

Shoot structure of *Symphytum officinale* L. (Boraginaceae) in relation to the nature of its axially shifted lateral branches

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Summary: Shoot structure of *Symphytum officinale* was studied in terms of its architecture, vascular anatomy and morphogenesis. The main stem and lower stems of secondary order typically bear axially shifted lateral branches (along with axillary ones). This results in development of internode-like stem section between the lateral branch and its subtending leaf. Each shifted branch possesses two stem leaves (prophylls) and a terminal inflorescence. All lateral buds are initiated in the leaf axils. At later developmental stages some of them become shifted due to the intercalary growth of the stem between them and their subtending leaves. The intercalary stem portion possesses internodal stele structure, and the stele of the lateral stem branches from the main stele almost at the level of lateral stem insertion. This phenomenon can be treated as concaulescence (i.e. congenital fusion), though no strict evidences for phylogenetic fusion were found. Stems of *Symphytum officinale* also bear green wings of leafy nature. They run downwards along the stem pairwise from each leaf base and bear vascular bundles which originate from the veins of leaf blade of second to fourth order.

Keywords: axial shift, Boraginaceae, concaulescence, congenital fusion, hemmaxilar plants, heterotopy, intercalary growth, metatopy, stem, *Symphytum officinale*, vasculature

The seed plants in general are considered to be hemmaxilar, i.e. their lateral shoots develop only from buds in the leaf axils (STORK 1956; SINNOTT 1963; DICKINSON 1978; ESAU 1980; SEREBRYAKOVA & VORONIN 1988; LOTOVA 2000; TIMONIN 2007). However, some species of this group are known to possess shoots (vegetative ones or flowers and inflorescences) which seem to be extra-axillary. These cases are usually treated as ‘metatopies’ (ENDRESS 2010). In respect of the plant vegetative sphere, the term ‘shift’ is more commonly used as synonym for ‘metatopy’ (e.g., DICKINSON & SATTTLER 1975). Two types of metatopies are well known to date: the axial shift (concaulescence) and the epiphyllous shift (recaulescence). Axial shift is the development of the lateral bud on a stem considerably above its subtending leaf (DUDKA et al. 1984; KOROVKIN 2007). Epiphyllous shift is the development of the lateral bud on its subtending leaf (TROLL 1937; GRUSHVITSKY 1981; SHORINA 1988). Numerous examples of axial shifts are reported from Boraginaceae (e.g., *Anchusa italica*, *Borago officinalis*, *Symphytum officinale*) and Solanaceae (e.g., *Lycopersicon esculentum*, *Solanum dulcamara*) (TROLL 1937; POYARKOVA 1955; DICKINSON 1978; SEREBRYAKOVA & VORONIN 1988; SOKOLOFF 2009). Epiphyllous shifts usually occur in flowers and inflorescences, for instance, in Helwingiaceae (STORK 1956; JOHNSON 1958; DICKINSON & SATTTLER 1975; GRUSHVITSKY 1981), *Bougainvillea glabra* (Nyctaginaceae) (COOPER 1932) and certain species of *Thesium* (Santalaceae) (TAKHTAJAN 1981). According to DICKINSON (1978) and GRUSHVITSKY (1981), the metatopies are most frequent for plant species of tropical and subtropical areas. However, some of these species are found far from the tropics as in the tundra, e.g., *Streptopus amplexifolius* (Convallariaceae) (FEDCHENKO 1935; TROLL 1937). A critical discussion of the terms, as well as the mentioned phenomena is urgently needed.

The deviations from the hemmaxilar shoot structure are almost always interpreted as congenital fusion of the proximal part of axial shoot to various structures of the main shoot (concaulescence and recaulescence sensu ENDRESS (2010), respectively for axial and epiphyllous shift; see also examples and references above). However, these fusions can appear due to various reasons. DICKINSON (1978) draws out three developmental processes which lead to the occurrence of epiphyllous structures: (1) ontogenic displacement, due to intercalary or zonal growth; (2) postgenital fusion between leaf and structure; (3) heterotopy, i.e. a switch of the position of the structure initiation from the usual (axial or terminal) place to the leaf. These three elementary processes can also act in combination with each other. Within the first two processes, the epiphyllous structure is initially axillary and becomes shifted during ontogenesis; in case of heterotopy, this structure should be initiated within the leaf tissues. Ontogenic displacement includes cases which were interpreted as congenital fusion (recaulescence) by other researchers. However, the congenital (or phylogenetic) fusion has never been observed and can be proved only by evidence of vascular anatomy; the ontogenic displacement, in contrast, can be observed during the organ development, and is applicable even in cases where vascular structure cannot support the idea of congenital fusion (DICKINSON 1978). One can also imagine an epiphyllous structure which is initiated within the leaf tissue and receives vascular bundles from the main axis separately from leaf veins. This case shows an example of congenital fusion (following the idea of vascular conservatism, see DICKINSON 1978 and references therein). It is probably a combination of ontogenic displacement and heterotopy sensu Dickinson.

The occurrence of ontogenic displacement is reported from *Turnera ulmifolia* (Turneraceae) (JOHNSON 1958). Heterotopic inflorescences are known in *Begonia hispida* (DICKINSON 1978), *Phyllonoma ruscifolia* and *P. integerrima* (Saxifragaceae) (STORK 1956; DICKINSON & SATTLER 1974). There are also species with controversial hypotheses about the origin of their epiphyllous shifts. DeCandolle assumed epiphyllous inflorescences of *Helwingia japonica* to be postgenitally united with the leaf; this point of view was argued by Gravis, Velenovsky, Goebel and Stork (cited from DICKINSON (1978)). STORK (1956) showed that ontogenic fusion does not take place here and the inflorescence meristem is initiated on the leaf midrib. DICKINSON & SATTLER (1975) found out that the inflorescence of this species is initiated at the base of the subtending leaf primordium near its axil, and then it appears to be 'moved' to the leaf blade due to the intercalary growth of the leaf base.

In contrast to epiphyllous shifts, probably no interpretations besides the concaulescence were suggested for axial shifts. However, one can extrapolate the diversity of epiphyllous shift origin to the axial shifts. Since the cases of axial shifts are often less studied in terms of anatomy and development, this extrapolation may occur useful for such investigations.

The object of the present study is *Symphytum officinale* L. (Boraginaceae) which occurs at swampy meadows, flood-plain bogs and stream banks. It is a perennial herbaceous plant, 50–120 cm high and with violet corolla. The stem of *S. officinale* always possesses several wings (MAJOROV 2006). The main shoot of this species commonly bears axillary lateral shoots as well as lateral shoots without subtending leaves at their base (i.e. axially shifted shoots). TROLL (1937) noticed *S. officinale* as an example of morphological deviation from the typical shoot organization of Boraginaceae. He indicated these deviations as 'Konkauleszenz' which length increases acropetally. Each lateral branch, which undergoes concaulescence, bears an inflorescence. Thus,

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concaulescences can be observed only in flowering specimens. Lower shifted branches possess quite short concaulescences at their bases, while the upper ones can be 'moved' up to one and a half internode from its supposed subtending leaf (TROLL 1937). TROLL (l.c.) also noticed that *S. officinale* is an understudied species and the nature of its concaulescences should be uncovered after investigation of its bud development. He also referred to Schumann who found for *Anchusa italica* (another member of Boraginaceae) the following developmental features: lateral buds are initially axillary but at later stages they appear to be situated at the internodes (TROLL 1937). SHORINA (1988) assumed the axial shifts in inflorescence of *Borago officinalis* (Boraginaceae) as fusions of the pedicels with the main inflorescence axis. However, she did not indicate whether these fusions are postgenital or congenital.

