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FLORAL ANATOMY OF ASIAN *Schefflera* (ARALIACEAE, APIALES): COMPARING VARIATION OF FLOWER GROUNDPLAN AND VASCULAR PATTERNS

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Floral morphology and vascular anatomy in members of the Asian *Schefflera* clade (Araliaceae) are studied. This clade is of special interest because of secondary loss of flower groundplan stability and increase of merism. Among five species studied, three have isomerous pentamerous flowers, one has (almost) isomerous polymerous flowers, and one has nonisomerous flowers as a result of increased carpel number. Loss of calyx innervation and reduction of sepals are suggested as apomorphic for the subclade *Heptapleurum* s.l. *Tupidanthus calyptratus*, a member of this subclade with the most polymerous gynoecium among asterids, shares those features, too. Range of petal venation diversity within the species examined exceeds what was previously estimated for the family Araliaceae and the order Apiales. Formation of anastomoses between the bundles of petals and stamens in bisexual flowers of *Schefflera venulosa* is suggested as an effect of high auxin production in developing anthers. A shift of the ovule supply from ventral bundles to lateral ones occurs in different lineages of Apiales. Fusion between peripheral and dorsal bundles is an effect of flower topography that may not be considered an advanced character state. Strong differences in floral vasculature between closely related species with the same flower groundplan are highlighted.

Keywords: vascular bundles, flower, evolution, development, Apiales, Araliaceae, *Schefflera*, *Tupidanthus*.

Online enhancement: appendix figure.

Introduction

Araliaceae is a moderately sized plant family of 41 genera and 1350–1400 species (Lowry et al. 2004). This family was traditionally recognized as a close relative of Umbelliferae (Apiaceae; von Wettstein 1924; Hutchinson 1959; Melchior 1964; Takhtajan 1966, 1987, 1997, 2009; Cronquist 1968, 1981, 1988; Grushvitsky 1981; Tikhomirov 1985; Dahlgren 1989; Thorne 2000). This view is supported by molecular phylogenetics (Plunkett et al. 1996, 1997, 2004a; APG III 2009; Moore et al. 2010). These two families share many common morphological traits, including some flower features. Both Umbelliferae and most of Araliaceae have polysymmetric, tetracyclic, pentamerous (often except the gynoecium) flowers, which are also typical in other families belonging to the order Apiales (Pittosporaceae, Myodocarpaceae, Griselinaceae, Torricelliaceae, and Pennantiaceae), as well as the vast majority of euasterids in general (Endress 1990; Jabbour et al. 2008; Takhtajan 2009; Leins and Erbar 2010; Ronse De Craene 2010). In some genera of Araliaceae (in contrast to Umbelliferae and other Apiales), multistaminate androecia and multicarpellate gynoecia, as well as other significant deviations from this groundplan, occur (Eyde and Tseng 1971; Endress 2002, 2006; Sokoloff et al. 2007; Nuraliev et al. 2010).

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Before the late 1960s of the twentieth century, the occurrence of numerous floral parts was commonly accepted as a primitive condition in Araliaceae. This led researchers of Araliaceae (Bentham 1867; Harms 1898; Li 1942; Takhtajan 1966; Grushvitsky and Skvortsova 1973) to consider the genera with polymerous flowers (*Tupidanthus*, *Plerandra*, *Tetraplasandra*, *Gastonia*, *Osmoxylon*) as early-divergent members of the family. Cronquist (1968, 1981) was the first to consider polymerous flowers as derived from pentamerous ones in Araliaceae. His suggestion was supported by the studies of floral anatomy (Eyde and Tseng 1971; these authors considered, however, only highly polymerous flowers to be advanced), wood anatomy (Oskolski 1994), and molecular phylogenetics (Plunkett et al. 1996, 1997, 2004a, 2004b, 2005; Plunkett and Lowry 2001), which provided strong evidence for the independent origin of taxa with polymerous androecium and/or gynoecium in at least four different clades within Araliaceae (Nuraliev et al. 2010). These cases afford a good opportunity for studies of the evolution of floral merism in euasterids.

The disymmetric flower of *Tupidanthus calyptratus* Hook. f. & Thoms., with calyptate corolla, up to 170 stamens, and up to 130 carpels, is the most prominent case of polymery among asterids (Hemsley 1901; Sokoloff et al. 2007). The data of gross morphology, wood anatomy, and molecular phylogenetics (Lowry et al. 1989; Oskolski 1994; Plunkett et al. 2004b, 2005) strongly supported the placement of this species, which is the only member of *Tupidanthus* Hook. f. & Thoms., within the Asian *Schefflera* clade sensu Plunkett

et al. (2005). This clade, comprising species from east and southeast Asia, Malesia, and Australia, is one of five mutually remote clades revealed within the polyphyletic genus *Schefflera* by molecular phylogenetic analysis (Plunkett et al. 2005).

Most species of the Asian *Schefflera* clade share bisexual polysymmetric, tetracyclic, pentamerous, (hemi)epigynous flowers, i.e., the common floral groundplan within Araliaceae (Nuraliev et al. 2010). Some traits of the *Tupidanthus* flower occur, however, in a few other members of this clade. The Australian species *Schefflera actinophylla* (Endl.) Harms and other members of the informal *Brassaia* group have slightly polymerous flowers (e.g., 10–12 elements in each whorl) with disymmetric gynoeceum (Frodin 1975; Frodin et al. 2010). More numerous stamens and carpels, in combination with calyptrate corolla, occur in the Asian species *S. subintegra* (Craib) C.B. Shang, with up to 27 stamens and 23 carpels in disymmetric arrangement, and *S. hemiepiphytica* (Grushv. & Skvortsova) C.B. Shang, with up to 22 stamens and 13 carpels (Grushvitzky and Skvortsova 1973; Frodin and Govaerts 2004).

This article investigates floral anatomy of five species belonging to the Asian *Schefflera* clade in order to clarify transformations of flower structure related to the evolutionary changes in the numbers of stamens and carpels. Four species (*S. venulosa* [Wight & Arnott] Harms, *S. delavayi* [Franchet] Harms, *S. incisa* Viguier, and *S. heptaphylla* [L.] Frodin) possess typically pentamerous flowers (except *S. heptaphylla*, with six to nine carpels). The fifth species studied here, *S. actinophylla*, has 10–12-merous flowers. The data on floral anatomy of these five species are compared with the flower structure of *T. calyptratus* (Sokoloff et al. 2007; Nuraliev et al. 2009). Results of our former study of the flower structure in *S. venulosa* and *S. delavayi* (Nuraliev et al. 2009) are given here, supplemented by much more detailed anatomical descriptions and illustrations based on new observations.

Phylogenetic relationships of species studied here within the large Asian *Schefflera* clade can be briefly summarized as follows (M. S. Nuraliev, G. V. Degtareva, D. D. Sokoloff, A. A. Oskolski, T. H. Samigullin, and C. M. Valiejo-Roman, unpublished manuscript; see also Frodin et al. 2010; Plunkett et al. 2010): *S. actinophylla*, *S. incisa*, and *S. venulosa*, together with *T. calyptratus* and many other species, belong to the */Heptapleurum* s.l. subclade. Within this large subclade, *S. incisa* and *S. venulosa* belong to a smaller subclade called */Heptapleurum* s.str., while *S. actinophylla* is closer to *T. calyptratus* than to the members of the */Heptapleurum* s.str. subclade. *Schefflera heptaphylla* belongs to the */Heptaphylla* subclade, and *S. delavayi* belongs to the */Agalma* subclade. */Heptaphylla* is closer to */Heptapleurum* than to */Agalma*. Therefore, the following formula represents putative relationships between *T. calyptratus* and the species examined here: (*S. delavayi* (*S. heptaphylla* ((*S. venulosa* + *S. incisa*) (*S. actinophylla* + *T. calyptratus*)))).

This study focuses on the diversity of the floral conductive systems. Views on the significance of floral vasculature and its bearing on establishing homologies varied among botanists in the twentieth century. At first, vascular patterns were viewed as highly significant because of the assumption of their evolutionary conservatism (reviewed in Puri 1951); vascular data played a crucial role in several theories of the origin of the angiosperm flower (Melville 1962). These views

were then much criticized (Carlquist 1970; Schmid 1972; Endress 1994). Nevertheless, we believe that an evolutionary analysis of floral vascular patterns is a promising field for investigation. The evolution of floral vasculature can be interpreted in light of what is known about the phylogeny of particular angiosperm groups. It is now accepted that vasculature is linked with the physiological needs of flowers. If the vasculature depends on floral functions and physiological aspects, studies of vasculature open a door to understanding these highly important issues. It is demonstrated that prepaterning of procambial strands (ultimately giving rise to the conductive tissue) is controlled by polar auxin transport in young organs (Sachs 1991; Benková et al. 2003; Aloni 2004; Scarpella et al. 2006, 2010). Considerable progress is achieved in studies of regulation of leaf venation patterning, but much less is known about flowers. Because the free auxin production starts at the tips of leaves and floral organs such as perianth members, stamens, and carpels, the vascular system develops basipetally, from the tip downward. The pattern of conductive bundles can be considered a trace of polar auxin transport in early floral development (Choob 2009; Lock et al. 2011). Therefore, a comparative analysis of floral vasculature in a phylogenetic context can help in understanding the evolution of patterns of polar auxin transport in floral meristems. Importantly, this method allows involving fossils where direct physiological studies cannot be conducted.

Material and Methods

Plants for anatomical and morphological studies were collected from those cultivated in the Tsitsin Main Botanical Garden of the Russian Academy of Sciences, Moscow, Russia, in 2005 (*Schefflera venulosa*); the Komarov Botanical Institute, St. Petersburg, Russia, in 2007–2008 (*S. venulosa* and *S. incisa*); the Royal Botanic Gardens, Kew, United Kingdom, in 2005 (*S. delavayi*); the Fairy Lake Botanical Gardens, Shenzhen, China, in 2005 (*S. actinophylla* and *S. heptaphylla*); and on the campus of the University of Johannesburg, South Africa, in 2007 (*S. actinophylla*).

Flowers were fixed in FAA or 70% ethanol and stored in 70% ethanol. For light microscope observations, material was sectioned using standard methods of paraffin or paraplast embedding and serial sectioning at 15- μ m thickness (Barykina et al. 2004). Sections were stained in picroindigocarmine and carbolic fuchsin (Axenov 1967) and mounted in Canadian balsam or Biomount. Cross sections, as well as longitudinal serial sections, were made. Sections were examined, and images of them were taken using a Zeiss Axioplan microscope. Several flowers of each species were sectioned and used for clarification of floral anatomical and morphological species-specific floral features.

For scanning electron microscopy (SEM), parts of inflorescences and flowers 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 Cam-Scan 4DV scanning electron microscope. SEM images were

treated (and some of them colored) using Adobe Photoshop Elements and Inkscape, version 0.46.

In “Results,” the material is organized following putative phylogenetic relationships between examined species: (*S. delavayi* (*S. heptaphylla* ((*S. venulosa* + *S. incisa*) *S. actinophylla*)). Illustrations are organized according to representation of material, to facilitate comparing data for different species. Figures 1–3 (and fig. A1 in the online edition of the *International Journal of Plant Sciences*) show general flower morphology. Figure 4 shows diagrammatic schemes of vascular supply of sectors of flowers of each examined species. Each diagram shows the vasculature of one carpel and one petal together with the stamens (and sepals, when vascularized) of adjacent radii. Figures 5–7 comprise schematic drawings of serial cross sections of flowers and three-dimensional diagrams showing the course of vascular bundles between the levels of selected sections. Figures 8–14 show photographs of anatomical cross sections.

Results

Schefflera delavayi

Organography. The flowers lack bracteoles. Mature flower buds are ~1.5–2.5 mm in diameter. Flowers are strictly isomerous and pentamerous, with precise alternation of adjacent whorls (figs. 1A, 8). All flowers are bisexual (figs. 1B, 8). The calyx of mature flowers consists of five tiny sepals united at their base. In contrast to mature flowers, in early stages of flower development, the calyx has five free sepals that cover inner floral elements (fig. 1A). Therefore, the sepals show late congenital fusion. (We follow Sokoloff et al. 2006 in using more general terms, such as “late/early congenital organ fusion,” that expand the concept of late/early sympetaly of Erbar and Leins 1996.) The corolla is of five free petals with their tips bent inward toward the ovary apex in floral bud. Before anthesis, the petals are tightly conjoint to each other at their lateral sides and at abaxial sides of their tips (fig. 1B). Stamen filaments are also curved inward. After flower opening, petals abscise individually, not forming a calyptera. The gynoecium consists of carpels united throughout their entire length (fig. 1B). The synascidiate zone is much longer than the symplicate zone. The gynoecium bears a distinct style (fig. 1B). Stigmas are flat, situated on the style tip. Each locule contains a fertile ovule and, in most cases, a sterile ovule. The sterile ovules look like subtle protuberances of the ovary wall, located laterally relative to the fertile ovule. The ovary is semi-inferior (fig. 1B). The cross zone lies approximately at the same level as the border between inferior and superior ovary parts.

Vasculature (figs. 4A, 5A–5F, 6A). Each sepal is supplied by a single vascular bundle (fig. 4A) that passes through the calyx tube up to the free lobe (fig. 5C, 5D). Each petal contains one vein in median position; the lateral petal veins are absent (fig. 5C–5F). Stamens are each innervated by a single vascular bundle. The gynoecium vascular system consists of two rings of bundles: five bundles near the flower center alternating with locular radii and five dorsal carpel bundles. Occasionally, the central ring consists of four bundles only (fig. 5A, 5B).

Fifteen or 14 bundles in two rings enter the flower from the pedicel. Five or four bundles of the inner ring are located on interocular radii, while the outer ring contains 10 bundles on locular and interocular radii (see fig. 6A, lower section). Bundles of the inner pedicel ring extend directly into the inner ring of carpellary bundles. These bundles are bicollateral, i.e., possess phloem both outside of xylem and inside of xylem; that is why they cannot be distinguished as inverted or noninverted. Bundles of the outer ring are not inverted. At the level of the lower parts of locules, each bundle of this inner ring divides tangentially into two bundles, supplying two adjacent locules. These bundles shift centrifugally into septa (see fig. 6A, middle and upper sections). As a result, each locule appears to be surrounded by two branches of different bundles of this ring. One of these branches supplies the fertile ovule (fig. 4A), whereas the sterile ovule is not vascularized. At a higher level, these branches join the dorsal bundle of the carpel (fig. 4A).

Below the level of sepal attachment, each of the five bundles of the outer pedicel ring that lie on interocular radii splits in a radial plane into a stamen bundle and a sepal bundle (figs. 5A, 5B, 6A). At the level of the lower parts of locules, each of five bundles of the outer pedicel ring situated on locular radii is divided in a radial plane into inner and outer branches, i.e., the dorsal carpellary bundle and the petal bundle (fig. 6A). Petal bundles have no anastomoses with the vascular system of androecium (figs. 4A, 6A).

Schefflera heptaphylla

Organography. Partial inflorescences are umbels (fig. A1D). Each flower possesses a pair of bracteoles. Mature flower buds are ~1.5–2 mm in diameter. Although this species was reported as andromonoecious (Shang and Lowry 2007), inflorescences bear only bisexual flowers in our material.

