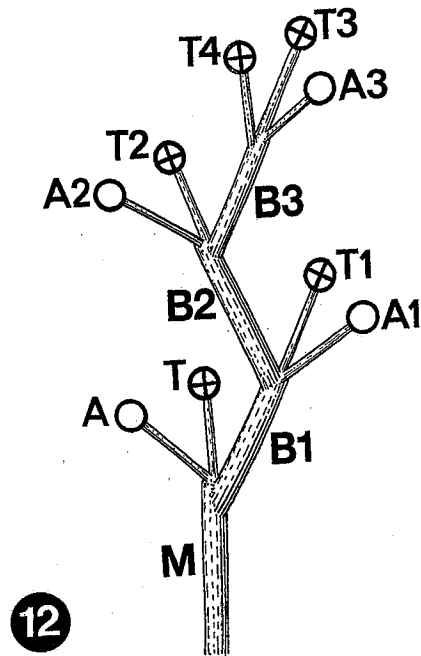
the helicoid inflorescence gradually becomes erect through continuous intercalary growth bringing about further elongation of consecutive branch axes while floral organs develop (Figs. 11, 1).

Discussion

The nature of the pair-flowered cyme in *Whytockia*. In Gesneriaceae, the development of pair-flowered cymes shows that the main



axis of inflorescences ends with a true terminal flower and an additional flower, i.e. frontal flower emerging slightly below the terminal flower in the axil of the front-median bract that is frequently suppressed (Weber 1978b, 1982b). Two lateral products (two lateral flowers or two lateral branches, i.e. paraclades) arise respectively in the axils of two opposite lateral bracts below the terminal flower. The following branches continuously repeat the same pattern, in which each branch ends with a terminal flower and an additional flower, i.e. a frontal flower (Weber 1978b, 1982b). In *Whytockia*, the inflorescence apex also transforms into a terminal flower. The main axis is closed by this main-axis terminal flower that is homologous to that of other Gesneriaceae. Below the main-axis terminal flower, two simultaneously initiated flowers function as the main-axis additional flower and the first-level-branch terminal flower, respectively. The main axis additional flower stays beside the main-axis terminal flower and there is no further branching below it. Meanwhile, the first-level-branch terminal flower is pushed up by intercalary growth, ending the first branch axis, and further development and branching continue downward below it (Fig. 12). Besides, the first-level-branch additional flower is initiated earlier than the second-level-branch terminal flower below the first-level-branch terminal flower. This time difference in initiation indicates that the first-level-branch additional flower and the second-level-branch are born at different nodes of the first-level-branch axis, in which the node bearing the former is higher than the one bearing the latter (Fig. 12). The following flowering and branching repeats the same pattern and forms terminal flowers alternately, in which the additional flowers are located above the next branches (Fig. 12). This developmental pattern thus results in a zigzag monochasial branching system of pair-flowered cyme in *Whytockia* (Fig. 12). The inflorescence in *Whytockia* is in fact flowering downward in a basipetal sequence, and the seemingly acropetal flowering sequences result from the vigorous development of the consec-



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Fig. 12. Diagram of the structure of the pair-flowered cyme in *Whytockia*, showing that the inflorescence is in fact a zigzag monochasial branching system, i.e. the consecutive front-lateral (alternate right and left) branches, in which the main axis or each branch axis ends with a terminal flower and an additional flower located on the front-lateral (alternate right and left) side of its related terminal flower

utive front-lateral (alternate right and left) branches (Fig. 12). Each of the consecutive front-lateral axes of cymose distal branches is aligned in the direction of the main axis, and so its respective terminal flower is pushed to one side together with an additional flower (Fig. 1). For that reason, the pair-flowered cyme in *Whytockia* looks unbranched and racemose (Fig. 1). In addition, even though the development of the pair-flowered cyme in *Whytockia* basically conforms to that of most members in Gesneriaceae, the additional flower beside the terminal one in *Whytockia* is not exactly equivalent to the frontal flower as in other Gesneriaceae because the former is located in the front-lateral position (Fig. 12) while the latter in the front-median position (Weber 1978b, 1982b). Moreover, the zigzag monochasial branching system in *Whytockia* represents the consecutive front-lateral

branches (Fig. 12) rather than the lateral branches as in other Gesneriaceae (Weber 1978b, 1982b). Apparently, the pair-flowered cyme of *Whytockia* is not exactly homologous to those in other Gesneriaceae. It represents a distinctively different kind of pair-flowered cyme in Gesneriaceae.

Weber (1978b, 1982b) suggested that the pair-flowered cyme in Gesneriaceae originated from a paniculate system through progressive loss of its upper branches, and the frontal flower was the remnant of a median branch above the prophyll-branches. According to Weber's suggestion (1978b, 1982b), each two initial flowers below the terminal one in *Whytockia* may be derived from two front-lateral branches, respectively. In the two front-lateral (alternate right and left) branches, the superior one becomes reduced to a single flower through progressive loss of its lateral flowers except the terminal one, while the inferior one still maintains the characteristics of branching. This view is further confirmed by the two suppressed floral primordia below the main-axis additional flower. In fact, two suppressed floral primordia are frequently present below the additional flowers in following branches. So, if the flower pair of the cyme in *Whytockia* is considered as derived from inflorescence branches of a paniculate system, the additional flower should be interpreted as the remnant of a front-lateral branch rather than a median branch. The zigzag monochasial branching system has probably originated from another front-lateral branch but not from a lateral branch as the branching system in other Gesneriaceae. These front-lateral axes are produced from the main axis below the main-axis terminal flower, and in a certain sense repeat the architecture of the main shoot.