Thus, in the literature available the information about the development of axial shifts is quite poor, and anatomical investigations are lacking.

The stem wings of *S. officinale* are believed to be decurrent parts of leaf bases (SOKOLOFF 2009). However, this assumption was not confirmed by any anatomical evidence.

Most of anatomical and morphological investigations of Boraginaceae species contain descriptions of the arrangement of stem tissues at the cross sections but not the spatial shoot vascular structure in its entirety (e.g., ALDRIDGE 1981; AKCIN et al. 2004; AKCIN 2005; AKCIN & BAKI 2007; AKCIN & ULU 2007; BINZET & ORCAN 2009; AKCIN & BINZET 2010). In relation to the vascular system of the genus *Symphytum*, it is known only that it comprises collateral bundles of various size (AKCIN 2007).

Symphytum officinale possesses a cymose inflorescence which is usually classified as double cincinni, i.e. a terminal flower with two lateral monochasia (SHORINA 1988). In the recent comprehensive review of monochasial elementary inflorescences, the monochasium of *S. officinale* was treated as boragoid (BUYS & HILGER 2003).

The main aim of this study is to uncover the nature of axial shifts in *S. officinale* and also to examine anatomy of stem wings of this species.

Materials and methods

Plants of *S. officinale* were collected on 22 June 2010 at the left bank of Usmanka river, Voronezh region, Russia, and on 7 September 2010, 2 October 2010, 14 March 2011 and 8 May 2011 in 'Vorobjevy Gory' reserved area, Moscow, Russia. Shoot architecture was studied in 27 flowering above-ground shoots.

For anatomical and morphogenetical investigations, parts of *S. officinale* were fixed and stored in 70% ethanol. Shoot vascular anatomy was investigated in two plants, one from each of the collection sites. For light microscope observations, the whole main stem of flowering above-ground shoots was cut with a hand razor into serial cross sections. Selected sections were stained using traditional methods of phloroglucin test for lignin (BARYKINA et al. 2004) and drawn. The drawings were used for reconstruction of three-dimensional shoot vascular structure. Images of the sections were taken using MDC200 camera combined with MBS-10 dissecting microscope and saved using ScopePhoto application.

For scanning electron microscopy (SEM), parts of winter regeneration buds were dehydrated in 96% ethanol and 100% acetone. Dehydrated material was critical-point dried using a Hitachi

critical-point dryer, mounted onto SEM stubs using double-sided tape and sputter-coated with Pt/Pd using a Giko IB-3 ion coater. Stubs were examined using a CamScan 4DV scanning electron microscope. SEM images were treated using GIMP 2.6.11 and Inkscape 0.48.

Results

Shoot architecture

Each of the flowering shoots observed bears 2 to 6 axial shifts (Fig. 1). This was the only deviation from the hemimaxilar organization concept found. For instance, a shoot can possess 9 stem leaves and 3 shifted lateral branches, or 11 leaves and 4 shifted branches. Overall stem leaf number varies from 4 to 13. Overall lateral branch number never exceeds leaf number. Strictly below each shifted branch a leaf can be found which does not subtend any other branch and therefore can be assumed as a candidate for being the subtending leaf of the shifted branch. The average relative shift length is $\frac{1}{2}$ – $\frac{2}{3}$ of internode. The maximum shift length registered was 25–30 cm, with the plant's height more than 90 cm. The shifts are found on the main shoot as well as on lateral shoots.

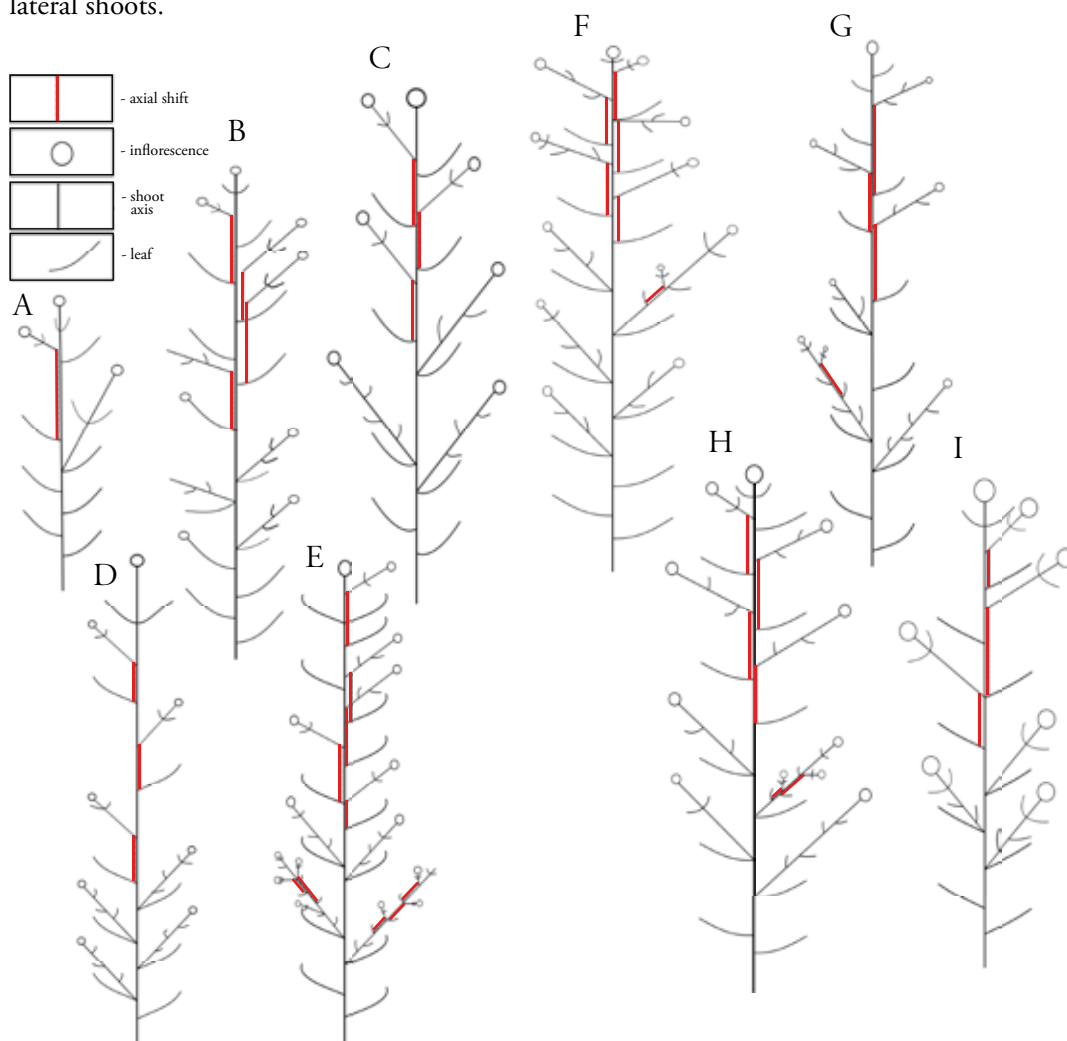


Figure 1. A–I, Schemes of shoot architecture of *Symphytum officinale*.