In contrast to other *Schefflera* species examined, both pre-anthetic and anthetic flowers of *S. heptaphylla* (fig. 1C–1E) bear a distinctive massive calyx with a relatively long tube (half the corolla in the flower bud) and five small free lobes. The calyx tube is nearly as thick as the petals (fig. 9D). The corolla is of five free petals with their tips bent inward toward the ovary apex in floral bud (figs. 1C, 1D, 9E). Before anthesis, the petals are tightly conjoint to each other at their margins and at abaxial sides of their tips (fig. 9E, 9F). After flower opening, petals abscise individually. The androecium is of five stamens (figs. 9D, 9E, A1E). Stamen filaments are curved inward (at abaxial sides) before flowering. Alternation between the members of isomerous whorls (i.e., between sepals, petals, and stamens) is precise. The gynoecium consists of six (fig. 10), seven (fig. 9A, 9B), or up to nine carpels united throughout their length, with a long synascidiate zone and a short symplicate one. The ovary is semi-inferior. A short, broad style is present. The style is slightly elliptic in top view (fig. 1E), with unstable orientation of symmetry plane in relation to the inflorescence axis. Receptive parts of stigmas are horseshoe-shaped regions situated dorsally near the carpel tips. Ventral parts of carpel tips are shorter than the dorsal ones, which makes the top of the gynoecium slightly concave. In our material, postgenital closure of carpel margins was absent in the uppermost part of the gynoecium,

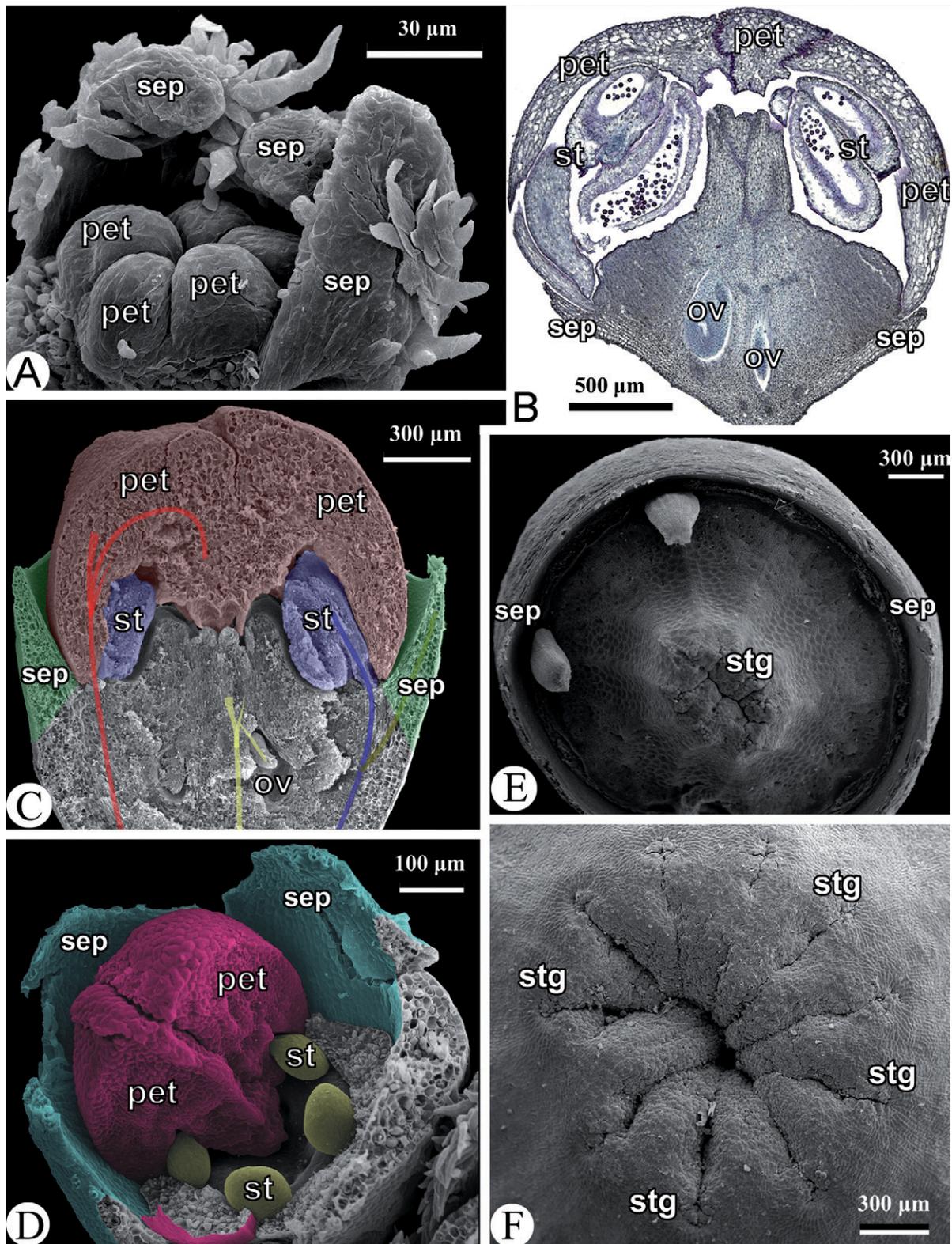


Fig. 1 Morphology of flowers (all except *B*, SEM; *B*, light microscopy). *A*, *B*, *Schefflera delavayi*. *A*, Young flower with two of five sepals removed. *B*, Preanthetic flower in longitudinal section. *C*–*E*, *Schefflera heptaphylla*. *C*, Flower bud longitudinally dissected, with partial diagram of vasculature superimposed (red lines = petal bundles; yellow lines = carpel bundles; blue line = stamen bundle). *D*, Young flower with three of five petals removed and calyx partially removed; note petal tips curved inward. *E*, Anthetic flower with corolla and androecium removed. *F*, *Schefflera actinophylla*, top view of gynoecium of anthetic flower. *ov* = ovule; *pet* = petal; *sep* = sepal; *st* = stamen; *stg* = stigma.

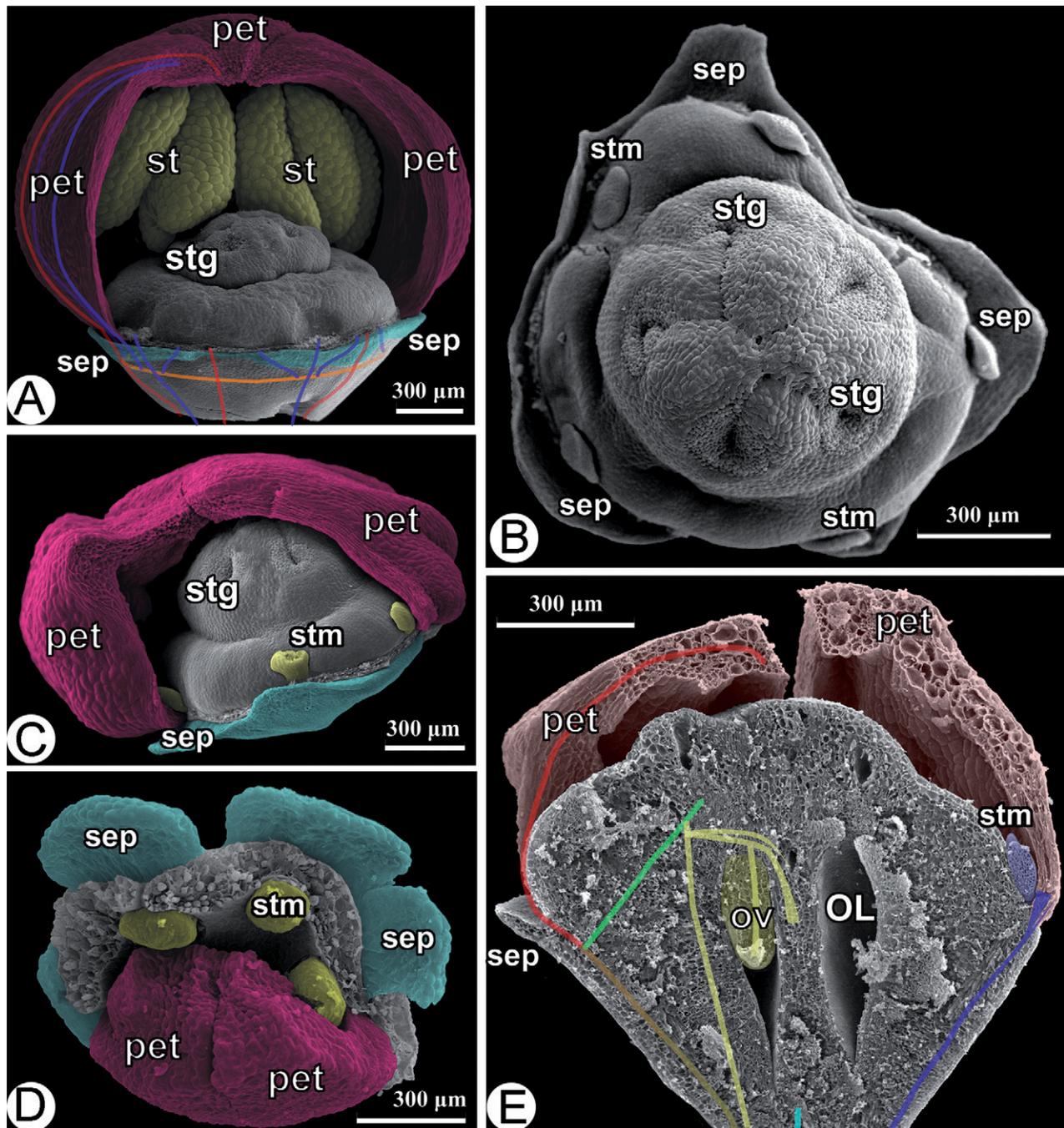


Fig. 2 *Schefflera venulosa*, morphology of flowers (SEM). *A*, Side view of bisexual flower, with scheme of its vascular structure superimposed; two petals and three stamens removed. *B*, Top view of functionally female flower; corolla removed. *C*, Side view of preanthetic functionally female flower; two petals removed. Note the short calyx tube. *D*, Young flower with three petals removed. *E*, Longitudinal section of functionally female flower, with scheme of its vascular structure superimposed. For legend of colors used in schemes of vasculature, see fig. 3. *OL* = ovary locule; *ov* = ovule; *pet* = petal; *sep* = sepal; *st* = stamen; *stm* = staminode; *stg* = stigma.

and a starlike inner space of the gynoecium was visible in cross section (fig. 10A). Lines of the postgenital carpel closure are visible on cross sections in the lower part of the symplicate zone (fig. 10B). Pollen tube transmitting tissue strands follow from stigmas to a compitum, which repeats carpel junction lines in its shape. Each locule contains a single fer-

tile ovule attached at cross zone; no sterile ovules were observed. The cross zone lies slightly below the border between inferior and superior ovary parts.

Vasculature (figs. 5G–5L, 6B). Each sepal is supplied by a single vascular bundle that passes through the calyx tube and continues into the free lobe (fig. 5J–5L). Petals usually

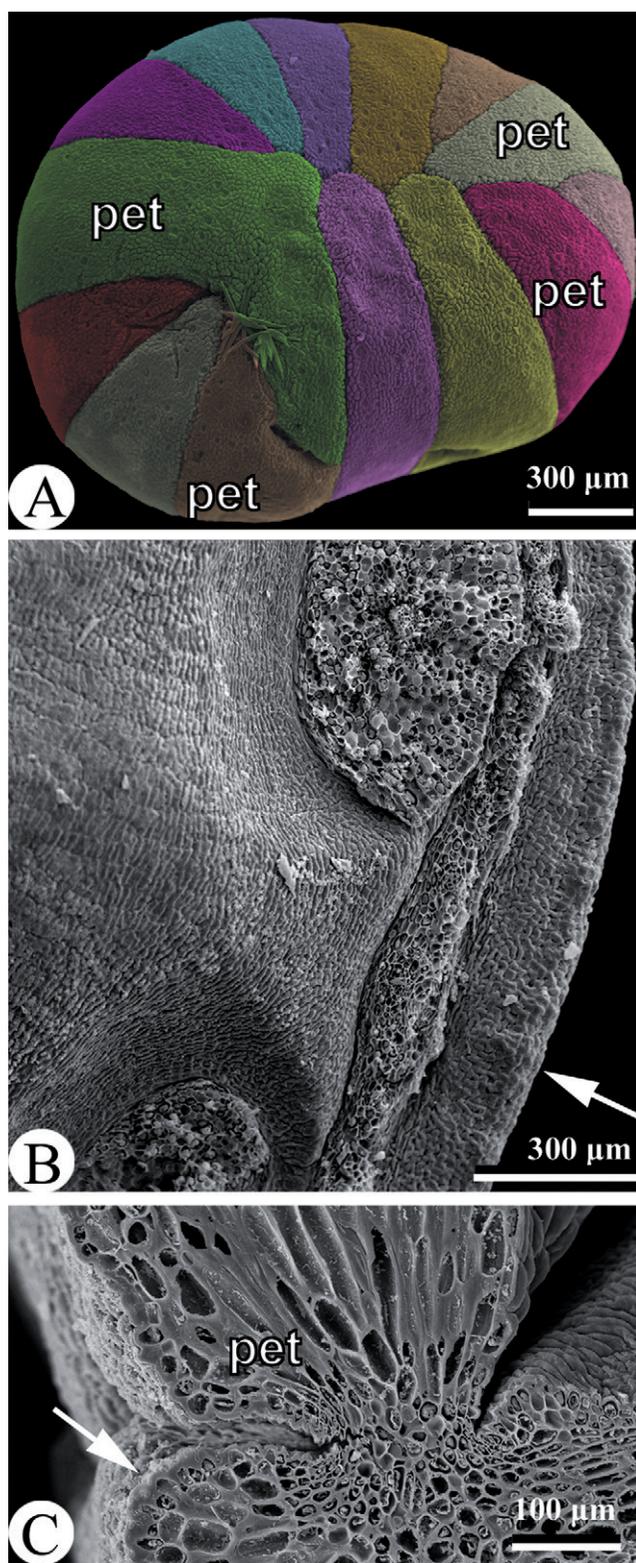


Fig. 3 *Schefflera actinophylla*, morphology of flowers (SEM). A, Top view of corolla in preanthetic flower. B, Fragment of flower, top view; corolla and androecium removed. C, Fragment of flower longitudinal section, showing place of perianth elements attachment. arrow = calyx; *pet* = petal.

have a median vein and two lateral veins (fig. 6B); sometimes, however, one to three additional lateral veins occur (fig. 5K). The median vein enters the petal base and continues to the petal tip. The lateral petal veins appear as branches of the median bundle (fig. 6B), and they join the median vein again in the upper part of the petal (i.e., the petal venation is closed). Each stamen is supplied by a single bundle (fig. 5J, 5K). In the gynoecium, only ventral bundles are well pronounced; they are fused in a heterocarpellary way and lie in the septa between locules instead of at the ovary center (fig. 5I). It should be noticed that in contrast to other species examined, in *S. heptaphylla*, fusion of heterocarpellate ventral bundles occurs above the level of departure of ovular branches from these bundles. Below this very level, the ventral vascular ring in this species shows a more complex organization. Therefore, this case of occurrence of heterocarpellary ventral bundles cannot be directly compared with those of other species. Dorsal bundles occur in less than half of carpels, they are quite thin, and they do not make contact with any other bundles.

The pedicel contains a single ring of five robust bundles that seem to lie on the same radii as sepals and stamens. After entering the flower, these bundles divide several times, giving rise to the inner ring of ventral carpel bundles and the outer group of rings that comprises dorsal carpel bundles and bundles of outer floral elements (fig. 5G). Below the level of departure of ovule branches, ventral bundles are less numerous than carpels (e.g., four instead of seven in fig. 5G). The ventral bundles are not inverted; i.e., they possess phloem outside of xylem. At the middle ovary level, they usually split into two branches, forming multiple irregular anastomoses with adjacent branches of the ventral vascular ring (fig. 6B). At this level, part of these bundles send branches to ovules. Slightly above, the branches join each other again and form heterocarpellary ventral bundles lying in the septa (fig. 5I). At the upper ovary part, the ventral bundles end blindly.

Because of the lack of isomery between the gynoecium and other floral whorls, the bundles of the outer floral whorls are oriented randomly in the ovary wall relative to the ovarian locules. Petal bundles probably appear in flower, independent from dorsal carpellary bundles, and form no anastomoses. Sepal and stamen bundles are fused in pairs that come apart at the middle ovary level (fig. 6B).

Schefflera venulosa

Organography. Each flower is situated in the axil of a broad triangular bract; the pedicel bears no bracteoles. Mature flower buds are ~2 mm in diameter. Both bisexual flowers with well-developed stamens and carpels (figs. 2A, A1A, A1C) and functionally female flowers with robust ovary and tiny staminodes (fig. 2B–2D) occur. Flowers are isomeric (i.e., organ number is the same in all whorls), with precise alternation of adjacent whorls. The flowers are mostly pentamerous, but tetramerous flowers of both sexual types sometimes occur. Moreover, a gynoecium of six carpels was found in a few functionally female flowers (preanthetic flowers of this type were not found, and perianth was not available for examination).

The calyx is almost inconspicuous in mature flowers because its growth is arrested early in flower development (fig.