In addition to the inflorescence development, some morphological features are also exclusive with Epithemateae in Gesneriaceae, such as the terminal racemes (in *Rhynchoglossum*), short ovoid ovary sharply contracted into the style, presence of secretory canal, and four separate ventral vascular bundles (in *Whytockia*) and so on (Burt 1977, 1998; Wang

et al. 1997; Wang and Pan 1998). Based on morphological characters, it is frequently suggested that the Epithemateae should be removed from Cyrtandroideae to a subfamily (Burt 1977, 1998; Smith 1996; Wang and Pan 1998). The cladistic analysis based on *ndhF* sequence data also shows that the tribe Epithemateae is monophyletic and is the sister group to the remainder of the Gesneriaceae (Smith et al. 1997). The inclusion of Epithemateae within the subfamily Cyrtandroideae would lead to a paraphyletic Cyrtandroideae, and the removal of this tribe to a subfamily would result in monophyletic Cyrtandroideae (Smith et al. 1997). Apparently, the evidence both from morphology and DNA sequence is strongly in favour of the interpretation for the pair-flowered cyme in *Whytockia*. The two kinds of pair-flowered cymes in Gesneriaceae are probably both derived from a paniculate axillary system. Evolution may have started from the same ancestral paniculate type and proceeded to two distinctively different kinds of pair-flowered cymes.

Comparison of the inflorescence between *Whytockia* and allies. Weber (1977, 1978a, 1982a) argued that the vegetative apical growth existed only in *Whytockia*, and that the simple and ebracteate pair-flowered racemose-cyme of *Whytockia* was the truly axillary inflorescence in Epithemateae. This consideration made him interpret the inflorescence of *Whytockia* as the basic unit in the inflorescence evolution of Epithemateae. The different types of bracteate inflorescence, such as the paniculate pair-flowered or one-flowered cymes, racemes and capitate-cincinnal cymes, are considered to be derived from the flower-bearing portion of the stem in *Whytockia* through suppression of the vegetative apical growth in phylogeny (Weber 1976b, 1977, 1978a, 1982a). The racemose inflorescence of *Rhynchoglossum* can be derived from the flower-bearing portion of the stem in *Whytockia* by further extreme condensation of the stem internodes, reduction of epicotyledonary leaves to tiny bracts, and each inflorescence to a single flower during phylogeny (Weber

1978a). Even though the erect and simple stem seems monopodial, the growth of the stem in *Whytockia* is not the truly apical activity (Wang 2000). In fact, the aerial part of *Whytockia* branches in a sympodial way (Wang 2000). Its so-called simple stems are the different level branch systems formed by the successive sprouts of the lateral buds in the axils of the small leaves (Wang 2000). The development of the stem in *Whytockia* is not in favour of the precondition of Weber's interpretation for the inflorescence evolution in Epithemateae (Weber 1978a, 1982a). Besides, the inflorescence primordium in *Whytockia* wholly transforms into a terminal flower and the following flowering continues downward below the terminal one. However, the apical meristem of the inflorescence in *Rhynchoglossum* remains active throughout the inflorescence development and permanently detaches floral primordia alternately in two directions at the front side (Weber 1978a, Wang et al. 1997). The inflorescence development of *Whytockia* is derived as compared to that of *Rhynchoglossum*. Furthermore, the initiation of flowers in two directions on the front side both in *Rhynchoglossum* and *Whytockia* implies a relationship between the inflorescence developments of the two genera. The development of this peculiar pair-flowered cyme in *Whytockia* may be connected with that of the raceme in *Rhynchoglossum*.

Except for *Rhynchoglossum*, the available detailed data of inflorescence development in Epithemateae are only from *Epithema*. In *Epithema*, the apical meristem of inflorescence is permanently present and detaches floral primordia alternately in two directions on the front side (Weber 1988). The inflorescence apex is completely undivided and maintains a shape of slightly asymmetrical, triangular pillow throughout the developmental process (Weber 1988). The development of the inflorescence in *Epithema* is evidently similar to that of *Rhynchoglossum* except for an extreme ontogenetic condensation of the inflorescence internodes. The development of inflorescence in *Epithema* is truly indeterminate and

monopodial like that of *Rhynchoglossum* rather than determinate and sympodial as Weber (1988) has interpreted it.

In addition, the development of the valvate calyx in *Epithema* also follows exactly the same pattern as that of *Rhynchoglossum*, which is distinctive from that of other Epithemateae (Weber 1976c, 1988; Wang et al. 1997). Besides, two fertile stamens exist only in the two genera in Epithemateae. The comparative data confirm the suggestion that the development of inflorescence in *Epithema* is more closely affined to that of *Rhynchoglossum* than to that of *Whytockia*.

According to Weber (1975), the inflorescence meristem of *Monophyllaea* is wholly transformed into a floral primordium. The following flower pairs are initiated in a basipetal sequence, and several flower pairs are born in two rows on the front side of the inflorescence axis like that in *Whytockia*. In addition, even though the vegetative organs of the two genera, *Monophyllaea* and *Whytockia*, are distinctly different from each other, their flowers are evidently similar in structure (Weber 1976b, Wang and Pan 1998). The initiation and development of floral organs basically follow the same pattern in the two genera, which is sharply distinctive from that of others in Epithemateae (Weber 1976a; Wang et al. 1996, 2002). As Weber pointed out (1976b), certain anatomical and flower morphological characters occurring exclusively in the two genera underlined the very close affinity of *Monophyllaea* and *Whytockia*, and *Whytockia* was the phylogenetic progenitor of *Monophyllaea*. The similarity of the inflorescence development in *Whytockia* and *Monophyllaea* additionally confirms Weber's suggestion. However, the final conclusion about the relationship of the inflorescence between *Monophyllaea* and *Whytockia* waits for detailed studies on inflorescence development of *Monophyllaea*.

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