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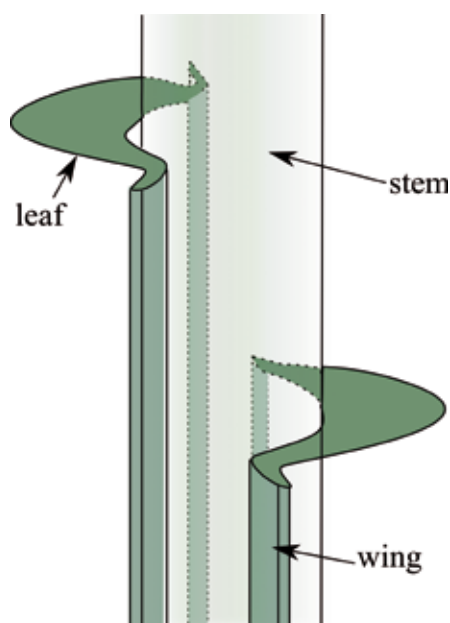


Figure 2. Stem wings arrangement in *Symphytum officinale*.

Within the inflorescence each pedicel of the monochasia seems to be fused basally with the pedicel of the previous order (Fig. 3A). However, the floral bracts are probably caducous and cannot be observed on the flowering specimens. For this reason the establishing of axial shifts in the inflorescence is problematic.

Green wings are present along the whole length of the stem (Fig. 2). They start in pairs at the base of each stem leaf and run downwards along the stem over one or two internodes. Thus, each internode bears up to two pairs of wings which start from two consequent leaves. The wings in each pair usually differ in length in several mm.

Shoot vascular structure

Stem vascular cylinder is organized as eustele (Fig. 5A, B). The stele at the internode level consists at the cross section of numerous collateral bundles which are tightly arranged into a circle and interconnected

with lignified parenchyma. In a longitudinal view, the bundles fuse with each other and then divide again. Some internodes possess pith cavities.

The separating of leaf vascular system from the stem stele takes place through a leaf gap with 5 leaf traces (Figs 6, 7). The median leaf trace branches off first (Fig. 6B), followed by 2 inner lateral traces (Fig. 6C) and then – 2 outer lateral traces (Fig. 6D).

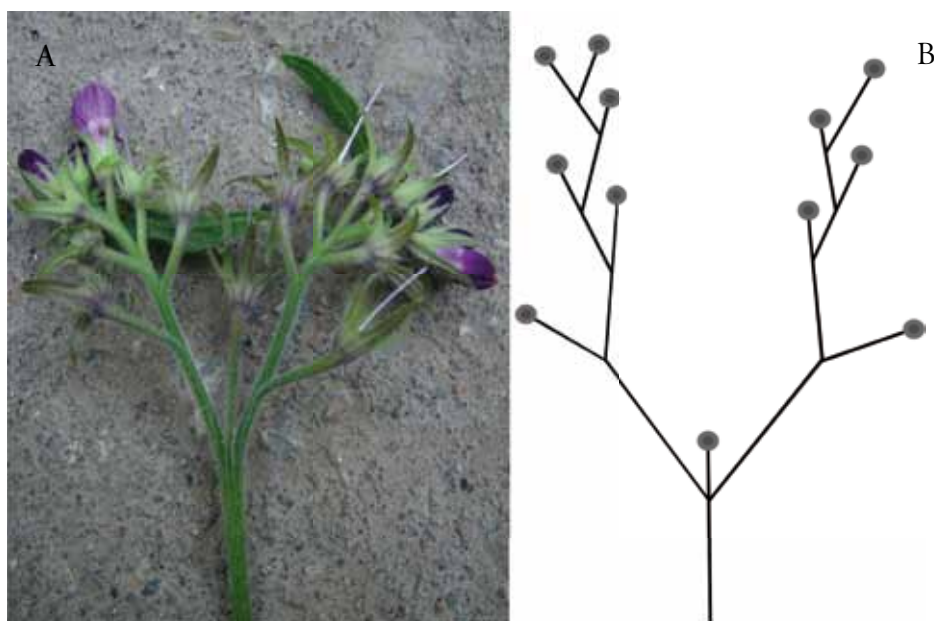


Figure 3. Inflorescence of *Symphytum officinale*. A, Photograph. B, Scheme.

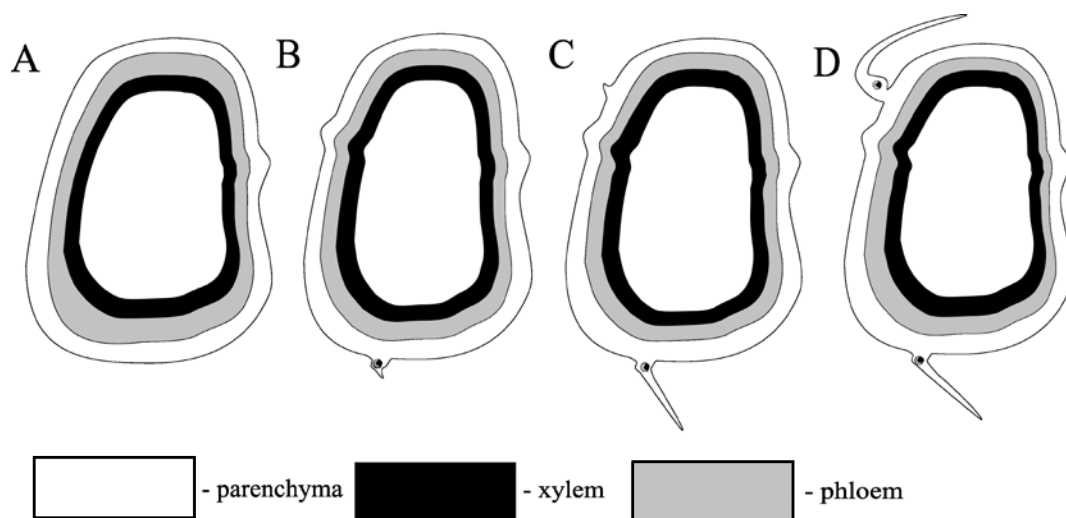


Figure 4. A–D, Ascending series of schemes of anatomical cross sections of an internode of *Symphytum officinale*. Note the vascularized stem wings.

The separating of lateral shoot vascular system in case of ‘true’ axillary branching (without shift) occurs through the following steps. Immediately after the subtending leaf traces branch off, the stem stele splits into two horseshoe-shaped parts (Fig. 6D): the remnant from the main stele (the bigger part) and the lateral stem stele (the smaller part). Above that the main stele restores its circular shape (at the cross section) and width (Fig. 6F); the lateral stele also obtains the circular shape (Fig. 6E) and branches to the lateral stem at once.

The origination of the lateral stem stele in case of a shifted lateral branch occurs in the same manner. However, in contrast to the axillary branching (see above), here the lateral stele splits

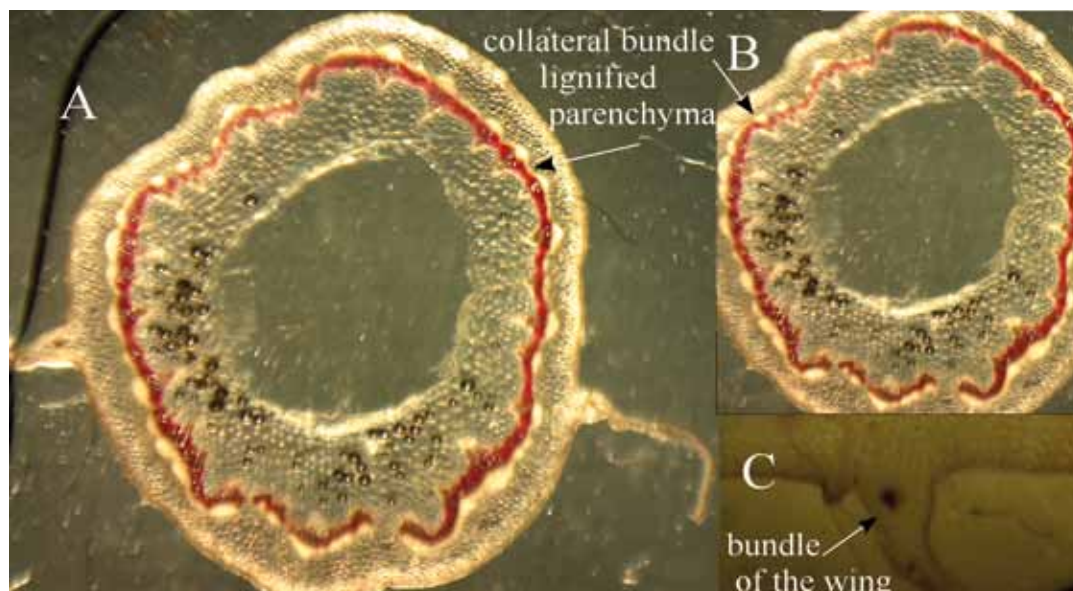


Figure 5. Anatomical cross sections of main stem of *Symphytum officinale* at the level of internode. A, General view. B, Stele. C, Stem wing.