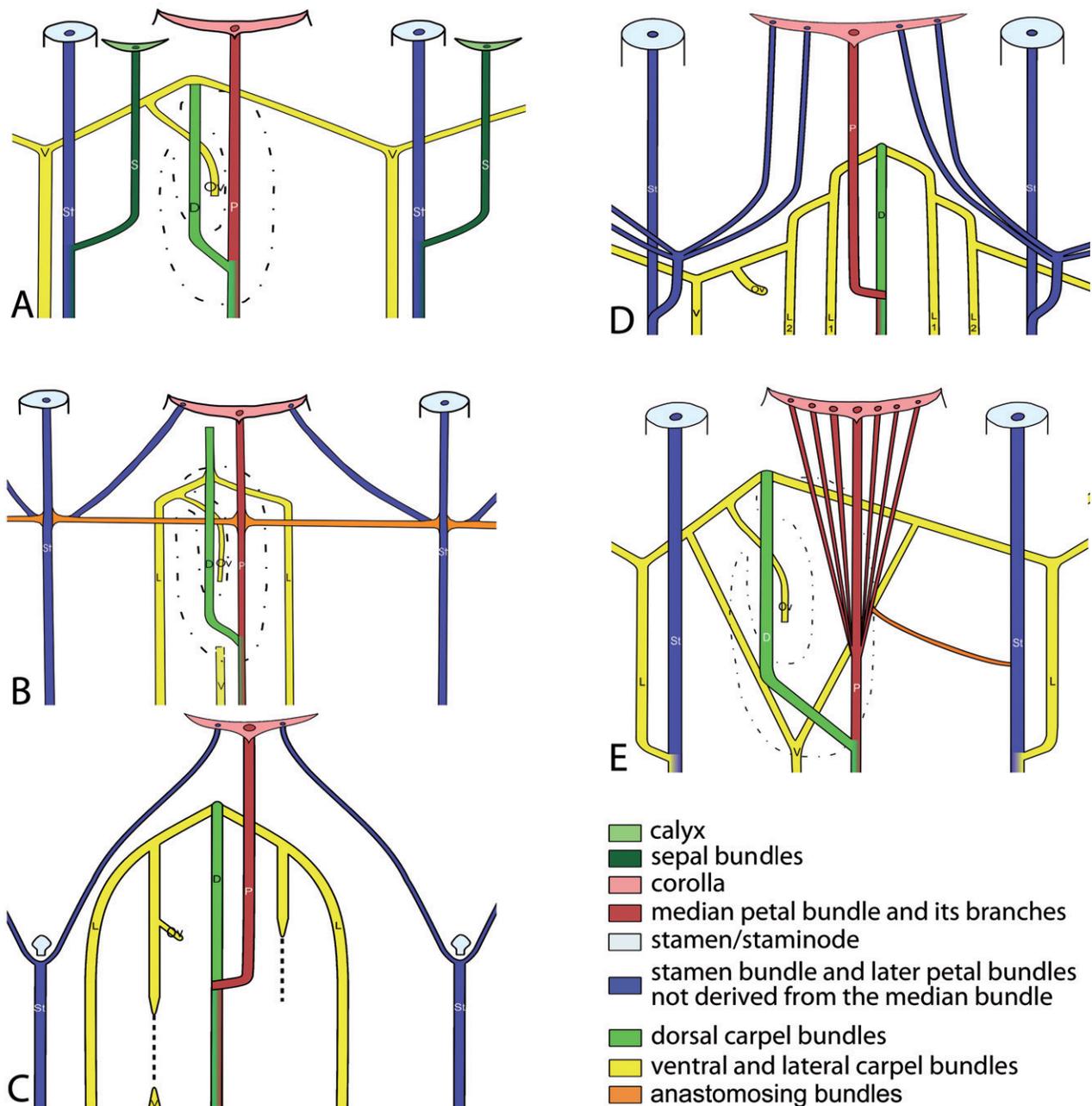


Fig. 4 Diagrams of vascular structure. Each diagram shows vasculature of one carpel and one petal together with the stamens (and sepals, when vascularized) of adjacent radii. A, *Schefflera delavayi*; B, *S. venulosa*, bisexual flower; C, *S. venulosa*, functionally female flower; D, *S. incisa*; E, *S. actinophylla*. Since the flowers of *S. heptaphylla* are not isomerous, a diagram is not given for this species. D = dorsal bundle; L = lateral gynoceium bundle; L1 = inner lateral bundle; L2 = outer lateral bundle; Ov = ovule bundle; P = petal bundle; S = sepal bundle; St = stamen (staminode) bundle; V = ventral bundle.

A1B). The calyx consists of a short tube (fig. 2C) and tiny free lobes (fig. 2A–2C, 2E). Sepal fusion is late congenital. The corolla is of free petals (fig. A1B) with petal tips bent inward toward the ovary apex in floral bud. Before anthesis, the petals are tightly conjoint to each other at their lateral sides and at abaxial sides of their tips. Stamen filaments in bisexual flowers are also curved inward. After the flower opens, its petals abscise separately (rather than forming

a calyptra). Carpels are united throughout their entire length. A prominent style is missing (fig. 2A–2C). The synasciadiate zone is much longer than the symplicate zone. Each carpel has a fertile ovule inserted in cross zone and pendent into a locule of the synasciadiate zone (fig. 2E). No sterile ovules were found. In anthetic flowers, the ovarian locule(s) is not present in the symplicate zone as a result of complete post-genital fusion of adjacent morphological inner surfaces. The

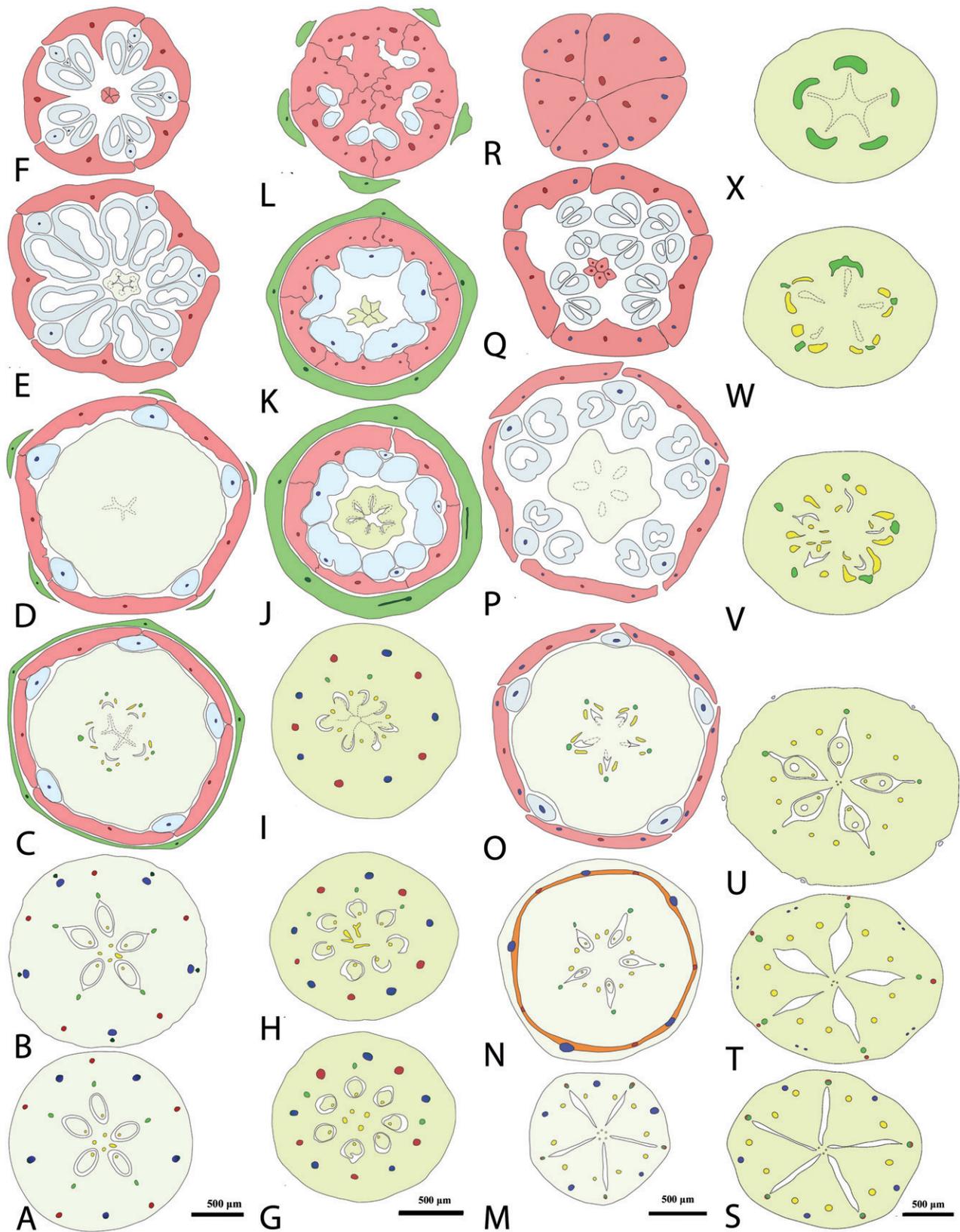


Fig. 5 Ascending series of schemes of anatomical cross sections of flowers, showing their vasculature. For legend of colors used, see fig. 3. A–F, *Schefflera delavayi*. A, B, Middle part of synascidiate zone of gynoecium with locules and ovules inside them. C, Lower part of symplicate zone

ovary is semi-inferior (fig. 2A, 2E). In bisexual flowers, the cross zone lies at the same level as the border between inferior and superior ovary parts; in functionally female flowers, the cross zone lies above this border. Flat stigmas with short unicellular papillae that occupy horseshoe-shaped areas on dorsal sides of carpel tips surround the line of postgenital carpel closure (fig. 2B). Since ventral sides of carpel tips are slightly longer than the dorsal ones, the stigmas are situated slightly below the apex of the gynoecium, where lines of postgenital closure of the gynoecium are clearly visible. Typically, only three of five carpels make apical contact (fig. 2B). Cross sections of the upper part of the ovary show postgenitally united carpel margins that form a star-shaped (sometimes imperfectly star-shaped) line (fig. 11C). Five strands of pollen tube transmitting tissue begin from stigmas (figs. 11C, 12E–12F) and form a star-shaped compitum above the locules (figs. 11B, 12D). Slightly below the level of the compitum, the rays of pollen tube transmitting tissue reach the ovules.

Vasculature of bisexual flowers (figs. 2A, 4B, 5M–5R, 6C). The calyx lacks vascular supply. Petal venation is open, formed by one median vein and two lateral veins. Each stamen carries a single vascular bundle. The gynoecium vascular system consists of three rings of bundles: five bundles in the ovary center alternating with ovarian locules, 10 paired bundles in septa between ovarian locules, and five dorsal carpel bundles.

The pedicel of a pentamerous bisexual flower contains 25 vascular bundles in three rings. The same bundles can be seen on cross sections through the lowermost part of the ovary (fig. 5M). All of these bundles are not inverted; i.e., they possess phloem outside of xylem. The inner ring consists of five bundles located on the interlocular radii alternating with ovarian locules. The middle ring contains 10 bundles arranged in pairs (each pair on locular radius). Ten bundles of the outer ring are arranged on locular and interlocular radii. The inner ring bundles extend immediately into five bundles situated in the ovary center that follow the lower part of the synascidiate zone without any fusions with any other bundles. Ten bundles of the second ring extend directly into 10 paired bundles situated in the ovarian septa and send branches to the ovules (one branch from every pair of bundles). At the level of the middle of the synascidiate zone, five bundles of the outer ring located on locular radii split radially into the inner branch, which is the dorsal carpellary bundle, and the outer branch continues into the median petal bundle (fig. 6C). Each dorsal carpellary bundle fuses with two carpellary bundles from the

ovarian septa (one bundle from each of two adjacent septa; fig. 5O) into the joint bundle (conventionally colored green in figures 4B and 6C as a dorsal bundle), which extends almost up to the ovary tip. Another set of five bundles of the outer ring (those that lie on interlocular radii) continue into the stamen bundles (figs. 5M–5O, 6C). A single bundle of each stamen extends up to the connective and gives two branches into thecae.

Each petal receives a median bundle, which extends up to the petal tip, and two shorter lateral bundles. Below the level of insertion of the petals, each median petal bundle joins with two adjacent stamen bundles by horizontal anastomoses. These anastomoses are arranged into a vascular circle connecting all stamen bundles and median petal bundles around the flower (figs. 4B, 5N, 6C). Ten lateral petal bundles begin from this circle near the stamen bundles (figs. 3B, 5C).

Vasculature of functionally female flowers (figs. 4C, 5S–5X, 6D, 12). Functionally female flowers show the following differences in their vascular anatomy compared with that of bisexual flowers. Staminodes are not vascularized (fig. 4C), but five bundles that correspond to androecium bundles of bisexual flowers in their position in the pedicel and the ovary wall are present (figs. 5S, 6D). Below the level of staminode attachment, each of these bundles branches dichotomically in tangential plane (figs. 5S, 5T, 6D). These 10 branches become lateral petal bundles. Thus, each petal contains three veins, i.e., the median bundle joined to the dorsal carpel bundle in the pedicel and two lateral bundles. The functionally female flower has no anastomoses between median and lateral petal traces (fig. 4C).

In the lower part of the ovary (fig. 5S–5U), there are bundles in the ovary center that correspond to the inner gynoecium vascular ring in bisexual flowers, but they are very thin and less numerous (from one to three) than the carpels. At the level of upper parts of locules, these bundles join the well-developed lateral carpel bundles. Below the point of joining, they send branches to ovules (fig. 6D). Since bundles of the ring in the ovary center are less numerous than ovules, some of them send branches to more than one ovule. The bundles of the inner gynoecium ring mostly consist only of phloem, which makes it difficult to decide whether they are inverted.

Schefflera incisa

Organography. Bracteoles were not found in our material with anthetic flowers and fully formed floral buds; the observations of early development are needed to clarify their pres-

with upper parts of locules and basal parts of outer floral elements; note the pollen tube transmitting tissue forming an irregularly star-shaped compitum. *D*, Middle part of symplicate zone with basal parts of outer floral elements. *E*, Style and outer floral elements. *F*, Outer floral elements; note the petal apices curved inward. *G–L*, *S. heptaphylla*. *G*, *H*, Synascidiate gynoecium zone with locules and ovules inside them and basal parts of outer floral elements. *I*, Ovary at the level of cross zone; note the line of postgenital fusion of ventral carpel parts. *J*, Basal style part and outer floral elements. *K*, Style tip and outer floral elements. *L*, Outer floral elements. *M–R*, *S. venulosa*, bisexual flower. *M*, Lower part of synascidiate gynoecium zone with locules. *N*, Middle part of synascidiate gynoecium zone with locules and ovules inside them; note the vascular ring connecting stamen and petal bundles. *O*, *P*, Symplicate gynoecium zone with basal parts of outer floral elements. *Q*, Outer floral elements; note the petal apices curved inward. *R*, Upper part of corolla. *S–X*, *S. venulosa*, gynoecium of functionally female flower (petals abscised). *S*, *T*, Lower part of synascidiate zone of gynoecium with locules. *U*, Middle part of synascidiate zone with locules and ovules inside them; note the tiny staminodes. *V*, Cross zone. *W*, Symplicate zone. *X*, Upper part of symplicate zone; note the pollen tube transmitting tissue forming a star-shaped compitum. dash-dotted line = border of pollen tube transmitting tissue; dotted line = line of postgenital fusion of carpel ventral parts.