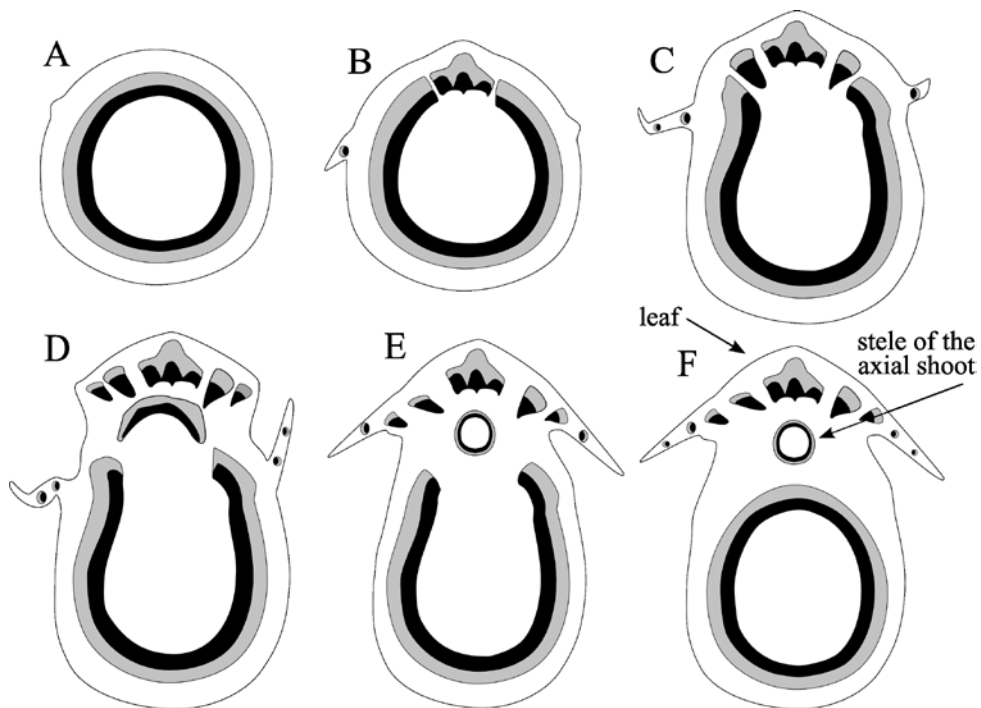
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Figure 6. Ascending series of schemes of anatomical cross sections of a node of normal structure (without axial shift) in *Symphytum officinale*. A, Upper part of subjacent internode. B–C, Branching of leaf traces from the stele. D, Branching of lateral stem stele from the main stele. E–F, Restoration of the internodal stem structure. For legend see Fig. 4.

from the main stem stele at the internode considerably above the level of the leaf insertion of the supposed subtending leaf (Figs 9, 11). As a consequence, an appreciable section of stem with internodal stele structure is observed between the supposed subtending leaf and the lateral shoot (Fig. 9D, E). The lateral stele branches to the lateral stem slightly above the level of main stele splitting, and thus the lateral stele runs upwards through the main stem cortex parallel to its stele no longer than 1 cm (Fig. 9G).

In the basal part of the inflorescence (see Fig. 3) the main stele splits into 3 horseshoe-shaped parts: the pedicel of the terminal flower (the smaller part) and the basal axes of 2 lateral monochasia (2 bigger parts) (Figs 8, 10).

The stem wings are vascularized and possess collateral bundles which originate from the leaf veins (Fig. 5C). In the basal part of each leaf blade several lateral veins of second to fourth order run backwards parallel to the midvein and enter the wings (Fig. 14). Each wing receives one to several bundles (Figs 4, 6, 7, 10). The width of wing bundles coincides with that of leaf veins. The bundles within a wing can branch and fuse with each other.

Shoot organogenesis

Plants of *S. officinale* overwinter as underground rhizomes which produce regeneration buds. In the autumn buds, the internodes are not developed and all the buds of lateral shoots occupy axillary positions (Fig. 15). In March buds, a single shifted lateral shoot was found at the level slightly below the terminal inflorescence (Fig. 12A). It was inserted 0.4 mm above its supposed subtending leaf.

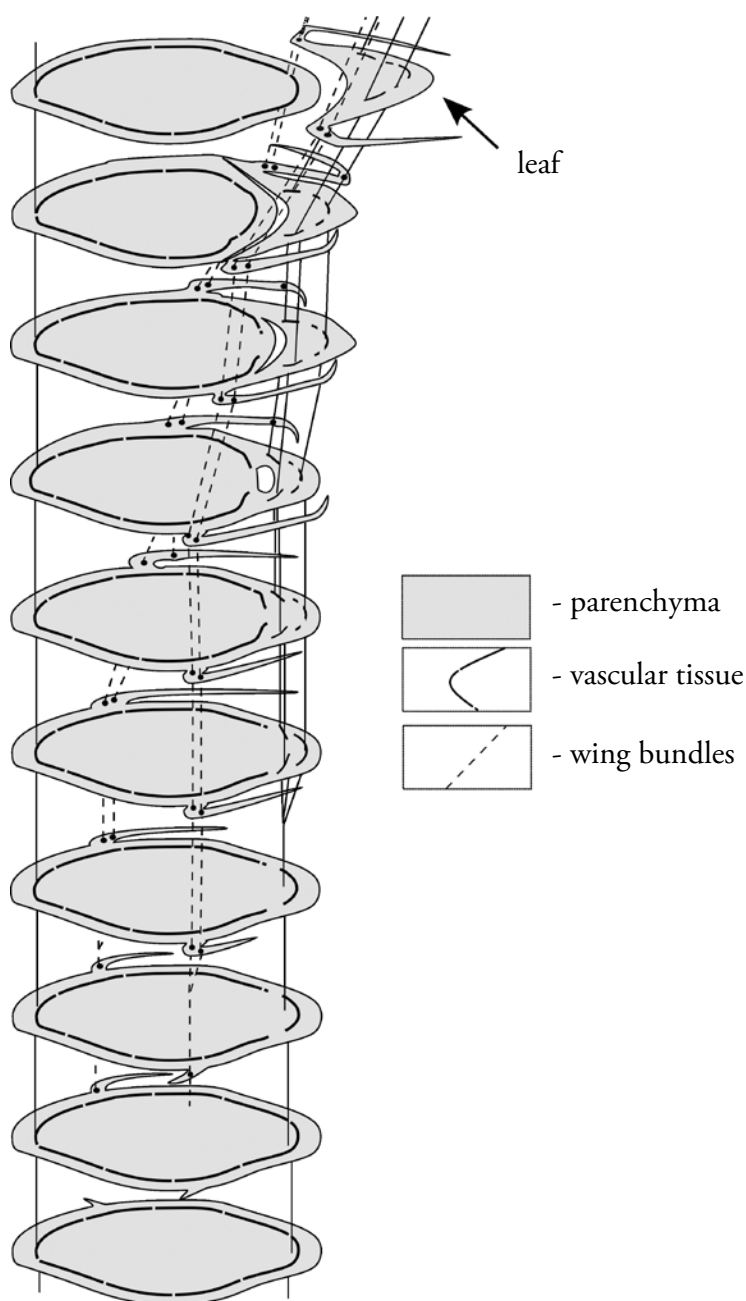


Figure 7. Scheme of shoot vascular system at the level of leaf insertion in *Symphytum officinale*.

Almost all young above-ground shoots (collected in early May) possess shifted lateral branches in the upper part of the main stem (Figs 12C, 13). The shifted lateral branches were never found below the fourth stem leaf.

Inflorescences at various developmental stages were found in the autumn and spring underground regeneration buds (e.g., Figs 12A, 13). The young flowers are subtended by bracts (Fig. 12B). However, no shifts can be observed in the developing inflorescences (in contrast to the blooming ones) since all the inflorescence axes are not elongated yet at these stages.

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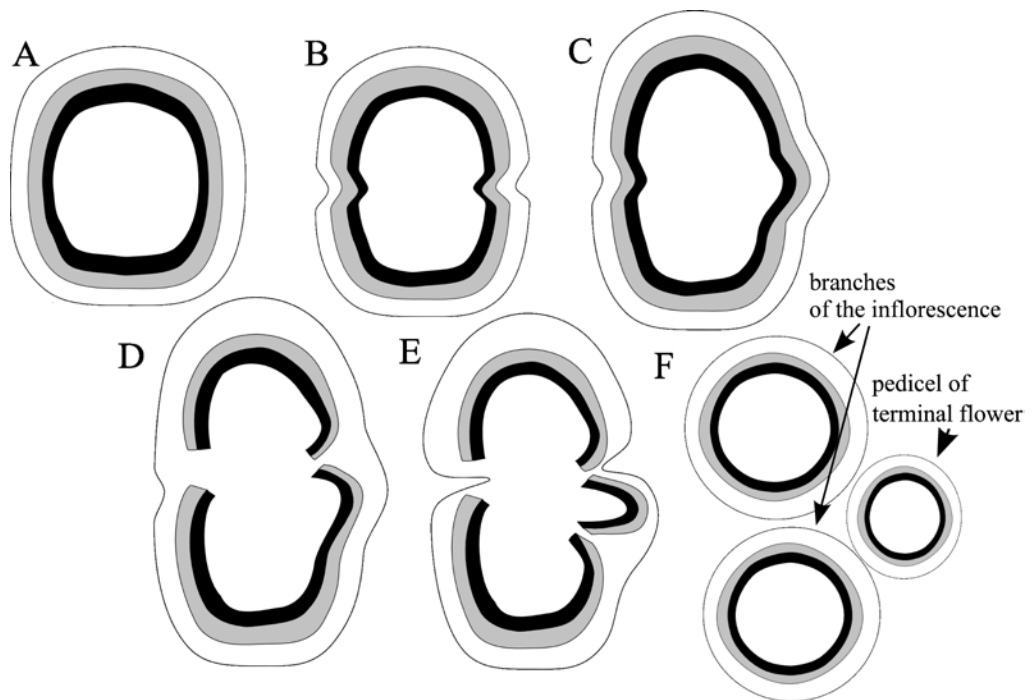


Figure 8. Ascending series of schemes of anatomical cross sections of the basal part of inflorescence in *Symphytum officinale*. A–C, Upper part of main stem. D, E, Splitting of the main stem stele. F, Inflorescence at the level of insertion of terminal flower and lateral branches. For legend see Fig. 4.

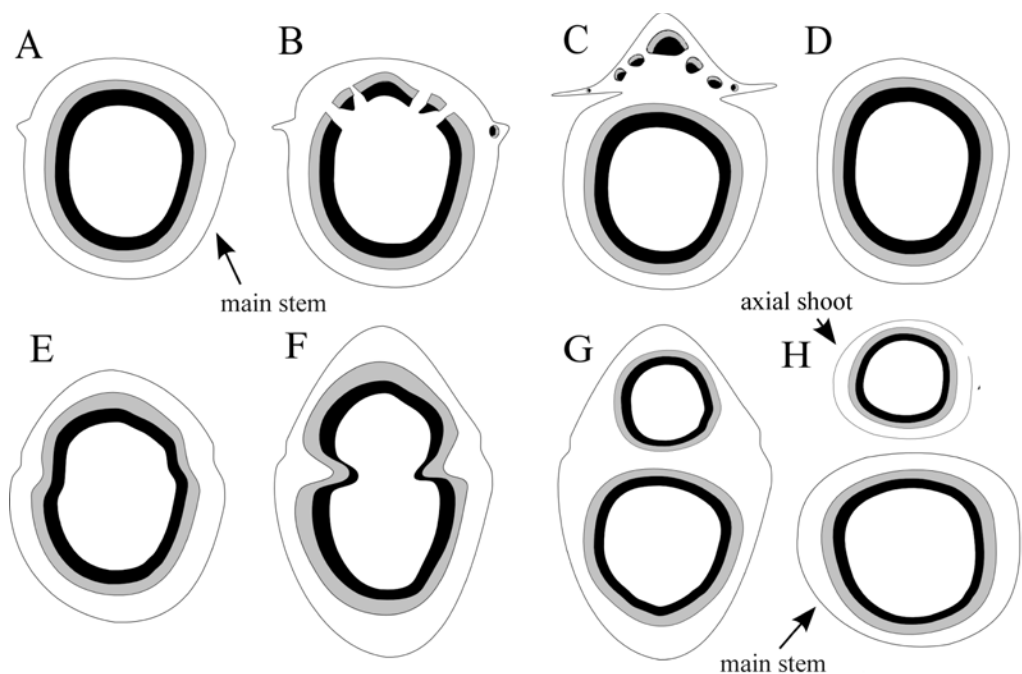


Figure 9. Ascending series of schemes of anatomical cross sections at the level of axial shift in *Symphytum officinale*. A, Upper part of subjacent internode. B, Branching of leaf traces from the stele. C, Leaf insertion. D, E, Stem section between the leaf and the lateral branch. F–H, Branching of lateral stem stele from the main stele. For legend see Fig. 4.