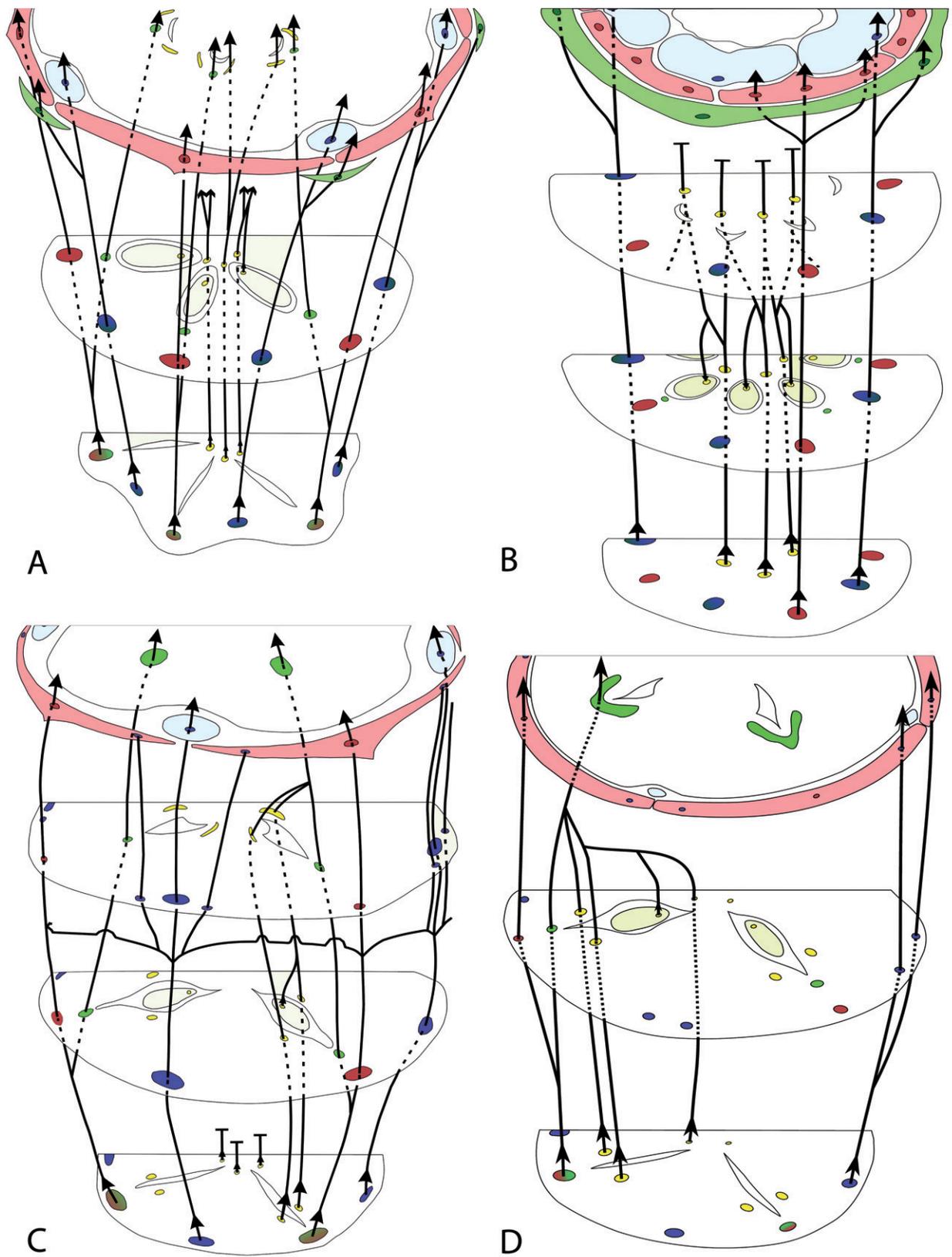


Fig. 6 Schemes of floral vascular systems. For legend of colors used, see fig. 3. A, *Schefflera delavayi*; B, *S. heptaphylla*; C, D, *S. venulosa*. C, Bisexual flower. D, Functionally female flower.

ence. Mature flower buds are ~4 mm in diameter. Flowers are isomerous and pentamerous, with regular alternation of whorls (fig. 13).

The calyx of anthetic flowers appears as a tiny tube with five free, faintly discernible lobes. Petal tips bend inward toward the ovary apex in floral buds. Petals are initially free but soon become tightly conjoined to each other at their lateral sides and at abaxial sides of their tips. In contrast to *S. delavayi*, *S. heptaphylla*, and *S. venulosa*, only proximal parts of petals are separated from each other when a flower opens in *S. incisa*, whereas their distal (incurved) parts remain postgenitally united. As a result, the whole corolla is abscised in a calyptra-like manner (fig. A1F). The stamen filaments are curved inward in flower bud. The gynoecium consists of carpels united throughout their entire length. A style is absent. Stigmas lie slightly below the tip of the gynoecium. Strands of pollen tube transmitting tissue form a star-shaped compitum (fig. 13B). Each locule contains a fertile ovule. No sterile ovules were observed. The ovary is semi-inferior. The cross zone lies just above the border between inferior and superior ovary parts.

Vasculature (figs. 4D, 7A–7E, 7M, 13). The calyx is not vascularized (fig. 7B). Petals are usually supplied by five (rarely six or seven) bundles each (figs. 4D, 7B–7E, 7M, 13C, 13D). Median and two inner lateral veins continue up to their junction near the petal tip; two outer lateral veins join the inner bundles below the petal tip. Thus, petal venation is closed. Each stamen is supplied by a single bundle (figs. 4D, 7B–7E, 7M, 13B–13D), which lasts up to the connective and gives two branches into thecae. The gynoecium vascular system consists of four rings of bundles: the innermost ring of five heterocarpellary ventral carpel bundles that lie in the ovary center alternating with ovarian locules, 10 inner lateral carpel bundles arranged in pairs on each side of the locules, 10 outer lateral carpel bundles situated on the same radii as inner lateral carpel bundles, and five dorsal carpel bundles on the radii of locules (fig. 7B).

Thirty-five bundles in four rings enter the flower from the pedicel. All of these bundles are not inverted; i.e., they possess phloem outside of xylem. The innermost ring contains five bundles located on radii alternating with ovarian locules. Two middle rings contain 10 bundles each, which are arranged in pairs (each pair on a locular radius). The outermost ring consists of 10 bundles on locular and interocular radii. The same 35 bundles are visible in the lowermost part of the ovary wall (fig. 7A). Bundles of the innermost pedicel ring extend directly into the inner ring of carpellary bundles (heterocarpellary ventral bundles). Bundles of both middle pedicel rings extend into their corresponding inner and outer lateral carpel bundles. At the middle level of the ovary, the heterocarpellary ventral carpel bundles are divided tangentially into two branches each. In the ovarian septa, each of these two branches joins sequentially inner and outer lateral carpellary bundles of the same radii and then attaches to the dorsal bundle. Below its junction, one ventral bundle branch of each carpel sends an extension to the ovule. Occasionally, the third ring of lateral bundles branches from the outer lateral bundles and joins the dorsal bundles.

At the middle level of the ovary, each of five bundles of the outermost pedicel ring situated on locular radii divides in

a radial plane into two branches (fig. 7M), i.e., into the dorsal carpellary bundle (the inner branch) and the median petal bundle (the outer branch).

Below the level of sepal attachment, each of five bundles of the outermost pedicel ring located on interocular radii is divided in a radial plane into the inner branch supplying the adjacent stamen and the outer branch that splits tangentially into four branches, diverging in pairs to bases of two adjacent petals forming their lateral petal veins (figs. 4D, 7M). No anastomoses were found between the derivatives of the bundles of the outermost pedicel ring in the wall of the inferior ovary (figs. 4D, 7M).

Schefflera actinophylla

Organography. Each flower possesses three bracteoles: two of them lie in the transversal plane, and the third one lies in the median adaxial position. Mature flower buds are ~7–8 mm in diameter. The calyx of anthetic flowers appears as a narrow rim ~0.1 mm broad at the base of the corolla (fig. 3B, 3C), without any traits of sepal tips. The number of sepals remains unknown because the early stages of calyx development were not examined. The corolla is usually of 12 (figs. 7H–7L, 14E) or sometimes 11–14 petals with their tips bent inward toward the ovary apex of the floral bud (this is why each petal appears twice in sections illustrated in figs. 7K and 14E). Figure 3A shows a flower with 14 petals, of which 13 have tips bent inward; one petal (colored green) has its tip bent in a counterclockwise direction. In a flower bud viewed from the top, the petals tend to be arranged into two alternate rows along a line and their tips close up in nearly alternate position along a zigzag line (figs. 3A, 7K, 7L) rather than in a central point, as it occurs in completely polysymmetric flowers. In preanthetic and anthetic flowers, the petals are postgenitally united in pairs joining each other along their lateral edges (fig. A1G). Using cross sections of flower buds (fig. 14F), one cannot predict the pattern in which the petals will remain united in pairs at anthesis. The stamen filaments are slightly curved inward. The androecium and gynoecium are usually isomerous with the corolla, with precise alternation of whorls (fig. A1H). In hemi-isomerous flowers, the merism of each whorl varies independently. In the flower illustrated in figures 7G–7L and 14, there are 12 petals, 12 stamens, and 11 carpels. The gynoecium is of carpels united throughout their entire length with a well-developed multilocular synascidiate zone and a short symplicate zone. Every locule contains a fertile ovule and usually a sterile ovule. Stigmas are horseshoe shaped and occupy the ovary top near the flower margin (from the top view), slightly protruding over the ovary surface (fig. 1F). Carpels tend to be arranged into two rows in a manner similar to the arrangement of petals. Ventral carpel margins in the symplicate zone of the gynoecium are postgenitally fused along a line, and each carpel contacts only with three or four adjacent carpels (fig. 1F). Correspondingly, the upper (symplicate) part of the ovary is elliptic in cross section (fig. 14D). The symmetry plane of the flower occupies an unstable position in relation to the inflorescence axis. In the upper part of the symplicate gynoecium zone, the pollen tube transmitting tissue is represented by the radially elongated strands united into the com-

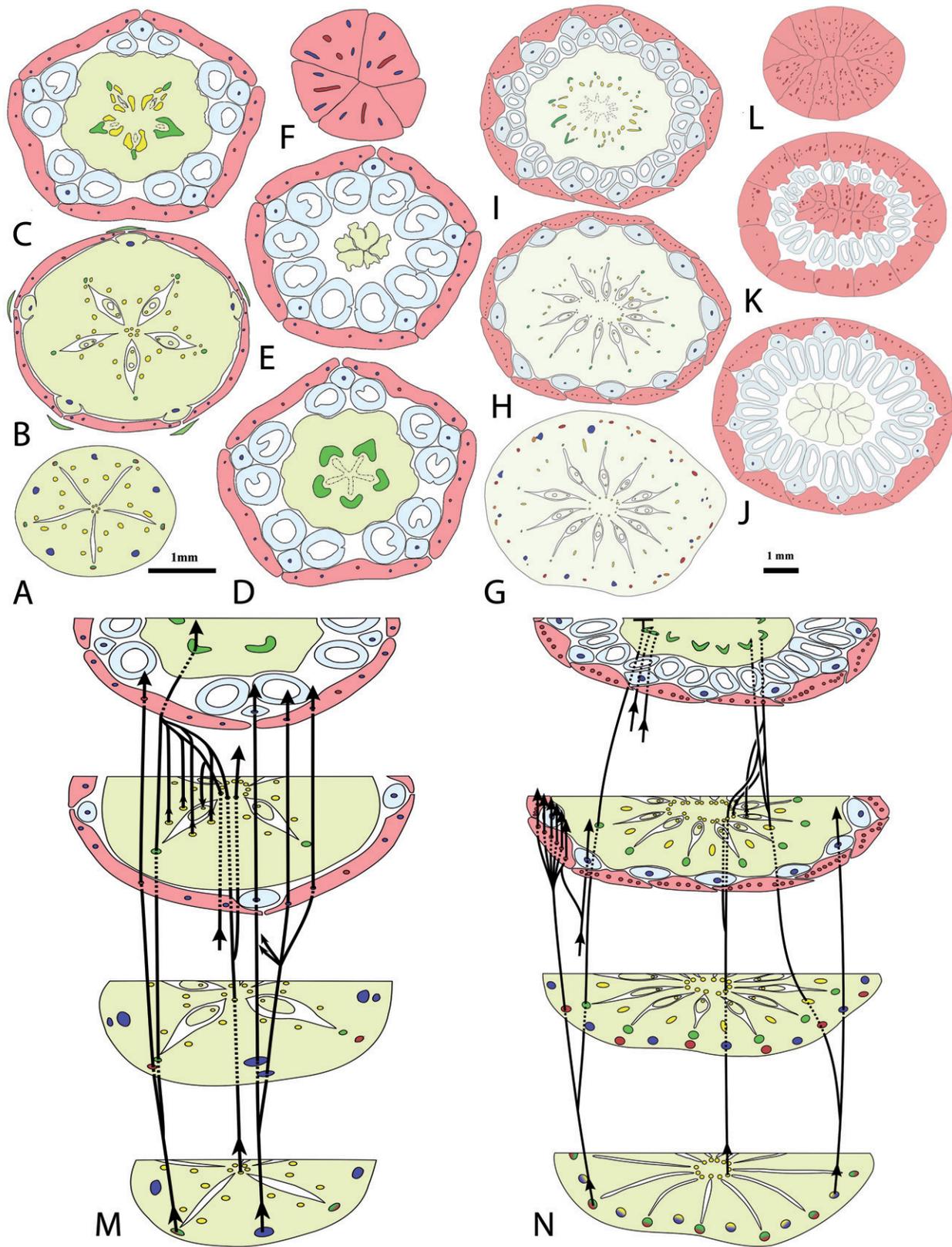


Fig. 7 A–L, Ascending series of schemes of anatomical cross sections of flowers, showing their vasculature. A–F, *Schefflera incisa*. A, Lower part of synascidiate zone of gynoecium with locules. B, Middle part of synascidiate zone with locules and ovules inside them and basal parts of

pitum above locules. The compitum is oblong-star-shaped in cross section, and the plane of elongation corresponds to the elliptic shape of the symplicate zone (fig. 14C). Slightly below this level, the compitum breaks apart into thin strands leading to ovules. The cross zone lies above the border between inferior and superior ovary parts.

Vasculature (figs. 4E, 7G–7L, 7N). The tiny calyx is not vascularized. Each petal contains seven to nine thin parallel veins (figs. 4E, 7H–7J, 7N). Petal venation is closed. Each stamen is supplied by a single bundle (fig. 7H–7J, 7N) that lasts up to the connective and gives two branches into thecae. Carpels have two bundles at their ventral sides fused in a homocarpellary way in the pedicel, two lateral bundles (basally united in a heterocarpellary way with lateral bundles of adjacent carpels), and one dorsal bundle each (fig. 7N, second section from the bottom).

Approximately 36 bundles (this number varies depending on flower merism) in two rings enter the flower from the pedicel (see the lower section in fig. 7N). Twelve bundles of the inner ring lie on the radii of the ovarian locules, while the outer ring contains 24 bundles on locular and interlocular radii. The inner ring bundles extend directly into the innermost carpel bundles, i.e., the ventral bundles in homocarpellary position. The ventral bundles are partly inverted and partly noninverted; i.e., the phloem is correspondingly located inside or outside of xylem. Within the synascidiate zone of the gynoecium, the homocarpellary ventral bundles are divided tangentially into two branches arranged into a ring around the ovary center (fig. 7H). Twelve bundles of the outer pedicel ring that lie on locular radii are split radially into dorsal carpel bundles and petal bundles (figs. 4E, 7N). Each petal bundle ramifies several times into a median and six to eight lateral petal veins below the petal base. The remaining 12 bundles of the outer pedicel ring occupy the periphery of the ovary wall, alternating with locules. These bundles also ramify radially into lateral carpellary bundles and stamen bundles (figs. 4E, 7N). Each lateral carpellary bundle is divided tangentially into a pair of lateral bundles supplying two adjacent locules. Branches of homocarpellary ventral carpel bundles go around locules and join lateral bundles of corresponding carpels. These combined bundles send branches to ovules and join dorsal bundles at the level of upper parts of locules (fig. 4E). Rare and irregular anastomoses between stamen bundles and lateral petal bundles occur (fig. 4E).

Discussion

According to Philipson (1970), the floral vascular system of Araliaceae can be subdivided into (1) peripheral bundles that supply two perianth whorls and stamens, (2) dorsal and lateral carpellary bundles, and (3) ventral bundles that usu-

ally supply the ovules. The peripheral bundles are usually connected with dorsal carpellary bundles. The ventral bundles enter the receptacle separately from the bundles of other types (Philipson 1970). The *Schefflera* species examined here follow this general pattern of flower vasculature. Within the limits of this general pattern, however, the members of the Asian *Schefflera* clade show great variability of their floral vascular systems. The gynoecium innervation is especially diverse within the species examined, whereas their androecium vasculature is rather constant. We will discuss different aspects of floral vasculature in members of the Asian *Schefflera* clade. Major characteristics of flower structure in the species under study are presented in table 1.