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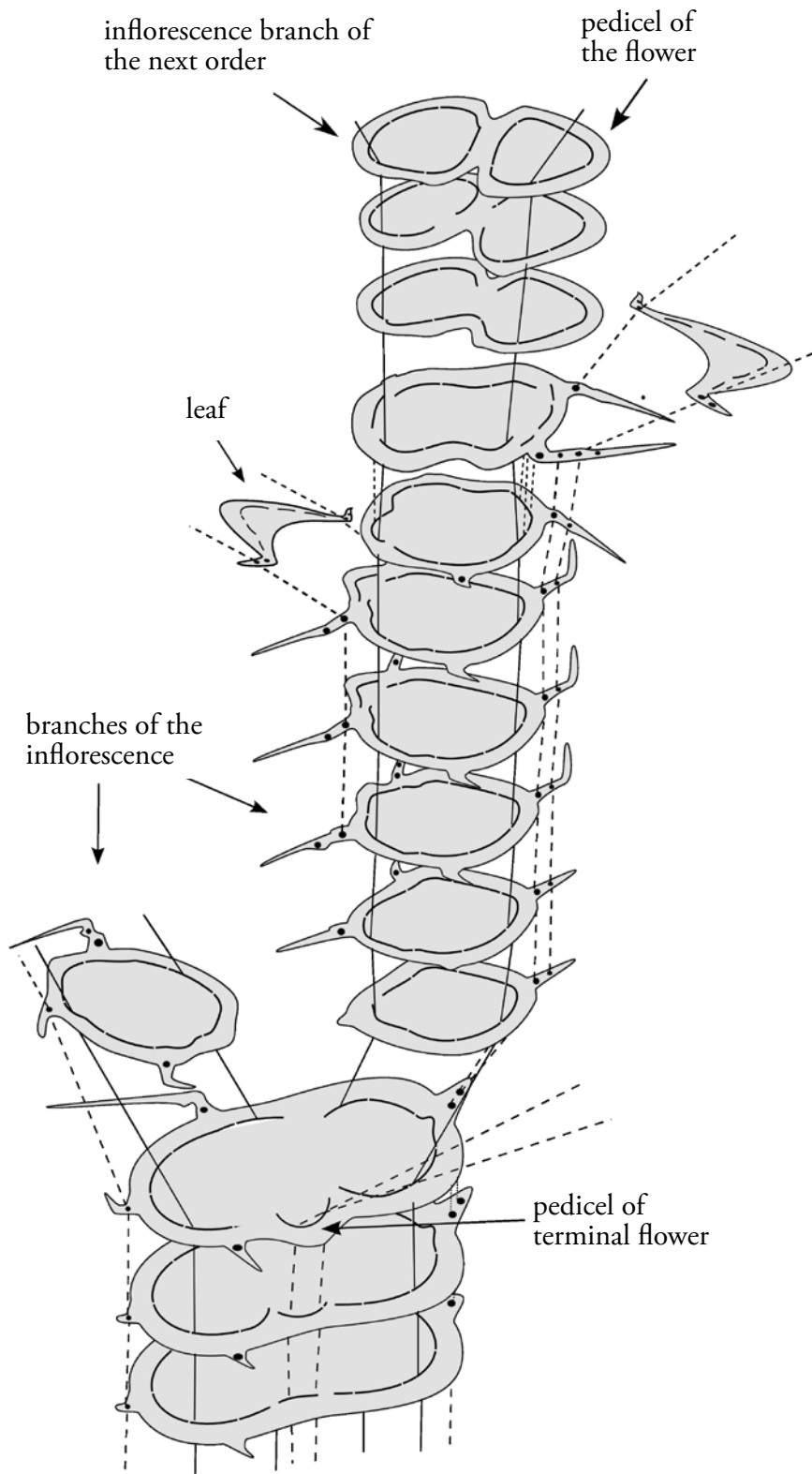
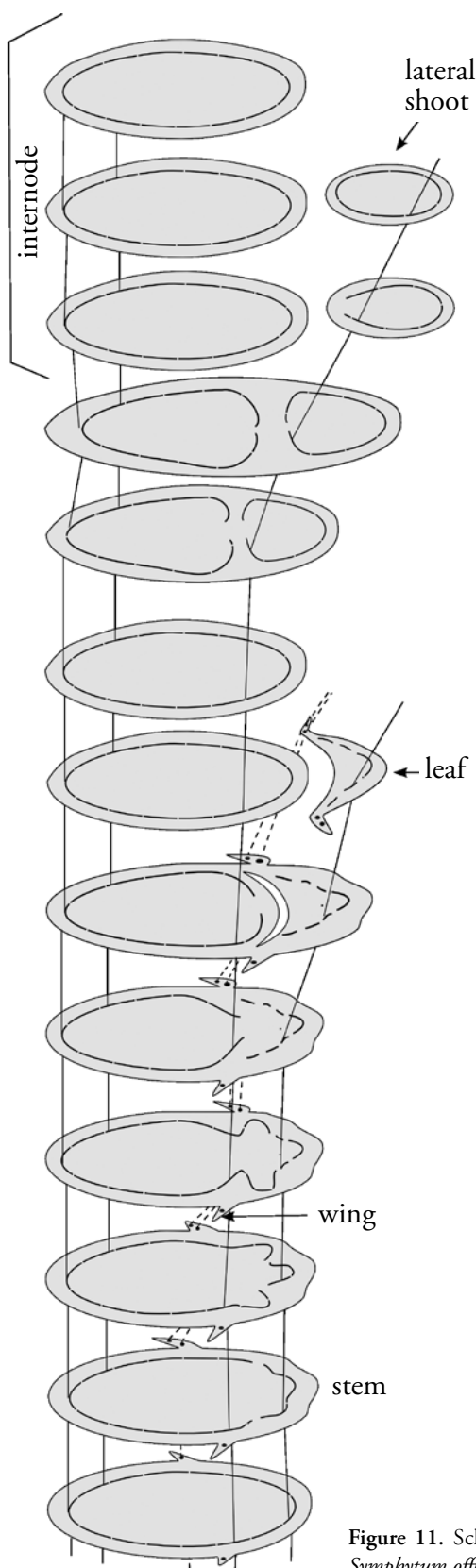


Figure 10. Scheme of shoot vascular system in the basal part of the inflorescence in *Symphytum officinale*. For legend see Fig. 7.

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Within the flowering plant the shifted lateral branches are found throughout the whole stem length (except the basal 3 internodes) and they are more frequent in the upper part. Each shifted branch bears 2 stem leaves (prophylls) and a terminal inflorescence (Fig. 12D). The length of each shift increases correspondingly to the internode growth till the end of flowering period. In a certain moment of the development the shift length increases acropetally along the stem.

Discussion

The shoot architecture as well as the vascular structure of *S. officinale* virtually agrees to the general characteristics of the dicots (Serebryakova & Voronin 1988; Lotova 2000). The only difference is the presence of axially shifted lateral branches, which is also reflected by the separation of lateral stem stele branching from the subtending leaf traces.

The classification of epiphyllous structures provided by Dickinson (1978) should be also useful for investigations of axial shifts, because together with the broadly assumed concaulescence hypothesis it seems to cover all the logically possible ways of shifted shoot origin (in ontogenetic and phylogenetic sense). Since all lateral buds of *S. officinale* are initiated in leaf axils, this species obviously possesses hemmaxillary shoot structure, and the supposed subtending leaves of shifted branches are indeed their true subtending leaves. Furthermore, this evidence makes us reject the opportunity of heterotopy, which implies extra-axillary bud initiation. Then, the 'moving' of the buds from axillary position to the internode during the development does not contradict the idea of postgenital fusion of basal portion of lateral stem with the main axis. However, in this case one should expect

Figure 11. Scheme of shoot vascular system at the level of axial shift in *Symphytum officinale*. For legend see Fig. 7.