Perianth Innervation

It is generally accepted that nodal anatomy (i.e., the number and arrangement of vascular bundles that enter the phylome from the stem stele) of angiosperm sepals is often similar to that of vegetative leaves, and three veins usually enter the sepal base; in contrast, petal venation typically resembles the stamen vascular system, and, therefore, a single vein enters the petal base (Eames 1931; Puri 1951; Hiepkö 1965; Pervukhina 1979). These differences in vasculature are closely linked with developmental (and functional) differences between sepals and petals (Endress 1994). Sepals typically have a broad base, an acuminate tip, and rapid growth, while petals often have a narrow base, a broad tip, and delayed growth. However, the occurrence of one-traced sepals and/or multitraced petals is documented in many eudicot lineages (Eames 1931; Puri 1951; Dickison 1975; Gustafsson 1995; Kärehed 2003; Ronse De Craene 2007, 2008). Three- and multitraced petals should be expected in flowers with rapid petal growth and a wide petal base (see Ronse De Craene 2007, 2008). When rapidly growing petals have a protective function in flower bud, a tendency to calyx reduction can be expected, as well as the occurrence of one-traced sepals. These features are well pronounced in the order Apiales. Although three-traced sepals and one-traced petals are documented in *Pittosporum* (Pittosporaceae; Narayana and Radhakrishnaiah 1982), it is not surprising that most members of Apiales studied so far, including Araliaceae, possess one-traced or nonvascularized sepals and one or more petal traces (Jackson 1933; Philipson 1967; Theobald 1967; Philipson and Stone 1980; this study). It is interesting that examined members of Apiales (mostly representing Apioideae) seem to possess one-traced petals, while some Araliaceae have more than one petal trace. Reduron (1978) documented the occurrence of multiple veins in petals of some Apiales, but he did not examine the nodal anatomy, so the petals could be still one traced, though the question needs further examination.

outer floral elements. C, Lower part of symplicate zone with outer floral elements. D, Middle part of symplicate zone with outer floral elements; note the pollen tube transmitting tissue forming a star-shaped compitum. E, Upper part of symplicate zone and outer floral elements. F, Upper part of corolla. G–L, *S. actinophylla*. G, Middle part of synascidiate zone of gynoecium with locules and ovules inside them. H, Upper part of synascidiate zone with locules and ovules inside them and basal parts of outer floral elements. I, Lower part of symplicate zone and outer floral elements; note the oblong star-shaped compitum. J, Upper part of symplicate zone and outer floral elements. K, Outer floral elements; note the petal apices curved inward. L, Upper part of corolla. M, N, Schemes of floral vascular systems. M, *S. incisa*. N, *S. actinophylla*. For legend of colors used, see fig. 3. dash-dotted line = border of pollen tube transmitting tissue; dotted line = line of postgenital fusion of carpel ventral parts.

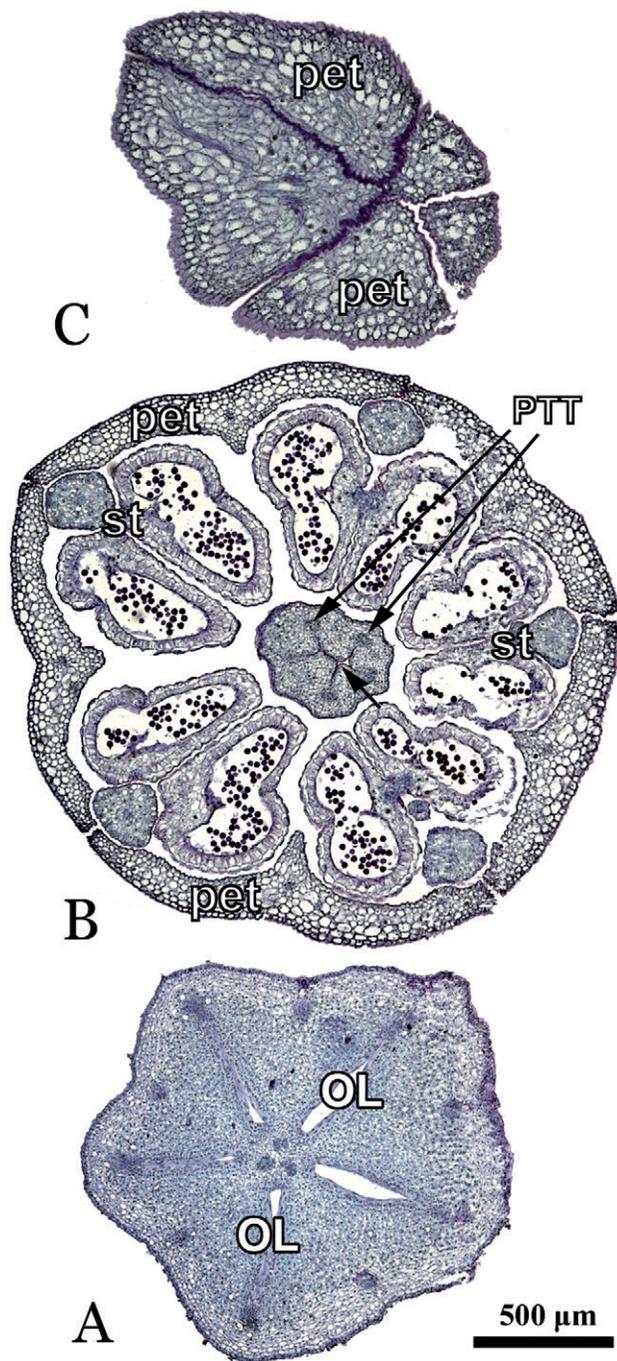


Fig. 8 *Schefflera delavayi*. A–C, Selection from an ascending series of anatomical cross sections of a flower. A, Lower part of synascidiate gynoecium zone with locules. B, Style and outer floral elements; arrow = postgenital fusion of ventral parts of carpels. C, Upper part of corolla. OL = ovarian locule; pet = petal; PTT = pollen tube transmitting tissue; st = stamen.

Within the species of the Asian *Schefflera* clade examined to date, the vascularized calyx is found only in *Schefflera delavayi* and *S. heptaphylla*, whereas small sepals in *S. incisa* and *S. venulosa* are not supplied by vascular bundles. As for *S. actinophylla* and *Tupidanthus calyptratus* (Sokoloff et al.

2007; Nuraliev et al. 2009), both these species show neither distinctive sepals nor traits of calyx innervation. The occurrence of bundles in calyx is not strictly dependent, however, on size and prominence of the sepals, which are not much larger in *S. delavayi* than in *S. incisa*. Rather, the loss of calyx innervation combined with partial or complete reduction of sepals could be suggested as an apomorphic feature for the *Heptapleurum* s.l. subclade (Frodin et al. 2010; Plunkett et al. 2010), which comprises *S. incisa*, *S. venulosa*, *S. actinophylla*, and *T. calyptratus*. This conclusion will remain tentative until more species are examined with respect to details of floral structure. So far, detailed anatomical data are available for only a small fraction of species included in molecular phylogenetic analyses.

According to the morphological data matrix of Kärehed (2003), petal venation seems to be an important character in Apiales because petals are scored as three veined to five veined in Pennantiaceae, Torricelliaceae s.l., and Pittosporaceae (according to Gustafsson 1995, the veins are fusing or at least converging at the petal base in Pittosporaceae) but one veined in Griselinaceae, Araliaceae, Myodocarpaceae, and Apiaceae s.l. Our study shows that Araliaceae are, in fact, variable in the number of petal veins. The examined species show surprising variation in petal innervation: almost all possible combinations of its characters were found therein. When a petal has multiple veins, the venation can be either closed (*S. incisa*, *S. heptaphylla*, *S. actinophylla*) or open (*S. venulosa*). Lateral petal veins can be of different origin. In two species, they unite with the median vein of the same petal above (*S. heptaphylla*) or below (*S. actinophylla*) the place of petal insertion in the ovary wall. In *S. venulosa* and *S. incisa*, lateral veins of adjacent petals are connected with the stamen bundle. These two species are closest to each other among taxa examined here and belong to the *Heptapleurum* s.str. subclade. A hypothesis that the occurrence of connections between the lateral petal and stamen bundles is a synapomorphy of the *Heptapleurum* s.str. subclade requires further testing. It is noteworthy that the connection between the lateral petal and stamen bundles occurs in either a tangential plane (*S. venulosa*) or a radial plane (*S. incisa*). It is interesting that the differences in petal innervations between bisexual flowers of closely related species *S. incisa* and *S. venulosa* occur in spite of the same organ number and position and similarity in relative sizes of all floral organs. This leaves an open question about morphogenetic factors of strong differences in vasculature.

Gustafsson (1995) found that petal venation is an important character in higher-level systematics of asterids. According to Gustafsson (1995), Asteraceae, Calyceraceae, Goodeniaceae, and Menyanthaceae share a presence of prominent marginal veins entering the petal, independent of the midvein, but meeting at the apex of the petal. He stressed that this feature was not found in any other asterid family he surveyed (including Apiaceae, Araliaceae, and Pittosporaceae). However, our data for *S. incisa* meet closely the description of Gustafsson. This means that differences in petal innervations observed among closely related *Schefflera* species with morphologically uniform pentamerous flowers are of the same kind that have been suggested to distinguish major asterid clades.

*Morphological Interpretation of the
Gynoecium Vascular System*

Looking through the descriptions of carpel innervation above, one can notice difficulties with establishing homologies between carpel bundles of different species. Most of the difficulties are due to ambiguous interpretations of ventral bundles. In general, the ventral bundles in angiosperm gynoecia with united carpels can be identified either (1) as the bundles that send branches to the ovules or (2) as the bundles of the innermost ring in a flower (see Eames 1931, 1961; Dickison 1975). These two criteria, however, imply radically different interpretations for the vascular system of the gynoecium. Using the first one, we should reject the possibility of ovules being innervated by any other bundles (which is clearly not the case at least for some angiosperms; Puri 1951; Eames 1961); the second criterion does not imply the existence of axial bundles in the center of a syncarpous gynoecium. Such ambiguity occurs in those cases where ovules are not innervated by the inner ring of gynoecium bundles. This very case was found in bisexual flowers of *S. venulosa*, where ovules are supplied by the second ring of bundles (counting from the flower center).

Assessing homologies of gynoecium bundles is also problematic in many other angiosperms. Some species are reported to possess ovules innervated by bundles of different rings (ventral, dorsal, and their anastomoses) within the same flower, though this function is more often realized by ventral bundles (Eames 1931, 1961). In the gynoecium of *Cornus* spp. (Cornaceae), ovules are innervated by heterocarpellary bundles that lie in the ovary wall on the radii of the septa (Eyde 1967). Eyde (1967) could not decide whether these bundles are ventral or whether true ventral bundles had been lost; he suggested several hypotheses to explain this phenomenon. Most Cunoniaceae possess two ventral bundles in each carpel, but some species appear to have increased numbers of these bundles: three in *Spiraeanthemum graeffei* and two pairs in *Acsmithia vitiensis* (Dickison 1975). In most of Magnoliaceae, ovules are supplied by branches of stelar carpel bundles, while ventral bundles join them above the level of ovarian branch insertion; in *Liriodendron*, the stellar bundle entirely becomes the ovular bundles, and no connection between them and ventral bundles occurs (Canright 1960). Carpels of some *Ranunculus* species (Ranunculaceae) have undergone a complete loss of ventral bundles, the ovule being innervated by the dorsal bundle (Eames 1931). Furthermore, some investigators knowingly do not use the term “ventral bundles” and name vascular bundles of gynoecium correspondingly to their function. For example, Sterling (1964), describing the floral vascular system of *Prunus* (Rosaceae), distinguishes “ovular” and “vegetative” carpel bundles; among vegetative bundles, he defines dorsal and wing bundles (the latter are those that lie next to ovular bundles). Sterling (1964, p. 37) points out that the ventral bundle in Rosaceae “appears to be morphologically a combination of the ovular bundle and wing bundle.”

As for the examined *Schefflera* species, they show different patterns of ovule innervation. Ovules are supplied by the branches derived from the bundles of the inner gynoecium ring in *S. delavayi* and *S. heptaphylla*, from the lateral bun-

dles in bisexual flowers of *S. venulosa*, and from the connection between central and lateral bundles in *S. actinophylla*, *S. incisa*, and the functionally female flower of *S. venulosa*. Following criterion 1, all those bundles should be considered ventrals. Then the bundles of the inner ring in bisexual flowers of *S. venulosa*, which end in the basal part of ovary, can be thought of as axial ones, whereas its ventral bundles should be located in the septa on each side of the ovarian loculi.

Such position of ventral bundles is not observed, however, in the functionally female flowers of *S. venulosa* and in other species under study as well. Moreover, the occurrence of free axial bundles above the carpel insertion has not been recorded for any member of Apiales investigated so far (Pervukhina 1953; Philipson 1967, 1970; Eyde and Tseng 1971; Narayana and Radhakrishnaiah 1982; Oskolski et al. 2010). Eames (1931, 1951) reported free axial bundles that extended above carpel insertion in some eudicots with free or nearly free carpels, such as *Aquilegia* (Ranunculales) and *Sedum* (Saxifragales), as well as in a number of eudicots with united carpels, including representatives of Caryophyllales (e.g., *Lychnis*), in *Pyrus* and *Cydonia* (Rosales), in *Citrus* (Sapindales), and in *Rhododendron* (Ericales). The example of *Rhododendron* (Eames 1951) is especially significant for our study because, like Araliaceae, it is a member of the asterid clade. In *Rhododendron*, the normally oriented axial bundles are surrounded by a ring of inverted (i.e., with xylem outside of phloem) ventral bundles. Eames (1951) suggested that xylem/phloem orientation is essential in identification of axial bundles. In contrast, Eyde (1975) found that an inverted bundle orientation in flowers, at least in some cases, could be explained by late timing of their initiation and initial absence of connections with other bundles. In this study, almost all the species possess normal orientation of bundles of inner gynoecium whorl, i.e., with phloem outside of xylem (in some cases xylem is surrounded by phloem). We believe that the bundles of the innermost ring in bisexual flowers of *S. venulosa* are considered (following criterion 2) remnants of reduced ventrals, whereas their ovules are innervated from the lateral bundles. In the closely related species *S. incisa*, ventral bundles are well developed. We conclude that the vascular pattern of gynoecium in bisexual flowers of *S. venulosa* can be derived from that of *S. incisa* by reduction of ventral bundles and one of two pairs of lateral bundles. As a result, a shift of the ovule supply from ventrals to inner lateral bundles occurs in the former species. It may be suggested that the reduction of carpellary bundles in *S. venulosa* is an effect of decrease in its flower size in comparison with that in *S. incisa*.

Similar to the ovules in *S. incisa*, those in *S. actinophylla* are also innervated by the branches that arise from the connection between central and lateral bundles. This species, however, is very distinctive from others in its homocarpellary ventrals, as well as in the heterocarpellary lateral bundles emerged from the peripheral stamen bundles. In that case, the vascular pattern of *S. actinophylla* is of little use for clarification of the morphological nature of the gynoecium bundles in *S. venulosa*, especially because these species are not closely related.

A shift of ovule innervation from ventral to lateral carpel bundles has been documented in other lineages of Apiales.

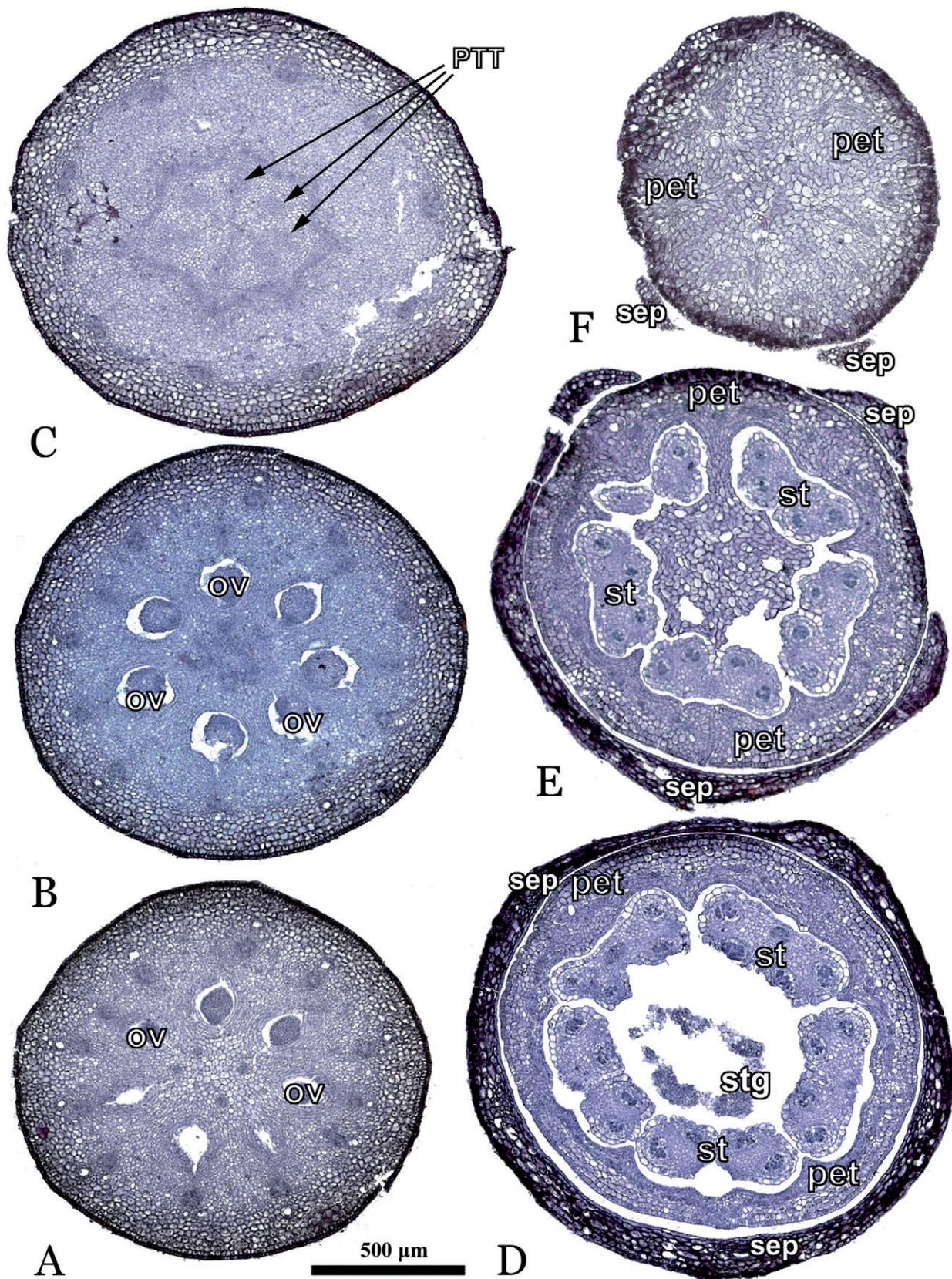


Fig. 9 *Schefflera heptaphylla*. A–F, Selection from an ascending series of anatomical cross sections of a flower. A, Lower part of synascidiate

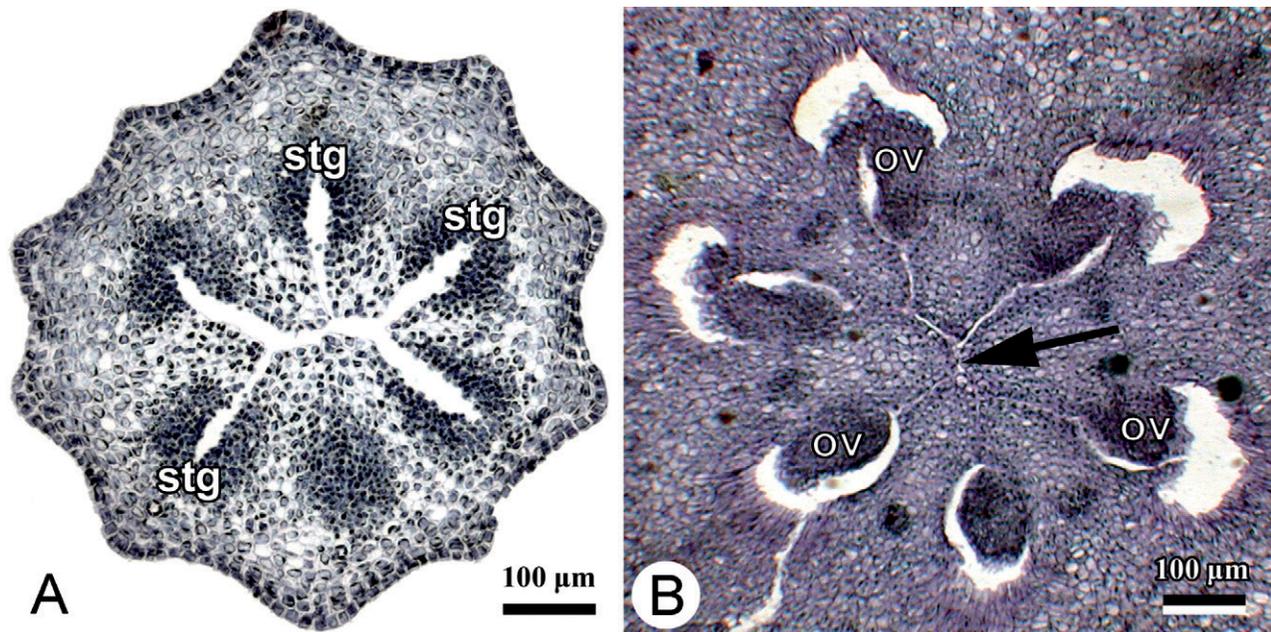


Fig. 10 *Schefflera heptaphylla*. Fragments of anatomical cross sections of a gynoecium. *A*, Style just below the tip. *B*, Middle ovary part with locules and ovules inside them. arrow = place of postgenital fusion of carpel ventral parts; *ov* = ovule; *stg* = stigma.

Jackson (1933, p. 144), in his review of gynoecium vasculature in Apiaceae (Umbelliferae), concluded that accompanying the specialization of the ventral traces due to carpophore formation, “the ovule bundles, which are primitively derived from the ventrals (the normal place of origin for ovule bundles), tend to get their physiological supply from the ‘laterals,’ the carpellary traces next in line.”

Position of United Ventral Bundles

Within the species under study, *S. venulosa*, *S. incisa*, and *S. delavayi* show the heterocarpellary fusion of ventral bundles, i.e., the pairwise union of ventrals belonging to adjacent carpels, as it can be distinguished by the position of fused bundles on interocular radii. Unlike them, the location of fused ventrals on locular radii that suggests the union of ventral bundles from two sides of the same carpel (the condition termed “homocarpellary fusion”) is observed in *S. actinophylla* (Konstantinova and Suchorukow 2010; this study) and also reported by Konstantinova and Suchorukow (2010) for *S. heptaphylla*. In the latter species, however, we found uncertain conditions when the carpels outnumber the ventral bundles (at least at the level of the synasciadiate zone).

In general, heterocarpellary ventral bundles are relatively common among angiosperms with united carpels (Eames 1931), including many representatives of the order Apiales (Jackson 1933; Tikhomirov 1958b; Eyde and Tseng 1971; Narayana and Radhakrishnaiah 1982; Tikhomirov and Konstantinova

1995; Konstantinova and Suchorukow 2010; Oskolski et al. 2010). Within Araliaceae, the homocarpellary ventral bundles occur only in *Trevesia*, *Aralia*, *Panax*, *Fatsia*, *Harmsioplanax*, some species of *Hedera*, *Oreoplanax*, and *Eleutherococcus* (Pervukhina 1953; Philipson 1970; Eyde and Tseng 1971), as well as *Stilbocarpa*, *Mackinlaya*, and *Delarbrea* (Eyde and Tseng 1971), placed now in other families among Apiales (Plunkett et al. 2004a). Therefore, heterocarpellary fusion of ventrals is the most common condition within Araliaceae.

Konstantinova and Suchorukow’s (2010) data and our data on gynoecium vasculature of *S. actinophylla* provide the first record of the occurrence of homocarpellary ventral bundles within the Asian *Schefflera* clade. It is noteworthy that the lateral carpel bundles of adjacent carpels in *S. actinophylla* are united in a heterocarpellary manner. Although these features have been reported for some angiosperms (Eames 1931), that condition is very distinctive within Araliaceae examined to date. The pathway from hetero- to homocarpellary ventral bundles in this lineage remains obscure.

Unlike the position of ventrals in *S. actinophylla* and three other species under study, that of ventrals in *S. heptaphylla* changes with the level of cross section. Through the lower level of the ovary, the five bundles are combined with six to nine carpels, so their position cannot be defined as homo- or heterocarpellary. Just above, the bundles split into two branches, forming multiple anastomoses with adjacent bundles (their homocarpellary arrangement was probably observed at this level by Konstantinova and Suchorukow [2010]). In the upper part of the ovary, the bundles are rearranged into a heter-

zone of gynoecium with locules. *B*, Middle part of synasciadiate zone with locules and ovules inside them. *C*, Lower part of symplicate zone. *D*, Stigmata and outer floral elements. *E*, Outer floral elements. *F*, Upper part of perianth. *ov* = ovule; *pet* = petal; *PTT* = pollen tube transmitting tissue; *sep* = sepal; *st* = stamen; *stg* = stigma.

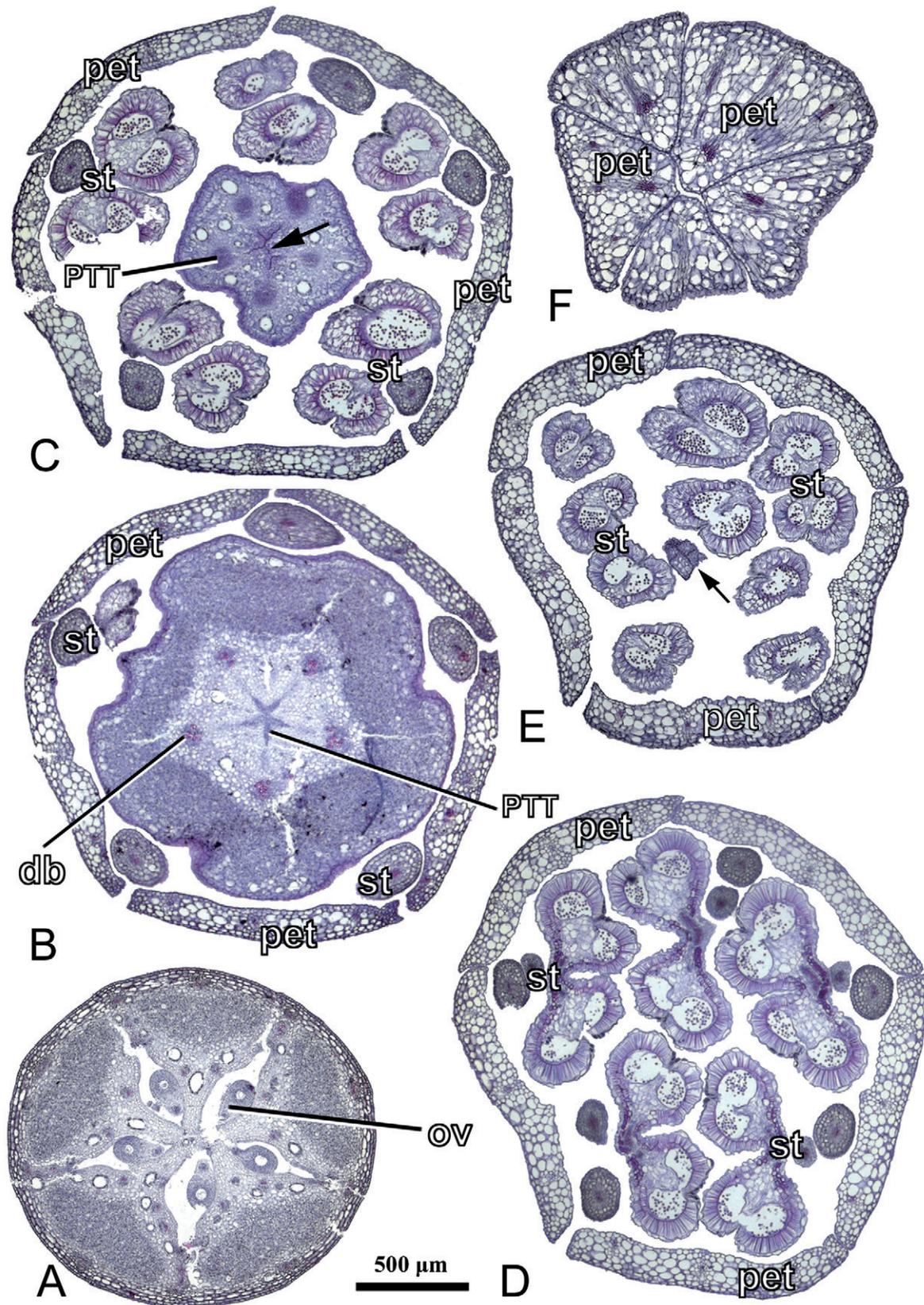


Fig. 11 *Schefflera venulosa*. A–F, Selection from an ascending series of anatomical cross sections of a bisexual flower. A, Middle part of

ocarpellary position. Similar cases of drastic alterations in the location of united ventral bundles within the ovary have also been reported (Eyde and Tseng 1971) in *Hedera*, *Fatsia*, and *Eleutherococcus*. Unlike these taxa, however, the ventrals at the upper level of the gynoecium in *S. heptaphylla* are arranged into a heterocarpellary pattern.

Composite ventral bundles, which are formed by fused ventrals from more than two adjacent carpels, occur in *T. calyptratus*, another member of the Asian *Schefflera* clade (Sokoloff et al. 2007; Nuraliev et al. 2009). Among angiosperms, the fusion of bundles belonging to more than two carpels is not unique for *Tupidanthus*. For example, the gynoecium of *Aphanopetalum* (Cunoniaceae) is composed of four carpels possessing a single ventral bundle, which is interpreted as a result of fusion of all ventral bundles (Dickison 1975). Unlike this genus, however, there are numerous composite bundles in *Tupidanthus* that may be considered an effect of its folding receptacle. Thus, positions of fused ventral bundles are very diverse within the members of the Asian *Schefflera* clade, and this feature seems not to be specific for the taxa of generic and infrafamilial rank.

While discussing the occurrence of homocarpellary versus heterocarpellary ventral bundles in gynoecia of Araliaceae, we should consider certain methodological problems with application of these terms. Indeed, the concept of heterocarpellary and homocarpellary bundles is based on the assumption that each carpel should ancestrally bear two ventral bundles, which can fuse in different ways in the course of evolution. This assumption is, in turn, based on an interpretation of carpels as conduplicate structures (e.g., folded phylomes). However, in Araliaceae, as well as in Apiaceae, the gynoecium consists of strongly ascidiate rather than conduplicate carpels (Tikhomirov 1958a; Magin 1977; Sokoloff et al. 2007; Oskolski et al. 2010). For free ascidiate carpels of various angiosperms, the most common condition is the occurrence of just one ventral bundle rather than two (Weberling 1989). In the case of Araliaceae, therefore, the heterocarpellary or homocarpellary positions of ventral bundles may not be considered an indicator of different modes of carpel margin fusion, as these terms suggest.

Connections of Peripheral Floral Bundles with Gynoecium Bundles

Fusion of bundles of outer floral elements with dorsal carpel bundles is assumed by Eyde and Tseng (1971) as one of the major trends in the evolution of the araliaceous flower. As they report, the cases of almost total isolation of peripheral bundles from dorsal carpel bundles (e.g., in *S. khasiana* and *T. calyptratus*), as well as the cases of their fusion along all the ovary, can be found among the taxa currently assigned to the Asian *Schefflera* clade. Our previous results (Sokoloff et al. 2007; Nuraliev et al. 2009) confirmed that *T. calyptratus* possessed free bundles of these two systems that are fused

only in the lowermost portion of the ovary. In *S. venulosa*, *S. delavayi*, *S. incisa*, and *S. actinophylla*, there is an intermediate level of bundle fusion: median petal bundles branch from dorsal carpel bundles in the middle ovary part, at the level of the lower part of the locules.

Thus, the peripheral bundles among Asian *Schefflera* (including *Tupidanthus*) can be either free from carpellar dorsals or partly or almost totally united with them. But should we, following Eyde and Tseng (1971), suppose an evolutionary trend in variation of this feature? Did gradual bundle fusion really take place in the evolution of this group?

If this opinion is accepted, *Tupidanthus*, with its bundles of two systems isolated from each other almost along their entire length, should be treated as a primitive form retaining ancestral features of Araliaceae. However, this interpretation obviously contradicts the morphological, anatomical, and molecular phylogenetic data, which show a derived nature of *Tupidanthus* (Oskolski 1994, 1995, 1996; Wen et al. 2001; Lowry et al. 2004; Plunkett et al. 2004b; Sokoloff et al. 2007). This evidence makes us doubt the irreversibility of fusion between peripheral and carpel dorsal bundles. We highlight the possibility of their secondary separation.