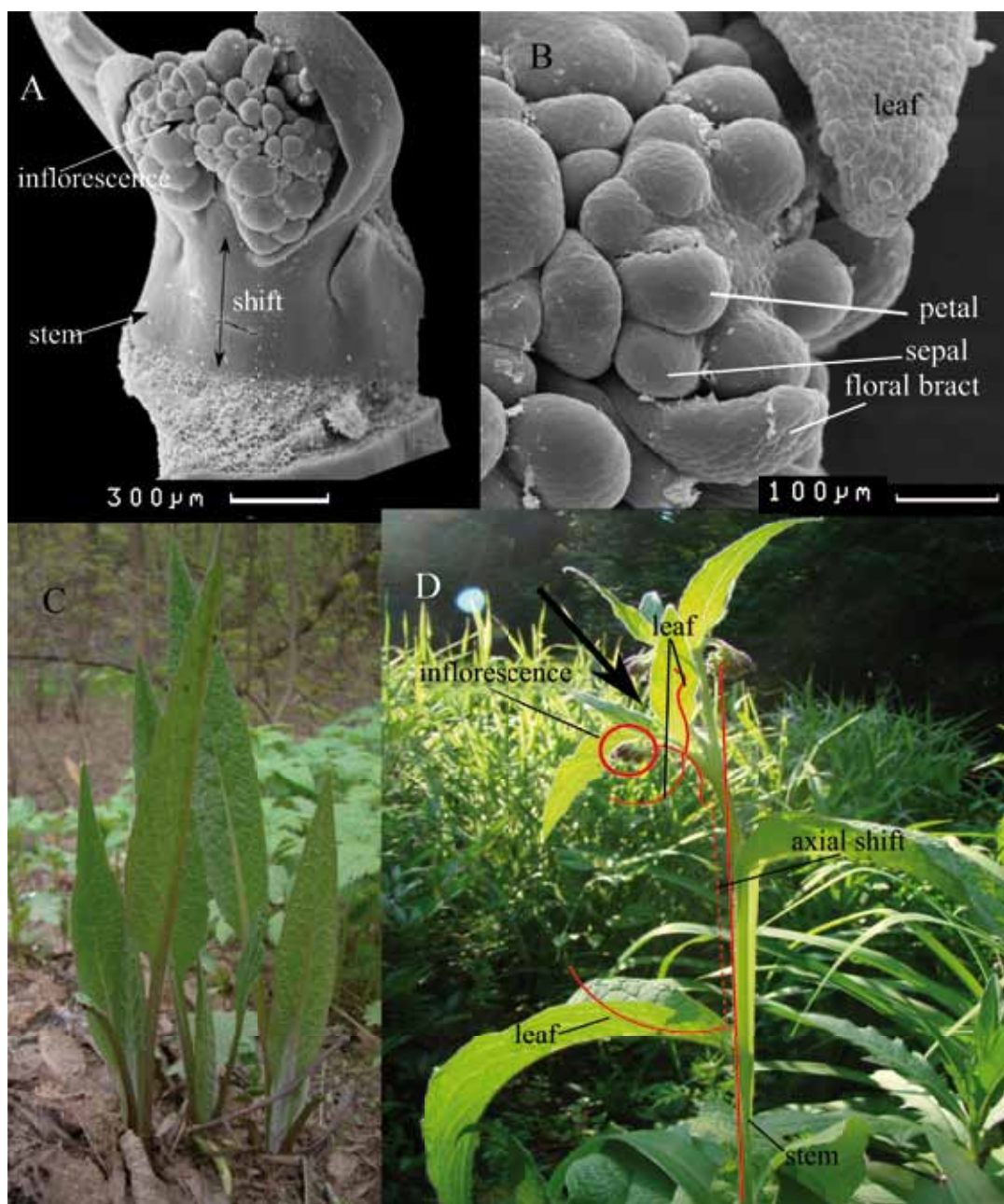


Figure 12. *Symphytum officinale*. A, Part of stem with axially shifted lateral shoot, collected in March (SEM). B, Part of inflorescence; note the floral bract (SEM). C, Above-ground shoot at the stage of leaf rosette, observed in May. D, Flowering shoot with scheme of its architecture superimposed; note the axially shifted lateral branch (arrow).

the nodal anatomy similar to that of a non-shifted lateral shoot, i.e. branching of lateral stem stele at the same level as subtending leaf traces and its arrangement in the cortex of the main stem till the level of shifted shoot insertion (two parallel steles should be observed in the stem section between the subtending leaf and the shifted lateral shoot). Since *S. officinale* shows a branching of the lateral stem stele from the main stele only slightly below the level of lateral shoot insertion, and a stem region with the internodal stele structure is present between the subtending leaf and

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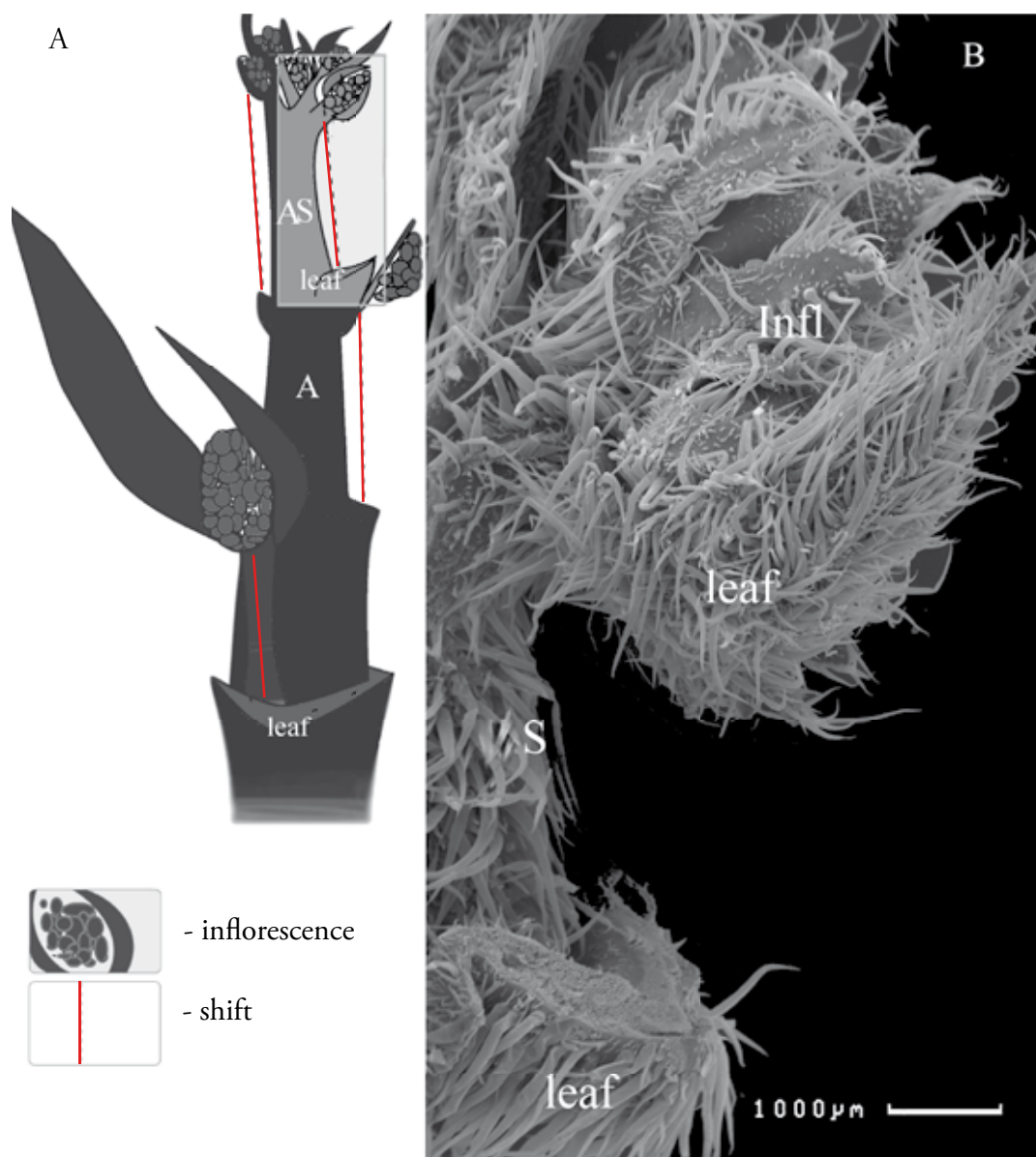


Figure 13. Upper part of the developing shoot of *Symphytum officinale*. A, Scheme. B, SEM image of the segment indicated in A. AS = axial shift; Infl = inflorescence; S = stem.

the lateral shoot, the idea of postgenital fusion does not correspond to shoot vascular structure of this species. Furthermore, no evidences of postgenital fusion were found at any stage of shoot development.