Not only *Tupidanthus* gives matter for such doubt. In several other genera (e.g., *Plerandra*, *Gastonia* [= *Peekeliopanax*, *Indokingia*, *Megalopanax*], *Reynoldsia*, *Tetraplasandra*, and *Trevesia*), separated peripheral and dorsal carpel bundles are associated with increased numbers of stamens and/or carpels (Eyde and Tseng 1971). Assuming the level of bundle fusion as an indicator of evolutionary advancement, Eyde and Tseng (1971) placed these genera at the base of several major branches of the Araliaceae phylogenetic tree and interpreted flower polymery as an ancestral condition for the entire family. Molecular phylogenetics, in contrast, shows that all the genera listed above are nested among taxa with pentamerous flowers (Wen et al. 2001; Lowry et al. 2004; Plunkett et al. 2004b). Furthermore, in *Osmoxylon* (= *Boerlagiodendron*), the only genus with frequently polymerous flowers that occupies an early-diverging position on molecular phylogenetic trees of Araliaceae (Wen et al. 2001; Lowry et al. 2004), peripheral floral bundles are not separated from gynoecium dorsal bundles but instead are fused with them (Eyde and Tseng 1971).

The inconsistency of viewpoints on phylogeny of Araliaceae and pathways of their floral evolution can be overcome by an assumption of secondary separation of peripheral and dorsal bundles. Fusion of these bundles is caused by congenital fusion of perianth, androecium, and gynoecium elements on formation of the inferior ovary wall (Eyde 1967; Kaplan 1967; Costello and Motley 2004). Their secondary separation could happen because of the disorder of arrangement of floral elements in different whorls, mainly the corolla and gynoecium.

For instance, a fusion of a median petal bundle with a dorsal carpel bundle is possible only in a case of their arrangement on the same flower radius. However, this arrangement can be altered because of deviations from precise isometry of

synascidiate zone of gynoecium with locules and ovules inside them. *B*, Symplicate zone with basal parts of outer floral elements; note the pollen tube transmitting tissue forming a star-shaped compitum. *C*, Upper part of symplicate zone with outer floral elements; arrow = place of postgenital fusion of carpel ventral parts. *D*, Outer floral elements. *E*, Outer floral elements; arrow = petal apices curved inward. *F*, Upper part of corolla. *db* = dorsal bundle; *ov* = ovule; *pet* = petal; *PTT* = pollen tube transmitting tissue; *st* = stamen; *stg* = stigma.

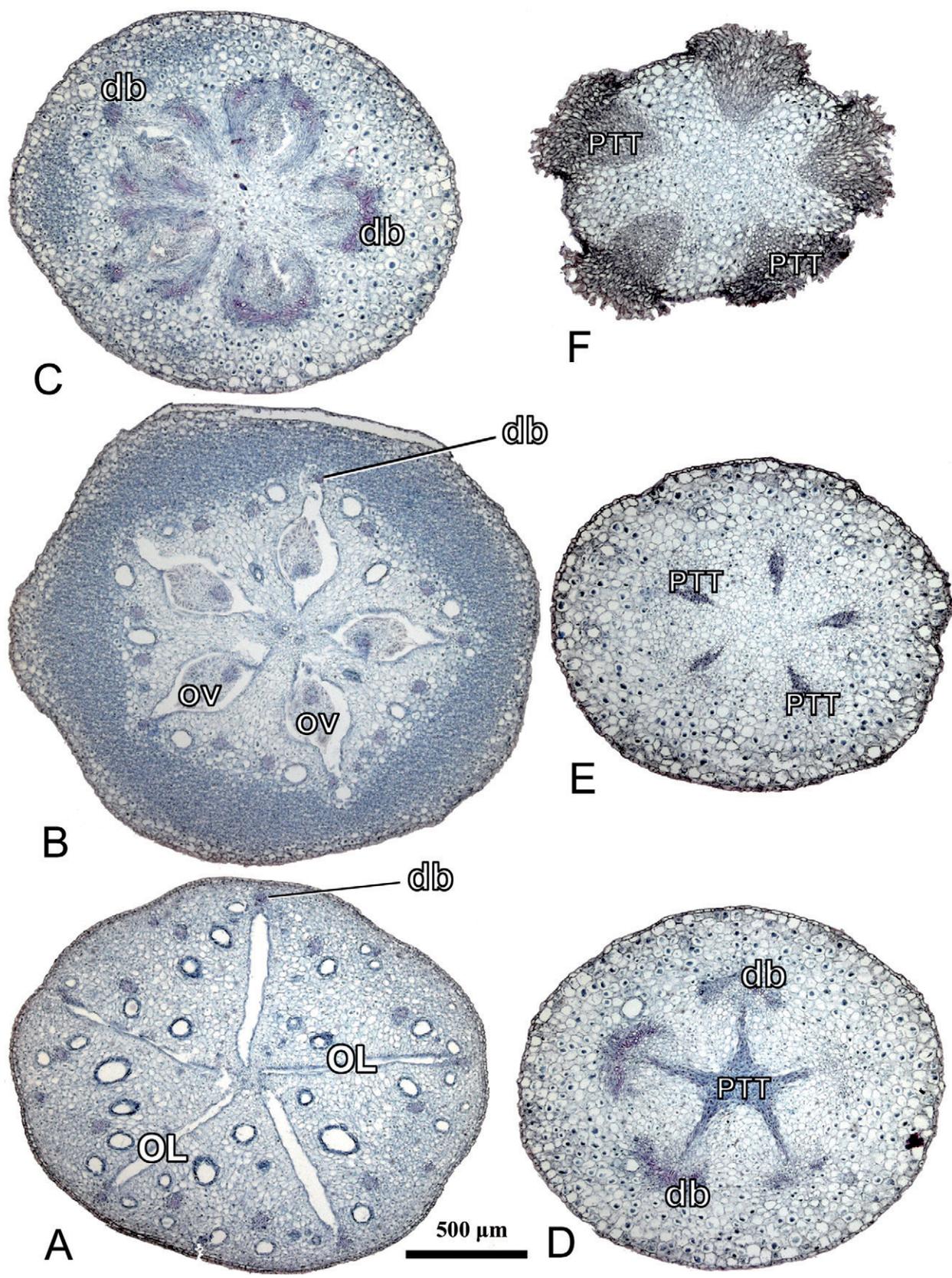


Fig. 12 *Schefflera venulosa*. Selection from an ascending series of anatomical cross sections of a functionally female flower; petals abscised. A,

corolla and gynoecium, i.e., increase or decrease of carpel number, as well as increase of petal number and/or loss of petal individuality, which takes place in flowers with petals congenitally united throughout their length, as in *Tupidanthus* and *Osmoxylon*. In these cases, independent formation of peripheral and gynoecium bundles, i.e., their isolation from each other at early stages of flower development, can be supposed.

Indeed, as Eyde and Tseng (1971) report, free or partially fused peripheral and dorsal bundles occur mainly in those genera of Araliaceae where merism variation within different flower whorls takes place, which causes corolla and gynoecium anisomery. These genera are, for instance, *Eleutherococcus* (= *Acanthopanax*), *Oreopanax*, and *Schefflera* (including *Didymopanax*), as well as many taxa with a dimerous gynoecium, but the greatest deviations from the isomerous flower groundplan are typical for polyandrous and/or polygynous flowers of *Tupidanthus*, *Plerandra*, *Tetraplasandra*, *Reynoldsia*, and *Gastonia*. These deviations that lead to the loss of adjacency between petals and stamens are probably connected with a correlation between presence of isolated bundles and flower polymery revealed by Eyde and Tseng (1971).

We suppose that in the evolution of Araliaceae, both fusion and separation of peripheral and dorsal carpel bundles took place; the latter is caused by the variation of flower meristic characteristics. However, the absence of strict relation between flower element arrangement and fusion/separation of peripheral and dorsal bundles should be noticed; for example, free bundles were found in *Trevesia* and *Dendropanax*, which possess isomerous corolla and gynoecium (Eyde and Tseng 1971). Our hypothesis needs verification by comparison of morphogenetic and vascular anatomical data of different Araliaceae species. Clearly, other factors responsible for the formation of common bundles could be considered, too, e.g., the relative timing of initiation of different organs on the same radii.

An additional argument for our hypothesis can be the arrangement of peripheral bundles in the species examined. Both species with vascularized sepals (*S. delavayi* and *S. heptaphylla*) have calyx and androecium bundles fused in the inferior ovary wall. On the other hand, none of the species shows fusion between median petal bundles and stamen bundles (only anastomoses between them were observed, which do not lead to the appearance of these bundles of neighboring whorls on the same radius). These features finely correlate with the fact that stamens lie on the same radii with sepals but not with petals (Nuraliev et al. 2009). The floral vascular system structure of Asian *Schefflera* species corresponds to those of many other angiosperms that possess fusion between bundles of different whorls (adnation sensu Eames 1931) only in the case of their arrangement on the same radii.

It is noteworthy in this context that flowers of Apiaceae, at least those with both carpels normally developed (Jackson 1933; Magin 1977), exhibit a high degree and stable pattern of fusion between carpel bundles and peripheral floral bun-

dles in spite of anisomery between the gynoecium (which is dimerous) and other floral whorls (which are pentamerous). In Apiaceae, each carpel has, apart from ventral bundle(s) and a dorsal bundle, four additional lateral bundles. The total of gynoecium bundles in the outer wall of the inferior part of the bicarpellate ovary is 10 (i.e., two dorsals and four plus four laterals). Five of the 10 bundles lie on the radii of petals and unite with petal traces, while five other bundles lie on the radii of sepals and stamens and unite with their traces (or with stamen traces only if sepals are not vascularized). Note that the dorsal bundle of one carpel is united with sepal trace while the dorsal bundle of another carpel is united with petal trace (Jackson 1933). The vascular construction described above can be seen as one of the most effective ones for this number and arrangement of floral parts, which may be partly responsible for the stability of flower structure in Apiaceae. A number of Araliaceae (including some early-divergent lineages) possess the same number and arrangement of floral parts as Apiaceae (i.e., flowers are pentamerous with dimerous gynoecium). A vascular system similar to that in Apiaceae is documented for at least some of these taxa (*Hydrocotyle* [Jackson 1933], *Uldinia* [Theobald 1967], and *Pseudopanax* [Philipson 1967]). Strong similarity in vascularization of pentamerous flowers with dimerous gynoecia in Apiaceae and Araliaceae may reflect the fact that this flower type is plesiomorphic for Araliaceae (see also Plunkett et al. 1996; Nuraliev et al. 2010), even though Eyde and Tseng (1971, p. 217) stressed that “no one doubts that 2-merous gynoecia are derived.” On the other hand, the similarity in vasculature may just reflect the fact that several lineages acquired independently the most effective condition.

Another way of producing a highly synorganized vascular system can be seen for completely isomerous flowers by fusion between dorsal bundles of all carpels and corresponding petal bundles. In such a construction, one may expect the absence of lateral carpel bundles. Actually, we can see considerable variation in the presence and number of lateral carpel bundles in pentamerous gynoecia of *Schefflera*. Should the occurrence of two pairs of lateral carpel bundles (as in *S. incisa*) be viewed as a primitive condition because the same is present in dimerous gynoecia? This remains an open question.

There are no easy ways of synorganization between vascular systems of gynoecium and peripheral floral bundles in pentamerous flowers with three carpels. Is it a coincidence that the stabilized occurrence of a trimerous gynoecium is rare among the members of Araliaceae (see Eyde and Tseng 1971; Nuraliev et al. 2010)? Possibly, the rarity of trimerous gynoecia in Araliaceae reflects difficulties in establishing a synorganized vascular system. Kärehed (2003) stressed the fact that the early-divergent members of Apiales tend to possess trimerous gynoecia (though two of three carpels can be sterile) and hypothesized that this feature may represent an ancestral condition in the order. *Aralidium* (Torricelliaceae s.l.) is an early-divergent member of Apiales with a pentamer-

Lower part of synascidiate zone of gynoecium with locules. *B*, Middle part of synascidiate zone with locules and ovules inside them. *C*, Ovary at the level of cross zone with ovules attached. *D*, Middle part of symplicate zone; note the pollen tube transmitting tissue forming a star-shaped compitum. *E*, Upper part of symplicate zone. *F*, Ovary tip with well-developed stigmas. *db* = dorsal bundle; *OL* = ovarian locule; *PTT* = pollen tube transmitting tissue.

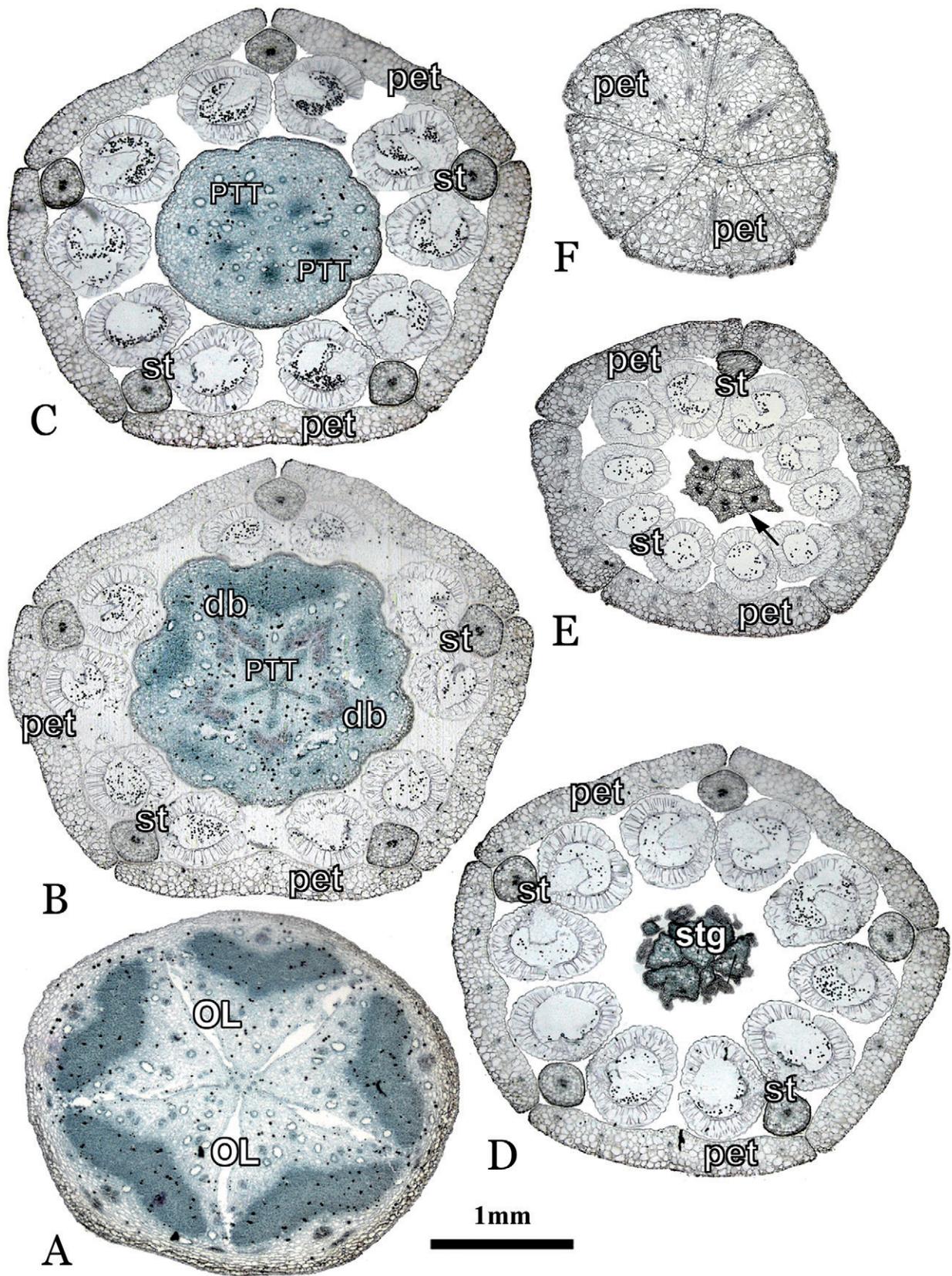


Fig. 13 *Schefflera incisa*. A–F, Selection from an ascending series of anatomical cross sections of a flower. A, Lower part of synascidiate zone of

ous perianth and androecium, trimerous gynoecium, and inferior ovary whose floral vascular anatomy has been studied in detail (Philipson and Stone 1980). It is important that gynoecium bundles of *Aralidium* are not united with any peripheral bundles.

Modes of Floral Vascular Bundle Fusion

The fusion of bundles and their reduction and amplification were considered by Puri (1962) as major evolutionary transformations of floral structure. The transition from isolated bundles to fused ones is commonly regarded as a general evolutionary trend within angiosperms (Eames 1931; Sterling 1964; Dickison 1975). Should this be the case, the most condensed vascular system would occur in flowers with the most advanced taxa. Eames (1931) distinguished between cohesion and adnation as two forms of fusion between floral organs and their bundles. The cohesion is a tangential fusion of neighboring elements within a single whorl that leads to union of their bundles. The adnation is a fusion of elements from different (including neighboring) whorls that leads to radial fusion of bundles (Eames 1931).

Although no constraints on the adnation of any neighboring floral vascular bundles from different whorls were suggested by these authors, numerous examples show that such fusion is possible only if the bundles lie strictly on the same radii. Radial bundle fusion was registered, for instance, between sepal and stamen traces in *Tetracentron* (Trochodendraceae; Eames 1931), median sepal and stamen traces in numerous species of Cunoniaceae, and also lateral sepal traces, single petal traces, and dorsal carpel bundles in *Aphanopetalum resinsum* (Cunoniaceae; Dickison 1975) and sepal and outer stamen and petal and inner stamen traces in Ericaceae (Eames 1931).

Within the Asian *Schefflera*, congenital fusion of carpels accompanied by union of ventral bundles (in *S. actinophylla* of lateral bundles) is the only example of cohesion sensu Eames (1931). In all other cases of con- or postgenital fusion of elements belonging to the same whorl, their bundles remain separate. Unlike many eudicots that show cohesion of lateral sepal bundles in calyx tube (Eames 1931), the sepals of *Schefflera* species bear only median veins (if any) whose tangential fusion is impossible. *Schefflera incisa* and functionally female flowers of *S. venulosa* show, however, the fusion of lateral bundles from two adjacent petals with the stamen (or staminode) bundle that lie on the radius between them. These cases can be interpreted as coincidences of cohesion with adnation, where the lateral petal bundles cohere to each other and then adnate to the stamen bundle.

Comparison of Floral Features between *Tupidanthus* and Other Members of the Asian *Schefflera* Clade

The flower of *T. calyptratus* has several crucial differences when compared with the typical flowers of the members of

the Asian *Schefflera* clade, such as its relatively large size, extremely high merism, unusual bisymmetric receptacle shape, thick calyptra formed by complete congenital fusion of adjacent petals with loss of their individuality, and postgenital closure of the corolla at the top (Sokoloff et al. 2007; Nuraliev et al. 2009, 2010). As for vascular anatomy, the flower of *T. calyptratus* also strongly differs from other members of the Asian *Schefflera* clade (Nuraliev et al. 2009), mainly by such features as (1) highly irregular vascular system in flower; (2) continuity of corolla innervation, without any traits of separate innervation of petals; (3) presence of several (from two to four) bundles in stamens; (4) paired dorsal carpel bundles; and (5) connections between ventral bundles of several neighboring carpels.

Peripheral floral bundles of *T. calyptratus* are arranged into an irregular vascular network with multiple anastomoses that innervate the corolla. Stamen bundles arise from this network, too (Sokoloff et al. 2007; Nuraliev et al. 2009). Within Araliaceae, a similar floral vascular system was found in *Plerandra stabliana* (Philipson 1970), which also possesses polymeric flowers. Furthermore, the presence of such vascular plexus is reported for many other taxa with numerous stamens and/or elements of other floral whorls (Ronse De Craene 1992) and, consequently, increased density of vascular bundles (Nuraliev et al. 2009).

The peculiar morphology of the corolla in *T. calyptratus* provides no way to count its petals, neither at the earliest stages of flower development (Sokoloff et al. 2007) nor by any traits of its vasculature (Nuraliev et al. 2009). Therefore, the number of petals forming the corolla of this species remains obscure. Another unusual feature of *T. calyptratus* is the presence of numerous (two to four) veins in its stamen filament. Within Araliaceae, this feature is known also in *S. subintegra* Craib and in other members of the *Scheffleropsis* group (Grushvitsky and Skvortsova 1973). *Schefflera subintegra* is suggested to be the closest relative of *T. calyptratus* (Konstantinova and Suchorukow 2010; Plunkett et al. 2010). While a single vein is a typical condition for the angiosperm stamen, two- or three-veined stamens are known among some members of several families that belong to different major groups of flowering plants, e.g., *Victoria* (Nymphaeaceae, basal angiosperms), *Degeneria* (Degeneriaceae) and some other magnoliids, and *Harperocallis* (Tofieldiaceae, basal monocots; Canright 1952; Takhtajan 1966; Schneider 1976; Remizowa et al. 2011). A higher number of veins in stamens is usually linked with an increase in flower size. Indeed, flowers of *Tupidanthus*, *Harperocallis*, and *Victoria* are larger than flowers of their relatives.

Like other members of the *Heptapleurum* s.l. subclade (Plunkett et al. 2010), *T. calyptratus* shows reduced calyx without innervation, multiple veins in the corolla, and connections between them and stamen bundles; this species looks, however, equally dissimilar to other species of the Asian *Schefflera* clade in its floral groundplan and vascular

gynoecium with locules. *B*, Lower part of symplicate zone with basal parts of outer floral elements; note the pollen tube transmitting tissue forming a star-shaped compitum. *C*, Middle part of symplicate zone with outer floral elements. *D*, Stigmas and outer floral elements. *E*, Outer floral elements; arrow = petal apices curved inward. *F*, Upper part of corolla. *db* = dorsal bundle; *OL* = ovarian locule; *pet* = petal; *PTT* = pollen tube transmitting tissue; *st* = stamen; *stg* = stigma.

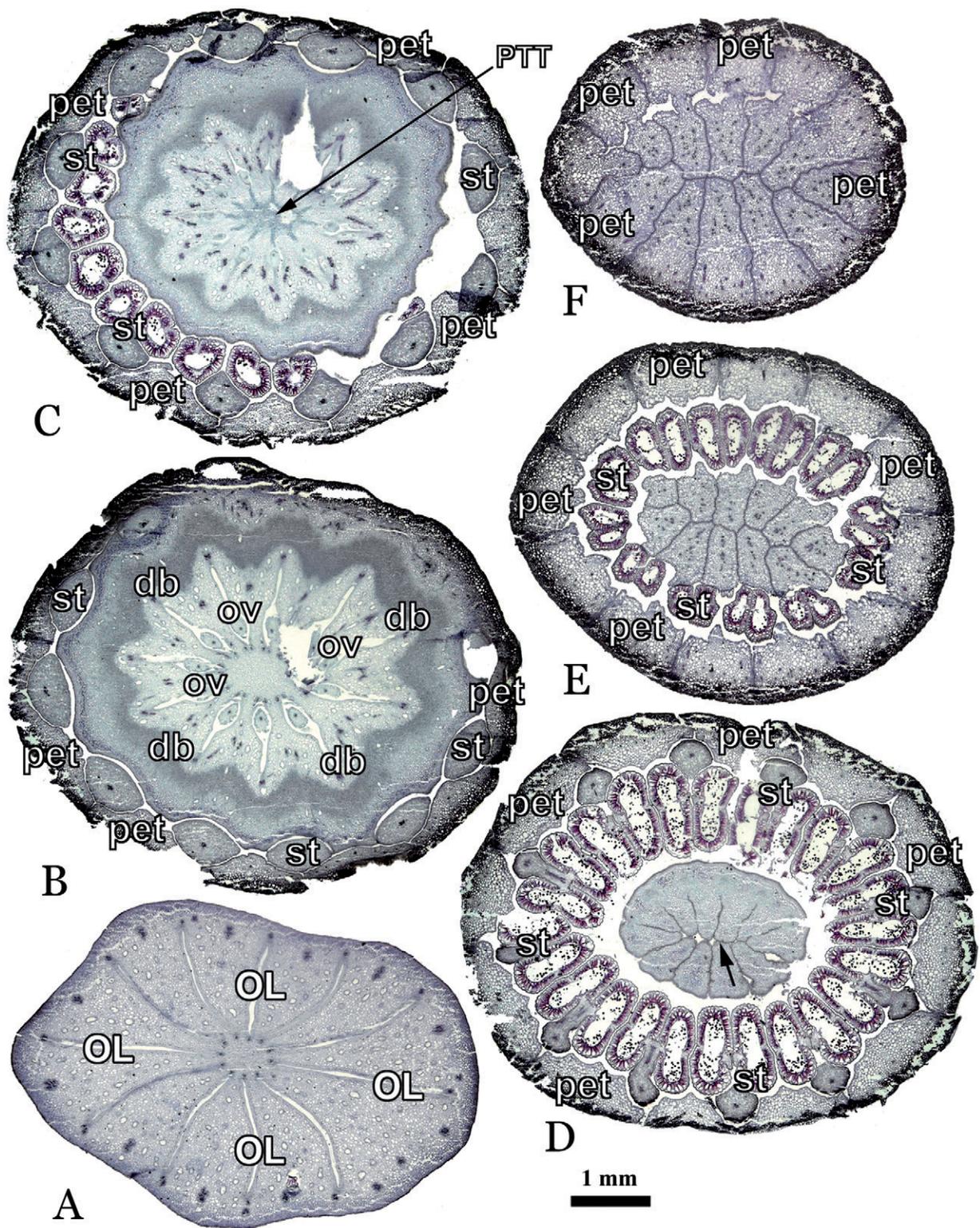


Fig. 14 *Schefflera actinophylla*. A–F, Selection from an ascending series of anatomical cross sections of a flower. A, Lower part of synascidiate zone of gynoecium with locules. B, Middle part of synascidiate zone with locules and ovules inside them and basal parts of outer floral elements. C, Lower part of symplicate zone and outer floral elements; note the oblong star-shaped compitum. D, Upper part of symplicate zone with carpel tips arranged along a line and outer floral elements; arrow = place of postgenital fusion of carpel ventral parts. E, Outer floral elements; note the petal apices curved inward. F, Upper part of corolla with petals arranged along a line. *db* = dorsal bundle; *OL* = ovary locule; *ov* = ovule; *pet* = petal; *PTT* = pollen tube transmitting tissue; *st* = stamen.

Table 1
Morphological and Anatomical Characters of *Schefflera* Species

	<i>Schefflera delavayi</i>	<i>Schefflera heptaphylla</i>	<i>Schefflera venulosa</i> bisexual flower	<i>Schefflera venulosa</i> functionally female flower	<i>Schefflera incisa</i>	<i>Schefflera actinophylla</i>
Bracteole no.	0	2	0	0	0	3
Floral formula	$K_{(5)}C_5A_5G_{-(5)-}$	$K_{(5)}C_5A_5G_{-(5-9)-}$	$K_{(5)}C_5A_5G_{-(5)-}$	$K_{(5)}C_5A_{5st}G_{-(5)-}$	$K_{(5)}C_5A_5G_{-(5)-}$	$K_{(n)}C_{12}A_{11-13}G_{-(11-12)-}$
Presence of calyx bundles	Yes	Yes	No	No	No	No
Postgenital petal fusion	No	No	No	No	Yes (by tips)	Yes—pairwise at the base
No. bundles in petal	1	3 or more	3	3	5	Many (3 groups)
Origin of lateral petal veins	...	From medial petal bundle	From anastomoses between median petal and stamen bundles	From stamen bundles	From stamen bundles	From medial petal bundle
Anastomoses between stamen and petal bundles	No	No	Yes (vascular ring)	No	No	Yes
No. bundles in stamen	1	1	1	0	1	1
Fusion of dorsal and petal bundles	Yes	No	Yes	Yes	Yes	Yes
Presence of lateral carpal bundles	No	No	Yes	Yes	2–3 pairs	Yes
Ventral bundles	Heterocarpellary	Uncertain	Heterocarpellary	Heterocarpellary or uncertain	Heterocarpellary	Homocarpellary
Bundles supplying ovules	Ventral	Ventral	Lateral	Ventral + lateral	Ventral + lateral	Ventral + lateral
Presence of axial bundles	No	No	No	No	No	No

anatomy. For instance, *S. actinophylla* resembles *T. calyptratus* more than other *Schefflera* species under study in its relatively large polymerous flowers with the carpels arranged in two rows. However, *S. actinophylla* is very distinctive from the latter species by its nearly isomerous floral whorls, single bundles in stamens connected with lateral bundles of carpels, and homocarpellary fusion of ventral bundles. Probably some traits of floral vasculature characteristic for *T. calyptratus* can also be found within the species of the *Scheffleropsis* group (Grushvitsky and Skvortsova 1973; Plunkett et al. 2010), but the vascular anatomy of their flowers has not been sufficiently studied so far.

Variation of Floral Vasculature and Speculations on Regulation of Vascular Patterning

We believe that the data on variation of vasculature across examined species might be a kind of evidence about regulation of vascular patterning, even though we are making the first steps in understanding this issue. Initiation and early development of leaf primordia occur at the same time as formation of major veins (Dengler and Kang 2001; Scarpella et al. 2010), and such temporary coincidence may also be expected for primordia of floral organs. No traces of vasculature, however, were observed in sepals of *S. venulosa* and *S. incisa*, determining precise positions of petals, as well as in staminodes of functionally female flowers in the former species. We hypothesize that in these two species, the production of auxin or its extensive polar transport from the sites of initiation of sepals or staminodes can

be arrested at very early stages before the procambium initiation but after the determination of organ positions. The loss of vascular bundles in floral organs (gynoecium-like structures) of *Arabidopsis* has also been reported by Cheng et al. (2006) for some multiple mutants of the *YUC* genes involved in the control of auxin biosynthesis. As these authors suggest, certain thresholds of auxin concentration have to be reached in order for vascular tissue to form.

The loss of vascular bundles in staminodes of functionally female flowers of *S. venulosa* is accompanied by the elimination of circular anastomoses between the bundles of stamens and those of petals present in bisexual flowers of this species. These anastomosing bundles can be considered higher-order veins in relation to lateral and median bundles of petals. Such minor veins in the *Arabidopsis* leaves are initiated later than midrib and lateral veins of second order (Kang and Dengler 2002, 2004) on the condition that the local auxin concentration exceeds some critical level (Cheng et al. 2006; Sawchuk et al. 2008; Scarpella et al. 2010). To all appearances, the venation pattern in petals and stamens is formed in a way similar to that of leaves. Should this be the case, the initiation of anastomosing preprocambial strands in flowers of *S. venulosa* could be an effect of high auxin concentration provided by developing anthers. As the anthers in *Arabidopsis* are reportedly the major sites of free auxin production (Aloni et al. 2006), we may suggest that the staminodes in functionally female flowers of *S. venulosa* cannot establish the auxin level that is sufficient for formation of higher-order bundles.

Conclusions

Flowers of Araliaceae are well known as being much more diverse than those of Apiaceae in terms of number and arrangement of sepals, petals, stamens, and carpels. It is now commonly accepted that multiple origins of polymeric flowers took place in different lineages of Araliaceae. Nuralliev et al. (2010) stressed the enigmatic nature of multiple origins of polymery and highlighted the question of possible preconditions to loss of stability of flower groundplan. These preconditions are to be discovered already at the ancestral level of pentamerous flowers. Although we are far from understanding this issue, it is highly important that pentamerous flowers of Araliaceae appear to be much more diverse in terms of vasculature than pentamerous flowers of Apiaceae. This hidden diversity of pentamerous flowers should be taken into account together with the diversity of nonpentamerous flowers of Araliaceae. This study supports the view that relative spatial arrangement of different floral organs is a crucial factor responsible for the occurrence of fusion between dorsal carpel bundles and peripheral floral bundles. As such, the occurrence of bundle fusion tells us little about the level of advancement of a taxon. High synorganization of vasculature can be lost in lineages with secondary loss of stability of

flower groundplan, e.g., in *Tupidanthus*. We argue that completely isomerous flowers and flowers with dimerous gynoecium plus pentamerous calyx, corolla, and androecium represent two floral types that allow the highest possible degree of synorganization in vasculature in Apiales. Furthermore, our study shows a homoplastic nature of transferring ovule innervations from ventral to lateral carpel bundles in Apiales. Finally, we believe that future studies of variation of floral venation taken into a phylogenetic context will contribute to understanding floral evolution and regulation of floral development in Apiales.

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