Two possibilities left are the ontogenic displacement due to the intercalary growth and the concaulescence (the congenital fusion). Both assumptions do not contradict the vascular anatomy of *S. officinale*. The choice between them could be theoretically made according the place of lateral bud initiation: near the subtending leaf in case of intercalary growth and on the internode in case of congenital fusion. Since all the internodes are shortened at the beginning of the shoot system development, the axillary bud cannot be initiated at any other level than the next to its

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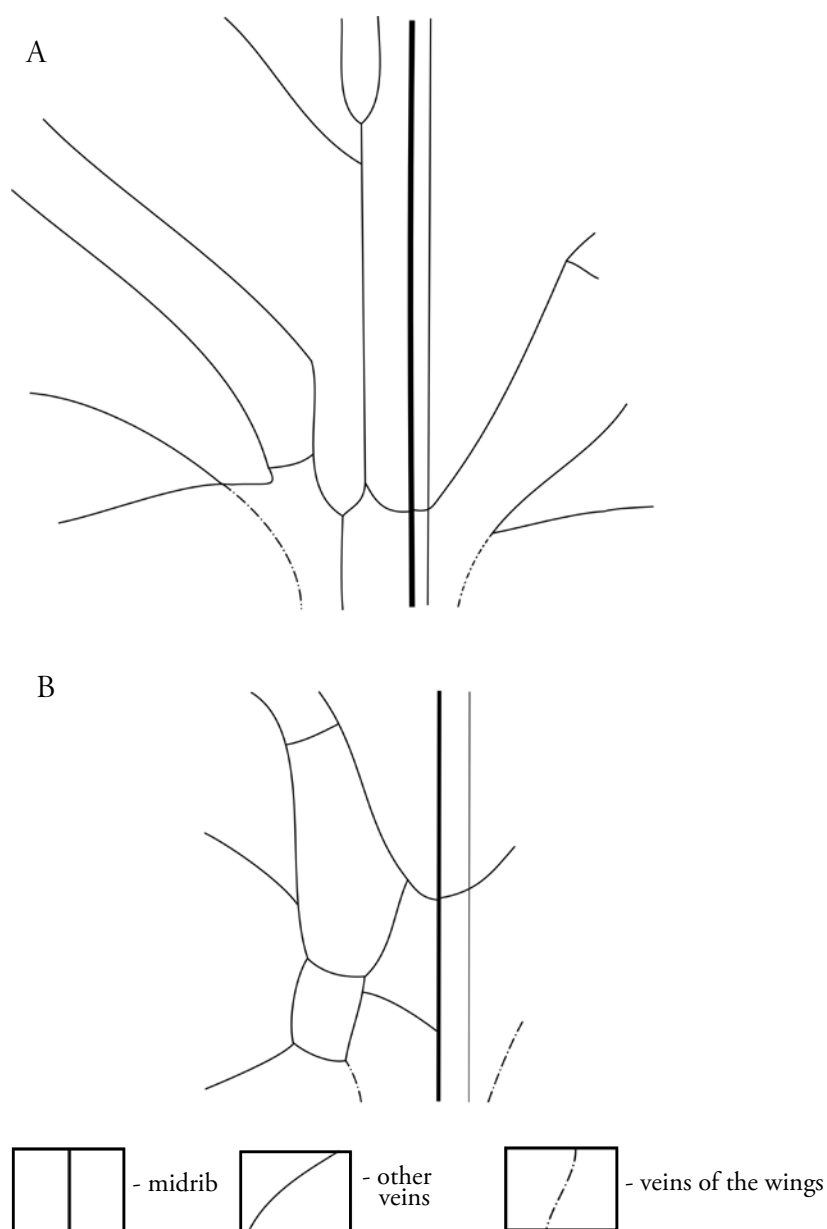


Figure 14. A, B, Schemes of venation of basal parts of leaf blades with veins branching off to the wings.

subtending leaf. Thus, a selection is impossible. The intercalary growth, however, seems to be more plausible, because the stem portion between the leaf and the shifted lateral branch finely resembles an internode in its structure. On the other hand, the ontogenetic process (intercalary growth) is compared to the phylogenetic one (congenital fusion) here. This could be probably more correctly treated as two sides of the same phenomenon: evolutionary fusion through developmental intercalary growth.

Thus, our data agree with the broadly accepted assumption of axial shift as a result of concaulescence or congenital fusion, at least within Boraginaceae, which was pointed out by TROLL (1937) and favoured by later researchers (see ENDRESS 2010). The present study supports this assumption

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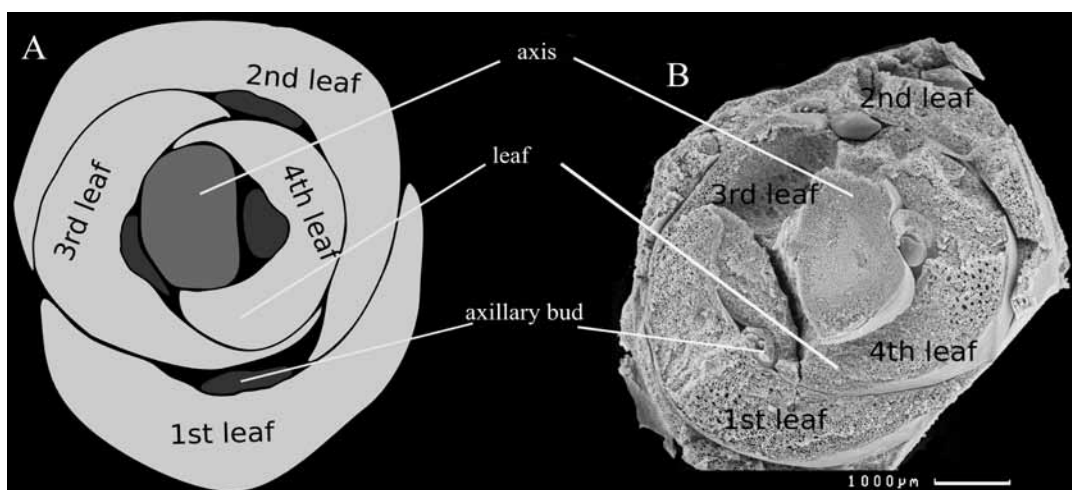


Figure 15. Underground terminal regeneration bud of *Symphytum officinale* collected in October. Note the shortened internodes and all lateral buds in axils of subtending leaves. A, Scheme. B, SEM image.

with anatomical and developmental evidences and suggests intercalary growth as a manner of axial shift development.

The stem wings of *S. officinale* run downwards from each leaf base and possess vascular bundles which branch from the veins of leaf blade. Thus, this anatomical evidence strictly supports the earlier assumption of the leafy nature of the wings (SOKOLOFF 2009).

Conclusions

Axially shifted lateral branches of *S. officinale* develop from axillary buds and are most probably a result of congenital fusion between the basal parts of the lateral stems and the main axis.

Development of the axial shift occurs through intercalary growth of stem section between the lateral shoot and its subtending leaf.

Morphologically, stem wings of *S. officinale* are parts of leaf bases and receive their vascular supply from leaf veins.

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